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NICHE, DISTRIBUTION AND GLOBAL CHANGES: MODELING INSIGHTS INTO BIOGEOGRAPHY AND CONSERVATION BIOLOGY

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SUMMARY

Evidences are accumulating that biodiversity is facing the effects of global change. The most influential drivers of change in ecosystems are land-use change, alien species invasions and climate change impacts. Accurate projections of species' responses to these changes are needed to propose mitigation measures to slow down the on-going erosion of biodiversity. Niche-based models (NBM) currently represent one of the only tools for such projections. However, their application in the context of global changes relies on restrictive assumptions, calling for cautious interpretations. In this thesis I aim to assess the effectiveness and shortcomings of niche-based models for the study of global change impacts on biodiversity though the investigation of specific unsolved limitations and suggestion of new approaches.

Two studies investigating threats to rare and endangered plants are presented. I review the ecogeographic characteristic of 118 endangered plants with high conservation priority in Switzerland. The prevalence of rarity types among plant species is analyzed in relation to IUCN extinction risks. The review underlines the importance of regional vs. global conservation and shows that a global assessment of rarity might be misleading for some species because it can fail to account for different degrees of rarity at a variety of spatial scales. The second study tests a modeling framework including iterative steps of modeling and field surveys to improve the sampling of rare species. The approach is illustrated with a rare alpine plant, *Eryngium alpinum* and shows promise for complementing conservation practices and reducing sampling costs.

Two studies illustrate the impacts of climate change on African taxa. The first one assesses the sensitivity of 277 mammals at African scale to climate change by 2050 in terms of species richness and turnover. It shows that a substantial number of species could be critically endangered in the future. National parks situated in xeric ecosystems are not expected to meet their mandate of protecting current species diversity in the future. The second study model the distribution in 2050 of 975 endemic plant species in southern Africa. The study proposes the inclusion of new methodological insights improving the accuracy and ecological realism of predictions of global changes studies. It also investigates the possibility to estimate *a priori* the sensitivity of a species to climate changes from the geographical distribution and ecological proprieties of the species.

Three studies illustrate the application of NBM in the study of biological invasions. The first one investigates the Northwards expansion of *Lactuca serriola L.* in Europe during the last 250 years in relation with climate changes. In last two decades, the species could not track climate change due to non climatic influences. A second study analyses the potential invasion extent of spotted knapweed, a European weed first introduced into North America in the 1890s. The study provides one of the first empirical evidence that an invasive species can occupy climatically distinct niche spaces following its introduction into a new area. Models fail to predict the current full extent of the invasion, but correctly predict areas of introduction. An alternative approach, involving the calibration of models with pooled data from both ranges, is proposed to improve predictions of the extent of invasion on models based solely on the native range.

I finally present a review on the dynamic nature of ecological niches in space and time. It synthesizes the recent theoretical developments to the niche conservatism issues and proposes solutions to improve confidence in NBM predictions of the impacts of climate change and species invasions on species distributions.

RÉSUMÉ

Les évidences montrant que les changements globaux affectent la biodiversité s'accumulent. Les facteurs les plus influant dans ce processus sont les changements et destructions d'habitat, l'expansion des espèces envahissante et l'impact des changements climatiques. Une évaluation pertinente de la réponse des espèces face à ces changements est essentielle pour proposer des mesures permettant de réduire le déclin actuel de la biodiversité. La modélisation de la répartition d'espèces basée sur la niche (NBM) est l'un des rares outils permettant cette évaluation. Néanmoins, leur application dans le contexte des changements globaux repose sur des hypothèses restrictives et demande une interprétation critique. Ce travail présente une série d'études de cas investiguant les possibilités et limitations de cette approche pour prédire l'impact des changements globaux.

Deux études traitant des menaces sur les espèces rares et en danger d'extinction sont présentées. Les caractéristiques éco-géographiques de 118 plantes avec un haut degré de priorité de conservation sont revues. La prévalence des types de rareté sont analysées en relation avec leur risque d'extinction UICN. La revue souligne l'importance de la conservation régionale en regard de celle globale. Une évaluation de la rareté à échelle globale peut être trompeuse pour certaine espèces car elle ne tient pas en compte des différents degrés de rareté que présente une espèce à différentes échelles spatiales. La deuxième étude test une approche pour améliorer l'échantillonnage d'espèces rares en incluant des phases itératives de modélisation et l'échantillonnage sur le terrain. L'application de l'approche en biologie de la conservation (illustrée ici par le cas du chardon bleu, *Eryngium alpinum*), permettrait de réduire le temps et les coûts d'échantillonnage.

Deux études sur l'impact des changements climatiques sur la faune et la flore africaine sont présentées. La première étude évalue la sensibilité en 2050 de 227 mammifères africains face aux climatiques. Elle montre qu'un nombre important d'espèce pourrait être bientôt être en danger d'extinction et que les parcs nationaux africains (principalement ceux situé en milieux xériques) pourraient ne pas remplir leur mandat de protection de la biodiversité dans le future. La seconde étude modélise l'aire de répartition en 2050 de 975 espèces de plantes endémiques du sud de l'Afrique. L'étude propose l'inclusion d'améliorations méthodologiques améliorant la prédiction des risques liés aux changements climatiques. Elle propose également une méthode pour estimer a priori la sensibilité d'une espèce aux changements climatique à partir de ses propriétés écologiques et des caractéristiques de son aire de répartition.

Trois études illustrent l'utilisation des modèles dans l'étude des invasions biologiques. Une première étude relate l'expansion de la laitue sauvage (*Lactuca serriola*) vers le nord de l'Europe en lien avec les changements du climat depuis 250 ans. La deuxième étude analyse le potentiel d'invasion de la centaurée tachetée, une mauvaise herbe importée en Amérique du nord vers 1890. L'étude apporte la preuve qu'une espèce envahissante peut occuper une niche climatique différente après introduction sur un autre continent. Les modèles basé sur l'aire native prédisent de manière incorrecte l'entier de l'aire envahie mais permettent de prévoir les aires d'introduction potentielles. Une méthode alternative, incluant la calibration du modèle à partir des deux aires où l'espèce est présente, est proposée pour améliorer les prédictions de l'invasion en Amérique du nord.

Je présente finalement une revue de la littérature sur la dynamique de la niche écologique dans le temps et l'espace. Elle synthétise les récents développements théoriques concernant le conservatisme de la niche et propose des solutions pour améliorer la pertinence des prédictions d'impact des changements climatiques et des invasions biologiques.

"Be fruitful and multiply and fill the earth and subdue it and have dominion over the fish of the sea and over the birds of the heavens and over every living thing that moves on the earth." Genesis 1:28

Chapter 1

INTRODUCTION

Today, there is little debate among scientists and conservationists about the importance of human influence on ecosystems (e.g. Sanderson *et al.* 2002). The impact of human activities on the ecological functioning of the planet can no longer be ignored. Evidences are accumulating that biodiversity is facing the effects of global change at various scales. The unprecedented escalation in both human population and consumption in the 20th century has resulted in environmental crises never before encountered in the history of humankind and the world (Sanderson *et al.* 2002). It would now take four Earths to meet the consumption demands of the current human population, if every human consumed at the level of the average US inhabitant (Wilson 2002).

Human enterprises such as agriculture, industry, fishing, and international commerce transform the land surface through cropping, forestry, and urbanization. Moreover, addition or removal of species and genetically distinct populations in most of Earth's ecosystems ultimately alters the major biogeochemical cycles (e.g. Vitousek *et al.* 1997; Sala *et al.* 2000; Wilson 2002; MEA 2005; IPCC 2007a; fig 1).

Figure 1, redrawn from the Millennium Ecosystem Assessment report (MEA 2005), provides a global picture of the current impacts of global change in different ecosystems. It shows that the impacts are not uniform over the planet and that some drivers of change are prevalent in some ecosystems, while other drivers are prevalent in other ecosystems. The most important direct drivers of change in ecosystems are habitat change (land-use change and physical modification of rivers or water withdrawal from rivers), overexploitation, invasive alien species, pollution, and climate change (MEA 2005). In the rest of the manuscript I will pool land-use change, habitat destruction, overexploitation and physical modification of rivers or water in the same group of global change. For convenience and the coherence of the manuscript, I will call it land-use change. I also put in this category the analyses of species risk of endangerment (e.g. IUCN 2004) since they currently mainly result from the direct action of land-use change (e.g. Vitousek *et al.* 1997; Wilcove *et al.* 1998; Sala *et al.* 2000; Lavergne *et al.* 2005).

In 9 of the 14 terrestrial biomes examined in the Millennium Ecosystem Assessment (Fig. 1), approximately one half of the area has been transformed, largely to croplands. Only biomes relatively unsuited to crop plants, such as deserts, boreal forests, and tundra, have remained largely untransformed by human action. In tropical, inland water and marine ecosystem, threats are projected to further increase in the next decades. Biological invasions by alien species are an increasing threat to biodiversity, with many ecosystems being already profoundly altered, especially island, inland water, costal and Mediterranean ecosystems. The latter is projected to be particularly susceptible in the future. Climate change impacts are still low (except in Polar Regions where impacts are already noticeable), but the current trends are indicating an overall very rapid increase of the impacts.

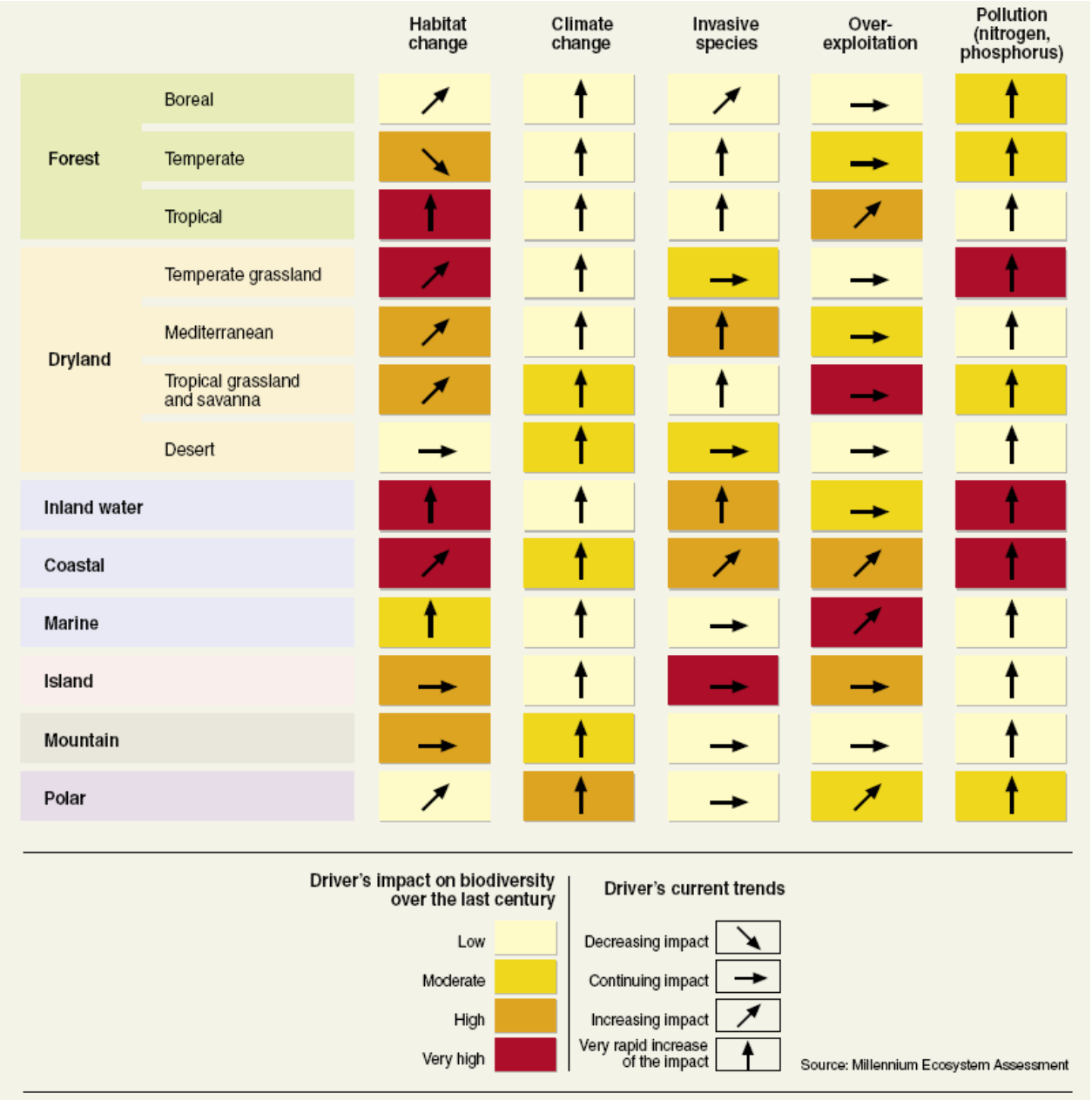


Fig. 1 – Main drivers of change in biodiversity and ecosystems. The cell color indicates impact of each driver on biodiversity in each type of ecosystem over the past 50–100 years. The arrows indicate the trend in the driver. This figure is based on expert opinion consistent with and based on the analysis of drivers of change. Redrawn from MEA 2005.

To face this unprecedented biodiversity crisis, ecologists and conservationists need to identify which biodiversity change already happened and to understand the processes leading to these changes. In **section 1.1**, I present a review of the currently known biological fingerprints of global changes on biodiversity. I aimed here to present the evidences of biological fingerprints from the global to the local scale.

Governments and societies concerns on the effects of global changes have tremendously increased in the last few decades. In reaction to the unbalanced distribution of threats towards developing countries and the difficulties in coordinating efficient actions above the state level, international environmental conventions have been set up to prioritize and optimize conservation practices on a global scale. In **section 1.2**, I review the main tools, policies and approaches used in conservation biology to conserve and prevent further losses of biodiversity.

Given the rate of projected environmental change for the 21st century, urgent adaptation and mitigation measures are required to slow down the on-going erosion of biodiversity. Even though increasing evidence shows that recent human-induced environmental changes have already triggered species' range shifts, changes in phenology and species' extinctions, accurate projections of species' responses to future environmental changes are more difficult to ascertain. The continued increase of losses in the last decades asks the question whether the investigation of current situations is sufficient to face the problem. This is problematic, since there is a growing awareness of the need to adopt proactive conservation planning measures using forecasts of species' responses to future environmental changes. In order to ensure that the current prioritization and optimization of biodiversity will be efficient for the durability of biodiversity in the future, projections of the future threats to biodiversity are needed. In **section 1.3**, I present niche-based models (NBMs) as a tool to help predicting and anticipating impacts of global change and review their main applications in assessing land-use, climate change and biological invasion impacts on biodiversity. The NBM approach is used in all the studies developed in the chapters of this PhD dissertation. This is not the only approach to provide predictions of the impacts of global change, but this is the most commonly applied and it has proven to provide valuable results.

In **section 1.4**, I finally present the objectives and the structure of the chapters of this PhD dissertation.

1.1 - A CHANGING WORLD: BIOLOGICAL FINGERPRINTS OF GLOBAL CHANGE

Land-use changes

Habitat destruction is not a recent phenomenon. Clearing, and deforestation, has been intricately tied to conditions of population growth and economic development for the past 14 to 15,000 years (Williams 2003). Major human influences on vegetation, mostly through deforestation, was effective since the end of the Neolithic (Williams 2003) and has not stopped since then. For example, Klein Goldewijk (2001) estimates that, compared with their extent before significant human disturbance, forest/woodland has declined in area by 29%, steppe/savanna/grassland by 49% and shrubland by 74%. One of the most well known examples of this is found in the region of the Mediterranean Basin (Reille & Pons 1992; Blondel 2008). Since the end of the Neolithic, this region has been deeply modified by human activity through active deforestation by fast-growing human societies that needed open, grassy spaces for developing agriculture and animal husbandry. Pollen analyses indicated that the most severe deforestation period occurred after the conquest by the Romans, and did not stop through classical antiquity up to the 13th century (Reille & Pons 1992). The most dramatic vegetation changes were the replacement of deciduous tree species by sclerophyllous tree species. This replacement has been associated, everywhere in the Mediterranean Basin, with a general desiccation of the region (Butzer 2005).

Scientists agree that habitat destruction is today the primary lethal agent to biodiversity (e.g. Vitousek *et al.* 1997; Wilcove *et al.* 1998; Sala *et al.* 2000; Lavergne *et al.* 2005). The use of land to yield goods and services represents the most substantial human alteration of the Earth system. Land use changes have an immediate and strong effect on agriculture, forestry, rural communities, biodiversity and landscapes. According to scientists' reports, we appropriate over 40% of the net primary productivity (the green material) produced on Earth each year (Vitousek *et al.* 1986; Rojstaczer *et al.* 2001). We consume 35% of the productivity of the oceanic shelf (Pauly & Christensen 1995), and we use 60% of freshwater run-off (Postel *et al.* 1996). The influence of human beings on the planet has become so pervasive that it is hard to find adults in any country who have not seen the environment around them reduced in natural values during their lifetimes - woodlots converted to agriculture, agricultural lands converted to suburban development, suburban development converted to urban areas. Human appropriation of net primary production (HANPP), the aggregate impact of land use on biomass available each year in ecosystems, is a prominent measure of the human domination of the biosphere. Figure 2, quantifying human-induced changes in trophic energy flows in ecosystems, illustrate the spatial patterns in the human domination of ecosystems, thus emphasizing land use as a pervasive factor of global importance (Imhoff *et al.* 2004). This analysis reveals the uneven footprint of human consumption and related environmental impacts indicate the degree to which human populations depend on net primary production imports.

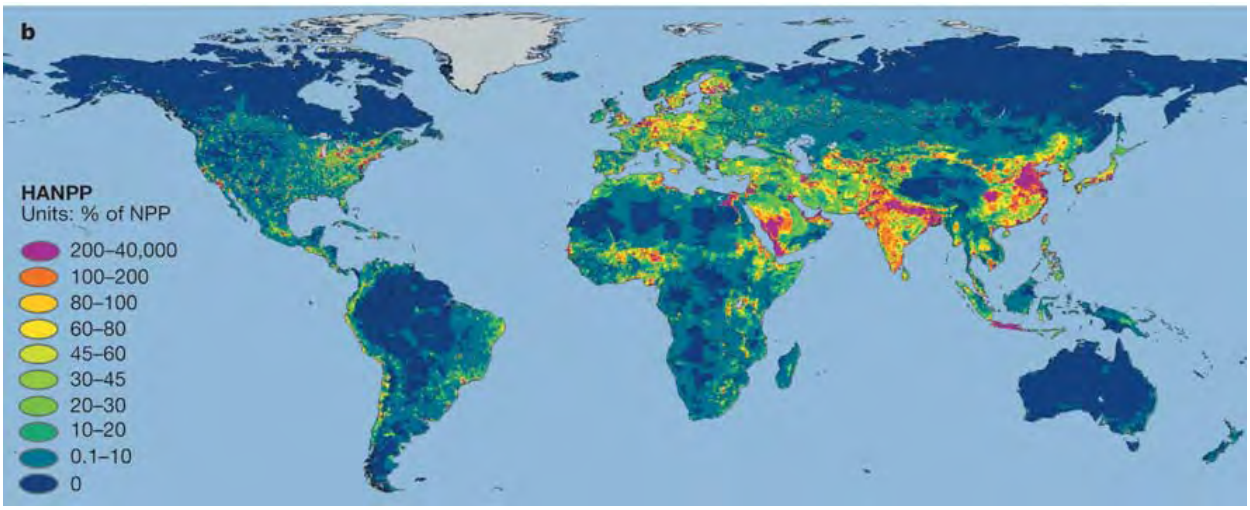


Fig. 2 - Spatial distribution of the annual net primary productivity (NPP) resources required by the human population, measured as a percentage of local NPP (from Imhoff *et al.* 2004).

On a local scale, this appropriation of land by human activities translates into destruction and fragmentation of natural habitats. In many cases, the decrease in surface of suitable habitat no longer ensures sufficient resources for wildlife survival and reproduction. Moreover, the threat due to habitat destruction itself is accentuated by the habitat fragmentation, which decreases the connectivity between suitable habitats. Because of the small numbers of individuals, rare species are disproportionately vulnerable to extinction in the short term, particularly in the face of the diverse pressures that human activities exert. In consequence, such species have come to dominate lists of species of conservation priority and have thus also received much consideration from conservation biologists (Caughley & Gunn 1995; IUCN 2004; Lavergne *et al.* 2005). It has been estimated that the current species extinction rate is between 1,000 and 10,000 times higher than it would naturally be (IUCN 2004). Habitat loss will remain a dominant threat, as there is no sign that human transformation of the landscape is slowing.

Human impacts on nature vary widely, on taxonomical and spatial dimensions (Balmford & Bond 2005). Taxonomically, certain groups are more vulnerable than others: for instance, amphibians as well as freshwater fish and invertebrates generally, are currently more threatened and undergoing steeper rates of population decline than groups such as birds or mammals (Houlahan *et al.* 2000; IUCN 2004; Loh *et al.* 2005). Within groups, species with narrow distribution ranges (for which localized threats can cause global extinction) are typically also more threatened (McKinney 1997; Owens & Bennett 2000; Purvis *et al.* 2000). Larger-bodied and specialized species (which have more specific ecological requirements) are more likely to be at risk (Owens & Bennett 2000; Purvis *et al.* 2000). Human impacts also vary spatially. Ongoing changes are more marked in tropical regions (e.g. Loh 2000). Habitat losses are disproportionately concentrated in endemic-rich parts of the tropics, where areas of dense human settlement and high species richness coincide (Cincotta *et al.* 2000; Balmford *et al.* 2001; IUCN 2004). Tropical wet forests are particularly at risk because of human demographic

pressure resulting in deforestation through logging and conversion of pristine forest to agricultural plots (FAO 2005). Moreover, the low resilience of those ecosystems makes these losses virtually irremediable. The majority of the Hotspot of biodiversity is concentrated in those regions (Myers *et al.* 2000). The Tropical Andes, Sundaland, Madagascar, Brazil's Atlantic Forest and the Caribbean contain endemic plants and vertebrates amounting to at least 2% of total species world-wide. Together, they comprise 20% and 16%, respectively, of all plants and vertebrates, and 45% of all the hotspots' endemic plants and vertebrates alike, but they comprise a mere 0.4% of the Earth's land surface. At the same time, they feature some of the most depleted habitats: the Caribbean retains only 11.3% of its primary vegetation, Madagascar 9.9%, Sundaland 7.8% and Brazil's Atlantic Forest 7.5% (Myers *et al.* 2000). Forest cover in tropical regions has continued to decline sharply, with annual loss estimates for the 1990s ranging from 0.4% (for humid forests, Achard *et al.* 2002) to 0.8% (for all tropical forests, FAO 2005).

Biological invasions

For millennia, the natural barriers of oceans, mountains, rivers and deserts provided the isolation essential for unique species and ecosystems to evolve (McNeely 1999). From the 15th century onwards, European explorers began to travel extensively around the world and to transport samples of the endemic flora and fauna of one continent to another, putting in contact species that had evolved separately and had previously had no chance to encounter each other since millions of years. In just a few hundred years these barriers have been rendered ineffective and alien species were enabled to travel vast distances to new habitats. The deliberate redistribution of plant species beyond the geographical barriers restricting them to areas of their evolutionary origin had very positive implication for the development of agriculture and greatly improved living conditions of Humans all over the planet (McNeely 1999). For example, food crops (such as corn and wheat) and fiber-producing crops (such as cotton) are often grown outside their native range to great advantage, as are livestock (such as sheep) that produce food and material for clothing, and trees (such as eucalypts) that produce wood for paper and building materials.

Although human translocation of plants has occurred for millennia in some regions (e.g. Tellman 2002) the problem has greatly increased during the last century due to growing global commerce and the increased rates of movements of goods and people around the world (McNeely 1999). This resulted in increased redistribution opportunities and increasingly common conditions favorable to non-native plant establishment. Some alien species have been able to establish self-sustaining populations in the absence of human assistance and started to spread at the expense of native species. During the second part of the 20th century, this phenomenon was set up at its paroxysm and some alien invasive species are beginning to threaten indigenous flora and displace local ecosystem equilibrium (e.g. Vitousek *et al.* 1996).

Non-native plant species arrive in new areas by deliberate human agency but also accidentally as hidden travelers on cars, clothes, seeds or on other imported organisms (Mack & Lonsdale 2001). Deliberately transported plants are often selected for their suitability to the climatic and soil conditions of the destination area and, once there, considerable efforts are made to ensure survival and reproduction (Mack *et al.* 2000). Successful establishment seems to be closely correlated with propagule pressure (the combination of the number of times and locations that a species is introduced and the number of individuals in each introduction; Williamson 1996). Only about 10% (with a confidence interval of 5–20%) of imported species appear in the wild, and of those species only about 10% go on to naturalize and only 10% of these penetrate intact habitats to become 'invaders' ('Tens Rule'; Williamson & Fitter 1996, fig 3). Once established, non-native plants may either become relatively benign or either dominate native communities. A number of factors have been identified as contributing to the likelihood that an established species will spread and become dominant. Species with greater phenotypic and genetic plasticity may be more likely to spread, due to the increased chance of eventually overcoming a fitness deficit (Rejmanek 1999). Successful invasives often appear to have the ability to reallocate resources to biomass, accumulation which may contribute to their ability to outcompete native species that invest in defensive compounds to cope with co-adapted pests and pathogens (Blossey & Notzold 1995). There is also evidence that increased vigour in some non-native plants is due to founder effects (introduction of small populations from native parents with more vigorous growth rates than the average native populations; Willis *et al.* 1999). The transition from benign to dominant invader is generally characterized by an apparent timelag (Crooks & Soulé 1999). Four competing explanations (Henderson *et al.* 2006) for apparent time lags are: 1) slow-growing populations are not noticed in the first stages of exponential growth; 2) genotypic adaptations eventually occur; and 3) cyclical disturbance or novel combinations of environmental conditions arise to 'release' the species from relative obscurity (Hobbs & Humphries 1995). 4) emergence of species from latency following lag periods as conditions amenable to their proliferation arise over time. The two most basic models of spread are diffusion dispersal, with slow expansion along a front, and saltation or punctuated dispersal, with expansion out from a number of sites that spring up at a distance from the parental population (Davis *et al.* 2000). The former more often occurs in species with limited dispersal ability, and in relatively homogeneous areas. The latter pattern is more common in species that have extensive dispersal ability or that are found in a heterogeneous environment.

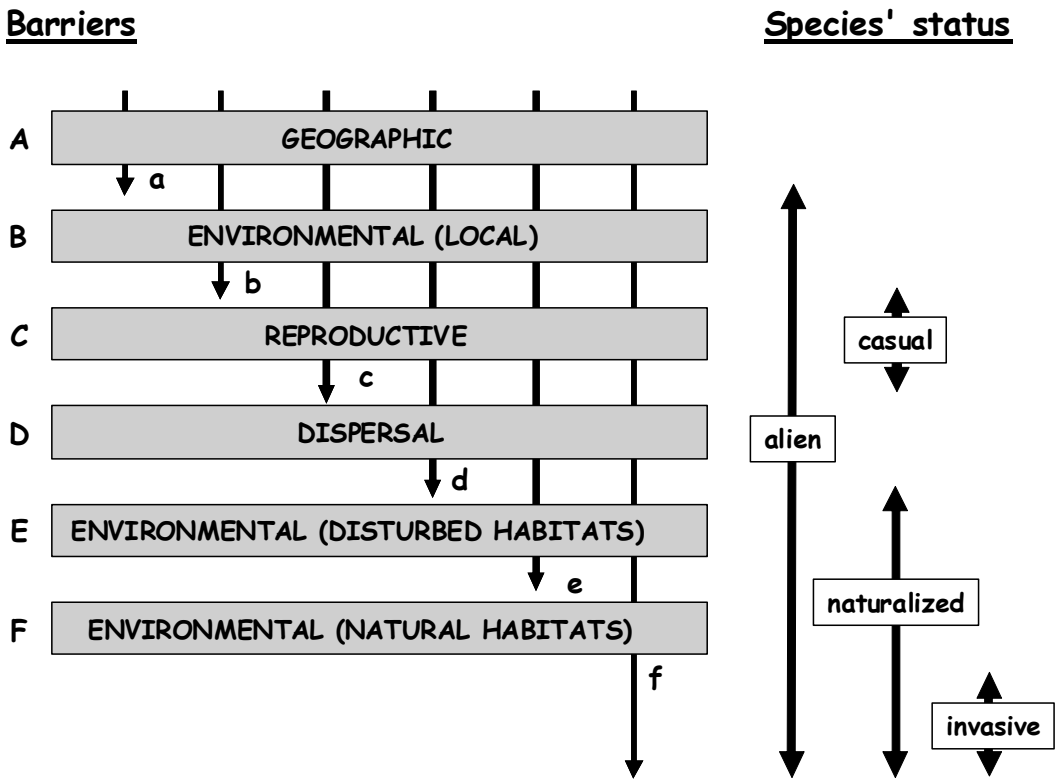


Figure 3 - Schematic representation of major barriers limiting the spread of introduced plants. The barriers are: A) intercontinental or infra-continental geographical barriers; B) abiotic and biotic environmental barriers at the site of introduction; C) Prevention against vegetative or generative production of offspring; D) local and regional dispersal barriers; E) Environmental barries in human-modified or alien dominated vegetation; and F) environmental barriers in natural or semi-natural vegetation. Arrows **a** to **f** indicate the paths followed by taxa to reach different states from introduced to invasive in natural vegetation. Redrawn from Richardson *et al.* 2000.

Recent works have addressed the economic impact of biological invasions (e.g. Pimentel *et al.* 2000; Perrings *et al.* 2001). For example, estimates of cost to the US economy are estimated about 138 billion US$ annually (Pimentel *et al.* 2000). Agricultural losses result from reduced forage yields, grazing interference, toxicity to animals, increased management and livestock production costs, and reduced land values (DiTomaso 2000). One striking example of such a problematic alien weed is spotted knapweed (*Centaurea maculosa*). It was first introduced in the 1890s from Europe into western North America, where it now infests over 3 x 10^6 ha of rangeland and pasture in 14 states and two Canadian provinces (Story *et al.* 2006) and may cause an estimated >150 million US$ in economic damage each year (Story 2002).

More difficult to estimate are the nonmonetary losses such as reduced human amenity value resulting from the inability to visit pristine wildlands and the loss of unique cultural landscapes. Biological invasions are now acknowledged by scientists and governments to be one of the major threats to native biological diversity. The impacts of alien invasive species are insidious, and usually irreversible. A lot of recent extinctions of terrestrial species have been concentrated on islands due to introduction of alien species (Pimm *et al.* 1995). Naturalized

alien species have caused or contributed to the extinction of many native species, as exemplified by introduced rats and cats on islands (Blackburn *et al.* 2004). In natural areas, invasive species are a leading factor in the listing of about 42% of species protected by the Endangered Species Act in the USA (Pimentel *et al.* 2000). In the United States, an estimated 5000 of 25,000 non-native plants have escaped into natural or seminatural systems (Morse *et al.* 1995). In other regions, up to 80% of the endangered species are threatened by non-native plants and animals (Armstrong 1995).

In some cases, a single invader can change the ecosystem variables over the tolerance of native species and can control the characteristics of the whole ecosystem' (Vitousek & Walker 1989). For example, the invasive nitrogen-fixing *Myrica faya* (firetree) in Hawaii quadruples nitrogen levels on young volcanic soils to the detriment of native vegetation (Vitousek *et al.* 1987). Ecosystem modification also occurs through altered disturbance regimes. In shrub-steppe habitat in the Idaho and Utah parts of the Great Basin the estimated historic return period for fire was about 60–100 years (Whisenant 1990). Since the invasion of *Bromus tectorum* (European cheatgrass), fires have occurred every 3–5 years, which retards regeneration of native shrubs and results in virtual monocultures that cover almost 5 million hectares (Whisenant 1990).

Climate change impacts

In the last two decades, current scientific and popular concern has increasingly emphasized the possible implications of climate change. Since industrialization in developed countries since the middle of 19th century and further industrialization in developing countries in the 20th century, strong evidence suggests that atmospheric concentrations of greenhouse gases (particularly carbon dioxide and methane) are increasing. The global atmospheric concentration of carbon dioxide has increased from 280 ppm[3] to 379 ppm[3] in 2005 and today exceeds by far the natural range over the last 650'000 years (Siegenthaler *et al.* 2005; Spahni *et al.* 2005).

The increasing concentration of this chemical compound in the atmosphere is very likely changing the physical proprieties and functioning of the climate of the earth. The Earth's climate has warmed by approximately 0.61° (+/- 0.18°) over the past 100 years (Root *et al.* 2003; IPCC 2007b). For some regions, this warming has been even higher. For example, temperatures in Europe have increased by 0.9°C from 1901 to 2005, together with changes in precipitation regimes, wind patterns and an increase in extreme events (IPCC 2007b). Between 1945 and 1976, the rate of warming has been greater than any other time during the last 1000 years (IPCC 2007b). This global warming has important consequence on the physical features of the planet. There is irrefutable evidence of an increase in widespread melting of snow and ice and rising global average sea level during the last century (IPCC 2007b). The global sea level has risen by 10–25 cm over the past 100 years. Warming is consistent with the observed sea-level rise owing to thermal expansion. There has been a

nearly continuous, below normal summer sea ice coverage since 1990 in the Arctic sea. The average extent of the ice pack was reduced by 9% in 1990–1995 as compared to 1979–1989 (Maslanik *et al.* 1996).

Observational evidence from all continents and most oceans shows that many natural systems are being affected by global climate changes (IPCC 2007b). However, the links between small and large-scale processes, and the relative roles in these processes on climate means as compared with climatic variability or extreme events are much less studied (Easterling *et al.* 2000). Regional changes are highly spatially heterogeneous (Schlesinger & Ramankutty 1994). For example, large-scale climatic fluctuations such as the North Atlantic (NAO; Hurrell 1995) or El Niño Southern Oscillation (ENSO; Holmgren *et al.* 2001) are being altered, changing induced pulses of enhanced plant productivity and ultimately cascade upward through the food web, and can cause open dryland ecosystems to shift to permanent woodlands (Stenseth *et al.* 2002a). One other major concern is that an increase in extreme events is likely occurring. Results of observational studies suggest that in many areas that have been analyzed, changes in total precipitation are amplified at the tails (i.e. changes in precipitation mostly occur through an increased frequency of extreme events). Changes in some temperature extremes have also been observed. Model's output shows changes in extreme events for future climates, such as increases in extreme high temperatures, decreases in extreme low temperatures, and increases in intense precipitation events (Easterling *et al.* 2000).

Adapting to this high rate of change is a challenge for human society as well as for natural ecosystems (MEA 2005). Evidence from long-term monitoring studies is now accumulating and suggests recent climatic trends are already affecting species physiology, distribution and phenology. Impacts of warming climate have already been shown to modify the phenology and physiology of species, or to induce displacements of species distributions that may ultimately lead to increased extinction rates (eg. Hughes 2000; Stenseth *et al.* 2002a; Root *et al.* 2003; Parmesan *et al.* 2005; Walther *et al.* 2005). Below, I detail four main effects:

1) Changes in physiology - changes in atmospheric carbon dioxide concentration directly affect metabolic and developmental rates in many animals, and processes such as photosynthesis, respiration, growth and tissue composition in plants. For example, several studies have shown that the stomatal densities of plants collected recently are significantly lower than in herbarium specimens of the same species collected between 70 and 200 years ago (Beerling & Kelly 1997).

2) Changes in species' phenologies - Life cycle events triggered by environmental cued might be altered, leading to decoupling of phenological relationships within and between species (Hughes 2000). Insects in particular are expected to pass through their larval stages faster and to become adults earlier. Five species of aphids in the UK have shown an advance in flight phenology of three to six days over the past 25 years (Fleming & Tatchell 1995). Phenology changes have also been reported for butterflies (Sparks & Yates 1997; Roy & Sparks 2000). As a result of long-time observations among ornithologists, changes in phenology for birds have been frequently published, such as migration changes (Both & Visser 2001; Jonzen *et al.* 2006), and changes in nesting time, mismatches in pollination and predator-prey interrelationships (Crick *et al.* 1997; Visser *et al.* 1998; Crick & Sparks 1999; Visser & Holleman 2001;

Penuelas *et al.* 2002). Parallel trends in earlier reproduction have been reported for several British amphibians over the period 1978–1994, with every 1°C increase in maximum temperature corresponding to an advance in spawning date by nine to ten days (Beebee 1995). Warmer conditions are expected to advance phenological events such as flowering and fruiting in plants. Few long-term data sets for plants have been analyzed in detail because long term surveys are needed. One exception is the study of 385 British plant species which shows that the average first flowering date has advanced by 4.5 days during the past decade compared with the previous four decades. 16% of species flowered significantly earlier in the 1990s than previously, with an average advancement of 15 days in a decade (Fitter & Fitter 2002)

3) Change in Species' distribution – A growing body of evidence is becoming available on climate driven changes in species distributions (e.g. Woodward 1987; Parmesan *et al.* 1999; Root *et al.* 2003; Parmesan 2006). Most of these examples are species whose distributions are most obviously limited by climate or organisms that are highly mobile at some stage of their life cycle (Hughes 2000). A 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude (in the temperate zone) or 500-600 m in elevation. Therefore, species are expected to move upwards in elevation or towards the poles in latitude in response to shifting climate zones (Parmesan 2006). The most striking examples are found in alpine areas, where upward movement of plant species has been widely reported (e.g. Grabherr *et al.* 1994; Kullman 2001; Dobbertin *et al.* 2005; Vittoz *et al.* 2008). For example, plant species richness on 30 peaks in the European Alps in 1992–1993 compared with 50 to 100 years ago show an increase at 70% of the sites, presumably because of upward colonization have been found at many other locations (Grabherr *et al.* 1994). Range shifts upward in elevation have been mostly reported for plant species but also for butterflies (Konvicka *et al.* 2003). Range shifts northwards in latitude are often observed for well-studied species groups such as birds (e.g. Thomas & Lennon 19991999) and butterflies (e.g. Hill *et al.* 1999; Parmesan *et al.* 1999).

4) Evolutionary changes - Species with short generation times and rapid population growth rates might undergo micro *in situ* evolutionary changes. Studies on fruit flies (*drosophila subobscura*) for example have suggested that the population is rapidly evolving in response to new environmental conditions, and has lost a significant amount of chromosomal diversity (18.3% in 16 years). (Rodríguez-Trelles & Rodríguez 1998). Another example in the Galapagos, drought years induced by El Niño cause evolution of larger beak size in Darwin's finches (*Geospiza fortis*), while extremely wet years cause evolution of small beak size (Boag & Grant 1984; for an example with plants, see Etterson & Shaw 2001; Davis *et al.* 2005; Botkin *et al.* 2007).

With future climate scenarios (Nakicenovic & Swart 2000) predicting a rise of temperature between 1.1 and 6.4 °C by 2100, there is little doubt that the impacts on species diversity will increase in the future and that climate change impacts could become the most threatening component of global change to biodiversity. For example, projections for the 21st century in Europe indicate that the mean annual temperature is likely to

increase by 2.2°C to 5.3°C under the most severe IPCC scenario (A1B), which is more than the projected planetary average increase (Christensen *et al.* 2007). The warming is likely to be largest in winter for northern Europe, but in summer for the Mediterranean region (Christensen *et al.* 2007). Annual precipitation is very likely to increase in northern Europe, while decreasing in most of the Mediterranean region (Christensen *et al.* 2007). In northern Europe, precipitation increases will likely be most pronounced in winter, while in the Mediterranean rainfall will likely decrease mostly in the summer, when water is already highly limiting in today's climate (Schröter *et al.* 2005; Christensen & Christensen 2007). Furthermore, the frequency of extreme climatic events is expected to increase in Europe, with heavier precipitation events and longer dry spells (Christensen and Christensen 2003). Projections of climate change impacts on biodiversity for the 21st century are projected to be even greater (Thomas *et al.* 2004; Thuiller *et al.* 2005a)

1.2 - HOW TO PRESERVE BIODIVERSITY: TOOLS & POLICIES IN CONSERVATION BIOLOGY

Governments and societies concern on the effects of global changes has tremendously increased in the last few decades. In order to conserve biodiversity and prevent further losses, the most consensual approach is to protect valuable areas (nature reserves, natural parks) against all interference by men and leave the entire flora and fauna to their natural development. National parks and protected area have a long tradition in developed countries. For example the Yellowstone national park was established in 1872 already. Today, protected areas are the cornerstone of conservation policy, an inter-generational legacy of the planet's most valuable assets and special places. Unfortunately, these nature reserves are mostly created in developed countries whereas the most urgent biodiversity threats are located in developing countries. Approximately 90% of the $6 billion of annual conservation funding originates in and is still spent within economically rich countries (James *et al.* 1999). Obviously, this framework is inefficient to achieve global conservation goals.

In response to the increase of global change, the unbalanced distribution of threats towards developing countries and the difficulties in coordinating efficient actions above the state level, international environmental conventions have been set up to prioritize and optimize conservation practices on a global scale (table 1). From the 50's to the 80's, the main conventions concern mainly the limitation of specific habitat destruction, mainly linked to the protection of natural resources. In the 90's however, conventions like the Convention on Biological Diversity (CBD) and the United Nations Framework Convention on Climate Change (FCCC) and the accompanying Kyoto Protocol tried to find solutions to ensure the global sustainability of the planet, including all global change impacts. An important new step in international law consisted in giving those conventions the legal mandate to remove environmentally damaging subsidies, through the implementation of the Global Environmental Facility (GEF) as a structure for transferring subsidy

to developing countries. Since its inception in 1992, the GEF has invested over $1 billion in biodiversity projects worldwide (IUCN 2004).

In parallel, International intergovernmental organizations (e.g. Commission for Environmental Cooperation (CEC), European Environment Agency (EEA), Intergovernmental Panel on Climate Change (IPCC) and the United Nations Environment Programme (UNEP)) have been established through international conventions or other commitments. One remarkable example of such an intergovernmental organization is the Millennium Ecosystem Assessment (MEA 2005), launched in June 2001. It hinges on contributions from a large and diverse suite of natural and social scientists. The Millennium Ecosystem Assessment aims to provide decision makers and the public with a broad scientific evaluation of the consequences of current and projected global changes in ecosystems for human well-being, and of policy options for addressing those changes (Reid & Mace 2003; MEA 2005). It has been designed to meet the needs of existing international conventions (the CBD, the Convention to Combat Desertification and the Wetlands Convention), and is working at multiple scales, from local to global.

Numerous private organizations (Environmental NGOs) were also created to increase specific lobbying (e.g. Greenpeace), advocacy (e.g. Conservation Law Foundation) and conservation efforts (e.g. IUCN, WWF, Nature Conservancy, and Conservation International).

Box 1 - the International Union for Conservation of Nature (IUCN)

The world oldest and largest global environmental network, founded in 1948 is the International Union for Conservation of Nature (IUCN). IUCN is a democratic membership union with more than 1,000 government and NGO member organizations, and some 10,000 volunteer scientists in more than 160 countries. IUCN helps develop conservation science, manages field projects all over the world, and brings together players from different domains and sectors to develop and implement policies, laws and best practice. This organization notably administrates the World Commission on Protected Areas and produces a global catalogue of classified Earth's land protected area (IUCN/UNEP/WCMC 2005). They also produce the IUCN Red List of Threatened Species (IUCN 2004), which is essentially a checklist of taxa that have undergone an extinction risk assessment using the IUCN Red List Categories and Criteria (IUCN 2001). The assessments appearing on the IUCN Red List are carried out by experts, in general members of the IUCN Species Survival Commission Specialist.

Table 1 – Main international environmental convention

Convention name	Starting date	Signatory countries	Aims
International Convention for the Regulation of Whaling	Washington 1946	59	Regulate the commercial, scientific, and aboriginal subsistence whaling practices
Convention on Fishing and Conservation of Living Resources of the High Seas	1958, 1991	38 (20 ratification)	Conserve living resources of the high seas and protect it from overexploitation
Antartic Treaty System (ATS) + Protocol on Environmental Protection	1959	46	Regulate international relations in Antarctica (South of 60° latitude). The accompanying protocol prevents commercial and military developments and protects fauna and flora
Convention on the Prevention of Marine Pollution (London Convention or LC 72)	London, 1972	81	Control pollution of the sea by dumping
Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)	1973	172	Ensure that international trade in specimens of wild animals and plants does not threaten their survival
Convention on Wetlands of International Importance (Ramsar Convention)	Ramsar, 1975	157	Conservation and sustainable utilization of wetlands. The Ramsar List of Wetlands of International Importance includes 1,708 sites Ramsar sites covering 1,530,000 km²
Convention on Long-Range Transboundary Air Pollution (CLRTAP)	1979	51	Protect the human environment against air pollution and to gradually reduce and prevent long-range air pollution
Convention on the Conservation of Migratory Species of Wild Animals (CMS or Bonn Convention)	Bonn 1979	100	Protect terrestrial, marine and avian migratory species throughout their range
Vienna Convention for the Protection of the Ozone Layer + Montreal Protocol	Vienna 1985, Montreal 1987	191	Protect the ozone layer. The Montreal Protocol on Substances That Deplete the Ozone Layer accompany the convention by phasing out the production of a number of substances believed to be responsible for ozone depletion
Basel Convention on the Control of Transboundary Movements of Hazardous Wastes and Their Disposal)	Basel, 1989	170 (US has not ratified yet)	Reduce the movements of hazardous waste between nations, and specifically to prevent transfer of hazardous waste from developed to less developed countries
Convention on Biological Diversity (CBD)	Rio de Janeiro 1992	189 (US has not ratified yet)	Develop national strategies for the conservation and sustainable use of biological diversity. The convention initiated the International Treaty on Plant Genetic Resources for Food and Agriculture
United Nations Framework Convention on Climate Change (FCCC) + Kyoto Protocol	Rio de Janeiro 1992, Kyoto 1997	175 (US and KZ have not ratified yet)	Reduce emissions of greenhouse gases in order to prevent global warming. The accompanying Kyoto Protocol enforces signatory governments of industrialized countries to reduce of 5.2% greenhouse gases emissions by 2012
United Nations Convention to Combat Desertification	Paris 1994	192	Combat desertification and mitigate the effects of drought through national action programs that incorporate long-term strategies
International Tropical Timber Agreement	1994	58	Ensure that exports of tropical timber originated from sustainably managed sources
Stockholm Convention on Persistent Organic Polllutants	Stockholm 2001	151	Ban chemical substances that persist in the environment and bio-accumulate through the food web

Conservation planning at global scale

Conservation planning is the process of locating, configuring, implementing and maintaining areas that are managed to promote the persistence of biodiversity and other natural values (Pressey *et al.* 2007). The establishment of global conservation priorities is extremely influential in providing a big-picture perspective on the current and projected status of biodiversity on the planet and ultimately in directing resources toward broad regions. The central and most widely accepted concept in conservation planning theory implies the maximization of biodiversity through the combined examination of irreplaceability and vulnerability of natural systems (Margules & Pressey 2000 for a review). The logic for this is that the greater the number of endemic species in a region, the more biodiversity is lost if that region is lost. In addition to the number of endemic species, other aspects of irreplaceability have been proposed, including taxonomic uniqueness, unusual phenomena, and global rarity of major habitat types (Olson *et al.* 2001), but these remain difficult to quantify. Different conservation planning approaches have been proposed to map regions of the world deserving the most urgent conservation actions (e.g. Biodiversity Hotspots (Myers *et al.* 2000), Global 200 Ecoregions (Olson & Dinerstein 1998), Last of the Wild (Sanderson *et al.* 2002); see Brooks *et al.* 2006 for a review). Most of these templates prioritize highly irreplaceable regions, but two approaches exist to incorporate vulnerability: reactive (prioritizing areas of high threat and high irreplaceability) and proactive (prioritizing areas of low threat but high irreplaceability). The former are considered the most urgent priorities in conservation planning theory (Margules & Pressey 2000) because unless immediate conservation action is taken within them, unique biodiversity will soon be lost. The latter are often de facto priorities, because the opportunities for conservation in these are considerable (Cardillo *et al.* 2006). Biodiversity conservation clearly needs both approaches, but the implementation of each may correspond to different methods.

Global conservation planning is a key for strategic allocation of flexible resources. Despite divergence in methods between the different schemes, an overall picture is emerging in which a few regions, particularly in the tropics and in Mediterranean-type environments, are consistently emphasized as priorities for biodiversity conservation. However, it is through the conservation of actual sites that biodiversity will ultimately be preserved or lost, and thus drawing the lessons of global conservation prioritization down to a much finer scale is now the primary concern for conservation planning (Brooks *et al.* 2006).

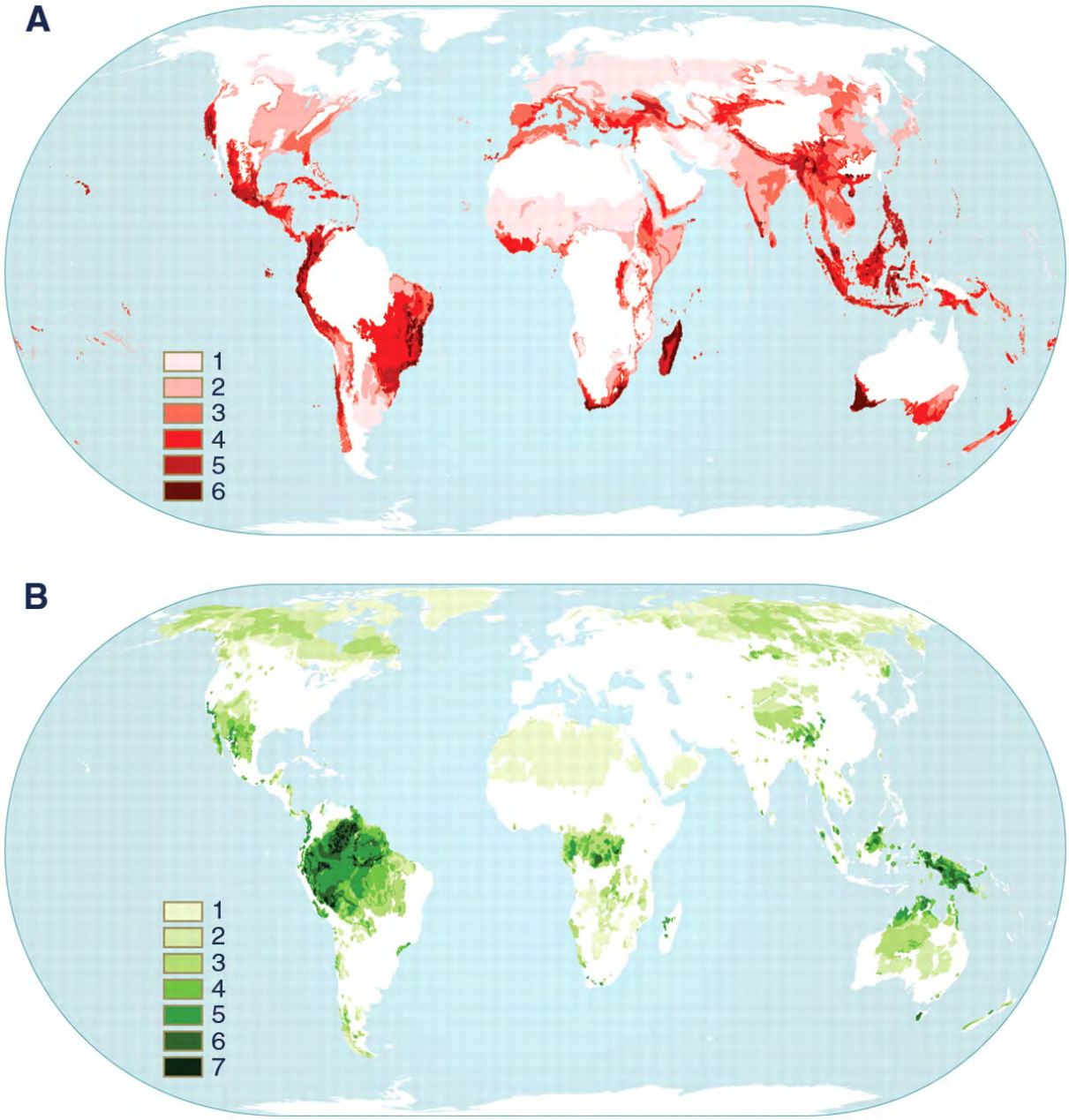


Fig 4 - Mapping the overlay of approaches prioritizing reactive and proactive conservation. (**A**) Reactive approaches which prioritize regions of high threat and those that do not incorporate vulnerability (**B**) Proactive approaches, which prioritize regions of low threat and those that do not incorporate vulnerability. Shading denotes the number of global biodiversity conservation prioritization templates that prioritize the shaded region, in both (A) and (B). Redrawn from Brooks *et al.* 2006

Conservation planning at regional scale

The mismatch between the scale of global assessments and the scale at which actual land-use and management decisions shape regional landscapes may result in a tendency for such assessments to overestimate the representativeness of the world's protected-area system or, conversely, to underestimate the global consequences of habitat loss. Furthermore, in using global assessments based on coarse-resolution surrogates to direct conservation attention to priority regions or "hotspots," there is a risk that important finer-scale priorities may be overlooked, and therefore never receive the conservation attention they deserve (Ferrier 2002). Regional systematic approaches to conservation planning have been developed over the last two decades to guide the efficient allocation of the scarce resources available for protecting biodiversity (Ferrier *et al.* 2004; Pressey *et al.* 2007):

1) Gap analysis – this planning approach is based on the assessment of the comprehensiveness of existing protected area networks and the identification of gaps in coverage (Scott & Panetta 1993). Numerous gap analyses at regional scales reveal that coverage of biodiversity by existing networks of protected areas is inadequate (Scott *et al.* 2001; Andelman & Willig 2003), skewed towards particular ecosystems, often those that are less economically valuable, leaving others inadequately protected (Peres & Lake 2003) .

2) Satellite remote sensing - The routine collection of imagery for most of Earth's surface by satellites provides an invaluable historical record covering more than three decades. This revolutionary development makes it possible to assess the quality and extent of terrestrial ecosystems for most regions of the world for this time period. Remote sensing data have been used in a wide range of applications such as biodiversity and species richness monitoring (e.g. Seto *et al.* 2004), mapping of wetlands extent (e.g. Prigent *et al.* 2001), inventory of forest quality and quantity (e.g. Woodcock *et al.* 1997), monitoring the rate and extent of desertification (e.g. Stephenne & Lambin 2001), inventory of farmland (Seto *et al.* 2000) and measuring atmospheric pollution (Husar *et al.* 1997).

3) Emergent properties of biodiversity using generalized dissimilarity modeling - this technique developed by Ferrier *et al.* (GDM; Ferrier *et al.* 2004) consists in the statistical modeling of spatial patterns of species richness and compositional turnover at fine scales by combining point data for diverse taxa with high-resolution mapping of environmental attributes. The method has proven to predict overall irreplaceability of biodiversity matching with existing conservation priorities (Ferrier *et al.* 2004). However, this method has so far focused on describing spatial patterns in emergent (or collective) properties of species-level biodiversity, rather than attempting to describe distributions of individual species.

While being a fundamental tool for prioritizing conservation action for guiding the efficient allocation of the scarce resources available for protecting biodiversity, conservation planning has mostly focused on preserving pattern and has acted reactively. However, scientists and stakeholders recognize that the dynamic nature of biodiversity requires to include proactive planning and focusing on processes rather than patterns (Cabeza & Moilanen 2001; Pressey *et al.* 2007). However, proactive responses are limited without forecasting and the implementation of advanced models to do this. Accurate predictions of the impact of global changes on biodiversity are needed. Responses of biodiversity to land-use, climate change and biological invasions are receiving increasing attention in conservation planning science, with decision tools being developed to incorporate such forecasts (Hannah *et al.* 2007; Pressey *et al.* 2007). Two approaches have been developed (Botkin *et al.* 2007; Thuiller *et al.* 2008):

1) process-based models - these types of model use mechanistic links between the growth and fitness of species, or more abstract plant functional types (PFTs), and a range of environmental or biological (e.g. competing species or PFTs) variables. Examples range from dynamic vegetation model (based on PFTs, e.g. Woodward 1992), population viability analysis (based on population dynamics, e.g. Possingham & Davies 1995), plant population modeling (e.g. Jeltsch *et al.* 2008), phenological models (based on phenology; e.g. Chuine *et al.* 2000), or diffusion/spread models (e.g. King & With 2002).

2) Niche-based models (NBM, also called niche distribution models or habitat models) – these statistical modeling approaches relate the physical nature (biotic and abiotic) of a region with respect to a species, with no direct mechanistic links necessarily occurring between those descriptors and the species (static modeling). Typical habitat models are reviewed in (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). They are purely descriptive and relate to a particular space and time.

All the following chapters of this PhD thesis will present studies developed on the use the NBM approaches. The next section specifically develops the state of the art of NBMs and presents how this tool can help anticipating impacts of global change.

1.3 - NICHE-BASED MODELS: A TOOL TO HELP ANTICIPATING IMPACTS OF GLOBAL CHANGE

Niche-based models are empirical models relating field observations to environmental predictor variables based on statistically or theoretically derived response surfaces (Guisan & Thuiller 2005; Fig. 5). By integrating known occurrences of species with environmental GIS layers that summarize meaningful niche dimensions, it is possible to determine the key combinations of environmental conditions enabling a species to grow and reproduce.

NBMs take advantage of revolutionary advances in the field of geographical information systems (GIS) and biodiversity informatics (Graham *et al.* 2004a; Kozak *et al.* 2008), which result in the higher availability and quality of two major sources of data:

1) Environmental predictors, including global coverage of digital terrain, climate, soil, and land-cover surfaces are now available at relatively fine spatial resolution (mostly 1 km grids), thanks to recent advances in interpolating climatic data from meteorological stations and remote sensing technologies. Environmental predictors can exert direct or indirect effects on species (Austin 2002), and are optimally chosen to reflect the three main types of influences on the species: (i) *limiting factors* (or *regulators*; Huston 2002) defined as factors controlling species eco-physiology (e.g. temperature, water, soil composition); (ii) *disturbances*, defined as all types of perturbations affecting environmental systems (natural or human-induced) and (iii) *resources*, defined as all compounds that can be assimilated by organisms (e.g. energy and water).

2) Species data sets from biological surveys and natural history collections. Species data can be simple presence, presence–absence or abundance observations based on random or stratified field sampling, or observations obtained opportunistically, such as those in natural history collections (Graham *et al.* 2004a). The accessibility of such data is improving dramatically as a result of rapid advances in the digitization of museum and herbarium specimen collections which contain the locations of observation or collection for large numbers of species across a wide range of higher taxa (Bisby 2000; Graham *et al.* 2004a).

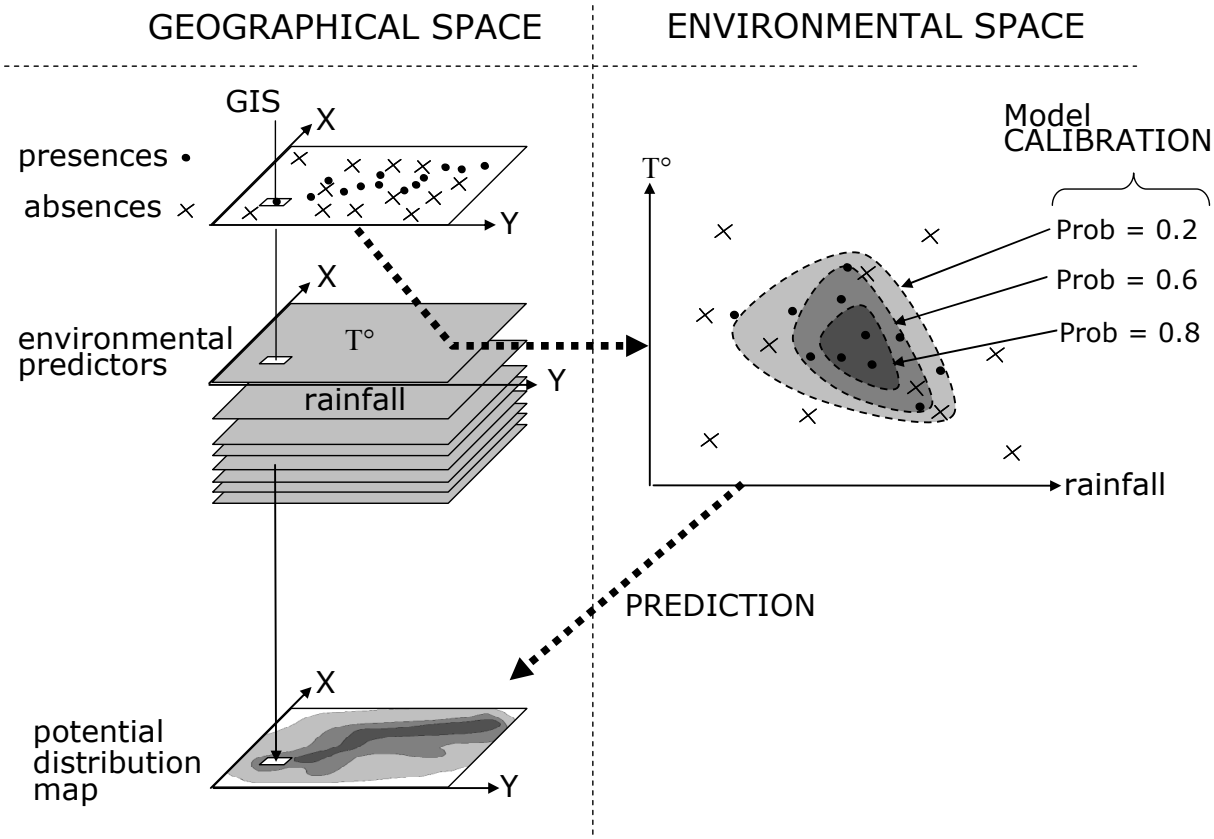


Fig 5 – Schematic representation illustrating the main steps of niche-based modeling. The distribution of the species data are shown on geographical and environmental spaces. The presence (dots) and absence (crosses) data are linked to environmental predictors in a geographic information system (GIS) and environmental values are attributed to them. Statistical response surfaces are then derived in the environmental space and predicted back to the geographical space to build a potential distribution map. The predictions on the map indicate the probability of presence of the species in each region of the study area.

Today, an impressive diversity of modeling techniques are available for modeling species distribution (see Guisan & Thuiller 2005; Table 2), depending on the type of response variables and predictors at hand. The choice of the right statistical method in a specific modeling context is now supported by many published comparisons (Elith *et al.* 2006for a review). These modeling techniques usually include an algorithm to select the most influential predictors in the model (Johnson & Omland 2004). The most popular – but also controversial - technique consists in the stepwise selection procedure (see Guisan *et al.* 2002). Starting with a full model including all the variables, variables are sequentially introduced and removed in the model. At each step, predefined rules such as deviance reduction inform to keep or remove the specific predictor.

Niche-based models are useful if they are robust. Addressing ecological questions with a model that is statistically significant but only explains a low proportion of variance might lead to weak, possibly

erroneous, conclusions (Mac Nally 2002). Similar problems may well arise in the opposite case, when a model is over-fitted. Even though no absolute measure of robustness of a model exists (Araujo *et al.* 2005a), techniques for statistically evaluating models and their predictions are available and have considerably improved in many ways (Fielding & Bell 1997; Pearce & Ferrier 2000, see also Box 2).

Table 2 - Published predictive NBM packages, reference paper, related modeling methods. ANN, artificial neural networks; BA, bayesian approach; BRT, boosted regression trees; CE, climatic envelop; CART; classification and regression trees; ENFA, ecological niche factor analysis; GA, genetic algorithm, GAM, generalized additive models; GDM, generalized dissimilarity modeling; GLM, generalized linear modles; ME, maximum entropy; MDA, multiple discriminant analyisi; MARS, multiple adaptive regression splines; RF, random forest. From Guisan and Thuiller 2005.

Tool	**Reference**	**Methods implemented**
BIOCLIM	Busby 1991	CE
ANUCLIM	See BIOCLIM	CE
BAYES	Aspinall 1992	BA
BIOMAPPER	Hirzel *et al.* 2002	ENFA
BIOMOD	Thuiller 2003a	GLM, GAM, CART, ANN, BRT, RF, MDA, MARS
DIVA	Hijmans *et al.* 2001	CE
DOMAIN	Carpenter *et al.* 1993	CE
ECOSPAT	Unpublished data	GLM, GAM
GARP	Stockwell & Peters 1999	GA (incl. CE,GLM,ANN)
GDM	Ferrier 2002	GDM
GRASP	Lehmann *et al.* 2002b	GLM, GAM
MAXENT	Phillips *et al.* 2006	ME
SPECIES	Pearson *et al.* 2002	ANN

The calibration of NBMs should be preceded by an initial conceptual phase, which consist in defining an up-to-date conceptual model of the system to be simulated based on sound ecological thinking and clearly defined objectives (Austin 2002; Huston 2002). Notably, a special attention must be drawn on the setting of working hypotheses (e.g. *pseudo-equilibrium ;*Guisan & Theurillat 2000*)*, the assessment of available and missing occurrence data, the relevance of environmental predictors for the focal species and the given scale (Thuiller *et al.* 2004c), and choice of the appropriate spatio-temporal resolution and geographic extent for the study. These aspects have been reviewed in a recent paper by Guisan and Thuiller (2005).

Lacks of consideration in these aspects can be potentially leading to:

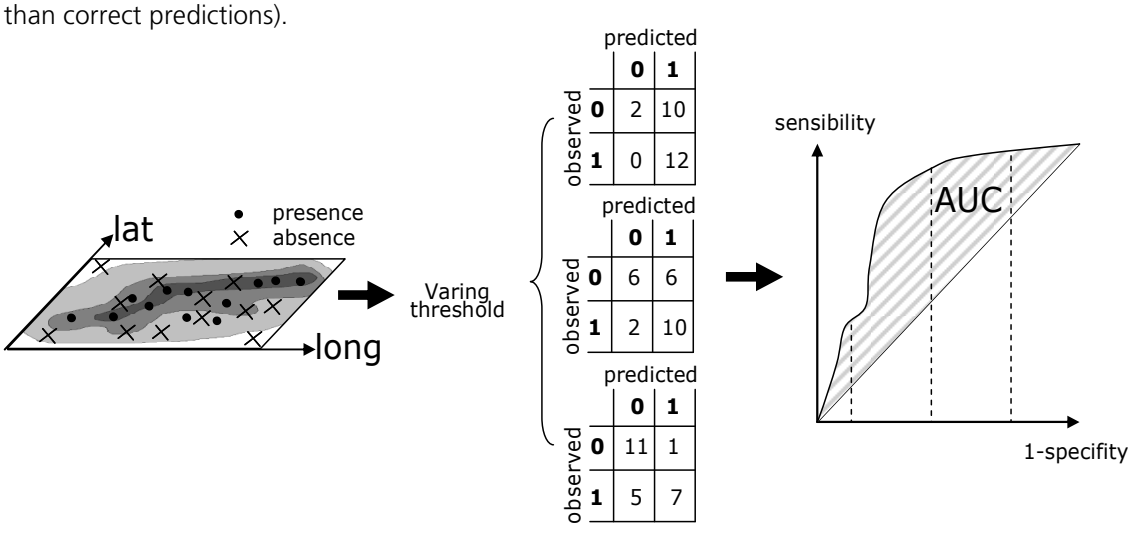
i) Poor predictive ability (e.g. due to taxonomic and geographic biases, missing of relevance of environmental predictors at particular scales or missing availability of absence data).

ii) Consistent over- or underoptimism in predictions with new data. (e.g. due to spatial autocorrelation, wrong choice of the modeling technique, small samplings)

iii) Apparent responses to environmental conditions inconsistent with biological understanding (e.g. due to spatial autocorrelation, small samplings, spurious response curves on incompletely sampled gradients; Van Horn 2002; Thuiller *et al.* 2004c)

Box 2- AUC validation

The predictive power of a model can be assessed through the area under the curve (AUC) of a receiver-operating characteristics plot (ROC; Fielding & Bell 1997; Elith *et al.* 2006). A varying threshold is applied to transform the prediction into a binary response. At each threshold, the sensibility (the number of true positive) and the 1- specificity (the number of false negative) is plotted. The area under the ROC curve indicates (AUC) the degree of matching between the known and predicted distribution of the species. Following Swets' scale (Swets 1988), predictions are considered random when they do not differ from 0.5, poor when they are in the range 0.5–0.7, and useful in the range 0.7–0.9. Predictions greater than 0.9 are considered good to excellent (1 = perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct predictions).



Niche-based models relying on data from natural history collection contribute significantly to conservation efforts that are directed toward species of concern, multi-species conservation prioritization schemes, prediction of the spread of invasive species, and predictions of biodiversity

consequences of climate change (Vaughan & Ormerod 2003; Rushton *et al.* 2004). NBM techniques thus offer unique opportunities to track distributional changes in relation to threatening processes and thereby anticipate future impacts.

NBMs in conservation planning

NBM research within the field of conservation planning has mainly focused on the development of theories and tools to design reserve networks that protect biodiversity in an efficient and representative manner (e.g. Araujo & Williams 2000; Araujo *et al.* 2002; Ferrier 2002; Cabeza *et al.* 2004). Predicted species distribution data from NBMs are commonly used for conservation planning because the alternatives (e.g. survey data) are often incomplete or biased spatially (Austin 1998; Andelman & Willig 2002). Moreover, NBMs and reserve selection algorithms are used together to investigate the pertinence of reserve networks under future global climate change. Several studies have assessed the ability of existing reserve-selection methods to secure species in a climate-change context (e.g. Araujo *et al.* 2004; Thuiller *et al.* 2006a). They concluded that opportunities exist to minimize species extinctions within reserves, but that new approaches are needed to account for impacts of climate change on species; particularly for those projected to have temporally non-overlapping distributions. Such achievement can be carried out with NBMs coupled with very simple dispersal model and reserve-selection methods to identify minimum-dispersal corridors allowing species migration across reserve networks under climate change and land transformation scenarios (Wiliams *et al.* 2005).

Niche-based predictions often include areas in which a species is currently not known to occur. This is especially helpful in the case of rare and endangered species. When species are rare, standard sampling methods such as simple or stratified random sampling, based on a simple combination of the main environmental gradients, can be highly inefficient (Rushton *et al.* 2004). Directing the sampling to ensure inclusion of units with a higher probability of hosting the species is thus a desirable approach for increasing survey efficiency and reducing sampling costs. Predictions from niche-based models of species distribution are promising tools in this respect (Côté & Reynolds 2002; Edwards *et al.* 2005; Guisan *et al.* 2006) as a way to improve the sampling of species of conservation interest. Moreover, the approach is also helpful to determine schemes to mitigate species declines or to target candidate sites for reintroduction programs (Rushton *et al.* 2004).

NBMs in biological invasions

Biological invasions represent a growing threat to biodiversity (Pimentel *et al.* 2000) and once introduced species are established, they become difficult to eradicate (Genovesi 2005). Thus, anticipating and preventing future invasions is the most cost-effective form of management. The

essential role of prevention is stipulated in the Convention on Biological Diversity and the Global Strategy of the Global Invasive Species Programme (McNeely *et al.* 2001). Preventative measures are also required post-introduction. The invasive potential of recently introduced alien species needs to be reassessed regularly, since many alien species undergo a clear 'lag phase', sometimes for decades following introduction, before the species shows any signs of becoming invasive (Crooks & Soulé 1999). Many alien species already present in a region and that currently show no signs of being invasive will invade in the future.

Niche-based models (Guisan & Thuiller 2005) have been used to predict the invasion extents of various organisms, including beetles (e.g. Peterson & Vieglais 2001), fishes (e.g. Chen *et al.* 2007), birds and plants (e.g. Peterson & Vieglais 2001; Peterson 2003; Peterson *et al.* 2003; Peterson & Robins 2003; Thuiller *et al.* 2005c).The potential spatial extents of species' invasion are usually predicted with models fitted with data from the native range (Peterson & Vieglais 2001). This is because the invasion process in the invaded range may not be achieved and the invading species may not yet occupy all environmental conditions suitable for its growth and reproduction. Subsequently, using occurrence data from the invaded range would bias NBMs and result in an underprediction of the full potential extent of the invasion.

However, a crucial assumption is made when applying these models calibrated in the native range. The environmental niche of the species – its ecological requirements - is assumed to be conserved across space and time (niche conservatism; reviewed in Wiens & Graham 2005; Pearman *et al.* 2008a). Departures from this assumption may have important effects not only on the prediction of the invasion extent in the present (e.g.Broennimann *et al.* 2007), but also on predictions of future extents under warming scenarios (Araujo *et al.* 2005c).

Projecting NBMs into future climates

Even though increasing evidence shows that recent human-induced environmental changes have already triggered species' range shifts, changes in phenology and species' extinctions, accurate projections of species' responses to future climate changes are adopt proactive conservation planning measures using forecasts of species' responses to future environmental changes**.** To predict the future distribution of a species, NBMs quantify the species-environment relationships in the present and project the response curves on altered climate data translating climate change (i.e. climate change scenarios). The percentage of species turnover (defined as an index of dissimilarity between the current and future species composition within a given area) and the percentage of species that could persist in, disappear from, and colonize that area are often considered as a good measures of the degree of ecosystem perturbation, and have been used to assess the potential impact of climate change at regional to continental scales (Peterson *et al.* 2002). Since the

development of finer scale climate change scenarios in the past decade (e.g. Nakicenovic & Swart 2000), niche-based models that project future suitable habitat from current distributions have suggested that species turnover may be very high in some regions, potentially resulting in modifications of community structure strong enough to lead to ecosystem disruption (e.g. Bakkenes *et al.* 2002; Erasmus *et al.* 2002; Peterson *et al.* 2002; Midgley *et al.* 2003b; Thomas *et al.* 2004; Thuiller *et al.* 2005b). The application of NBMs to climate change analyses was highlighted by a recent, massive study assessing global species extinction risk (Thomas *et al.* 2004).

1.4 - OBJECTIVES & STRUCTURE OF THE THESIS

The general aim of this PhD thesis is to assess the usefulness, effectiveness and shortcomings of niche-based models calibrated on natural history collections data for the conservation of biodiversity, by investigating important unsolved limitations and suggesting new approaches. Given the broad scope of the issue, this will be achieved by conducting specific studies aiming to answer particular important - but yet unsolved – questions in studies of global change impact:

- **Chapter 2 presents two studies on the threat to rare and endangered plants**. First, a review **(2.1)** of the ecogeographic characteristic of 118 endangered plants with high conservation priority in Switzerland is presented. The prevalence of rarity types among plant species in Switzerland is assessed and analyzed in relation to IUCN extinction risks. The study underlines the importance of regional vs. global conservation practices in regard to rare and endangered species. The second study **(2.2)** proposes and tests a modeling framework including iterative steps of modeling and field surveys to improve the sampling of rare species. The approach is illustrated with a rare alpine plant, *Eryngium alpinum*.
- **Chapter 3 presents two studies on the impacts of climate change on biodiversity**. Both illustrate the case of African taxa. The first study **(3.1)** assess the sensitivity of 277 mammals at African scale to climate change by 2050 and 2080 using static land transformation assumptions and estimate the sensitivity of 141 African National Parks in terms of both species richness and turnover. The second study **(3.2)** model the distribution in 2050 of 975 endemic plant species in southern Africa distributed among seven life forms and provides new methodological insights improving the accuracy and ecological realism of predictions of global changes studies. It also investigates the possibility to estimate *a priori* the sensitivity of a species to climate changes from the geographical distribution and ecological proprieties of the species.

- **Chapter 4 presents four studies on the modeling of the spread of invasive alien plants.** The first study **(4.1)** assesses the historical biogeography of *Lactuca serriola L.* in Europe during the last 250 years. It shows the Northwards expansion of the species during the 19th in relation with climate changes during the same period. The second study **(4.2)** models the potential invasion extent of spotted knapweed, a European weed first introduced into North America in the 1890s. The study tests if the species conserved its climatic requirements in the invaded ranges. We further discuss the implication of a niche shift on the predictions in the invaded range. The third study **(4.3)** builds on the results of the latter to propose an alternative method using pooled data from the native and invasive ranges to accurately model the geographical extent of species invasions. The study investigates the uncertainties inherent to the methods when the models are projected into a future warming climate.

- **Chapter 5 presents synthesis and perspectives on the use of niche-based models to the study of global change impacts on biodiversity.** A review on the dynamic nature of ecological niches in space and time is presented**.** It synthesizes the recent application of NBMs and phylogenetic methods to analysis of niche characteristics and presents conceptual and theoretical developments to the niche conservatism issues evocated in chapter 4 concerning biological invasion. It further proposes solutions to improve confidence in NBM predictions of the impacts of climate change and species invasions on species distributions and biodiversity.

- **Chapter 6 presents a synthesis of the work** presented in the core of the manuscript and illustrates its usefulness through the impacts and debates generated in the recent literature. I further discuss the current limitations and possible improvements of the NBM approach to assess the impact of global change (**6.2** & **6.3**) and finish the chapter with a discussion of the interactions between the different drivers of global change (**6.4**).

Chapter 2

THREATS TO RARE AND ENDANGERED PLANTS

Chapter 2.1 Rarity types among plant species with high conservation priority in Switzerland

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ABSTRACT

We investigated the ecogeographic characteristics of 118 Swiss plant species listed as those deserving highest conservation priority in a national conservation guide and classified them into the seven Rabinowitz' rarity types, taking geographic distribution, habitat rarity and local population size into account. Our analysis revealed that species with high conservation priority in Switzerland mostly have a very restricted geographic distribution in Switzerland and generally occur in rare habitats, but do not necessarily constitute small populations and are generally not endemics on a global scale. Moreover, species that are geographically very restricted on a regional scale are not generally restricted on a global scale. By analysing relationships between rarity and IUCN extinction risks for Switzerland, we demonstrated that species with the highest risk of extinction are those with the most restricted geographic distribution; whereas species with lower risk of extinction (but still high conservation priority) include many regional endemics. Habitat rarity and local population size appeared to be of minor importance for the assessment of extinction risk in Switzerland, but the total number of fulfilled rarity criteria still correlated positively with the severity of extinction risk. Our classification is the first preliminary assessment of the relative importance of each rarity type among endangered plant species of the Swiss flora and our results underline the need to distinguish between a regional and a global responsibility for the conservation of rare and endangered species.

Key words: Rabinowitz' rarity types, conservation practice, extinction risk, geographic distribution, rarity assessment, vascular plants.

CONTRIBUTION TO THE PROJECT

I gathered, sorted and managed the occurrence data from the Swiss Floristic Network (CRSF) in Geneva and performed the analyses of the type of rarity. I also produced all the figures, performed the literature survey, wrote the first draft of the manuscript and supervised the reviewing of the paper.

INTRODUCTION

In the effort to conserve biodiversity worldwide, resources are often directed toward protecting rare species since these are assumed to undergo the highest risk of extinction (Gaston 1994). But is this assumption true? To answer this question, it is first necessary to define "rare" species, which is a non-trivial issue. Each researcher or practitioner probably has his own intuitive definition of what makes a species rare in the landscape (Gaston 1994), and there is no universal definition and measure of rarity. Depending on how it is defined, rarity may relate differently to extinction risk, so that an explicit and appropriate definition is essential if conservation priorities are based on rarity. The explicit definition of rarity is also important in studies that try to explain why species are rare, e.g. by comparing traits of rare and common species (Bevill & Louda 1999; Murray *et al.* 2002; Lavergne *et al.* 2004; Pohlman *et al.* 2005) or by searching for factors that limit the abundance of individual species (Schemske *et al.* 1994; Yates & Broadhurst 2002; Burns *et al.* 2003; Evans *et al.* 2004; Yates & Ladd 2004). The fact that no single cause of rarity has been identified by these studies may be due to the many forms that rarity can take in nature. The simplest way to assess the degree of rarity of a species is to quantify its geographic distribution. Two measures applied by the IUCN (2001) are the extent of occurrence (EOO; area in square kilometers of the minimum convex polygon including all known populations of a species) and the area of occupancy (AOO; sum of kilometer plots containing populations).These measures are easily applicable and require little information about the species, but they do not take into account the different forms of rarity that exist in nature. For example, the IUCN criteria cannot be used to compare the rarity of two endemic Alpine species, *Artemisia nivalis* (a species forming very small populations and restricted to *Drabion hoppeanae* communities at 3000 m a.s.l.) and *Carex baldensis* (which forms large colonies in several vegetation types). Both species have approximately the same EOO and AOO but their demographic and ecological characteristics are completely different, so that *A. nivalis* is actually much rarer than *C. baldensis*.

A more comprehensive measure of rarity has been proposed by Rabinowitz (1981; Rabinowitz *et al.* 1986), who defined seven rarity types based on a (i) *geographic range*, (ii) *habitat specificity* and (iii) *local population size* (Tab. 1). Species are rare if they have a restricted range, if they occur only in one or few specific habitats, and/or if their populations are always small. Species fulfilling two or three of the criteria are particularly rare, those fulfilling none of the criteria are common (Tab. 1). Rabinowitz' classification has been applied to numerous taxa and locations in the world (Kattan 1992; Arita 1993; Saetersdal & Birks 1997; Pitman *et al.* 1999; Yu & Dobson 2000). Rabinowitz' rarity types also lead to a more differentiated view on the relationship between rarity and extinction risk (Gaston 1994) in that the type of rarity may determine how endangered a species is. If so, measures to conserve biodiversity should not focus on rare species in general but more specifically on those with certain rarity features. Furthermore, as the rarity criteria can be assessed at regional scale (e.g. one country) or global scale (worldwide), they may lead to different priorities for the conservation of

regional and global biodiversity. In this study we characterise the rarity of 118 plant species from the Swiss flora, which have been selected as those deserving highest conservation priority in Switzerland. We address the following specific questions: (1) What types of rarity characterize these species with high conservation priority? (2) How does rarity relate to extinction risk across this set of species? (3) Do species that are geographically restricted at a regional scale also have a restricted distribution at global scale? We finally discuss some implications for the regional versus global conservational responsibility for rare and endangered species.

MATERIALS AND METHODS

Species data

The plant species analysed in this paper are those described in the Swiss guide for conservation of flowering plants and ferns (Käsermann & Moser 1999). This guide compiles information about 132 plant species in Switzerland resulting from detailed surveys during the past ten years. It provides a baseline to conserve the existing sites and to propose further actions that need to be taken for the conservation.The data on which this guide was elaborated (all species observations with their locations and population sizes) were provided by the Swiss Floristic Network in Geneva (www.villege.ch/cjb/rsf). Among the 132 species, presently extinct ones were included in the analysis if possible, based on their ecological and demographical features just before they become extinct. However, 14 extinct or critically endangered species had to be excluded because no information about local population size was available, leaving 118 species for the analysis.

Rarity criteria and rarity types

The geographic distribution of each species in Switzerland was quantified from the dot maps of the Swiss guide for conservation (Käsermann & Moser 1999). Only indications of presences or probable presences since 1998 were taken into account. Probable presences correspond to recent convincing information that have not been checked in the field for diverse reasons (lack of time, inappropriate weather or phenology during the sampling) or to historical populations not confirmed recently but probably still existing since occurring in undisturbed habitats (Käsermann & Moser 1999). On a grid of 226 plots of 16 16 km2 covering the whole Swiss territory, the number of plots occupied by each species was counted and expressed as percentage of all plots (hereafter called % coverage). A narrow geographic distribution was defined as a coverage of less than 1% (≤ 2 plots) or less than 10% (≤ 23 plots). To see whether species geographically restricted on a regional scale also tend to be restricted on a global scale, worldwide geographic distribution was assessed using the information about "general distribution and threats" in the guide for conservation. A distribution was considered to be narrow at worldwide scale if the species is endemic to a small region of Europe (for example: Orobic, Insubrian or Pennian Alps).

Table 1 - Rabinowitz' typology of rarity. Categories represent different rarity types based on the combinations of three dichotomic ecogeographic criteria as defined by Rabinowitz *et al.* (1986). When possible, an example of the flora present in Switzerland is given for each rarity type.

Geographic distribution		Wide		Narrow (restricted)	
Habitat rarity		Unspecific	Specific	Unspecific	Specific
Local population size	Somewhere large	Common *Trifolium pratense*	Type A *Spiranthes aestivalis*	Type D *Tulipa sylvestris* subsp. *australis*	Type E *Myosotis rehsteineri*
	Everywhere small	Type B ?	Type C *Dianthus gratianopolitanus*	Type F *Senecio halleri*	Type G *Artemisia nivalis*

The habitat of each species is indicated in the guide for conservation following a published habitat typology (Delarze *et al.* 1998).We classified the rarity of these habitats on the basis of the Swiss ordinance concerning the protection of nature and landscape (OPN 451.1), which edicts the list of habitats deserving protection in Switzerland. Habitats listed in this ordinance have been scientifically recognized as rare or irreplaceable for threatened and rare animals and plants (OPN 451.1). Species occurring only in rare habitats according to this list were considered as having a restricted habitat. For species occurring evenly in two habitats, the more abundant habitat was decisive, whereas for species occurring in several habitats but predominantly in one of them, the main habitat was evaluated. The habitat rarity criterion applied in this paper does not correspond to habitat specificity as defined by Rabinowitz *et al.* (1986) as it measures the rarity of the habitat instead of considering the specificity of a species to a few habitats. This is, to our point of view, a better estimation of the availability of suitable sites for a species in the landscape. Population size was indicated on a six-point ordinal scale (less than 10 individuals, 11 to 20, 21 to 50, 51 to 100, 101 to 200 and more than 200) for most species observations in the database of the Swiss Floristic Network. In clonal plants, "individuals" were units that could easily be counted, i.e. either single ramets or entire tussocks, depending on the growth form. A species was considered to have local populations "everywhere small" when all known population consisted of less than 200 individuals. Rarity types were attributed following the dichotomic procedure described by Rabinowitz *et al.* (1986; Tab. 1), using both thresholds for a restricted geographic distribution in Switzerland (1% and 10% coverage, respectively). A list of the evaluated species with their local population size, habitat rarity, geographic distribution and rarity type is given in Appendix 1.

Relationship between rarity type and extinction risk

The risk of extinction for every species was obtained from the guide for conservation (Käsermann & Moser 1999). It corresponds to the risk of extinction in Switzerland as defined by the IUCN/SSC (1994).This classification does not correspond exactly to that of the last Swiss Red List (Moser *et al.* 2002), but it was used here because it was based on the same data as our attribution of rarity types. The 1994 classification differs from the 2001 classification in that includes a category LR (lower risk), which was subsequently split into NT (near threatened) and LC (least concern). For each IUCN category, we determined the proportion of species fulfilling each of the three rarity criteria – restricted geographic distribution, rare habitat or small population size. Chi square tests were then performed to test if the proportion of species fulfilling a specific rarity criterion differed among IUCN categories. The tests were computed by considering the overall proportion of species fulfilling the rarity criteria as expected values.

RESULTS

The main ecogeographic characteristic of the plant species with high conservation priority in Switzerland is a restricted geographic distribution in this country: 94% of the 118 species cover less than 10% of the 16x16 km plots, and 39% of them even cover less than 1% (Fig 1). In contrast, the proportion of regional endemics is fairly low (24.6%) and unrelated to coverage in Switzerland (Fig. 1a).The two other rarity criteria are mostly fulfilled by species with a relatively broad distribution in Switzerland: 81.3% of the species with more than 5% coverage have rare habitats, but only 59.8% of the species with less than 5% coverage (Fig. 1b). Likewise, 85.7% of the species with more than 10% coverage have everywhere small populations, but only 41.4% of the species with less than 10% coverage (Fig. 1c). The rarity types attributed to each species are given in Appendix 1. Table 2 summarizes the number of species per rarity type for each of the two geographic distribution thresholds (1% and 10% coverage, respectively). With the 1% threshold, rarity types are represented in the sequence A > G > C > D > B = E > F, with 17 species considered as common. With the 10% threshold, types A, B, C and common are less frequent. The rank order is then E > G > D > F > A > C > B, with only one species classified as common (*Dracocephalum ruyschiana*). Rarity types differ significantly among IUCN categories of extinction risk (Tab. 3). The percentage of regional endemic species is greatest (74%) for species with low risk of extinction (LR) and decreases with increasing extinction risk; 0% of the extinct species are regional endemics (Tab. 3).The pattern is opposite for geographic distribution in Switzerland: only 21% of the species with low risk of extinction have a restricted geographic distribution in Switzerland (< 1% coverage), whereas 68% of the species with high risk of extinction and all extinct species do so (Tab. 3). The other relationships between IUCN categories and rarity features are not statistically supported. However, the percentages of species with rare habitat and of species with small populations also tend to increase with the risk of

extinction (Tab. 3). The IUCN risk of extinction correlates positively with the number of fulfilled rarity criteria for both geographic distribution thresholds (Fig. 2).

DISCUSSION

Ecogeographic characteristics of highly endangered plants in Switzerland

We have underlined the prevalent demographical and ecological features that characterize species with high conservation priority in Switzerland. Most of them are narrowly distributed on a local scale (Fig. 1). Interestingly, almost all widely distributed species – *Liparis loeselii*, *Spiranthes aestivalis*, *Cypripedium calceolus*, *Eryngium alpinum*, *Aquilegia alpina*, *Dracocephalum ruyschiana* – are well known forbs with attractive flowers, which may have biased botanists toward considering these species to be highly endangered (i.e. risk of picking).We also demonstrated that species with high conservation priority generally occur in rare habitats, but do not necessarily constitute small populations (Fig. 1).

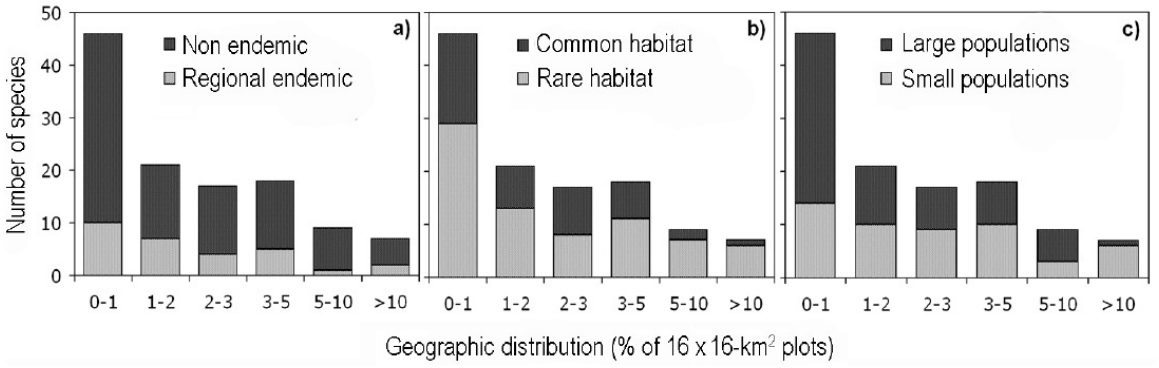

Figure 1 - Ecogeographic characteristics of 118 endangered plant species in relation to their geographic distribution in Switzerland: (a) proportion of regional endemics, (b) proportion of species occurring in rare habitats, and (c) proportion of species with everywhere small populations.

Rarity types, IUCN categories and conservation priority in Switzerland

The percentage of species in a flora attributed to each rarity type obviously depends on the criteria and thresholds used to define the classes (Tab. 1). Nevertheless, we strongly believe that this classification provides a useful preliminary assessment of the relative importance of each rarity type among threatened plant species in the Swiss flora. Some patterns might even hold more generally: the rank order of rarity types found here with the 1% threshold for geographic distribution resembles the sequence found in Britain (A > E > C = D > G > B > F; Rabinowitz *et al.* 1986). In both studies, type A is most frequent and type F least frequent.

Table 2 - Rarity types in the endangered Swiss flora (118 species with high conservation priority): number of species classified in each rarity type using a geographic distribution threshold of 1% and in parentheses, 10% (percentage of 16 16 km2 plots covered). See Methods section for a definition of the rarity criteria.

Geographic distribution		Wide		Narrow (restricted)	
Habitat rarity		Common	Rare	Common	Rare
Local population size	Somewhere large	**17** (1)	**30** (5)	**11** (29)	**10** (35)
	Everywhere small	**10** (0)	**15** (1)	**6** (14)	**19** (33)

Table 3 - Relationship between rarity and extinction risk. The percentage of species fulfilling various rarity criteria is given for the entire data set (total) as well as for each IUCN category. $\chi 2$ values and p-values indicate whether the percentages differ significantly among IUCN categories.

IUCN category	Total	LR	VU	EN	CR	EX	χ^2	p
Number of species	118	19	31	39	22	7		
% of regional endemics	24	74	29	10	9	0	26.00	0.000
% in <1% of 16×16 km^2 plots	38	21	19	36	68	100	16.22	0.003
% in <10% of 16×16 km^2 plots	94	84	87	100	100	100	0.61	0.962
% with rare habitat	62	26	65	77	55	100	7.07	0.132
% with small populations	44	37	29	46	55	86	5.16	0.272

We also demonstrated that species with the highest risk of extinction are those with the most restricted geographic distributions in Switzerland. In contrast, rare habitats and small populations, when considered alone, did not seem to constitute pertinent factors to assess extinction risk, which is surprising at first sight. This pattern reveals that geographic distribution is presently the most important criterion to decide if a species is endangered or not. It reflects the overriding importance given to the *criteria extent of occurrence* (EOO) and *area of occupancy* (AOO) in the definition of the IUCN categories (IUCN 1994, 2001). However, the significant positive correlation found here between the number of fulfilled rarity criteria and IUCN risks shows that habitat rarity and small population size also contribute to making a species prone to extinction.

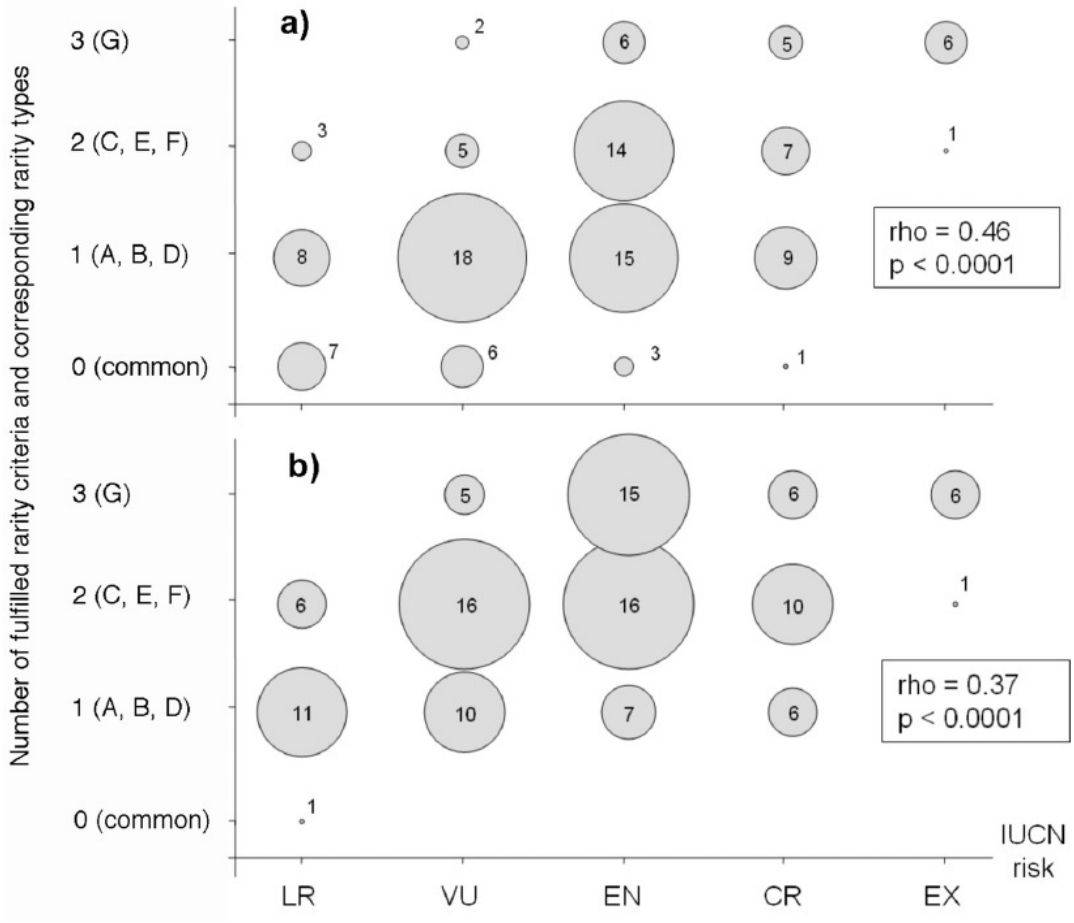

Figure 2 - Relationship between the number of fulfilled rarity criteria (categories as in Tab. 1) and IUCN extinction risks. Bubble size and numbers in the plots represent the number of species in each category, using a threshold of (a) 1% and (b) 10% for geographic distribution in Switzerland. IUCN categories of extinction risk are LR = low risk, VU = vulnerable, EN = endangered, CR = critically endangered, EX = extinct. Spearman rank correlations and their significance are given.

This result provides further support to the use of rarity classifications in conservation practice. Since species with a high degree of rarity usually undergo a severe risk of extinction, they deserve high local concern and conservation priority. Thus, Rabinowitz' rarity criteria could complement Red Lists as tools to identify species deserving priority in conservation action.

Global versus regional implications

The ecogeographic characteristics of the plant species analyzed in the study are specific to Switzerland. A different classification would have been obtained for some species if rarity criteria had been based on worldwide eco-floristic data. Such classifications would require global databases, which are unfortunately not yet available. However, we clearly demonstrated that very few highly endangered species in Switzerland are both regionally restricted and endemic on a worldwide scale. This might be due to the small area of the country and to the fact that Swiss frontiers do not coincide with ecogeographic boundaries. For example, many Mediterranean species have their

northern distribution limit within Switzerland because they cannot migrate to the other side of the Alps. This contrast supports the view of Murray and Lepschi (2004) that theories trying to account for local rarity are incomplete for the majority of species because they fail to account for different degrees of rarity in different places. This problem was already noted by Rabinowitz *et al.* (1986), who argued that differences in rarity status depending on the geographic area considered are not a drawback of their classification, but rather emphasize that rarity must be considered at a variety of spatial scales. Nevertheless, differences between local and worldwide rarity raise the more fundamental question of local versus global responsibility for species conservation. This question is underlined in our study by the relationship between extinction risk in Switzerland and worldwide endemicity (Tab. 3): species with the highest risk of local extinction were not endemics on a global scale. As these particular species are not endemics, they are likely to receive high conservation priority only when they become highly endangered at a local scale. The worst risk of not attributing a high conservation priority to a species that would be largely distributed over the world, but becoming rare at each national scale (e.g. due to increasing habitat destruction and fragmentation) would be to observe simultaneous extinctions in all countries. Although an unlikely situation, it remains a possible option that deserves to be considered seriously in national and international conservation strategies.

CONCLUSIONS

Our study shows that species given high conservation priority in Switzerland can be subdivided into three subsets: (1) species characterised by a restricted coverage of the Swiss territory and generally having a high risk of extinction in Switzerland; (2) endemic species that do not face a particularly high risk of extinction in Switzerland but have still been given conservation priority because of their endemicity on a global scale; and (3) species with a broad geographic distribution but either rare habitats or small populations or attractive flowers (high risk of picking).We believe that taking all these criteria into account – e.g. by calculating Rabinowitz' rarity types – would allow a better assessment of the endangerment of species before their extinction risk increases to the point that it is denoted by a restricted geographic distribution.

Appendix 1. Ecogeographic attributes and rarity classification for 118 endangered species listed by the Swiss Floristic Network (CRSF). Local population size (from the CRSF database): median and maximal number of individuals. Habitat specificity: habitat number following Delarze et al. (1998) and habitat rarity following the Ordinance for Nature Protection (OPN: "+" = frequent, "–" = rare). Geographic distribution: percentage of 16×16 km^2 plots covered in Switzerland (CH%) and regional endemicity (Käsermann and Moser 1999). Rarity types: determined following Rabinowitz (1981, 1986) using a geographic distribution (CH) threshold of 1% or 10%. IUCN Category = risk of extinction for Switzerland (Käsermann and Moser 1999).

Species	Local population size		Habitat specificity		Geographic distribution		Rarity types		IUCN
	Median	Max	Habitat	OPN	CH (%)	Regional endemicity	CH 1%	CH 10%	Category
Adenophora liliifolia	11-25	26-50	2.3.1	–	0.4	-	G	G	EN
Aldrovanda vesiculosa	>200	>200	2.1.1	–	0.9	-	E	E	EN
Allium angulosum	101-200	>200	2.3.1	–	8.5	-	A	E	VU
Allium rotundum	<10	11-25	8.2.3.2 (4.5.1)	+	0.9	-	D	D	CR
Anagallis minima	11-25	>200	2.5.1	–	6.3	-	A	E	EN
Anagallis tenella	<10	11-25	2.3.1	–	0.4	-	G	G	CR
Androsace brevis	11-25	>200	4.3.4	–	0.4	Orobic & Insubrian Alps	E	E	EN
Androsace septentrionalis	11-25	>200	4.1.4 (4.2.1.1)	+	4.0	-	common	F	VU
Anemone sylvestris	11-25	101-200	5.1.1	–	0.4	-	G	G	CR
Anogramma leptophylla	11-25	101-200	3.4.1.3	+	2.2	-	B	F	EN
Apium repens	<10	<10	7.1.1	–	0.0	-	G	G	EX
Aquilegia alpina	11-25	>200	4.3.3 (5.4.5)	–	29.6	Western Alps	A	A	LR
Aquilegia einseleana	26-50	26-50	4.3.1 / 3.3.1.4	+	0.4	Eastern Prealps	F	F	LR
Artemisia nivalis	11-25	101-200	3.3.1.3	–	0.4	Pennine Alps	G	G	VU
Asplenium adulterinum	<10	11-25	3.4.2.3	–	3.6	-	C	G	LR
Asplenium billotii	<10	101-200	3.4.2.2	+	0.4	-	F	F	CR
Asplenium foreziense	<10	101-200	3.4.2.2	+	0.9	-	F	F	CR
Baldellia ranunculoides	<10	11-25	2.1.3	–	0.9	-	G	G	CR
Betula humilis Schrank	<10	>200	5.3.7	+	0.4	-	F	F	CR
Blackstonia acuminata	<10	11-25	2.5.1	–	3.6	-	C	G	EN
Botrychium lanceolatum	<10	<10	4.3.5	+	2.2	-	B	F	CR

Species	Local population size		Habitat specificity		Geographic distribution		Rarity types		IUCN
	Median	Max	Habitat	OPN	CH (%)	Regional endemicity	CH 1%	CH 10%	Category
Botrychium matricariifolium	<10	<10	5.4.1 (4.3.5)	–	0.0	-	G	G	EX
Botrychium simplex	<10	11-25	5.4.1 (4.3.5)	–	0.0	-	G	G	EX
Botrychium virginianum	<10	<10	6.1.3 / 6.6.2	+	2.2	-	B	D	CR
Bromus grossus	<10	>200	8.2.1.1	+	1.3	-	common	D	CR
Bufonia paniculata	26-50	>200	8.2.3.4	+	0.9	-	D	D	EN
Cardamine matthiolii	26-50	>200	4.5.1	+	0.9	-	D	D	CR
Carex baldensis	101-200	>200	4.3.1 (6.4.2)	+	0.4	Central & Western Alps	D	D	LR
Carex chordorrhiza	26-50	>200	2.2.4	–	3.6	-	A	E	VU
Carex fimbriata	>200	>200	4.3.7	–	1.3	Pennine Alps	common	F	LR
Carex hartmanii	26-50	51-100	2.3.1	–	1.3	-	C	G	VU
Carex heleonastes	11-25	51-100	2.2.4	–	4.0	-	C	G	EN
Carpesium cernuum	11-25	>200	5.1.5	–	1.8	-	A	E	CR
Cypripedium calceolus	<10	51-100	6.2.1 (6.4.1)	–	48.0	-	C	C	VU
Cytisus decumbens	<10	>200	5.1.1 (4.2.4)	–	1.3	-	A	E	EN
Cytisus emeriflorus	51-100	>200	4.3.2	–	0.4	Insubrian Alps	F	F	VU
Deschampsia littoralis	<10	51-100	2.1.3	–	2.7	Central Europe	C	G	EN
Dianthus gratianopolitanus	<10	26-50	4.1.1 (4.3.1)	–	6.7	-	C	G	VU
Diphasiastrum complanatum	26-50	51-100	6.4.4	–	4.5	-	C	G	EN
Draba ladina	<10	>200	3.4.1.2	–	0.9	Switzerland	D	D	EN
Dracocephalum austriacum	51-100	>200	4.2.1.1 (4.2.4)	–	2.7	-	A	E	VU
Dracocephalum ruyschiana	26-50	>200	4.3.6 / 5.1.1 (4.3.1)	–	17.0	-	common	common	LR
Eriophorum gracile	11-25	>200	2.2.4	–	7.2	-	A	E	EN
Eryngium alpinum	<10	51-100	4.3.3 (5.2.3)	–	11.7	Western Prealps	A	A	VU
Erythronium dens-canis	51-100	>200	6.3.4 (6.3.3)	–	2.2	-	A	E	VU
Euphrasia christii	51-100	>200	4.3.6	+	4.5	Western Alps	common	D	LR
Falcaria vulgaris	11-25	>200	4.6.1 / 8.2.1.2	+	2.7	-	common	D	EN
Gagea pratensis	<10	>200	8.2.3.2	+	2.2	-	common	D	EN
Galium triflorum	11-25	>200	6.6.2	+	1.3	-	common	F	VU
Gentiana prostrata	11-25	101-200	4.3.4	–	1.3	-	C	G	EN
Gladiolus imbricatus	<10	<10	2.3.1 (4.2.4)	–	0.9	-	G	G	EN
Gladiolus italicus	<10	>200	8.2.1.2	+	0.4	-	D	D	CR
Gladiolus palustris	11-25	>200	2.3.1	–	5.8	-	A	E	EN
Gratiola officinalis	11-25	26-50	2.3.1 (2.1.3 / 7.1.1)	–	5.8	-	C	G	EN
Hammarbya paludosa	<10	51-100	2.2.4	–	0.9	-	G	G	EN

Species	Local population size		Habitat specificity		Geographic distribution		Rarity types		IUCN
	Median	Max	Habitat	OPN	CH (%)	Regional endemicity	CH 1%	CH 10%	Category
Pulmonaria helvetica	11-25	>200	6.1.4 / 6.2.3	+	2.2	Switzerland	common	D	VU
Ranunculus gramineus	11-25	>200	4.2.1.1 (4.1.3)	–	1.3	-	A	E	EN
Ranunculus pygmaeus	26-50	51-100	4.2.2	–	0.9	-	G	G	VU
Ranunculus rionii	<10	>200	1.1.2	–	0.9	-	E	E	CR
Sagina nodosa	26-50	26-50	2.5.1	–	2.7	-	C	G	VU
Salix myrtilloides	11-25	101-200	5.3.7	–	0.4	-	G	G	CR
Saponaria lutea	11-25	>200	4.3.1	+	0.9	Pennine Alps	D	D	VU
Saxifraga diapensioides	11-25	>200	3.4.1.2	+	1.8	Central & Western Alps	common	D	LR
Saxifraga hirculus	11-25	>200	2.2.4	–	0.4	-	E	E	EN
Scorzonera laciniata s.str.	11-25	>200	4.6.1	+	4.5	-	common	D	LR
Sedum rubens	26-50	>200	4.1.3 (7.1)	–	3.1	-	A	E	VU
Senecio halleri	26-50	101-200	4.3.7	+	4.9	Pennine Alps	B	F	LR
Senecio incanus subsp. insubricus	11-25	26-50	4.3.6	+	1.8	Central & Southern Alps	B	D	LR
Sisymbrium supinum	<10	>200	2.5.2 (2.1.3)	–	0.9	-	E	E	CR
Spiranthes aestivalis	11-25	>200	2.2.3	–	13.9	-	A	A	LR
Teucrium scordium	51-100	>200	7.1.1 (2.2.1.1)	–	3.6	-	A	E	EN
Thlaspi leresheanum	<10	>200	3.3.2.2	–	3.1	Western Alps	A	E	LR
Trifolium saxatile	11-25	>200	3.2.1.1 (3.2.2.1)	–	1.8	Central Alps	A	E	VU
Trochiscanthes nodiflora	11-25	>200	6.2.1	–	2.2	Western & Apennine Alps	A	E	VU
Tulipa sylvestris subsp. australis	101-200	>200	4.2.1.1 / 4.5.2	+	2.2	-	common	D	VU
Typha minima	<10	>200	2.2.3	–	3.1	-	A	E	CR
Typha shuttleworthii	11-25	>200	2.1.2.1 (2.2.3)	–	12.6	-	A	A	VU
Utricularia bremii	101-200	>200	2.1.1	–	2.2	-	A	E	EN
Valeriana celtica	26-50	11-25	4.3.6 (4.3.7)	+	0.9	Pennine Alps	F	F	LR
Veronica austriaca	11-25	26-50	4.2.2	–	0.4	-	G	G	EN
Vicia orobus	11-25	101-200	5.1.2	+	0.4	-	D	D	CR
Viola elatior	<10	>200	2.3.1	–	0.9	-	E	E	EN
Viola persicifolia	26-50	>200	2.3.1	–	3.6	-	A	E	EN

Helianthemum salicifolium	11-25	101-200	4.1.3	–	0.4	-	G	G	EN
Iberis saxatilis	<10	>200	4.1.2	+	0.4	-	D	D	VU
Inula britannica	11-25	>200	7.1.1	–	2.7	-	A	E	EN
Inula helvetica	>200	>200	5.1.3	+	8.5	Western Submediterranean	common	D	VU
Inula spiraeifolia	11-25	>200	4.2.1.2 (4.2.2 /6.3.4)	–	1.3	-	A	E	VU
Isoëtes lacustris	51-100	>200	2.1.3	–	1.3	-	A	E	VU
Isopyrum thalictroides	51-100	51-100	6.3.3	–	1.8	-	C	G	EN
Juncus stygius	11-25	>200	2.2.4	–	0.4	-	E	E	EN
Knautia godetii	11-25	11-25	4.5.2 (4.2.4)	+	4.0	Central & Subatlantic Europe	B	D	LR
Lathyrus bauhinia	11-25	>200	4.5.2	+	0.4	-	D	D	EN
Lathyrus sphaericus	11-25	>200	4.6.1 (4.2 /8.2.3)	+	1.8	-	common	D	VU
Leucojum aestivum	>200	>200	6.1.2	–	0.9	-	E	E	LR
Linaria alpina subsp. petraea	<10	26-50	3.3.1.5	+	2.7	Jura	B	F	VU
Lindernia procumbens	26-50	101-200	2.5.1	–	0.0	-	G	G	EX
Liparis loeselii	<10	>200	2.2.3 (2.2.4)	–	15.7	-	A	A	VU
Littorella uniflora	26-50	101-200	2.1.3	–	4.5	-	C	G	EN
Lomatogonium carinthiacum	11-25	>200	2.2.5	–	1.8	-	A	E	VU
Lysimachia thyrsiflora	26-50	>200	2.2.1.1	–	9.4	-	A	E	VU
Melampyrum nemorosum	<10	51-100	5.1.2 (5.1.1 /6.3.3)	+	1.3	-	B	D	EN
Minuartia cherlerioides subsp. rionii	11-25	>200	3.4.2.2	+	4.0	Central Alps	common	D	LR
Myosotis rehsteineri	26-50	>200	2.1.3	–	1.8	Prealps	A	E	EN
Nigella arvensis	11-25	51-100	8.2.1.2	+	3.1	-	B	D	EN
Notholaena marantae	<10	>200	3.4.2.3	–	0.4	-	E	E	CR
Nuphar pumila	11-25	26-50	1.1.4	–	2.2	-	C	G	EN
Orchis laxiflora	<10	26-50	2.2.3 / 2.3.2	–	0.4	-	G	G	EX
Orchis papilionacea	11-25	51-100	4.2.4	–	0.4	-	G	G	EX
Orchis provincialis	<10	<10	4.2.3 (6.3.4 / 6.3.5)	–	1.3	-	C	G	CR
Orchis spitzelii	<10	101-200	5.4.4	–	0.4	-	G	G	CR
Phyteuma humile	<10	101-200	3.4.2.2	+	1.3	Pennine Alps	B	D	LR
Pilularia globulifera	11-25	>200	2.1.3 (2.5.1)	–	0.4	-	E	E	EX
Pinguicula grandiflora s.str.	11-25	26-50	2.2.3	–	0.4	-	G	G	EN
Potentilla alpicola	11-25	>200	4.2.1.1 (4.1.4 /4.1.3)	–	1.8	Central & Western Alps	A	E	CR
Potentilla grammopetala	11-25	>200	3.4.2.2	+	2.7	Western Alps	common	D	LR
Potentilla inclinata	11-25	>200	4.1.4 (4.2.4 / 4.5.1)	+	5.4	-	common	F	EN
Primula daonensis	11-25	26-50	4.3.7	+	0.9	Rhaetic Alps	D	D	VU

Chapter 2.2 USING NICHE-BASED MODELS TO IMPROVE THE SAMPLING OF RARE SPECIES

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ABSTRACT

Because data on rare species usually are sparse, it is important to have efficient ways to sample additional data. Traditional sampling approaches are of limited value for rare species because a very large proportion of randomly chosen sampling sites are unlikely to shelter the species. For these species, spatial predictions from niche-based distribution models can be used to stratify the sampling and increase sampling efficiency. New data sampled are then used to improve the initial model. Applying this approach repeatedly is an adaptive process that may allow increasing the number of new occurrences found. We illustrate the approach with a case study of a rare and endangered plant species in Switzerland and a simulation experiment. Our field survey confirmed that the method helps in the discovery of new populations of the target species in remote areas where the predicted habitat suitability is high. In our simulations the model-based approach provided a significant improvement (by a factor of 1.8 to 4 times, depending on the measure) over simple random sampling. In terms of cost this approach may save up to 70% of the time spent in the field.

Keywords: efficiency, endangered species, *Eryngium alpinum*, habitat suitability maps, population discovery, predicted species distribution, prospective sampling

CONTRIBUTION TO THE PROJECT

I gathered, sorted and managed the occurrence data from the Swiss Floristic Network (CRSF) in Geneva and performed the model-based field sampling of *Eryngium alpinum* in the entire Swiss Alps except for the Eastern part. I performed the niche-based modeling work and produced the distribution maps. Finally, I contributed to the writing and the reviewing of the paper through discussions with Antoine Guisan.

INTRODUCTION

Monitoring populations of rare and endangered species has become a priority for most conservation agencies. It provides the major source of data for updating World Conservation Union and national red lists (Lamoreux *et al.* 2003), the main use of which is setting the long-term goals of conservation programs, such as helping identify biotopes or areas particularly in need of protection (Prendergast *et al.* 1993). Although precise quantitative and qualitative criteria are used to assign a particular status to a species (IUCN 2001), such decisions depend on the way the target species populations are monitored and on the sampling design used for data collection. A range of sampling schemes can be used to estimate the state of the system and its rate of change, the most efficient of which usually combine repeated (random) samples among existing sites with additional independent random samples at unvisited locations (Yoccoz *et al.* 2001; Stauffer *et al.* 2002).

Yet this random component is seldom considered in conservation surveys of rare species, although it is fundamental for ensuring unbiased population estimates and calculating unbiased estimates of distributional and population states. For example, remote populations may differ from accessible ones with respect to important environmental and management variables. In the context of distribution modeling, bias is thus likely to affect the quantification of the realized niche of a species and therefore the assessments that could be based on it. These include assessing the impact of climate change on species distribution and associated risks of extinction or searching for reintroduction sites for a species.

When species are rare, standard sampling methods such as simple or stratified random sampling, based on a simple combination of the main environmental gradients, can be highly inefficient (Rushton *et al.* 2004). For instance, in a sample of 550 plots surveyed in a random-stratified way based on the elevation, slope, and aspect of the plot during two consecutive summers in the Swiss Alps (704.2 km^2), not one occurrence of the rare and endangered plant species *Eryngium alpinum* L. was recorded. This was despite the species being easily detectable

if present and independent records of the species existing in the area within similar vegetation types. Directing the sampling to ensure inclusion of units with a higher probability of hosting the species is thus a desirable approach for increasing survey efficiency and reducing sampling costs.

Predictions from niche-based models of species distribution (Guisan & Zimmermann 2000) are promising tools in this respect (Côté & Reynolds 2002; Edwards *et al.* 2005) as a way to improve the sampling of species of conservation interest. Although population viability analyses have long been used in rare species management (Brook *et al.* 2000), spatially explicit, predictive, habitat distribution models have only recently been used in conservation biology (Vaughan & Ormerod 2003; Rushton *et al.* 2004). The majority of predictive models published in the literature were developed for common plant and animal species or for biodiversity. To date, relatively few successful applications of this

approach have been published for rare and endangered plant species (but see Miller 1986; Elith & Burgman 2002; Engler *et al.* 2004), although reliable spatial predictions are essential for species of great conservation interest. Paucity of data, spatial inaccuracy, and lack of valid absences are the main reasons identified for this shortcoming (Engler *et al.* 2004).

Recent methodological progress (Guisan & Thuiller 2005), such as improved predictive algorithms and more causal environmental predictors at a better spatial resolution, has made predictive models more reliable and applicable to the sampling of rare and endangered species

(Ferrier 2002). Here, we propose a procedure for using niche-based models of species distribution to direct a random-stratified prospect of the study area and improve the sampling of rare and endangered species. We illustrate the approach with the rare species *E. alpinum* by using data taken from a modeling study of endangered plant species in Switzerland (O.B., unpublished).We also tested the approach through simulations. Finally, we discuss the conditions for the successful application of this approach, highlight some of its main limitations, and make suggestions for future research.

METHODS

A General Procedure for Model-Based Sampling of Species Distribution

The general procedure for model-based sampling of species distribution is pictured in Fig. 1. A first model is fitted with available data. These data include information on monitored populations or records of species that are typically extracted from a computer data bank, such as those developed in botanical conservatories, museums, or biological data centers (Graham *et al.* 2004a). Spatial predictions derived from this initial model are then used to stratify the field sampling. Data gathered during this first sampling campaign serve to update the training data set and fit improved models that are used to direct the next sampling stage, and so on iteratively over several field seasons (Fig. 1). The higher prediction strata are expected to reveal those occurrences of suitable environmental conditions for the species where undetected or newly established populations, not recorded in the initial data set, might prevail. This iterative process can be repeated during the same field season or over consecutive seasons, and its success is mainly measured by the number of new occurrences found at each stage.

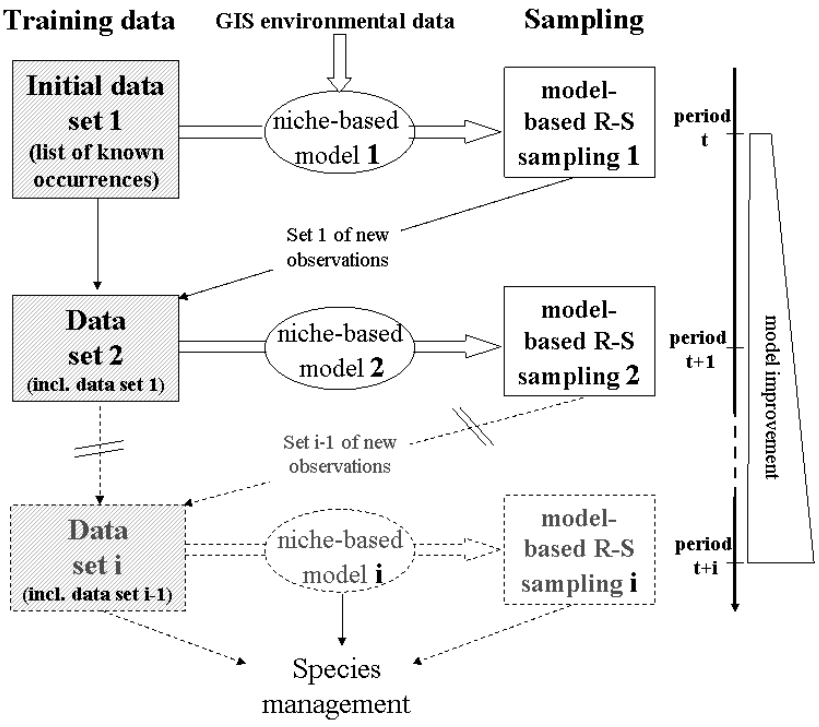

Figure 1 - Analytical procedure illustrating the iterative model-based sampling process.

Study Area and Species Data

The study area is the same as in Engler *et al.* (2004). We illustrate the proposed approach with *E. alpinum*, commonly called alpine eryngo, an emblematic species endangered in most parts of the calcareous European Alps. It grows mainly on deep and moist soils with intermediate to high level of nutrients, preferably on steep slopes where screes of large blocks occur and solar radiation is rather high. The exact reasons for its recent decline are still unknown, but possible threats could be picking and changes in pastoral practices (Engler *et al.* 2004). Original species data on *E. alpinum* were provided by the Swiss Floristic Network (CRSF) in Geneva (data can be ordered from http://www.crsf.ch). These records are usually provided by various volunteers and professionals, and thus they share the same idiosyncrasies as those in other natural history collections (Graham *et al.* 2004a) except that, in our case, information on the positional accuracy of each record is also provided. Only data with a minimum horizontal accuracy of 25 m were retained for the analyses, to match the resolution of environmental data layers used. Remaining data were used for visual evaluation of the prediction maps. Because only presence observations were initially available in the database, fitting the initial model required the generation of pseudoabsences.This was based on occurrences of 11 other rare species. With easily detectable and well-known rare species, like *E. alpinum*, this method of generating pseudoabsences works well because providers of rare species observations usually have a good knowledge of most other rare species. Thus, for each single observation of a rare species one can confidently assume the absence of all other possible rare species that usually share the same type of habitat. A total of 92 presences and 2380 absences were used to develop the initial predictive model. Following the recommendations of Manel *et al.* (Manel *et al.* 2001), we weighted the absences in the generalized linear models (GLMs) to ensure an equal prevalence (0.5) between presences and absences. This was achieved by providing a vector of weights with "1" for presences and "92/2380" for absences; so the total weight of absences was equal to the total weight (sum) of presences.

Environmental Predictors

We selected quantitative predictors to reflect the main biophysical gradients with a recognized, physiological influence on plants. We generated maps of monthly precipitation sums and monthly temperature averages from the Swiss meteorological network (normals 1961–1990) and a 25-m digital elevation model (DEM) and used them to derive predictors with a more causal effect on the fitness and survival of species. Topographic positions and slope angle were additionally derived from the DEM to express microclimatic corrections and disturbance effects. Table 1 lists all the predictors that were used to fit the models. Details on these predictors can be found in Zimmermann and Kienast (1999). Qualitative predictors were broken down into disjunctive classes, which were then used to filter the predictions made by the models. For qualitative filters we used simplified maps of geology and land cover types.

Table 1 - Quantitative geographic information system predictor variables used to fit the models for *Eryngium alpinum*.

Variables	***Description***
Seasonal indices of precipitation	obtained by a principal component analysis on monthly precipitation maps; axis 1 is the yearly sum of precipitation, whereas axes 2 and 3 express two seasonal variations trends
Monthly average of potential daily global radiation in March and July	calculated from the digital elevation model (DEM) as the sum of direct and diffuse radiation
Number of days of precipitation per growing season	calculated from a regionalized regression model of the annual number of days with rainfall of more than 1 mm on elevation
Degree-days of growing season	calculated as the sum of interpolated temperatures above the threshold of 3◦ C
Number of frost days	defined as a sudden drop of the daily minimum temperature below 2° C preceded by a period of at least 1 day above 3° C; expresses the core 90% of the vegetation period
Topographic position	relative topographic exposure of a pixel compared with its local neighborhood; indicates ridge tops, regular slopes, or valley bottoms
Site water balance	estimate of the water available to plants during a water year, based on precipitation, evapotranspiration, and the soil bucket size derived from the soil suitability map of Switzerland and topographic position
Slope angle	derived from the DEM

Niche-Based Statistical Models

We used generalized additive models (GAMs; Hastie & Tibishirani 1986) with a binomial distribution and logistic link function to fit the models based on topographic and climatic predictors (hereafter topoclimatic models). Model selection followed a stepwise algorithm based on Akaike's information criterion (AIC) that operates both backward and forward from an initial full model. We used splines as smoothers, with up to four degrees of freedom allowed in the stepwise procedure, as set by default in the program GRASP (Generalized Regression Analysis and Spatial Prediction; Lehmann *et al.* 2002b).

Each topoclimatic model was filtered by the binary variables derived from the qualitative predictors. To be a filter, the species must never occur on any pixel of the corresponding disjunctive class. Typical filters for *E. alpinum* include forested areas and all classes of siliceous bedrock. Although this might have the potential to bias the future sampling, for instance if the original data are biased against some rock or vegetation classes, such a risk is mostly reduced by also sampling outside the suitable areas (see below). Care should thus be taken when using such filters in other situations.

The agreement between predictions and observations was assessed using the standard area-under-the-curve (AUC) measure of a receiver-operating characteristic (ROC) plot (Fielding & Bell 1997) and its cross-validated version (AUC_{CV}). Values of AUC vary between 0.5 for an uninformative, random model and 1 for a model with perfect discrimination. Cross-validation was performed by splitting the data set into five partitions (5-fold CV) and reestimating the model coefficients at each loop.

The minimal predicted area (MPA; Engler *et al.* 2004) was calculated to complement the other evaluation measures and compare the predicted maps obtained after each loop of the reiterative modeling/field testing process (Fig. 1). It also constituted the primary stratification factor for the field sampling. The MPA is the surface obtained by considering all pixels with predicted values above the probability threshold that still encompasses 100% of the species occurrences (rule of parsimony). The resulting MPA map is binary, with 0 for cells where the habitat is predicted unsuitable and 1 for cells where it is predicted suitable.

To make spatial predictions of species distributions on a large data set possible (64 million pixels at 25-m resolution for Switzerland), we used lookup tables generated from the GAM models. A custom script was used in the ArcView geographic information software (ESRI, Redland, California) to implement the models and calculate the final potential maps.

The entire procedure, except the use of filters, was automated with the GRASP library of S-PLUS (Insightful Corp., Seattle, Washington) functions (Lehmann *et al.* 2002*b*; GRASP and the ArcView script are available online from http://www.cscf.ch/grasp).

Implementing the Model-Based, Random-Stratified Sampling

The model-based sampling was designed as follows. First, we fitted a model for the species based on topographic and climatic predictors, filtered by binary classes of qualitative predictors and used to predict the species distribution over the study area. Second, we calculated the MPA. Third, we superimposed the MPA map on a relief map and distinguished subareas of similar geological substratum belonging to the same macrotopographic unit (e.g., large massifs) (Fig. 2a). Because of limited sampling resources, only subareas including at least one patch of cells with high habitat suitability for the species (i.e., above the MPA threshold) were considered further for the sampling (Fig. 2a). We visited a random selection of these subareas in the field, according to a standardized field methodology. Hence we did not formally use a probability sample of the whole area, and the results should not be interpreted outside the range of the candidate subareas that define our target population.

We conducted survey walks in visited subareas, following a random trajectory based on the MPA map and designed to cross approximately an equal number of suitable and unsuitable pixels. In an attempt to reduce costs and increase survey efficiency, we opted for survey walks across the

probability gradient rather than a strict random stratified procedure, based on sampling individual pixels randomly in both strata (within and outside MPA), because surveying all of Switzerland was not possible. The full trajectory was recorded using a GPS system (Garmin eTrex Summit, Olathe, Kansas, locational accuracy <10m). New occurrences, when found, were recorded and georeferenced using the GPS. A series of points without species observations were also sampled at regular intervals (at least 500 m, to avoid spatial autocorrelation) along the recorded trajectory to generate likely absences for the species.

All new and updated presences and absences were used to fit a second, improved model to be used as a next step to redirect the sampling effort (Fig. 1). New observed absences force the model to be more discriminating at locations where the prior model was predicting high suitability values. On the other hand new observations of presences help remove bias from predictions and narrow the species realized niche. A bias may for instance be introduced in the original model if the species observations offered only a partial view of the species niche, which could result if only some geographic areas were subjectively sampled. Because visual detectability was high for *E. alpinum*, absences generated in this way are likely to be reliable. This is unlikely to hold for inconspicuous species; thus field sampling and modeling approaches, including detectability (Stauffer *et al.* 2002; Edwards *et al.* 2005; MacKenzie *et al.* 2005), should be used in these cases. The status of each binary class of qualitative predictor used as a filter was also revised after field sampling (Fig.1) by checking that no new presence occurred in any of them.

Testing the Approach by Simulation

To test sampling improvement over several iterations, we conducted simulations with a virtual species in a real landscape (Hirzel & Guisan 2002). The distribution of a virtual species can be defined from the available environmental predictors by specifying response curves for each predictor and combining them to draw a habitat suitability map. The final species distribution map is then obtained by cutting the previous suitability map into a presence-absence map reflecting presence and absence of the virtual species in each pixel of the study area. The advantage here is that the truth is known; thus model predictions can always be compared with this original "true" distribution of the species.

In our case, the true distribution of the virtual species in the study area was artificially derived from the first model for *E. alpinum* so that it remained as close as possible to a real situation (same type of distribution, same study area). To turn the probabilistic map into a binary presence-absence map, we used a cut-off value of 0.8, yielding a distribution restricted to about 5% of the study area. This map reflected the true distribution of the virtual species. This way, field iterations could be simulated simply by checking the presence or absence of the virtual species at each sampling site on this map. After each iteration, the predicted distribution map was reclassified using the MPA threshold—as

required by the model-based stratification of the sampling—and the resulting binary predictions were compared with the virtual distribution with the kappa coefficient (Cohen 1960).We used kappa here instead of the AUC because the comparisons involved directly two binary variables. Hence it provided a reliable measure of model improvement over time (here, the successive iterations), reflecting a convergence, or no convergence, toward the true distribution. For computational reasons the simulations were not run over the entire Swiss landscape but on a subset of 500,000 pixels selected in a random-stratified way across the main environmental gradients. This subset of pixels accurately reflected the prevalence of the different habitat suitability classes of the virtual species.

The iterative, model-based, random-stratified sampling procedure was simulated as follows:

1. An initial data set of 30 presences and 30 absences was randomly selected among the pools of 92 presences and 2380 absences used to calibrate the "true distribution" of our virtual species. Hereafter we refer to this data set as the training data set.
2. Using the training data set, a GAM was fitted and predictions were made across the entire study area (i.e., the 500,000 randomly chosen pixels). We used the MPA threshold to transform probabilistic predictions into binary values (presence or absence of the species).
3. The agreement between the binary predictions map and the known binary distribution of the virtual species was evaluated using the kappa coefficient.
4. An equal number of sample sites were selected randomly within (predicted presence) and outside (predicted absence) theMPA (i.e., the two sampling strata).
5. To avoid spatial autocorrelation we did not allow the selection of new sample sites within a radius of 500 m of any already sampled site.
6. The fieldwork was simulated by checking, from the virtual distribution, for true presence or absence in each sample site. At this stage we recorded the number of new occurrence sites found. All new and updated observations were then added to the training data.
7. Steps 2 to 5 were repeated 10 times (e.g., simulating a 10-year survey). Because the selection of the new sample sites involved randomness, we repeated each loop 20 times to quantify the related uncertainty (Fig. 3).

We ran this simulation procedure for three different experiments: sample 30, sample 60, and sample 120. Numbers indicate the initial number of observations and the number of sites sampled at each iteration (e.g., 30 means 15 sites sampled within the "predicted presence" strata and 15 sites within the "predicted absence" strata). Additionally, control simulations in which the new sample sites were chosen completely at random in the landscape, rather than on a model-based stratification basis, were run for each scenario (Fig. 3). We repeated these control simulations 20 times. Differences between model-based and full-random-sampling simulations were assessed with paired *t* tests or Wilcoxon signed rank tests when normality was not satisfied. When values were > 0.05, the difference between the two curves was not significant.

RESULTS

A New Picture of the Species' Distribution

Hardly any of the records from the eastern part of the Swiss Alps were confirmed by revisiting existing occurrence localities in 2003, thus offering a very different view of the species range at the end of the field campaign from that suggested by the historical data records. Based on confirmed records only, the status of the species in the Swiss red list would qualify for a downgrade from vulnerable to endangered. Interestingly, most of the unconfirmed records seemed to be specimens that had escaped from nearby gardens, where the plant was cultivated artificially, and in most cases in areas that do not appear naturally suitable to the species long-term survival.

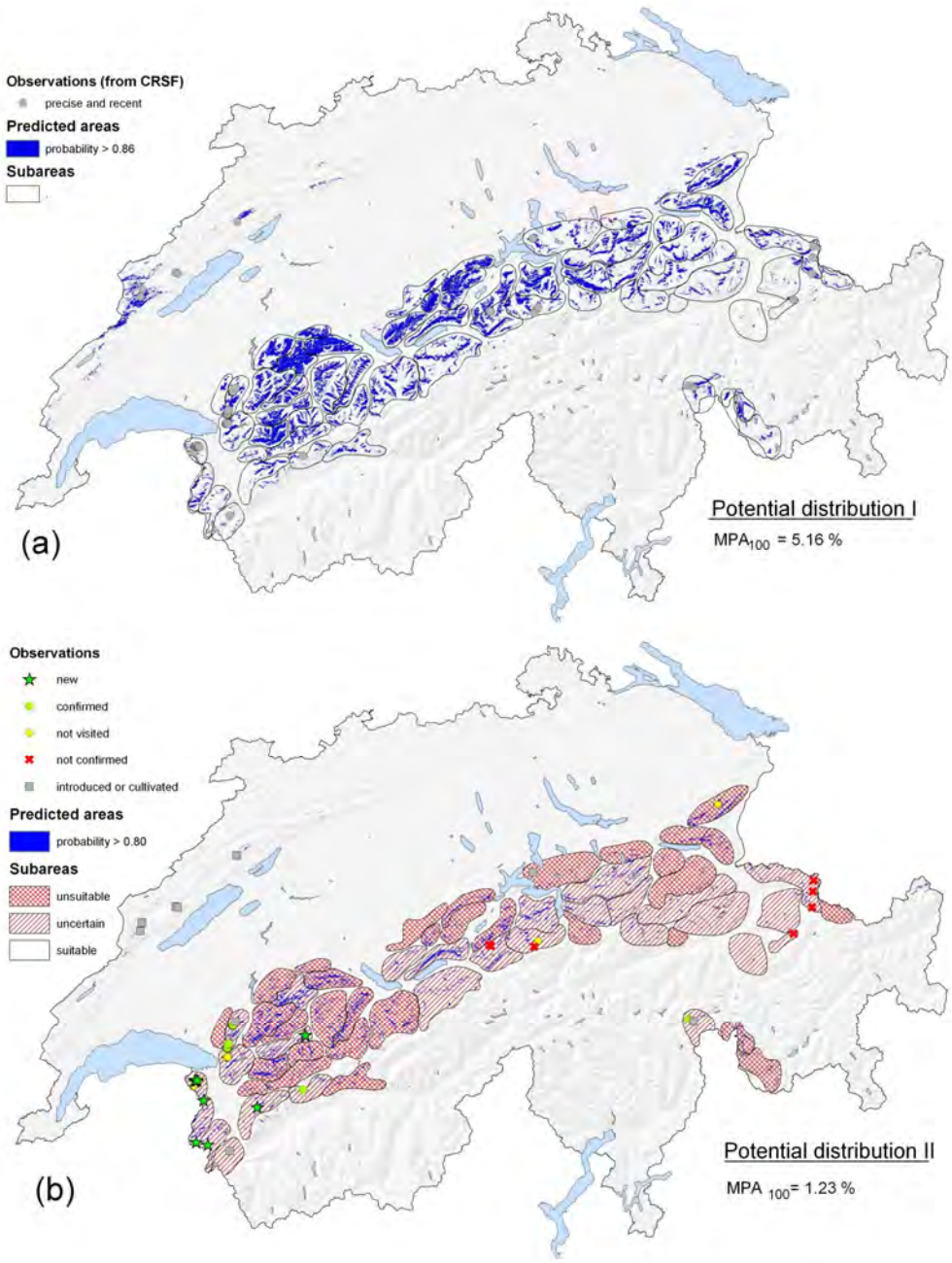

Figure 2 - Potential distribution maps for Eryngium alpinum in Switzerland. (a) Model 1, used to stratify the sampling. Subareas used for sampling are also shown (polygons; see text). Observations correspond to recent (1995 or later) and precise (25-m accuracy) observations. (b) Model 2, improved from model 1 with data sampled in the field. Updated knowledge on geological units important for the species, derived from the field campaign, is also shown (polygons with various shading). The predicted area appears in both maps as dark grey and corresponds to the minimal predicted area (MPA; see methods) containing 100% of observations (MPA_{100}).

Model-Based, Random-Stratified Sampling for E. alpinum

The first predictive model for *E. alpinum* yielded values of simple evaluation and cross-validation AUC of 0.97 and 0.96, respectively, and the corresponding map was filtered using several qualitative variables (Fig. 2a). Positive filter classes for the species were land use (1, bushes in a 200-m buffer zone from meadow/pasture; 2, rocks in a 200-m buffer zone from meadow/pasture; 3, drain stone; 4, meadow/pasture) and geology (rock and soil) (1, sand and silts; 2, coarse screes [fallen blocks]; 3, marl; 4, marly schist; 5, calcareous phyllites; 6, massive limestone; 7, sandy limestone). For any other qualitative class, predictions were reset to 0. The 100% threshold for this first map was at $p = 0.86$, and the MPA covered 5.1% of the entire Swiss territory. The resulting binary mapwas superimposed on the shaded relief and divided into subareas (Fig. 2a). A random selection of nearly half the subareas (45.7%, covering 1438 km^2) was visited during summer 2003. Seventy-nine survey walks adequately sampled the two sampling strata, with 56.9% of the paths in areas outside MPA ($p < 0.86$) and the remaining 43.1% of paths within MPA areas ($p \geq 0.86$).

Overall, seven new populations were discovered, which were not previously recorded in the database or the literature. All the new populations occurred in western Switzerland, within highly suitable landscape patches (probability of presence > 91%), and were subsequently used to fit an improved model for the species (Fig. 1). The second model, improved from a field-based update of the initial data (new observations, update of historical records, and a set of field-checked absences), and revised filters (land use 1 and geology [1–3] removed; classes of slope and aspect added) provided a much narrower prediction of the species range (MPA of 1.2%) that better reflected its actual niche, distribution (local and patchy), and endangered status in the Swiss Alps (Fig. 2b). The same predictors were retained; thus only their coefficientswere updated. Most subareas where the

species was previously predicted by the primary model, but where no species occurrence could be found, no longer included any suitable patch in the map drawn from the improved model (Fig. 2b). This second model and related spatial predictions had simple validation and cross validation AUC coefficients of 0.99 and 0.98, respectively.

Simulations

In all three scenarios the number of new presences found over 10 iterations was always much higher when using the model-based stratification approach (about four times in all simulations; Fig. 3). For instance, at a sample size of 30, only 6 iterations were needed with the model-based sampling to double the initial number of presences (i.e., to pass from 30 to 60), whereas nearly 20 iterations would have been needed with simple random sampling. In this case, the model-based approach was 3.3 times faster, corresponding to a net gain in time of 70%. At a sample size of 60, the model-based approach was still 2.3 times faster (considering the doubling case), allowing a 55% gain of time compared with random sampling. In all experiments, the cumulative number of new occurrences found by model-based sampling after 10 iterations was always about 4 times greater than those found by a simple random sampling.

Averages and standard errors of the adequacy between the predictions and the true distribution of the virtual species are also reported for all simulations (Fig. 3). Except for the sample120 scenario, where no significant difference was found, the model-based sampling approach led, on average, to a predicted distribution that had higher agreement with the true distribution of the virtual species than that obtained with the random sampling.

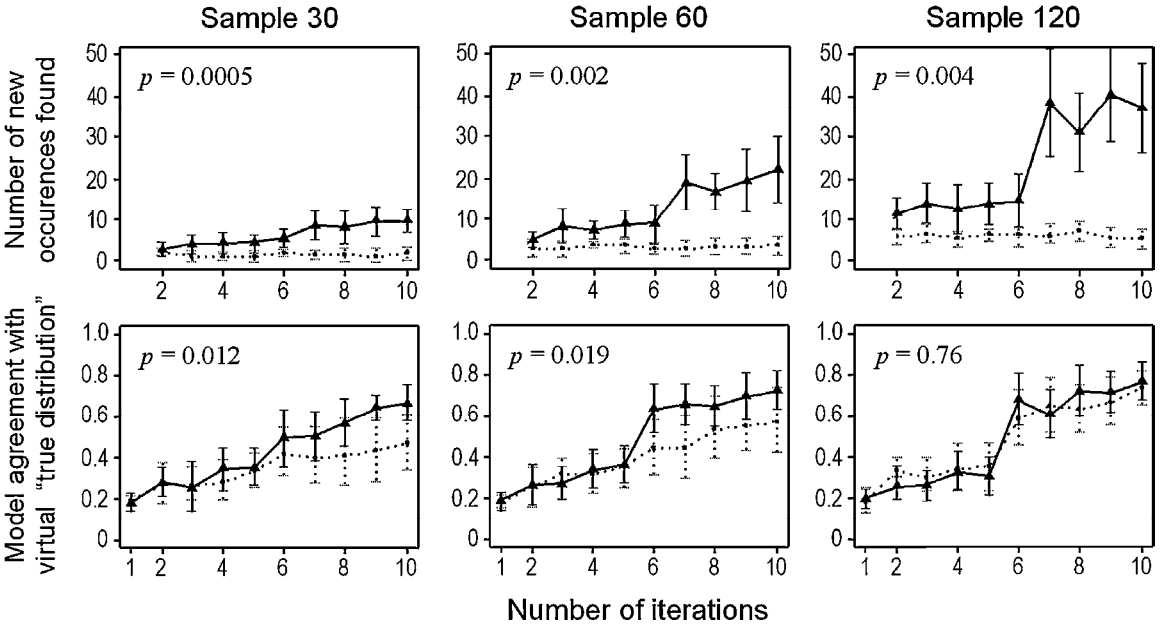

Figure 3 - Average (±SE) number of new occurrences of Eryngium alpinum at each iteration (upper graphs), and the kappa agreement between the predictive model built at each iteration and the true distribution of the virtual species (lower graphs). Solid lines represent simulation with model-based stratification when selecting the new locations to sample. Dashed lines are the control simulation, where the new points to be sampled were chosen completely at random. The horizontal series of graphs correspond to increasing number of sample points visited at each iteration (30, 60, 120). The p values are only indicative because they depend on the number of simulations. Each point on a graph was obtained as an average of 20 runs. The field work of iteration i + 1 is done using the model of iteration i. This explains why the "number of new occurrences found" starts at iteration 2.

DISCUSSION

We have presented and illustrated the use of predictions obtained from niche-based species distribution models for stratifying sampling and improving data sets on rare and endangered species. Similar approaches based on simple models (e.g., bioclimatic envelope models) have been published independently (Parris 2002; Poon & Margules 2004). The procedure has the advantage of fitting an existing sampling design in ecology and conservation biology (random-stratified approach), and it adds a new model-based sampling scheme that is expected to increase sampling efficiency, particularly the chance to discover new populations of rare species. The approach was successfully verified through field checking—with seven new populations discovered for the severely endangered species *E. alpinum*—and in computer simulations.

Robust Modeling Approaches Needed for Stratification

To be efficient, the stratification ideally has to be based on as robust an initial model as possible to reduce costs by reiterating only a few sampling stages. Thus the modeling strategy itself is important. Four elements can contribute to a successful modeling effort when species data from such heterogeneous data banks are used. First, species occurrences need to be carefully selected before conducting the statistical analyses by considering the positional accuracy of site location (when recorded in the database). In our study we dropped several occurrences from the original data set, keeping only those corresponding to the grain size and positional accuracy used for the modeling. Such operations limit measurement errors significantly (Engler *et al.* 2004).

Second, close attention needs to be given to preparing and selecting predictors, including only those expected to have a causal physiological effect on the species (Austin 2002). Third, using an appropriate modeling technique for the data at hand (e.g., when sufficient occurrences are available, use a flexible semi parametric modeling approach such as GAM) allows for the calculation of response curves that more closely fit the data (Guisan *et al.* 2002; Lehmann *et al.* 2002a). This is particularly appealing when the predictions are to be made in the same area that was used to calibrate the model. Response plots in GAMs may additionally allow one to check plot density along each environmental predictor and improve the sampling of unevenly sampled predictors during the next field campaign. When fewer data are available, more simple approaches such as climatic envelopes (e.g., BIOCLIM) can be used instead (Guisan & Thuiller 2005). Finally, fourth, when absences are not available from a systematic survey, generating pseudoabsences from presence sites of other rare species seems a promising approach (A.L., unpublished).

Use of Survey Routes

Survey routes recorded on GPS may be a valuable way to explore sampling frameworks further, as a means to lower survey costs and provide additional absences for improving the models. As our results show, generating absences along survey routes can be useful to increase the discriminatory power of the models. Some important limitations exist, however, and should be highlighted before this approach can be further promoted.

Although our species was easily detectable, which was convenient for the first test of the approach, many species will indeed be much harder to detect in the field. Species detectability (MacKenzie *et al.* 2005) is a major component to consider because it can affect the whole modelbased approach in two ways: (1) as additional cost during the field sampling (e.g., more time might be needed to detect cryptic than conspicuous species) and (2) in the way absences are derived from survey routes because these absences might not have the same reliability for different species. The latter aspect is of prime importance when presence-only data are the sole initial source of species data available at the start of the study, as is the case with data from natural history collections (Graham *et al.* 2004a; Rushton *et al.* 2004).

The use of survey routes across stratifying gradients (in our case, predicted presence or absence of the species) is specific to cases where survey costs need to be reduced. The approach is similar to the cost-reduction "gradsec" sampling technique described by Austin and Heyligers (1989), although applied to a model-based stratified sampling situation rather than to an environmentally based stratification of sampling. Refinements might come here from such guided transects across the stratifying gradients (Stahl *et al.* 2000; Thompson *et al.* 2004) rather than survey routes.

In cases where there is no need to reduce survey costs, a strict model-based, random-stratified approach (i.e., no survey route, no gradsec) in which target cells are randomly chosen in each prediction strata throughout the whole study area should be preferred. The latter is the approach that was used in our simulations.

Confirmation by Simulations

Our simulation results showed that using a model-based rather than a simple random sampling (control) yields both a greater number of presences and a higher adequacy of model predictions. Obtaining such improvement over a random sampling is not surprising because no one would sample rare species randomly in the field, but it provides a standardized and objective measure of improvement. This is, however, mostly true below a certain sample size. With 120 sites (or more) sampled at each iteration, the model based approach did not converge significantly faster toward the true distribution than the simple random sampling, but the number of new presences found remained much greater (nearly four times). With a sample size of 30 and 60 sites visited at each iteration, the improvement was very apparent, with a significantly greater number of presences found. Thus, the fewer the number of sites sampled at each iteration, the more valuable the use of the model-based approach. This has direct implications for reducing costs of surveys in nature conservation.

A Flexible, Adaptive Approach

One advantage of this approach is to let the model reflect the current state of a species distribution (or of a set of species). In this sense, it is adaptive. This is particularly important because some environmental conditions or the fitness of some populations might change during the course of the survey, possibly resulting in a temporary lower model evaluation. Such a temporary decrease in model performance may also happen under stable conditions, as observed by simulations (internal variation within the 20 replicates; see error bars in Fig. 3). In the latter cases, the model returned rapidly (usually within the next iteration) to a situation of higher agreement with the true geographic distribution. The same might be expected after an environmental change, which is thus only likely to delay model convergence by some number of iterations.

Which Method for Which Data?

In this study, we had recourse to GAMs to predict the distribution of a rare species for which 92 occurrences were initially available. GAMs, however, are relatively data-hungry modeling techniques. As such they need a sufficient number of occurrences to be fitted. In many cases fewer occurrences will be available at the start of the study, as in the case of many rare and endangered species in data-poor countries, which will prevent the use of such an advanced technique. When too few species occurrences are available (say < 20), alternative approaches must be found. Alternatives can be (1) a simpler technique such as climatic envelopes (Poon & Margules 2004); (2) a modeling approach at the community level (Ferrier 2002), where the data for more common species may help support the modeling of less frequent species; or (3) models for more common species that are frequently

associated with the rare target species. In the last case, Edwards *et al.* (2005) show that a model-based stratified sampling based on common species can significantly improve detectability of rare species in coarse-scale surveys.

The resolution used in our study was also much finer than often available elsewhere. Although this approach could theoretically be conducted at any resolution, problems may well appear when the size of the sampling unit becomes too large to be properly surveyed in the field. Again, the choice of an appropriate resolution and survey design is likely to depend primarily on a species' detectability (screening a large sampling cell is easier for a conspicuous than for a cryptic species). Future tests of the method may thus need to take detection probability into account in the sampling design and related statistical inferences (MacKenzie *et al.* 2005).

Sampling Bias and Predictors Used

There might be a risk of converging toward a biased model, because of the influence of some of the initial parameters (e.g., initial sample size, number of sites sampled at each field iteration, initial environmental or geographic bias in the data). As long as the area is sampled probabilistically in both the suitable and unsuitable strata, however, the model iterations should converge rapidly toward unbiased estimates.

Besides an initial sampling bias, predictions may additionally be weakened—and thus with it the strength of the approach—if one or several proximal environmental predictors (Austin 2002) are not included in the initial model or if the model is severely overfitted. It is thus critical to decide which predictors should be included and how strict the limitation of the final number of predictors

in the model should be. With only a few species occurrences, a limitation rule that is too strict (e.g., a stepwise procedure in a regression model, based on the Bayesian information criterion) may prevent the inclusion of some proximal predictors, whereas including too many predictors may cause the model to direct the sampling too narrowly toward some situations. In both cases the effect is likely to be a reduction in sampling efficiency. Hence a tradeoff has to be found, which still requires further investigation.

Future Research Directions

Where multiple species and overall biodiversity are the focus, distinct sampling designs could be used (Ferrier 2002; Edwards *et al.* 2005) or the same model-based, random-stratified design might be adapted to a multispecies situation. The use of alternative modeling methods such as community modeling (Ferrier 2002) should also be investigated, within a similar model-based sampling

framework, when too few occurrences are available at the start of the study but more common species were jointly inventoried (which was not the situation in our case).

Improved field design may also be implemented within such a model-based approach, such as adaptive cluster sampling (Thompson & Seber 1996). In adaptive cluster sampling, a more intensive search of the species in neighbor plots is made every time the species is met at one of the plots included in the original design. The search is conducted within a neighborhood window of specified shape. Every time the species is found again within this window, the same procedure is repeated until no additional occurrence is found. This design is optimal when improved estimates of the whole population size in the area are requested and is particularly efficient for sampling rare, clustered species (Thompson & Seber 1996; Christman 2004). Hence it will be particularly suited for the case of rare species with large populations in the areas where they occur (i.e., the "urban" type described in Collins *et al.* 1993). Such adaptive cluster sampling was for instance successfully tested in a parallel study of an invasive species—*Heracleum mantegazzianum*—that has still a scattered distribution in the study area (A.G., unpublished results).

Model-based sampling of rare species, involving reiterative alternation of modeling and field sampling phases, shows great promise for strengthening and complementing conservation practices and reducing sampling costs. It would be optimal if applied together with the monitoring of those additional parameters required by population management (e.g., accessibility of sites as a surrogate for picking; agricultural practices as a surrogate for grazing). The approach would still deserve more thorough testing, however, especially in the field, before it can be applied more widely. Once more broadly validated, it may be seen as a valuable approach for nature conservation agencies.

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Chapter 3

CLIMATE CHANGE IMPACTS ON BIODIVERSITY

Chapter 3.1

Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions

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ABSTRACT

Recent observations show that human-induced climate change (CC) and land transformation (LT) are threatening wildlife globally. Thus, there is a need to assess the sensitivity of wildlife on large spatial scales and evaluate whether national parks (NPs), a key conservation tools used to protect species, will meet their mandate under future CC and LT conditions. Here, we assess the sensitivity of 277 mammals at African scale to CC at 10' resolution, using static LT assumptions in a 'first-cut' estimate, in the absence of credible future LT trends. We examine the relationship between species' current distribution and macroclimatic variables using generalized additive models, and include LT indirectly as a filter. Future projections are derived using two CC scenarios (for 2050 and 2080) to estimate the spatial patterns of loss and gain in species richness that might ultimately result. We then apply the IUCN Red List criteria A3(c) of potential range loss to evaluate species sensitivity. We finally estimate the sensitivity of 141 NPs in terms of both species richness and turnover. Assuming no spread of species, 10–15% of the species are projected to fall within the critically endangered or extinct categories by 2050 and between 25% and 40% by 2080. Assuming unlimited species spread, less extreme results show proportions dropping to approximately 10–20% by 2080. Spatial patterns of richness loss and gain show contrasting latitudinal patterns with a westward range shift of species around the species-rich equatorial zone in central Africa, and an eastward shift in southern Africa, mainly because of latitudinal aridity gradients across these ecological transition zones. Xeric shrubland NPs may face significant richness losses not compensated by species influxes. Other NPs might expect substantial losses and influxes of species. On balance, the NPs might ultimately realize a substantial shift in the mammalian species composition of a magnitude unprecedented in recent geological time. To conclude, the effects of global CC and LT on wildlife communities may be most noticeable not as a loss of species from their current ranges, but instead as a fundamental change in community composition.

Keywords: Africa, climate change, extinction risk, IPCC storylines, land transformation, mammals, national parks, species distribution models

CONTRIBUTION TO THE PROJECT

I spent three months in Kirstenbosh, Cape Town, South Africa where I trained the models for the 277 mammal species and assessed the projected spatial patterns of richness loss and gain. I calculated the rate of extinctions and species range changes. I was also in charge of the retrieving and upscaling of the land transformation data. I prepared most of the figures and tables. Furthermore, I participated to the reviewing of the manuscript.

INTRODUCTION

Future changes in atmospheric CO2 and climate will directly affect the distribution, abundance and life cycles of most species and ecosystems (Araujo *et al.* 2005a; Schröter *et al.* 2005). Species are generally expected to respond individualistically to these changes, for example by shifting their distributions as they track moving climate zones (Prentice 1986; Huntley 1990; Graham 1992). Hypothetically, the geographic ranges and/or coincidence of species that currently interact may therefore progressively move apart, while species that do not presently coexist may do so in the future (Araujo *et al.* 2005a). Thus, great potential exists for novel species combinations to occur, and for present day relationships to become increasingly decoupled (Hughes 2000). Recent meta-analyses have already shown species' range shifts because of climate change (CC) during the last century for both animal and plant taxa (Parmesan & Yohe 2003; Root *et al.* 2003). Land transformation (LT) by humans restructures the landscape, enhancing or, more often, perturbing species range migrations that may be induced by CC. These synergistic human-induced global changes therefore threaten wildlife and vegetation around the globe (Sala *et al.* 2000), and decisions may have to be made to optimize the persistence of this biodiversity (Araujo *et al.* 2004).

In the past decade, several papers have related climate to the distribution of species (Huntley *et al.* 1995; Sykes 2001; Bakkenes *et al.* 2002; Peterson *et al.* 2002; Thuiller *et al.* 2005a), plant functional types (Box 1996; Smith *et al.* 2001; Sitch *et al.* 2003; Thuiller *et al.* 2006b) or biomes (Malcolm *et al.* 2002), estimating the likely impacts of CC under a range of possible future scenarios. However, few studies have attempted to assess the impacts of global change on animal distributions, and especially mammals (but see Erasmus *et al.* 2002; Burns *et al.* 2003). Animals, as consumers at higher trophic levels, are influenced both by climate that potentially limits physiological processes, and by vegetation that determines resource availability and habitat. They are, therefore, likely co-limited by vegetation and climate (Grayson 2000). Evidence from paleo-ecological studies suggests that mammals responded abruptly to Middle-Holocene CC, especially around the Great Basin of the western US (Grayson 2000), by showing a decrease in species richness and evenness, driven largely by a series of local extinctions and near-extinctions coupled with a dramatic increase in the abundance of xerophytic taxa (Graham 1992; Grayson 2000). It is, therefore, likely that similar dynamics will occur in response to the projected CC for the 21st century, probably exacerbated by the increase of LT (Sanderson *et al.* 2002). National parks (NPs) and bio-reserves are key conservation tools used to protect species and their habitats within the confines of fixed boundaries. With the distributional changes expected with CC comes a great uncertainty about the future ability of parks and protected areas to meet their conservation mandates (Burns *et al.* 2003).

In this paper, we assess the relative sensitivity of wild African mammals to CC taking into account the patterns of anthropogenic LT that have occurred on the continent in order to prevent an unrealistic assessment, and we evaluate the ability of African NPs to protect mammals into the

future. Projections of future LT are not available for Africa, and are contingent on a plethora of socioeconomic drivers that may increase or decrease pressure on the expansion of land-use activities. Consequently, the use of current LT data provides a pragmatic first approximation of the future situation. We first relate the current distribution of 277 mammal species to present-day climate. Then, a LT map is used to filter the current potential distribution of every species by removing completely transformed climatically suitable habitats. We then project the future potential climatically suitable habitats of every species under two CC scenario extremes for 2050 and 2080. Finally, we address the following questions:

1. How sensitive are African mammals to CC, given current LT patterns?

2. What regions are most at risk to the impacts of CC on mammal ranges?

3. What level of species turnover may be experienced in the 141 selected African NPs under CC?

MATERIALS

Species datasets

Distributions for 277 species, belonging to 12 orders and 28 families, were extracted from the African Mammals Databank, an atlas of medium to large mammals (AMD; IEA 1998). Species included orders of Primates, Carnivora, Perissodactyla (except rhinoceros for security reasons), Hyracoidea, Tubulidentata, Artiodactyla, Pholidota, Lagomorpha, Macroscelidea and seven species of the Rodentia. The distributions from the AMD were extracted for each species in the form of extent of occurrence (EO), which defines the boundaries of a polygon in which observers have recorded occurrences of the species. The EO does not incorporate recorded absences inside the EO, and does not give any information about how abundance varies across the range. In order to match the resolution of environmental data, species' range polygons were rasterized to a 10' x 10' grid.

Climate datasets

The CRU CL 2.0 dataset (New *et al.* 2000a) at a resolution of 10' x 10' was chosen to represent current climate. Future (~2050 and ~ 2080) climate predictions were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HadCM3 General Circulation Model using the A2 and B2 IPCC SRES scenarios (Nakicenovic & Swart 2000) in accordance with globally accepted guidelines for climate impact assessment (IPCC-TGCIA 1999).

We used six uncorrelated variables (selected after cross-correlation evaluation from principal component analysis) representing the major climatic gradients in Africa, namely: mean annual

potential evapotranspiration, annual growing-degree days, minimum temperature of the coldest month, maximum temperature of the warmest month, mean annual temperature and annual sum of precipitation.

LT dataset

Data on LT at a resolution of 100 _100 were resampled from the 0.50 resolution 'Human Footprint' dataset (Sanderson *et al.* 2002). At present, this represents the most consistent source of LT on a global basis. The human footprint dataset is similar to the ecological footprint, a set of techniques for estimating the amount of land or sea necessary to support the consumption habits of one individual, population, product, activity or service (Wackernagel & Rees 1996). The human footprint represents in some sense the total sum of ecological footprints of the human population. It expresses that sum not as a single number, however, but as a continuum of human influence stretched across the land surface, revealing through its variation the major patterns of human influence on nature. The Human Footprint uses four types of data as proxies for human influence: population density, LT, accessibility and electrical power infrastructure. It ranges from 0 to 1, proceeding from natural to completely transformed and inadequate habitat for wildlife.

Unfortunately, there is no available dataset for future LT in Africa. Because LT on the continent is driven by such a wide range of socioeconomic drivers, and is even subject to uncertainties as unpredictable as political instability, we concluded that simple estimates, such as extrapolations of past LT trends, are likely to be misleading. It was, thus, assumed that future LT is best conservatively described by the current LT dataset as this represents a conservative prognosis of the future and limits additional uncertainty owing to future LT projections.

METHODS

Generalized additive models (GAM, Hastie & Tibshirani 1990) implemented into the Splus-based BIOMOD application (Thuiller 2003a), relating the mammal species distributions to the six bioclimatic variables, were calibrated using a random sample of the initial data (70%) and a stepwise selection methodology, with the most parsimonious model being selected using the Akaike information criterion (AIC) (e.g. Thuiller *et al.* 2003, 2004a). The predictive power of each model was evaluated on the remaining 30% of the initial dataset using the values obtained for the area under the curve (AUC) of a receiver operating characteristic (ROC) plot of sensitivity against (one specificity) (Swets 1988). Sensitivity was defined as the proportion of true positives correctly predicted, whereas specificity was the proportion of true negatives correctly predicted. We used the following

conservative rough guide for AUC: <0.8, null model; 0.8<AUC<0.9, fair model; 0.9<AUC<0.95, good model and 0.95<AUC<1, very good model. We only used the ROC curve procedure as it is does not require the estimation of an artificial threshold to transform probability of occurrence to binary data and it is not biased by prevalence like Cohen's k index (Fielding & Bell 1997; Pearce & Ferrier 2000).

The probabilities of occurrence from the mammal models were then filtered by the LT information. We applied this filter by weighting the probability of occurrence by the human footprint following: $FP_i = IP_i \times LT_i$, where FP is the final probability of occurrence in the pixel i, IP is the initial probability of occurrence in the pixel i, and LT is the percentage of land untransformed in the pixel i. For instance, if the probability of occurrence of a species based only on climate in a given pixel is 0.5, and the habitat is 90% transformed: FP = 0.5 x 0.1 = 0.05. Finally, the probabilities of occurrence from the filtered mammal models were converted into presence/ absence using a threshold maximizing the percentage of presence and absence correctly predicted (Pearce & Ferrier, 2000).

The GAM models were then used to make projections into the future using the different CC scenarios for the two time slices considered, and weighting by the human footprint was applied to the future probabilities of occurrence. After transformation of the probabilities of occurrence into presence–absence values using the same threshold determined for current presence, we estimated indices of vulnerability. These indices have been estimated according two extreme assumptions concerning the ability of species to spread or colonize into new climatic suitable habitat. Either we assumed no spread ability of species (null spread), or unlimited spread (full spread). The full spread assumption assumes the spread to be instantaneous and fully effective, so that ranges that have become newly suitable are invariably colonized. Under the null spread assumption, spread is assumed to be totally limiting, and individuals are unable to occupy a new range. Neither of these approximations is satisfactory, as spread rates depend to a large extent on the characteristics of each individual species. However, based on current knowledge and modeling frameworks, they allow the expected impact on ranges to be bracketed.

Extinction risk

We assigned each species to a threat category (IUCN 2001), or classified it as lower risk (LR), depending on the projected reduction in range size from present to 2050 or 2080. Present and future range size (area of occupancy) was estimated from the number of pixels where a species was predicted to occur. Loss in range size was calculated by subtracting future range size from present range size. In line with IUCN Red List criterion A3(c) the following thresholds were then used to assign a species to a threat category (IUCN 2001). Extinct (EX): species with a projected range loss of 100% in 50 or 80 years; critically endangered (CR): projected range loss of >80%; endangered (EN):

projected range loss of >50%; and vulnerable (VU): projected range loss of >30%. It is important to note that our Red Listing approach is simplistic, general and considers only the future effects of rapid anthropogenic CC and static LT. More details and pro and con discussions on the use of Red Listing approach to derive extinction risks of species can be found in Bomhard *et al.* (2005).

Spatial index

To evaluate the percentage of extinction at pixel level, we summed the predicted number of species lost (L) by pixel and related it to the predicted current species richness (SR) by pixel. The procedure was also used to assess the percentage of species gained (G) by pixel (under full spread assumption).

Protected areas

The areas of African land especially dedicated to the protection and maintenance of biological diversity and managed through legal or other effective means were extracted from the World Database on Protected Areas 2005 (WPDA; IUCN/UNEP/WCMC 2005). The WPDA is the most comprehensive global catalogue of protected areas, and includes data on size, locations and Word Conservation Union (IUCN) classifications of management designation. Protected areas in categories I–IV were explicitly designed for biodiversity protection while those in categories V and VI were designed with multiple-management objectives in mind (IUCN 2001). At the African continental scale, we only focused on the NPs (category II; Fig. 1) (category II), representing natural area of land designated to (a) protect the ecological integrity of ecosystems for present and future generations, (b) exclude exploitation inimical to the purposes of designation of the area and (c) provide a environmentally and culturally compatible foundation for spiritual, scientific, educational, recreational and visitor opportunities (IUCN 2001). Finally, we assessed the sensitivity of each NP to CC estimating the predicted number of species lost, gained and the related turnover according to the different CC scenarios and time slices.

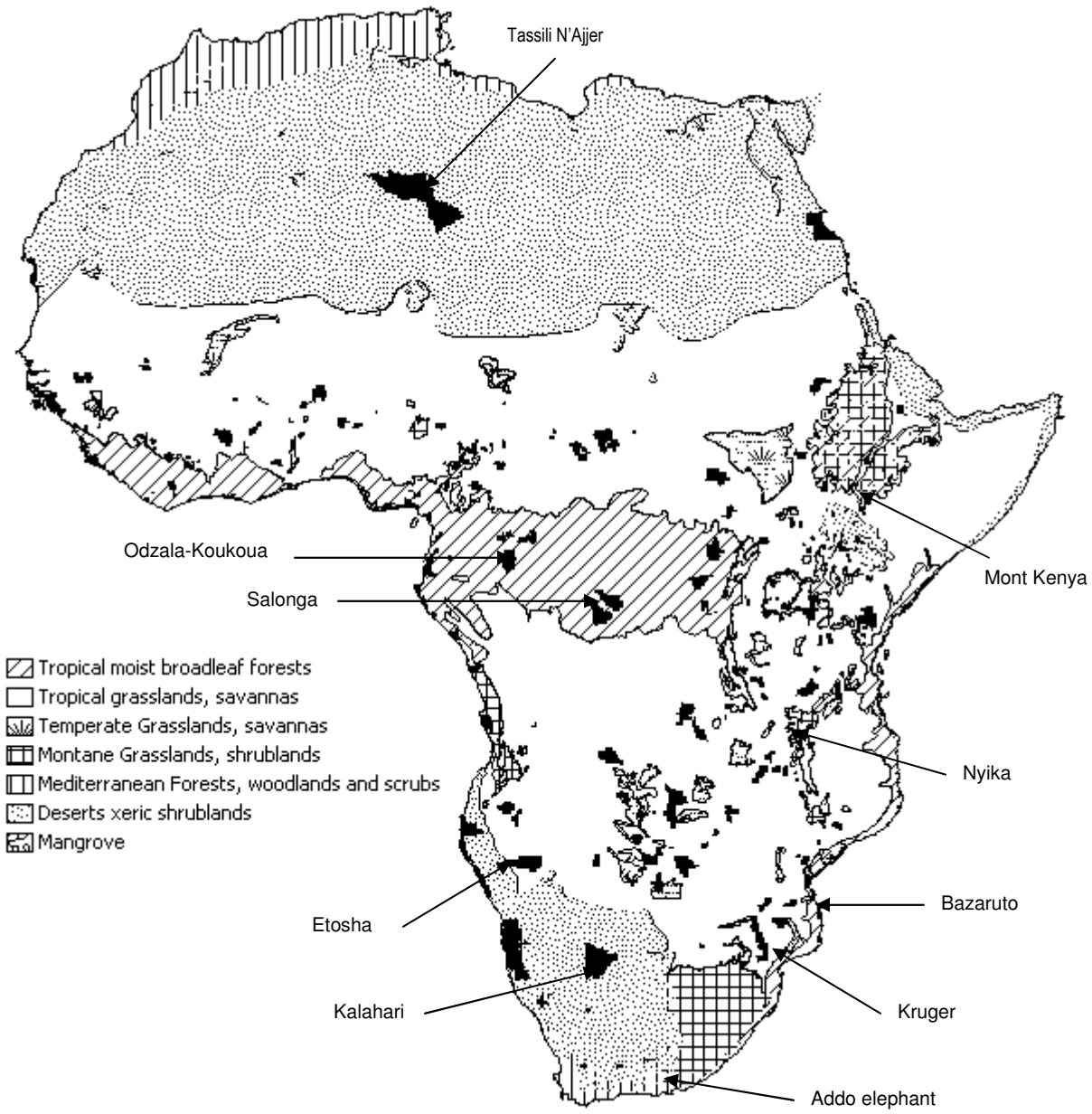

Fig. 1 - Spatial distribution of African biomes and the representation of the national parks (NPs) in Africa. Named NPs correspond to those highlighted in Table 1.

RESULTS

Model evaluation

The mammal models filtered by the LT showed a good predictive power with a mean AUC of around 0.98 estimated on the evaluation data (Fig. 2). The minimum accuracy value was 0.85 recorded for the common hippopotamus (Hippopotamus amphibious) almost certainly because our analysis did not include wetland habitats. The maximum accuracy value was 1.0 recorded for the bovid Silver dik-dik (Madoqua piacentini), which showed perfect prediction (see Fig. 3). Such a high accuracy may be expected considering the spatial resolution of the analysis, as large-scale patterns are easier to predict than finer scale ones. For this reason, we consider an AUC of 0.85 as a weak model, although at a fine scale this would usually be considered a good model.

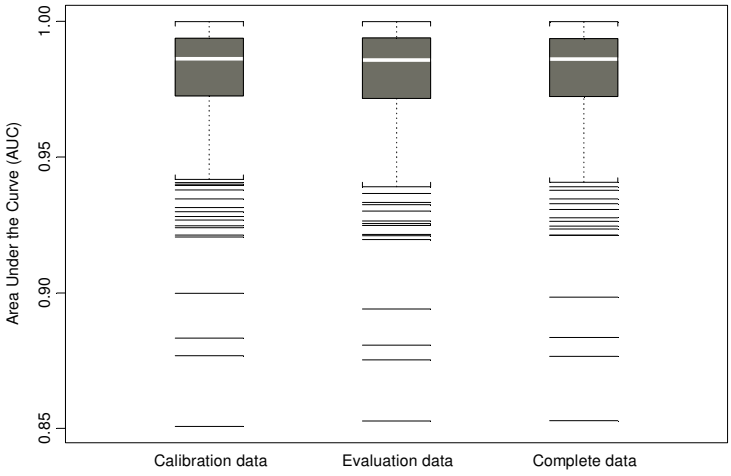

Fig. 2 - Summary of the area under the curve (AUC) generated from the mammal models, using the calibration data used to calibrate the models (70% of the complete data), using the evaluation (the remaining 30%) and the complete dataset. Single horizontal bars represent outliers of the relationships.

Species-specific sensitivity

Example results demonstrated the idiosyncratic response of species to potential CC and current LT (Fig. 3). The Jackson's mongoose (Bdeogale jacksoni), for instance, was predicted to be fairly stable and could potentially gain few suitable habitats closeby its current range. Inversely, the Silver dik-dik, a species currently classified as VU by the Red List, was predicted to experience an almost complete disappearance of its climatically suitable habitat. Our poor predictive ability for the hippopotamus was clearly apparent (Fig. 3). Nevertheless, the species was predicted to gain some potential climatically suitable habitat in the equatorial belt. The grey-cheeked mangabey (Lophocebus albigena), which was very well predicted under current conditions (AUC = 0.99), was also predicted to lose a large amount of climatically suitable habitat, mainly in the middle of its current range, dividing its potential future range into two disjunct zones. The last two examples highlight the uncertainty provided by the two crude spread assumptions. The CR Sahara oryx (Oryx dammah) was predicted to lose almost all its current climatically suitable habitat in the Sahara desert, but to gain substantially in Namibia and Botswana, in a region to which it was unlikely to spread without human intervention. Similarly, while the current climatically suitable habitat of the Ru¨ppell's fox (Vulpes ruepelli) was predicted to remain fairly stable in the future (Fig. 3), this species appeared to have current and future climatically suitable habitats in Namibia and South Africa although it had never been recorded in this region.

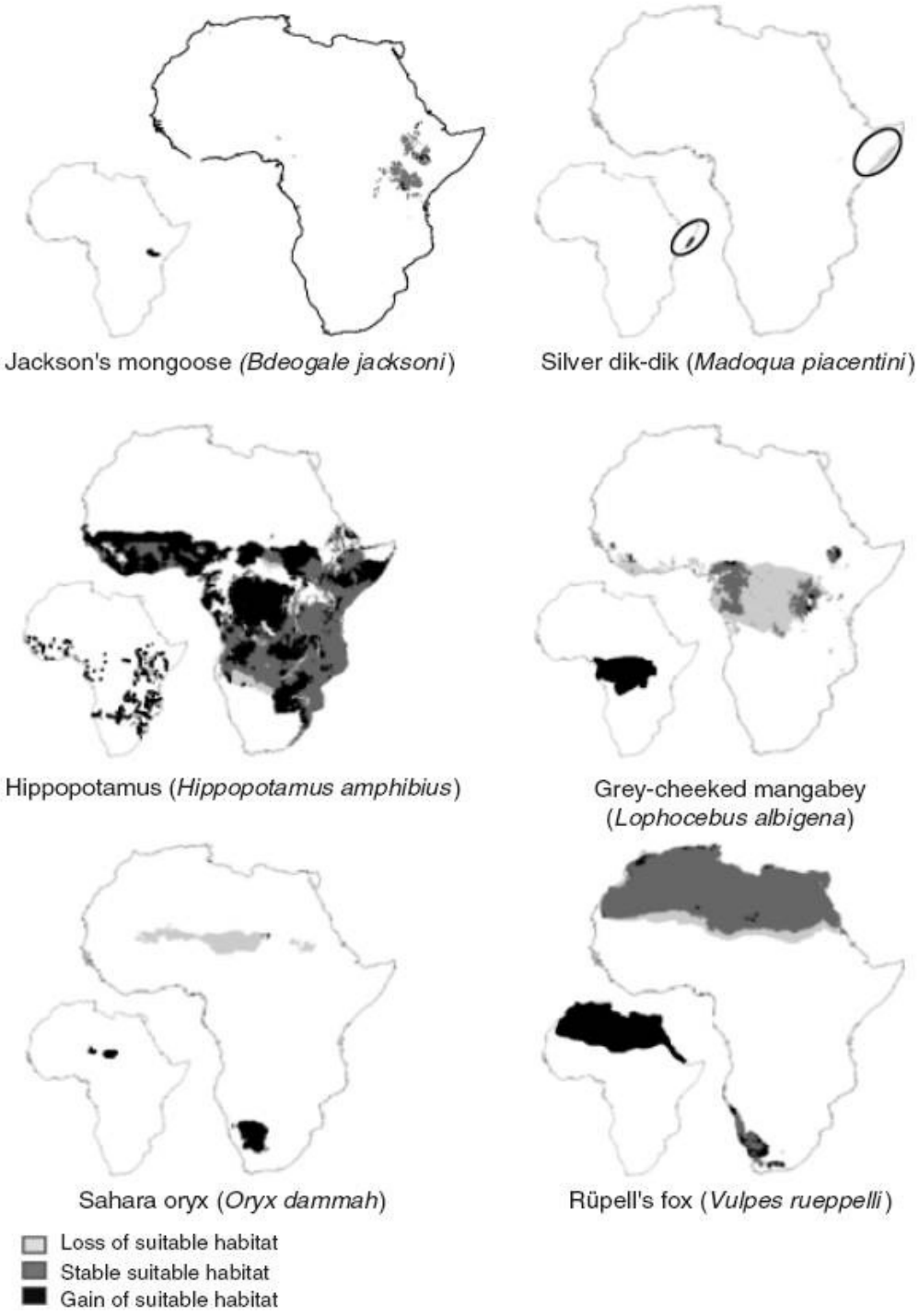

Fig. 3 - Observed and predicted distribution under the HadCM3 A2 2050 scenario for six species. For each couple of maps, the small one is the observed distribution from the AMD, and the larger one is the predicted one. Clear grey indicates current climatic suitable habitats predicted to be unsuitable by 2050, moderate grey indicates the current climatic suitable habitats predicted to stay suitable by 2050 and dark grey indicates the current climatic nonsuitable habitats predicted to be suitable by 2050.

Our simple application of a single IUCN Red List A3(c) criterion highlighted that in the worst-case scenario, up to 4% of the African mammals species appeared severely threatened by future CC and current LT (Fig. 4). Under the assumption of null spread ability, between 40% and 50% of the species were classified at LR (respectively, for scenarios HadCM3-A2 and HadCM3-B2) for 2050 and 25% and 35% for 2080. Very few species were classified as EX under the null spread ability, but under the HadCM3-A2 storyline, 37.5% of the species were predicted to become CR after 2080. For both time slices, CC and LT affected species less under the full migration assumption because of the potential for species to move across landscapes and occupy new ranges. Under the full migration ability, between 56% and 62% of the species were classified as LR (respectively, for HadCM3-A2 and HadCM3-B2 storylines) for 2050 and between 39% and 50% for 2080. The HadCM3-A2 storyline was more severe for wildlife distribution than the HadCM3-B2 storyline, reflecting economic vs. sustainable development strategies. As expected, projections for 2080 displayed more negative impacts than 2050 projections.

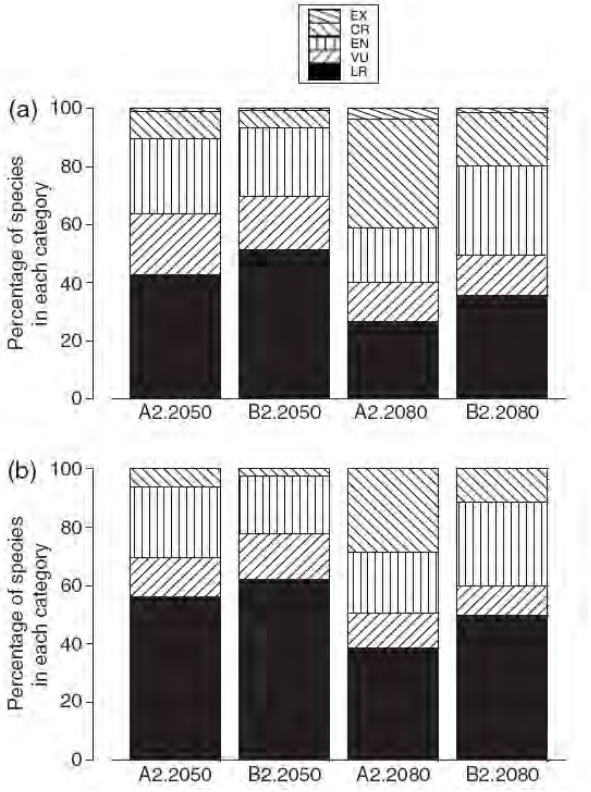

Fig. 4 - Barplots representing the percentage of species classified according to our IUCN Red list assessment for each time slice and under both assumption on species' migration. (a) no migration ability, (b) full migration ability. EX, extinct; CR, critically endangered; EN, endangered; VU, vulnerable; LR, lower risk.

Spatial wildlife sensitivity

For both time slices and storylines, two regions of high species loss were discernible (Fig. 5). The first was situated in species-rich central Africa (mostly in the Congo Basin), which exhibited very high species losses (50–60% for A2 2050 and 60–75% for A2 2080) and extending patchily westwards along coastal regions. The second region was centred on the Kalahari region in arid Namibia, northern South Africa and Botswana, but extending patchily to the Mozambique coastline. The absolute numbers of species loss here were lower than for the central African region, but higher in relative terms (70–80% for A2 2050 and 80–100% for A2 2080). Similar to the species-specific projections, rates of species loss were exacerbated for 2080 under the storylines used in this study.

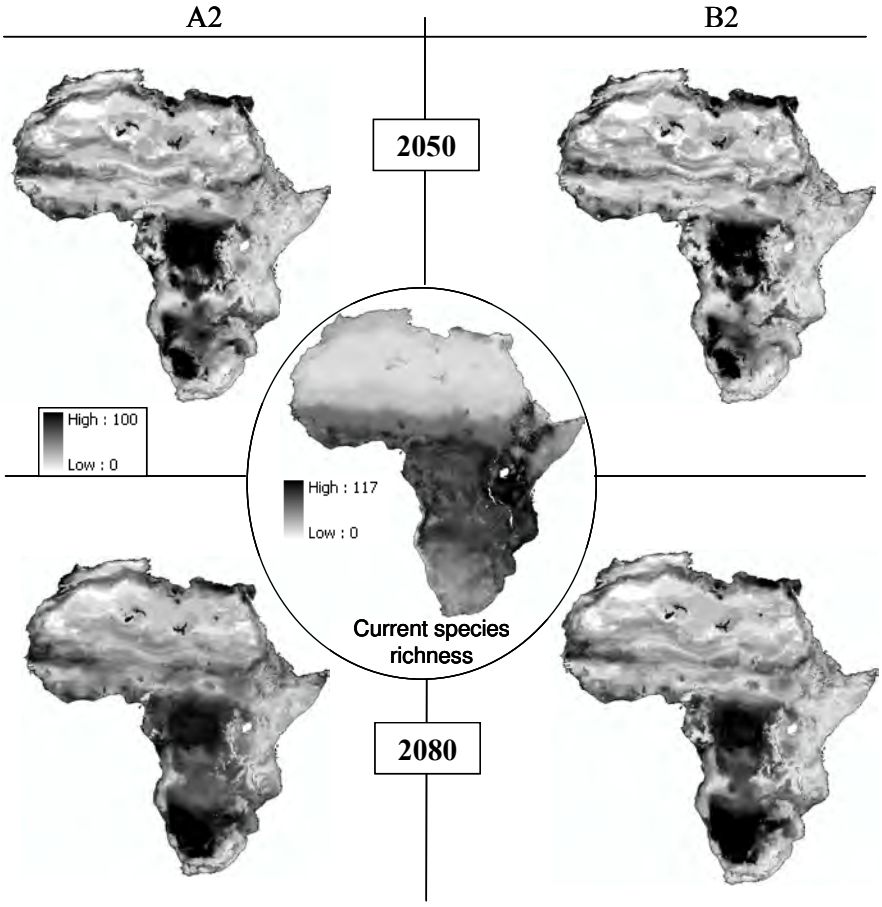

Fig. 5 - Relative number of predicted species lost by pixel for the two time slices (2050 and 2080) and the two storylines (A2 and B2). Current species richness is displayed at the centre of the figure. The rate of species gain was likely to be less reliable than rate of species loss, as we did not explicitly model spread across the landscape in our analysis. However, they provided insights into the directional trend of change. Interestingly, two regions of high species gains were detectible at the same latitude as the highest areas of species loss (Fig. 6). Nevertheless, there was a different longitudinal pattern. The northern region was situated around Gabon, western Zaire and northwestern Angola with an average of 40% gain for A2 2050 and 65% for A2 2080. The southern region occurred in northeastern South Africa and adjacent southern Mozambique with an increase in richness of 50% for A2 2050 and 80% for A2 2080.

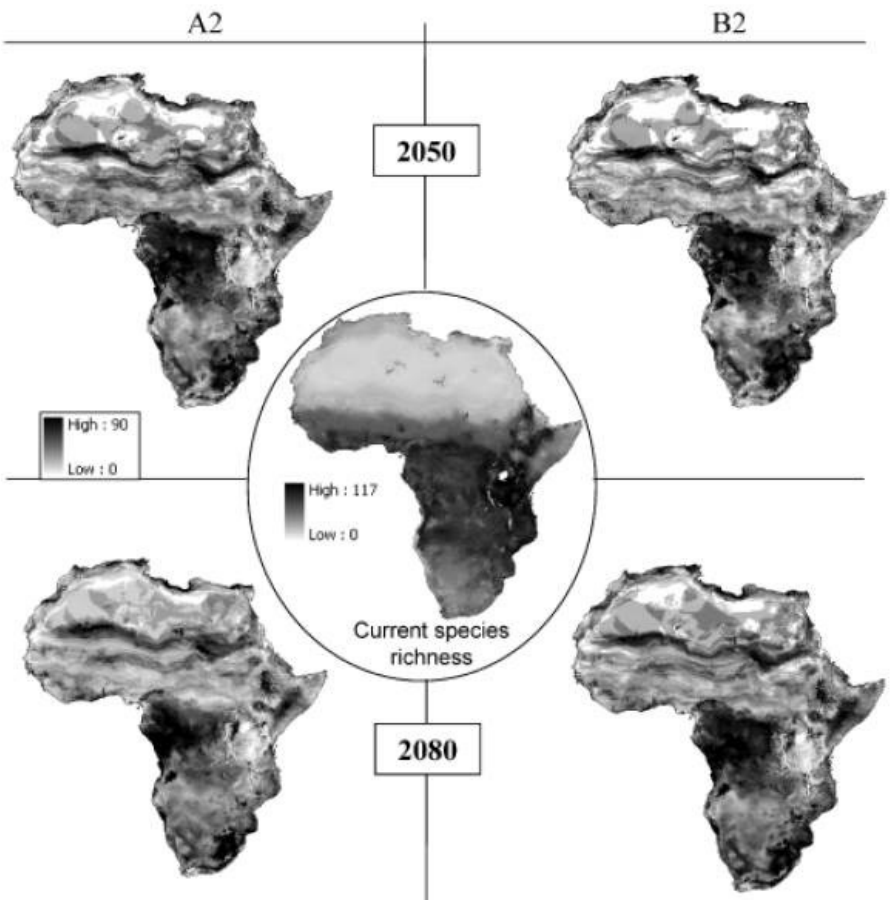

Fig. 6 - Relative number of predicted species gained by pixel for the two time slices (2050 and 2080) and the two storylines (A2 and B2). Current species richness is displayed at the centre of the figure.

Spatial patterns were quite clear and mostly related to the aridity gradients (Fig. 7): CC and land-use transformation could cause a substantial loss of species in the middle of the central Africa region and a substantial gain in the western region depending on the ability of mammals to move across the landscape. The Congo Basin was, for instance, projected to undergo a major reshuffling in species composition. The eastern part of the Congo Basin might experience a high rate of species loss while the western part might gain a substantial number of new species. There was a spatial shift of species towards cooler and moister areas (see east–west gradient on Fig. 7) causing major reshuffling in community composition. In southern Africa, this latitudinal trend was reversed with a decrease of species richness in the western region and an increase in the eastern region. This inverse trend was mainly explained by west–east temperature and precipitation gradients, causing an eastward species shift towards cooler and moister areas (Fig. 7). These results suggested that the effects of CC on wildlife community may be most noticeable not only as a substantial loss of species from their current ranges but also as a fundamental change in community structure as species associations shift with influxes of new species.

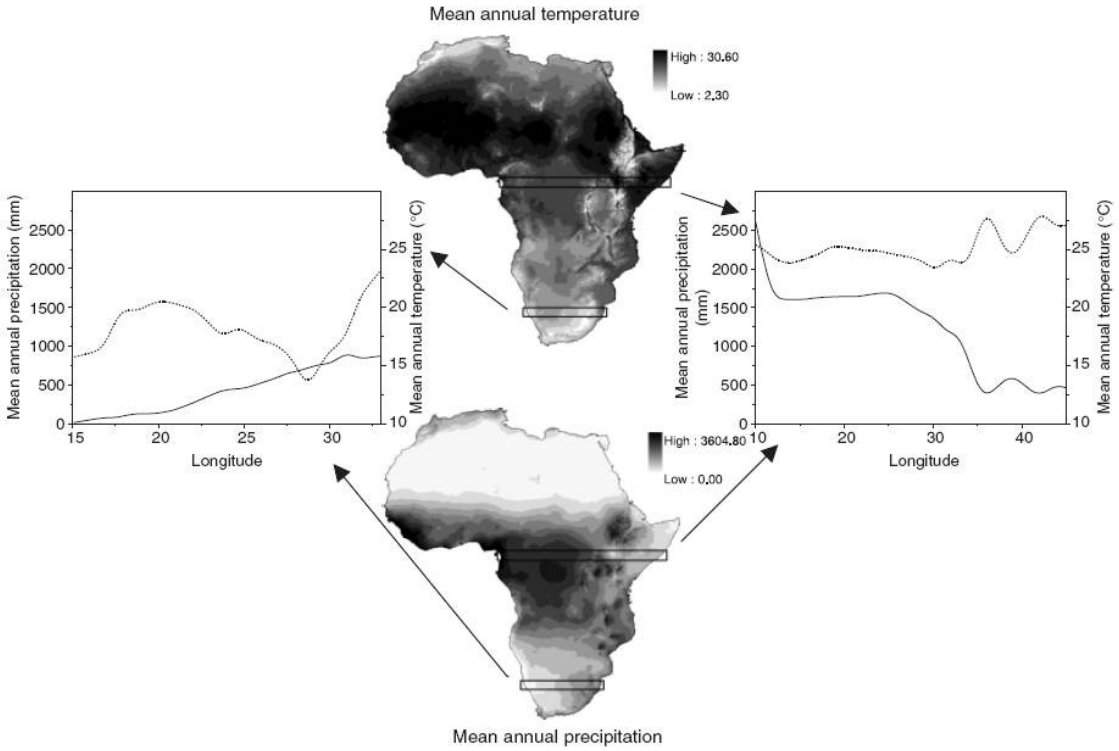

Fig. 7 - Current mean annual temperature and mean annual precipitation along two east–west gradients. Dashed lines indicates temperature values along the transects while continuous lines indicates precipitation values along the transects.

The influence of LT on estimates of species sensitivity was not substantial for the relative predicted species lost per pixel (Fig. 8). If LT by 2050 was similar to the current situation, it would slightly increase the relative predicted species lost per pixel under CC alone. However, the impact of LT on the potential predicted species gained per pixel was more pronounced. It suggested that the current LT pattern would reduce (or preclude) the potential for species to spread to future climatically suitable habitats (Fig. 8). This analysis highlights the need for future LT scenarios, and stresses the critical need for assessments of 'corridor' approaches to facilitate species range shifts (e.g. Hannah *et al.* 2002).

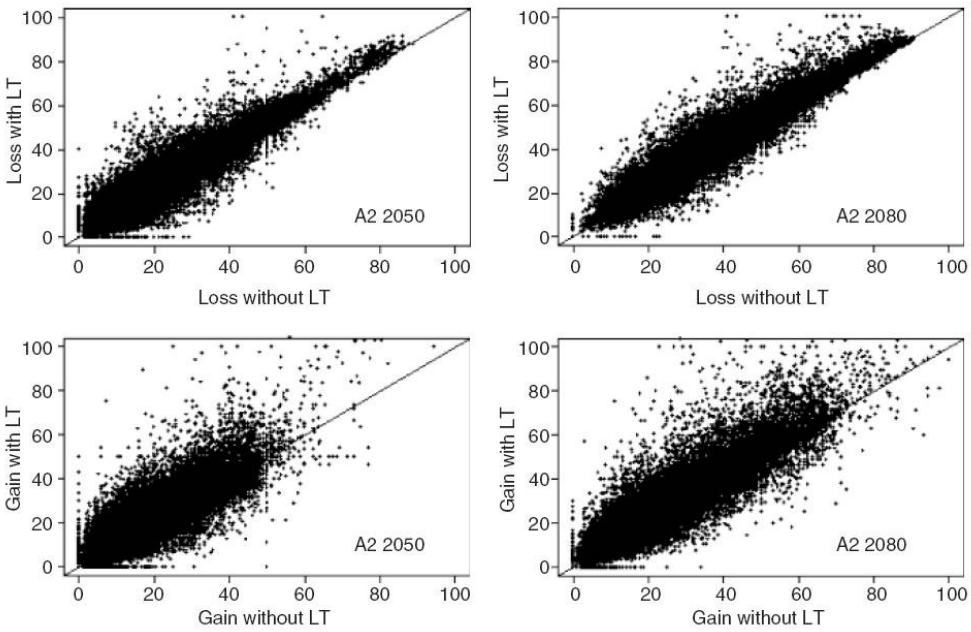

Fig. 8 - Relationship between the relative numbers of predicted species lost/gained per pixel with climate change (loss and gain without LT) alone against the relative numbers of predicted species lost/gained per pixel accounting for current land transformation (loss and gain with LT). Only the results using the scenario A2 are represented here for both time slices (2050 and 2080).

Sensitivity of African NPs

We estimated the current and future species richness of the African NPs to highlight the degree to which they may be VU to CC (Fig. 9, see also Fig. 1). In order to provide a ranking, we grouped NPs by the dominant biome in which they are situated, using the classification and mapping of biomes by Olson *et al.* (2001).We present results only for A2 HadCM3. Results for B2 HadCM3 were spatially similar to A2 but with a lower impact, while results for 2080 were more extreme than for 2050. NPs mostly situated in desert and xeric shrubland biomes were most sensitive to CC (Figs 9 and 1) as almost all these NPs here showed a marked decrease in species richness. These include mainly southwestern NPs (Kalahari Gemsbok), and the Algerian NP (Tassili N'Ajjer) where a very high number of species might be lost (>50%) with few immigrations (<10%) for all the scenarios and time slices (Table 1). The NPs situated in rare and patchy biomes (Mediterranean forest and mangroves) showed a neutral pattern where few losses and gains were projected. NPs situated in montane grassland biomes showed a positive response to CC (Figs 9 and 1) with a few neutral response exceptions. For instance, Mount Kenya and Nyika NPs were projected to gain a substantial number of species (i.e. Mt Kenya: 50% for A2 2050 and 80% of A2 2080), and retain most of their species currently found within their boundaries, suggesting that altitudinal species shifts towards currently cooler areas allow species persistence in the face of CC.

NPs situated mainly in tropical and subtropical montane grasslands, as well as tropical moist broadleaf forest did not exhibit unilateral patterns (Fig. 9), but the majority might experience an increase in species richness, enhancing a positive net turnover (Table 1).

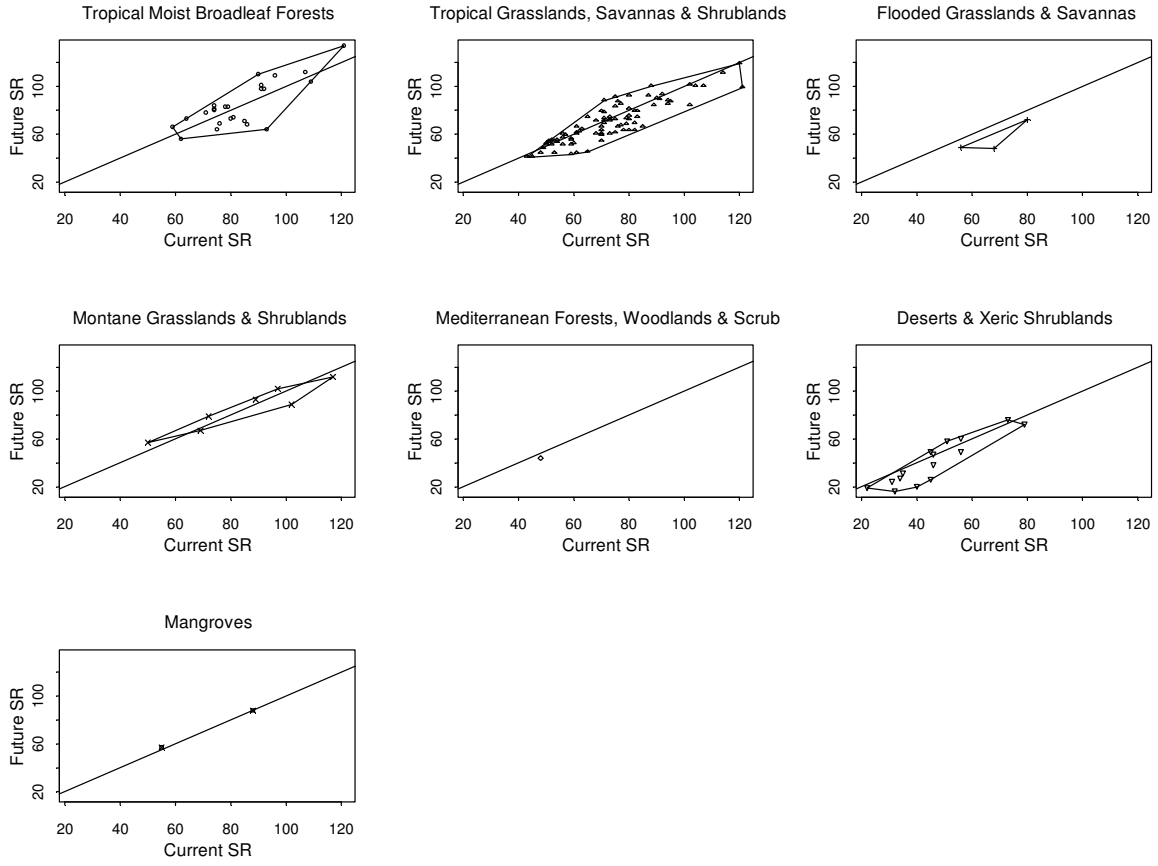

Fig. 9 - Current and future species richness (under the A2 scenario for 2050) assuming full migration inside the African national parks ranked according to the biome where they occur. Lines indicate the steady-state situation (no species richness gain or loss).

Table 1 - Current modeled species found in selected African national parks and projected species losses, gains and net turnover under different climate change scenarios and time-slices. SR means species richness, Sp lost, Sp gained represent respectively the number of species expected to be lost or gained by the selected national parks. Turnover calculated as species gained minus species lost independently of current species richness.

			2050						2080					
			A2			B2			A2			B2		
Park	Biome	Current SR	Sp lost	Sp gained	Turn over	Sp lost	Sp gained	Turn over	Sp lost	Sp gained	Turn over	Sp lost	Sp gained	Turn over
Kalahari	Desert an Xeric shrublands	45	25	6	-19	23	7	-16	39	10	-29	39	8	-31
Tassili N'Ajjer	Desert an Xeric shrublands	40	21	1	-20	21	1	-20	27	20	-25	25	1	-24
Etosha	Flooded grasslands	80	22	14	-8	18	13	-5	27	20	-7	27	16	-11
Bazaruto	Mangroves	88	12	12	0	7	10	3	29	18	-11	17	12	-5
Addo Elephant	Mediterranean forests	48	10	6	-4	7	3	-4	15	17	2	13	11	-2
Mont Kenya	Montane grasslands	50	18	25	7	12	26	14	18	39	21	16	35	19
Nyika	Montane grasslands	97	5	10	5	6	4	-2	10	10	0	12	7	-5
Kruger	Tropical grasslands	87	11	16	5	10	18	8	20	20	0	13	19	6
Serengeti	Tropical grasslands	120	7	6	-1	6	3	-3	15	14	-1	9	9	0
Odzala-Koukoua	Tropical moist broadleaf forests	74	16	23	7	12	19	7	42	37	-5	29	28	-1
Salonga	Tropical moist broadleaf forests	80	36	28	-7	20	25	5	53	34	-19	43	37	-6

DISCUSSION

Limitations

Several recent papers discuss the broader theoretical limitations of the approach that we develop in this analysis (Pearson & Dawson 2003; Hampe 2004; Thuiller *et al.* 2004a; Thuiller *et al.* 2004b; Araujo *et al.* 2005a; Guisan & Thuiller 2005); hence, we focus this discussion to limitations and assumptions strictly relevant to this particular analysis. A primary limitation is the lack of recorded absences inside the EO of the species. This is a common weakness of most of the animal atlases that only massive sampling efforts could remediate. However, it is the most reliable data available for mobile organisms, and GAM models have been shown to exhibit a relatively good performance even for highly mobile taxa (Brotons *et al.* 2004; Huntley *et al.* 2004; Araujo *et al.* 2005a).

A further limitation is based on the relevance of the variables we used to assess the sensitivity of mammals. Here, we used climatic variables to produce climatically suitable habitat for every species and then weighted projected ranges by the LT variable. Our use of this approach does not mean that we are unaware that climate is only one of several determinants of species distribution (Araujo *et al.* 2005b). Rather, we reason that while other factors, such as both competition and trophic interactions in ecosystems (Davis *et al.* 1998a; Davis *et al.* 1998b; Hochberg & Ives 1999), and the phylogenetic history of taxa (Myers & Giller 1988; Brown *et al.* 1998), are likely to influence species geographical distribution at a fine scale, mainly, geographical distributions at large spatial scale and resolution are likely to be determined to a large degree by climate (Root 1988; Rogers & Williams 1994; Chown & Gaston 1999; Spicer & Gaston 1999; Fischer *et al.* 2001).

The influence of climate, especially rainfall conditions, on mammal distributions and abundances has been widely documented in Africa (Owen-Smith 1990; Mills *et al.* 1995; Owen-Smith & Ogutu 2003). For instance, in the Kruger Park in South Africa, almost all of the ungulate species, except conspicuously the giraffe, seem extremely sensitive to lack of rainfall during the dry season, which is projected to be exacerbated into the future (Hulme *et al.* 2001). Dry season rainfall may be directly important by influencing the retention of some green forage during this critical period when malnutrition takes hold (Owen-Smith & Ogutu 2003).

Another concerns specific habitat, dietary or disturbance requirements of particular species. For instance, a number of mammal species (e.g. H. amphibious) strongly depend on fresh water availability (Sinibaldi *et al.* 2004), a parameter that was not included in our analysis. Thus, models on freshwater-dependent mammals exhibited the lowest predictive power in our analysis. While river coverages do exist at the African scale, these represent only primary rivers and lakes and we believe that at the resolution of the analysis (16 kmx16 km), they would only bias the results and not add useful information.

It is also clear that many animal species are dependent on habitat structure as well as climatic requirements for their persistence. Under future climate and atmospheric CO2 change, habitat structure, such as the dominance of trees vs. grasses in savannas, may be altered through changes in fire regime (e.g. Bond *et al.* 2003), with significant impacts on fauna.

A final problem is related to the crude assumptions about the potential spread of species, and their ability to track CC across transformed or untransformed landscapes. The consequence of such assumptions was highlighted in Fig. 3 for the Sahara oryx or the fox species. Clearly, it is very unlikely that these two species could reach these potential suitable habitats without human intervention. The spread of animals or migration of plants in the context of environmental change has raised great concern in the ecological community as they are likely to be unpredictable (Higgins *et al.* 2003). Current knowledge on these issues is so poor that it is currently difficult to estimate even a maximum spread of the species we analysed in this study. This is a major weakness of the niche-based modeling approach and needs urgent attention in order to develop more reliable conservation plans (Wiliams *et al.* 2005). The assumptions we used (no spread, universal spread) are debatable but this is currently the only way to deal with this issue.

An additional problem is the use of current LT as a conservative prognosis of future LT. We made this assumption because of the lack of reliable and sufficiently fine resolution projections of LT by 2050 or 2080. Moreover, the inclusion of LT would probably add a substantial amount of uncertainty, which combines with those from data, model, species biology and climate model uncertainty to increase overall uncertainty greatly. Case study evidence highlights the uncertainty and surprises inherent in the processes of land-use intensification and LT, as well as the importance of decision making by land managers when facing a range of response options (Lambin *et al.* 2000), components that are currently poorly known at the African scale and relatively fine resolution. Notwithstanding these weaknesses, the model used here represents a pragmatic estimate for a provisional estimate of the likely impacts of CC and LT on the mammals at the African scale.

Species extinction risks

Of the 277 species we examined, none were committed to extinction assuming full migration ability of species across the landscape, and a maximum of 10 species when assuming no migration under the A2 HadCM3 scenario for 2080. This number of expected extinctions corroborates a South African study on animal taxa using a similar approach (Erasmus *et al.* 2002), noting that 2.2% of the modeled species could be committed to extinction under a double CO2 climate.

However, our extinction risk analysis highlights that a substantial number of African mammals species might be severely threatened by future CC and LT (Fig. 2). Indeed, assuming unlimited migration ability of species across the landscape, which is a likely overestimate, and under the

extreme scenario (A2 HadCM3 2080), 30% of the species are classified as CR, while 40% are classified at LR. It is only when assuming that species are not able to migrate across the landscape that some species are predicted to lose 100% of their suitable habitats.

Because so many of the species we examined here show substantial range contraction (median = -49%, mean = -18% under A2 HadCM3 2080), it is this facet of range alterations that is of most concern. This concern is especially warranted because the range contractions we have predicted here may be underestimates and a conservative prognosis because of LT inhibiting the free migration of species across the landscape.

The major reason for concern regarding range contractions has to do with the negative relationship between range size and extinction probability (Gaston 1994). A reduction in the absolute range of a species is likely to lead to an increased risk of local extinction (Thomas *et al.* 2004; Thuiller *et al.* 2005b). Indeed, a decrease in range size could mean that smaller stochastic events affect a larger proportion of the species' total population, especially in the context of fragmented landscapes. For instance, if a species becomes restricted to a few sites, then local catastrophic events (such as drought or disease outbreak) or an increase of LT by humans could easily cause the extinction of that species (Lawton & May 1995). This is especially the case of mammals that directly threaten human lives, compete with humans for resources and/or are restricted inside artificial boundaries.

Furthermore, additional drivers could enhance the risks of species extinctions because of CC and LTs. For instance, rainfall conditions can affect the susceptibility of animals to disease outbreaks, and particularly anthrax. The marked population decline by buffalo into the Kruger Park after 1990, and to some extent also that of kudu, was largely the result of an anthrax outbreak affecting these species resulting from unusually humid dry season. Life cycles of ticks or other parasites are also particularly influenced by climate variation and could exacerbate risks of extinctions. For instance, unusually warm winter in 1998 (1–2 *1*C warmer than the long-term average) allowed the tick Boophilus decoloratus larvae to peak twice in southern Kruger, once in June–July (unusual) and again in November–December (usual), implying that ticks had undergone an extra cycle that year (Bengis *et al.* 2003). Finally, competitive interactions may also influence some species according to the CC, especially waterbuck, which inhabit regions close to water likely to be most severely affected by other grazers during dry periods (Owen-Smith & Ogutu 2003).

Spatial patterns

Spatial patterns of loss and gain show three contrasting patterns following the latitudinal position of the species. First, northern Africa does not exhibit a high number of loss and gain because of the very low number of mammals occurring in this area. The second pattern is a westward range shift of species in the Zaire and the Congo Basin. Given the pronounced west–east temperature and

precipitation gradient across Africa (Fig. 7) at this latitude, the general decline in species richness in this direction, and replacements over this gradient of species that differ markedly in their physiological tolerances, these changes are undoubtedly a realistic reflection of the likely impacts of CC weighted by the substantial human pressure in these areas (Hulme *et al.* 2001; Sanderson *et al.* 2002). The third pattern mirrors the second one but is situated in the Kalahari region of southern Africa and centred on Namibia, Botswana, northern South Africa and Mozambique. In this area, there is an east–west aridity gradient (Fig. 7) across these countries (Rutherford & Westfall 1986; Schulze 1997), and this results in the same emerging relationships as around the equatorial transition zone (Freitag & vanJaarsveld 1995; Gelderblom *et al.* 1995). This pattern corroborates Erasmus *et al.*'s (2002) analysis carried out on a broad range of animals, highlighting the same eastward range shift towards the moister (cooler, higher altitude) end of the aridity gradient for most of the modeled species.

The extent to which predicted shifts in range and spatial modifications of species richness will translate into realized alterations in range position and species richness change will obviously also vary between taxa. If species are capable of adapting to local conditions by behavioural or physiological means, realized range shift may not be as pronounced as those projected. However, information on the relationships between species ranges and behavioural patterns and physiological tolerances, and the extent to which behavioural and physiological flexibility influence species ranges is very limited and inconsistent across the African mammals. However, we could argue that most of the predators, and especially cats, could be less susceptible to climate as they can easily supplement water availability with prey fluids (Kitchener 1991; Bailey 1993; Ogutu & Dublin 2002). This fact would lead us to believe that predators would mainly follow their prey rather than explicitly tracking CC. Uncertainty also emerges with the complex response of large predators to long-term ecological change. For instance, Packer *et al.* (2005) showed that despite gradual changes in prey availability and vegetative cover, regional populations of Serengeti lions remained stable for 10–20-year periods and only shifted to new equilibriums in sudden leaps (Packer *et al.* 2005; Ranta & Kaitala 2005).

Landscape alteration in the central part of Africa as well as in the eastern and central portion of South Africa will also have a marked impact on the extent to which the predicted changes will be realized. We included LT in our assessment as a variable constraining the climatically suitable areas of species, but we did not consider migration of species across the transformed land. Extensive habitat alteration could create large gaps between suitable patches (Brown *et al.* 1998; Tokeshi 1999) and, thus prevent free migration of species to keep pace with CC. If a species is unable to move into an area because of a lack of a suitable habitat, or because that area is too distant from the closest source population of that species, then area is effectively unavailable to the species and local extinction is the most likely outcome.

Sensitivity of NPs

The sensitivity of NPs to CC shows a very distinct pattern in accordance with the biomes in which the parks occur. NPs situated in xeric and desert shrublands are not expected to meet their mandate of protecting current mammalian species diversity within park boundaries. Indeed, these NPs are expected to face significant losses of species diversity that are not compensated by species influxes. The other NPs should expect both substantial losses of species and significant species influxes. On balance, the NPs will realize a substantial shift in mammalian species composition of a magnitude unprecedented in recent geological time. This conclusion is based on the assumptions that all species will reshuffle en masse in an orderly manner (Pimm 2001), and that the rate of distribution change is commensurate with geographic shifts in habitat. These assumptions are debatable in general (Pimm 2001), although comparatively rapid (20–50 years) range adjustments are not entirely out of the questions for mammals.

In addition, we must consider that, even when significant species losses are not anticipated, there may be repercussions because of indirect effects caused by the rearrangement of mammal communities and change in the patterns of interspecific interactions (see Stenseth *et al.* 2002b) for a review). Indeed, as shifting species forge new ecological relationships with each other and with current park species, the character of species interactions and fundamental ecosystem processes stands to become transformed in unforeseen ways (Walther *et al.* 2002; Schmitz *et al.* 2003). For instance, an influx of new species may alter existing competitive interactions and influence trophic dynamics with changes in predator–prey interactions. Further, climate warming is likely to result in phonological shifts, including changes in spring breeding dates, flowering and budburst (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003), which can further disrupt current species associations. In some cases, it is possible that shifting species assemblages may lead to irreversible state changes, in which the relative abundance of species in different trophic levels can be radically altered (Schmitz *et al.* 2003). The outcome of these new species interactions may be particularity difficult to predict for nonlinearities that may emerge, for example.

CONCLUSION

Our results suggest that the effects of global CC and LT on wildlife communities may be most noticeable not as a drastic loss of species from their current range (even if some species could experience complete loss of suitable habitats), but instead as a fundamental change in community structure as species associations shift because of both species losses and influxes of new species. Our extinction risk assessment shows, however, that a substantial number of species could be CR because of CC and LT. Obtaining a clearer insight into these fine-scale effects rests squarely on developing more detailed models that better account for CC effects on species and the mosaic of habitat types within a geographic region, and on developing an understanding of ecosystem structural/functional change such as changes in tree/grass balance in savannas and fire frequency (Midgley & Thuiller 2005). Better distribution data including true presence–absence or even abundance are urgently needed. Therefore, direct resources for animals should also be fully included to the process to provide more robust projections into the future, even though they are generally difficult to acquire for a large sample of species. Finally, the role of changes in habitat structure on faunal distribution, through the impacts of fire regime (e.g. Bond *et al.* 2003), should be incorporated in the future work of this nature.

Nevertheless, our prognosis for the extent and degree of change in Africa and specifically in park mammals can be viewed as a null hypothesis of distributional expectations (Peterson *et al.* 2002). Models that are more detailed will likely give a finer resolution, but the overall message is likely to be similar. In general, we should observe major changes in mammalian species composition in central Africa (tropical and subtropical areas) with a westward shift of diversity, and major losses of species in southern Africa with an eastward shift of mammal diversity. In addition, species interactions could increase the toll of species losses above and beyond what we find in this study (Pimm 2001; Root *et al.* 2003).

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Chapter 3.2

Do geographic distribution, niche property and life form explain plants' vulnerability to global change?

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ABSTRACT

We modeled the future distribution in 2050 of 975 endemic plant species in southern Africa distributed among seven life forms, including new methodological insights improving the accuracy and ecological realism of predictions of global changes studies by: (i) using only endemic species as a way to capture the full realized niche of species, (ii) considering the direct impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' migration into account. Our analysis shows important promises for predicting the impacts of climate change in conjunction with land transformation. We have shown that the endemic flora of Southern Africa on average decreases with 41% in species richness among habitats and with 39% on species distribution range for the most optimistic scenario. We also compared the patterns of species' sensitivity with global change across life forms, using ecological and geographic characteristics of species. We demonstrate here that species and life form vulnerability to global changes can be partly explained according to species' (i) geographical distribution along climatic and biogeographic gradients, like climate anomalies, (ii) niche breadth or (iii) proximity to barrier preventing migration. Our results confirm that the sensitivity of a given species to global environmental changes depends upon its geographical distribution and ecological proprieties, and makes it possible to estimate a priori its potential sensitivity to these changes.

Keywords: biodiversity, biogeographic gradients, Cape floristic region, climate change scenarios, land transformation, Succulent Karoo

CONTRIBUTION TO THE PROJECT

I trained the models for the 975 endemic plant species in Southern Africa and assessed the projected spatial patterns of richness loss and gain. I calculated the rate of extinctions and species range changes. I developed the Biomod script to take into account migration limitation of species during climate change. I prepared all the figures. I wrote the initial manuscript and supervised the reviewing.

INTRODUCTION

Ecologists commonly agree that biodiversity is already facing the effects of climate change at various scales, revealed for instance in modifications of the phenology and physiology of species, or in induced displacements of species distributions that may ultimately lead to increased extinction rates (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). Another major threat to biodiversity is habitat destruction and fragmentation caused by the intensification of human land use practices. Both have been recognized as a major threat to biodiversity (Wilcove *et al.* 1998; Hughes *et al.* 2002). There is now substantial evidence that these global changes are increasingly affecting ecosystems.

In order to anticipate threats and prioritize conservation actions, ecologists have developed various modeling tools to predict species and diversity distribution in the future, in order to help develop planning responses to the impacts of global environmental change on biodiversity (Schröter *et al.* 2005). One such tool is to apply species distribution models (SDMs; see Guisan & Zimmermann 2000; Austin 2002; Guisan & Thuiller 2005) to assess the potential responses of individual species to climate change. These models relate present day distributions to current climate, and then project the fitted climatic envelopes under future scenarios to identify how and where spatial shifts could occur (e.g. Huntley *et al.* 1995; Iverson & Prasad 1998; Bakkenes *et al.* 2002; Peterson *et al.* 2002; Thomas *et al.* 2004; Thuiller *et al.* 2005b). Species turnover – the net change in number of species that could persist in, disappear from, or colonize a particular area – has been used as a measure of the community composition change (Erasmus *et al.* 2002; Peterson *et al.* 2002). Accordingly, it has been widely used to assess the potential impact of climate change from regional to continental scales (e.gErasmus *et al.* 2002; Peterson *et al.* 2002; Thuiller 2004).

Species' vulnerability to global change can result from both ecological and geographical characteristics. Emphasis has been placed on the assumption that marginal species – (i.e. species with requirements which do not correspond to the mean climate conditions prevailing in the study area) – should be more sensitive to climate change than species that have their optimum close to or coinciding with the centroid of the realized environmental space (Swihart *et al.* 2003). Furthermore, generalist species (e.g. species with a large niche breadth) should have broader tolerances to climate changes than specialist species (Brown *et al.* 1995). Thuiller *et al.* (Thuiller *et al.* 2004d) demonstrated that such a relationship between the ecological and distributional properties of species could be successfully drawn from modeling studies. Moreover, because climate changes are not predicted to be uniform over landmasses, particular patterns of change in future distributions of species could also result from the geographical coincidences between species' range and spatial patterns of climate change anomalies. Disentangling these physiological and geographical effects on the future distribution of species would greatly improve our ability to predict patterns of change.

Several shortcomings are associated with most studies predicting climate change ecological impact conducted so far (Loehle & LeBlanc 1996; Davis *et al.* 1998a; Pearson & Dawson 2003; Hampe 2004; Guisan & Thuiller 2005). Firstly, modelers often have to model species inside arbitrary boundaries (e.g. political borders). Hence, resulting response curves are often incomplete descriptions of species' responses to environmental predictors. As a result, difficulties in projecting species' distributions in different areas or times than those used to calibrate the models may arise (Van Horn 2002; Thuiller *et al.* 2004c). Using species restricted to the area under study, like endemics, should allow capturing their full realized niche and prevent biased projections at range limits, in both geographic and environmental space.

Secondly, land transformation is rarely included in climate change impact scenarios (but see Dirnbock *et al.* 2003a; Thuiller *et al.* 2006a), although it is a major cause of biodiversity loss (Sala *et al.* 2000; Lavergne *et al.* 2005). There are at least two reasons for this: (i) reliable land use data do not exist for key regions; and (ii) climate change studies are hampered by a lack of fine scale species and climate data, and as such are often conducted at such large extent and coarse resolution that accounting for land use is difficult (Pearson *et al.* 2004; Thuiller *et al.* 2004a). At the continental scale, climate can be considered the prevailing factor, whereas factors including topography and land-cover type become increasingly important toward more local scales (Guisan & Thuiller 2005). A simple approach is to use aggregated land use data to weight or filter predictions of species' occurrence (e.g. Guisan *et al.* 1998; Thuiller *et al.* 2006a), rather than including them within the statistical component of models.

Thirdly, dispersal ability is usually not taken explicitly into account when projecting species distribution in the future (Pearson 2006, but see Iverson *et al.* 1999b; Wiliams *et al.* 2005). Instead, either dispersal is assumed to be fully effective, so that ranges that have become newly suitable are invariably colonized ('unlimited dispersal' hypothesis), or dispersal is assumed to be zero, so that all individuals of the study are unable to shift to their new ranges ('no dispersal' hypothesis; e.g. Thomas *et al.* 2004; Thuiller *et al.* 2005b). These two extremes encompass the range of possible migration rates, but neither of these approximations is satisfactory because migration rate depends to a large extent on the capacity of each individual species to migrate, which itself is a composite of individual's various abilities. The first hypothesis would be a realistic approximation only if the climate was changing slowly enough to allow the species to track changes, and the second would only be realistic if the migration rate was negligible compared with the extent of the study area. The extent to which plants will be able to track climate change by migration is still largely debated (Ronce 2002; Pearson 2006; for a review, Pitelka *et al.* 1997). Fossil evidence of plant migrations following climatic upheavals in the Holocene, shows a wide range of migration rates among trees (Clark 1998). Today, anthropogenic habitat loss and fragmentation are likely to substantially constrain migrations compared with those measured in the past (Schwartz 1993; Dyer 1994, 1995; Malanson & Cairns

1997; Peters & Thackway 1998; Iverson *et al.* 1999b; Collingham & Huntley 2000). According to some authors, long-distance dispersal events might also play a crucial role for some species (Clark *et al.* 1998; Cain *et al.* 2003), but whether this is a general or a marginal phenomenon among plants is still under debate. For some taxa, lags in their response to past climate change tend rather to indicate that no long-distance event occurred that helped them to keep pace with the changing climate (Huntley 1991). Hence, including even an unspecific and overestimated migration rate would greatly refine predicted species distributions under climate change.

Finally, comparisons between groups of species or systems should thus provide a powerful approach for examining hypotheses on species' distribution (Parmesan *et al.* 2005). In this way, assessing effects of climate changes by life form or plant functional types (PFTs) should allow the identification of future trends in ecosystem structure (Dawson & Chapin 1993; Lavorel *et al.* 1997). Although individual species are expected to respond idiosyncratically to climate change, some species that share the same ecological properties (e.g. life history traits, life forms, history) might respond in the same way (Thuiller *et al.* 2005a). Although this approach is central in the conceptual and theoretical framework of dynamic global vegetation models (DGVM, Daly *et al.* 2000; Sitch *et al.* 2003; Woodward & Lomas 2004), it has been rarely tested in climate change impact studies involving SDMs (but Thuiller *et al.* 2006b). To date, SDMs have concentrated on quantifying species' range changes, with few efforts to explain the predicted ecological patterns (but see Guisan & Theurillat 2000; Peterson & Holt 2003; Thuiller *et al.* 2005a). Identifying which particular species or group of species might be at greater risk is a major issue that remains to be investigated.

Here, we derive projections for a large set of 975 endemic plant species in southern Africa belonging to seven different life forms. This region exhibits high levels of endemism and harbours two of the five African hotspots: the Cape floristic region (CFR) and the Succulent Karoo hotspots (Myers *et al.* 2000) which were identified as candidate areas of prime importance to become a world floristic heritage (www.conservation.org). Some studies in southern Africa have concentrated on the global change impacts on plant species of the Proteaceae family (Midgley *et al.* 2002; Midgley *et al.* 2003b; Bomhard *et al.* 2005), however, few studies have dealt with other taxa in this region (Erasmus *et al.* 2002; Simmons *et al.* 2004; Thuiller *et al.* 2006a). Focusing on endemics is a priority task for conservation in its own right, but it also avoids one frequent shortcoming in modeling, which is to fit only a part of a species' niche, as the entire geographic range of a species can be modeled (Guisan & Thuiller 2005). Biodiversity hotspots are the biologically richest yet among the most threatened places on Earth (Howlett 2000; but see Orme *et al.* 2005), where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. As much as 44% of all species of vascular plants and 35% of all species in four vertebrate groups are confined to 25 hotspots that only cover 1.4% of the Earth's land surface (Myers *et al.* 2000). If all threatened species cannot be conserved, focusing on hotspots is one way to protect a maximum of species at a minimum cost (Myers *et al.* 2000).

Our main objectives are:

(1) to assess the relative sensitivity of endemic species of Namibia and South Africa to both climate change and land transformation by 2050. (2) to compare the predicted patterns of species sensitivity with global change across life forms, using ecological and geographic characteristics of the species in the study area. We ask particularly whether some species or specific groups are constrained in their migration toward cooler seacoasts or areas at higher elevation. (3) to propose an improved modeling approach that considers the three limitations previously discussed: (i) use of endemic species only to capture the full realized niche of species, (ii) impose constraints by land transformation types, and (iii) impose constraints related to species' ability to migrate.

MATERIAL

Study area

The study area encompasses four southern African countries namely Namibia, South Africa, Lesotho and Swaziland. It harbors two of the five African biodiversity hotspots, namely the CFR of South Africa and the Succulent Karoo of South Africa and Namibia. The CFR, located at the southwestern tip of Africa, is one of five Mediterranean-type systems included in nearly all assessments of global conservation priorities. As the smallest floral kingdom, it occupies only 90 000km^2, yet contains nearly 3% of the world's plant species on 0.05% of the land area. The Succulent Karoo covers an area of approximately 116 000km2 stretching from South Africa's Little Karoo along the arid western side of the country into southern Namibia. It is the richest arid region in the world to be declared as a biodiversity hotspot and includes a spectacular array of 6356 species, of which over 40% are endemic.

Species data

We used a subset of the PRECIS Database (National Herbarium Pretoria Computerised Information Service; Germishuizen & Meyer 2003), which contains records for more than 736 000 specimens in 24 500 taxa (species and infraspecies) from southern African countries. Species endemic to the region including Namibia and South Africa were selected, and those with less than 20 records in the dataset were excluded from analysis to reduce errors associated with excessively small sample sizes (Stockwell & Peters 1999). The 975 remaining species were distributed among life forms as follows: 59 trees, 278 shrubs, 168 perennial herbs, 100 annual herbs, 62 grasses, 230 geophytes and 68 succulent plants. The classification of species into life forms was achieved by sorting the PRECIS specimen database and by retaining the 'higher' life form presented by the species (for example, when a plant was found either as a tree or a shrub, it was classified as a tree). In ambiguous cases,

we used expert knowledge (M. Rutherford, personal communication). This PRECIS locality data were recorded by quarter degree grid (QDS) cells (~ 25x 25 km^2 at this latitude).

Climate data

We used the CRU CL 2.0 dataset (New *et al.*, 2000) to represent current climate and to derive six climatic variables considered critical to plant physiological function and survival (Bartlein *et al.* 1986; Woodward 1987). In order to produce consistent datasets, all subsequent data layers were developed at a spatial resolution of 10' and resampled at QDS scale for model calibration. Climate data were averaged for the period 1961–1990 and included mean annual potential evapotranspiration, mean annual growing degree days (410 1C), mean annual temperature, mean temperature of the coldest month of the year, mean temperature of the warmest month of the year and mean annual precipitation sum. Potential evapotranspiration estimates were obtained using the FAO 56 Penman Monteith combination equation (Allen *et al.* 1998). These variables were already used successfully elsewhere to predict species distribution (e.g. Huntley *et al.* 2004; Thuiller *et al.* 2005a).

Future climate predictions by 2050 were produced by perturbing the current climatic data with anomalies derived from climatic simulations produced by the HadCM3 general circulation model (GCM) using the A1, A2, B1 and B2 IPCC SRES scenarios (Nakicenovic & Swart 2000). The A1 storyline describes a future world of very rapid economic growth, global population that peaks by mid-century and then declines, and the rapid introduction of new and more efficient technologies. The A2 storyline describes a very heterogeneous world, preserving local identities. Economic development is primarily regionally oriented and per capita economic growth and technological changes are more fragmented and slower than in the other storylines. The B1 storyline describes a convergent world that peaks by mid-century and declines thereafter, but with rapid change in economic structures towards a service and information economy, with the introduction of clean and resource efficient technologies. The B2 storyline describes a world in which the emphasis is on local solutions to economic, social and environment sustainability (Nakicenovic & Swart 2000).

Land transformation data The 'human footprint' (Sanderson *et al.* 2002) is a regionally consistent way to represent land transformation on a global scale. It represents the sum of the ecological footprints of the human population as a continuum of human influence stretched across the land surface. This dataset use four types of data as surrogates for human influence: population density, land transformation, accessibility and electrical power infrastructure. The footprint index ranges from 0 to 1, from natural to completely transformed habitat. The original GIS layer at a resolution of 1 km was resampled to a 10' resolution.

METHODS

Current potential distributions

Statistical modeling - SDMs were fitted to climatic data using the BIOMOD package in SPLUS (Thuiller, 2003). For each species, generalized linear model (GLM), generalized additive model (GAM), classification tree analysis (CTA) and artificial neural networks (ANN) were fitted on a random sample (70%) of the initial data. Then for every species the accuracy of each model was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) curve on the remaining 30% of the initial data (test set for independent evaluation; Guisan & Zimmermann 2000; Pearce & Ferrier 2000; Liu *et al.* 2005).

Land use filters - We used the 'human footprint' dataset to filter the resulting climatic potential distributions. We applied this filter by weighting the probability of occurrence by the 'human footprint' index. We assumed that completely transformed pixels corresponded to unsuitable habitat for wildlife, and their probability of occurrence was set to 0. Finally, the probabilities of occurrence from the filtered models were converted to presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted.

Future potential distributions

Statistical modeling - Models calibrated under current conditions were then used to generate projections of future climatically suitable habitat under the scenarios HadCM3 A1, A2, B1 and B2 for 2050. Only the best model for each species according to the ROC curve criterion was used to project future potential climatic suitable habitats (Thuiller 2004).

Land use filters - As no dataset of future land transformation was available for each IPCC scenario, we assumed future land transformation to be best described by the current land transformation dataset, as this represents a conservative prognosis of the future (i.e. a 'best case' scenario) and limits additional uncertainty owing to future land transformation projections. Accounting for current land transformation in this way was expected to be better than ignoring it, as it is very unlikely that currently transformed areas will revert to 'untransformed' areas in the future (although there may be few exceptions). The future potential distribution maps were filtered following the same procedure as the current distribution maps. Finally, the probabilities of occurrence from the filtered models were converted to presence/absence using a threshold maximizing the percentage of presence and absence correctly predicted.

Migration limits - In order to avoid unreliable future potential distributions, we constrained the migration of any species to no more than ~1 $kmyr^{-1}$ (based on data by Clark *et al.* 1998), even if the

climate becomes suitable at larger distances. This has the effect to restrict species movement to maximum 0.51 for the 50-year period until 2050. For every species, if any pixels geographically more distant than 0.51 from the source pixel became suitable under climate change, its probability value was set to 0.

Climate change impact measurements

Spatial patterns - For each pixel, we calculated the number of species predicted both under present and future climatic conditions. From these values, we assessed the number and percentage of species predicted to no longer be present in the pixel in the future (species loss) as well as the number and percentage of species predicted to newly arrive (species gain). The difference between species loss and species gain allowed us to quantify the intensity of species reshuffling (species turnover): $sp_{turnover} = 100 \times (sp_{gain} + species_{loss}) / (initial\ sp_{richness} + sp_{gain})$. A turnover value of 0 indicates that the assemblage of species is predicted to remain the same in the future (i.e. no loss or gain of species), whereas a value of 100 indicates that the assemblage of species is completely different (i.e. the species loss equals the initial species richness; e.g. Thuiller *et al.* 2005b).

Sensitivity of species - For each species, we calculated the percentage of pixels that remain suitable for the species under both present and future climatic conditions. The remaining grid cells, predicted to become unsuitable, were used to calculate the percent of lost habitat (habitat loss). We also calculated the percent of new suitable habitats (habitat gain), defined as the pixels unsuitable at present but predicted to become suitable after climate change, according to the assumption of constrained dispersal. Finally, for each species the percentage of range expansion or contraction (species range change) was calculated as the relative difference between habitat loss and habitat gain.

Ecological and geographical drivers of vulnerability

To investigate the spatial patterns of species vulnerability (expressed as species range changes), we derived a set of factors summarizing the ecological and geographic properties of the species expected to respond to climate change.

Niche breadth - The ecological niche of a species can be described by its mean position and breadth along various environmental axes (Schoener 1989). Here, niche breadth along climatic axes was described using the multivariate coinertia analysis outlying mean index (OMI: Doledec *et al.* 2000), which makes no assumption about the shape of species response curves to the environment, and gives equal weights to species-rich and species-poor pixels (for more details see Thuiller *et al.* 2004d).

Spatial patterns of climate change - We derived maps of mean temperature and precipitation anomalies (differences between present and future values) over the study area, and related these to the present distributions of species. Only temperature and precipitation anomalies were used as a surrogate of global climate changes, because these two variables explain the major variation in future climate (Hulme *et al.* 2001), and allow straightforward interpretations.

Change in proximity to seacoast - For each species, we calculated the centroid of the current and future distribution, and calculated the distance of both centroids to the seacoast. This allowed calculating how much closer the centroid of the distribution moved toward seacoast. This estimate highlighted if a species would move toward or in the opposite direction to the coast, and if these movements could explain the species' sensitivity to climate change. The scale of the change in proximity to seacoasts axis represents the percent change of the proximity of the range centroid to seacoast after climate change.

Altitudinal rise - We calculated the centroid of present and future distributions of each species, and used it to calculate the expected altitudinal rise of species in the future. The scale of the altitudinal rise axis represents the absolute elevation change (in meters) of the centre of the distribution after climate change.

The influence of these factors on the vulnerability of species to climate change was then assessed by identifying the statistically supported relationships between these factors and predicted species' range changes using a linear regression fitted for each different life form. Note that some factors may act directly on the sensitivity of species to climate change (niche breadth, temperature anomalies and precipitation anomalies), whereas some others may act indirectly by constraining the response of the species (change in proximity to seacoast and altitudinal rise). The relationships between response and these explanatory variables were assumed to be linear, and no interaction term was allowed in the models to facilitate interpretation. An iterative stepwise analysis was performed to remove variables that did not significantly contribute to the explained deviance. This analysis was only carried out for the scenario A2 HadCM3, because this socio-economic scenario was understood as being reasonably credible in the future and showed important impacts on species, allowing a detailed investigation of the relationships between climate changes and species traits (including characteristics of species' range change). To facilitate the interpretation of the resulting trends, we further examined the mean position of each species along the ecoclimatic and biogeographic gradients.

RESULTS

Modelling current and future species distribution

Model accuracy - The average AUC calculated from the evaluation dataset is 0.95 ± 0.04 (Fig. 1). This reflects an excellent predictive accuracy (AUC40.9; Swets 1988). Only three species show a poor predictive accuracy (AUC < 0.7; Swets 1988). Although AUC is high for every life form, the model accuracy of annuals and succulents is slightly lower than for others. By contrast, geophytes are in average almost perfectly modeled (mean AUC = 0.97).

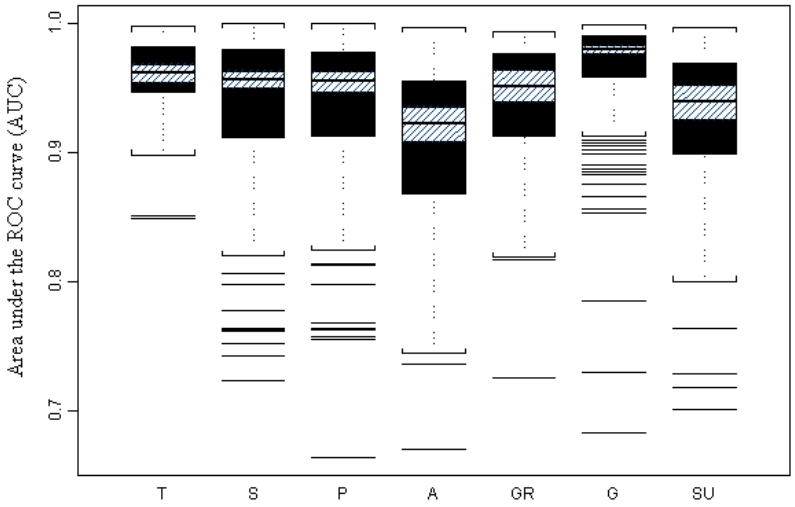

Fig. 1 - Summary of the area under the curve (AUC) generating from the models using the evaluation dataset (30% of the total dataset). AUC 0.90–1, excellent; 0.80–0.90, good; 0.70–0.80, fair; 0.60–0.70, poor; 0.50–0.60, fail (). The boxplots indicate the accuracy of models for T, trees; S, shrubs; P, perennials; A, annuals; GR, grasses; G, geophytes; SU, succulents. The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the interquartile range of data whereas the whisker lines symbolize the centiles 5 and 95. Single horizontal bars represent outliers of the relationships.

An example of a species model is shown for Heliophila deserticola (Fig. 2) for scenario A2-HadCM3 by 2050, with potentially stable, lost and gained habitat in the future, as well as presence data used to calibrate the model. A predicted southeast distributional shift of the species in the future is denoted for this rare and endemic annual herb, characteristic of the Succulent Karoo and Nama Karoo Biomes. The obviously erroneous outlier observations outside the relevant biomes (crosses surrounded by circles, Fig. 2) illustrate the difficulty of using herbarium data. These observations may reflect errors in determination, database handling or the presence of specimens in botanical gardens. However, the resulting predicted distributions correspond globally well to the known distribution of the species, highlighting the fact that the model is not particularly sensitive to such outliers.

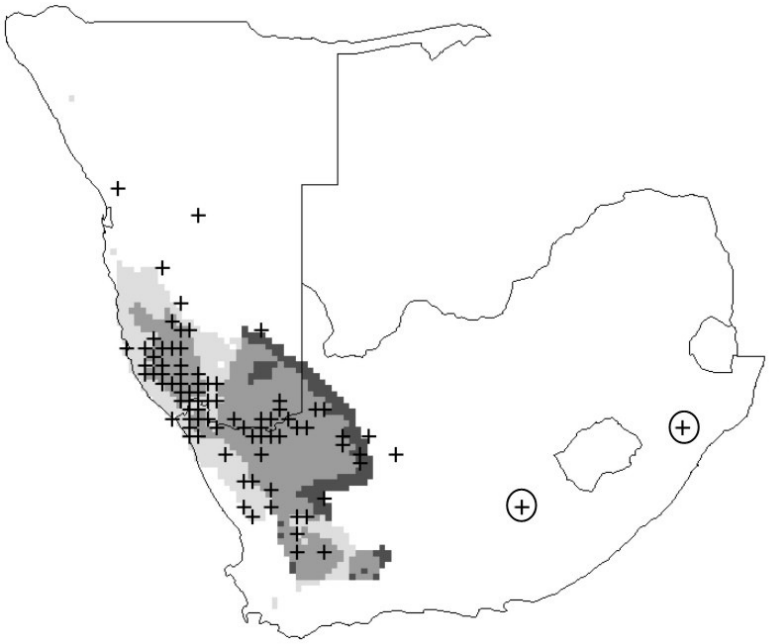

Fig. 2 - Examples of species model (Heliophila deserticola) for the scenario HadCm3 A22 050. Areas in light grey correspond to habitat predicted to be lost in the future, in mid grey those predicted to be stable habitat and in dark grey those predicted to be potentially colonized according to the dispersal assumptions used in this study. Crosses point out observation presences used to calibrate the model. Crosses surrounded by circles indicate erroneous outlier observations outside the relevant biomes.

Spatial patterns - Consequences of climate change for the species richness of endemic plants are predicted to be fairly severe (Table 1, Fig. 3). By 2050, each pixel of the study area is predicted to lose, on average, 41–51% of its current endemic species richness, whereas only gaining 30–33% of new species. This is predicted to result in a high species turnover (54–62%). Some biomes are predicted to be more severely affected than others (Table 1). The Namib Desert and Fynbos are the less affected biomes with 30–40% of species turnover predicted by 2050. By contrast, Albany Thicket, Grassland and Savanna are predicted to undergo 60–70% turnover. In term of absolute number of species however, the results are quite different, because of the high disparity of species richness among biomes. The CFR in the southwestern part of South Africa in particular is predicted to suffer a massive loss of endemic species, with up to 273 species lost in areas at the transitions zones between Fynbos and Succulent Karoo and between Fynbos and Nama-Karoo.

Table 1 – Average percent of species losses, gains and turnover. The range of average values across scenarios is presented here for time slice 2050. Values are calculated for the biomes occurring in the study area. The mean species richness by biome is also indicated.

Biome	Endemic species richness	% of species loss	% of species gain	% of turnover
Global	94	41-51	30-33	54-62
Namib Desert	151	20-28	14-18	30-39
Succulent Karoo	203	36-49	14-21	45-56
Nama Karoo	90	35-43	33-38	51-57
Fynbos	415	24-35	7-12	30-41
Albany Thicket	200	56-67	10-16	60-72
Grassland	67	51-64	27-28	62-73
Savanna	57	45-57	36-40	59-67
Forest (1pixel)	176	24-34	15-21	33-45

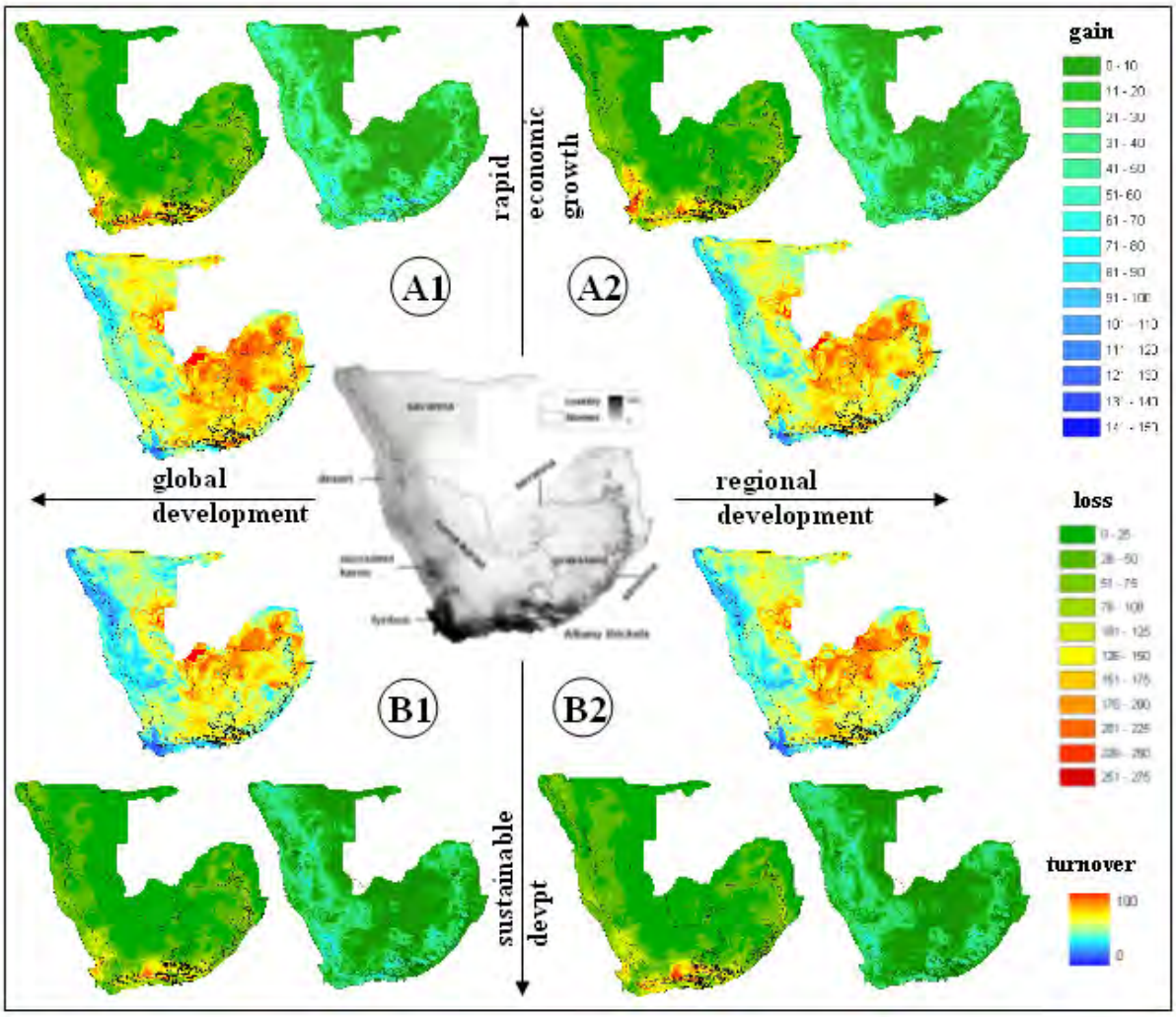

Fig. 3 – Species loss, species gain and percentage of turnover in 2050. The absolute number of species predicted to be lost (species loss; green to red scale), the absolute number of species predicted to be gained (species gain; green to blue scale) and the percentage of species turnover are shown for scenarios HadCm3 A1 (upper left corner), HadCm3 A2 (upper right corner), HadCM3 B1 (lower left) corner and HadCM3 B2 (lower right corner) by 2050. For each scenario, species loss is on the left and species gain is on the right. Predicted endemic species richness at present time is shown in the centre of the figure.

Sensitivity of species - Consequences of climate change and land transformation on selected endemic plant distributions are first analysed globally (all life forms together) and then by life form, namely: trees, shrubs, perennials, annuals, grasses, geophytes and succulents. Effects on selected endemic plants are predicted to be fairly severe, broadly the same order of magnitude as found on species richness (Fig. 4). By 2050, plants of this study would lose on average 39–49% of their current suitable habitat, whereas mean percentage of gained habitat ranges from 16% to 21%. This results in mean species range changes between -21% and -29%. Extremes percentages of stable suitable habitats range from 0% (e.g. Baphia massaiensis) to 100% (e.g. Agapanthus campanulatus), highlighting the idiosyncratic response of species. By contrast, median range changes by life forms reveal more consistent patterns (Fig. 4), with a variance among life forms higher than that among the different climate change scenarios by 2050 (GLM: species range change ~ scenarios + life forms; life forms: $F = 52.59$, $P<0.00001$; scenarios: $F = 7.77$, $P = 0.00003$). Annual herbs in particular show a very different pattern than all other life forms. It is the only life form not predicted to undergo a globally significant decrease in species ranges (-4% to 2%) by 2050. By contrast, geophytes are predicted to consistently suffer higher decreases in species ranges (-36% to -45%). Other life forms share more similar patterns, with a decrease of species range of about 20% for the less extreme scenarios and of about 30% for the most extreme scenarios (trees: -18% to -27%; perennials -23% to -31%; shrubs: -19% to -28%; grasses: -19% to -27% and succulents: -23% to -31% of decrease in species range).

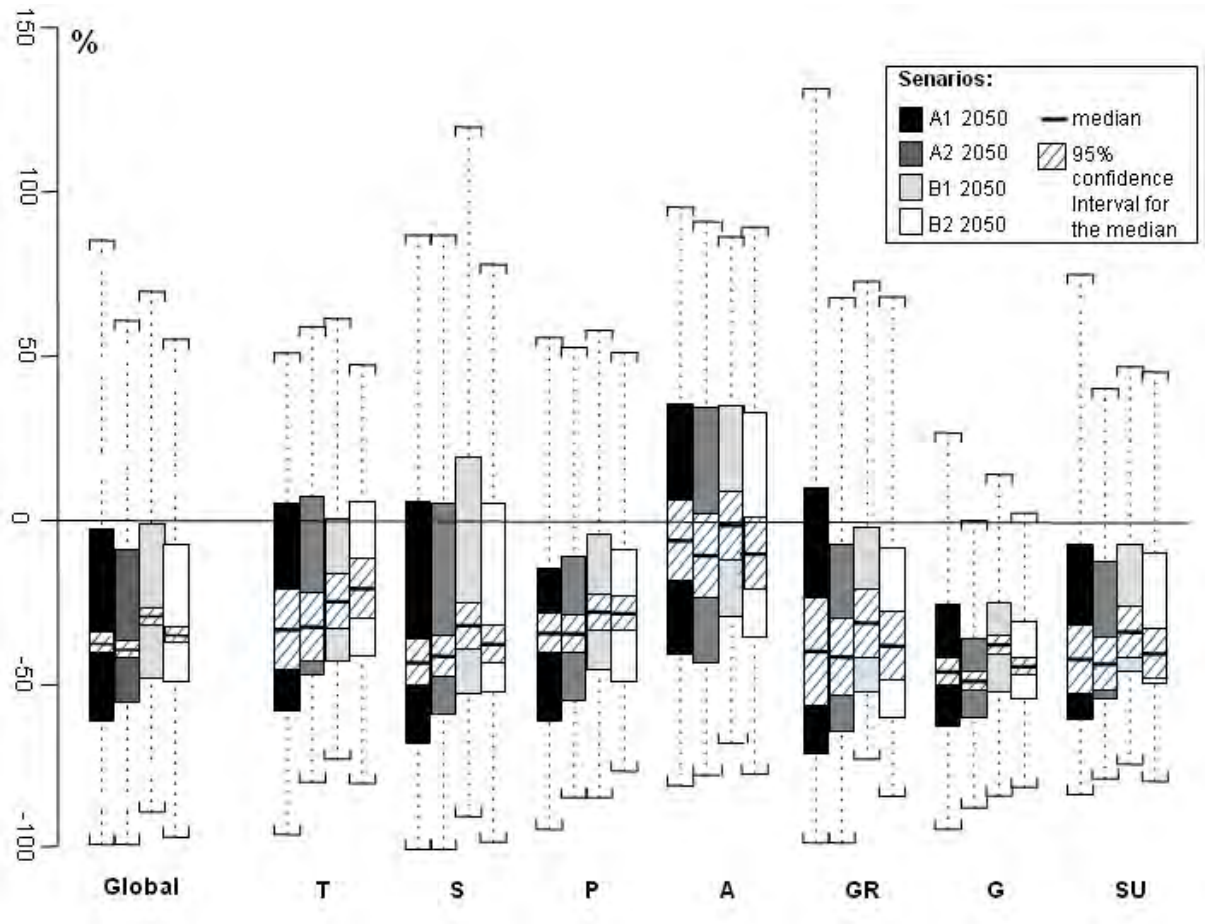

Fig. 4 - Percentage of species' range change between present and 2050. Global) whole dataset, T) trees (69 sp), S) shrubs (278 sp), P) perennial herbs (168 sp), A) annual herbs (100 sp), GR) grasses (62 sp), G) geophytes (230 sp), SU) succulents (68 sp). Boxplots in black, dark grey, light grey and white represent results for scenario HadCM3 2050 A1, A2, B1 and B2 respectively. The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the inter-quartile range of data while the whisker lines symbolize the centiles 5 and 95.

Ecological and geographical explanation of spatial patterns of vulnerability

For the variable niche breadth, we estimated the variability of habitat conditions used by each species by calculating the variance of the positions of each occurrence on the first axis of the OMI analysis (Fig. 5c). This axis captures a continental gradient (Table 2) running from the seacoast to the centre of the African continent. We only used the first OMI axis, because it explained most of the variance among data (70.28%), and because there was no distinct hierarchy between the contributions of other axis.

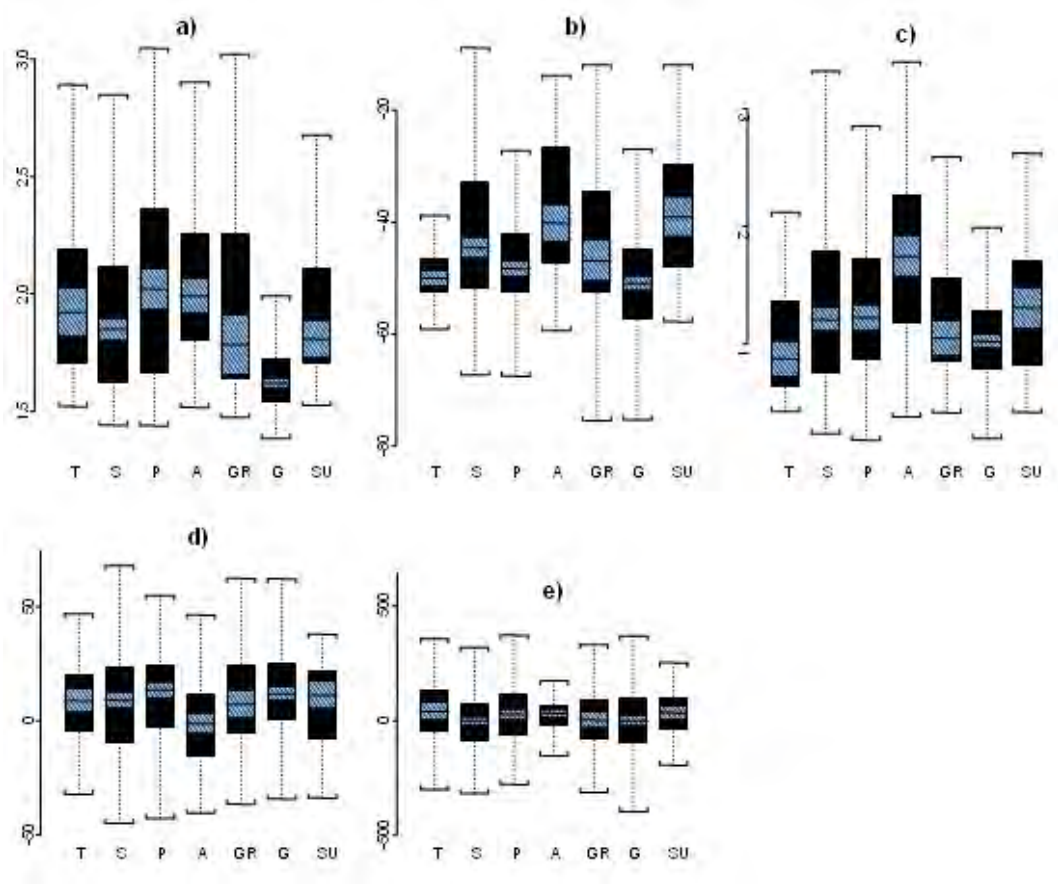

Fig 5 – Mean position of species along geoclimatic and biogeographicgeographic gradients. The boxplots indicates the mean position of modelled species on the geoclimatic and biogeographic gradients, namely: a) temperature anomalies, b) precipitation anomalies, c) niche breadth, d) closure to seacoast and e) altitudinal rise. For each ecogeographic variable, each life form is analyzed separately (T= Tree, S=Shrubs, P=perennials, A=annuals, GR= grasses, G=geophytes and SU=succulents). The medians of range changes are shown (black horizontal lines) with their respective 95% confidence interval (hatched boxes). The core boxes of boxplots indicate the inter-quartile range of data while the whisker lines symbolize the centiles 5 and 95.

Table 2 - OMI analyse. The respective importance of climate variables in the first axe of the co-inertia analysis Outlying Mean Index (OMI: Doledec *et al.* 2000) is presented.

Climate variable	Niche breadth
mean annual potential evapotranspiration	-0.80
mean annual growing degree days (>10°)	-0.66
mean temperature of the coldest month	0.24
mean temperature of the warmest month	-0.70
mean annual precipitation sum	0.67
mean annual temperature	-0.62

Multivariate GLMs identifying statistically supported relationships between biogeographical variables and species range changes are presented in Table 3. When considering the pool of species globally, temperature anomalies are positively correlated with species range changes, which indicate that in our study area, higher temperature anomalies tend to be associated with an expansion of species ranges. Niche breadth is also positively correlated with species range change, which indicates that species having a broad niche breadth tend to be less affected by climate change in the future. On the contrary, change in proximity to seacoasts and altitudinal rise are negatively correlated with species range change, meaning that species predicted to shift toward seacoasts and higher elevations are the most affected by climate changes. Precipitation anomalies do have a significant relationship with species range change when considering all species together.

The response of some life forms seems to depend upon specific geoclimatic and biogeographic patterns. Temperature anomalies, change in proximity to seacoasts and altitudinal rise have a stronger influence on the vulnerability of species and act similarly on the majority of life forms, whereas others – precipitation anomalies and niche breadth – only affect particular life forms.

The range changes for trees, shrubs, annuals and succulents' are best explained by the same factors (temperature anomalies, change in proximity to seacoasts and altitudinal rise), while the response of perennial species are additionally influenced by their niche breadth. Grasses and geophytes exhibit distinct patterns. Grasses seem affected by precipitation anomalies and niche breadth whereas geophytes are influenced by all variables except temperature anomalies. Note, however, that the influence of such geographic factors, even significant, does not always explain a large part of the deviance of the models. Models for annuals and grasses, for instance, have a particularly low explained deviance (D^2 = 50.49 and 0.40, respectively; Table 3).

The mean value of species along geoclimatic and biogeographic gradients (Fig. 5) allows further investigation of the statistically supported relationships. Not all results are described here (see Fig. 5), but some life forms show interesting patterns. For instance, annuals is the only life form which does not overall move seawards (-1.25% proximity, whereas the entire set of species will experience an average change in proximity of 19.13%). By contrast, geophytes have more restricted niche breadths compared with other life forms (1.32, whereas 1.56 for the entire set of species), and will undergo stronger precipitation reduction in the future (-50.93mm, whereas -47.07mm for the entire set of species).

Table 3- ecological and geographical variables determining species range changes. Results of the stepwise GLM between species range change (with scenario HadCM3 A2 2050) vs. temperature and precipitation anomalies, niche breadth, proximity to seacoasts and altitudinal rise for each life form are shown. Details provide explained deviance (D2) as well as the shape of the partial relationship between response and explicative variables with their relative statistical significance (*: $0.05 < p < 1x10^{-4}$, **: $1x10^{-5} < p < 1x10^{-7}$; **: $1x10^{-8} < p < 1x10^{-10}$; **: $p < 1x10^{-11}$).

Life form	D2	Temperature anomalies	Precipitation anomalies	Niche breadth	Proximity to seacoasts	Altitudinal rise
Trees	0.71	Positive *	ns	ns	Negative *	Negative *
Shrubs	0.56	Positive ****	ns	ns	Negative ****	Negative ****
Perennials	0.56	Positive *	ns	Positive ****	Negative ***	Negative **
Annuals	0.49	Positive ***	ns	ns	Negative ****	Negative **
Grasses	0.40	Positive *	Positive ***	Positive ***	ns	ns
Geophytes	0.75	ns	Negative *	Positive **	Negative **	Negative **
Succulents	0.59	Positive **	ns	ns	Negative **	Negative **
Global	0.59	Positive ****	ns	Positive ****	Negative ****	Negative ****

DISCUSSION

Vulnerability of South African and Namibian endemic flora to global change

In this study, we modeled 975 endemic plant species in southern Africa distributed among seven life forms. Our results predict that impacts of climate change and current land transformation on endemic plant species in the study area are likely to be fairly severe, both at a geographic scale and a systematic level, with a 41% average decrease in species richness among habitats and a 39% average decrease of species distribution range for even the most optimistic scenario. The analysis of contraction or expansion of species distributions revealed highly idiosyncratic responses across species. However, two life forms – annuals and geophytes – revealed particular and consistent patterns of changes. The annual life form is the only one not predicted to undergo a global significant decrease in species ranges, whereas by contrast, geophytes are consistently predicted to suffer high decreases in species range.

Interpreting habitat exposure to climate change – i.e. losses, gains and resulting turnovers – requires careful consideration of both absolute and relative numbers of species. Pinpointing regions with high absolute numbers of species lost or gained is of prime importance for conservation planning,

whereas regions with high percentage turnover may experience a high reshuffling of biological assemblages, which may further lead to some ecosystem disruptions (Bakkenes *et al.* 2002; Erasmus *et al.* 2002; Peterson *et al.* 2002). For instance, the CFR is predicted to suffer particularly massive losses of endemic species. These high absolute losses compared with other regions can be partly explained by the fact that this region shelters the majority of species present in the study area. However, losses in certain part of the CFR cannot be explained by initial species richness. Regions in the west and at the northern edge with the Nama Karoo are predicted to face the highest percentage of species loss. This echoes the results of Midgley *et al.* (Midgley *et al.* 2003b), who showed that these regions were particularly vulnerable to climate changes. On the contrary, the central parts of CFR that constitute the core of the Fynbos biome are predicted to face attenuated losses.

Our analysis concerns only a portion of the total Namibian and South African plant diversity, and cannot be extrapolated to the whole plant diversity of the area. Nevertheless, the geographical patterns in percentage of species turnover probably depict fairly well the general trends of changes expected in this region, because our species dataset comprises a fair representation of life forms. Moreover, our predictions concern only endemic species, and thus the most sensitive part of the biodiversity. Predicted trends of extinction should therefore be considered as a very serious threat to this world floristic heritage.

Species vulnerability as a function of geographic properties and niche traits

The basic idea suggested by our analyses is that the sensitivity to climate change of a given species depends on its geographical distribution and ecological niche properties. The most vulnerable species are those with a restricted niche breadth (and thus often a restricted distribution) distributed within regions most exposed to climate change (i.e. high anomalies), or which direction of range change hits barriers to migration like seacoasts or mountains. This suggests that the potential sensitivity of species to climate change can be – at least partly – estimated a priori from their distribution along these gradients and from their niche characteristics.

Indeed, the linear analyses by life forms of the relationships between species' range change and species' position along geoclimatic and biogeographic gradients allowed us to identify variables that can significantly explain species vulnerability to climate changes in our study area. Species are likely to suffer less of a range decrease in the future when their geographic distribution is predicted to move away from seacoasts, hence providing species with larger areas to colonize. For instance, in our study, annuals is the only life form that does not get overall closer to seacoasts, which can explain why it does not show high susceptibility to climate change. All other life forms are predicted to undergo serious distributional shrinkage. Similarly, in agreement with ecological niche theory (Brown

et al. 1995), we assume the high vulnerability of geophytes to be related to their restricted niches, which results in a lower probability of establishment elsewhere. Also for geophytes, their high vulnerability seems to result from the greater reduction in rainfall in their distribution range. This is not surprising, because precipitation is considered to be the most critical factor to plant physiological function and survival (Bartlein *et al.* 1986; Woodward 1987).

Curiously, species occurring at places of greater climatic anomalies are not predicted to lose more of their range than other species. A likely explanation is that when considered alone, temperature anomalies may be positively correlated to species range change, but once other variables are included in the linear model, the correlation becomes negative because of geographic patterns and correlations with other variables.

Improvements to previous projections and remaining limitations

Our modeling was improved as much as possible over three usual shortcomings of SDMs (Guisan & Thuiller 2005), by: (i) using endemic species as a way to capture the full realized niche of species, (ii) considering the impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' dispersal into account.

Considering endemics prevents the risk of fitting truncated response curves of species to the main environmental gradients, which can result in limited transferability of models to new environmental conditions (Thuiller *et al.* 2004c; Guisan & Thuiller 2005).

By using the human footprint dataset (Sanderson *et al.* 2002) to weight probability of presence in areas with high human pressure, we accounted for human influence on the landscape. We assumed species to be absent from areas heavily influenced by human, either because habitats are not suitable or because they are suitable but not valuable for conservation purposes. Unfortunately, there was no available dataset on future land transformation for the study area. It was thus assumed that future land transformation is best conservatively described by the current land transformation dataset, as this represents a conservative prognosis of the future and limits additional uncertainty owing to future land transformation projections. As our way of taking land use into account is not species specific, the influence of land use might have been exaggerated for some species and underestimated for others. One way to take species specificity into account in future work would be to include land use variables directly in the models, taking care not to overfit models. But this would require specific knowledge about the susceptibility of every modeled species to land use impact. Hence, we advocate that such a method using land use variables separately is a reasonable compromise for incorporating such variables in global studies, because land use variables are distal predictors that do not act as direct factors constraining plant physiology or providing energetic

resource (Austin 2002). To avoid overfitting and provide better generality, proximal variables should be included preferentially in models (Guisan & Zimmermann 2000).

Restricting migration of species to 1 km yr^{-1} was considered a more realistic approach than considering the two extreme hypothesis – 'no dispersal' and 'unlimited dispersal' – that are usually considered in this type of studies (e.g Thomas *et al.* 2004; Thuiller *et al.* 2005b). This extent of migration, corresponding to the maximum rates observed in ancient climate changes in the Holocene (Clark *et al.* 1998), allows avoidance of spurious distribution areas that would appear when modeling future species distribution with no dispersal limit. This approach is not species specific, but it has the potential to be implemented meaningfully with large species datasets. Specific implementation of migration requires specific knowledge on the dispersal ability, which is impractical in many studies, as necessary data are lacking for most species even in well-studied areas. One possible – although still crude – approach to overcome this limitation would be to consider groups of species with particular dispersal syndromes and to allow each group to migrate with a particular rate (e.g. entomochory vs. zoochory vs. wind dispersal; G. F. Midgley *et al.*, unpublished).

Notwithstanding our effort to account for possible bias in the models, some weaknesses still remain to be investigated. For example, fire regime – type of fire, intensity, frequency, season, duration – is known to be an important ecosystem regulator in southern Africa (Bond *et al.* 2003), but is not available as a coherent dataset over the whole study area and could thus not be incorporated in our modeling framework. Nor did we account for species persistence and inertia of ecological systems. Niche base modeling techniques predict the habitat suitability of species at a given time and not, per se, the presence of the species. For instance, a long-lived plant can persist several decades even if its habitat has become unsuitable. But as no more suitable habitat will be available in the neighborhood, the population will experience a decrease in offspring recruitment, becoming a sink population (Pulliam 2000). It will survive only until the youngest individuals, born before the habitat became unsuitable, die. When predicting extinctions, we include the possible persistence of individuals in unsuitable habitat even after decades or centuries, depending on species lifespan.

CONCLUSION

Our analysis shows important promise concerning the impact of climate changes on the endemic flora of southern Africa. A better understanding of the likely impacts will allow the prediction and prioritization of global conservation strategies to prevent massive loss of biodiversity. In particular, we demonstrated that:

1. CFR and the Succulent Karoo hotspot are predicted to undergo a minimum of 41% loss of species richness and 39% species range reduction by 2050. However, species with core distributions in Fynbos and the Namib Desert biomes, as well as species belonging to particular life forms, like annuals, may suffer attenuated – but yet considerable – consequences of future global changes. Because CFR and the Succulent Karoo constitute a world floristic heritage of prime global and regional importance, our results underline the necessity to take political decisions in order to circumvent major biodiversity impacts in that region.

2. Species and life form vulnerability to climate change can be partly explained according to (i) the position of their geographical distribution along geoclimatic and biogeographic gradients, like climate anomalies, (ii) their niche breadth or (iii) their proximity to barriers preventing migration and expansion. Our results confirm that the sensitivity of a given species to climate change depends upon its geographical distribution and ecological properties, which can be used for predictive purposes.

3. New methodological insights can be implemented for improving the accuracy and ecological realism of predictions, avoiding three usual limitations inherent to many global or continental climate changes studies. These are: (i) using endemic species only as a way to capture the full realized niche of species, (ii) considering the impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' migration into account.

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Chapter 4

SPREAD OF INVASIVE ALIEN PLANTS

Chapter 4.1 Historical biogeography of Lactuca serriola L. (Asteraceae) in Europe

In review in Journal of Biogeography

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ABSTRACT

The spread of *Lactuca serriola* in Europe during the last 250 years and its relation to global change was investigated through the use of historical material and geographical analyses.

We modelled the distribution of the bioclimatic niche of the species using occurrences and climatic data for five time periods during the last century and tested whether the observed distribution of *L. serriola* could be explained for each time period, maintaining the same niche characteristics.

The species has spread northward since the beginning of the 19th century. We showed that climate warming in Europe increased the number of sites suitable for the species at northern latitudes. Until the late 1970s, the distribution of the species corresponded to the climatically suitable sites available. For the last two decades of the century, however, we could not show any significant relationship between this increase and the distributional range change of *L. serriola*. Predominantly non-climatic influences of global change contributed to its rapid spread.

Our work highlights the importance of historical floristic and herbarium data for understanding the expansion of a species. Data from past events can form the basis for managing modern environmental problems such as the species' reaction to environmental change.

Keywords: Bioclimatic niche, climate change, distribution shift, disturbance, global change, historical biogeography, *Lactuca serriola*, prickly lettuce.

CONTRIBUTIONS TO THE PROJECT

I developed and performed models of the bioclimatic niche of L. serriola for five time periods during the last century and tested whether the observed distribution of *L. serriola* could be explained for each time period. I wrote the sections related to these analyses and participated in the reviewing of the manuscript.

INTRODUCT ION

Lactuca serriola L. or prickly lettuce (Asteraceae) is a large spring or winter annual herb native to the summer-dry Mediterranean climate (Gallardo *et al.* 1996). It was originally distributed in southern Europe, northern Africa, and western Asia**,** but has been widely introduced in other regions (Carter & Prince 1985; Zohary 1991). It increased in geographical range toward northern Europe and now has a worldwide synanthropic distribution. The species belongs to a group of Mediterranean ruderal plants that have enlarged their distribution area during the last few centuries (Landolt 2001). It poses problems in agricultural fields in Australia and North America (http://www.weedscience.org/in.asp).

The spread of *L. serriola* is very closely related to human activities, mainly increases in transport (Lebeda *et al.* 2001) and changing patterns of land use. These processes have led to greater availability and better connectivity for disturbed and ruderal habitats favourable to *L. serriola,* such as wastelands, embankments, sides of ditches and roads, field margins, and fallow fields (Feràkovà 1977; Zohary 1991; Lebeda *et al.* 2001).

Global change, whose components are linked to global industrialisation and global trade, is a concept that brings together many environmental changes and subsequent ecological consequences. It includes the invasion of alien species into natural environments, biodiversity changes, climate changes, increased nitrogen deposition, and changing patterns of land use such as destruction and fragmentation of habitats (Dukes & Mooney 1999). Recently, concern about the impact of the current climate change on organisms and the environment has greatly increased. Distributional latitudinal shifts have already been documented for many kinds of organisms (Huntley *et al.* 1995; Walther *et al.* 2002; Root *et al.* 2003; Walther *et al.* 2005). It has also been demonstrated that climate warming can affect the dynamics of plant communities and influence the range expansion and contraction of species as well as their phenology and physiology (Davis & Shaw 2001; Parmesan & Yohe 2003). Root *et al*. (2005) showed recently that a significant portion of the changes observed in plants and animals can be attributed to increases in global temperature caused by human activity. However, correlations between climate changes and single species distribution range shifts are mostly investigated for small geographical areas (Kennedy 1995; Pounds *et al.* 1999; Sturm *et al.* 2001; Johnstone & Chapin 2003; but see also Walther *et al.* 2005) or at upper elevation limits (Kullman 2002; Penuelas & Boada 2003).

Over the next century, increases in annual precipitation and temperature at the medium and high latitudes of the Northern hemisphere and a global warming of 1.4 to 5.8°C are expected, depending on the climate change scenario considered (Dukes & Mooney 1999; IPCC 2001). Since the end of the 19th century, the global temperature has increased by 0.6 °C, on average; this figure is even higher if only landmasses are considered. From 1946 to 1975, temperatures decreased in the Mediterranean, Central Europe, and Great Britain, while they continued to rise in Scandinavia and the rest of Europe.

From 1976 to the present-day, temperatures increased rapidly across Europe, with the 1990s being the warmest decade of the 20th century (IPCC 2007b).

Improving our understanding of how climate and dispersal dynamics interact to drive migration rates is important for predicting future ecosystem responses to global change (Higgins *et al.* 2003). It has been found that the geographical distribution limit of *L. serriola* in Great Britain corresponds to climatic variables related to the warmth and dryness of the summer Prince *et al.* 1985. This strongly suggests that climate factors exert a dynamic control over the distribution limit of this species. For instance, temperature and photoperiod are likely two determinant factors controlling blooming Prince *et al.* 1978. Moreover, seed germination is affected by climatic variables such as rainfall and temperature (Carter & Prince 1985).

Seed production and germination are crucial factors of colonisation success for *L. serriola*. Using a population dynamics epidemic model, Carter and Prince (1981) simulated a small change in the production of seeds, showing that such a change was sufficient to change the balance of colonisation and extinction rates, and, therefore, explain a sharp biogeographic range limit. We thus hypothesize that climate has contributed to variations in the geographic range of *L. serriola* in the past, indirectly via the environmental variables that affect its establishment and/or directly through traits such as flowering time or seed set production.

We focus here on describing the spread of *L. serriola* in Europe and assessing the influence of climate on the distribution of the species. For this purpose, we compiled historical data from natural history collections as well as literature and related these to the past and present climate (e.g., Walther *et al.* 2005). Until now, no study has documented the spread of *L. serriola* in time and space or tested the hypothesis of a climatically induced distribution shift of *L. serriola* during the past few centuries in Europe. The results are discussed in the context of climate change and also consider the hypotheses regarding the increase in human disturbance.

MATERIALS AND METHODS

Species occurrence data

Data on the geographic distribution of *L. serriola* were assembled through a literature search as well as floristic and herbarium surveys. A floristic investigation of literature from 25 European countries resulted in 1365 occurrence records for *L. serriola*. The literature survey focused mainly on Germany, Austria and Great Britain (975 occurrences, 71% of the dataset). In addition, 24 herbaria from 15 other European countries were also screened, resulting in 1785 *L. serriola* herbarium sheets. The herbarium data were more equally distributed than the literature data amongst all European countries. Within this herbarium and literature data, we searched for the geographical coordinates of *L. serriola* localities. Six categories of precision were used: (i) exact coordinates, (ii) precision to 50 km, (iii) precision to 100 km, (iv) precision to 300 km, (v) precision to 500 km, and (vi) precision to more than 500 km. On maps, only locations with coordinates of up to 100 km precision for the herbaria and up to 300 km for the literature were considered. The indication of abundance (if present in the literature) was divided into six categories: ND – no data; A – absent; P – present without indication of abundance; R – very rare to scarce; S – scattered; and F – common to frequent. Herbaria sheets provided no information about abundance; therefore, only the "P" abundance category was used.

Distribution data for L. serriola

Maps of the spread of *L. serriola* in Central and Northern Europe were prepared based on occurrences using all herbarium data. We divided Europe into a 50 km x 50 km grid for this purpose. We considered a square to be colonised if it contained at least one occurrence. It has been shown that *Lactuca serriola* exhibits invasive behaviour (Cottet & Castella 1891; Jaquet 1930; Landolt 2001; Purro & Kozlowski 2003; Hooftman *et al.* 2006) and easily colonises disturbed areas; it has also been repeatedly observed that, at this scale, the species persists once established. Thus, the occurrences of *L. serriola* were added cumulatively to the sequence of maps. The southern limit of the study area is defined by the Pyrenees mountains, Southern France, and Northern Italy; it is limited to the east by the borders of Austria, the Czech Republic, Germany, and Scandinavia (Fig.1). Six time periods were defined. The first time period was 1765-1820, followed by six 30-year periods: 1821-1850, 1851-1880, 1881-1910, 1911-1940, 1941-1970, and 1971-2000. As previously mentioned, we had sufficient occurrences (more than 50 *L. serriola* literature locality indications) that were well-distributed over the time periods for three countries: Germany, Great Britain, and Austria. To follow the spread of *L. serriola* in these countries more accurately, we additionally divided the data according to the administrative units (counties for Great Britain and "Bundesländer" for Germany and Austria), abundance, and six time periods. In order to balance the data between categories, the time periods used were different than those used to build herbarium maps. The first time interval was between 1632 and 1800, followed by five 40-year periods: 1801-1840, 1841-1880, 1881-1920, 1921-1960 and 1961-2000. The herbarium and floristic occurrences of *L. serriola* were plotted on maps (except

for category A – absent). To test the role of climate in the distributional shift, we split the species data set from the 19th century into five periods of 20 years (1901 to 1920, 1921 to 1940, 1941 to 1960, 1961 to 1980 and 1981 to 2000). Hereafter, these time slices are called the 1910, 1930, 1950, 1970, and 1990 time slices, respectively. Other time periods could not be tested because of the lack of climate data before 1900.

Climate data

We used the CRU TS 2.0 data set (Climatic Research Unit, University of East Anglia, United Kingdom; http://www.cru.uea.ac.uk/~timm/grid/CRU_TS_2_0.html), which provides monthly means, maxima, and minima for temperature as well as for precipitation from 1901 to 2000 for a 0.5° x 0.5° grid resolution (i.e., about 55 km x 55 km). These data were obtained by the interpolation of observed climatic data from more than 20,000 weather stations all over the world (New *et al.* 2000b). We used a grid of points for Europe that contains 8566 points. Using the same time slices considered for species data, we calculated a set of eight climatic predictors comprising the mean sum of precipitation during the winter (December to February), spring (March to May), summer (June to August), and autumn (September to November), the mean temperature of the spring and summer, the mean number of months with a minimum temperature above 10°C (the temperature required for seed germination), and, finally, the mean number of months without frost.

Distribution modelling

Species distribution models (Guisan & Zimmermann 2000; Guisan & Thuiller 2005) were fitted using species occurrences and associated climatic data. Absence of the species was randomly sampled in areas where the plant has never been known to occur. First, a generalised additive model (GAM; Hastie & Tibishirani 1986; Yee & Mitchell 1991; Guisan *et al.* 2002) was fitted in R (R Development Core Team, 2005) using all occurrences jointly (pooled from different time periods) to determine the optimal climatic conditions for the species to grow. It was assumed that the climatic niche of the species was conserved across time. Then, for each time slice, GAMs were fitted following a k-fold cross-validation procedure (Hastie *et al.* 2001). The dataset was divided into five independent partitions corresponding to each time slice, then four of those were used to calibrate the model. Finally, the model performance was computed for the partition that had been eliminated. This procedure was repeated five times (once for each time slice), each time excluding the partition of the time slice to be evaluated. Moreover, within each time slice partition, the data was divided into ten independent sub-partitions. This allowed for the calculation ten independent measures of the model performance for each time slice. Model performance was assessed through the calculation of the *area under the curve* (AUC) of a *receiver operating characteristic* (ROC) curve (Fielding & Bell 1997; Pearce & Ferrier 2000). AUC values indicate the correspondence between the predictions and the

observations for the same time period. An AUC value of 1 means perfect agreement, an AUC of 0.5 means that predictions are not significantly different from random, and values between 0 and 0.5 means the model's predictions are worse than random. The following interpretation scale is typically used for ranking model predictions based on AUC (Swets 1988): > 0.9 good, 0.7-0.9 useful, and < 0.7 poor. The calibrated models were then used to generate a projection of suitable habitats under the climatic conditions of each time slice.

RESULTS

Colonisation of Europe from herbarium data

The changing distribution patterns are shown in Figure 1. The maps showed a northward spread of the species beginning in the early 19th century. Moreover, the results indicated that colonisation in Great Britain and Scandinavia moved across the area from southeast to the northwest. The first occurrence of *L. serriola* in Europe, according to the herbarium survey, was reported in Belgium in 1765. Until 1820, few records of the species were available; *L. serriola* was present in Belgium as well as in southern France and Germany (not shown). In Switzerland, prickly lettuce had colonised the country and was found both north and south of the Alps. Interestingly, it was already being found at high altitudes by 1802 (e.g., Zermatt, 1620m). The species was collected for the first time in southeast England (Northfleet) in 1830 and in Sweden (Lund) in 1828 (Fig. 1a). Therefore, the first steps of the colonisation of Great Britain and Scandinavia had already taken place at the beginning of the 19th century. By 1850, *L. serriola* was widespread in Central Europe (France, Belgium and Germany) (Fig. 1a). From 1851 to 1880, the number of records increased in Central Europe, and the spread northwards continued; prickly lettuce was recorded on the north-eastern coast of England (Hartlepool, Cleveland). In Sweden, the species progressed from the coast of the Baltic Sea to Ostergötland (Fig. 1b) and colonised regions below 100 meters. The next thirty years (1880 to 1910) were characterised by a westward spread; *L. serriola* progressed to the Norwegian border (herbarium record (HR) in 1903 in Langbro, Sweden) and settled in the centre of Norway by 1906 (Bratsberg). It colonised Wales, Cornwall, and Devon in Great Britain (Fig. 1c), staying below 100 meters and avoiding the Cambrian Mountains and the centre of the mainland. The first herbarium record in Denmark (Copenhagen) is dated 1881, after Swedish colonisation. The colonisation of the Netherlands started at the very beginning of the 20th century, with the first herbarium sheet dated 1904. Prickly lettuce then colonised the centre of Great Britain, the northwestern coast of Wales and England through 1940; it also migrated above 100 meters in Cirencester. In Sweden, *L. serriola* progressed northward as shown in Figure 1d, colonizing altitudes above 100 meters. From 1941 to the end of the 20th century, the species progressed 700 km northward along the Swedish coast (Fig.

1e, f). Occasionally, herbarium sheets provided information about the dynamics of populations and the circumstances in which *L. serriola* arrived. A herbarium sheet from Besançon (France) dated 1874 noted that prickly lettuce had been "abundant since the construction of the railway". In a herbarium sheet from 1915 collected in Somerton (GB), *L. serriola* was recorded as "ballast alien"; in a 1922 sheet collected in Penryndendreath (GB), it was recorded as "adventive by railway". In 1936, a sheet from Colchester observed: "not noticed for some years, abundant for this year".

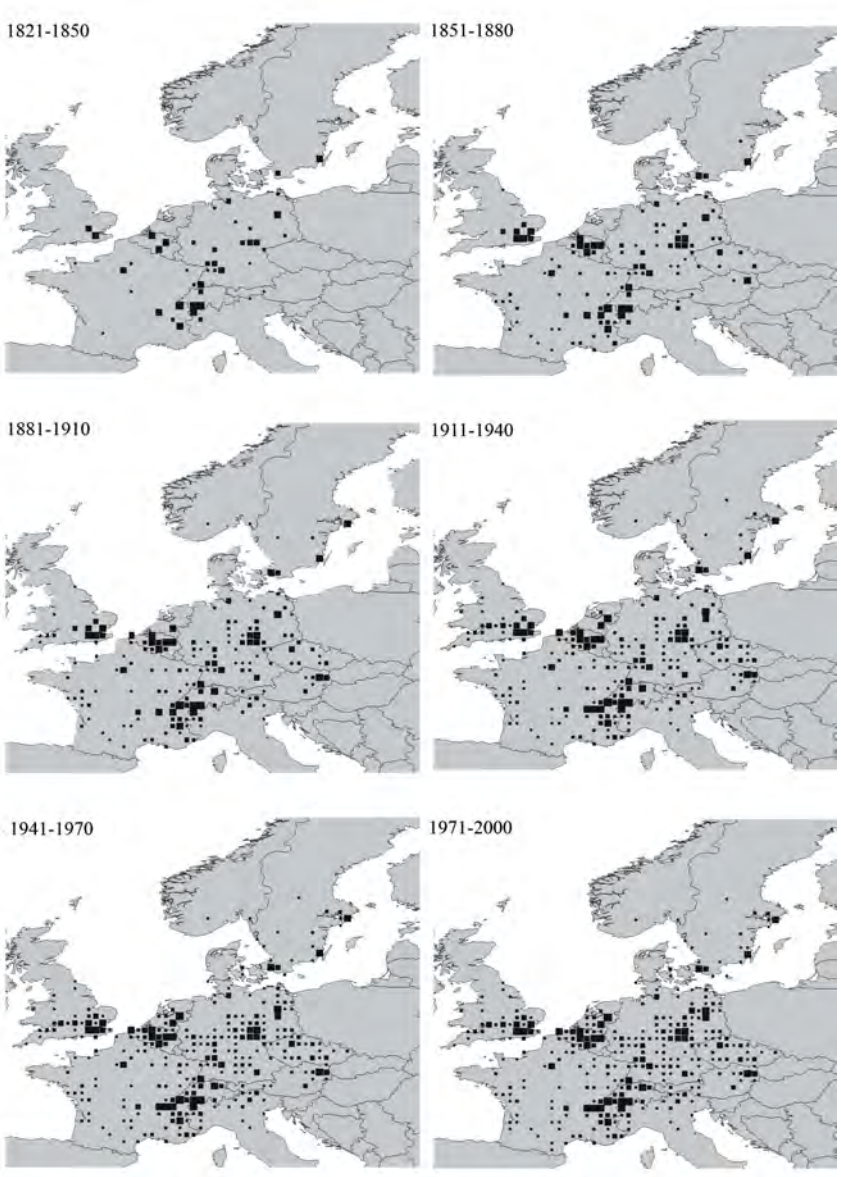

Fig. 1 - distribution pattern taken from herbarium data for (a) 1821-1850, (b) 1851-1880, (c) 1881-1910, (d) 1911-1940, (e) 1941-1970, and (f) 1971-2000. The square size increases with the number of occurrences.

Colonisation of Austria, Germany and Great Britain from floristic and herbarium data

Since both types of data (floristic and herbarium) are used together, records coming from our herbarium survey will be annotated as HR.

Austria is of particular interest due to its orographic relief. However, only two items dating from before 1840 are available (Fig. 2b). One is the absence of *L. serriola* in the "*Enumeratio Stirpium Plantarum quae sponte crescunt in agro Vindobonensi*" of Jacquin (1762) (Fig. 2a); the other is an HR of 1819 in Clausen (Tirol) (Fig. 2b). The mountainous region of the centre was colonised later. "Die Flora von Bad Aussee" indicated the absence of prickly lettuce in 1956, while it is currently mentioned as rare (Fig. 2f) (Rechinger 1956).

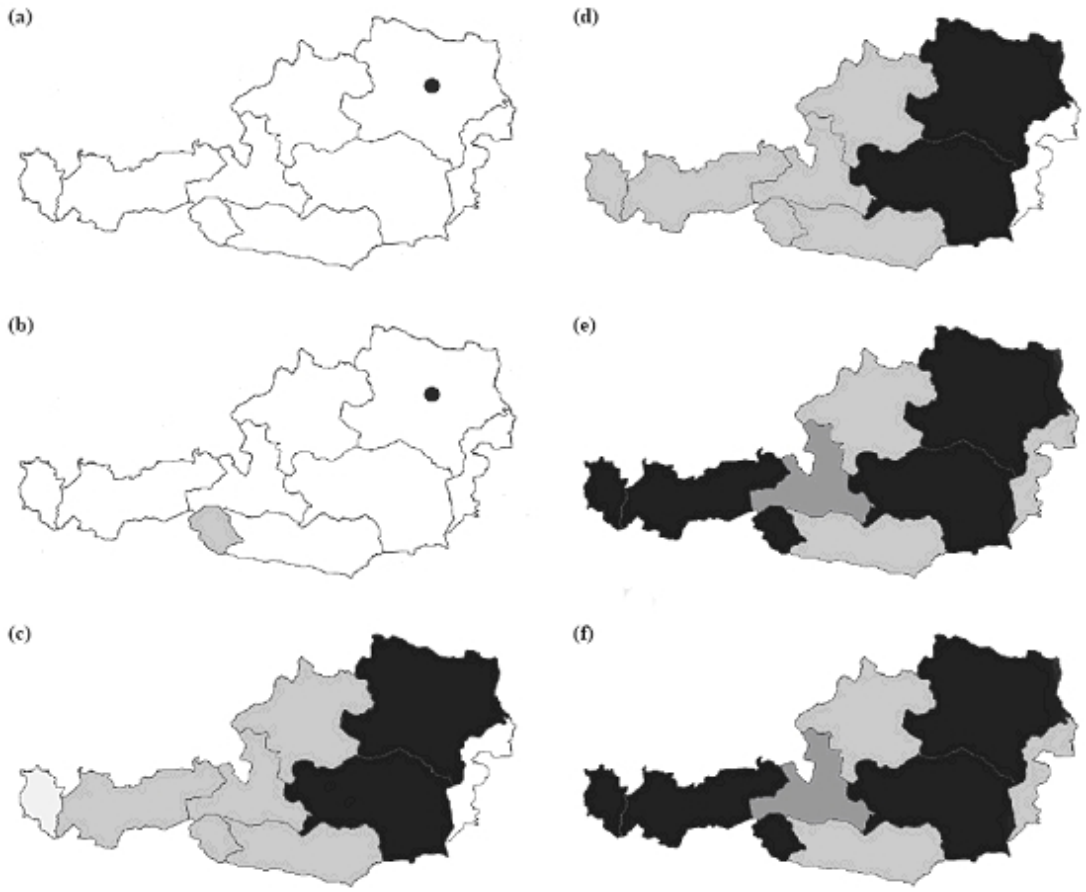

Fig. 2 - Distribution pattern of *L. serriola* in Austria taken from literature data for (a) 1632-1800, (b) 1632-1840, (c) 1632-1880, (d) 1632-1920, (e) 1632-1960, and (f) 1632-2000. Dots correspond to an absence of the species. The gray shade corresponds to the abundance of the species: white = no data, light gray = present without indication of abundance, gray = very rare to scarce, dark grey = scattered and black to common to frequent.

Germany was rapidly colonised. The species was mentioned for the first time in the Flora Halen in 1761 (Leyser 1761). The first HR was in 1819 in Plauen-Dresden. By 1800, *L. serriola* was found everywhere except in Saarland (southwest Germany); its absence there was probably due to lack of data and not to any real absence (Fig. 3a). From 1800, its abundance increased from the south to the north (Fig. 3b, c), until Germany was almost totally colonised by the beginning of the 20th century (Fig. 3d).

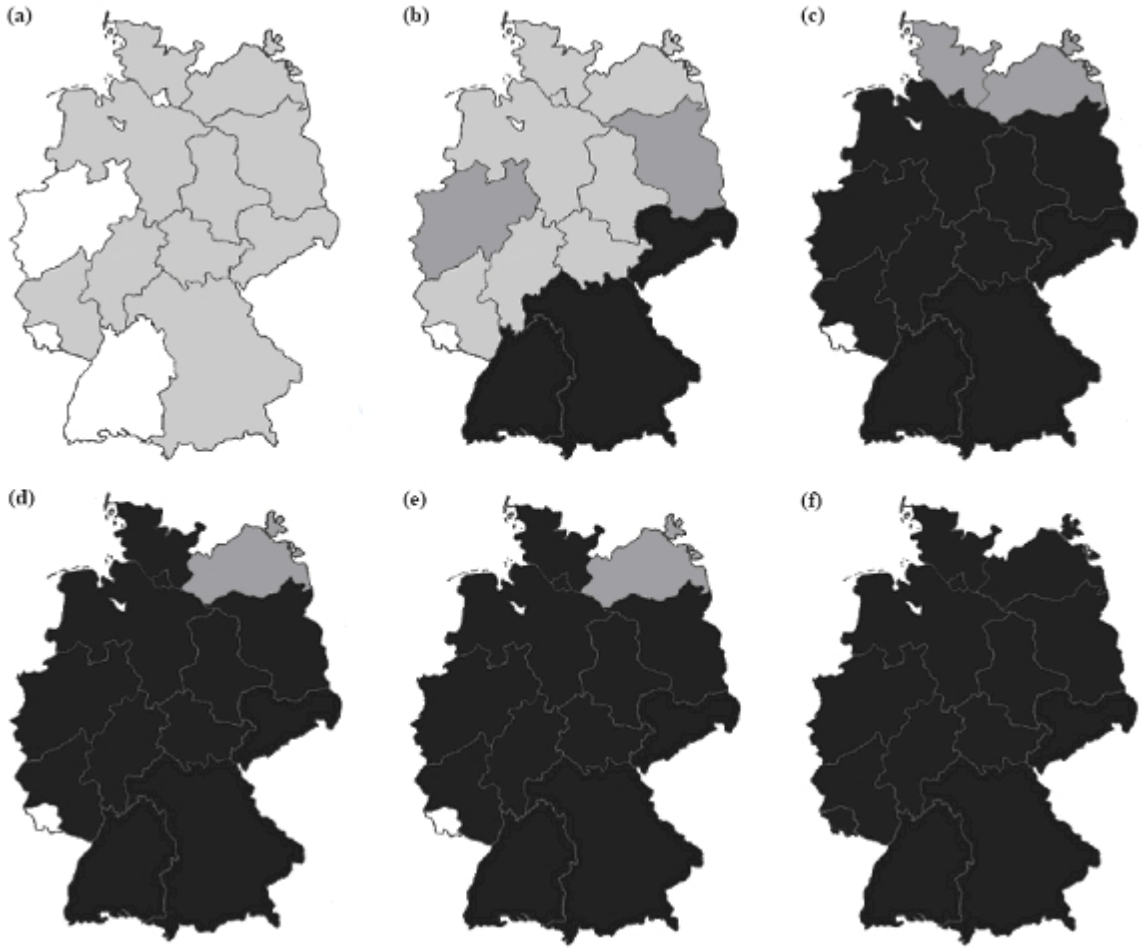

Fig. 3 - Distribution pattern of *L. serriola* in Germany taken from literature data for (a) 1632-1800, (b) 1632-1840, (c) 1632-1880, (d) 1632-1920, (e) 1632-1960, and (f) 1632-2000. Dots correspond to an absence of the species. The gray shade corresponds to the abundance of the species: white = no data, light gray = present without indication of abundance, gray = very rare to scarce, dark grey = scattered and black to common to frequent.

Great Britain is presented in Figure 4. The oldest mention of *L. serriola* is a record of 1632 Flora of Middlesex in 1869 (Trimen 1869). However, Prince and Carter (1977) stated that the general practice was to call unlobed-leaved plants *L. virosa*; therefore, they concluded that most pre-1930 records might easily refer to *L. serriola* as to *L. virosa*. According to Oswald (2000), "the confusion occasioned by the failure of most British Flora of the nineteenth century to recognise that *L. serriola* can have simple leaves has led to some uncertainties about the past status of this species and *L. virosa* in Britain". The expansion of *L. serriola* in Great Britain started from the southeast. In 1785, *L. serriola* was mentioned in the Flora Cantabrigiensis (Relhan 1785) of the Isle of Ely (Fig. 4a). Until 1880, *L. serriola* remained confined to the southeast, spreading from the initial record location to reach Hartlepool (Cleveland) in 1866 (HR) (Fig. 4b). Increasing records at the end of the 19th century indicate the colonization of eastern and northeastern England (Fig. 4c). In 1889, the first HR for Wales (Bangor, Wrexham) was registered. In the Flora of Glamorgan (Wade 1994), *L. serriola* is mentioned in Porthcowl in 1897. Then, in 1902 and 1907, prickly lettuce was recorded in Pembrokeshire and Cardiff, respectively. In 1901, *L. serriola* was mentioned as casual in the Flora of Cornwall (Davey 1909), and an HR was registered in Par in 1908. It was collected along a railway bank near Newton Abbot (Devon) in 1909 (Fig. 4c). At the beginning of the 20th century, prickly lettuce expanded to the western part of the mainland (Fig. 4d). Intriguingly, at this time, *L. serriola* was mentioned as absent from the central part of the flora of Wiltshire (Preston 1888), Bournemouth (Linton 1919) and Warwickshire (Bagnall 1891). Thereafter, it colonised the southern and central parts of England and finally spread to Scotland, where the first record in the Flora of Angus appeared in 1967 (Ingram 1981; Fig. 4e, f). Since 1950, *L. serriola* increased in abundance in the colonised areas, such as Warwickshire, in which prickly lettuce was recorded for the first time in 1959 and the populations subsequently exploded (Bowra 1992). Similar expansions are described for the Netherlands (Hooftman *et al.* 2006) and Switzerland (Cottet & Castella 1891; Jaquet 1930; Landolt 2001; Purro & Kozlowski 2003), and are probably occurring in many other countries.

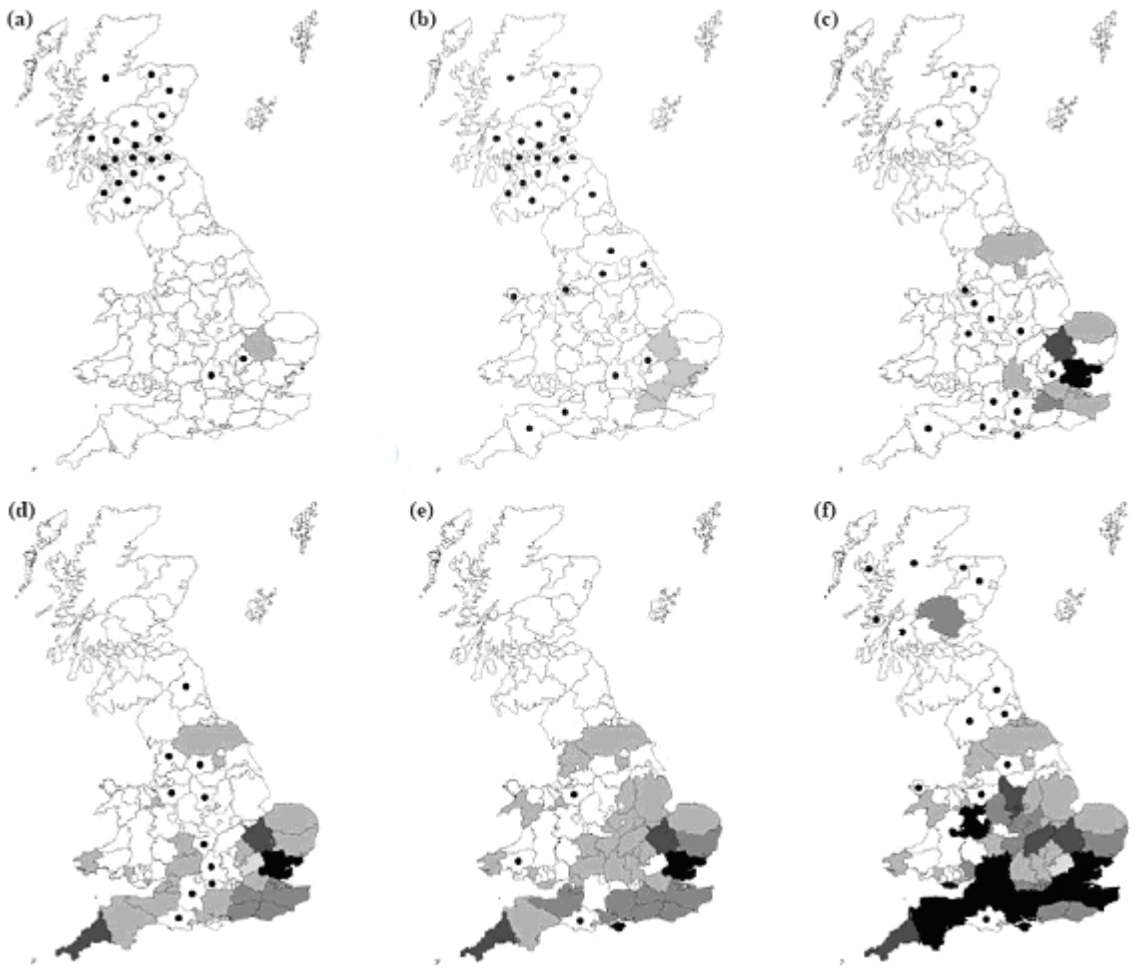

Fig. 4 - Distribution pattern of *L. serriola* in Great Britain taken from literature data for (a) 1632-1800, (b) 1632-1840, (c) 1632-1880, (d) 1632-1920, (e) 1632-1960, and (f) 1632-2000. Dots correspond to an absence of the species. The gray shade corresponds to the abundance of the species: white = no data, light gray = present without indication of abundance, gray = very rare to scarce, dark grey = scattered and black to common to frequent.

Distribution modelling & climate-induced shift

The model using all occurrences retained seven out of eight environmental predictors, each of these statistically significant in explaining the distribution of the species. The model explained 56% of the variance of the data, indicating that meaningful climate predictors were incorporated in the model. The climatic conditions that were found to favour the presence of *L. serriola* in Europe were: temperatures in the spring of >5°C, temperatures in the summer between 7 and 15°C, two to ten months of temperatures >10°C, less than 300 mm of rain in the winter, more than 300 mm of rain in the spring and summer, and less than 200 mm of rain in autumn (Fig. 5).

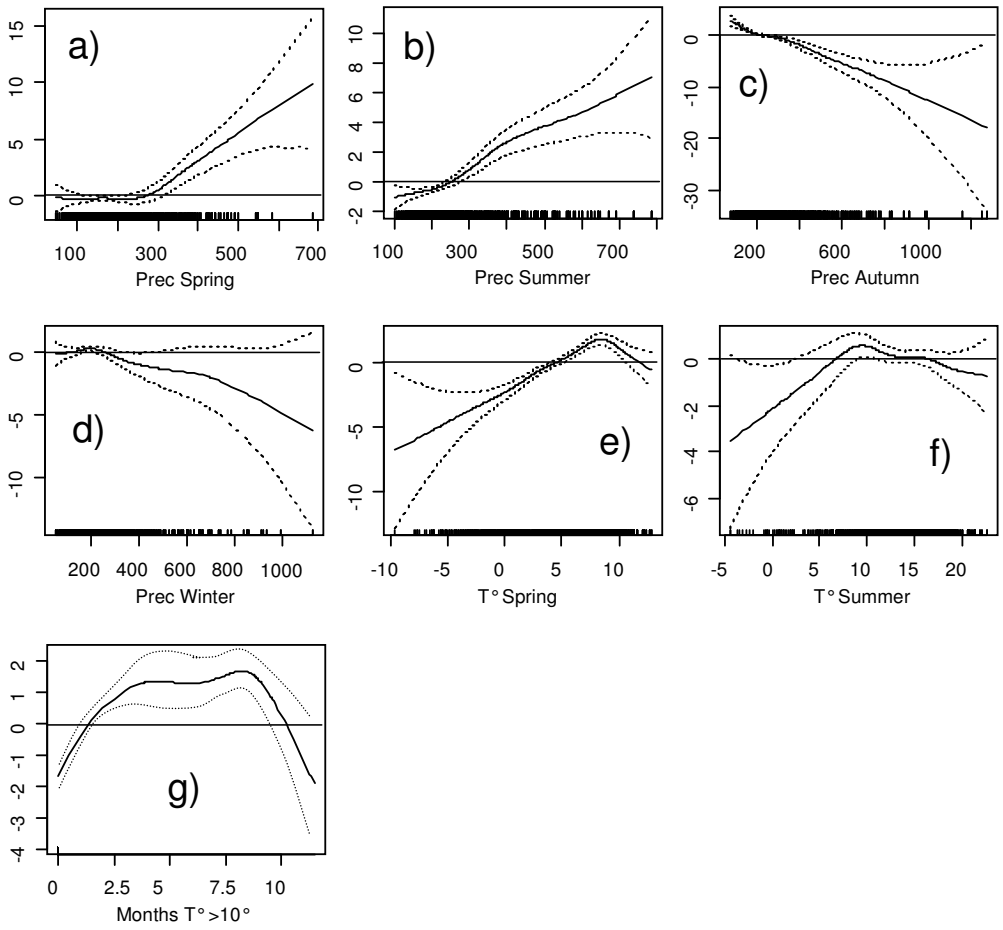

Figure 5 - GAM response curves. Plots of response curves of the GAM model, including all occurrences, are shown for the amount of seasonal precipitation (a-d), mean temperature in spring and summer (e-f) and the number of months with temperatures higher than 10°C (g). The response curves for each climatic predictor are shown here in the scale of linear predictors. Curves above zero indicate climatic situations that increase the probability of the species occurring.

The results from the k-fold validation procedure illustrate the ability of *L. serriola* to track climate change during the last century. Figure 6 (a-e) illustrates the predictions of areas suitable for colonisation and the known occurrences for each time period. At the beginning of the century, the species was predicted to have a high probability of presence in all of central Europe except the Mediterranean coast, the Aquitaine Atlantic coast, a large part of Scotland, and Scandinavia. Note, however, that the southern Swedish coast of the Baltic Sea had intermediate values of probability. In the subsequent time periods up until 1970, the suitable habitats for the species shifted slightly north, with areas in Scotland and South Scandinavia becoming more suitable (Fig. 6a-d). During the most recent time period, an enhanced northern distributional shift was predicted, with large parts of Scotland and Scandinavia becoming suitable (Fig. 6e); however, these new areas are not yet occupied by *L. serriola*.

The relationship between the potentially suitable areas and actual occurrence of the species is further illustrated with AUC values on validation datasets (Fig. 6f). From 1910 to 1970, AUC values fell between 0.85 and 0.90, indicating high levels of agreement between the predicted and observed data (Table 1). However, in 1990, the AUC value decreased to 0.47, indicating essentially random conformity between predicted and observed data. This result is due primarily to the large areas in Sweden that were predicted to be suitable, but had not yet been colonised by the species.

Table 1 - Performance of Generalised Additive Models. The AUC calibration values correspond to the models' performances on the four data partitions used for calibration (not including the focal period). The evaluation values correspond to the models' performances on the remaining data partition. The values shown here correspond to the average of the AUC calculated for ten sub-partitions.

Time slice	**1910**	**1930**	**1950**	**1970**	**1990**
Mean AUC Calibration	0.979	0.983	0.979	0.983	0.981
Mean AUC Validation	0.882	0.892	0.903	0.851	0.473

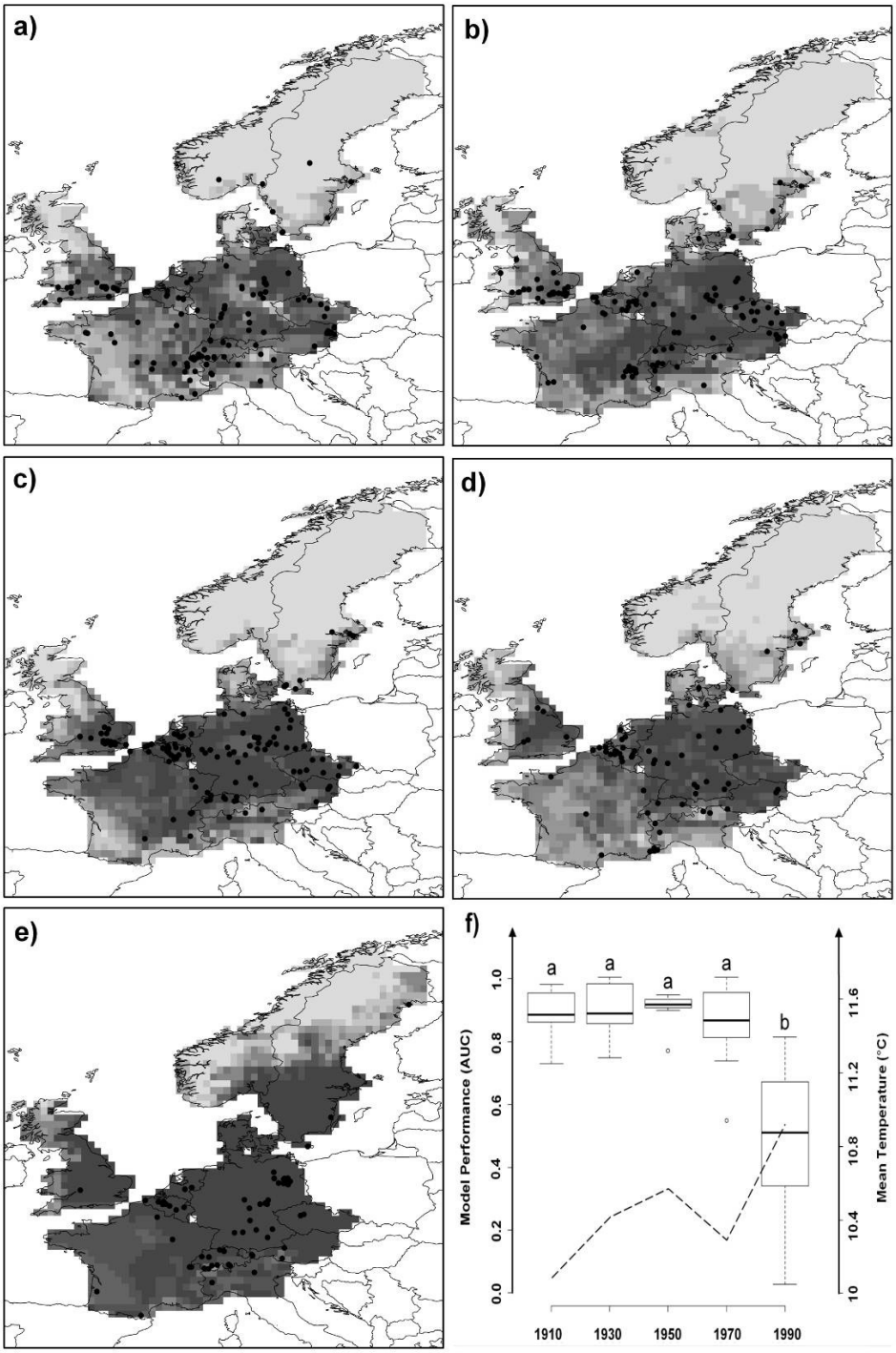

Figure 6 - Climate-induced distributional shifts. Light and dark grey correspond to areas with low suitability and high suitability, respectively, for *L. serriola*. Dots illustrate occurrences, while crosses correspond to absences (places where the species was never shown to occur). Maps (a-e) show the potential distribution of the species for the 1910, 1930, 1950, 1970 and 1990 time periods. Boxplots (f) show agreement between potential distribution maps and actual occurrences data. The dashed line indicates the mean temperature in the study area for each time period. The rise of temperature in the last two decades coincides with the low agreement between known and potential distributions.

DISCUSSION

Using natural history collection data to quantify range change

For this study, it was hypothesized that the effects of climate change are already visible for prickly lettuce, and, in particular, that these effects caused the distribution of the species to shift toward the poles. Using herbarium specimens introduces several biases including problems identifying the plant in the field, accessibility of the sampling sites, and variability of the sampling effort over a long period of time. Some groups of species (e.g., aliens or garden escapes) were recorded less consistently (Delisle *et al.* 2003), whereas other groups were more frequently recorded (rare, endangered or conspicuous species). Nevertheless, our floristic and herbarium data revealed consistent trends: the colonisation of Northern Europe by *L. serriola* happened in the end of the 18th century and the first decades of the 19th century. At the same time, *L. serriola* increased its abundance in Central Europe. By the beginning of the 20th century, the species had colonised most of Europe. Locally, westward migration of the species was observed, moving from Sweden to Norway, South England to Wales, Wales to Ireland (first record in 1996; Preston *et al.* 2002), and from the eastern part of Austria to the west. Our dataset does not allow us to draw any inferences about the colonisation of the Iberian Peninsula, either from France or from North Africa. In Scandinavia, although the first steps of colonisation took place in the south relatively early, the species is still not yet widespread. Presently, the northern boundary of the distribution area runs near 66° north, through Sweden.

Colonisation of lower altitudes and flat countries took place more rapidly than colonisation of mountainous regions. Mountains are significant obstacles for plant migration, making transportation from one valley to the next more likely to take place by human intervention. In southern Europe, *L. serriola* has generally been observed at higher altitudes than in northern areas, although it has been collected at 680 meters in Bratsberg, Norway. *L. serriola* is now abundant in Central Europe (Lebeda *et al.* 2001) and England (Bowra 1992) and is still in a dynamic state of colonisation. For instance, Hooftman *et al.* (2006) showed that *L. serriola* is spreading rapidly through the Netherlands. In Switzerland, the species was recorded as rare before 1900, but had totally colonised the country by the end of the 20th century.

Different factors such as global change (including climate change), increases in disturbances caused by the development of trade routes and urban areas as well as the intensification of transportation may have contributed to the spread of *L. serriola*. In the following section, we discuss how each factor might have influenced the distribution of prickly lettuce. Assessing their relative importance is difficult, as these factors may interact with each other.

Climate change

The only studies that have investigated the relationship between the distribution of *L. serriola* and climate were carried out in Great Britain. Prince & Carter (1985) concluded that the response to climate observed in *L. serriola* beyond its distribution limit was too small for the limit to be explained in terms of failure of the individual plants. In controlled environments, they found that the rate of development toward flowering was strongly related to temperature. Flowering was always faster within the distribution limit than beyond it, but no difference in fecundity was detected between the areas. Nevertheless, the authors stressed that even if undetectable physiological responses slightly reduced the performance of the plant at the individual level, the secondary effects induced on the populations or the tertiary effects on the dynamics of metapopulations could be significant. Carter and Prince (1985) concluded that extremely subtle climatic changes are responsible for controlling *L. serriola*. For instance, hot, dry weather in the summer may favour the fruiting and/or the establishment of the plant in the following autumn. Even in the absence of any direct physiological effects, climate can have a significant effect on the persistence of *L. serriola*; for example, lower rainfall might lead to slower closure of open habitats suitable for prickly lettuce. Thus, some aspects of the climate likely exert dynamic control over the distribution of prickly lettuce. Thus, when a year is climatically exceptional, *L. serriola* may extend its geographical and altitudinal ranges (Carter & Prince 1985; Prince & Carter 1985). Climatic factors such as temperature, photoperiod, and precipitation, which influence the environment and the establishment of the plant and/or its flowering and fruiting, may have a significant effect on the ability of individual plants to build viable populations and colonise new sites.

Modelling the distribution of the climatic niche of the species shows that from the beginning of the century to the late 1970s, the distribution of *L. serriola* corresponds to the climatically suitable sites available. This indicates that the species distribution range was in equilibrium with its climatic niche. The highest increase in temperature in the northern hemisphere during the last century actually occurred during the last two decades (Brohan *et al.* 2006) and coincides with a sudden increase in areas predicted to be climatically suitable for *L. serriola*. However, we were not able to show a significant relationship between this increase and the known species distributional range change towards northern latitudes. This may signify that climate changes are happening too fast for *L. serriola* to track them; however, it does suggest the potential dispersion range of the species in the future. Another interpretation of this inadequacy would be that a time lag phase is necessary for the species to develop adaptive mutations or receive additional gene flow, or for migrants to overcome competitive constraints (Sakai *et al.* 2001; Levin 2003). An alternative explanation would be that the non-significant relationship found between climate change and dispersion in the last time series could be due to an underestimation of the actual dispersion of the species. Botanists tend to collect more

rare species. It is therefore probable that the sampling effort during the two last decades became less important in northern Europe as *L. serriola* became more abundant there.

The climate models predict a slight decrease in habitat suitability in the middle of the century at the southern limit of the distribution (southern France). This decrease is not confirmed by current knowledge about the distribution of the species in this region. This decrease in habitat suitability is obviously a modelling artefact resulting from our failure to account for the entire distribution of the species when calibrating the model, as Spanish populations were not included in the analysis. If such southern populations had been taken into account, this region would probably have been situated in the middle of the response curve and would have been less affected by the climate shift.

Our models also did not correctly predict the presence of *L. serriola* in northern Scandinavia at the beginning of the century. One possible explanation is that our resolution (50 km) did not permit the detection of all the favourable microsites for the species. Another explanation is that most of the herbarium sheets in Scandinavia were collected around urbanised centres, where temperatures are always higher than in the natural environment. Our model is generated using mean monthly climate values that cannot reflect short-lived climatic events or extreme conditions that may have an important influence on population dynamic (e.g., a very hot and dry summer that affects the autumnal establishment of the plant).

Distribution limits can also extend without relation to the climate or biology in a climatically favourable zone. For instance, in epidemic models, the increase of susceptible sites near to, but beyond, a plant's distribution limit could displace its climatic equilibrium distribution limit without changes in the climate or in the biology (Carter & Prince 1981). Thus, the availability and accessibility of colonisable habitats are also important factors for understanding the spread of a species. It is therefore of great importance to consider the interaction between landscape structure and climate change when trying to understand a plant's distribution limit in time and space.

Disturbance, habitat availability and dispersal

Non-climatic influences of global change, such as habitat modification, may dominate locally and are of great importance for the spread of species (Parmesan & Yohe 2003). No data are available yet to quantify the impact of a disturbance on the population dynamics of *L. serriola*, but it has been noted that a population generally establishes within one year. Its persistence depends then on the continued availability of open areas uncolonised by plants in later stages of succession (Carter & Prince 1985). The influence of disturbance on population expansion as well as seed germination and establishment has already been shown for other ruderal plants (Bossard 1991; Steinlein *et al.* 1996). The expansion of *L. serriola* in anthropogenic urbanised ecosystems is discernable from occurrence data (Prince & Carter 1985; Bowra 1992; Hill *et al.* 2002) and historical records.

The opportunity to be transported from one available habitat to another is a key factor for enabling colonisation. As it has already been stressed, the modern expansion of international traffic is likely to be accompanied by an expansion in the range of aggressive road-side weeds like *L. serriola* (Clifford 1959). These species should be the first to shift their ranges (Dukes & Mooney 1999; Parendes & Jones 2000; Landolt 2001). In this context, Central and Northern Europe witnessed a tremendous development in man-made habitats and transport networks during the past 250 years (construction of motorways, rails, airports, canals, built-up areas, and agriculture), permitting *L. serriola* to expand rapidly. Indeed, roads and railways interconnect anthropogenic ecosystems and facilitate the expansion of plant species such as *L. serriola*, which possess life history traits that confer good colonisation abilities and rapid generation turn-over (Forman & Alexander 1998; Lebeda & Astley 1999; Trombulak & Frissell 2000; Dolezalovà *et al.* 2001; Landolt 2001; Hill *et al.* 2002; Kowarik 2003; Lebeda *et al.* 2004). Roads and railways provide corridors along which the species can migrate (Parendes & Jones 2000). Indeed, the seeds can be easily transported from one site to another through, for instance, the mud attached to cars and trucks and/or by transport of various materials over long distance (Pitelka *et al.* 1997).

Occupation of new regions occurs through passive seed dispersal and the establishment of seedlings in sites where conditions are suitable (Davis & Shaw 2001). However, the ability of species to migrate rapidly across large distances might be driven primarily by infrequent long-distance dispersal events that are difficult to quantify (Higgins & Richardson 1999; Malcolm *et al.* 2002). Prince *et al.* (1985) already underlined the importance of long-distance seed-dispersal events for building new *L. serriola* colonies, which is impossible to prove from our results. However, several first records of the species at short time intervals, but long distances from each other, could indicate that such events did happen. uch long dispersal events could lead to the formation of outlier populations, exerting a continual outward pull (Cain *et al.* 2000a) and resulting in a more rapid migration than that along a single population front (rapid in-filling of the intervening space). However, outlier populations may fail to build viable populations, making the frequency of introduction and the number of seeds introduced beyond the distribution limit of great importance. In this context, the growth in the volume of trade along commercial routes greatly increases the frequency with which introductions are repeated (Perrings *et al.* 2005). Moreover, the seed bank formed from one year can substitute for a lack of immigrant seeds the next year; one single plant of *L. serriola* can produce a huge number of wind-dispersed seeds and potentially form a short-term (one to three year) seed bank (Weaver & Downs 2003).

The dual influences of human habitat modification and anthropogenic climate change likely favour mobile species (Warren *et al.* 2001); the combination of both factors probably favoured the rapid spread of *L. serriola.*

CONCLUSION

Our results highlight the possible impact of components of global change, such as climate warming or habitat disturbance, on the expansion of Mediterranean plant species like *L. serriola* toward northern regions in Europe. Our work shows the importance of floristic and herbarium data for a global understanding of the spread of a species. Historical data can thus form the basis for detailed studies and for the management of modern environmental issues, such as the influence of changing environmental factors on the response of a species, invasion or biodiversity changes. Validating models through comparison of observed range shifts against model predictions is a key step forward in order to improve projections of climate change on species and their viability (IPCC, 2007). Finally, our study, using *L. serriola* as a model species for studying colonisation routes in Europe, will help to better predict and manage future expansion of the species. These data could also serve as a basis for further molecular studies on migration routes and genetic diversity of this species in Europe

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Chapter 4.2 Evidence of climatic niche shift during biological Invasion

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ABSTRACT

Niche-based models calibrated in the native range by relating species observations to climatic variables are commonly used to predict the potential spatial extent of species' invasion. This climate matching approach relies on the assumption that invasive species conserve their climatic niche in the invaded ranges. We test this assumption by analyzing the climatic niche spaces of Spotted Knapweed in western North America and Europe. We show with robust cross-continental data that a shift of the observed climatic niche occurred between native and non-native ranges, providing the first empirical evidence that an invasive species can occupy climatically distinct niche spaces following its introduction into a new area. The models fail to predict the current invaded distribution, but correctly predict areas of introduction. Climate matching is thus a useful approach to identify areas at risk of introduction and establishment of newly or not-yet-introduced neophytes, but may not predict the full extent of invasions.

Keywords: Biological invasion, *Centaurea maculosa*, climate matching, niche conservatism, niche shift, niche-based models, Spotted Knapweed

CONTRIBUTIONS TO THE PROJECT

I developed a contact network for gathering occurrence data of Spotted Knapweed in Europe and North Western America and contributed to a thorough field sampling of the species in those areas during summer 05. I developed and performed the analyses of the niche of the species in the climatic and geographic space. I did a survey of the literature, analyzed the results, wrote the manuscript and leaded the reviewing.

INTRODUCT ION

Niche conservatism, the tendency of species to maintain ancestral ecological requirements (Wiens & Graham 2005), is a necessary assumption in niche-based geographical predictions of biological invasions. Under this pivotal assumption, invasion ranges can be predicted with models fitted with data from the native range (Peterson & Vieglais 2001). Anticipating future distributions of invasive species is essential for prioritization, early detection and control. Niche-based models (Guisan & Thuiller 2005) have been used to predict the invasion extents of various organisms, including beetles (e.g. Peterson & Vieglais 2001), fishes (e.g. Chen *et al.* 2007), birds and plants (e.g. Peterson & Vieglais 2001; Peterson *et al.* 2003; Thuiller *et al.* 2005c). Although all of these studies assume niche conservatism in their projections, they usually do not put emphasis on quantifying possible niche shifts (e.g. percentage of divergence) as an alternative hypothesis.

Two distinct formulations of the niche conservatism concept exist that focus on either a single species or on sister taxa. In the latter multiple species situation, niche conservatism is tested by reconstructing the phylogeny of a group of related species and by testing if sister taxa are more ecologically similar than expected by random evolutionary divergence (Prinzing *et al.* 2001; Ackerly 2003; Losos *et al.* 2003). In the single species situation discussed here, niche conservatism is assessed in time or space (Martinez-Meyer *et al.* 2004) aiming to test whether a single taxon has retained similar ecological requirements across different geographical ranges or time periods.

Both niche conservatism and niche shifts can have important implications for understanding speciation, effects of climate change and biological invasions (Wiens & Graham 2005). For instance, niche shifts are important in sympatric speciation (Losos *et al.* 2003; Levin 2005), whereas niche conservatism can explain allopatric speciation (Huntley *et al.* 1989; Peterson & Holt 2003; Wiens & Graham 2005). Niche conservatism in many species may have led to migration in response to past climate changes, and thus might drive future responses as well (Martinez-Meyer *et al.* 2004), but climate change may also create opportunities for niche differentiation and evolution, e.g. when empty niches are created at rear edges of range shifts (Ackerly 2003).

In the case of biological invasions, two factors can cause exotic species to expand beyond their predicted climate envelope in the invaded range, thus exhibiting niche differentiation between native and introduced ranges. Such niche differentiation, in effect, may result from changes in either the fundamental niche of the species (i.e. the sum of ecological situations where populations of an organism can have a positive growth; Holt *et al.* 2005b), or the realized niche (i.e. the fundamental niche constrained by biotic interactions; Chase & Leibold 2003; Guisan & Thuiller 2005) or both.

First, release from biotic and abiotic constraints, such as the absence of competitors, predators or pathogens

(Mitchell & Power 2003; Torchin *et al.* 2003; Callaway & Maron 2006; Mitchell *et al.* 2006) or the availability of empty niches (Hierro *et al.* 2005) may lead to a niche shift in the introduced range. These causes affect the realized niche of the species. Second, an exotic species may evolve in the new range allowing it to expand into new niches. Evolutionary changes can occur through genetic drift or through selection in the introduced range (Müller-Schärer *et al.* 2004; Müller-Schärer & Steinger 2004), thus affecting the fundamental niche of the species. Evolutionary processes may take place during and after the time lag generally observed between introduction and the spread of invasive species (Kowarik 1995; Dietz & Edwards 2006), leading to subsequent demographic and range expansion. Hence, both ecological and evolutionary changes can potentially allow a plant to shift into new habitats and climate zones, and an observed shift can equally result from a change of the realized niche, of the fundamental niche, or of both.

Empirical field evidence of climatic niche shifts during biological invasions is still lacking. Experimental studies (e.g. Sexton *et al.* 2002; DeWalt *et al.* 2004; Maron *et al.* 2004) provide some support for such processes but have limitations. For instance, growth chambers experiments (e.g. Sexton *et al.* 2002) underestimate biotic interactions effects and their conclusions are only applicable to the fundamental niche of the species. Field studies (e.g. DeWalt *et al.* 2004) and common garden experiments (e.g. Maron *et al.* 2004) only include a very limited number of experimental sites and are most often focusing on the introduced range (Hierro *et al.* 2005). Studies investigating the realized niche of invasive species at biogeographical scales in both native and non-native ranges are necessary to quantify niche shifts accurately (Hierro *et al.* 2005). Reciprocal geographic predictability between the two ranges is one approach that has been suggested (Wiens & Graham 2005).

We conducted a large biogeographical study on the herbaceous spotted knapweed *Centaurea maculosa* L. This is an excellent species for testing the hypothesis of niche shift associated with biological invasions. It was first introduced in the 1890s from Europe into western North America, where it now infests over 3 x 10^6 ha of rangeland and pasture in 14 states and two Canadian provinces (Story *et al.* 2006) and may cause an estimated >150 x 10^6 US$ in economic damage each year (Story 2002). In both ranges, the species occurs in disturbed and natural grassland habitats, but it rarely reaches densities in the native range as high as observed in the invaded range (Müller 1989a). The species has not undergone any artificial selection nor hybridization to improve ornamental traits, which ensures that an observed niche shift is likely to result from natural processes.

We examined the climatic niche of *C. maculosa* in its native and invaded ranges to test whether the species exhibits niche conservatism, a pivotal assumption for enabling reciprocal geographic predictability between the two ranges. We used comprehensive occurrence data from all regions where the species is present in Europe and western North America, fully covering the relevant large climatic gradients and eliminating risk of fitting truncated response curves and thus only partially

fitting models to the species' realized niche (Thuiller *et al.* 2004c). The niche we define here thus reflects all climatic conditions where the plant can survive and reproduce in the presence of biotic interactions. We are not aware of comparably robust data for any other invasive species across two ranges.

MATERIALS AND METHODS

Species occurrence data collection

We collected all occurrences available for *Centaurea maculosa* Lam. (syn C. stoebe L.) in Europe and western North America. The taxonomic treatment of *C. maculosa* is unclear (Ochsmann 2000, Flora Europaea database 2007; http://rbg-web2.rbge.org.uk/FE/fe.htm). Therefore, we considered *C. maculosa* s.l. as the taxonomic entity. Two subspecies have been suggested for the species, associated with its two ploidy levels*: C. stoebe* L. subsp*. stoebe* (diploid) and *C. stoebe* L. subsp. *micranthos* (Gugler) Hayek (tetraploid; Ochsmann 2001). Although it was hypothesized that the species' distribution was restricted to south-central and south-east Europe at the time of introduction to North-America (Ochsmann 2001), models fitted based on a more restricted native range would result in a larger niche shift, making our approach conservative. The same applies for a more narrow taxonomic treatment.

Occurrences for Europe were acquired through herbarium data and completed by several field surveys done by the two first authors during summer 2005. For western North America, occurrences were obtained through different land management and state agencies. Only occurrences with locational accuracy equal to or finer than the resolution of climate data were kept. The final database consisted of 275 occurrences for Europe and 1685 for western North America.

Climate data

We used global climatic data sets used in previous studies of plant distributions (Guisan & Thuiller 2005; Thuiller *et al.* 2005b) that have been recommended for cross-continental tests of niche conservatism (Wiens & Graham 2005). As the choice of climatic data may influence the result, we performed separate series of analyses based on three existing global coverage climate maps, CRU 0.5° (New *et al.* 1999), CRU 10′ (New *et al.* 2000b) and WORLDCLIM (Hijmans *et al.* 2005) (Table 1). As these sets of maps were independently prepared at three different resolutions (10′ and 0.5° and 1 km respectively), we ensured the replicability and reliability of the analyses.

The 19 original WORLDCLIM bioclimatic variables were used without modifications. From the original CRU 10° base maps we derived a data set containing eight bioclimatic variables commonly used in other studies. A data set of five coarser annual variables from CRU 0.5° was also tested (Table 1).

Table 1 - List of predictors available in each climatic data set

Data set	Variable	Description
WORLDCLIM	BIO1	Annual mean temperature
	BIO2	Mean diurnal range
	BIO3	Isothermality
	BIO4	Temperature seasonality
	BIO5	Max temperature of warmest month
	BIO6	Min temperature of coldest month
	BIO7	Temperature annual range
	BIO8	Mean temperature of wettest quarter
	BIO9	Mean temperature of driest quarter
	BIO10	Mean temperature of warmest quarter
	BIO11	Mean temperature of coldest quarter
	BIO12	Annual precipitation
	BIO13	Precipitation of wettest month
	BIO14	Precipitation of driest month
	BIO15	Precipitation seasonality
	BIO16	Precipitation of wettest quarter
	BIO17	Precipitation of driest quarter
	BIO18	Precipitation of warmest quarter
	BIO19	Precipitation of coldest quarter
CRU 10´	aet/pet	Ratio of actual to potential evapotranspiration
	pet	Potential evapotranspiration
	std_prec	Annual amount of precipitations
	tmin	Annual variation of precipitations
	tmp	Minimum temperature of the coldest month
	tmax	Annual mean temperature
	gdd	Maximum temperature of the warmest month
		Growing degree-days above 5 °C
CRU 0.5°	tmin	Minimum temperature of the coldest month
	tmp	Annual mean temperature
	tmax	Maximum temperature of the warmest month
	rad	Annual amount of radiations
	prec	Annual amount of precipitations

Testing for climatic niche conservatism

Principal component analysis (PCA) was run to compare the position of occurrences from the native and invaded range in the climatic space, using the ade4 library in the R software. Occurrences were weighted to ensure an equal representation of the two ranges in the analyses. The magnitude and statistical significance of the niche shift between the two occurrence clouds in the PCA graph were assessed using a between-class analysis, yielding a between class inertia percentage (Doledec & Chessel 1987). We further tested this ratio with 99 Monte-Carlo randomizations (Romesburg 1985). To locate the climatic position of the species inside European and Western North American climates, we projected all pixels of study areas in the same PCA climatic space.

Fitting niche-based species distribution models

It has been recently shown that different modeling techniques calibrated on the same species can produce different results (Thuiller *et al.* 2004c; Araujo *et al.* 2005c). As recently suggested, we use a combination of these techniques to adjust for the inherent uncertainty from these models and to find the optimal solution from an ensemble of predictions (Thuiller 2004; Araujo & New 2007).

For such a purpose, we used the latest release of the BIOMOD tool (Thuiller 2003a) implemented into the R software (R Development Core Team 2005), including four additional techniques. The following eight techniques were used for our reciprocal modeling analyses: artificial neural networks (ANN), boosted regression trees (BRT), classification tree analyses (CTA), generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), mixture discriminant analysis (MDA) and random forests (RF). GLM, GAM, CTA and ANN are described and discussed in the original BIOMOD paper (Thuiller 2003a). BRT and MARS were recently tested, together with GLM, GAM and CTA in a large study comparing 16 predictive techniques (Elith *et al.* 2006), BRT ranking best. MDA (Hastie & Tibshirani 1996) and RF (Breiman 2001) were also added as promising modeling methods. As only occurrences were available, pseudo-absences were generated (Graham *et al.* 2004a) to fill the absence component of the models. Following recent recommendations (Elith *et al.* 2006), this was done randomly. The procedure was repeated 100 times with each technique, using a different set of calibrating presences and absences within each iteration to ensure robustness of the predictions and provide uncertainty estimates (Fig. 2).

Model evaluation

We tested the predictive power of each model in the range where it was calibrated, using an independent data set (30% of the total), as well as in the range where it was projected, by comparing model predictions to real observations, using the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Fielding & Bell 1997; Elith *et al.* 2006). The AUC allowed testing of whether the pattern predicted in the other range differed significantly from a random prediction, compared to the prediction achieved in the same range. Following Swets' scale (Swets 1988), predictions are considered random when they do not differ from 0.5, poor when they are in the range 0.5–0.7, and useful in the range 0.7–0.9. Predictions greater than 0.9 are considered good to excellent (1 = perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct predictions).

RESULTS

The analyses provided the same results and supported the same conclusions whatever the climatic data set used. Only the results conducted with the eight CRU 10° climatic maps are presented here, because 1) these were considered biologically more relevant for the species (Guisan & Thuiller 2005) and 2) they constitute the baseline data set used by the Intergovernmental Panel for Climate Change and were already used in similar studies (Thuiller *et al.* 2005c). The eight CRU 10′ climatic maps were: ratio of actual to potential evapotranspiration (aet/pet), potential evapotranspiration (pet), annual amount of precipitations (prec), annual variation of precipitations (std_prec), minimum temperature of the coldest month (tmin), annual mean temperature (tmp), maximum temperature of the warmest month (tmax) and growing degree-days above 5 °C (gdd). Results obtained with other climatic data sets are available in the Supplementary Material.

Principal component analysis of the pooled climatic data revealed two significant axes of climatic variation, defining a realized climate space of reduced dimensionality which allows the investigation of niche conservatism (Fig. 1). The enclosed correlation circle (Fig. 1, see also Table 2) indicates the relative contributions of climatic predictor variables to axis 1 and 2. The two axes are associated closely with water availability and heat energy, respectively. Examination of the position of the species in climate space reveals that niche centroids differ strongly between the native and introduced ranges of the species (between group inertia: 31.8%; $P < 0.01$), in spite of extensive overlap of European and western North American climates (Fig. 1). The niche shift occurs principally along axis 1, indicating water availability as the underlying gradient of niche differentiation. Supporting this idea, spotted knapweed in North America is known to be highly efficient at capturing available moisture, allowing it to exploit drier sites (Story 2002).

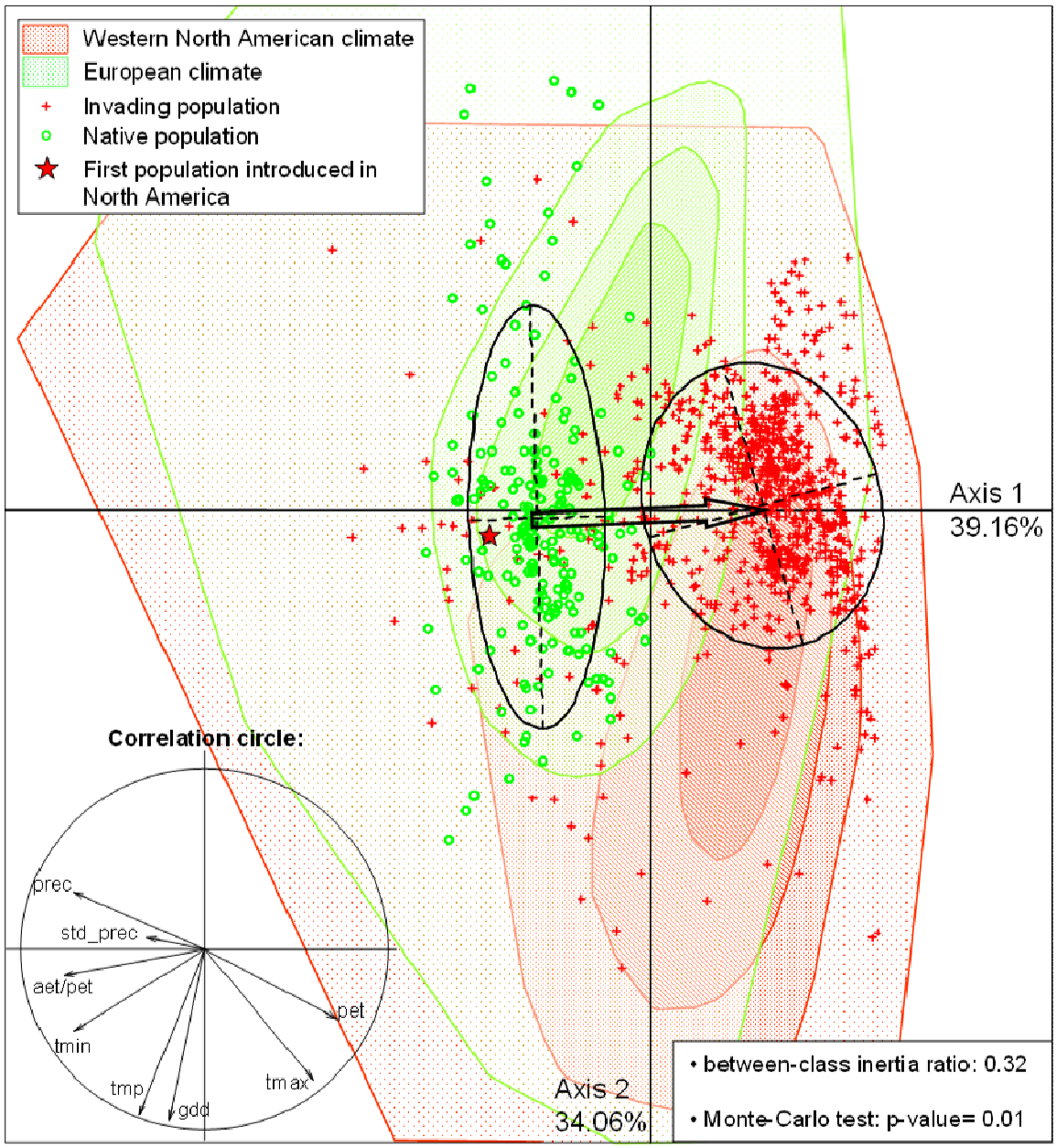

Figure 1 - Bioclimatic space with illustration of niche shift. The position of occurrences, from the native and invaded ranges along the principal climatic gradients is indicated with green dots and red crosses respectively. The red star shows the climatic position of the first population introduced in North America (Victoria, BC). The arrow linking the centroids of the 1.5 inertia ellipses for the two ranges illustrates the niche shift. The enclosed correlation circle indicates the importance of each bioclimatic variable on the two significant axes of the principal component analysis (PCA), which jointly explain 73.22% of the variance in the data. A between-class analysis, yielding a betweenclass inertia ratio, was further conducted and tested with 99 Monte-Carlo randomizations. The convex hulls indicate the prevalence (25, 50, 75 and 100% of sites included) of the global climate conditions in the two ranges. Climatic predictors are: tmp = annual mean temperature, tmax = maximum temperature of the warmest month, tmin = minimum temperature of the coldest month, prec = annual sum of precipitation, std_prec = annual variation of precipitation, gdd = annual growing-degree days above 5 °C, aet/pet = ratio of actual to potential evapotranspiration, pet = annual potential evapotranspiration.

Reciprocal prediction of the species´ distribution between the two ranges further confirmed this niche shift. If realized niches were conserved, models fitted in the native range would predict the extent of potential invasion in the new range (Wiens & Graham 2005). However, models of *C. maculosa* fitted in Europe failed to predict the western North American distribution and vice versa, independent of modeling technique and climatic data set (Fig. 2). To avoid methodological artifacts, we derived geographical predictions using eight different modeling techniques, and subsequently fitted each model 100 times with resampled data to quantify uncertainties in predictions (Fig. 2). Interestingly, fitting models at coarser resolution with annual climatic parameters not accounting for seasonal variability somehow reduced the divergence of predictions between the two ranges (AUC increased 7.9% in average among the eight modeling techniques using CRU0.5 data set; see Supplementary Material), hypothesizing either that niche differentiation may occur more in the seasonally relevant climatic variables than in coarse climatic features or that the bioclimatic parameters may be over-specifying niche models, reducing their generality.

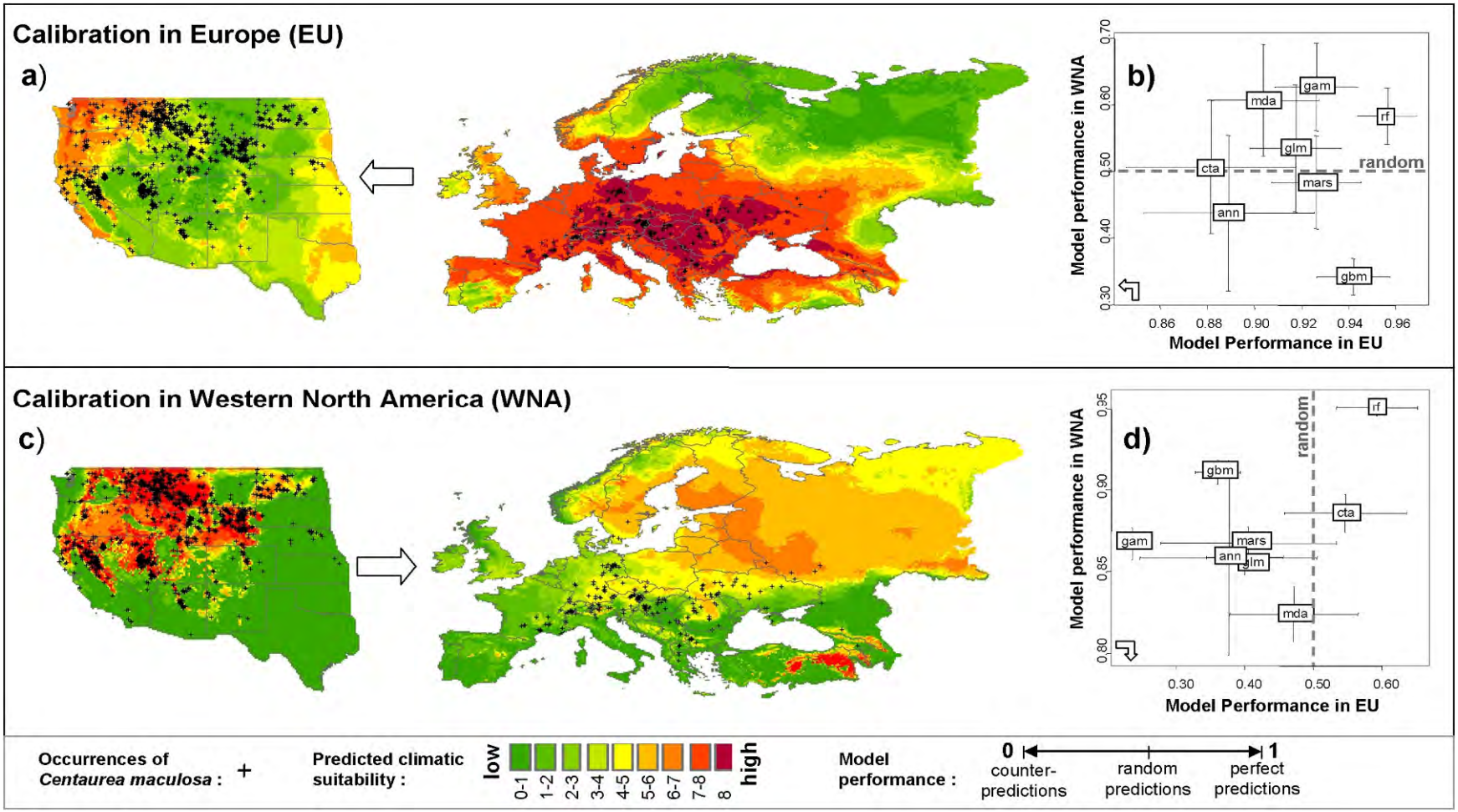

Figure 2 - Prediction maps and model evaluation. The upper and lower boxes illustrate, respectively, the results obtained from models calibrated in Europe (EU; a, b) and Western North America (WNA; c, d), and projected into the other range. The maps (a, c) show the predicted climatic suitability (mean number of models, among eight modeling techniques, predicting the species present). The series of graphs (b, d) plot model performance [area under the curve (AUC)] for 100 repetitions of each technique, based on random re-sampling of the data. The AUC (see Supplementary Material) of a receiver-operating characteristic (ROC) curve calculated on independent data is currently the most objective measure of model performance for presence–absence data, with 1 indicating perfect prediction, 0.5 not different than random and 0 a perfect counter prediction. The horizontal axis indicates the model performance of the predictions in the native area (EU). The vertical axis indicates the model performance of the predictions in the invaded area (WNA). The horizontal and vertical dashed lines indicate predictions that do not differ from random (AUC = 0.5) when projected in the other area (WNA in b; EU in d). Error bars indicate the standard deviation of each modeling technique for the 100 repetitions. As (b) and (d) show, both reciprocal predictions fail, with AUC values centered on 0.6 for the best technique, but for most others being not significantly different from 0.5 or below (counter-predictions).

DISCUSSION

Our results clearly suggest a climatic niche shift of Spotted Knapweed during or subsequent to invasion of this species. The study was based on a comprehensive occurrence data from all regions where the species is present in Europe and western North America, fully covering the relevant climatic gradients. Although distribution data of exotic species are increasingly available within their introduced ranges, obtaining similar data from the native range often remains difficult (Peterson 2003). We put particular effort in acquiring data from the native species range by performing our own field sampling. We are not aware of comparably robust data for other invasive species across two ranges.

These results have important implications for studies of biological invasions, as they provide the first empirical field evidence of such phenomenon. The distribution of invading and native population along climatic gradients (Fig. 1) shows that none of the native populations grows in a similar climate as the vast majority of the invading populations in western North America. However, some of the invading populations still grow under similar climatic conditions as the native populations, and thus have conserved their climatic niche. As none of the native populations can be found in the climatic core area of the invasion, the niche shift we illustrate here occurred in the invading range. Thus, it does not seem related to a specific subgroup of native populations.

In this study, the observed niche reflects the realized niche of the species, including effects of interactions with other species. Thus, the observed niche shift could result either from changes in the species' fundamental niche, as caused by an evolutionary process (e.g. hybridization or evolution of increased competitive ability; Blossey & Notzold 1995) or from changes in the realized niche, as caused by a different biotic environment in the introduced range (e.g. enemy-release hypothesis; Keane & Crawley 2002), or from both (Dietz & Edwards 2006).

From an ecological perspective, some climatic factors may be only indirectly related to the shift, and other more proximal non-climatic factors may have played a more prominent role. Shifts in other dimensions of the niche, such as soil types, could also be investigated in a similar way. In the new range, Spotted Knapweed has been shown to benefit from biotic release from competitive neighbors through novel weapons (Callaway *et al.* 2004, but see Blair *et al.* 2005; Blair *et al.* 2006), from soil pathogens (Hierro *et al.* 2005; Callaway & Maron 2006) and from escaping specialist root herbivore insects that dominate the complex of natural enemies in the native range (Story *et al.* 2006). However, in the latter biocontrol study, the insects can be abundant in very dense stands of knapweed, indicating that the plant may overcome the damages done by the insects in particular ecological situations. These three processes may have promoted niche shifts into climatic conditions from which the species was naturally excluded in its native range.

From an evolutionary perspective, the fact that the niche determinants may differ between native and invaded ranges is supported by experimental studies suggesting rapid evolution of invasive plants (Sexton *et al.* 2002; DeWalt *et al.* 2004; Maron *et al.* 2004). It was also hypothesized that both diploids and tetraploids of *C. maculosa* were introduced from the native range, but only tetraploids became invasive (Müller-Schärer *et al.* 2004). The observed niche shift may thus be solely associated with a shift in the frequency of ploidy levels. However, the fact that none of the native populations has climatic requirements similar to those observed in the climatic core area of the invasion (Fig. 1) refutes this hypothesis. This was further confirmed by a ploidy analysis showing a similarly large climatic shift between the European and North- American tetraploid populations (Treier *et al.* , in review).

Given that gene flow between the two ranges is low or absent, likely factors influencing niche evolution include time since invasion in which evolutionary processes can have occurred, and the magnitude of environmental (climatic or biotic) differences. Evolutionary niche shift may therefore only be quantifiable for species present for sufficient time in the new range (> 120 years for *C. maculosa*). As supporting evidence, the first accidental introduction of *C. maculosa* was in Victoria, BC (Roche *et al.* 1986), a place predicted as highly suitable by the European models (Figs 1 and 2a).

The invaders database (http://invader.dbs.umt.edu) provides a chronological description of the species spread in north-western USA. A first specimen was recorded in Ravalli, Montana, in 1920. The high number of records done in drier habitats in Montana and north-western America during the succeeding years seems to indicate that the date of introduction of the plant there occurred approximately at the same period, 30 years after its introduction in Victoria, BC. This is, to our knowledge, the only documented chronology of introduction available for this plant. Multiple, possibly simultaneous, introductions could have occurred, but only phylogenetic studies can answer this question.

Our results have particularly important implications for application of niche-based species distribution models to predict future areas prone to invasions (Peterson & Vieglais 2001; Thuiller *et al.* 2005c). Our results report, for the first time, a climatic niche shift during biological invasion, and thus support the hypothesis that species can spread into new habitats never been used before by the species (Dietz & Edwards 2006). In particular, this means that an invasive species can occupy new niches that are not predictable from knowledge of the native range alone, calling for more cautionary interpretation of model predictions. Nonetheless, the areas where the species was first introduced proved to be correctly predicted by models. Therefore, the approach of using niche-based models to predict the spread of potential invaders into new areas is still useful to identify areas at risk of successful introduction and establishment of newly or not-yet-introduced neophytes. However, it may not predict the full invasion potential in the new range.

As a further step, our results could provide a framework to design more local and proximal studies of niche shifts, for instance by investigating shifts along biotic factors or identifying other more mechanistic processes behind such climatic niche shifts, at contrasted climatic sites as revealed by predicted species distribution maps.

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SUPPLEMENTARY MATERIAL

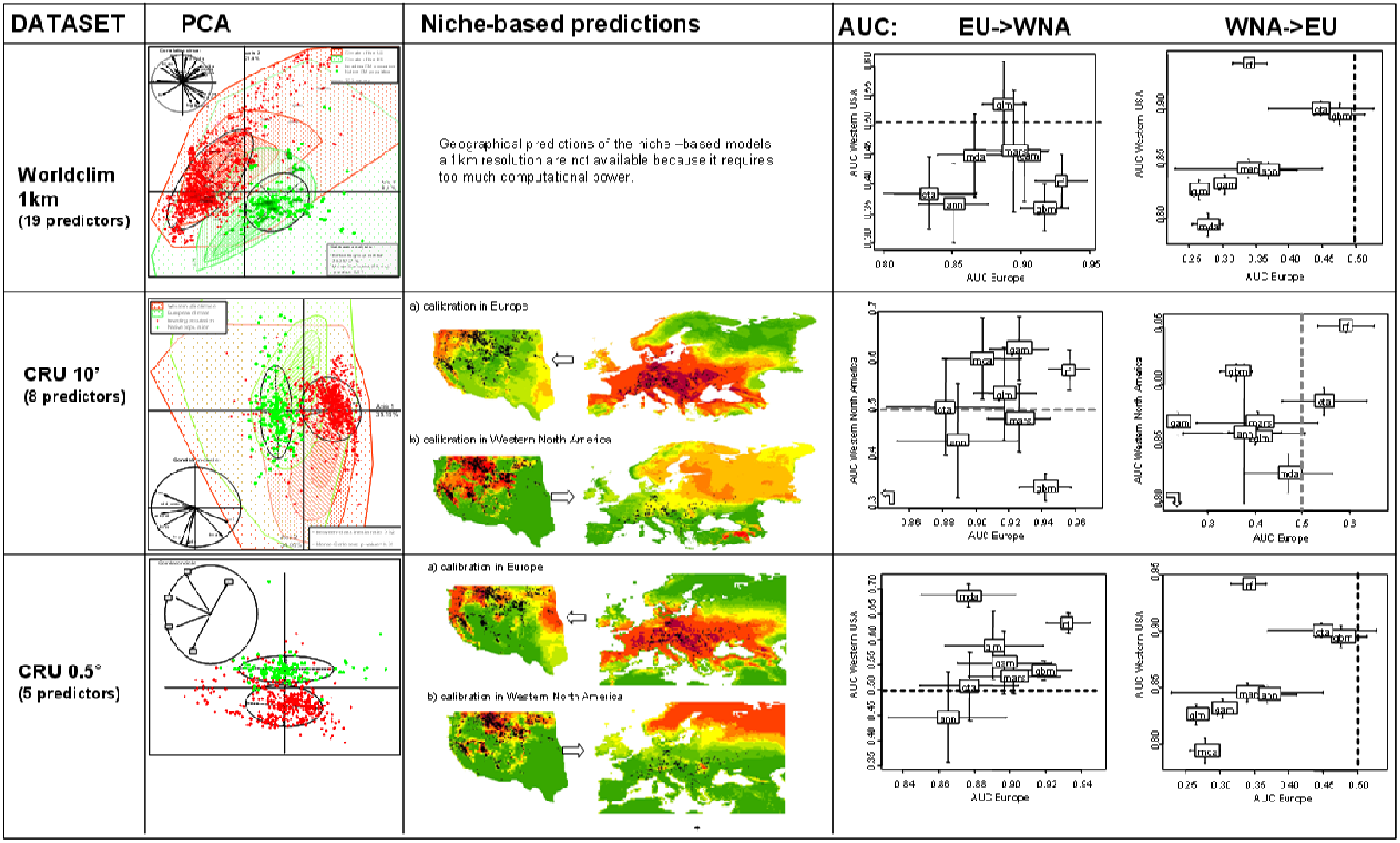

Figure S1 - Results obtained with other climatic data sets. Results of PCA analyses, niche-based predictions and model evaluations are given for each of the following climatic datasets:CRU 0.5 (New *et al.* 1999), CRU 10' (New *et al.* 2000) and WORLDCLIM (Hijmans *et al.* 2005). These results support the same niche shift as illustrated in the main manuscript. More detailed explanations about the interpretation of results are given in the legend of Figure 1 and 2.

Chapter 4.3

Predicting current and future biological invasions: both native and invaded ranges matter

Biology letters: in review

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ABSTRACT

The classical approach to predicting the geographical extent of species invasions consists in training models in the native range and projecting them in distinct, potentially invasible areas. However, recent studies have demonstrated that this approach would be hampered by a change of the realized climatic niche, allowing invasive species to spread into habitats in the invaded range that are climatically distinct from those occupied in the native range. We propose an alternative approach that involves fitting models with pooled data from both ranges. We show that this pooled approach improves prediction of the extent of invasion of spotted knapweed (*Centaurea maculosa)* in North America on models based solely on the European native range. Furthermore, it performs equally well as models based on the invaded range, while ensuring the inclusion of area with similar climate to the European niche, where the species is likely to further spread. We then compare projections from these models for 2080 under a severe climate warming scenario. Projections from the pooled models show fewer areas of intermediate climatic suitability than projections from the native or invaded range models, suggesting a better consensus among modelling techniques and reduced uncertainty.

Keywords: Niche-based modeling, niche shift, climate change, Spotted Knapweed

CONTRIBUTION TO THE PROJECT

I ran all the analyses, created the figures, performed the literature review and wrote the initial draft of the manuscript. I also leaded the reviewing of the manuscript.

INTRODUCTION

Biological invasions represent a growing threat to biodiversity (Pimentel *et al.* 2000). Once introduced species are established, they become difficult to eradicate (Genovesi 2005). Thus, anticipating and preventing future invasions is the most cost-effective form of management.

Niche-based models (NBM, Guisan & Thuiller 2005) are increasingly used to estimate risks of biological invasions (e.g. Thuiller *et al.* 2005d). Two crucial assumptions are made when applying these models. First, the species is assumed to be in equilibrium with its environment in the range used to train the model. Second, the environmental niche of the species is assumed to be static across space and time (niche conservatism; reviewed in Pearman *et al.* 2008a; Wiens & Graham 2005).

So far, NBM approaches have developed models by using observations either from the invaded range (e.g Mau-Crimmins *et al.* 2006) or from the native range (e.g Peterson & Vieglais 2001; Thuiller *et al.* 2005d) and then predicted the potential extent of invasions. An obvious problem with the first approach is that in the invaded range, the invasion process may not be completed and thus, the invading species may not yet occupy all environmental conditions suitable for its growth and reproduction (Wilson *et al.* 2007). Such a violation of the equilibrium assumption can subsequently bias the model, under-predicting the full potential for invasion. A problem with the second approach is that the ecological requirements of the species might have changed during the invasion process (Pearman *et al.* 2008a), thus violating the assumption of niche conservatism.

We recently evidenced (Broennimann *et al.* 2007) a shift of the climatic niche of spotted knapweed (*Centaurea maculosa* Lam.), a weed introduced in the 1890s from Europe into western North America, where it now infests over $3x10^6$ ha of disturbed and natural grassland habitats (Supplementary material S2). A consequence of this difference was that models fitted in the native range could successfully predict areas of introduction in North America, but were unable to predict the full extent of invasion. Current NBM approaches used to predict spread and ultimate distributions may thus be inadequate for several invasive species. Moreover, distinct model training strategies may not only yield distinct predictions in the present, but also on future predictions in warmer climates (Araujo *et al.* 2005c).

Here, we assess uncertainties in predictions of Spotted Knapweed invasion obtained with models trained in: i) the native range, ii) the invaded range, and iii) both ranges, as similarly explored by Kriticos & Randall (2001). We further investigate the outcome of these training strategies with regard to the outcome of predictions under a severe warming scenario by 2080 (HadCM SRES A1FI; Nakicenovic & Swart 2000). Attempts to predict future distributions of invasive species in a warmer climate are few (e.g. Beerling 1993).

METHODS

Species occurrence data

We used the occurrence database described in Broennimann *et al.* 2007, complemented with occurrences from Canada (*www.eflora.bc.ca*), Eastern USA and Russia (Müller-Schärer, unpublished data), resulting in a robust cross-continental dataset of 373 occurrences for Europe and 2972 occurrences for North America. A corresponding number of pseudo-absences were sampled randomly (see Elith *et al.* 2006) across both native and invaded ranges.

Climate data

We used the CRU05 climate data at 0.5° (New *et al.* 2000a) to derive the following set of meaningful predictors (Guisan & Thuiller 2005): mean annual temperature (t_{AN}), annual sum of precipitation (p_{AN}), mean annual daily temperature range (dtr_{AN}), minimum temperature (t_{MIN}), maximum temperature (t_{MAX}), total precipitation of the wettest quarter (p_{WETQ}), total precipitation of the driest quarter (p_{DRYQ}), and potential evaporation (pet; following Samani & Pessarakli 1986). The HadCM-A1FI climate scenarios anomalies were retrieved from the CRU-TS2 dataset (Mitchell *et al.* 2004) and added to present climate maps to obtain future climate predictors for 2080.

Statistical modelling

Models were fitted and evaluated using a standard split-sample strategy. Models were trained using three subsets (70%) of occurrence data: (i) from Europe (modEU), (ii) from North America (modNA) only and (iii) from both ranges (modEUNA). We used the same BIOMOD modelling framework (Thuiller 2003b) as Broennimann *et al.* (2007), fitting for each species: generalised linear models (GLM), generalised additive models (GAM), boosted regression trees (BRT) and random forest (RF). Models were validated in each case with the remaining 30% independent data (Thuiller 2003b). The whole training-evaluation procedure was repeated 100 times. The predictive power of the models was tested using the area under the receiver operator characteristic function (AUC; Thuiller 2003b; Elith *et al.* 2006; Supplementary material S1). Models were projected into future climates to generate species distribution maps for 2080.

RESULTS

The modEU models (Fig. 1a and 1b) predict the distribution significantly better in EU than in NA (Table 1). In NA, they correctly predict areas of introduction (Victoria, British Columbia) but not the full invasion extent. They also predict areas in Eastern NA, where the plant is present, but still infrequent. Similarly, the modNA models (Fig. 1e, 1f) predict the distribution significantly better in NA than in EU (Wilcoxon tests; Table 1). They predict the species in Southern EU where it is absent and fail to predict most of its actual native distribution. The modEUNA models (Fig. 1c, 1d) predict in both ranges as accurately as modEU and modNA predict in EU and NA, respectively (Table 1).

Table 1 – Model accuracy on evaluation dataset (30% independent data) using Area Under the Curve criteria (AUC). Standard deviations (±) indicate the variability of model accuracy through 100 iterations. AUC values for models calibrated in Europe (EU), North America (NA) and both (EU+NA) are indicated for each modeling technique. The differences in model accuracy between ranges within and between models were tested with a paired Wilcoxon signed rank test (ns = non significant; * = $0.05<p<1x10^{-5}$; ** = $p<1x10^{-5}$).

	Calibration in EU				Calibration in EU+NA				Calibration in NA		
	NA	↔	EU	↔	EU	↔	NA	↔	NA	↔	EU
GLM	.77±.07	**	.87±.03	ns	.86±.03	**	.96±.01	ns	.96±.01	**	.73±.04
GAM	.89±.05	*	.88±.03	ns	.87±.03	**	.96±.01	ns	.96±.01	**	.70±.04
GBM	.85±.02	**	.89±.03	ns	.88±.03	**	.96±.01	ns	.97±.01	**	.76±.04
RF	.84±.03	**	.90±.02	ns	.90±.03	**	.97±.01	ns	.98±.01	**	.76±.03

When projected for 2080, the three strategies yielded distinct predictions (Fig. 2). The modEU predictions were correlated 66% with the modEUNA predictions (66% in EU, 62% in NA) and only 40% with modNA predictions (45% in EU, 32% in NA). The modEUNA predictions were correlated 76% with the modNA predictions (79% in EU, 73% in NA). In EU, the modEU models predicted the species to persist in the Alps and to colonise Sweden, the Baltic countries, Caucasus, and North-Eastern Russia (Fig. 2b), whereas it predicted the colonisation of British Columbia, Quebec and Labrador in the invaded range. In contrast, the modNA models predicted a decreased suitability in the EU and the migration of the species to British Columbia and the Central Rockies in NA. The models calibrated on both ranges indicated convergent patterns of distribution in EU and NA when compared to modEU and modNA alone (comparing Fig. 2d to 2b and 2c to 2e).

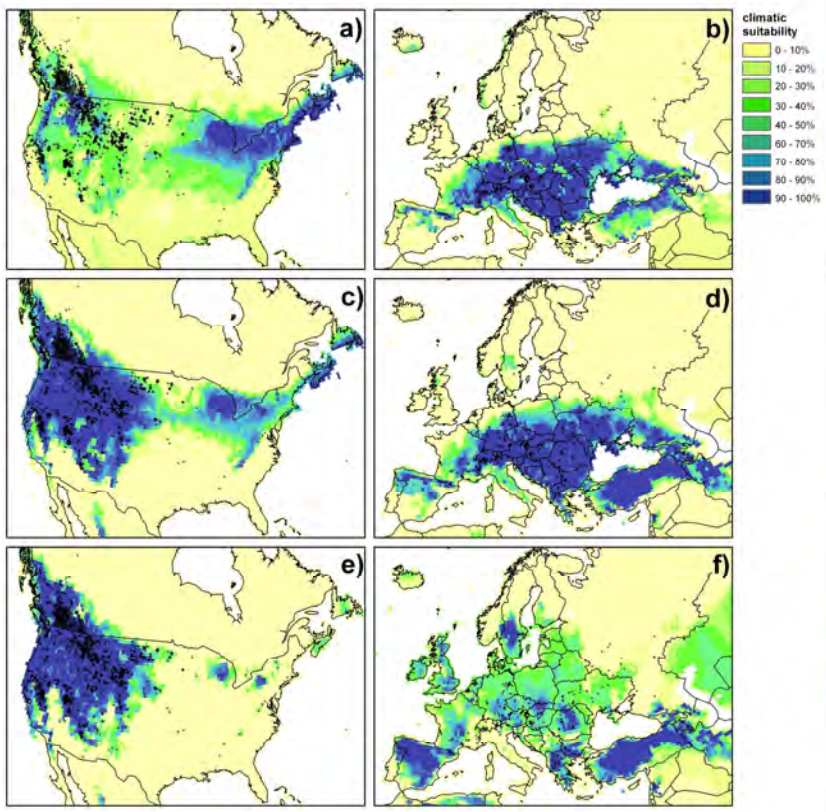

Figure 1 – Geographic predictions of Spotted Knapweed at the present time. Models calibrated in Europe only (modEU; a,b), in both North America and Europe (modEUNA; c,d) and North America only (modNA; e,f) are projected respectively to North America (a,c,e) and Europe (b,c,d). The climatic suitability (yellow to blue scale) indicates the percent of models (all techniques pooled) predicting the species in the present.

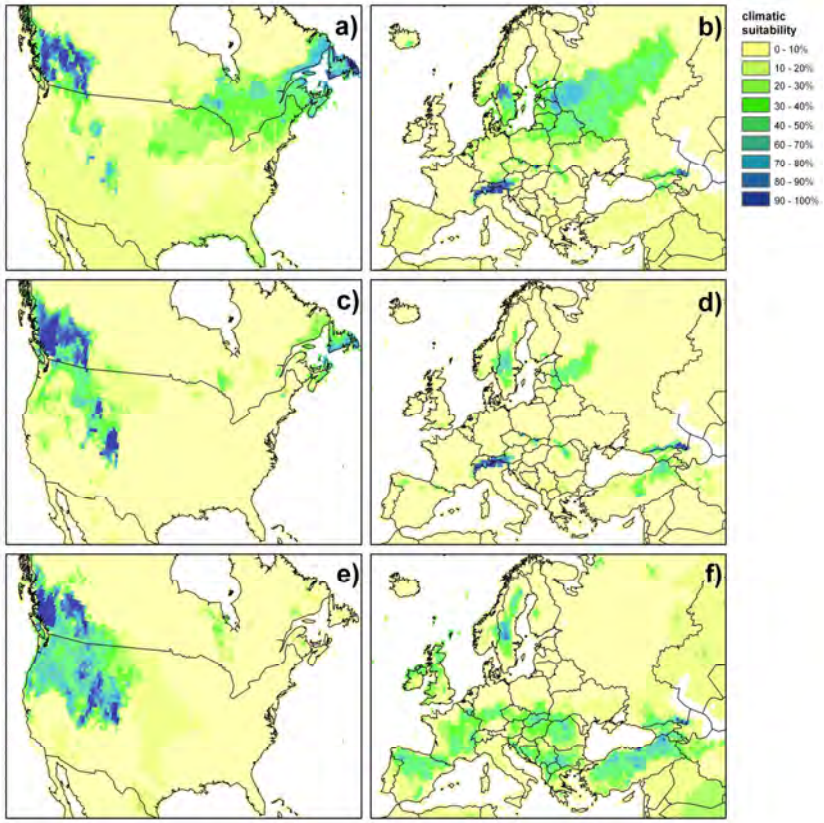

Figure 2 – Geographic predictions of Spotted Knapweed by 2080 under HadCM A1FI warming climate scenario. (see details of fig. 1 for the description of the models and color scale)

DISCUSSION

Studying invasive species in their native and invaded ranges offers new opportunities for addressing theoretical challenges associated with niche-based modelling and the prediction of biological invasions. As we showed, a main challenge is the uncertainty of conservatism of the climatic niche between ranges, whether observed shifts result from a change in the fundamental and/or the realised niche (Pearman *et al.* 2008a), and how such shifts can further affect predictions of biological invasions.

Using Spotted Knapweed as a model species, we confirm that the current practice, consisting of training models in the native range, fails to predict the full extent of biological invasions (Broennimann *et al.* 2007). As a better alternative, we propose that models be trained using data from both native and invaded ranges, which ensures that the models can predict the future spread of the species in areas of the invaded range that are not yet invaded but where suitable conditions similar to the native range occur. We show that this approach yields accurate predictions across both ranges (Fig. 1, Table 1). Furthermore, the prediction of the extent of invasion in North America improves on models based solely on the distribution in the native range and equally performs as models based on the invaded range, while ensuring the inclusion of area with similar climate to the European niche, where the species is likely to further spread.

There are several factors that could contribute to the improvement demonstrated by our approach. In the native range, biotic constraints (e.g. competitors, herbivores) can exclude the species from part of the climatic envelope within which it could otherwise grow and reproduce (i.e. the *fundamental* niche is constrained to the *realized* niche). In the invaded range however, many of these natural enemies are absent (e.g. specialist root-feeding herbivores; Müller 1989b). Such biotic release may allow the species to occupy climatic situations (i.e. additional parts of the fundamental niche) from which it is excluded in the native range. Models trained in the native range will fail to account for these newly occupied climates. By taking both ranges into account in the training process, the niche implicitly fitted can be expanded to express a larger part of the fundamental niche in the invaded range. Conversely, the pooled model should indicate, in Europe, areas where the species does not occur, potentially due to these negative biotic interactions. Interestingly, Fig 1d reveals such areas in Turkey and Southern and Eastern Ukraine, where a potential competitor - *C. diffusa* - is present. Further testing on a larger number of invasive species is required to validate such pooled approach.

In addition to considerations of changes of the realised niche, one cannot exclude the fact that the fundamental niche might have evolved in the invaded range, because of evolutionary processes taking place after introduction (Dietz & Edwards 2006; Pearman *et al.* 2008a). Disentangling changes in the realized (ecological process) versus in the fundamental niche (evolutionary process) is currently impossible based on empirical distribution data only. Further contributions from experimentalists and ecophysiologists are required.

Future predictions of invasions in a warmer climate based on the pooled approach exhibit similar patterns of prediction than models trained and projected within the same range (Fig. 2). However, the pooled approach significantly reduces areas of future predictions, forecasting a much reduced invasion extent for the species by 2080. Interestingly, the reduction mainly concerns areas with limited consensus between modelling techniques, thus reducing uncertainty. However, our projections cannot be confronted to future species occurrence data. A strong testing would be to predict current patterns of invasions from data on past invasions, but dated observations are currently missing for such analysis.

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SUPPLEMENTARY MATERIAL

S1 - METHODS (see also Broennimann *et al.* 2007)

Statistical modelling

The following 4 techniques were used for our reciprocal modelling analyses: boosted regression trees (BRT), generalized linear models (GLM), generalized additive models (GAM) random forests (RF). These techniques were chosen because they have proven to be the current most effective niche-based models in a recent large study comparing 16 predictive techniques (Elith *et al.* 2006). As only occurrences were available, pseudo-absences were generated (Graham *et al.* 2004) to fill the absence component of the models. Following recent recommendations (Elith *et al.* 2006), this was done randomly. The procedure was repeated 100 times with each technique, using a different set of calibrating presences and absences within each iteration to ensure robustness of the predictions and provide uncertainty estimates.

Model evaluation

We tested the predictive power of each model in the range where it was calibrated, using an independent data set (30% of the total), as well as in the range where it was projected, by comparing model predictions to real observations, using in both cases the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Fielding & Bell 1997; Elith *et al.* 2006). The AUC allowed testing of whether the pattern predicted in the other range differ significantly from a random prediction, compared to the prediction achieved in the same range. Following Swets' scale (Swets 1988), predictions are considered random when they do not differ from 0.5, poor when they are in the range 0.5–0.7, and useful in the range 0.7–0.9. Predictions greater than 0.9 are considered good to excellent (1 = perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct predictions). AUC values should be interpreted with caution because it does not give information about the spatial distribution of model errors and because the total geographic extent to which models are carried out can influence the rate of well-

predicted absences (see Lobo *et al.* 2008). However, in this specific study, we did not use the AUC values as an absolute value of goodness of fit but rather as a relative measure of predictive power to compare the outcome of different training strategies, always in the same study area, and with a prevalence of 0.5 in the presence/absence data, thus limiting the risks of flaws. Two types of errors are influencing AUC: omission (wrongly predicted absence) and commission (wrongly predicted presence; see for instance Fielding & Bell 1997, Pulliam 2000). With invasive species, though, the main issue is not to find occurrences in locations where in theory they could exist (not observed with our species, at least in the western US where the species was introduced), because these sites might simply not have been yet colonized, but rather to find occurrences in locations where they are not predicted to occur (omission error), as shown here by the species invading new climatic conditions.

S2 – INVASION HISTORY OF SPOTTED KNAPWEED (see also Broennimann *et al.* 2007)

Spotted knapweed (*Centaurea maculosa* L.) was first introduced in the 1890s from Europe into western North America, where it now infests over $3x10^6$ ha of rangeland and pasture in 14 states and two Canadian provinces (Story *et al.* 2006) and may cause an estimated >150 · 106 US$ in economic damage each year (Story 2002). In both ranges, the species occurs in disturbed and natural grassland habitats, but it rarely reaches densities in the native range as high as observed in the invaded range (Müller 1989). The species has not undergone any artificial selection nor hybridization to improve ornamental traits. The first accidental introduction of C. maculosa was in Victoria, BC (Roche *et al.* 1986). The invaders database (http://invader.dbs.umt.edu) provides a chronological description of the species spread in north-western USA. A first specimen was recorded in Ravalli, Montana, in 1920. The high number of records done in drier habitats in Montana and north-western America during the succeeding years seems to indicate that the date of introduction of the plant there occurred approximately at the same period, 30 years after its introduction in Victoria, BC. This is, to our knowledge, the only documented chronology of introduction available for this plant. Multiple, possibly simultaneous, introductions could have occurred, but only phylogenetic studies can answer this question.

S3 - ASSESSING THE CONTRIBUTIONS OF CLIMATIC PREDICTORS

The contribution of climatic variables was assessed by spatial permutations. Predictions based on 100 randomized variables were correlated to the original predictions (Thuiller *et al.* 2008) and then averaged and rescaled to measure the predictors' importance in the models. The lower the correlation, the more important the variable is in the model.

The climatic variables contribute differently to the models depending on the training area. While p_{AN}, t_{MAX}, dtr_{AN}, p_{WETQ} and p_{DRYQ} only provide little contribution, regardless of the model, t_{AN}, t_{MIN} and pet

have important, but contrasting contributions (table S1). While t_{MIN} provides the greatest contribution to modNA, the greatest contributor to modEU is pet. Interestingly, predictors having little importance in modEU and modNA (p_{AN}, t_{MAX}, dtr_{AN}, p_{WETQ}) gain importance in modEUNA.

In the manuscript, we propose training models using data from both native and invaded ranges as an alternative to the current modeling of biological invasion approach based on the training of the models in the native range. We show that this approach yields satisfying predictions in both ranges (see the discussion, Fig. 1, Table 1), and we discuss the reasons that may explain this superiority. Additional support is provided by the varying importance of climatic variables between the different modeling strategies. Models trained on both ranges exhibit a pattern of climatic variables contribution similar to models trained in the native range, with potential evapotranspiration being the most influential predictor, but also includes contributions of minimum temperatures, a variable contributing much in the models trained in the invaded range. Hence, we show that climatic variables with small contributions in models trained in Europe and North America gain more importance in models trained on both ranges. This may result from the fact that some climatic features can only be expressed along sufficiently large climatic gradients, which only become available when pooling climatic data from the two ranges.

Table S1 – Importance of the climatic variables. The importance of climatic variables for models calibrated in Europe (EU), North America (NA) and both (EU+NA), are indicated for each modeling technique.

Calibration area	modeling technique	t_{AN}	p_{AN}	dtr_{AN}	t_{MIN}	t_{MAX}	p_{WETQ}	p_{DRYQ}	pet
EU	GLM	0.28	0.02	0.04	0.72	0.19	0.03	0.04	1.00
	GAM	0.10	0.01	0.01	0.32	0.27	0.01	0.04	1.00
	GBM	0.02	0.09	0.05	0.52	0.07	0.05	0.10	1.00
	RF	0.21	0.16	0.09	0.53	0.12	0.14	0.14	1.00
EU+NA	GLM	0.31	0.11	0.22	0.61	0.23	0.11	0.08	1.00
	GAM	0.22	0.03	0.14	0.57	0.23	0.04	0.04	1.00
	GBM	0.06	0.01	0.22	1.00	0.22	0.04	0.07	0.59
	RF	0.12	0.03	0.27	1.00	0.22	0.06	0.11	0.61
NA	GLM	1.00	0.06	0.31	0.85	0.12	0.04	0.06	0.59
	GAM	0.56	0.01	0.13	1.00	0.15	0.02	0.02	0.26
	GBM	0.11	0.00	0.06	1.00	0.20	0.02	0.05	0.08
	RF	0.27	0.02	0.09	1.00	0.38	0.06	0.13	0.36

Chapter 5

NICHE DYNAMICS IN SPACE AND TIME

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ABSTRACT

Niche conservatism, the tendency of a species niche to remain unchanged over time, is often assumed when discussing, explaining or predicting biogeographical patterns. Unfortunately, there has been no basis for predicting niche dynamics over relevant timescales, from tens to a few hundreds of years. The recent application of species distribution models (SDMs) and phylogenetic methods to analysis of niche characteristics has provided insight to niche dynamics. Niche shifts and conservatism have both occurred within the last 100 years, with recent speciation events, and deep within clades of species. There is increasing evidence that coordinated application of these methods can help to identify species which likely fulfill one key assumption in the predictive application of SDMs: an unchanging niche. This will improve confidence in SDM-based predictions of the impacts of climate change and species invasions on species distributions and biodiversity.

CONTRIBUTION TO THE PROJECT

I took part to the survey of the literature and early discussions. Together with Peter Pearman and Antoine Guisan, I contributed to the elaboration of the plan of the manuscript. I further created or modified all the figures in the manuscript and participated to the reviewing of the paper.

INTRODUCTION: THE FUNDAMENTAL CHALLENGE FACING PREDICTIVE APPLICATION OF NICHE-BASED SPECIES DISTRIBUTION MODELS

The assumption that the niche of a species might remain unchanged (Huntley *et al.* 1989; Peterson *et al.* 1999; Wen 1999; Qian & Ricklefs 2004), or change only slowly over hundreds to millions of years (i.e. niche conservatism; see Glossary, Webb *et al.* 2002; Ackerly 2003, 2004), currently influences the study of species distributions and has generated considerable debate (Wiens & Graham 2005). This is because pervasive niche-conservatism is used as a justification for applying species distribution models (SDMs; see Glossary; Gallardo *et al.* 1996; Guisan & Zimmermann 2000; Guisan & Thuiller 2005) to predict species distributions in space and across time. In this way, authors assume slow or absent change in the niche to study species diversification and geographical distributions (Hugall *et al.* 2002; Rice *et al.* 2003; Graham *et al.* 2004b; Levin 2005; Knouft *et al.* 2006), to forecast species extinction and biodiversity loss in response to climate change (Peterson *et al.* 2002; Martinez-Meyer *et al.* 2004; Thomas *et al.* 2004) and to predict the establishment and spread of invasive species (Peterson & Vieglais 2001; Dirnbock *et al.* 2003b; Thuiller *et al.* 2005c).

In reality, there is little basis for evaluating whether the assumption of an unchanging niche holds when predicting changes in species distributions in space and time. If niches of species are not static, then they can expand, contract or shift. These niche dynamics, if they occur over the time period or area of interest, probably invalidate conclusions based on the application of niche-based SDMs. One crucial issue in developing an evaluative framework for niche dynamics is resolving which niche concept(s) is most pertinent for the application of SDMs (Araujo & Guisan 2006). Niche-based SDMs are discussed and applied in the context of Hutchinson's niche (Hutchinson 1957) — defined by a combination of environmental characteristics (i.e. his 'hypervolume') — in which populations of a species can maintain a positive net growth rate. Hutchinson further distinguished between the fundamental environmental niche (see Glossary), which is genetically and physiologically determined, and the realized environmental niche (see Glossary), which includes, additionally, constraints arising from interspecific competition (Figure 1) (Pulliam 2000; Silvertown 2004). The distinction between realized and fundamental niches is important for describing and understanding niche dynamics. This is because a niche-shift (see Glossary) could result from changing ecological processes influencing the realized niche as when, for example, an exotic species experiences release from natural enemies in the new environment. Alternatively, a niche-shift could involve both the realized and fundamental niches if, for example, the genetically determined environmental tolerances of a species were to respond to selection during range expansion (Figure 1).

GLOSSARY

Allopatric speciation: speciation following the division of a large population into at least two new populations that are separated by a geographic barrier.

Brownian motion model: niche attributes of a species or clade are affected by genetic drift or selection in directions that are random and vary independently over time.

Climatic niche: an aspect of the environmental niche that is defined by limits in climatic variation. Outside of this niche, a population cannot maintain a positive net rate of population increase (e.g. owing to excessively low minimum winter temperature, insufficient growing season precipitation, etc).

Directional selection: occurs when natural selection favors phenotypic values that tend to lie either above or below the mean phenotypic value in a population.

Environmental niche: all environmental conditions that meet the physiological requirements of a species necessary for positive population growth rates (compare fundamental and realized niches, described below).

Founder effect: the tendency for the few individuals that disperse and found a new population to carry only a small, and potentially unrepresentative, portion of the genetic variation that exists in their population(s) of origin.

Fundamental niche: the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions.

Niche: the requirements of a species to maintain positive population growth rates (see fundamental and realized niche).

Niche conservatism: the tendency for related species to have similar fundamental and/or realized niches; also, the tendency for the niche of a species to be little changed over time (i.e. to exhibit temporal autocorrelation).

Niche shift: any change in the position of either the fundamental or realized (Hutchinsonian) niche of a species.

Niche stasis: lack of any kind of change in the niche. Applies to either the fundamental or realized niche.

Null model: a model in which purely random processes create observed patterns; it is used in constructing a null hypothesis for statistical testing.

Phylogenetic signal: the tendency for more closely related species to have more similar characteristics.

Realized niche: the portion of the fundamental niche in which a species has positive population growth rates, given the constraining effects of biological interactions, such as competition.

Species distribution model (SDM): a model that describes or predicts the probability of the presence or absence of a species

Ideally, predictions of species distributions (e.g. in a modified climate or different area) should, first, be based on a quantification of the fundamental niche and, second, be constrained by the effects of biotic interactions. Given that the fundamental niche can only be estimated using costly manipulative experiments in the field and/or under controlled conditions, these estimates have only been conducted for a few species. In the absence of data from manipulative experiments, SDMs must be fitted with field observation data. However, observed distributions of species include effects of biotic interactions and for this reason only provide information on the realized environmental niche. Any change in biotic interactions might alter the realized niche (Davis *et al.* 1998a) and affect the accuracy of predictions of species distributions.

However, even if one could estimate the fundamental niche, the main issue remains that using SDMs to project species distributions in space and time assumes, potentially uncritically, that neither the fundamental nor the realized niche changes (Davis *et al.* 1998a). Recent findings suggest that niche shifts do occur in previously unrecognized situations, owing to ecological processes changing the realized niche, and/or evolutionary processes altering the fundamental niche (Ackerly 2003; Davis *et al.* 2005; Dietz & Edwards 2006). Furthermore, we still cannot predict which species will be affected by niche changes, nor is it clear under which ecological conditions or over what time periods these niche changes will be observed. Thus, it is crucial that we better understand the conditions that determine the range of niche dynamics — from rapidly changing niches (Box 1) to completely static niches (Box 2; see Glossary). Unfortunately, evidence for the occurrence of niche shifts is mixed and debated (Table 1).

The combination of niche-based SDMs, environmental data from the field, and phylogenetic information can help us to better define both the timescales over which shifts of the realized niche occur and which species are most likely to experience them. Additional empirical data on the life history characteristics, ecological circumstances and evolutionary histories that are associated with particular dynamics of species niches will also improve confidence in the predictions supplied by niche-based SDMs. Here, we examine how recent studies in ecology and phylogenetics have contributed to our understanding of the conditions, patterns, processes and timescales surrounding niche dynamics. We build on recent theoretical and empirical studies of niche change and stasis across different timescales to illustrate the observed variability in niche dynamics. Recent work has relied increasingly on the implementation of alternative models to guide hypothesis testing and has emphasized the need to identify factors that might affect the detection and quantification of niche shifts. These advances provide new understanding of niche dynamics that could help us to identify the conditions under which either niche stasis is a supportable assumption or the potential for niche shifts appears large. This in turn will improve our ability to assess the risk of establishment and invasion by exotic species, and to develop justifiable confidence in predictions of species response to climate change.

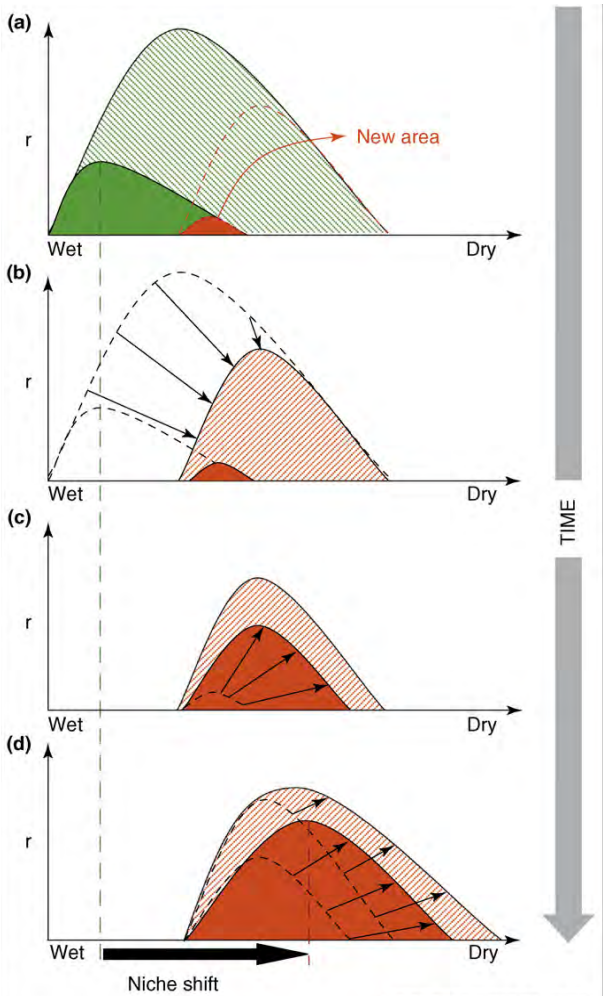

Figure 1 - The relationship between fundamental and realized niche during a founder event and subsequent niche expansion along one environmental axis (relative moisture availability). There are four snapshots in time, which progresses from the top panel to the bottom. In each panel, the rate of increase of populations (r, on the y-axis) is shown as a function of location along a moisture gradient (on the x-axis). (a) The realized niche (dark green) of the species in comparison with its fundamental niche (light green), the reproductive rates that would occur in the absence of competitors. The dashed green line indicates the moisture optimum in relation to the original realized niche of the species. A collection of individuals from one end of the moisture gradient, together defining a realized niche (red area) and a fundamental niche (dashed red line), disperse to establish populations in a new area with similar conditions. (b) In the new area, populations of the species establish somewhere within the original realized and fundamental niches (red and light red areas, respectively), which are small in comparison to those of the species in its original range (change in fundamental niche shown by black arrows). (c) In the newly colonized area, the species expands (black arrows) its use of habitats (i.e. its realized niche) to portions of the fundamental niche that were not occupied in the original range, which might happen because of competitive release in the new area. (d) With time, directional selection acts to favor individuals that tolerate drier conditions than those potentially tolerated by the first colonists. This happens because populations now experience conditions that were not within the realized niche in the original range. Thin black arrows indicate the evolution of the fundamental niche and expansion of the realized niche in the invaded range. The cumulative shift in realized niche is also shown.

Box 1. The case for rapid change of environmental niche

Support for rapid niche shifts is found in diverse fields of ecology and evolution. Some theoretical models of speciation suggest rapid niche change (Orr & Smith 1998). For example, whereas strong differences in per capita survival and reproductive output between habitats (i.e. source-sink dynamics) favor niche stasis (Antonovics *et al.* 2001; Holt & Gomulkiewicz 2004), weak differences, temporally correlated variation in fitness, and gene flow from source to sink might promote niche expansion (Holt & Gomulkiewicz 2004). The effects of dispersal and selection interact to determine whether the species niche (and range) contracts or expands rapidly (Kirkpatrick & Barton 1997) (reviewed in Bridle & Vines 2007).

Evidence for rapid niche shifts comes from empirical studies of invasive species ecology (Broennimann *et al.* 2007; Fitzpatrick *et al.* 2007), phylogenetic analysis (Rice *et al.* 2003; Knouft *et al.* 2006; Silvertown *et al.* 2006) and community ecology (Silvertown 2004), and the occurrence of host shifts by pathogens is well documented (Ebert 1994; Roelke Parker *et al.* 1996). Insects can expand the range of habitats they occupy and evolve increased dispersal rates in response to climate change (Thomas *et al.* 2001). Niche shifts can also occur during invasion of new geographical areas by plants (Holt *et al.* 2005a; Dietz & Edwards 2006; Broennimann *et al.* 2007) and animals (Fitzpatrick *et al.* 2007), and have happened in less than 100 years. Niche shift might be a factor that enables successful invasion by exotic species (Broennimann *et al.* 2007).

Niche shifts have also been studied experimentally. Invasive exotic species can undergo rapid adaptation and population differentiation, as shown in field (Maron *et al.* 2004) and laboratory (Sexton *et al.* 2002) experiments. For example, Wright *et al.* (2006) examined the occurrence of a California annual plant, Collinsia sparsiflora, in an area of patchy serpentine soils. They used five environmental variables in SDMs to predict species distribution, survival of experimental plants and flowering performance. Their models predicted the flowering performance of experimental plants and two nearby populations from serpentine soil, and four additional serpentine species. The models did not, however, predict the performance of two nonserpentine populations of C. sparsiflora in serpentine soils, thus suggesting a niche shift. Wright *et al.* (2006) also showed that the models performed well in predicting plant performance when competitors were removed (i.e. predicting the fundamental niche), suggesting that the fundamental and realized niches of the species were similar. Another experimental study, on Pinus contorta in British Colombia, demonstrated that populations are locally adapted to climatic conditions (i.e. they differ in their fundamental niche), but that competitors exclude most individuals from optimal environments within each local population (i.e. limited to their realized niche; Holt & Gomulkiewicz 2004). Taken together, these studies show that rapid niche shift can occur in a variety of species and habitats.

Box 2. The case for niche stasis

Multiple studies support the existence of niche stasis and strong phylogenetic signal. Comparison of the effectiveness of environmental niche models in reciprocally predicting the distribution of sister taxa and non-sister taxa suggests that niches tend to remain similar during allopatric speciation (see Glossary; Peterson *et al.* 1999). Similarly, comparisons of the realized niche at the continental or intercontinental scales have supported the existence of niche stasis in beech (genus Fagus), Argentine ants (Linepithema humile) and in herbaceous plants (Huntley *et al.* 1989; Ricklefs & Latham 1992; Hoffmann 2005; Roura-Pascual *et al.* 2006). Other studies have compared ecological aspects of species and have inferred niche stasis from a significant similarity in the distributions (geographical or in environmental space) of pairs or larger groups of species. The migration of tree species in response to Quaternary climate change suggests that it is easier for some plants to migrate than to adapt to changing climate. Additionally, the positive correlation between areas of high species richness and high speciation rates in three clades of plankton suggests that their niches have barely changed, if at all (Allen & Gillooly 2006). One theoretical result is that natural selection should generally favor adaptation to source habitats because higher fitness in source habitats inside the realized niche and low rates of dispersal from sink to source habitats lead to little selection for adaptation to sink habitats (Holt 1996). Strong differences in fitness between sink and source habitats favor niche stasis (Antonovics *et al.* 2001; Holt & Gomulkiewicz 2004). Furthermore, little niche change is expected when the rate of adaptation of sink populations is slower than their rate of extinction, which depends primarily on the magnitude of gene flow (Pulliam 2000). Thus, little or no niche change is generally expected based on theory, and niche stasis might occur in a variety of systems (Table 1; main text

Table 1- Studies of niche conservatism or shift 1996–2007, showing the lack of association between the frequency of or propensity for niche shift and any particular ecological conditions, morphological characteristics or evolutionary history

TOPIC	SYSTEM	CONCLUSIONS	REFS
Character divergence	Theoretical	Character displacement among prey species is enhanced with some forms of predation	Abrams 2000
	Insect pest	Food resource and bill morphology change result from competition in a drought year	Grant & Grant 2006
Host shift	Darwin's finches	Insipient speciation involves genotype–environment interaction	Filchak *et al.* 2000
	Viruses and carnivores	Related viruses find hosts in dogs (Canis familiaris), lions (Panthera lio) and others	Roelke Parker *et al.* 1996
	Tephritid fruit flies	Hybrid speciation event is associated with host shift	Schwarz *et al.* 2005
	Butterflies (Papilio)	Host shift is supported by change in predation regime	Murphy 2004
Niche conservatism	Theoretical	Niche conservatism is due to higher fitness of individuals in source habitats than in sinks	Holt 1996, 2003
	Beech (Fagus)	Niche conservatism suggested by reciprocal modeling of beech in NA and EU	Huntley *et al.* 1989
	Plants and mammals	Conservatism supported by non-random association of occurrences with projected range	Martinez-Meyer *et al.* 2004; 2006
	Birds, mammals, butterflies	Niche conservatism displayed by sister taxa with adjacent distributions	Peterson *et al.* 1999
		Gene flow crucial to determining local adaptation and range changes	Kirkpatrick & Barton 1997
	Theoretical	Niche conservatism is shown by correlation in range size for disjunctive congeners	Ricklefs & Latham 1992
	Plant communities	Similarity between ants in native and introduced ranges revealed by niche modeling	Roura-Pascual *et al.* 2006
	Argentine ant	Diversity in tropics explainable by higher speciation rates and niche conservatism	Allen & Gillooly 2006
	Plankton diversity		
Niche cons. and shifts	Sundews (Drosera)	Niche shifts shown by clades, described by ancestral climate envelope reconstruction	Yesson & Culham 2006
Niche shift	Plant phenology	Radiation to new habitats is often accompanied by altered phenology	Levin 2006
	Copepods	Niche shifts are adaptive responses to environmental variability	Hairston & Bohonak 1998
	Plant invasions	Ecological and evolutionary processes change during successive stages of plant invasions	Dietz & Edwards 2006
	Genus Arabidopsis	Recently evolved species show greater changes in range and climatic characteristics	Hoffmann 2005
	Invasive species	Niche shift shown by lack of reciprocal predictability between native and invaded ranges	Broennimann *et al.* 2007
	Plant communities	No phylogenetic signal in comparison of occupied plant niches suggests niche shifts	Silvertown *et al.* 2006
	Introduced plant	Introduced populations rapidly adapt to conditions at local latitude	Maron *et al.* 2004
	Pinus contorta	Populations vary in optima of fundamental niche	Rehfeldt *et al.* 1999
	Bivalves	Shifts supported by species origin in warm waters and adaptation to polar regions	Goldberg *et al.* 2005
	Oaks (Quercus)	Niche characteristics and habitat occupancy suggest phylogenetic overdispersion	Cavender-Bares *et al.* 2004; 2006
Niche shifts / speciation	Dendrobatid frogs	Divergence in climatic niche occurred during speciation of Ecuadorian frogs	Graham *et al.* 2004b
Niche size	Edaphic conditions	Niche size is maintained by gene flow and strong selection	Sambatti & Rice 2006
	Invasive plant/labo	Plasticity and niche evolution both contribute to invasive ability	Sexton *et al.* 2002
	Edaphic conditions	Modelling of niche affected by ecotypic variation in soil chemistry tolerance	Wright *et al.* 2006
Phylogenetic / ecological relatedness	Lizards (Anolis)	No relationship exists between clade phylogeny and climate or habitat niches	Losos *et al.* 2003
	New World warblers	Niche conservatism occurs in recently diverged species, shifts at deeper branches	Lovette & Hochachka 2006
	European plants	Niche positions explained by phylogenetic distance and taxonomic levels	Prinzing *et al.* 2001
	Aphelocoma jays	Pervasive niche shifts unrelated to phylogenetic distance	Rice *et al.* 2003
Range limits Sp. richness	Theoretical	Niche limits and demographic process interact to influence range limits	Holt *et al.* 2005a
	New World Birds	Niche conservatism, extinction in basal clades explains species richness gradient	Hawkins *et al.* 2006

NICHE CONSERVATISM MEETS PHYLOGENETICS

The use of the term niche conservatism in the literature is inconsistent. Niche conservatism has been used to signify that niches appear to be statistically correlated over time (Martinez-Meyer *et al.* 2004; Knouft *et al.* 2006; Martinez-Meyer & Peterson 2006), and that the fundamental niche has a tendency to resist evolution (Levin 2005). This latter definition is similar to phylogenetic inertia, in which species have not evolved to reach ecological optima because of the lack of heritable variation or the presence of evolutionary constraints that prohibit occupation of some areas of niche space. The term is also similar to phylogenetic signal (see Glossary), in which trait variation among species remains associated with phylogenetic relationships (Blomberg & Garland 2002). Thus, niche conservatism might be assigned to various patterns resulting from niche dynamics. For example, stasis of the fundamental and realized niches (e.g. through stabilizing selection and competitive dominance, respectively), phylogenetic signal (e.g. owing to finite rates of random divergence of the fundamental or realized niche of species over time) and evolutionary constraints (Blomberg & Garland 2002) could all be considered as niche conservatism. Nonetheless, these relationships remain vague until it is possible to identify the amount of niche change expected over time owing to random processes. Because of these terminological, conceptual and operational difficulties, we suggest that the terms 'niche stasis', 'niche shift' and 'phylogenetic signal' be used predominantly, to minimize confusion in studying niche dynamics.

HOW DOES SPECIES DISTRIBUTION MODELING CONTRIBUTE TO UNDERSTANDING NICHE DYNAMICS?

The use of SDMs has been suggested as a tool with two particular applications: for identifying niche characteristics in natural systems and at spatial scales that make experimentation infeasible (Guisan and Thuiller 2005); and for studying niche dynamics (Wiens & Graham 2005). One way to model and test for niche shifts in response to climate change or speciation events is to predict past species distributions from models fitted under current climate conditions (Graham *et al.* 2004b; Martinez-Meyer *et al.* 2004; Araújo & Rahbek 2006; Benito Garzón *et al.* 2007) (i.e. hindcasting), or similarly to forecast current distributions from models fitted using historical records (Araujo *et al.* 2005c; Walther *et al.* 2005). Some hindcasting studies claim support for minimal niche change using a null hypothesis of change to randomly distributed, independent niches (Martinez-Meyer *et al.* 2004; Martinez-Meyer & Peterson 2006). Nonetheless, methods to estimate the amount of niche change to be expected owing to random processes and to examine species data for deviation from random niche divergence have not been fully developed.

Niche-based SDMs have been used to demonstrate rapid niche changes during invasions by exotic species, for example fire ants (Solenopsis invicta; Fitzpatrick *et al.* 2007) and spotted knapweed (*Centaurea maculosa*, Figure 2; Broennimann *et al.* 2007). By contrast, the invasive Argentine ant (Linepithema humile) in North America shows little evidence of niche shift (Roura-Pascual *et al.* 2006). These examples of using SDMs to compare niche properties between species' native and invaded ranges (over tens to a few hundreds of years), and niches between the present and the late Pleistocene (over thousands of years; Martinez-Meyer *et al.* 2004; Martinez-Meyer & Peterson 2006), show that change in the realized niche can occur over different timescales (Box 1; Table 1). Thus, SDMs can contribute to detecting niche shifts that occur in a species over time or between populations separated in geographic space. This is accomplished by fitting models with occurrence data on the species at one time or in one part of its range, then evaluating the performance of the models when they are projected in time (as in hindcasting) or in geographic space (as with invasive species). Furthermore, these empirical results suggest that the uncritical assumption of niche stasis, so as to allow prediction using SDMs, appears to be questionable at best. New approaches are thus needed to keep predictive modelling from being at the mercy of an untested and understudied assumption. These approaches include consideration of phylogenetics and evolutionary models so as to improve understanding of niche dynamics.

HOW CAN PHYLOGENETICS CONTRIBUTE TO UNDERSTANDING NICHE DYNAMICS?

In the absence of extensive phylogenetic data, comparisons of characteristics of the realized niche in one species over time, or among putative sister-species, have used the criterion of non-random association of pairs of niche measurements to conclude that species niches show limited divergence over time or maintain a phylogenetic signal (Ricklefs & Latham 1992; Peterson *et al.* 1999; Martinez-Meyer *et al.* 2004; Martinez-Meyer & Peterson 2006). These comparisons of realized niches are of limited use in detecting niche change because they involve only relative differences among pairs of species. Also, given enough time, niche stasis is not the null expectation for evolution of the fundamental niche (Blomberg & Garland 2002). Furthermore, the possibility of parallel directional selection (see Glossary), the arbitrariness of taxonomic levels and the lack of knowledge of how much change should be expected given the amount of elapsed time make broader interpretation of simple among-species comparisons difficult.

In contrast to comparisons of species pairs, comparisons based on combining phylogenetic methods with empirical data on environmental niche characteristics might contribute to a better understanding of niche dynamics by providing a framework in which different patterns of distribution of niche characteristics on tree nodes are expected (e.g. Losos *et al.* 2003; Cavender-Bares *et al.* 2004), based on underlying ecological and evolutionary mechanisms (Box 3). For example, a distance matrix that is derived from niche characteristics of species can be compared with a matrix of phylogenetic distances among the species by using a Mantel test or similar

randomization. The presence or absence of significant correlation between corresponding elements of the two matrices is interpreted as the presence or absence of phylogenetic signal in the trait (e.g. Losos *et al.* 2003; Knouft *et al.* 2006; Lovette & Hochachka 2006). Nonetheless, this approach reduces a phylogeny to a distance matrix that, while providing a measure of the concordance between ecological and phylogenetic distances, omits information on the timing and distribution of niche changes on the tree.

In the presence of significant correlation between phylogenetic distance and distance among environmental niche values of species, the question becomes whether there is more or less niche similarity than expected, given the amount of genetic change that has occurred. To address this, phylogenetic analysis, using information contained in tree topology, can be applied to characteristics of the realized niche in a similar way to how it is applied to analyze the evolution of morphological characters (e.g. Silvertown *et al.* 2001; Graham *et al.* 2004b). At the same time, interpretation of the analysis should recognize that niche characteristics observed in the field, as with morphological characteristics of specimens, are influenced by both genetic and environmental factors.

Box 3. A case study: Florida oak niches

Niche shift and niche stasis are unlikely to be a simple dichotomy. A recent study by Cavender-Bares *et al.* (2004) addressed the distribution of species niches and how this varied at different levels of a phylogeny. The authors used ecological, physiological and phylogenetic information to address the co-occurrence of 17 oak (*Quercus*) species that dominate forests in north Central Florida. The authors developed a phylogeny for these species using sequences from two nuclear genes, and evaluated the physiological and physical characters of each species as seedlings (in laboratory experiments) and as adults (in the field). At the community level, they measured ecological habitat characteristics, including soil moisture and fire return interval, and used them to describe niche overlap among species. They then tested for phylogenetic signal by randomizing the phylogenetic distance scores among species. By comparing species co-occurrence frequencies and niche overlap at different levels of phylogenetic resolution, Cavender-Bares *et al.* identified clades at multiple phylogenetic levels in which niche overlap and co-occurrence were either more or less extensive than expected on the basis of a randomization test.

Cavender-Bares *et al.* found that species niches were overdispersed among the major clades in the oak phylogeny, indicating that niche shifts occurred extensively within oak clades and that species within clades were less ecologically similar than would be expected by chance (Figure 1a). Nonetheless, species niche distribution within subclades at intermediate phylogenetic resolution showed greater levels of over-dispersion than occurred either at the species level or in the basal oak clades. Furthermore, the authors suggested that a negative correlation between phylogenetic distance and differences in soil moisture preferences hints at niche convergence among distantly related species. In contrast, consideration of wider taxonomic and environmental scope revealed phylogenetic signal (Figure 1b).

Other studies that used phylogenetic information identified patterns of ecological differences in terms of evolutionary relatedness. For example, patterns in North American wood-warblers (Parulidae) suggest the presence of phylogenetic signal in niche traits in recent speciation, but niche shifts deeper in the evolutionary pasts of the clades (Lovette & Hochachka 2006). In addition, the combination of niche-based distribution models and molecular phylogenies of dendrobatid frogs to estimate ancestral states of niche dimensions suggests niche divergence and complementarity in association with speciation (Graham *et al.* 2004b). Thus, recent studies have documented substantial niche shifts, but niches do not seem to be widely divergent in some cases, with the degree of shift varying with phylogenetic level within

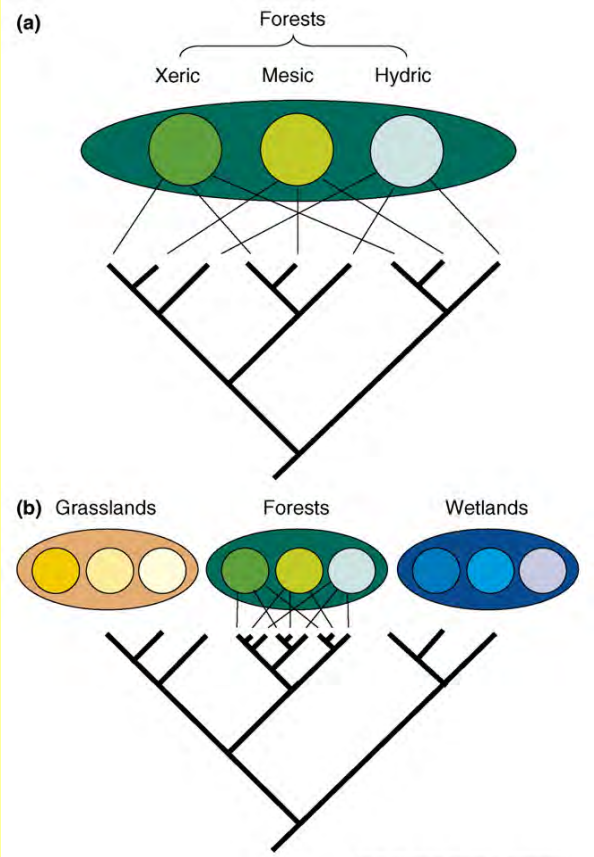

Figure 1- Detecting a phylogenetic signal in the environmental niches of oaks (*Quercus*) depends on environmental variation and phylogenetic tree size. (a) Niche shifts are shown by the over-dispersed pattern of the occurrence of related species in relation to the moisture differences among types of forest (xeric, mesic and hydric); there is no phylogenetic signal. (b) With larger environmental and taxonomic scope, phylogenetic signal in habitat preference is observed when comparing clades at deeper levels on the expanded phylogenetic tree. Dryer conditions occur towards the left of the figure and wetter conditions to the right, both among the three habitat types (grasslands, forests and wetlands) and within each of these groups. Redrawn with permission from (Cavender-Bares 2006).

HOW CAN EVOLUTIONARY MODELS CONTRIBUTE TO INFERENCE ON NICHE DYNAMICS?

The application of evolutionary models of character change supports our understanding of niche dynamics by helping us to choose among particular evolutionary processes that might have influenced patterns of niche change. For example, random evolution of a character (e.g. an aspect of the environmental niche of a species) over time can be modeled by the Brownian motion model, a null model (see Glossary) of character evolution in which direction and degree of change vary randomly over time and for which there are no additional constraints (Felsenstein 1988). The resulting among-species distribution of the magnitude and direction of character change is Gaussian (bell-shaped), with a single expectation of no change and a finite standard deviation. This process results in among-species variance in character values (e.g. niche metrics) that increases with the square root of elapsed time (Felsenstein 1988).

A family of models, of which Brownian motion character-change is a special case, incorporates the possibility that selection can act, in addition to random effects, as a source of character differences among species (Hansen 1997). Selection in these models can include both directional and stabilizing selection through a series of hierarchical models that include one or more terms for ecological optima for extant species, in addition to a term for Brownian motion (Butler & King 2004). Parameter estimation is possible through the use of likelihood methods, whereas a model comparison approach can determine which model of character change is most supported by the data (Butler & King 2004). For example, Losos *et al.* (2003) failed to reject a Brownian motion model in favor of constrained evolution affecting the realized niche (Box 4). Other methods to detect non-Brownian evolution (e.g. by detecting that potential environmental niches are filled non-randomly in association with speciation events) are also possible by correlating phylogenetic contrasts with the height of the nodes at which the contrasts are assembled. A significant correlation leads to rejection of the Brownian motion model because trait evolution occurs systematically throughout the tree (Freckleton & Harvey 2006).

Box 4. Absence of phylogenetic signal in an Anolis assemblage

Niche conservatism (in the sense of evolutionary constraint through stabilizing selection) might be supported if species in a phylogeny had diverged less than would be expected from a Brownian motion model of evolution. Losos *et al.* (2003) tested for constrained niche evolution by determining whether 11 Anolis lizards in an evolutionary radiation on Cuba are less distantly related ecologically than predicted, given the time since their divergence. The authors evaluated environmental, behavioral and morphological variables using principal component analysis, placing the 11 species in a four dimensional multivariate character space, and also reported the development of a phylogenetic tree of 129 Anolis species, including the species on Cuba, using mitochondrial DNA. For this insular lizard assemblage, Losos *et al.* used Mantel tests to examine the relationship between phylogenetic distance and character similarity, but found no significant correlation. The authors interpreted the lack of phylogenetic structuring of the traits to indicate that niche shifts have dominated the evolution of the assemblage.

Losos *et al.* also constructed additional phylogenetic trees using maximum likelihood methods that were constrained in various ways to hold ecologically similar species as sister taxa. These trees were also rejected, providing more evidence for ecological difference between closely related species. These results also indicated that, for the two clades they examined, the species of the two groups were not less similar than expected under a Brownian motion model of divergence, suggesting that niche evolution has not been constrained. One explanation for Anolis divergence could be that behavioral characters are more likely to be involved in niche shifts than are other types of traits, because some evidence suggests that behavioral traits are less evolutionarily constrained than morphological traits (Blomberg *et al.* 2003). Six of the seven traits measured by Losos *et al.* were behaviorally mediated, such as body temperature, the use of rocks, and perch diameter, but such behavioral characteristics are often associated with phenotypic differences.

HOW HAVE ENVIRONMENTAL NICHE DATA, PHYLOGENETICS AND EVOLUTIONARY MODELS BEEN COMBINED?

The combination of niche modeling and the use of phylogenetic methods has demonstrated shifts of realized environmental niche that are associated with speciation and ecological diversification. For example, Knouft *et al.* (2006) examined the degree to which phylogenetic similarity parallels similarity of realized climatic niches (see Glossary) of Cuban Anolis lizards. The authors recognized that a negative correlation between evolutionary distance and niche similarity would suggest that niches tend to show phylogenetic signal, perhaps similar to Brownian motion evolution. They used a phylogenetic tree of 11 Cuban Anolis species to calculate the sum of the branch lengths between pairs of individuals, each representing a distinct species, and determined the niche similarity of the species in terms of climatic niche dimensions. The authors found no significant correlation between niche similarity and phylogenetic distance, indicating no detectable phylogenetic signal in the characteristics of the climatic niche.

In another example, Graham *et al.* (2004b) used climatic variables, species occurrence data, niche modeling and a phylogeny to describe the relationships among niches of species in three clades of dendrobatid frogs in Ecuador. Because the authors' methods hinged on reconstruction of the ancestral climate niche, and given that these reconstructions are error-prone (Schluter *et al.* 1997),

the authors tested for directionality in the evolution of pairs of sister species y comparing the phylogeny of the frogs (a maximum likelihood tree) with what might be produced if trait evolution were to follow a Brownian motion model. They failed to reject the adequacy of invoking a Brownian-like evolutionary process to explain among-species differences in niche traits. They also found, however, that sister species generally showed niche divergence along gradients of moisture and seasonality.

IS SCALE IMPORTANT IN STUDYING NICHE DYNAMICS? A CAVEAT

Recent studies have shown that the scale of investigation, be it spatial, temporal, environmental or phylogenetic, is important in studies of niche dynamics. The effects of scale (e.g. in studying the climatic niche) can be tied to the spatial resolution at which climatic information or species distribution data are available (Figure 3). In some cases, data will thus need to be collected and/or analyzed at multiple resolutions and extents. For instance, Broennimann *et al.* (2007) showed that rapid niche change was detectable when both native (European) and invaded (North American) ranges of an exotic plant were compared (Figure 2). The temporal period in their study was only 120 years, but the geographical extent was large, encompassing Europe and the western United States. Similarly, the statistical power to detect phylogenetic signal within a clade depends on tree size and the taxonomic inclusiveness of the study (Blomberg *et al.* 2003, Cavender-Bares *et al.* 2006). In their biogeographical study of native vegetation in northern Florida, Cavender-Bares *et al.* (2006) (Box 3) found that phylogenetic signal was more evident when more environments and a larger phylogenetic tree were used to examine the phylogenetic structure of oak (Quercus) and other plant communities (Box 3, Figure I).

Variation in choice of scale thus influences our ability to identify niche shifts, to determine their prevalence within a phylogeny, and to evaluate their magnitude. These results suggest that multi-scale studies of niche shifts, using both phylogenetic trees and niche-based SDMs, will help us to identify clades that are especially prone to shifts in environmental niche. Multi-scale studies will also produce empirical guidance regarding the scales at which studies of environmental niche need to be conducted to describe adequately niche-shift prevalence and magnitude.

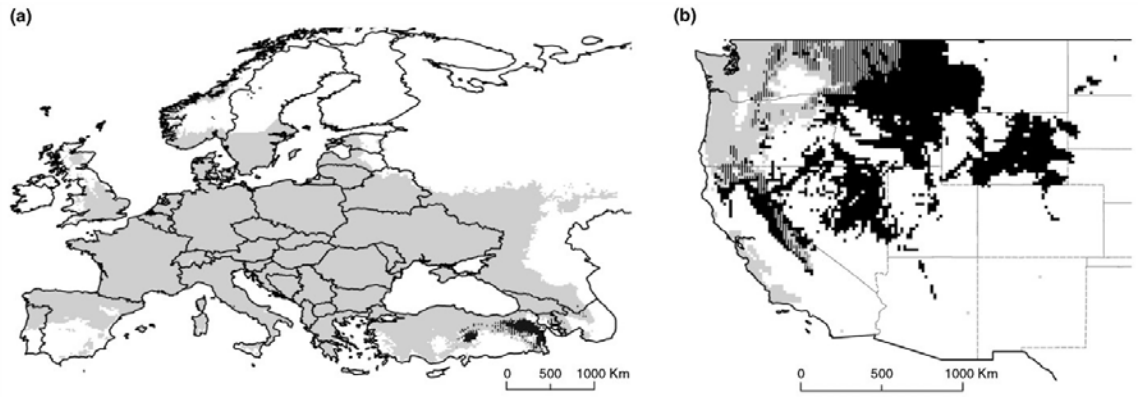

Figure 2 - Niche shift in an invasive plant, spotted knapweed (*Centaurea maculosa*). The distribution of spotted knapweed was modeled with eight modeling techniques, and consensus predictions are shown (six of eight models). (a) The modeled distribution of spotted knapweed in Europe. Here, the gray area indicates predicted presence when the models have been calibrated with occurrence data from the European range. When this 'European model' is projected to the western United States (b), the predicted range of the species is shown again in gray. However, when the models are calibrated with occurrence data from the USA, the species is predicted to occur in the black area. Projection of the 'United States' model to Europe (a) leads to predicted presence, shown also in black. The gray and black hatched areas in both panels show that there is little area that both models predict as being occupied by the plant and, thus, provide a spatially explicit representation of a shift in the species realized climatic niche. Adapted with permission from Broennimann *et al.* 2007.

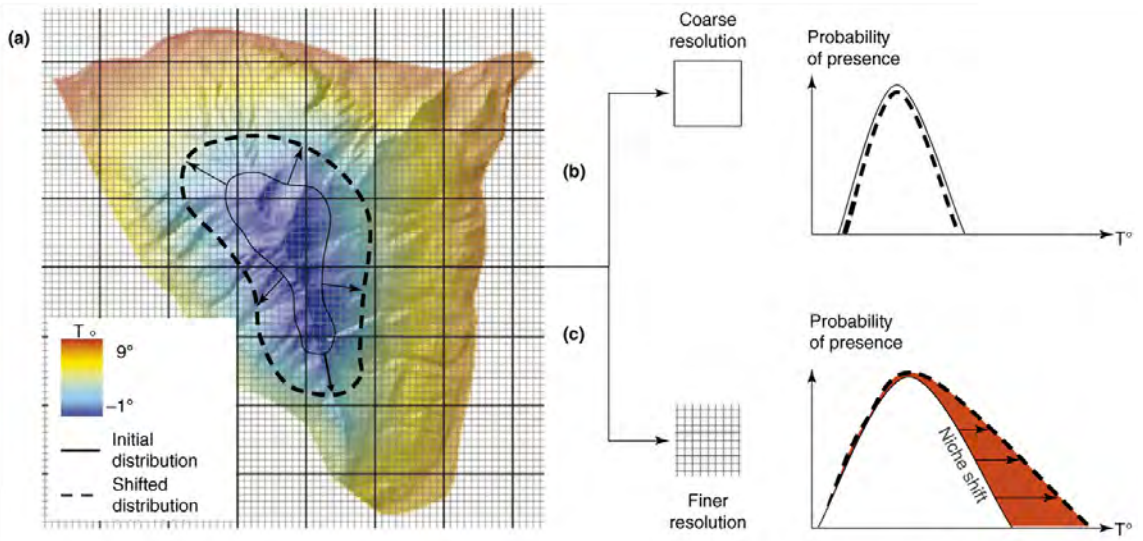

Figure 3. Effect of sampling resolution on detecting an environmental niche shift. (a) A hypothetical gradient of annual mean temperature is shown by color shading on a mountain peak. The realized niche of a hypothetical plant shifts to include warmer temperatures, with a corresponding expansion of the distribution of the plant to lower altitudes. The initial and expanded distributions of the species are shown by solid and dashed lines, respectively. Large and small cells (squares) show a difference in spatial resolution (in this case, 10x) of data on species occurrence and local temperature, as might be obtained from a sampling program. (b) When temperature variation (and/or species presence) is expressed at a coarse resolution, both initial and shifted niches result in estimated species distributions that show identical probabilities of species presence as a function of temperature. (c) Expression of spatial variation at a finer spatial resolution enables detection of the niche shift, shown by the increased probability that species will be present at higher temperatures (i.e. lower elevation).

WHAT CAN WE CONCLUDE REGARDING THE DYNAMICS OF THE ENVIRONMENTAL NICHE?

Understanding niche dynamics is a prerequisite to predicting patterns of biodiversity in future climates or in areas distinct from where models are fitted. However, neither niche stasis nor rapid niche shift prevail in current studies (Table 1). It would be helpful to know whether niche shifts are likely to occur in the case of biological invasions, and whether niche stasis predominates in the case of climatically induced range shifts within a region. However, the necessary data for these conclusions do not exist. In the case of biological invasions, a strong founder effect (see Glossary) followed by genetic drift, directional selection or hybridization might occur frequently, but sufficient studies to support this possibility have not yet been conducted. Clearly, studies that combine phylogenetic and ecological data show that closely related species can frequently diverge along one or more environmental gradients (Rice *et al.* 2003; Cavender-Bares *et al.* 2004; Graham *et al.* 2004b; Cavender-Bares *et al.* 2006). Nonetheless, the degree to which niche dynamics might affect predictive modeling is not yet known, which should weaken confidence in the conclusions of studies relying on SDMs to predict effects of climate change or species invasions. The most important action that can be taken to boost this confidence is to collect the data necessary to identify biological factors, both current and historical, that are associated with patterns of niche dynamics.

WHAT REMAINS TO BE DONE?

The patterns of niche dynamics over time need rigorous study. Sufficient empirical work is needed to conduct meaningful meta-analyses of correlates of niche dynamics. Confidence in the use of niche-based SDMs for prediction will increase markedly with a general understanding of how environmental conditions influence rates of niche change, the spatial and temporal variability of these rates, their variation with time-span under consideration, focal clade, the life-history variability of the component species in the clade, and phylogenetic tree size. For example, we speculate that clades that have high rates of polyploidy, species with strongly bimodal dispersal distances, and ample genetic variation within species are more prone to rapid niche shifts than are clades where these characteristics are absent. Similarly, the realized niche of competitively dominant species might be unlikely to change over any timescale. Other possibilities could be suggested, and supportable hypotheses should be tested.

There is an additional need for comparative studies that identify both the groups of species that are characterized by environmental niche stasis or shifts, (e.g. Yesson & Culham 2006) and the attributes that these species share. Similarly, the question of which characteristics of the realized niche need to be measured should be addressed. One could, for example, first estimate a variety of modeling parameters that describe niche traits (e.g. environmental limits, estimated environmental optima, niche position etc.) and then analyze whether and how use of these parameters affects discernable

phylogenetic patterns of niche change. Probably, models that describe the realized niche using variables that are closely related to functional and physiological species characteristics will provide more meaningful ecological and evolutionary information than do models using other variables.

Increasing refinement of alternative hypotheses, such as alternative models of the evolution of the environmental niche, are likely to contribute to understanding evolutionary and ecological factors associated with patterns of niche dynamics. Furthermore, alternative models for character change have recently been developed in both phylogenetics (Mooers *et al.* 1999; Pie & Weitz 2005) and quantitative genetics (Estes & Arnold 2007). These methods enable one to identify trends in niche dynamics, for example, clade propensities for experiencing stabilizing and/or directional selection, the contribution of random evolution to niche dynamics, and the existence of evolutionary stable lineages within portions of clades. These approaches have yet to be applied to environmental niche related characters, in general, and specifically to characteristics of the climate niche. New studies can attempt to identify lineages in which niche shifts are either overwhelmingly small or unlikely, such as lineages with a strong phylogenetic signal, evidence of a long history of stabilizing selection, and maintenance of niche characteristics in spite of wide geographical separation of species distributions. Species identified in these studies will be good candidates for more confident predictions of their response to climate change.

The relative contributions of directional and stabilizing selection to among-species variation in niche characteristics can now be analyzed with new tools (Butler and King 2005). By helping us to choose species with conservative evolutionary histories, these analyses will provide additional confidence in predictions made with SDMs. By contrast, estimating the propensity for niche change, and the historical rate and magnitude of niche change in clades could help us to identify lineages in which the probability of future niche change is great relative to other lineages. Studies that put trait variability into a phylogenetic context are likely to identify lineages with a propensity for niche change and, for example, identify species that might become invasive when introduced to new areas. To do this, we require greater understanding of the relationship between the rate of niche change over phylogenetically meaningful time spans and the rate of niche change over a hundred to several hundred years. This will help us to predict the frequency of niche shifts and other niche dynamics over the short term. The interpretation of phylogenetic data in the context of rapid niche change might involve the use of calibrated trees for which the actual rate of niche change could be calculated. These areas remain open for investigation.

Finally, although observed changes in environmental niche might be due to evolution of the fundamental niche, currently there is no method to evaluate the relative influence of fundamental and realized environmental niches to niche variation arising from either speciation or change within a species over time. We suggest that innovative combination of phylogenetic methods and physiological experimentation to model the fundamental niche (e.g. Kearney & Porter 2004) could

answer, if only partially, the question of the relative importance of changes in the fundamental and realized niches in observed patterns of niche dynamics.

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Chapter 6

SYNTHESIS & PERSPECTIVE

6.1 - SYNTHESIS & IMPLICATIONS IN RECENT LITERATURE

The three main chapters of this PhD thesis present original studies focusing on the use of NBMs to investigate the impact of global changes on biodiversity.

Chapter 2 illustrates the case of endangered plant species in Switzerland and proposes analyses and methods to implement or support conservation planning approaches. The first study (chapter 2.1) demonstrates that very few highly endangered species in Switzerland are both regionally restricted and endemic on a worldwide scale. Therefore, a global assessment of rarity might be misleading for some species because it can fail to account for different degrees of rarity in different places. Rarity should rather be considered at a variety of spatial scales. The worst risk of not attributing a high conservation priority to a species that would be largely distributed over the world, but becoming rare at each national scale would be to observe simultaneous extinctions in all countries. This option deserves to be considered more seriously in national and international conservation strategies.

The particular case study (chapter 2.2) on *Eryngium alpinum* further demonstrates that a model-based sampling (MBS) of rare species, involving reiterative alternation of modeling and field sampling phases, shows great promise for strengthening and complementing conservation practices and reducing sampling costs. Hughes *et al.* (2008) use a similar approach to identify unsurveyed areas which may harbor isolated populations of the riverine rabbit endemic to South Africa or offer opportunities for re-introduction or introduction of the species. Similarly, Aitken *et al.* (2007) developed predictive maps for four endemic plants in the Great Basin of western North America on which a field survey was performed. They validated their approach and developed final models through a similar iterative process, in which data collected during the field validation were incorporated into subsequent predictive models. Zimmermann *et al.* (2007) further propose to strengthen the method by including remote sensing-based predictors in the model because there are many reasons why a species may be rare, and not all these reasons may be modeled from topo-climatic predictors (Edwards *et al.* 2005). Remotely sensed predictors may capture subtle differences in either the soil/vegetation characteristics or in the phenology linked with the rare species. A further suggestion of future work could be to assess for which type of rarity the MBS approach would yield the best improvement

Chapter 3 illustrates the application of NBMs in the assessment of the impact of climate change on biodiversity. The first study (chapter 3.1), investigating the vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions, shows that a substantial number of species could be critically endangered in the future because of climate change and land transformation. It further highlights that the sensitivity of African national parks show a very distinct pattern in accordance with the biomes in which they occur. National parks situated in xeric and desert shrublands are not expected to meet their mandate

of protecting current mammalian species diversity within park boundaries in the future. This study has been cited as example of threat of global extinction of large-herbivore (e.g. Gaston & Fuller 2007; Robinet *et al.* 2007; Ritchie *et al.* 2008). Furthermore, two recent papers (Rodriguez *et al.* 2007; Thuiller *et al.* 2008), reviewing the future challenges in predicting global change impacts on plant species' distribution, cite this study as an example for including the dynamic nature of biodiversity for the evaluation of the future performance of protected areas.

The second study (3.2) models the future distribution in 2050 of 975 endemic plant species in southern Africa distributed among seven life forms and shows important promises for predicting the impacts of climate change in conjunction with land transformation. The study further demonstrates that species and life form vulnerability to global changes can be partly explained according to species' (i) geographical distribution along climatic and biogeographic gradients, like climate anomalies, (ii) niche breadth or (iii) proximity to barrier preventing migration. These results confirm that the sensitivity of a given species to global environmental changes depends upon its geographical distribution and ecological proprieties, and makes it possible to estimate a priori its potential sensitivity to these changes.

The study proposes the inclusion of new methodological insights improving the accuracy and ecological realism of predictions of global changes studies by: (i) using only endemic species as a way to capture the full realized niche of species, (ii) considering the direct impact of human pressure on landscape and biodiversity jointly with climate, and (iii) taking species' migration into account. The use of explicit species' dispersal ability we proposed in this study has been recognized as an important issue for the improvement of climate change impact studies (Pearman *et al.* 2008a; Thuiller *et al.* 2008). For example, Manne *et al.* (2007) refined this approach to project future Fynbos species distributions in the Cape floristic region by assuming dispersal distance to be a maximum of 1.5 km in 10 years for ant- and rodent-dispersed species and a maximum of 4 km in 10 years for wind-dispersed species.

Chapter 4 illustrates the application of NBMs in the study of biological invasions. The first study (chapter 4.1) retrospectively analyzes the spread of *Lactuca serriola* in Europe in relation with climate change during the last century and shows that for the last two decades, the species could not track climate change due to non climatic influences predominately contributing to the spread of the species.

The second study (chapter 4.2) analyzes the climatic niche spaces of spotted knapweed in western North America and Europe and provides the first empirical evidence that an invasive species can occupy climatically distinct niche spaces following its introduction into a new area. This fact was further confirmed with similar studies on ants (Fitzpatrick *et al.* 2007; Steiner *et al.* 2008). This is problematic since NBMs predicting the potential spatial extent of species' invasion relies on the assumption that invasive species conserve their climatic niche in the invaded ranges. This issue has

been highlighted in recent reviews on ecological and evolutionary insights from species invasions (Sax *et al.* 2007) and on the integration of GIS-based environmental data into evolutionary biology (Kozak *et al.* 2008), on the future challenges when predicting global change impacts on plants distributions (Thuiller *et al.* 2008) and on the niche dynamics in space and time (Pearman *et al.* 2008a). Furthermore, the study has raised (together with the work of Fitzpatrick *et al.* 2007) a debate in the literature concerning the appropriate choice of environmental data sources (Peterson & Nakazawa 2008; Peterson & Nyari 2008). Peterson and co-authors argue that the geographical patterns predicted by NBMs may be contingent on environmental dataset chosen for the study and that, in the case of biological invasions, lack of correspondence between actual and predicted areas distribution in the invaded range is due to overfitting which does not imply biological considerations. Stimulated by a recent analysis (Fitzpatrick *et al.* 2007) showing niche shifts similar to those of our study on spotted knapweed, they further analyzed the invasion by fire ants (*Solenopsis invicta*) from their native distributional area in South America into the southern United States using six environmental data sets. They show differences in model generality when models are based on different environmental data sets, with one (out of six) dataset correctly predicting both the invaded and the native range using native range occurrences. However - and among other flaws - their conclusions are based on visual comparisons between actual and predicted distribution in the invaded range (the predictive power of models are not considered in the native range). The authors do not test the hypothesis of niche shift with an appropriate statistical alternative (see also Fitzpatrick *et al.* 2008). Their consideration of what constitutes a correct prediction may thus be subjective.

The third study (chapter 4.3) proposes, as an alternative to the calibration of models with occurrences from the native range, that models be trained using data from both native and invaded ranges. We show that this approach yields accurate predictions in the invaded range because i) the models can predict the future spread of the species in areas that are not yet invaded but where suitable conditions similar to the native range occur and ii) niches implicitly fitted by these models can express a larger part of the fundamental niche, translating the fact that biotic releases may allow the species to occupy climatic situations from which it was excluded in the native range. The study further demonstrates that this pooled approach significantly reduces areas of future predictions and reduce the uncertainty between modeling techniques.

6.2 - VALIDATING ASSESSMENTS OF GLOBAL CHANGE IMPACT

Increasing concern over the implications of global change for biodiversity has led to the use of NBMs to project species extinction risk under climate change scenarios, to quantify the effect of land-use change or to predict the future extent of species invasions. However, recent studies have demonstrated significant variability in model predictions and there remains a pressing need to validate models and to reduce uncertainties. For the investigation of climate change impacts, model validation is problematic as predictions are made for events that have not yet occurred. Similarly, for the investigation of biological invasions, this may be problematic because the invasion process may not be completed, leading to commission errors.

Re-substitution and data partitioning data sets are, therefore, commonly used to test the predictive performance of models. However, these approaches suffer from the problems of spatial and temporal autocorrelation in the calibration and validation sets. For climate change studies, uncertainty provided by the combination of different analyses, spatial resolutions, scales, modeling techniques and evaluation methods may be greater than the variability of using different climate change scenarios (Thuiller 2004). Over-predictions or over-parameterization greatly affect models and could explain why two NBMs calibrated on the same species could produce different projections (Thuiller 2004). Better understanding of the behaviour of models and better evaluations of their predictive power are both necessary to facilitate such projections (Boone & Krohn 2002). Recent developments, combining different algorithms within a common framework and exploring the central tendency (consensus) of model projections, may lead to improve agreement between projected and observed shifts (Thuiller 2004; Gelfand *et al.* 2005; Araujo & New 2007).

It may be argued that the predictive accuracy of NBMs can only be fully tested by means of validation studies using direct comparison of model predictions with independent empirical observations. Attempts to perform such tests are relatively rare. A limited number of studies have attempted independent validation using known distributions in different regions (e.g. Peterson 2003), data at different resolutions (e.g. Pearson *et al.* 2004; Araujo *et al.* 2005b), field observations in previously unsampled regions where species' occurrences are predicted (e.g. Raxworthy *et al.* 2003) and pollen or fossil records under past climates (e.g. Martinez-Meyer *et al.* 2004; Pearman *et al.* 2008b). Using observed distribution shifts among 116 British breeding-bird species over the past 20 years, Araujo *et al.* (2005a) provide a first independent validation of four envelope modeling techniques under climate change. Results showed good to fair predictive performance on independent validation. They showed that measures of performance on non-independent data provided optimistic estimates of models' predictive ability on independent data. This result supports cautious use of measurements of accuracy on non-independent data as a surrogate for accuracy on independent data

6.3 - IMPROVING NBM FOR THE ASSESSMENT OF GLOBAL CHANGE IMPACTS

Models are simplifications of reality and are often first conceived to help researchers to formalize their understanding of a particular process or pattern of interest. NBMs are static models and their validity and interpretability limited by the assumptions of niche conservatism and equilibrium with the environment. Consequently, this category of models does not explicitly take into consideration the effects of important ecological and evolutionary factors such as species dispersal biotic interactions between species or rapid adaptive evolution. Difficulties may therefore arise when such theoretical models are used to guide conservation planning, management and to support the formulation of policy decisions. As a result, conservation practitioners often prefer to avoid the uncertainties in projections and concentrate on protecting current patterns of biodiversity. To increase confidence in model projections, methodologies must acknowledge clearly the uncertainties involved and try to obtain conditional measurements of confidence in the forecasts made (Thuiller 2004; Schröter *et al.* 2005; Berry *et al.* 2006; Araujo & New 2007; Thuiller 2007). I do not review here the limitations inherent to NBM studies in general since several recent papers discuss this issue (Peterson *et al.* 2002; Hampe 2004; Thuiller *et al.* 2004c; Guisan & Thuiller 2005; Araujo & Guisan 2006). I rather focus on limitations and assumptions strictly relevant to the application of NBM for the study of global changes:

1) Biotic interactions - Natural systems consist in a complex web of interactions and feedbacks between species. Changes to the distribution of a single species could have significant feedbacks on the distributions of many other species. Biotic interactions are thus shown to have important impacts on species distributions. NBMs correlate climate variables with observed distributions, adopting the general assumption that the best indicator of a species' climatic requirements is its current distribution. Such correlative models thus characterize bioclimatic envelopes based on the *realized* niche, since observed species' distributions are constrained by non-climatic factors, including biotic interactions.

   In the case of global change however, the different species in presence are expected to respond idiosyncratically to various ecological forces. Thus, ecological communities may disassemble as individual species shift their ranges in different directions. When projecting NBMs in future warmer climate, biotic interactions may be altered (e.g. because of different migration rates). In such cases, projections of species distributions are likely to generate mistakes (Davis *et al.* 1998a). In principle, the same limitation exists when projecting NBMs to other areas with different floras or faunas. Testing the transferability of models in space may already provide a useful assessment on the validity of these future projections (Randin *et al.* 2006). In the case of biological invasions, interactions might change simply because of transplantation into natural communities that evolved separately since millennia. We demonstrated for instance (Broennimann *et al.* 2007) that the realized niche of spotted knapweed was altered after the

introduction of the species in its invading range, compromising the prediction of the full extent of the invasion from models fitted in the native range.

In addition to these considerations, there is a debate whether climate is driving species distributions at macroecological scales. It is argued that applying bioclimatic models at macro-scales, where climatic influences on species distributions are shown to be dominant, can minimize the impact of biotic interactions (Willis & Whittaker 2002; Pearson & Dawson 2003). In other words, the prevailing idea is that climate is the key limiting factor at macroecological scale; thus models that use present-day climate-species range relationships are expected to provide reasonable means to quantify the impacts of global change on species distributions at macroecological scale. It has already been shown that a number of correlative bioclimatic envelope models have been successfully used to simulate the distributions of higher plants in Europe (e.g. Huntley *et al.* 1995; Pearson *et al.* 2002; Thuiller *et al.* 2005b). These modeling results support the hypothesis that continental-scale distributions are principally determined by climate. It is thus suggested that many species distributions can in fact be considered to be in equilibrium with the current climate at the macro-scale.

However, for most species, it is unknown how much of its fundamental niche is represented by its realized niche. For instance we could expect this proportion to be related to its competitive and dispersal abilities. Several studies have demonstrated that some species are not in equilibrium with their environment (Pearson *et al.* 2002; Svenning *et al.* 2006) or have undergone a severe shift of their realized climatic niche over time (Pearman *et al.* 2008). For example, Skov and Svenning (2006) modeled the potential distribution of 55 European trees and compared their potential to their actual range. They found that the range filling of these tree species was low (38.3%). Such inaccuracies can be expected for species' distributions that show extensive fragmentation (for non-climatic reasons) within a species' climate space or if species ranges is strongly controlled by geographical dispersal constraints on post-glacial expansion. Araujo & Luoto (2007) showed that the effects of biotic interactions on individual species distributions at macroecological scales are contingent on the species, type of interaction and methods considered. They call for more evidence in support of the idea that purely climate-based modeling would be sufficient to quantify the impacts of climate change on species distributions (Araujo & Luoto 2007).

Process-based models do not make the assumption of equilibrium and are not dependent upon identifying a relationship between the current distribution and climate for characterizing the bioclimatic envelope of a species. It may thus be argued that in basing the model on physiological limits to a species' climatic tolerance, the bioclimatic envelope identified will better represent a species' absolute climatic limits than that identified through the correlative approach (Woodward 1987). However, such models are equally limited in their inability to account for

non-climatic influences and have a number of important limitations that may lead to model inaccuracies. Most importantly, fundamental niches are not realized, and nor will they be realized in the future. Thus, predicted future species distributions based on the physiologically determined fundamental niche are unlikely to be as accurate as those based on correlations between the observed distribution and the current realized niche. Moreover, these models require the parameterization of high number of demographic and physiological factors which are largely unavailable for most natural species (i.e. most physiological studies concern species of agricultural or forestry interest, thus most dynamic models only exist for forests). Since correlative techniques do not require detailed physiological data about individual species, they also have the advantage that they can easily be applied to a large number of species. This enables conclusions regarding the potential impacts of climate change on a wide range of species, and thus habitat assemblages, to be made (e.g. Berry *et al.* 2002).

It is apparent that there are limitations to both correlative and process-based modeling methodologies. An alternative approach would be to base predictive models on fundamental (i.e. physiological) responses obtained from field or laboratory experiments, and constrain these by general rules of biotic interactions, dispersal behavior and populations dynamics, in order to obtain more realistic predictions of species distribution under changing environments (Guisan & Thuiller 2005).

2) Dispersal limitations – NBMs do not account for species dispersal, but instead aim to predict the potential range of organisms under changed climate. In most projections, species dispersal is inappropriately taken into consideration, relying either on a *no dispersal*, or an *unlimited dispersal* scenario (e.g. Thomas *et al.* 2004; Thuiller *et al.* 2005b; Engler & Guisan in revision). These scenarios represent two rather unlikely extreme situations. With a *no dispersal* scenario, a species can only loose habitat as climate changes. This will be the case for sedentary species or poor dispersers which might occupy only current distributional areas that remain suitable under future climates (Collingham *et al.* 1996; Peterson *et al.* 2001; Engler & Guisan in revision). Conversely, with an *unlimited dispersal* scenario, all habitats that become suitable can be colonized. Sufficiently mobile species can be expected to track the geographical position of their bioclimatic envelope through dispersal. However, the ability of a species to migrate at a sufficient rate to keep up with the changing climate will be dependent on the dispersal characteristics of individual species, with future migration rates required to be at least equal to those of the early postglacial period (Collingham & Huntley 2000; Engler & Guisan in revision).

The ability to migrate is a function not only of individual species' characteristics, but also the structure of the landscape over which dispersal is occurring (Iverson *et al.* 1999a; Collingham & Huntley 2000). This includes the presence of natural barriers (such as mountain ranges) or the

anthropogenic fragmentation of habitats (e.g. through the growth of urban areas or deforestation). It can thus be expected that in many areas of the world, where artificial landscape fragmentation prevails and land-uses are changing rapidly, species will be unable to migrate at a sufficient rate to keep pace with the changing climate. In such cases predictions of future distributions derived from bioclimatic models will be erroneous (Pearson & Dawson 2003).

Accurate predictions of the future distribution of species will require detailed knowledge of the ability of species to migrate through dynamic heterogeneous landscapes within the constraint of changing bioclimatic envelopes. The simplest approach to include this knowledge is to attribute an estimate of migration rate per unit of time according to estimated migration rates in the past (for example from climatic upheavals in the Holocene; Broennimann *et al.* 2006) or according to the dispersal agent of the selected species (e.g. Wiliams *et al.* 2005). Such an approach is easily implemented within NBMs and could be used to assess risk in global change analyses. A second approach couples a landscape model simulating habitat fragmentation and dispersal events with NBMs (e.g. Carey 1996; Schwartz *et al.* 2001; Iverson *et al.* 2004; Engler & Guisan in revision), where the NBM current and future predictions represent the potential environmental shift required by species, while the cellular automaton predicts the more realistic continuous shifts based on dispersal abilities and colonization probabilities from varying suitable source populations (i.e. pixels) within a fragmented landscape.

Restricted species' dispersal presents an important limitation to the current bioclimatic modeling approach. However, there is evidence from the paleo-ecological record that climate change is sufficient to explain continental-scale patterns of plant migrations. The success of global bioclimatic reconstruction models in simulating Holocene changes in distribution for some species (e.g. Huntley *et al.* 1989) supports the hypothesis that organisms were able to migrate fast enough to allow their range limits to track climatic changes sufficiently to avoid getting extinct. It is expected that the ability of species to migrate rapidly across large distances is driven primarily by rare long-distance dispersal events (Clark *et al.* 1998). Indeed, recent studies have highlighted the extreme importance of long-distance dispersal events, with illustrative examples drawn not only from palaeoecology but also from contemporary observations of island colonization and alien plant spread (Clark *et al.* 1998; Cain *et al.* 2000b). In such cases, the assumption that species are able to migrate to occupy their suitable climate space may not be so unrealistic. Simulations of plant migrations along an elevation gradient also suggest that the unlimited dispersal scenario might yield realistic projections on average (across many species), but might remain overoptimistic for some species (Engler & Guisan in review).

3) Evolutionary changes – Genetic adaptation of species is rarely considered in the literature on the biotic effects of past and potential future global change. This is regardless of the fact that the implications of rapid evolutionary change are important for bioclimatic envelope modeling since the assumption of niche conservatism will be wrong for species experiencing sufficiently rapid adaptation.

In NBMs studies, it is usually expected that evolutionary change occurs only on long time scales and that the tolerance range of a species remains the same as it shifts its geographical range. Fossil record favors the hypothesis of niche conservatism for most species in a climate change context (Prinzing *et al.* 2001; Ackerly 2003; Wiens & Graham 2005). Some bioclimatic studies of past climate-species distribution relationships also provide evidence that adaptation to future climates will not occur for most species (Huntley *et al.* 1989; Peterson *et al.* 1999). For example, Huntley *et al*. (1989) fitted climate response surfaces to beech (*Fagus* spp.) distributions in Europe and eastern North America. They were able to simulate distribution patterns in Europe during the Holocene using the response surface derived for North America, and vice versa. This suggests that the North American and European beech populations have retained similar climatic tolerances since their separation between 25 and 10 My ago, supporting the hypothesis that, for this species, fundamental physiological limitations have been unaffected by evolutionary processes over this long timescale. Similarly, in an experimental study on a native legume of the American Great Plains (*Chamaecrista fasciculata*), Etterson & Shaw (2001) conclude that predicted rates of evolutionary response for plants of this kind are much slower than the predicted rate of climate change (due to antagonistic genetic correlations among traits within populations).

However, studies have shown that climate-induced range shifts can involve not only migration into newly suitable areas, but also selection against phenotypes that are poor dispersers or are poorly adapted to local conditions (e.g. Davis & Shaw 2001; Thomas *et al.* 2001). For example, the potential importance of rapid evolutionary change in the context of climate change has been demonstrated by Thomas *et al*. (2001) who examined insect species that have expanded their geographical ranges in Britain over the past 20 years. Two species of bush cricket (*Conocephalus discolor* and *Metrioptera roeselii*) were shown to have increased fractions of longer-winged (more dispersive) individuals in recently founded populations, whilst two butterfly species (*Hesperia comma* and *Aricia agestis*) have increased the variety of habitat types that they can colonize. Recent evidences of changes in the climatic requirements of invasive species after their introduction on a new continent (Broennimann *et al.* 2007; Steiner *et al.* 2008) support this view.

Predicting the effect of adaptive changes to species in response to global change presents a huge challenge to modelers and has not, to date, been accounted for within the NBM

framework. As we can see from the previous paragraphs, there is no unified view on how evolutionary changes will affect the predictions. Part of the problem probably comes from the fact that NBMs only predict how the entire distribution of a selected species (i.e. as a whole) will be modified in response to a given environmental change. The species is considered as a homogeneous and immutable entity and each population is assumed to be constrained by the same ecological requirements, whatever its position within the distribution (i.e. niche conservatism assumption). To predict the future distribution of a species, more attention should be given to simulating ecological and evolutionary processes at the leading and rear edges of the distribution where range change (i.e. migration, persistence, extinction, evolution) happens (Hampe & Petit 2005). Under climate change and during biological invasion, range expansions depend mostly on populations at the colonization front. The leading edge of species distributions is controlled by rare long-dispersal events followed by exponential population growth (Hewitt 1993; 2000; Hampe & Petit 2005). The investigation of such processes is fundamentally important because leading edges consist in small and isolated populations potentially driven by a greater degree of environmental stress and inbreeding depression (Willi *et al.* 2006). Under warming climate, rapid genetic adaptations are especially likely to happen for short-lived species, since evolutionary processes will take effect more rapidly. This is also expected in the case of invasive species, for which strong directional selection exerted by abiotic and/or biotic factors encountered in the introduced range can promote the appearance of newly adapted genotypes, outcompeting native species that invest in defensive compounds to cope with co-adapted pests and pathogens (Blossey & Notzold 1995)

Moreover, to predict the future distribution of a species, one has to consider not only its ability to colonize new sites, but also its ability to persist in current sites or face localized population extinction. The rear edge remains largely understudied, but recent reviews have demonstrated their crucial role by maintaining long-term stores of species' genetic diversity and places of speciation (Hampe & Petit 2005)

In the study of the global change impact on biodiversity, it appears to be imperative to move beyond treating species as genetic black boxes and to consider differentially population at the core, at the leading and at the rear edges of the distributions. Landscape genetics (reviewed in Manel *et al.* 2003) integrates information about the landscape features and micro-evolutionary processes, such as gene flow, genetic drift and selection. It can aid in identifying cryptic genetic boundaries, which are either breaks in the gene flow across populations caused by barriers, strong environmental gradients, or secondary contacts among previously isolated populations. The combined use of NBMs and landscape genetics holds promises to better understand the effect of global change on biodiversity.

Although major issues remain concerning the application of NBMs to climate change research, they currently represent one of the only tools for assessing the impacts of forecasted global change on a wide range of species, independent of the trophic level considered (Huntley *et al.* 2004). Process based (mechanistic) models (Chuine *et al.* 2000) and landscape genetics (Manel *et al.* 2003), while very appealing at the species level, are often too data-hungry to be of general use in nature management and biodiversity assessment (Guisan & Thuiller 2005).

6.4 - SYNERGISTIC INTERACTIONS BETWEEN DRIVERS OF GLOBAL CHANGE

Several recent reviews support the view that climate change is starting to affect biodiversity and will become a major driver of biodiversity losses (MEA 2005; IPCC 2007b). However, the predictive power of models is hindered by the effect of non climatic anthropogenic forces affecting natural systems. Areas with high concentrations of species also tend to have high concentrations of humans (e.g Balmford *et al.* 2001; Araujo 2003; Real *et al.* 2003; Vázquez & Gaston 2006; Luck 2007), and therefore of human activities, such as land conversion, water diversion, pollution and loss and increased fragmentation of habitats (e.g. Parmesan 2001; Metzger *et al.* 2006; Rounsevell *et al.* 2006). The complex nature of human decisions makes it difficult to predict future land uses with a high degree of confidence (Araujo *et al.* 2008). However, evidence is accumulating that human use of land alters the structure and functioning of ecosystems and ultimately alters how ecosystems interact with the atmosphere, with aquatic systems, and with surrounding land.

There is increasing concern that the interaction between land-use and climate change will magnify these negative effects on biodiversity (Sala *et al.* 2000). The complex interactions between land use and climate change make it difficult to attribute biodiversity changes to either one of these drivers and this has a consequence that current estimates of biodiversity loss might miss synergistic effects arising from such complex interactions (Sala *et al.* 2000). Not only are scenarios of global climate change predicting nonlinearities and surprises in the climate system, but if we incorporate the complexities of modern, human-dominated environments, then wildlife should also be expected to exhibit novel, unpredictable responses (Schneider & Root 1996).

Synergistic interactions between biological invasions and climate changes are also raising considerable concerns (Dukes & Mooney 1999): i) many invasive plants have been shown to respond positively to rising atmospheric carbon dioxide concentration (e.g. *Bromus tectorum*, Smith *et al.* 1987; *Pueraria lobata*, Sasek & Strain 1988; and *Lonicera japonica*, Sasek & Strain 1991). Elevated carbon dioxide levels stimulate plant growth and consequently increase fuel loading. This might have played a role in the invasion by cheatgrass (*Bromus tectorum)* of the intermountain West by contributing to an acceleration of fire regimes (Polley *et al.* 1996). Experimental studies suggest that rising carbon dioxide might slow the process of succession in grasslands (Vasseur & Potvin 1998),

which would increase the dominance of non-native species in many ecosystems. Rising carbon dioxide levels might have contributed to an increase in the abundance of mesquite (*Prosopis glandulosa*), a native C3 shrub, in North American C4 grasslands over the past century (Polley *et al.* 1996). We might predict that the world's major crops, which are mostly C3 species, will compete more successfully with the world's worst agricultural weeds, which are mostly C4 species (Alberto *et al.* 1996). ii) Invasive species might respond directly to changing climate (Dukes & Mooney 1999). Studies have shown that, in some ecosystems, shrubs will profit from a hotter climate. For example, simulated warming favored shrubs (primarily sagebrush, *Artemisia tridentata*) over forbs in Rocky Mountain meadows (Harte & Shaw 1995), and shrubs over nonvascular plants in arctic tundra (Chapin *et al.* 1995). Long-term observational studies suggest that an increase in annual precipitation in arid and semiarid regions could increase the dominance of invasive alien grasses, which are normally confined to small areas, but might outcompete much of the native vegetation if annual precipitation were to increase under climate change (Hobbs & Mooney 1991).

Three-part synergistic interactions between biological invasions, land use and climate changes might be expected (Dukes & Mooney 1999). Although a new climate might not directly favor alien plant species over natives, many invasive plant species share traits that could increase their dominance in a transitioning climate. A rapid anthropogenic climate change might disadvantage species that cannot quickly extend their ranges into newly suitable regions, such as plants with long generation times. Species that are able to shift ranges quickly would be at an advantage. Rapid dispersal is a characteristic of many biological invaders. In many areas of the world, alien plant species thrive along roadsides. With the help of vehicles, seeds of these species can quickly disperse over great distances (Lonsdale & Lane 1994) and often arrive in disturbed habitats. Thus, roadside weeds should be some of the earliest species to shift their ranges as climates change.

I performed a rapid review of 723 peer-reviewed papers using NBMs and selected the studies assessing the impacts of biological invasions and land use and/or climate changes on biodiversity (Fig 1). This analysis of the NBM literature is not meant to be exhaustive, but rather to provide a global picture of the current application of NBM in the field.

Out of the 723 papers, 301 studies are dealing with the prediction of the global changes impacts on biodiversity. This reveals the increasing interest of NBM in conservation biology. Out of these 301 studies, 135 studies are dealing with the forecast of climate change impacts and 118 with the investigation of the impacts of land destruction or transformation or with the investigation of endangered species. The study of invasive species appears to be less investigated so far, with only 70 studies published on this issue (Fig 1).

Only 25 studies are dealing jointly with two drivers (Fig 1), revealing that the vast majority of the studies take into consideration only one driver of biodiversity threats. The investigation of the effects of climate change with land-use changes is the most investigated synergy. While some studies

explicitly include estimates of land-use and climate change scenarios (Iverson *et al.* 1999a; Dirnbock *et al.* 2003a; Midgley *et al.* 2003a; Bomhard *et al.* 2005; Parra-Olea *et al.* 2005; Broennimann *et al.* 2006; del Barrio *et al.* 2006; Thuiller *et al.* 2006a; Peterson & Martinez-Meyer 2007; Golicher *et al.* 2008), some other indirectly investigate the effect of land use changes by assessing the IUCN risk of extinction (Saetersdal & Birks 1997; Skov & Svenning 2004; Thuiller *et al.* 2006a; Normand *et al.* 2007) or by verifying if current reserve-selection methods might provide solutions that are adequate to ensure species' long-term persistence within protected areas (Tellez-Valdes & Davila-Aranda 2003; Araujo *et al.* 2004; Tellez-Valdes *et al.* 2006; Thuiller *et al.* 2006a; Attorre *et al.* 2007; Hannah *et al.* 2007)

Five studies use models that correlate present climatic variables with present species distributions to forecast the future distribution of alien invasive species under climate change scenarios (Beerling *et al.* 1995; Rafoss & Saethre 2003; Roura-Pascual *et al.* 2004; D'Andrea *et al.* 2008; Broennimann & Guisan In review). Interestingly, some studies suggest that the consequence of climate change on invasive species could be a significantly reduced invasion extent (Beerling *et al.* 1995; Broennimann & Guisan In review).

Finally, I only found one NBM study considering the effect of biological invasion on endangered species conservation. Peterson & Robins (2003) developed models with predictions for the native distributions of Spotted owls (a species threatened by the destruction and fragmentation of primary forest in the Pacific Northwest) and for the invasive range of Barred Owls (a larger and aggressive Owl invading the Pacific Northwest). Overlap between the models for the two species suggests that most of the northern portion of the Spotted Owl's distribution is vulnerable to Barred Owl invasion.

Most interestingly, I was not able to find any study considering the three drivers jointly.

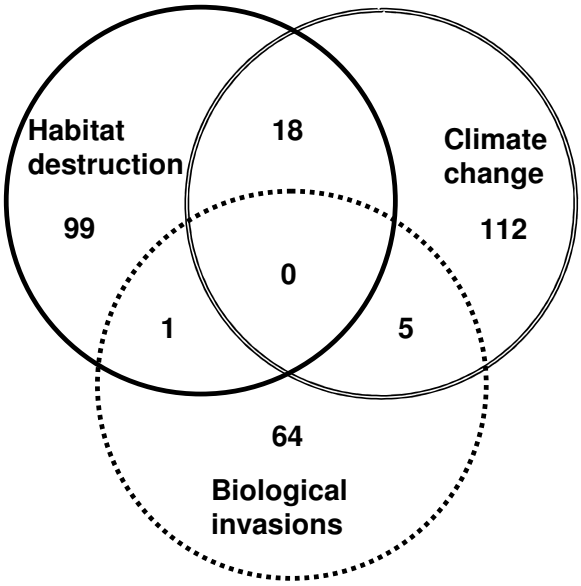

Fig. 1 – Review of the 723 studies using a NBM approach to investigate the impact of global changes. The circles represent the three major drivers of global change, respectively habitat destruction (including land-use changes and species endangerment), climate change impacts and biological invasions. The numbers indicate the amount of studies dealing with each driver. Studies taking into consideration several drivers of change are also shown.

Ecologists are beginning to understand how species and ecosystems respond to many single aspects of global change, but our understanding of the full array of responses to these three factors is rudimentary. In a recent study, Sala *et al.* (2000) developed global biodiversity scenarios for the year 2100 based on scenarios of changes in atmospheric carbon dioxide, climate, vegetation, and land use and the known sensitivity of biodiversity to these changes. This study identified a ranking of the importance of drivers of change, a ranking of the biomes with respect to expected changes, and the major sources of uncertainties. If diversity is assumed to respond to global changes without any interaction among drivers of change, Mediterranean and grassland ecosystems are projected to be most sensitive to change in the future. In contrast, arctic, alpine, and desert ecosystems will show only moderate changes. The range of changes among biomes projected by this scenario is relatively small. If the diversity in each biome is assumed to be determined only by the factor that has the greatest impact on diversity, then tropical and southern temperate forests are projected to experience substantial changes in diversity due to land-use changes and the arctic will experience changes due to climate changes. In this scenario, deserts and alpine regions will show the fewest diversity changes, because there is no single driver to which biodiversity in these biomes is extremely sensitive. If there are synergistic interactions among all causes of biodiversity change, Mediterranean and grassland ecosystems are projected to experience the greatest biodiversity change because diversity in these biomes is sensitive to all global-change drivers. In this scenario, tropical forest, arctic, and alpine ecosystems will show the fewest biodiversity changes, because there are several drivers of change to which these biomes are relatively insensitive. In contrast to the no-interaction scenario, in this case the range of expected change is quite broad, encompassing two orders of magnitude, because of the effect of synergistic interactions on amplifying differences among biomes.

Chapter 7

CONCLUSION

A HOMOGENIZING WORLD

While species richness is declining globally, species gains are frequently observed at regional and local scales as range-expanding generalists invade new species pools at the expense of rare, and often endemic, native species that disappear (Williamson 1996; Hobbs & Mooney 1998). These biotic replacements may be further accelerated by the growing influence of climate change. The process describing this non-random reshuffling of species pools is called biotic homogenization (McKinney & Lockwood 1999) and refers to an increase in the taxonomic similarity of two or more species pools through time as the result of species invasions and extinctions (Olden & Poff 2003; Olden & Rooney 2006). Biotic homogenization is recognized as an important component of anthropogenic global change (e.g. Vitousek *et al.* 1996; Myers 1997; Vitousek *et al.* 1997; Baskin 1998; Rahel 2000; Olden *et al.* 2004). Although biotic homogenization is a rapidly growing conservation issue in biology, understanding the dynamics of homogenization will be challenging because many complex aspects of the biodiversity crisis such as extinction and species introductions are involved.

Environmental changes are often viewed only in terms of their harmful impacts on the affected species. However, some species may also benefit (Morris & Heidinga 1997). If that change is widespread and persistent, the beneficiary species will expand their range and replace those that cannot survive. Thus, biotic homogenization occurs when a widespread environmental change promotes the geographic expansion of some species (winners) and the geographic reduction of others (losers) (Baskin 1998). Previous mass extinctions, for example, show that global climatic and geological disturbances often produce low-diversity biota dominated by a few widespread, broadly adapted species (Erwin 1998). The homogenization process can already be seen in island biota where the loss of endemic species and their replacement by widespread exotic species result in decreased beta diversity among the islands (Harrison 1993). The projected rise in species extinctions and species introductions will almost certainly increase homogenization at continental scales as well.

A common source for estimating the number of probable losers can be found in lists of threatened species (IUCN 2004). About 11% of all global bird species are listed on the IUCN Red List compared with a much higher proportion (70%) of species in decline. In the five major fossil mass extinctions, over 50% of all species became extinct (Myers 1997; Erwin 1998). If most species now in decline eventually become extinct then a mass extinction on the scale of previous events would occur (Wilson 2002). Winners are species that not only resist geographic range decline, but also expand their ranges. About 2% of bird (Lockwood 1999) and 1% of mammal (Lever 1987) species, worldwide, are currently identified as having been successfully introduced into new environments. About 2% of plant species are considered successful invasive weeds (Daehler 1998). Such tiny fractions of estimated successful biotic introductions probably underestimate the true number of ultimate winners, because many species that could be successfully introduced have not yet been

transported to the appropriate habitat, and because many winners are not perceived as invasive because they are undergoing only localized expansion in, or near, their native ranges.

Large-scale homogenization can be enhanced if the winning and losing species are not randomly distributed among taxonomic and ecological categories. Emerging evidence suggests that species extinction is taxonomically non-random at local and global scales. Some families are reported to contain substantially higher percentages of threatened species (global) or declining species (local) than others (McKinney & Lockwood 1999). The over-representation of specific family can have drastic taxonomic homogenizing effects where species-rich taxa have a very large concentration of exotic species. For example, the large grass family (Poacae) contains 180 more weed species than it would if 'weediness' were distributed randomly among plant families (Daehler 1998). These represent 180 closely related winners (almost 10% of the grass family) that would otherwise represent many other plant families within the set of global weeds. As with extinction-biasing traits, such clustering of winning species in certain families can be attributed to the non-random way that traits are shared among closely related species (McKinney 1997). Related species tend to share traits that promote successful transport and establishment in new environments (Reichard 1997). In plants, for example, invaders of croplands and other highly disturbed areas are concentrated in herbaceous families with rapid growth and wide environmental tolerances (Daehler 1998; Pysek 1998). By contrast, invaders of undisturbed natural areas are over-represented in a variety of woody families, including nitrogen-fixers that can live in nitrogen-poor soils (Daehler 1998). Similarly, families with many local winners apparently have clusters of traits that promote establishment in environments produced by human activities. Deforestation benefits moths (Sphingidae) with generalist adaptations to an open habitat, frogs (Hylidae) that breed in temporary ponds (Pearman 1997), and spiders (Lycosidae) with webs not confined to certain kinds of vegetation (Ingham & Samways 1996). Conversely, extinction-prone groups have a predominance of traits associated with specialization, slow reproduction and other traits not associated with opportunism (McKinney & Lockwood 1999). Interestingly, the same pattern has been suggested for mass extinctions, wherein widespread generalist and opportunistic species not only survive major crises, but often expand their ranges (Erwin 1998). The replacement of many losing species with a relatively small fraction of widespread winners will likely produce a much more spatially homogenized biosphere. The result would be fewer and simpler ecosystems. The ultimate degree of homogenization could exceed even that seen in the largest past mass extinctions, with repercussions for numerous ecosystem functions and services. Projections are needed to anticipate and prevent such crisis. NBMs currently represent one of the only tools for assessing the impacts of global change on a wide range of species. Since, they are independent of the trophic level considered and do not require detailed physiological data about individual species, they can easily be applied to a large number of species. This enables conclusions regarding the potential impacts of climate change on a wide range of species, and thus habitat assemblages, to be made (e.g. Berry *et al.* 2002; Guisan & Thuiller 2005; Ferrier & Guisan 2006).

8 – ACKNOWLEDGMENTS

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Chapter 10

ANNEXES

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LETTER

Prediction of plant species distributions across six millennia

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Abstract

The usefulness of species distribution models (SDMs) in predicting impacts of climate change on biodiversity is difficult to assess because changes in species ranges may take decades or centuries to occur. One alternative way to evaluate the predictive ability of SDMs across time is to compare their predictions with data on past species distributions. We use data on plant distributions, fossil pollen and current and mid-Holocene climate to test the ability of SDMs to predict past climate-change impacts. We find that species showing little change in the estimated position of their realized niche, with resulting good model performance, tend to be dominant competitors for light. Different mechanisms appear to be responsible for among-species differences in model performance. Confidence in predictions of the impacts of climate change could be improved by selecting species with characteristics that suggest little change is expected in the relationships between species occurrence and climate patterns.

Keywords

Climate change, global circulation model, hindcasting, Holocene, niche conservatism, PMIP, pollen, range filling, species distribution model.

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INTRODUCTION

The earth is currently experiencing rapid, anthropogenic climate change (Houghton *et al.* 2001) that is expected to impact species diversity, distribution and persistence (Thomas *et al.* 2004; Thuiller *et al.* 2005; Botkin *et al.* 2007). For example, the ranges of insects and birds are already expanding northward as more northerly areas become increasingly suitable (Walther *et al.* 2002; Parmesan & Yohe 2003). Similarly, plants in mountainous regions are responding by shifting elevation ranges upwards (Grabherr *et al.* 1994; Gehrig-Fasel *et al.* 2007). Potential effects of climate change on the distributions of species are often evaluated using niche-based species distribution models (SDMs), in which current climate and species distribution data are used to model the realized climatic niche (Hutchinson 1957). Niche models are then projected in geographic space using estimates of future climate patterns (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). Models suggest that species with limited dispersal abilities and/or high-elevation habitats will become threatened with extinction as suitable habitat becomes reduced and new areas remain unreachable due to natural and anthropogenic barriers to dispersal (Hannah *et al.* 2002; Broennimann *et al.* 2006). Nonetheless, predicted changes in species distribution are difficult to evaluate with empirical data because the predicted changes may take decades to centuries to occur (Lang 1994; Araújo *et al.* 2005; Bradshaw & Lindbladh 2005; Araújo & Rahbek 2006).

Predictions from SDMs can be affected by factors such as data resolution, sampling extent and choice of modelling algorithm (Elith *et al.* 2006; Randin *et al.* 2006; Guisan *et al.* 2007a; Thuiller *et al.* in press). While such effects may be mitigated by careful design regarding these aspects, shifts in species niche that are caused by dynamic ecological or evolutionary processes could bias or invalidate predictions of the biotic effects of climate change obtained from SDMs (Pearman *et al.* 2008). Prediction using SDMs of species' future distributions assumes that species niches do not change over the relevant time scale. However, some plant species seem to have undergone rapid niche shifts (Broennimann *et al.* 2007) while other plants appear to experience long periods of niche stability (Huntley *et al.* 1989). The unassessed potential for niche shift casts doubt upon the

validity of SDM-based predictions of climate-change impacts (Pearman *et al.* 2008). While future niche changes are unlikely predictable for particular species, increased reliability of SDM-based predictions may depend on understanding how potentials for niche change vary among species. The consistent association of species characteristics with unchanging distribution–climate relationships would assist ecologists in determining the quality of predictions and increase confidence in projected climate-change impacts obtained from SDMs.

The modelling and prediction of climate-change impacts on species distributions additionally assumes that species have migrated to fill the distribution that is accessible given the environmental requirements of the species and the outcome of competitive interactions (Pearson & Dawson 2003). If this is not the case, it may be difficult to develop SDMs that accurately represent species' niches. A difference in time between changes in the geographic distribution of climatic conditions that are suitable for a species and the colonization of newly suitable areas by the species (or transient persistence of slowly declining populations in areas no longer suitable) could be indistinguishable from a shift in a species niche. Changes in the observed relationship between climate and species distributions could, thus, be generated by temporal changes in proportion occupancy of a species potential geographic range (Davis & Shaw 2001; Svenning & Skov 2004). For example, European beech (*Fagus sylvatica* L.) might currently occupy most of its potential range and be at distributional equilibrium (Huntley *et al.* 1989) while *Abies alba* L. could occupy only 37% of its potential range (Svenning & Skov 2004). Incomplete range filling currently might result from dispersal limitation of range expansion from Pleistocene refugia (Svenning & Skov 2004). If so, then partial range filling may have been even more pronounced in some species during the mid-Holocene. It follows that if such limitations have already lasted thousands of years, dispersal limitation would likely be substantial in response to rapid climate warming. This would clearly impede accurate projections of future plant distributions unless dynamic dispersal is implicitly taken into account in the modelling (Thuiller *et al.* in press). Nonetheless, the effects that niche shifts and partial range filling may have on predictions from niche-based SDMs have never been investigated using appropriate independent data and rigorous statistical methods.

In this paper, we test the predictive ability of SDMs using forecasting and hindcasting of species distributions as functions of past and current climates (Araújo & Rahbek 2006). Forecasting is the process of fitting statistical models using data on present climate and distributions, and then projecting species potential distributions into the future using estimations of future climate. Similarly, one might calibrate models using data on past climate and species distributions and then evaluate model forecasts for current species distributions by comparing the predictions to known current distributions. In contrast, hindcasting is the process by which one calibrates models using data on current climatic conditions and species distributions, and then projects the modelled relationships into the past using independent estimates of prior climates. So far, only a few studies have used hindcasting to estimate previous species distributions, for example, in testing for niche changes between last glacial maximum and the present (Martinez-Meyer & Peterson 2006). Here, we explore hindcasting as a method to assess quantitatively the accuracy of predictions of climate-change impacts on biodiversity and species distributions, and of how predictions of species distributions vary when the assumptions behind predictive application of SDMs are violated.

To assess model predictive performance during hindcasting and forecasting, one needs sufficient, independent data on current and historical species distributions, and on present and past climate. We use atlas data on current plant distributions, pollen core data from two European databases and climate estimates from a global circulation model (GCM) to conduct an independent assessment of SDM performance upon hindcasting the distributions of tree species at the mid-Holocene, 6 ky BP. Similarly, we forecast current distributions of these species by using pollen data on species' mid-Holocene distributions to calibrate (i.e. fit) the models. We use multivariate techniques to estimate change in the niche position (i.e. change in 'marginality' of species in multivariate climate space, *sensu* Dolédec *et al.* 2000) of each species between the mid-Holocene and the present. We then evaluate the relationship between these estimated niche shifts and model predictive performance. Models for species would not likely perform identically as a consequence of potential interspecific variation in range filling, niche stability and data quality. We quantify the uncertainty surrounding among-species differences in model performance by providing bootstrapped 95% confidence intervals. Finally, we interpret variation in model performance among species in terms of species ecological characteristics, interspecific competition and range expansion.

DATA AND METHODS

Species distributions

Current distributions of plant species in Europe were taken from the digital Atlas Florae Europaeae (AFE) database (Jalas & Suominen 1972–1999). We eliminated off-shore grid cells, leaving a total of 1973 cells with which we determined species presence/absence. To determine species distributions at 6 ky BP, we examined pollen composition in the pooled sample of cores in the Alpine Palynological

Database and the European Pollen Database (http://www.europeanpollendatabase.net). Pollen data included the interval 6 ± 0.5 ky BP, using calibrated C^{14} dates. Pollen from wetland and aquatic plants were removed from the data so that the data reflected each species' pollen as a proportion of pollen from terrestrial species. We then averaged pollen percentages for each species across the 10 100-year periods.

Direct species-level determinations are generally not possible for pollen morphotypes because pollen differs little among species within a genus. To allow SDMs of species, we selected only those types of pollen that represented a single species in northern and central Europe and thus could not be confused with pollen arising from other members of a genus. To achieve this, we restricted chosen pollen sites to be north of a line drawn from the Adriatic Sea north-eastward, passing through northern Romania and continuing eastward *c.* 200 km north of the Black Sea. This left an area of continental Europe, Scandinavia and the United Kingdom/Ireland, and removed cores where species common in central and northern Europe might overlap in range with other congeners. We used data from all remaining 312 cores to maximize opportunity for model calibration and testing (Table 1).

Once the study species were identified, we established two threshold pollen percentages per species, based on expert knowledge, for determining species presence/absence. A lower threshold per cent for species presence was established to signify a level below which we considered the species unlikely to be present. Likely this would capture relatively small and recently established populations, but species presence determinations might be influenced by long-distance pollen transport (see Discussion in Latalowa & van der Knaap 2006). An upper threshold per cent, if exceeded, led us to consider a species as definitely present, minimizing the influence of pollen transport. For each species, pollen percentages were evaluated using the average percentages over the 10 100-year period centred on 6 ky BP. Here, we present results using the lower threshold, based on the observation that plant macrofossils often indicate a date for species arrival that is earlier than pollen evidence (Kullman 2001; Magri *et al.* 2006). Because of this phenomenon, the use of our high pollen thresholds for model calibration and evaluation may be unnecessarily conservative and in our data sets some species showed an insufficient number of presences for reliable modelling. We present analyses using the upper threshold in supplementary online materials.

Current climate

We used interpolated climate data at 1-km resolution from the WorldClim data set (Hijmans *et al.* 2005), downloaded 31 March 2006. We chose to use the variables 'annual mean temperature', 'mean temperature of the coldest month', 'total annual precipitation', 'precipitation December–March' and 'precipitation June–August' because of the close relationship of these or very similar variables to plant physiological limitations (Bartlein *et al.* 1986; Prentice *et al.* 1992). In a geographic information system, we sampled each climate variable map at locations corresponding to the centre of each of the 1973 AFE cells.

Mid-Holocene climate estimate

The use of climate estimates reconstructed from pollen composition in cores (Davis *et al.* 2003) for hindcasting mid-Holocene plant distributions would have generated circularities in the results. This is because the same pollen data were used to determine species distributions and resulting

Table 1 Current species distributions (presence/absence) based on Atlas Floreae Europaeae (AFE) and mid-Holocene presence/absence based on pollen percentages from the combined holding of the European Pollen Database and Alpine Palynological Database

	Current			Mid-Holocene	
	AFE	Pollen thresholds*		Presences/absences	
Species	Presences/absences	Low	High	Low threshold	High threshold
Abies alba	410/1573	0.01	0.02	71/241	62/250
Carpinus betulus	1000/983	0.005	0.02	14/289	8/304
Corylus avellana	1423/560	0.01	0.03	198/114	145/167
Fagus sylvatica	990/993	0.01	0.02	47/265	31/281
Juniperus communis	1486/497	0.01	0.02	21/291	10/302
Larix decidua	135/1848	0.005	0.015	19/293	12/300
Picea abies	783/1200	0.01	0.02	119/193	93/219

*Employed threshold values necessary for species presence when considering mean pollen percentage over 10 consecutive 100-year time periods in which pollen of the genus was detected.

biome maps upon which reconstructed climate estimates were ultimately based. To avoid this circularity we estimated mid-Holocene climate using two data sets. To obtain an estimate of the European climate anomaly between the current period and the mid-Holocene, we obtained projected climate data from the UBRIS-HadCM3 AO GCM (Gordon *et al.* 2000), generated as a part of the PMIP2 climate modelling comparison project (Gladstone *et al.* 2005). Comparison of the results of this GCM with climate reconstructions and other models show that the direction of climate change is in general correctly estimated in the PMIP2 models, although the degree of cooling in southern Europe is generally underestimated (Brewer *et al.* 2007). The UBRIS-HadCM3 model results were available for both the present (*c.* 1950) and for a 100-year period centred around 6 ky BP. We obtained average values for each variable for each month over the 100-year period. We then generated an anomaly map for each variable by subtracting values for the present, as modelled by the GCM, from the GCM estimated mid-Holocene values. These anomaly maps were then interpolated to 1-km resolution using inverse-distance weighting among the four nearest cells in ARCGIS 9.1 (ESRI 2005). Values in these interpolated maps were then added to the corresponding WorldClim values to generate estimated climate maps at 1-km resolution for Europe at the mid-Holocene. From these maps, we extracted climate data at the 312 pollen core sites from which we had obtained species presence/absence information.

Species distribution modelling

We modelled species distributions using an iterative computer learning algorithm called the gradient boosting machine (Friedman 2001; Ridgeway 2006). We used the algorithm as implemented in the package 'gbm: Generalized Boosted Regression Models', available on the R website (http://cran.r-project.org). Boosted regression trees are becoming increasingly popular in niche modelling because of their often superior performance in prediction (Elith *et al.* 2006; Thuiller *et al.* in press). For a full description of gbm and additional references, see Appendix S1 in Supplementary Material. We employed the 'area under the receiver operator characteristic curve' (*AUC*) as a criterion for evaluating the fit of gbm models to the calibration data set and in evaluating predictive performance (Fielding & Bell 1997). This measure of model fit is suited for comparing probabilistic predictions to observed presence–absences because it requires no arbitrarily defined threshold probability with which to establish prediction of species presence. In calibrating the model for each species, we generated an additional estimate of *AUC* by conducting 10-fold cross-validation on a calibration data set that was selected randomly from the complete data set and that conserved the overall proportion of presences/absences that was in the full data set (Efron & Tibshirani 1998; Randin *et al.* 2006). We retrieved directly from the gbm model (in fact, an R-object) the proportional contribution of each climate variable to the model.

We also developed a basis for understanding the statistical significance of differences in model performance among species by bootstrapping 95% percentile confidence intervals for *AUC* values of both model fit (i.e. to the calibration data) and upon prediction (Efron & Tibshirani 1998). To evaluate confidence intervals around the *AUC* value of model fit, for each species we generated 1000 bootstrap data sets from the calibration data (i.e. from the original 1973 observations from the AFE data set). For each bootstrap data set, we fit a gbm model and determined the *AUC* for model fit to the bootstrap data. We established the confidence interval for *AUC* by selecting values corresponding to the upper and lower 2.5% quantiles of the bootstrapped *AUC* distribution. We considered non-overlapping 95% confidence intervals as a sign of significant difference between species *AUC* values. Finally, preparing presence–absence maps for each species from probabilistic predictions requires use of a threshold. Therefore, we used maximized Kappa (Fielding & Bell 1997), choosing the threshold providing the maximum value for the Kappa coefficient of agreement (Cohen 1960), as reported by Randin *et al.* (2006).

Quantifying change in climate–distribution relationships

We determined the relationship between model predictive ability and change in species' estimated niche position by comparing these values between the mid-Holocene and the current period. For both periods, we estimated niche position (i.e. marginality) for all species simultaneously by multiplying the transpose of the species occurrence matrix by the corresponding matrix of normalized observed environmental values. We then conducted a principal components analysis on the difference between estimated current and mid-Holocene niche position for all species (for full details, see Appendix S2). Thus, the change in marginality for each species was calculated relative to the change in marginality of a hypothetical average species in the multivariate space spanned by both current and mid-Holocene climate data sets, using species presence/absence data.

Finally, we assessed model predictive performance as a function of estimated change in niche position by regressing species values of *AUC* on the absolute value of change in niche position from the PCA. We repeated the entire process that is described above to forecast current species distributions based on gbm models that were calibrated with the mid-Holocene data sets.

RESULTS

Species and distributions

We studied seven unambiguously identifiable taxa for which pollen data, when we excluded south-eastern Europe, represented the approximate distributions of the species at the mid-Holocene (Table 1). These species included four trees (*Abies alba*, *Fagus sylvestris*, *Larix decidua* and *Picea abies*) and three shrubs or small trees (*Carpinus betulus*, *Corylus avellana* and *Juniperus communis*) that varied in the AFE data regarding their current distribution across Europe (Figs 1a and 2a; also see Figs S1a–S5a, supplementary online materials). The species varied over an order of magnitude in the degree to which they were represented in pollen count

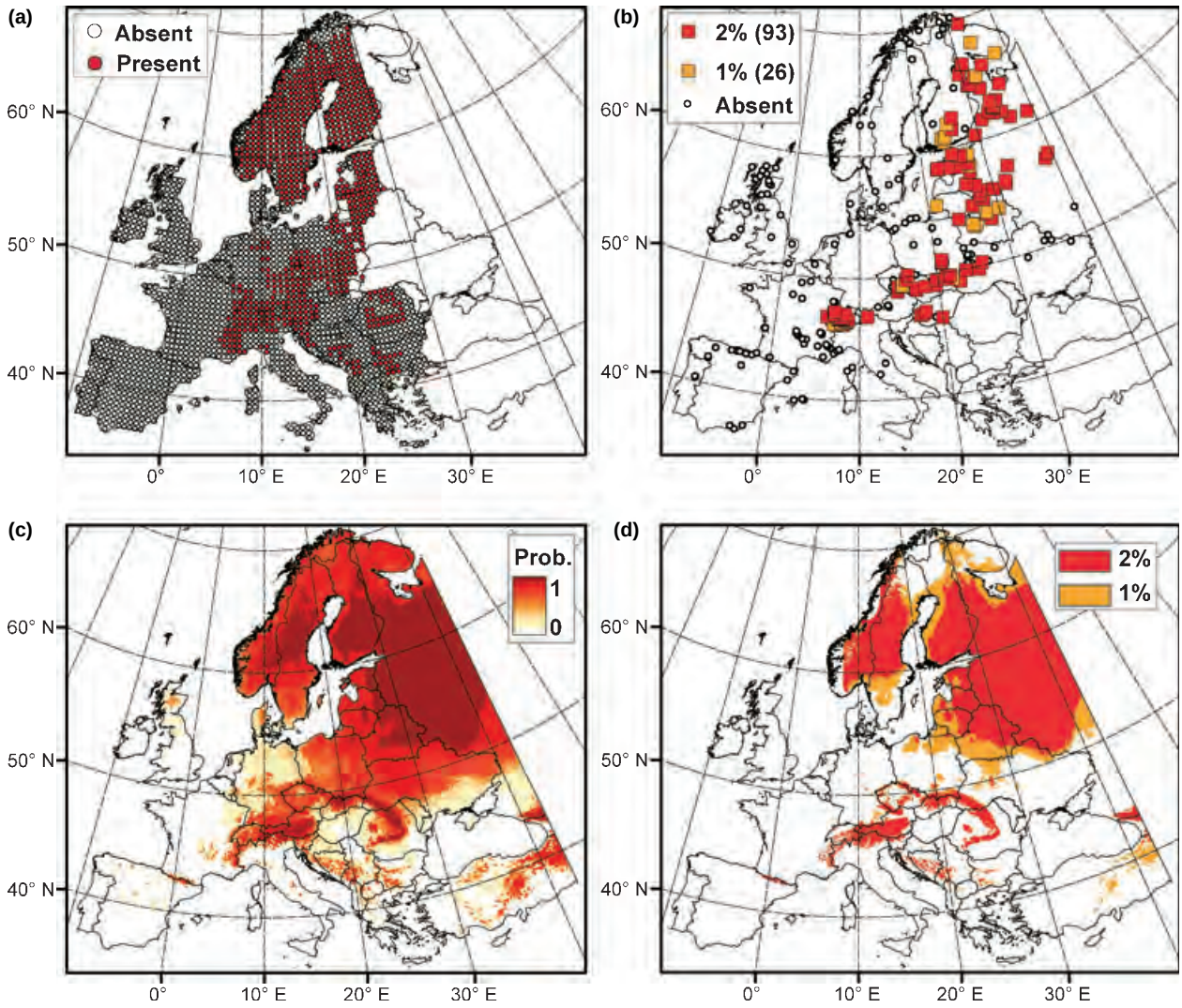

Figure 1 The current and mid-Holocene distributions of *Picea abies*, from empirical data and from niche-based species distribution models (SDMs). (a) The current distribution of the species in Europe, as determined with a digital version of the Atlas Florae Europaeae (AFE). (b) Presence of the species in pollen cores at the mid-Holocene, evaluated at two thresholds. Red squares indicate locations of cores in which pollen frequency of the species reached an average of 2% over the period 6 ky BP (± 500 years). Yellow points indicate additional cores in which the average pollen concentration of the species was ≥ 1% but < 2%. (c) A map of the probability of occurrence of the species currently, obtained by fitting an SDM with AFE data and projecting it over the study area. The probabilities are indicated by a colour band labelled 'Prob.'. (d) Map of the predicted distribution of the species at the mid-Holocene, established using an SDM-generated probability map for the species (i.e. in hindcasting) and a threshold determined by the maximum Kappa criterion, derived from pollen core data. The value of maximum Kappa was calculated using species presence according to high pollen (2%, red) and low pollen (1%, yellow) thresholds. The map thus represents the combination of a model of the estimated current realized niche and pollen data species distribution at 6 ky BP.

data (Table 1, Figs 1b, 2b and S1b–S5b). When evaluated at the high pollen threshold, three species had only a marginally sufficient number of presences (i.e. < 20) for model evaluation on hindcasting and model calibration in forecasting (Table 1).

Modelling results and evaluation

Although models calibrated with current distribution data described well the current distribution of the species (model verification, Figs 1c, 2c and S1c–S5c), model performance was poor for some species upon hindcasting mid-Holocene distributions (model validation; Figs 3a,c and S6a,c). When models were calibrated with current species distribution and climate data, all species models attained an $AUC > 0.8$ and had overlapping 95% confidence intervals for AUC in model verification (Figs 3a and S6a). Thus, we obtained useful models for all species (Swets 1988; Araújo *et al.* 2005) and model performance in fitting the calibration data was statistically indistinguishable among species (Figs 3a and S6). Total annual precipitation together with average annual temperature made by far the strongest contributions to all models (> 90%). In model validation (i.e. evaluation of hindcasted predictions) with the pollen data set and the low threshold for species presence, non-overlapping percentile confidence intervals indicated significant among-species differences in model performance (Fig. 3a), with a notably poor model performance for *J. communis*.

Forecasting current species distributions based on model calibration with pollen-based occurrence data demonstrated substantial uncertainty in the fit of models to the mid-Holocene calibration data, as shown by comparatively wide

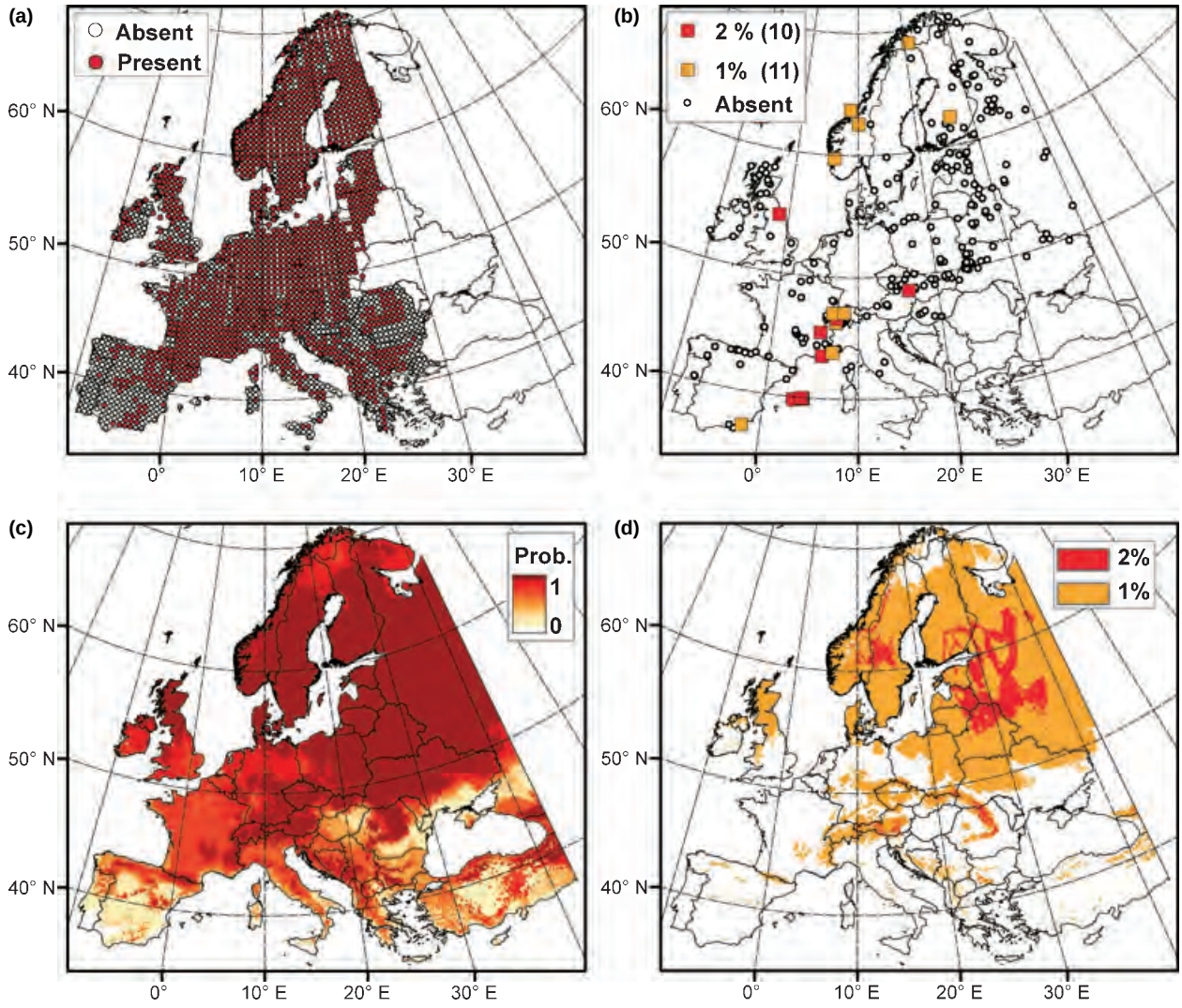

Figure 2 The distribution of *Juniperus communis*, with pollen thresholds as labelled. Otherwise as in Fig. 1.

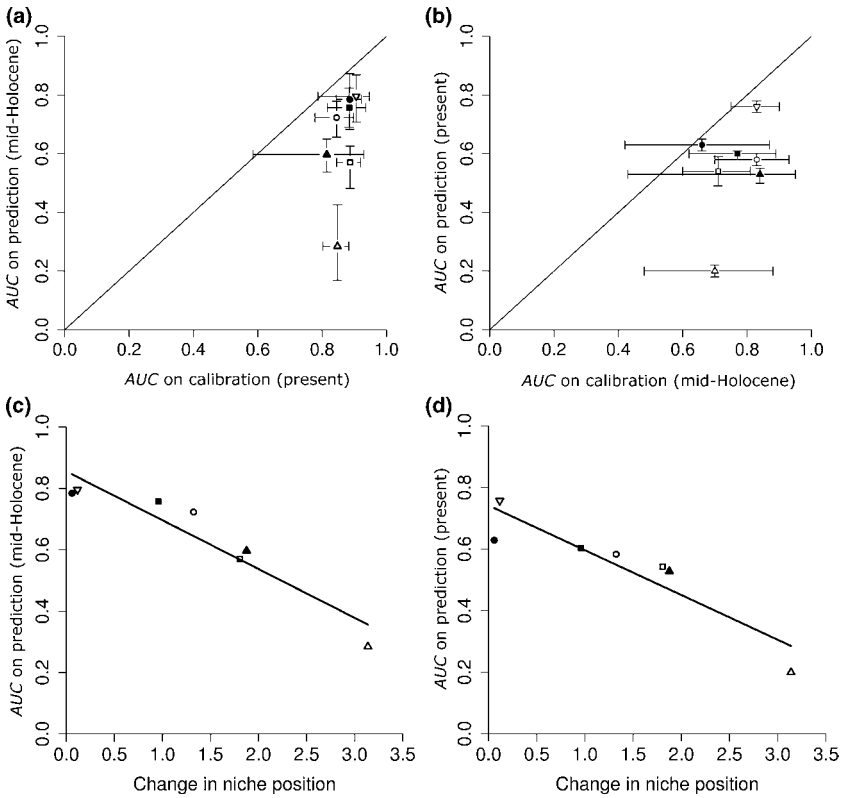

Figure 3 Mean values of the area under the receiver operator characteristic curve (*AUC*) and 95% confidence intervals (a and b), and model performance as a function of magnitude of niche shift (c and d). Top panels show (a) hindcasting with calibration of models using current distribution data and evaluation of predictions based on low pollen percentage thresholds; (b) forecasting current species distributions using mid-Holocene pollen data (low thresholds) for models calibration. Confidence intervals are bootstrapped percentage intervals (95%). Diagonal lines represent equal model performance in fitting and prediction. Species are *Abies alba* (○), *Carpinus betulus* (●), *Corylus avellana* (□), *Fagus sylvatica* (■), *Juniperus communus* (△), *Larix decidua* (▲) and *Picea abies* (▽). The lower panels show the predictive success of models as a function of estimated shift of a species niche position. The *x*-axis is the absolute value of change in estimated niche position, determined in principal component analyses by using low pollen thresholds for species presence. The *y*-axis presents *AUC* values obtained upon prediction, as seen in panels (a) and (b). Evaluations are of hindcasting mid-Holocene distributions (c) and forecasting current species distributions (d). The trend lines are from least-squares regression and are statistically significant. These regressions (c and d) remain significant with removal of *J. communis*. The three colonizing species (*C. avelana*, *J. communus* and *L. decidua*) demonstrate the greatest observed niche shift and the lowest model performance upon prediction.

95% confidence intervals (Figs 3b and S6b). Overlapping confidence intervals indicated that there were no significant differences among species upon model fitting. In contrast, species' models varied greatly in their abilities to forecast current species distributions (Fig. 3b). As in hindcasting, the model for *J. communis* performed much better in describing species occurrence in the calibration data (mid-Holocene) than in prediction (Fig. 3b). Two species' models performed similarly both in fitting the calibration data and in forecasting current distribution (*C. betulus* and *P. abies*). In both the forecasting and hindcasting exercises, there was generally less uncertainty in model performance (i.e. narrower confidence intervals) when using the data sets on current climate and species distributions than when using the mid-Holocene climate estimates and pollen data for model calibration.

Some notable disagreement existed between pollen-based species distribution and hindcasted predictions. *Fagus sylvatica* was predicted to be present in northern Europe but had not occupied this area by 6 ky BP (Fig. S4). *Larix decidua* occurred further south during the mid-Holocene than predicted upon hindcasting (Fig. S5). *Picea abies* was predicted to occupy Scandinavia but there we encountered no pollen evidence for this as of the mid-Holocene (Fig. 1). Finally, *J. communis* was largely absent from central and eastern Europe, although hindcasting predicts that these areas lie within the species potential mid-Holocene range (Fig. 2).

Table 2 Regression statistics and estimated coefficients for two scenarios, in an analysis of model performance (*AUC*) as a function of observed change in species estimated niche positions

Prediction	Pollen threshold	Adjusted r^2	β_0	β_1	SS_{model}	MS_{error}	F*	P-value
Hindcasting	Low	0.87	0.86	−0.16	0.199	0.004	46.97	0.001
Forecasting	Low	0.81	0.74	−0.15	6.42×10^{-14}	2.36×10^{-15}	27.186	0.003

Values for r^2, β_0 and β_1 describe regression lines illustrated in Fig. 1c,d. Statistics were obtained after transformation to meet assumption of normally distributed residuals. See Table S1 in supplementary online material for results using high pollen thresholds.
*All *F*-statistics have one numerator and five denominator degrees of freedom.

Estimated niche position change and model performance

Species varied in estimated difference between their current and mid-Holocene niche positions. *Picea abies* and *C. betulus* experienced less change in estimated niche position when compared to the other species (Figs 3c and S6c). In contrast, the estimated change in niche position of *J. communis* far exceeded that of the other species. The magnitude of species' niche shifts and performance of the models were strongly related, both in hindcasting and in forecasting. Models for species whose niche position had changed little between the mid-Holocene and the present generally performed better than models for species whose niche position had changed substantially relative to the other species (Fig. 3c,d; see also Fig. S6c,d). The significant negative relationships between change in niche position and model performance held for both hindcasting and forecasting, using both low- and high-pollen thresholds. The change in niche position and low *AUC* value of *J. communis* strongly influenced the regression equations (Table 2; see also Table S1). Nonetheless, a significant negative regression persisted when *J. communis* was not included (Fig. 3c,d; analysis not shown).

DISCUSSION

The results demonstrate that the effectiveness of niche-based SDMs in predicting species distributions over a period of 6 ky varies among species. In this way, our results are similar to those on the transfer of SDM predictions in geographic space (Randin *et al.* 2006; Broennimann *et al.* 2007), in which species varied in the accuracy with which they could be predicted in areas other than those where the models were calibrated. These results suggest that work is needed to identify species for which the relationship between distribution and climate likely remains unchanged over relevant time periods. There are a number of reasons why the distributions of some species may be predictable while for others, predictions are markedly erroneous. The realized environmental niche of species may change, either because of changes in either positive or negative biotic interactions in the community or because of evolutionary adaptation to the biotic and abiotic environment (i.e. a change in fundamental niches and realized niches; Broennimann *et al.* 2007; Pearman *et al.* 2008). As change in geographical patterns of climate proceeds, species can also vary in their ability to track these changes. These possibilities suggest further that a change in the mechanisms that limit a species distribution could alter the observed relationship between species distribution and climate (Guisan & Thuiller 2005). Additionally, prediction error might arise from any of the sources of data we used. Thus, understanding which species are more or less likely to be affected by these phenomena will improve confidence in predictions of climate-change impacts provided by niche-based SDMs.

Niche dynamics and species distribution

The degree to which species' niches remain unchanged over time has received substantial attention (Wiens & Graham 2005). Despite this, there has been no clearly identifiable pattern of niche dynamics useful in choosing species that likely provide reliable predictions of climate-change impacts (Pearman *et al.* 2008). We found that species vary in the degree to which estimates of their climate–distribution relationship (i.e. estimated niche position) differed between the mid-Holocene and the present. *Picea abies* and *C. betulus* had little estimated niche change relative to other species. In contrast, the estimated niche and predicted distribution of *J. communis* appears to differ radically between the mid-Holocene and the present. In general, although we have only seven data points, our analysis suggests that species that specialize in disturbed habitats and which are intolerant of shade might have been more likely than competitively dominant species to undergo shifts in estimated climate–distribution relationships during the last 6 ky (Fig. 3).

Likely, at the time scale we investigate here, initial post-glacial expansion of some pioneer species to near their full potential range was followed by reduction in density and/or exclusion from some areas by competitors (Lang 1994). In contrast, we suggest that species could respond differently to rapid climate change (and over a short period), relative to one another, than they do to changes over hundreds or

thousands of years. The actual species for which model projections produce accurate representation of changes in distribution in response to climate change could differ depending on the rate of change and the length of period over which the projections are made. In this regard, competitive ability, time to distribution equilibrium, niche size and the magnitude of displacement of the projection of the niche in geographic space could have large influences. Future research could use hindcasting and other methods to explore these possibilities.

Range filling and dispersal limitation

Similar to cases in which species niches are not stable over time, a tendency for limited range filling for some species would equally suggest that SDM-based predictions of climate-change impact on the geographic distribution of species may be encumbered with error. Incomplete range filling could affect model performance when making predictions of changes in species ranges over time. For example, *L. decidua* might fill < 18% of its current potential range (Svenning & Skov 2004). This species was predicted in hindcasting in the present study to occupy an area extending from the French Alps through the central Alps to eastern Austria. As of the mid-Holocene, evidence for *L. decidua* comes from the central Alps and north of the Adriatic Sea, but is missing from the great portion of the eastern part of its predicted range. A pattern of consistently wide confidence limits for *L. decidua* in both calibration and prediction (Fig. 3a,b) suggests that climate only partially determined the species' climate–distribution relationship by the mid-Holocene. This may in part be due to one or more known ecological properties of *L. decidua*, such as low migration rates, low competitiveness for light, ability to colonize poor soils or anthropogenic effects (Lang 1994; Gobet *et al.* 2003; Bradshaw & Lindbladh 2005). It might also be that although the mid-Holocene climate in central Europe is generally well predicted by GCMs (Brewer *et al.* 2007), some errors in climate estimation could be influential. Comparison of models derived from a variety of GCMs could be informative regarding these effects.

In another example, *F. sylvatica* was missing from much of the northerly portion of its predicted range as of the mid-Holocene (Fig. S4). Our models over-predict the mid-Holocene range of the species in northern Europe, as do physiological models (Giesecke *et al.* 2007). Those models predict a much broader distribution as of 6 ky BP than do the SDM results described here, although the two results are not directly comparable because of differing methodology and response variables. *Fagus sylvatica* only spread into its predicted suitable range with the advent of anthropogenic fires in the late-Holocene, in areas that up to that point were dominated by *P. abies* (Gobet *et al.* 2003; Bradshaw & Lindbladh 2005). We cannot, using only our data, distinguish with certainty the degree to which observed changes in estimated niche position and geographic range filling result from niche shift, competitive exclusion or some degree of dispersal limitation. Nonetheless, these results suggest that the mechanisms limiting the distribution of *F. sylvatica* may have changed over 6 ky.

Mechanisms influencing species distribution and niche position

Multiple processes surely influence species distributions and might change in importance over time, to the degree that the role of climate in limiting species distributions could have changed between the mid-Holocene and the present. This could result in a change in estimated niche position in multivariate climate space. For example, *P. abies* was a widely distributed species as of the mid-Holocene (Fig. 1b). Notably, *J. communis* had a similarly large predicted mid-Holocene range as *P. abies*. Pollen records show that *J. communis* was common and present at some sites in northern and western Europe before arrival of *P. abies* and full forest development (Lang 1994), suggesting that the late glacial and early Holocene distribution of *J. communis* was limited primarily by climate, not by competition. However, little pollen evidence for *J. communis* presence is available from much of its predicted mid-Holocene range in central Europe (Fig. 2b). Much of this area was by this time occupied by *P. abies* and mixed forest species (Lang 1994). *Juniperus communis* is a colonizer of disturbed and open areas due to its requirement for light and can tolerate soils with little development (Zoller 1981). This suggests that as of the mid-Holocene, competition had a larger influence on the distribution of *J. communis* than did climate.

It is unlikely that *J. communis* was completely absent from most of central Europe as of the mid-Holocene (i.e. absence of evidence is not evidence of absence), but the patterns we observe suggest that this species was at low density or absent across extensive areas of its potential range, which had come to be dominated by *P. abies* and other trees of closed canopy forest. The broad range but scattered distribution of *J. communis* in recent times (Fig. 2a) suggests that the species has benefited greatly from expanding anthropogenic disturbance, but may still be excluded from many optimal habitats by stronger competitors. Similar reasoning may explain the relatively poor fit of hindcasted models of *C. avellana*, a species which may have been absent locally within its predicted mid-Holocene range because of competition for light in closed canopy forest (Oberdorfer 1990; Burga & Perret 1998).

One further cause of prediction errors is that the mechanisms limiting species distributions could be hetero-

geneous, not just in time, but also over the range of the species. For example, it might be that in mapping *J. communis* occurrences in the mid-Holocene we included more (nominally) intraspecific variation by pooling closely related species or ecologically distinct populations when making or evaluating predictions. Another possibility is that just one or a few populations could be responsible for changes in species distribution. A case of differential range (and niche?) expansion of populations is known for *F. sylvatica*, in which only one population is thought to have expanded from its Pleistocene refugium to cover much of western Europe (Magri *et al.* 2006). This suggests that a niche shift affected this population, perhaps similar to the expansion of populations of invasive species in their introduced range (Broennimann *et al.* 2007). Intraspecific variation may also influence the local distribution and degree to which *L. decidua* is excluded by forest species such as *A. alba* and *F. sylvatica* (Zoller 1981).

Paleo-data, SDMs and prediction uncertainty

Fossil pollen data is often incomplete and the adequacy of the pollen record in representing species prior distributions can vary among species. For example, *L. decidua* produces and spreads small amounts of pollen (Zoller 1981). The pollen data on *L. decidua*, even at the low threshold we used here, probably underestimate the distribution of the tree. *Larix decidua* grows densely in a narrow elevation belt in mountains today (Fig. S5). Thus, pollen sites outside this belt likely record very little or no *L. decidua* pollen even when the species occurs relatively short distances away.

In another example, *P. abies* potentially might fill < 85% of its potential range currently (Svenning & Skov 2004). While the authors of that study (as here) may have failed to include one or more variables that are important to determining species distribution, this does not appear to affect model performance greatly upon hindcasting the mid-Holocene distribution of this species. Other species may be affected by choice of climate variables, but this is not possible to evaluate here. One possible explanation is that SDM performance may depend more on the degree to which a species has expanded to the limits of its niche than on expansion to its potential geographic range. Another possibility is that the spatial distribution of pollen cores might influence model performance differentially among species. For example, *P. abies* was absent from areas in Scandinavia that we predicted as suitable habitat as of the mid-Holocene. Over-prediction of the species in this area could conceivably have little influence on model fit because of the paucity in our data set of pollen cores from the area that is over-predicted, which corresponds to central Sweden (Fig. 1).

Limitations to the approach and future directions

We have shown that hindcasting and forecasting of species distributions using data from pollen cores are ways to evaluate model performance across time. While we used all available pollen data we could acquire electronically, continued growth of pollen databases will allow improved assessment of the effects on model performance of the choice of pollen thresholds. Increasing availability of plant macrofossils may eventually be sufficient as an additional source of data for modelling the distributions of some species. This may improve projections for species that can be present at low densities or otherwise produce little pollen.

A further limitation is that the equilibrium distribution of species cannot be estimated independently from competitive effects. Ideally, one would estimate the fundamental niche of a species, then constrain it with estimates of the effects of competitive interactions (Guisan *et al.* 2007b; Pearman *et al.* 2008). However, even with an understanding of the physiological limits that determine the fundamental niche, an estimation of the equilibrium distribution will require an operational understanding of how competitive interactions constrain the fundamental niche and result in an expected distribution based on the realized niche.

Future research on predictive modelling may result in better techniques, or an ensemble of techniques, with which to address effects of migration rates and predict levels of range filling (Botkin *et al.* 2007; Thuiller *et al.* in press). In the present study, we faced the additional problem of choosing a GCM for estimating past climate, because we were further constrained not to use comparison of GCM results with pollen-based climate reconstructions as a basis for our choice. Future work may approach effects of variation in predictions of past climate as a random factor to quantitatively estimate uncertainty generated by choice of climate model. For example, by model performance could be evaluated with a larger number of historical GCM runs for mid-Holocene climate (e.g. Brewer *et al.* 2007). Furthermore, variability in data quality that arises from any of our data sources could influence the observed relationship between distribution and climate (i.e. the realized climatic niche). Consideration of these issues and careful choice of additional species for analysis, both in Europe and elsewhere, will help improve our understanding of the ecological characteristics of species and the structural characteristics of data sets that influence predictions of plant response to climate change.

CONCLUSIONS

The increasing availability of data on plant distribution and climate allows testing SDMs by hindcasting and

forecasting. Model performance upon prediction depends on the estimated shift in a species' climate–distribution relationship. The ability to compete for light may be one factor that influences the relationship between a species distribution and geographic variability in climate. Additional effects likely include those of dispersal (migration) ability and range filling, elapsed time over which a prediction is made, and qualities of invariably imperfect data. The long time span used here, relative to predicted future climate change, likely affected in contrasting ways the estimated niche position changes in the study species. Future research should seek to improve quantitative understanding of the effects of these factors on predictions across time that are made with SDMs.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Niche and distribution modeling: boosted regression trees.

Appendix S2 Determination of change in estimated niche position in PCA climate space between two time periods.

Figure S1 The distribution of *Abies alba*, with pollen thresholds as labeled.

Figure S2 The distribution of *Carpinus betula*, with pollen thresholds as labeled.

Figure S3 The distribution of *Corylus avellana*, with pollen thresholds as labeled.

Figure S4 The distribution of *Fagus sylvatica*, with pollen thresholds as labeled.

Figure S5 The distribution of *Larix decidua*, with pollen thresholds as labeled.

Figure S6 Mean values of the area under the receiver operator characteristic curve (AUC) and 95% confidence intervals (a, b), and model performance as a function of magnitude of shift in climate space (c, d).

Table S1 Regression statistics and estimates of coefficients for two scenarios, in an analysis of model predictive ability (AUC) as a function of observed change in species realized climate niche position.

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Why are tetraploid Spotted Knapweeds (*Centaurea maculosa*) favored over diploids during biological invasion?

In review in Ecology

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ABSTRACT

Polyploidy is often assumed to increase the spread and thus the success of alien plant species, but few empirical studies exist. We tested this hypothesis with *Centaurea maculosa* Lam., a species native to Europe and introduced into North America about 120 years ago where it became highly invasive. We analyzed the ploidy level of more than 2000 plants from 93 native and 48 invasive *C. maculosa* populations and found a pronounced shift in the relative frequency of diploid and tetraploid cytotypes. In Europe diploid populations occur in higher frequencies than tetraploids and only four populations had both cytotypes, while in North America diploid plants were found in only one mixed population and thus tetraploids clearly dominated. Our results showed a pronounced climatic niche shift between tetraploid populations in the native and introduced range towards drier climate in North America, and a smaller difference between diploids and tetraploids in the native range, with tetraploids occurring in slightly drier climates. The field data indicate that diploids have a predominately monocarpic life cycle, while tetraploids are often polycarpic. Additionally, the polycarpic life form seems to be more prevalent among tetraploids in the introduced range than among tetraploids in the native range. Our study confirmed that both ploidy types of *C. maculosa* were introduced into North America, but tetraploids were favored over diploids during the invasion process. We thus conclude that the invasive success of *C. maculosa* is partly due to pre-adaptation of the tetraploid cytotype in Europe to dryer climate, and further adaptation to these conditions in the introduced range. The potential for earlier and longer seed production associated with the polycarpic life cycle constitutes an additional factor that may have favored the dominance of tetraploids over diploids in the introduced range.

INTRODUCTION

Several studies have tried to identify factors that make a species invasive (e.g., Blossey and Nötzold 1995, Mack et al. 2000, Keane and Crawley 2002, Callaway and Ridenour 2004) and because the proportion of polyploids is higher among invasive than among native species in some regional floras, several authors have recently suggested that polyploidy may constitute a favorable attribute for the success of alien plants (Verlaque et al. 2002, Pandit 2006, Pandit et al. 2006). Why polyploids are successful invasives remains unclear, however. Intuitively, the underlying mechanisms probably result from polyploidization, which can lead to increased and/or shifted ecological tolerance and alter functional traits including life form, herbivore resistance, self incompatibility, and competitive ability (Levin 2002).

Evidence for increased ecological tolerance (niche breadth) of polyploids comes from Stebbins' (1971) observation that tetraploids tend to have larger geographic ranges than diploids. A comprehensive study including all taxa of the genus *Clarkia* reports that polyploid taxa have significantly larger ranges than diploid taxa (Lowry and Lester 2006). Furthermore, among invasive species polyploids were found to colonize a larger variety of habitats (Verlaque et al. 2002). Polyploids may not only have a broader niche, they may also differ in their niche optima, thus mainly occurring under environmental conditions that differ from those of their diploid conspecifics. For example Hagerup (1933) reported, besides a wider distribution of the tetraploid compared to the diploid *Vaccinium uliginosum*, only slightly overlapping ranges between the two cytotypes. Similar differentiation between cytotypes was subsequently reported for various other diploid/polyploid complexes (e.g., Mosquin and Small 1971, Soltis and Soltis 1989, Van Dijk et al. 1992, Felber-Girard et al. 1996, Gauthier et al. 1998, Borgen and Hultgård 2003, Stuessy et al. 2004). In addition, Levin (2002) reports that polyploids, compared to their diploid conspecifics, can have an increased ability to grow at low nutrient levels, on dry and well drained soils, and at cold temperatures.

When neopolyploids originate within diploid populations, an increased or shifted ecological tolerance may allow them to establish and propagate despite a potential fitness disadvantage resulting from incompatible matings with diploid plants (Levin 1975). Here we argue that niche differentiation in the native range may provide an explanation for the observed increased invasive success of polyploids compared to diploids (Verlaque et al. 2002, Pandit 2006, Pandit et al. 2006). Let us consider a situation where environmental conditions in the introduced range differ from those in the native range. In this case, polyploids with increased ecological tolerance or a shifted niche optimum towards the environmental conditions in the introduced range are expected to have an advantage over diploids, because of a larger degree of niche overlap between the native and introduced range (i.e. polyploids are pre-adapted to ecological conditions in the introduced range). Furthermore, selection on traits responsible for the broader or shifted tolerance may further increase their fitness under the environmental conditions encountered in the new range (post-invasion evolution). Thus, due to pre-adaptation to these altered environmental conditions polyploids will become the dominant cytotype in the introduced range, and are expected to exhibit a shift in their niche optimum, compared to the combined niche of native diploids and polyploids. Furthermore their niche should be shifted in the same direction as the niche of the polyploids in the native range compared to the diploids.

Prolonged life span and polycarpy are commonly observed functional traits in polyploids that may increase seed output through earlier and repeated reproduction but also the buildup of higher herbivore loads (Lawton and Schroder 1977, Klinkhamer et al. 1997). For example, in *Centaurea maculosa*, specialized root-feeding herbivores were found to attack and kill larger plants preferentially (Müller 1989b, Müller et al. 1989). Even though such higher loads of natural enemies may disadvantage polyploids in the native range, a predominantly perennial, polycarpic life cycle may favor polyploids in environments that lack such natural enemies, e.g., after transcontinental introductions or island colonization (Müller-Schärer et al. 2004). In line with this argument, a clear trend towards a polycarpic life form and longer life span was observed for species on islands (Böhle et al. 1996).

Thus, an alternative mechanism for the increased invasive success of polyploids could be that they harbor traits providing them with an advantage when released from biotic constraints, e.g. specialist herbivores. Following the same line of arguments as the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995), polyploid genotypes which invest in repeated reproduction and thereby become more susceptible to natural enemies would be favored over diploid genotypes that try to escape from natural enemies by investing only once in reproduction (Klinkhamer et al. 1997, Müller-Schärer et al. 2004). In this situation, where release from biotic constrains is the main difference between the introduced and the native

range, with environmental conditions otherwise being similar, polyploids are expected to become the dominant cytotype in the introduced range through increased propagule pressure. In contrast to the situation where pre-adaptation to altered environmental conditions is important, here, the niche of the polyploids in the introduced range should not differ from the combined niche of the diploids and polyploids in the native range, neither in terms of niche breadth nor in terms of niche optimum.

In this study we provide a comprehensive assessment of the geographic distribution of the two ploidy types of *Centaurea maculosa* across its native (Europe) and introduced (North America) ranges, to access whether polyploids were favored during the invasion process, and to unravel the potential underlying mechanisms as outlined above. Specifically we ask: (1) Do the cytotypes differ in their niche breadth or niche optima in the native range, and did the niche optima further shift in the introduced range? (2) Does the niche of the polyploids in the introduced range differ from the combined niche of diploids and polyploids in the native range? (3) To what degree are life history traits linked to ploidy level? By answering these questions we seek support for either one or a combination of both of the outlined mechanisms: pre-adaptation to altered environmental conditions or increased competitive ability through altered life history traits as an explanation for the expected increased invasion success of polyploids.

METHODS

Study species

Centaura maculosa Lam. (syn. *C. stoebe* L.) is native to Europe, but a highly invasive plant species in North America, to where it was introduced 120 years ago (Roché et al. 1986). The taxonomy of *C. maculosa* is unclear (Ochsmann 2000, Royal Botanic Garden Edinburgh 2007) and presently under re-investigation. Ochsmann (2001) suggested subdividing the species according to the known ploidy levels: *C. stoebe* L. subsp. *stoebe* (diploid 2n = 18) and *C. stoebe* L. subsp. *micranthos* (Gugler) Hayek (tetraploid 2n = 36). Here, in order to include the complete native range and to ensure robust cross-continental comparison, we considered *C. maculosa* s.l. as the taxonomic entity.

Population data and environmental variables

For the present study we used data from 97 populations collected during our own field surveys in 2005 as well as from 44 additional populations sampled by colleagues, resulting in a total sample size of 141 *C. maculosa* populations (Fig. 1, Appendix A). Overall, data from 93 and 48 populations were available from Europe (EU) and North America (NA), respectively, with varying information per population. The field surveys were performed by sampling populations spaced by at least 16 km. Population sampling depended on the abundance of *C. maculosa* plants at each site: seeds from 16 randomly selected plants were sampled in populations with low abundance while plants were systematically sampled in populations with high abundance. Systematic sampling depended on the area covered by the population: we sampled 16 plants along a transect of 50 m 2 m (100 m2) or in two sub-transects (c. 25 m 2 m) if the spatial structure of the population did not allow sampling within one transect. Along the transect, 16 sampling points were defined, separated by three meters and starting at 2.5 m. In populations that covered only a small area not allowing transect sampling we defined 16 regularly spaced sampling points (1.5 m) across a quadrate of 4.5 m 4.5 m (20.25 m2). At all sampling points, we selected the nearest *C. maculosa* plant. For each selected plant we collected seeds from at least 10 seed heads, measured height and diameter (the mean of the maximum horizontal and its orthogonal plant extent), counted the number of stems, noted if the plant formed new lateral buds/shoots (an estimate of polycarpy), and scored herbivore damage (low, medium, or high) on different root parts (external, internal, and collar). If a selected plant did not carry seeds, we additionally chose the nearest fruiting plant for seed collection. We also estimated the area covered by the population in five classes (<100 m2; <250 m2; <1000 m2; >1000 m2 but extend less than 1 km; not determinable) and assessed population density by counting *C. maculosa* plants on an area of 20 m2 (in the transects every 5 m in a strip of 1 2 m) or 20.25 m2 (quadrate sampling).

We separately counted small and large rosettes as well as flowering plants, and noted if they formed new rosettes. At each site we determined habitat type (forest, grassland, ruderal, waterside), the degree of anthropogenic disturbance (low, medium, or high), slope, vegetation parameters (percentage of bare ground, grass and forb cover, mean grass and forb height), and various soil parameters (pH; Munsell Color (1975): value, chroma; clay content; and presence of

CaCO3, measured with an HCl reaction). In addition to the local field data, we used ArcGIS 9.0 (ESRI, Redlands, California) to retrieve climate data for all populations (potential evapo-transpiration, PET; ratio of actual to potential evapo-transpiration, AET/PET; annual precipitation, PREC; annual variation in precipitation, STD_PREC; minimum temperature of the coldest months, TMIN; maximum temperature of the warmest months, TMAX; growing degree days, GDD; CRU 10' dataset; New et al. 2002), land cover classification (forest, woodland s.l., grassland, cropland, urban; Hansen et al. 2000), and vegetation structure (datasets from http://edcdaac.usgs.gov/main.asp: remote sensing tree and bare ground cover (rm_tree, rm_bare;

"MOD44b" dataset) and primary productivity determined at three different times in the season from normalized difference vegetation indices (ndvi-3/22/05, ndvi-6/10/05, and ndvi-9/30/05; "MOD13q1v4" dataset)). See Appendix B for more details on the environmental variables.

Ploidy determination

We attempted to grow one offspring from each individually collected plant per population (in general 16, but available plants varied from 2-18). We also attempted to grow 16 plants if only population bulk seed samples were available. We successfully grew 2005 plants, on average 14 per population from which the DNA ploidy level was estimated using flow cytometry (for population details and number of plants analyzed see Appendix A). Populations were randomized and ploidy levels were determined with bulk samples. We only analyzed individual plants when both cytotypes were detected within a sample, thus for populations with mixed ploidy levels. In pre trials we determined that analyses of bulk samples with eight plants still allowed us to easily detect mixed ploidy levels within a sample. Samples were prepared in a petri dish by chopping 0.2 cm2 leaf tissue from eight plants for 30 seconds with a sharp razor blade in 500 µL of extraction buffer (Partec GmbH, Münster, Germany). Thereafter, 500 µL of extraction buffer was added. The mix was incubated for about one minute before filtering the nuclei suspension with a 30 µm CellTrics® disposable filter (Partec). Two mL of staining buffer (Partec; containing 20 µg RNAse) were added and the mix incubated for at least 30 min in darkness. We analyzed the extracted and stained nuclei with a CyFlow® SL Green 2P (CY-S-1022 HR, Partec). Data acquisition and analysis were done with the software FloMax® ver. 2.0 (Quantum Analysis, Münster, Germany). The fluorescence intensity at channel 100 was adjusted to a diploid plant of *C. maculosa* originating from population 44 (hereafter standard plant). Samples of the standard plant were prepared as described above, except that more leaf tissue was used (0.5 cm2). Samples of the standard plant were then analyzed in regular intervals between the other samples and fluorescence peak position of sample peaks were compared to the mean peak position of the standard plant. We classified each population or individuals in mixed populations as diploid (2x) or tetraploid (4x) since DNA ploidy proved to be consistent with ploidy determined by chromosome counts (Bancheva and Greilhuber 2006). Up to now only chromosome numbers of 2x = 18 and 4x = 36 were described for *C. maculosa*, with occurrence of B chromosomes (Ochsmann 1999). Exact DNA contents were not assessed due to methodological fluctuations in the measurement. Some populations showed ambiguous 4x DNA-ploidy levels (indicated by smaller or intermediate genome size measurements). This ambiguity of classification coincides with populations in southern France (Fig. 1, Appendix A) and all analyses were therefore performed with and without these populations. The results were in general consistent and therefore reported for all populations, except when differences were obtained. Based on the combination of the population's cytotypes (2x/4x) and geographical range (EU/NA), we assigned so-called geo-cytotypes (2xEU, 4xEU, 2xNA, and 4xNA) to each population for further analyses.

Data analysis

We analyzed for differences in niche optima (i.e. niche shifts) and niche breadth among geocytotypes with Outlying Mean Index analysis (OMI: Doledec et al. 2000), Chi-square tests, and logistic regression (Hosmer and Lemeshow 2000). The OMI analysis is a constrained ordination method used to estimate species niche optimum and niche breadth (i.e. ecological tolerance) along environmental gradients (Doledec et al. 2000). In OMI analyses, niche optima are estimated as the difference between the mean climatic conditions under which a given species occurred and the mean climatic conditions of all studied sites (Doledec et al. 2000). In our analyses, geo-cytotypes were treated as a "species" and mixed populations were included in the analyses according to the ratio of ploidy types. Niche shifts, i.e., differences in niche optima among geo-cytotypes were measured along the two OMI axes separately, and in the OMI plane defined by those axes. The latter was calculated as the Euclidian distance between the niche optima of geo-cytotypes, weighted by axis inertia. Niche breadth was calculated as the variance in the occurrences' position along the OMI axes (Thuiller et al. 2004, Thuiller et al. 2005), or as the ellipse surface in the OMI plane. The ellipses are a graphical summary of the cloud of points of each geo-cytotype, defined by the gravity centre of the cloud (i.e. the mid point) and 1.5 times the standard deviation of the projections of the points on the ellipse axis (drawn orthogonal with maximal dispersion). Differences in niche breadth among geo-cytotypes were calculated separately, as the difference between the variances on the two axes, and in ellipse surface weighted for axes inertia. We used 999 Monte Carlo randomizations to test for differences in niche breadth (two-sided tests) and for niche shifts (one-sided tests). Using the OMI analysis we tested for niche shifts and differences in niche breadth along climatic, local scale abiotic as well as large and local scale vegetation structure gradients (for variables see Appendix B). In addition, we tested if geocytotypes differ in niche breadth, by testing the difference in frequency of geo-cytotypes among habitat types with chi-square tests. Due to occurrences below the recommended minimum of five, we assessed the significance of the chi-square statistics by 9999 Monte Carlo randomizations (Sokal & Rohlf, 1995). We tried to disentangle the possible mechanisms causing niche shifts between geocytotypes in the two ranges with logistic regression models. We ran the models with geo-cytotype contrasts (2xEU vs. 4xEU and 4xEU vs. 4xNA) as response of one climatic or vegetation structure variable at the time. Each variable was included with both its linear and quadratic term. To examine if differences in niche optima between cytotypes in the native range indicate preadaptation of tetraploids to the conditions in the introduced range we assessed if logistic regression models built on the contrast between 2xEU and 4xEU could predict the differences between 4xEU and 4xNA. Data splitting (70% training and 30% test data) was performed to assess model accuracy with the area under the curve (AUC) of the receiver-operating characteristic plots (Fielding and Bell 1997). AUC values between 0.5 and 0.7 indicate no or poor discrimination, while values greater than 0.7 indicate reasonable discrimination between groups (Pearce and Ferrier 2000). We computed AUC values for 999 randomly split datasets to test if a given model provided better discrimination than random (AUC > 0.5). In addition, we calculated the conditional probability of correctly predicted geo-cytotypes, as the number of populations correctly assigned to a given geo-cytotype out of all populations of this geo-cytotype (cf. Fielding and Bell 1997). To assess a possible link between geo-cytotypes and population traits, we performed non21parametric tests and analyses of variance (ANOVAs). Due to non normality and unequal variance of several traits, we computed non-parametric Mann-Whitney U-tests to test for differences in the 15 population traits among ranges (native vs. introduced) and geo-cytotypes. *P*-values were corrected for multiple comparisons with the Dunn-Sidak method (Sokal and Rohlf 1995). We performed ANOVAs for traits where transformations allowed using parametric statistics. As the results of ANOVAs and Mann-Whitney U-tests did not differ, only results from the latter are reported. Anthropogenic disturbance may affect population traits since habitat disturbance is known to promote spread and establishment of invasive species. We therefore tested with two-way factorial ANOVAs if differences in population traits between geo-cytotypes are altered by the level of anthropogenic disturbance. ANOVAs and Chi-square tests were performed in SPSS for Windows (2003), Mann Whitney U-tests, Outlying Mean Index analysis (using the ade4 package: Dray and Dufour 2007) and logistic regressions were computed in the R environment (R Development Core Team 2007).

RESULTS

Geographical distribution of cytotypes

We determined the ploidy level of more than 2000 plants of *C. maculosa* originating from 141 natural populations spread across the whole geographical range. On average, we analyzed 13.7 individuals per population of the native range (Europe) and 15.2 individuals per population of the introduced range (North America). We observed a profound shift in the frequency of the two ploidy types between the native and introduced range, with 56% diploid, 40% tetraploid and 4% mixed populations in Europe and 98% tetraploid and 2% mixed populations in North America (Fig. 1). No obvious geographical pattern in the distribution of the two ploidy cytotypes was observed in the native range but given the ambiguity of ploidy determination in populations of southern France (attributed to 4x), in the native range, diploid populations seem to occur in higher frequencies than tetraploid populations. Overall, mixed populations were scarce (5 of 141 populations), and were therefore excluded from all except the OMI analyses. Three of the mixed populations were dominated by one ploidy type (1–2 plants of 14–16 of either the 2x or 4x cytotype) while more balanced frequencies (37–50%) were found in the two other populations. The introduced range was dominated by tetraploid plants with only two plants out of 731 being diploid (Fig. 1, Appendix A). In summary, three main geo-cytotypes could be distinguished: native diploids (2xEU), native tetraploids (4xEU), and invasive tetraploids (4xNA).

Differences in niche optima among geo-cytotypes

Cytotypes in the native range (2xEU vs. 4xEU) only differed significantly in niche optima along the second OMI axis (Table 1), which represents a temperature-energy gradient, indicating a shift of the EU tetraploids towards warmer climate (Fig. 2). At the local scale, tetraploids tended to occur more on soils with higher CaCO3. Native and invasive tetraploids had significantly different niche optima along climatic gradients, large and local scale vegetation structure, and local abiotic gradients (Table 1). For local scale and climatic gradients, we observed opposite shifts between native and invasive tetraploids compared to the shifts between cytotypes in the native range. For soil, these trends were only observed when southern France populations, showing ambiguous 4x DNA-ploidy levels, were included in the analysis. Results of additional OMI analyses testing for differences between the combined niche of native cytotypes and the niche of tetraploids in the introduced range were very similar to the results for the comparison of native and invasive tetraploids (Table 1). We found highly significant niche shifts for all four gradients in the OMI plane and along axis 1, while axis 2 had no importance in these analyses. The OMI analyses indicated that invasive tetraploids tended to grow in areas with warmer and dryer climates, more bare ground and lower primary productivity. At the local scale, invasive tetraploids occurred more on soils with increased chroma values and lower CaCO3 contents as well as vegetation characterized by lower forb cover but higher mean forb and grass height. Logistic regression models showed that GDD, TMAX and PET significantly discriminated between cytotypes in the native range. The models predicted 2xEU populations better than 4xEU (Table 2). Tetraploids between ranges were significantly discriminated by AET/PET, GDD, PET and TMIN; again, the models had lower prediction accuracy for the 4xEU populations (Table 2). GDD predicted both the differences between cytotypes in Europe and between the tetraploids in the two ranges, but with opposite signs. Two models which we calibrated on the two cytotypes in the native range showed AET/PET and PET as best predictors for the observed niche shift between native and invasive tetraploids (Table 2).

Differences in niche breadth among geo-cytotypes

Ecological tolerance along large scale vegetation structure gradients tended to increase from diploids to tetraploids in the native range and increased even further for tetraploids in the introduced range, as indicated by the OMI analyses (Table 1). At the local scale, ecological tolerance also tended to increase in native tetraploids but this trend clearly reversed for invasive tetraploids, which showed reduced niche breadth for local soil conditions (Table 1). Again, the overall contrast between the native and invasive cytotypes was very similar to the results for the comparison of native and invasive tetraploids (Table 1). Thus, niche breadth for large scale vegetation structure (increased) and local scale abiotic factors (decreased) differed significantly from the combined niche of the diploids and polyploids in the native range but in contrasting directions.

The geo-cytotypes did not differ in the number of different habitat types and landscape classes in which they occur (Table 3 and 4). Nevertheless, frequency of occurrence within major habitat types (forests, grasslands, ruderal sites, and along shores/rivers) differed significantly

(c2 [6] = 17.082, p = 0.009, Table 3). The contrast between diploid and tetraploid populations in the native range was significant (c2 [3] = 8.804, p = 0.035) while tetraploid populations between ranges did not differ significantly (c2 [3] = 2.837, p = 0.418). Diploid populations occurred predominantly in grasslands, especially natural dry meadows, while tetraploid populations had a more balanced occurrence among the different habitat types. The occurrence in ruderal sites was very similar for all geo-cytotypes while the occurrence in open forest habitats tends to increase in the introduced range. Using remote sensing data, we found that the three geo-cytotypes also differed significantly in their frequency among five different land cover classes (c2 [8] = 22.190, p = 0.004, Table 4). Again, the contrast between native diploid and tetraploid populations was significant (c2 [4] = 9.569, p = 0.047) while tetraploid populations between ranges did not differ significantly c [4] = 2.814, p = 0.589). In the native range, populations in southern France were most strongly associated with open forests or woodland habitats. Excluding these populations from the analyses, and thus accounting for ambiguous 4x DNA-ploidy level estimates, tetraploid cytotypes also tended to differ between ranges. We did not find any difference in frequency occurrence of geocytotypes in habitats with low, medium or high anthropogenic disturbance (c [4] = 1.542, p = 0.819). *Differences in population traits between geo-cytotypes* Data from our field survey revealed significant differences between native and invasive populations for some traits, with plants from the introduced range exhibiting more stems, an increased level of polycarpy (indicated by post-reproductive emergence of lateral buds/shoots) and increased damage by internal root feeders (Table 5). Invasive populations also tended to cover larger areas and to have higher densities of large rosettes and flowering plants (Table 5). In Europe, tetraploid populations, compared to their diploid conspecifics, showed a significant increase in the number of stems/plant, and also the level of polycarpy tended to be higher (Table 5). Moreover, invasive tetraploids had a significantly higher proportion of polycarpic plants, had lower damage levels of external root feeders, and covered larger areas than native tetraploids (Table 5). A two-way factorial ANOVA with stem number as the response variable and geo-cytotype (three levels: 2xEU, 4xEU, and 4xNA) and anthropogenic disturbance (three levels: low, medium, high) as explanatory factors gave significant results for geo-cytotype (F[2,34] = 5.103, $p < 0.001$) and the interaction term (F[4,34] = 4.095, p = 0.008). In highly disturbed habitats (e.g. road sides), 4xNA geo-cytotypes had increased number of stems compared with 4xEU and 2xEU while in habitats with low or intermediate disturbance, geo-cytotypes varied little in stem number.

DISCUSSION

This study represents the first global assessment of the geographical distribution of ploidy cytotypes in *C. maculosa* s.l.. We report a profound shift in the ratio of the two ploidy types between the native (Europe) and the introduced (North America) range. Furthermore, our study showed that, as previously hypothesized, both ploidy types of *C. maculosa* were introduced into North America, but tetraploids were selected over diploids during the invasion process. Two contrasting, but mutually nonexclusive hypotheses dominate the literature on plant invasion (Müller-Schärer and Steinger 2004). The first assumes that specific trait combinations pre-adapt species to become good invaders ('pre-adaptation hypothesis'), whereas the second postulates successful invasion as the outcome of rapid evolutionary change in the new habitat ('post-invasion evolution hypothesis'). Our results provide support for both hypotheses: The tetraploid cytotype of *C. maculosa* comprises genotypes that were pre-adapted to ecological conditions in the introduced range (1) through increased tolerance to dryer conditions and (2) through changes in functional traits, especially increased polycarpy, providing them with an advantage over diploids during the invasion process. Additionally, tetraploids may have further evolved through directional selection in the introduced range, as indicated by the shift in niche optima and climatic differences between ranges suggesting rapid post-invasion evolution (Fig. 2, Table 2, Broennimann et al. 2007).

As reported by Broennimann et al. (2007), *C. maculosa* shows a clear shift in the climatic niche space between the native and introduced range. Our findings confirmed this shift using various environmental gradients at different scales (Table 1). Interestingly, we additionally confirmed that these niche shifts also occurred within the tetraploid cytotypes and that a few climatic parameters – with potential evapotranspiration being the

most important – unravel a sequential shift between cytotypes in the native range and tetraploids between ranges towards dryer conditions (Table 2). Niche breadth of tetraploids in the native range increased for some of the gradients compared to diploids and it further increased for the large scale vegetation gradient in the introduced range, but decreased for local scale abiotic conditions (Table 1). Furthermore, diploids and tetraploids did not differ in the number of habitats they occupy although tetraploids have a more balanced occurrence across the different habitat types and land cover classes (Table 3 and 4). Thus, the pattern for niche breadth between cytotypes in the native range partly supports the expectation that polyploids may have increased ecological tolerance. Answering our first two questions, the cytotypes did differ in their niche breadth and optima in the native range, even though a large niche overlap was observed. Furthermore, the niche of the tetraploid cytotype further shifted in the introduced range and differed significantly from the combined niche of diploids and polyploids in the native range (Table 1, Fig. 2).

The observed niche differences between the two ranges thus supports the idea outlined in the introduction, that polyploidization in *C. maculosa* may have favored increased tolerance to warmer and dryer condition and thus, that the increased invasion success of polyploids is at least partly due to pre-adaptation to the altered environmental conditions in the introduced range. This view finds support in the introduction history of *C. maculosa*, a species introduced at least a few if not multiple times (Hufbauer and Sforza 2007) into North America and at least in two different areas (Roché et al. 1986). The earliest report dates to 1893 for Victoria BC, from where it subsequently spread into the coastal areas of British Columbia and Washington. The species, however, appears to have spread into Washington in greater numbers from the east and was abundant in Montana before it became common in eastern Washington (Roché et al. 1986). This strongly suggests that *C. maculosa* also was also introduced to Montana, probably as alfalfa seed contaminants. Today, Montana suffers from large infestations by this noxious invader and thus, may be regarded as one of today's core areas of *C. maculosa* invasion. Compared to the native range, the climatic conditions are dryer and warmer in these areas (Broennimann et al. 2007). Hence, after introduction the species was exposed to different climatic conditions and this gave tetraploids an advantage, as they were better adapted to these conditions. However, stochastic processes, such as a strongly biased or earlier introduction of tetraploids, or strong founder effects are further possible explanations for the profound shift in cytotype frequencies (Kliber and Eckert 2005). Molecular marker studies including a large set of populations of both ranges are needed to further disentangle these processes.

Although we found evidence for pre-adaptation through increased tolerance to the altered environmental condition in the introduced range, a combination with pre-adaptation through changes in functional traits can not be excluded. In agreement with earlier reports, our field study revealed that tetraploid populations consist of plants with more stems and a higher relative frequency of polycarpy than diploid populations (Müller 1989a, Ochsmann 2001). Our data suggest that this relationship is only partial, and thus, polycarpy and polyploidy are not strictly linked. Nevertheless, it implies that tetraploids have a higher tendency for a long lived, polycarpic life form, which most probably is genetically determined. In agreement with these findings, an older age structure for tetraploid than for diploid populations was recently confirmed for Europe (Christine Bollig, personal communication) and North American plants were reported to live up to 9 years (Boggs and Story 1987). Stem number and polycarpy was highest in the introduced range, which suggests selection favoring polycarpy and thus, repeated reproduction during establishment in the introduced range free of natural enemies. This confirms our expectations, as outlined in the introduction and predicted by the evolution of increased competitive ability (EICA) hypothesis (Blossey and Nötzold 1995).

By examining the patterns of root herbivory across the investigated populations in the field, we observed different patterns for external and internal root feeders. In the introduced range we scored higher internal damage while in the native range damages at the external part of the root were higher. Generalist arthropod herbivores are mainly external while specialist arthropod herbivores are internal feeders (Strong et al. 1984). Therefore, the high level of internal root herbivory in the introduced range can be seen as the result of the large-scale bio-control effort against this species (Müller-Schärer and Schroeder 1993). Nevertheless, up to now *C. maculosa* remains an uncontrollable invasive species despite considerable bio-control efforts over the past 46 years and recent observations of population declines at some sites (Story et al. 2006). Under the present management scheme, intentionally introduced specialized natural enemies do not (yet) seem to limit the abundance of the tetraploid cytotype. This does, however, not allow to conclude that the observed shift in cytotype occurrence was not influenced by their initial absence (for the first 70 years) in the introduced range. It seems reasonable that not only pre-adaptation of tetraploid genotypes and further selection to the altered

environmental conditions in the introduced range but also traits linked to this cytotypes, as the perennial, polycarpic life cycle with its earlier and repeated seed production, enforced the invasion success of tetraploids.

Interestingly, the populations located in southern France showed not only anomalies in DNA-ploidy but were also different in their position in the climatic niche space, occurring under high growing degree day conditions. This may lie in the difficult taxonomy of *C. maculosa* s.l (Hufbauer and Sforza 2007). Our study therefore highlights that morphological and molecular studies, including many plants from various populations of the native and introduced range, are needed to resolve the taxonomic problems in this group and the origin of the introduced populations. Hybridization is commonly observed and a possible hybrid origin of tetraploids as well as the mode of polyploidization (allo- vs. auto-polyploidization) needs additional clarification. Hybridization is increasingly recognized as an additional mechanism promoting the invasiveness in plants (Ellstrand and Schierenbeck 2000). In line with this, polyploid populations may maintain most of their genetic variation in spite of inbreeding and bottlenecks because each plant individual carries a large fraction of the populations gene pool in the form of fixed heterozygosity, while populations of out-crossing diploids typically become genetically depauperate when exposed to inbreeding and bottlenecks (Brochmann et al. 2004). This gives polyploids a further advantage, especially when dispersed over long distances by humans and introduced to new ranges. In addition to pre-adaptation to the altered ecological setup (climate or lack of natural enemies), hybridization may provide a further explanation for the dominance of the tetraploid cytotype in the introduced range.

For species showing ploidy variation, our study strongly advocates considering ploidy level as a further important factor promoting invasions. Ecological differences between cytotypes are increasingly recognized, even under autopolyploidy, and thus they may be considered as distinct biological entities (Soltis et al. 2007).

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Table 1: Outlying Mean Index (OMI) analyses for niche shifts and differences in niche breadth (ecological tolerance) along climate, vegetation structure, and local abiotic gradients.

VARIABLES	NICHE OPTIMUM			NICHE BREADTH		
	EU vs. **NA**†	**2xEU** vs. **4xEU**‡	**4xEU** vs. **4xNA**‡	**EU** vs. **NA**†	**2xEU** vs. **4xEU**‡	**4xEU** vs. **4xNA**‡
climate (large scale, N = 141)						
area	**0.001**	0.099	**0.012**	*ns*	*ns*	*ns*
axis 1[a)] (100%†, 81%‡)	**0.001** →	*ns*	**0.001** →	*ns*	*ns*	*ns*
axis 2[b)] (0%†, 19%‡)	-	**0.001** ↓	**0.001** ↑	-	*ns*	*ns*
vegetation (large scale, N = 140)						
area	**0.001**	*ns*	**0.026**	**0.002** ◄	0.098 ◄	*ns*
axis 1[c)] (99%†, 97%‡)	**0.001** →	*ns*	**0.013** →	**0.002** ◄	*ns*	**0.032** ◄
axis 2 (1%†, 3%‡)	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
abiotic (local scale, N = 73)						
area	**0.002**	*ns*	**0.039**	**0.044** ►	*ns*	**0.004** ►
axis 1[d)] (100%†, 85%‡)	**0.001** →	*ns*	**0.024** →	**0.010** ►	*ns*	*ns*
axis 2[e)] (0%†, 15%‡)	-	**0.017** ↓	0.064 ↑	-	0.070 ◄	**0.004** ►
vegetation (local scale, N = 80)						
area	**0.001**	*ns*	**0.002**	*ns*	*ns*	*ns*
axis 1[f)] (100%†, 93%‡)	**0.001** →	*ns*	**0.001** →	*ns*	*ns*	*ns*
axis 2 (0%†, 7%‡)	-	*ns*	*ns*	-	*ns*	*ns*

Notes: The direction of niche shifts along axes is indicated with arrows and increasing/decreasing of niche breadth with / symbols, boldface type indicates statistically significant at $p < 0.05$, ns = not significant. OMI analyses were performed separately, either for the contrast between ranges† (EU: Europe, NA: North America) or for the contrasts among geo-cytotypes‡ (2x: diploid, 4x: tetraploid). Significance of niche differences were assessed with permutation tests, either on the 2 dimensions area of OMI axis 1 and 2 (ellipse area and centroids, differences were weighted by the axis inertia) or on the niche projections on each OMI axes (niche centroids or variance of means). No values are given for axes inertia less than 0.5%, inertia are given in brackets. Correlations greater than 0.2 of variables with a given axis are given below (for variable descriptions see methods and Appendix B): a†) AET/PET (-0.68), PET (0.62), TMIN (-0.46), TMAX (0.37), GDD (-0.32), STD_PREC (0.25) a‡) AET/PET (-0.66), PET (0.64), TMAX (0.40), TMIN (-0.38), STD_PREC (0.30), GDD (-0.25) b‡) GDD (-0.38), TMAX (-0.26), TMIN (-0.23), PET (-0.21) c†) rm_bare (0.42), ndvi-9/30/05 (-0.30) c‡) rm_bare (0.41), ndvi-9/30/05 (-0.24) d†) $CaCO_3$ (-0.40), chroma (0.34), pH (-0.25), slope (-0.23) d‡) chroma (0.40), $CaCO_3$ (-0.37), slope (-0.29), pH (-0.26) e‡) $CaCO_3$ (-0.20) f†) gr_height (0.45), fo_height (0.38), forbs (-0.32) f‡) gr_height (0.46), fo_height (0.36), forbs (-0.35)

Table 2: Results of logistic regression models of contrasts between geo-cytotypes and single climatic variables (included with linear and polynomial terms).

	2xEU vs. **4xEU**			**4xEU** vs. **4xNA**			**2x4xEU to 4xEUNA**[a)]	
	AUC		**% correct** (2xEU; 4xEU)	**AUC**		**% correct** (4xEU; 4xNA)	**AUC**	**% correct** (4xEU; 4xNA)
AET/PET	*ns*		95 ; 4	0.88***	←	75 ; 78	0.87*	85 ; 60
GDD	0.76**	→	85 ; 46	0.85***	←	58 ; 86	*ns*	42 ; 10
PET	0.73**	→	92 ; 40	0.70*	→	60 ; 83	0.71*	49 ; 90
PREC	*ns*		95 ; 8	*ns*		5 ; 85	*ns*	92 ; 21
STD_PREC	*ns*		98 ; 1	*ns*		14 ; 83	*ns*	89 ; 23
TMAX	0.76**	→	87 ; 48	*ns*		20 ; 88	*ns*	40 ; 74
TMIN	*ns*		97 ; 5	0.79**	←	52 ; 81	*ns*	68 ; 4

Notes: Model accuracy is reported as mean AUC (on test data) and *p*-values calculated from 999 models run on randomly split datasets (70% for training, 30% for testing). In addition, we report the conditional probability of correctly predicted geo-cytotypes. Arrows indicate the shift direction along the gradient. For variable descriptions see Methods and Appendix B, EU: Europe, NA: North America, 2x: diploid, 4x: tetraploid. a) models were calibrated on cytotypes in the native range and subsequently applied to tetraploids in both ranges to predict niche shifts for the invasive cytotype along the single environmental gradients. Probabilities for AUC-values > 0.5: *** $p < 0.001$ ** $p < 0.01$, * $p < 0.05$, *ns* = not significant

Table 3: Occurrence of populations in major habitat types derived from field data.

GEO-CYTOTYPE	**HABITAT TYPE**				
	forest [a)]	**grassland** [b)]	**ruderal** [c)]	**waterside** [d)]	**N**
2xEU	2%	65%	31%	2%	45
4xEU	14%	43%	29%	14%	28
4xNA	27%	30%	36%	7%	30

Notes: Geo-cytotypes are defined as native diploids (2xEU), native tetraploids (4xEU), and invasive tetraploids (4xNA); EU: Europe, NA: North America. a) open forest habitats or forest edges b) meadows, pastures, or semi natural grasslands c) mainly roadsides, rarely other wasteland d) along rivers, lakes or sea-shores

Table 4: Occurrence of populations in major land-cover classes derived from remote sensing data.

GEO-CYTOTYPE	**LAND-COVER CLASSES**					
	forest	**woodland s.l.** [a)]	**grassland**	**cropland**	**urban** [b)]	**N**
2xEU	10%	23%	4%	60%	4%	52
4xEU	11%	43%	14%	30%	3%	37
4xNA	17%	41%	17%	17%	7%	46

Notes: Geo-cytotypes are defined as native diploids (2xEU), native tetraploids (4xEU), and invasive tetraploids (4xNA); EU: Europe, NA: North America. a) mainly woodland and wooded grassland, rarely shrub land b) urban and build-up areas

Table 5: Differences in population traits between ranges and geo-cytotypes.

TRAIT	EU ; NA			2xEU; 4xEU			4xEU ; 4xNA		
	N	medians	p-value	N	medians	p-value	N	medians	p-value
Population density [plants/m^2]	25 ; 14	6.96 ; 15.60	*ns*	14 ; 11	7.23 ; 5.65	*ns*	11 ; 14	5.65 ; 15.60	*ns*
small rosettes (SR)	25 ; 14	1.55 ; 1.25	*ns*	14 ; 11	2.13 ; 0.45	*ns*	11 ; 14	0.45 ; 1.25	*ns*
large rosettes (LR)	25 ; 14	0.50 ; 3.48	0.079	14 ; 11	0.55 ; 0.15	*ns*	11 ; 14	0.15 ; 3.48	*ns*
flowering plants (FP)	25 ; 14	3.95 ; 9.43	0.104	14 ; 11	4.00 ; 3.45	*ns*	11 ; 14	3.45 ; 9.43	*ns*
Proportion of SR (SR/[SR+LR+FP])	25 ; 14	0.26 ; 0.12	*ns*	14 ; 11	0.30 ; 0.16	*ns*	11 ; 14	0.16 ; 0.12	*ns*
Proportion of FP (FP/[SR+LR+FP])	25 ; 14	0.59 ; 0.61	*ns*	14 ; 11	0.58 ; 0.74	*ns*	11 ; 14	0.74 ; 0.61	*ns*
Area covered (area classes)	82 ; 29	3.5 ; 4.0	0.102	48 ; 34	4.0 ; 2.5	*ns*	34 ; 29	2.5 ; 4.0	**0.026**
Mean height of flowering plants [cm]	25 ; 18	58 ; 54	*ns*	14 ; 11	62 ; 46	*ns*	11 ; 18	46 ; 54	*ns*
Mean diameter of flowering plants [cm]	25 ; 18	22 ; 29	*ns*	14 ; 11	22 ; 22	*ns*	11 ; 18	22 ; 29	*ns*
Number of stems	25 ; 18	1.88 ; 5.47	**0.002**	14 ; 11	1.18 ; 3.14	**0.000**	11 ; 18	3.14 ; 5.47	*ns*
Polycarpy (new lateral buds/shoots)	25 ; 21	0 ; 1	**0.000**	14 ; 11	0 ; 0	0.074	11 ; 21	0 ; 1	**0.000**
Total root herbivore damages	25 ; 14	0.12 ; 0.17	*ns*	14 ; 11	0.06 ; 0.19	*ns*	11 ; 14	0.19 ; 0.17	*ns*
only external	25 ; 14	0.04 ; 0.00	0.084	14 ; 11	0.01 ; 0.08	*ns*	11 ; 14	0.08 ; 0.00	**0.033**
only internal	25 ; 14	0.10 ; 0.30	**0.023**	14 ; 11	0.05 ; 0.13	*ns*	11 ; 14	0.13 ; 0.30	*ns*
only collar	25 ; 14	0.19 ; 0.20	*ns*	14 ; 11	0.15 ; 0.31	*ns*	11 ; 14	0.31 ; 0.20	*ns*

Notes: Significance of the differences were determined with Mann-Whitney U-tests, *p*-values were corrected for multiple comparisons, boldface type indicates statistically significant differences at $p < 0.05$, ns = not significant. Geo-cytotypes are defined as native diploids (2xEU), native tetraploids (4xEU), and invasive tetraploids (4xNA); EU: Europe, NA: North America.

Fig. 1: Distribution of *Centaurea maculosa* s.l in its native (Europe, circles) and introduced (North America, diamonds) range. Open symbols indicate populations with diploid (2x), filled symbols with tetraploid (4x) plants, and half filled symbols with mixed occurrences. The enlargements (A, B) show areas in Europe where mixed populations occur. Note: the 4x DNA-ploidy level for populations in southern France is ambiguous. Exact locations of sampled populations are given in Appendix A.

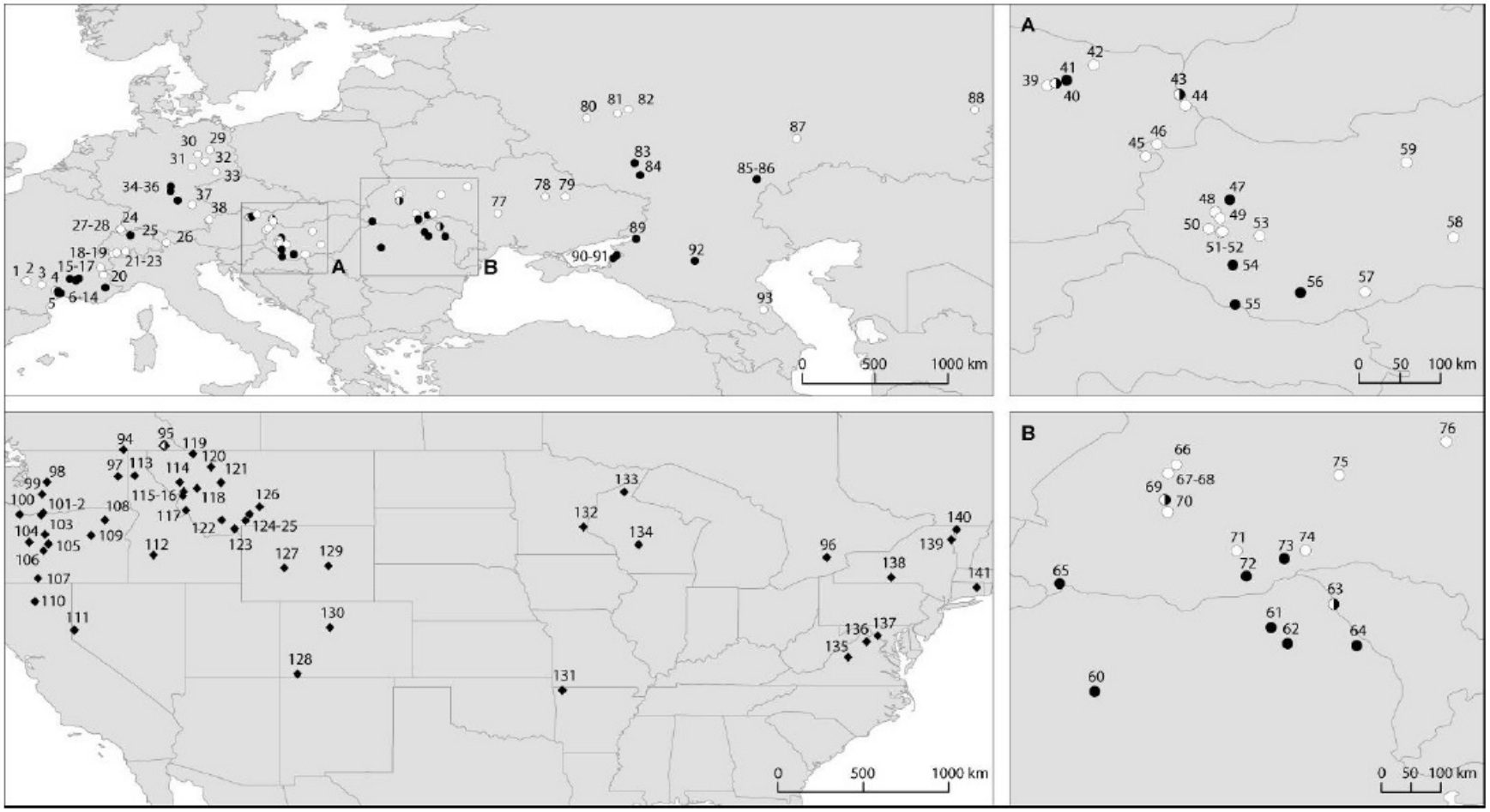
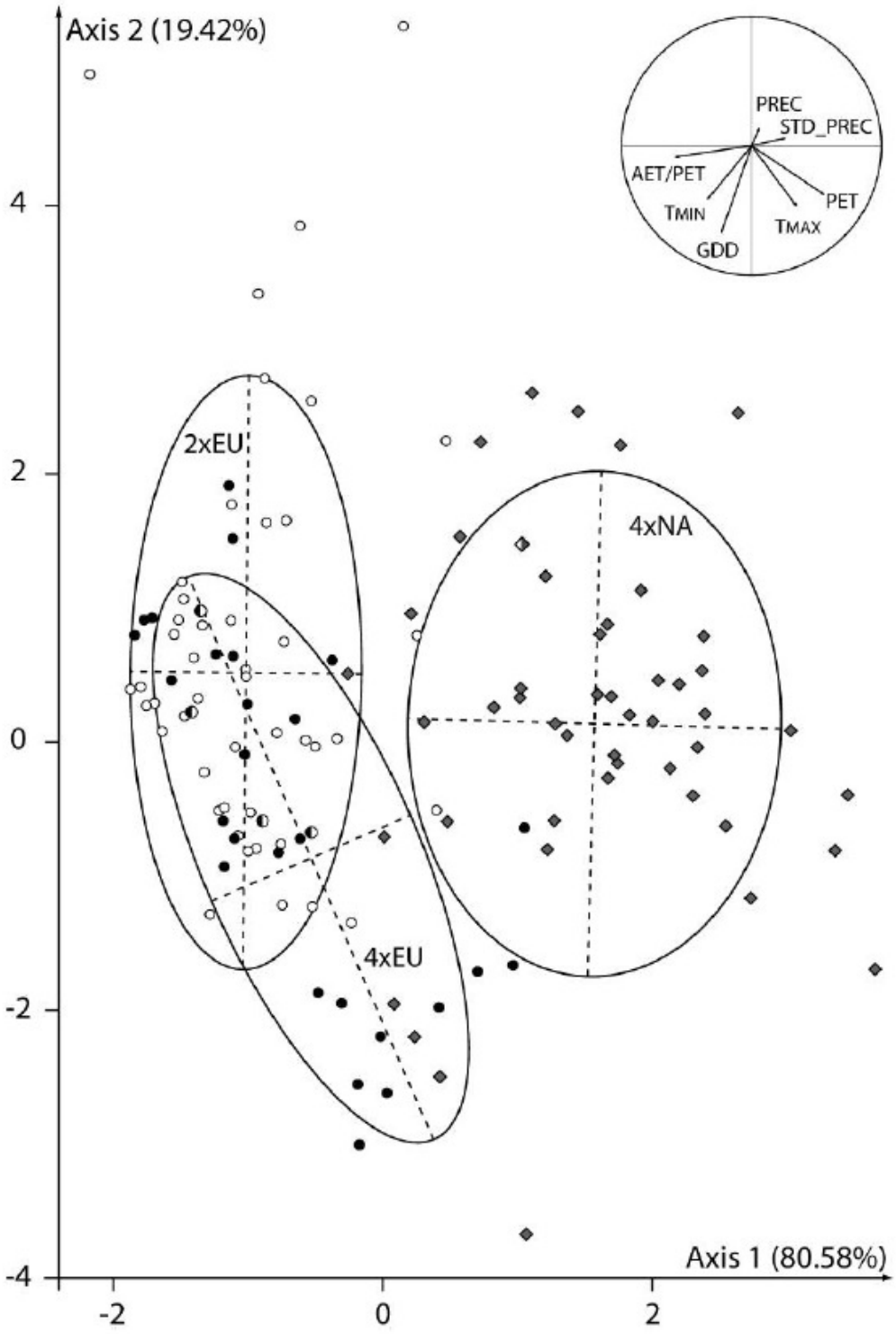


Fig. 2: Outlying Mean Index analysis (OMI) of 141 *C. maculosa* populations divided into three geo-cytotypes. The enclosed correlation circle (r = 1) shows the included climatic variables and their correlation with the OMI axes. For details on ellipses (1.5 SD) see Methods, symbols as in Fig. 1.



Characterization of plastid DNA polymorphisms in *Prunus serotina* var. *serotina* (Rosaceae), a North American tree invading Europe

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3180 words

SUMMARY

Black cherry (*Prunus serotina*) is a tree from North America, where it is often used for economical purposes, whereas it is widespread and invasive in Europe. Plastid DNA variation was first investigated in both its native and invasive ranges using microsatellite loci and sequences of three intergenic spacers (*trnT-trnL, trnD-trnT* and *trnS-trnG*). This analysis was focused on *P. serotina* var. *serotina*, with the inclusion of samples of closely related taxa. Length variation at a microsatellite locus (ccmp5) and a few sequence polymorphisms were identified among *P. serotina* samples. Four new primer pairs were then designed to specifically amplify variable regions and a combination of five markers was finally proposed for phylogeographic studies in *P. serotina*. These loci allow identification of six chlorotypes in *P. serotina* var. *serotina*, which may be particularly useful to depict the maternal origins of European invasive populations.

INTRODUCTION

Black cherry, *Prunus serotina* Ehrh. (Rosaceae), is a deciduous tree native to an area ranging from Mexico-Guatemala to south-east Canada (McVaugh, 1951; Little, 1971). Based on phenotypic characteristics such as the height of the trees and the thickness of the leaves, five varieties are usually recognised: 1) *P. serotina* var. *eximia* (Small) Little is confined to the Edwards Plateau in central Texas; 2-3) *P. serotina* var. *rufula* (Woot. & Standl.) McVaugh and *P. serotina* var. *virens* (Woot. & Standl.) McVaugh are distributed in Texas, New Mexico and Arizona; 4) *P. serotina* var. *salicifolia* (Kunth) Koehne [or subsp. *capuli* (Cav.) McVaugh] is found from Mexico to Guatemala; and 5) *P. serotina* var. *serotina* which is the most abundant and common variety and is particularly widespread in the eastern part of the USA and Canada. Black cherry is one of the most valued cabinet and furniture woods in North America (Little, 1971) but large, high-quality trees suited for commercial use (belonging to var. *serotina*) are found in a restricted range on the Allegheny Plateau of Pennsylvania, New York and West Virginia (Hough, 1965; Marquis, 1975).

Black cherry is now naturalized in several countries from northern South America, such as Ecuador and Peru (EPPO, 2007). In Europe, *P. serotina* var. *serotina* was first introduced in the early 17th century. This tree was recorded in France near Paris around 1630 (Starfinger, 2006), in England in 1629 (EPPO, 2007) and in Germany in 1685 (Starfinger and Kowarik, 2003), where it was particularly appreciated as an ornamental. Since the 19th century, the species was massively planted throughout Europe for timber production, but this objective was never achieved because the wood was of poor quality in the introduced range. The species is now widespread and invasive in north-eastern France, Belgium, the Netherlands, Germany, Denmark and Poland and locally abundant in Lithuania, Romania, Hungary, Switzerland and Italy (EPPO, 2007). Thanks to its tolerance to a very wide range of moisture conditions (Starfinger, 2006), black cherry can invade open habitats such as dry grasslands and heathlands. *Prunus serotina* also benefits from anthropogenic influences such as soil disturbance and/or eutrophication (Godefroid *et al.*, 2005). *Prunus serotina* disperses by seed (mainly through birds and frugivore mammals; Starfinger, 2006) but has also a very efficient vegetative reproduction by suckering and sprouting. If sufficiently exposed to light, trees produce abundant quantities of seeds (up to 10,000 per tree in invasive populations; Pairon *et al.*, 2006) after the age of approximately seven.

The use of genetic markers should be helpful to discern high-quality tree lineages in the native range and to depict the pattern of invasion of *P. serotina* in Europe. The plastid genome (cpDNA) is usually inherited from the female parent (as already reported in other *Prunus* species; Brettin *et al.*, 2000; Mohanty *et al.*, 2003) and only dispersed by seeds. Thus, the use of cpDNA markers is often more efficient to detect colonization routes than nuclear markers (e.g. Petit *et al.*, 2005) and is informative to depict the pattern of invasion. The combined use of plastid and nuclear markers is also very informative for a comparative study of gene dispersal by seeds vs. pollen (seed or pollen mediated gene flow). However, plastid DNA variation can be particularly low in forest trees (e.g. Magri *et al.*, 2007; Besnard, 2008; Vendramin *et al.*, 2008). Moreover, one can expect that European *P. serotina* populations could be genetically depauperate due to bottleneck effects, putatively leading to difficulties in the detection of useful polymorphisms for population genetic studies in the invasive area. Nevertheless, the successful use of highly variable cpDNA microsatellites has been reported for numerous trees (e.g. Harbourne *et al.*, 2005; Li *et al.*, 2006; Magri *et al.*, 2007) and such a methodology should be tested on *P. serotina*.

In the present paper, we investigate cpDNA polymorphism in *P. serotina* var. *serotina* using seven universal cpDNA microsatellite loci (Weising and Gardner, 1999) and sequences of three intergenic spacers. Based on sequence polymorphism, new primers for the characterization of polymorphic loci are developed to easily characterize large samples of trees. Lastly, a combination of loci for cpDNA genetic studies of *P. serotina* var. *serotina* is proposed to allow efficient characterization of cpDNA variation in black cherry populations.

MATERIAL AND METHODS

Plant sampling and DNA extraction

Eleven populations of *P. serotina* var. *serotina* were sampled throughout its distribution in both the native and invasive ranges (Table I). Five individuals per population were collected at least 15 meters from each other. In addition, two individuals of both *P. serotina* var. *rufula* and *P. virginiana* (a closely related species of *P. serotina*; Shaw and Small 2004) were also collected in Arizona and New Mexico, respectively (Table I). A total of 59 individuals were characterized. Approximately 20 mg of dry leaf material were ground in a 2-ml Eppendorf tube using a Tissuelyzer (QIAGEN) and three tungsten balls in each tube. Genomic DNA was extracted using a DNA-mini-extraction Kit (QIAGEN) according to the manufacturer's protocol.

Plastid DNA characterization

In order to characterize maternally inherited polymorphisms, seven cpDNA microsatellite loci (ccmp2, ccmp3, ccmp4, ccmp5, ccmp6, ccmp7 and ccmp10; Weising and Gardner 1999) were firstly tested on the whole plant sample. Each PCR reaction (25 µl) contained 10 ng DNA template, 1X reaction buffer, 0.2 mM dNTPs, 0.2 µmol of each primer (one labelled with a fluorochrome), and 0.75 Units *Taq* DNA polymerase (GoTaq, Promega, Madison, WI, USA). Reaction mixtures were incubated in a thermocycler (T1; Biometra, Göttingen, Germany) for 3 min at 94°C, followed by 36 cycles of 45 s at 94°C, 45 s at 53°C, and 60 s at 72°C. The last cycle was followed by a 10 min extension at 72°C. Electrophoresis procedures were used as described by Basic and Besnard (2006).

Three non-coding plastid regions (*trnT-trnL, trnD-trnT* and *trnS-trnG*) were sequenced on one *P. virginiana* tree (NM2) and eight *P. serotina* individuals originating from distant populations in the native (AZ1-1, NE2-1, PE7-2, IO1-7, SC1-2) and invasive ranges (UK1-1, IT1-8, FR1-4). For the PCR reactions, we used either universal primers for *trnT-trnL* and *trnD-trnT* (Taberlet et al. 1991; Demesure et al. 1995) or new specific primers for *trnS-trnG* (*trnS-trnG*-For: 5′GTGAAACTTTGGTTTCATC3′ and *trnS-trnG*-Rev: 5′GAAAAAAGAGAAGACTATGTTAC3′). Each PCR reaction (50 µl) contained 10 ng DNA template, 1X reaction buffer, 0.2 mM dNTPs, 0.2 µmol of each primer, and 0.75 Units *Taq* DNA polymerase (GoTaq, Promega, Madison, WI, USA). Reaction mixtures were incubated in a thermocycler (T1; Biometra, Göttingen, Germany) for 3 min at 94°C, followed by 36 cycles of 45 s at 94°C, 45 s at 53°C, and 120 s at 72°C. The last cycle was followed by a 10 min extension at 72°C. PCR products were then purified using a QIAquick Purification Kit (QIAGEN) following the manufacturers protocol. Direct sequencing was performed using Big Dye 3.1 Terminator sequencing cycle (Applied Biosystems) according to manufacturer's instructions and an ABI PRISM 3100 genetic analyzer (Applied Biosystems).

Based on cpDNA sequences, four loci were developed to characterize our plant samples. Primers (Table II) were designed in regions flanking polymorphisms (i.e. nucleotidic substitutions or length polymorphisms). Each PCR reaction (25 µl) contained 10 ng DNA template, 1X reaction buffer, 0.2 mM dNTPs, 0.2 µmol of each primer (one labelled with a fluorochrome; Table II), and 0.75 Units *Taq* DNA polymerase (GoTaq, Promega, Madison, WI, USA). Reaction mixtures were incubated in a thermocycler (T1; Biometra, Göttingen, Germany) for 3 min at 94°C, followed by 36 cycles of 30 s at 94°C, 30 s at the defined annealing temperature (Table II) and 30 s at 72°C. The last cycle was followed by a 10 min extension at 72°C. Furthermore, in *trnD-trnT-Tas*I and *trnS-trnG-Tas*I, nucleotidic substitutions were investigated using the RFLP (Restriction Fragment Length Polymorphism) methodology. Digestion of the PCR fragments was performed using the restriction enzyme *Tas*I (Fermentas, St Leon-Rot, Germany) according to the manufacturer's recommendations. Electrophoresis procedures were used as described by Basic and Besnard (2006).

The total gene diversity (H_T) was estimated using FSTAT (Goudet, 2005) for both native and invasive populations of *P. serotina* var. *serotina*. This parameter was estimated for each locus and on the multilocus profiles (considered as alleles from one locus). In addition, a reduced median network for *P. serotina* haplotypes was built based on the combined PCR-RFLP and microsatellite data. This maximum-parsimony analysis was performed using the NETWORK software (http://www.fluxus-engineering.com/sharenet.htm; Bandelt *et al.*, 1999).

RESULTS AND DISCUSSION

The characterization of the whole plant sample with seven ccmp loci (Weising and Gardner, 1999) allowed clear distinction between *P. virginiana* and *P. serotina* (using length variation at ccmp2, ccmp3, ccmp5 and ccmp6; Table III). This result supports that these two species are phylogenetically differentiated based on maternal markers. Additionally, our samples of *P. serotina* var. *serotina* and var. *rufula* can be distinguished based on ccmp5 (Table III). In *P. serotina* var. *serotina*, only one locus (ccmp5) was variable with one tree from SC1 (SC1-2) displaying a rare variant (i.e. 125 bp).

The lack of genetic polymorphism in *P. serotina* var. *serotina* revealed by the ccmp loci led us to investigate DNA sequence polymorphism in the intergenic spacers *trnT-trnL* (884 bp), *trnD-trnT* (1122 bp) and *trnS-trnG* (1245 bp). In *P. serotina*, only four variable sites were found, but var. *rufula* did not display specific polymorphism compared to var. *serotina*. On the *trnD-trnT* and *trnS-trnG* spacers, one T/A substitution was found at positions 200 and 496, respectively. On *trnT-trnL*, two length polymorphisms of one bp were found at positions 257 and 551, respectively in a poly-T (T_{10-11}) and a poly-A (A_{14-15}).

Four ptDNA primer pairs were developed (Table II) to amplify and characterize these polymorphisms on the whole plant sample. Our markers revealed various levels of gene diversity (H_T) and the most discriminating locus in both ranges was *trnD-trnT-Tas*I ($H_T \approx 0.5$; Table III). Combining these loci with ccmp5, six haplotypes (named ss1, ss2, ss3, ss4, ss5 and ss6) were found in *P. serotina* var. *serotina* (Table III). The reconstructed network (Fig. 1) showed that haplotypes are all interconnected with ss1 and ss4 at central positions. The outgroup haplotype (sr1) is branched on ss1 suggesting that the latter probably represents the ancestral profile. Three haplotypes (ss1, ss3 and ss4) were shared by both native and invasive populations, two haplotyes (ss2 and ss5) were just detected in the native area and one haplotype (ss6) was only found in the invasive range. Surprisingly, in our sample the global gene diversity was similar between the native (H_T = 0.661) and invasive ranges (H_T = 0.738) suggesting no reduction of gene diversity during the invasion. Interestingly, intrapopulation variation was also detected in several populations and even in the invasive range (PE2, PE7, IO1, NE2, SC1 and DA3; Table I).

This study showed that, even in presence of a low sequence polymorphism, substantial cpDNA diversity can be detected throughout the *P. serotina* distribution. Plastid DNA markers may be very useful for population genetic studies in *P. serotina*, and particularly here for var. *serotina* for which we recommend the combined use of three microsatellite loci (i.e. ccmp5, *trnT-trnL*-poly-T and *trnT-trnL*-poly-A) and two PCR-RFLPs (i.e. *trnS-trnG-Tas*I, *trnD-trnT-Tas*I). Moreover, their combined use with nuclear SSR markers (Pairon *et al.*, 2008) will also help to depict the origins and dispersal of invasive populations in Europe. The presence of distinct cpDNA haplotypes in Europe supports the hypothesis of multiple introductions in the invasive range. The molecular characterization of a more exhaustive sample in both the native and invasive ranges is now necessary to better document these introductions and then identify the pattern of colonization of this invasive species (M. Pairon, B. Petitpierre *et al.*, in prep.). Detection of the different invasive forms could also open new perspectives to understand invasion of the tree, particularly by integrating such information in niche-based modelling (Mau-Crimmins *et al.*, 2006; Broennimann *et al.*, 2007).

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FIG. 1. Reduced median network representing phylogenetic relationships of plastid DNA haplotypes of *Prunus serotina* var. *serotina*. Each haplotype is coded as reported in TABLE III. Haplotype sr1 (*P. serotina* var. *rufula*) is used as outgroup. This analysis is performed on five polymorphic loci.

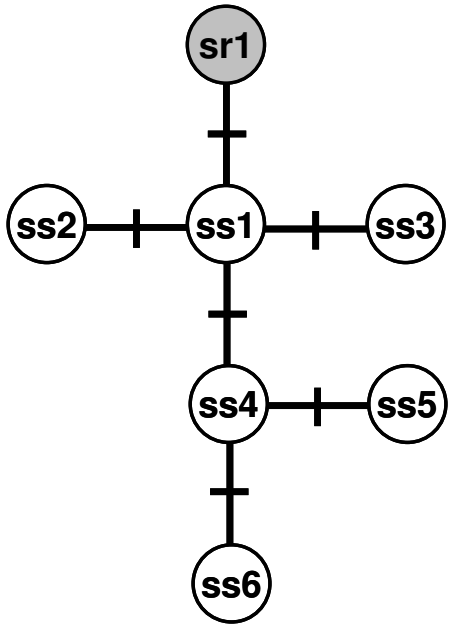

TABLE I. *Description of the* Prunus serotina *and* P. virginiana *populations analysed in the present study, including population code (Pop. code), geographic location, GPS coordinates, number of individuals characterized (N) and detected haplotypes*

* see TABLES II and III for haplotype definition

Taxon	Location	Pop. code	GPS coordinates		N	Haplotypes*
			Lat	Long		
Prunus serotina						
- var. *serotina*						
	Native range (USA)					
	- Charleston, South Carolina	SC1	32.45°N	79.54°W	5	ss4, ss5
	- Spruce Knob, Virginia	WV1	38.71°N	79.54°W	5	ss4
	- Achville, Ohio	OH3	39.67°N	82.93°W	5	ss1
	- Omaha, Nebraska	NE2	41.25°N	96.00°W	5	ss1, ss2
	- Ames, Iowa	IO1	41.35°N	92.30°W	5	ss1, ss2
	- Buckaloons, Pennsylvania	PE2	41.80°N	79.25°W	5	ss1, ss3, ss4
	- Galeton, Pennsylvania	PE7	41.77°N	77.82°W	5	ss1, ss4
	Invasive range (Europe)					
	- Ticino, Italy	IT1	45.52° N	08.72° E	5	ss6
	- Fontainebleau, France	FR1	48.38° N	02.75° E	5	ss3
	- Shakelford, UK	UK1	51.18° N	00.65° W	5	ss4
	- Aarhus, Denmark	DA3	56.18° N	09.65° E	5	ss1, ss4
- var. *rufula*	Native range (USA)					
	- Tanque Verde, Arizona	AZ1	32.37°N	110.69°W	2	sr1
P. virginiana	Native range (USA)					
	- Chloride, New Mexico	NM1	33.35°N	107.89°W	1	v1
	- Cloudcroft, New Mexico	NM2	32.96°N	105.75°W	1	v1

TABLE II. *Characteristics of new primers used to characterize cpDNA polymorphisms in* Prunus serotina*, including annealing temperature (Ta) in °C, the number of alleles (N) and the size of alleles in bp.*

Locus	GenBank	Primers	Ta	N	Allele sizes[a]
*trnS-trnG-Tas*I	AM950170 to AM950177	For. 5′CTATAATCATAGAAATCTAAATAAACA3′	47	2	A) 101 → 74[b] + 27
		Rev. FAM-5′TCGTAAATAAACTGATTTATTTGATT3′			B) 101 → 101[b]
*trnD-trnT-Tas*I	AM950153 to AM950160	For. 5′GGATAATCACTCTTTCAATGT3′	50	2	A) 109 → 87[b] + 22
		Rev. HEX-5′AATTCTGATCTTGCTAATGATC3′			B) 109 → 109[b]
trnT-trnL-poly-T	AM950162 to AM950169	For. FAM-5′ATTAGCTTAATTAGATAGTAAG3′	47	2	126, 127
		Rev. 5′CCGTTAATTTATAATTAGAAGA3′			
trnT-trnL-poly-A	AM950162 to AM950169	For. 5′TAATTCAGATCATAATGAAACA3′	47	2	106, 107
		Rev. FAM-5′GTGCAATTTTGAATACTTGAA3′			

[a] For *trnS-trnG-Tas*I and *trnD-trnT-Tas*I, the size of fragments before and after (→) restriction is given; [b] DNA fragment labelled with the fluorochrome (FAM or HEX).

TABLE III. *Multi-locus profiles of the eight cpDNA haplotypes detected in* Prunus serotina *(ss1 to ss6 in var.* serotina, *and sr1 in var.* rufula*) and* P. virginiana *(v1). The length (in bp) of each sized DNA fragment is given. Gene diversities in the native [$H_{T\ (N)}$] and invasive [$H_{T\ (I)}$] ranges are given for the* P. serotina var. serotina *populations*.

Locus	Multi-locus profile (haplotype)								$H_{T\,(N)}$	$H_{T\,(I)}$
	ss1	ss2	ss3	ss4	ss5	ss6	sr1	v1		
ccmp2	204	204	204	204	204	204	204	202	0	0
ccmp3	105	105	105	105	105	105	105	125	0	0
ccmp4	118	118	118	118	118	118	118	118	0	0
ccmp5	126	126	126	126	125	126	129	127	0.057	0
ccmp6	111	111	111	111	111	111	111	110	0	0
ccmp7	133	133	133	133	133	133	133	133	0	0
ccmp10	113	113	113	113	113	113	113	113	0	0
*trnS-trnG-Tas*I	101	101	74	101	101	101	101	68	0.057	0.375
*trnD-trnT-Tas*I	87	87	87	109	109	109	87	86	0.514	0.488
trnT-trnL-poly-T	126	126	126	126	126	127	126	131	0	0.375
trnT-trnL-poly-A	106	107	106	106	106	106	106	107	0.248	0
Total	-	-	-	-	-	-	-	-	0.661	0.738