



UNIL | Université de Lausanne

Faculté de biologie
et de médecine

Ecole de biologie

**What drives the success of the invasive tree Robinia
pseudoacacia: climate suitability, disturbance or land
management?**

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation**

Master Thesis of Science in Behaviour, Evolution and Conservation

par

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Janvier 2020

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Resumé

Les invasions biologiques sont un de composants majeurs du changement global. Pour cette raison, beaucoup d'études ont essayé de comprendre les vecteurs et les impacts des invasions, mais la variabilité dans le taux d'invasion entre et à l'intérieur de différentes aires géographiques n'a pas été beaucoup étudiée. Notre objectif était de mieux comprendre les facteurs humains et écologiques qui guident l'invasion d'une des espèces exotiques les plus envahissantes, l'arbre *R. pseudoacacia*, et de chercher d'expliquer la différence apparente entre les taux d'invasion de trois pays différents : Suisse, Italie et France. Pour ce faire on a appliqué différentes méthodes : on a modélisé l'adéquation de l'habitat de *R. pseudoacacia* à l'échelle globale et puis on l'a utilisé pour conduire un travail de terrain basé sur l'habitat modélisé pour évaluer présences et absences et la dynamique des populations à une échelle locale. Modèles d'habitat, analyses univariées et modèles mixtes multivariés ont été utilisés pour analyser les données. Le climat était le prédicteur le plus important pour expliquer la présence de *R. pseudoacacia* et la richesse en espèces natives semblait jouer un rôle dans la différence de densité atteinte par *R. pseudoacacia*. Cependant, aucun des prédicteurs étudiés pouvait expliquer entièrement la différence dans le taux d'invasion entre les différents pays. L'histoire de l'introduction (avec ses effets sur la pression de propagules), qui est différent dans les trois pays, pourrait avoir joué un rôle.

Abstract

Biological invasions are a major component of global change. For this reason, many studies have investigated the drivers and impacts of alien species invasions, but the variability in invasion rates between and within different areas has been poorly studied. Our aim was to better understand the anthropogenic and ecological factors that drive the invasion by a major invasive alien species, the tree *R. pseudoacacia*, and to try to explain the apparent difference in invasion rates between three different countries: Switzerland, Italy and France. To do this, we applied different methods: we modelled climatic suitability of *R. pseudoacacia* at a global level and then used it to conduct model-based fieldwork to assess presence-absence and population dynamics at a local level. Habitat suitability models, univariate analysis and multivariate mixed models were used to analyse the data. Climate was the most important predictor in explaining presence of *R. pseudoacacia* and native tree species richness seemed to play a role in the difference in density reached by it. However, none of the studied predictors could explain entirely the difference in invasion rates among countries. History of introduction (with its effect on propagule pressure), different in the three countries, could likely have played a role.

Key words

Robinia pseudoacacia; species distribution models; invasive alien species; environmental drivers; human drivers; habitat suitability; disturbance; generalized linear mixed models.

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Introduction

Invasive alien species (IAS) are an important component of global environmental change, and one of the major causes of biodiversity loss (e.g. Wilcove et al. 1998). They can impact local communities by altering nutrient cycling, by outcompeting native species, through hybridisation, and in general by influencing structure and composition of communities (e.g. D'Antonio & Corbin 2003; Liao et al. 2008). Due to their impact on the receiving environment (reduced crop productivity (Cook et al. 2011), recreational opportunities limited (Pyšek et al. 2007), increased frequency of wildfires (e.g. Brooks et al. 2004) just to give some examples), biological invasions can have important direct and indirect financial and social costs (McNeely 2001; Pyšek et al. 2009; Shackleton et al. 2019; Vilà et al. 2010.) The interest in biological invasions has greatly increased starting from the 1980s (Richardson & Pyšek 2006), together with their increase in threat due to globalization that allows species to cross their natural barriers (such as maximum dispersal capacity) and biogeographic boundaries (Lodge 1993; Richardson & Pyšek 2006; Seebens et al. 2017). Alien species can be introduced by humans both accidentally and on purpose. Concerning plants, the majority of species have been introduced following two principal pathways: (i) introduction for horticulture or ornamental purposes but escaped from cultivation; (ii) introduction for practical reasons in semi-wild habitats for erosion control and landscaping (Pyšek et al. 2009). More than 350 tree species are known worldwide to be invasive (Richardson & Rejmánek, 2011; van Wilgen & Richardson, 2014) and most of them were introduced for the second reason and were just later recognised as invasive species (Benesperi et al. 2012; Reichard and Hamilton, 1997).

Robinia pseudoacacia L. (commonly called robinia, acacia and black locust) is one of these tree species, for which the invasive potential was discovered after its introduction. It was first brought in Europe as an ornamental tree at the beginning of the 17th century, and then extensively planted for forestry purposes in the late 18th because of the increased demand in wood following the beginning of industrialization. Later, in the early 19th century, *R. pseudoacacia* was again promoted and planted but this time for erosion control after forest degradation and to support the sides of new railroads and highways (Göhre, 1952; Kowarik, 2010). Initial invasions of *R. pseudoacacia* are not well documented, but they have probably spread more from plantations than gardens (Vítková et al. 2017). The naturalization and spread of this tree were helped by the fact that it was not

perceived as a danger by many people; on the contrary, it entered and became adopted in European culture (Vítková et al. 2017). Furthermore, although nowadays its invasiveness and threats to native communities are well documented (e.g. Benesperi et al. 2012; Lazzaro et al. 2018), many countries continue to plant it for forest purposes and perceive it as part of the local flora (Vítková et al. 2017). However, *R. pseudoacacia* is also listed in many blacklists of invasive species (i.e. lists of species proven to be invasive and having important ecological, economic and/or social impacts in a certain area), often in the same countries that continue to plant it (e.g. Gruppo di Lavoro Specie Esotiche della Regione Piemonte (2014)).

In Switzerland, *R. pseudoacacia* was introduced in 1800 principally for apiculture and soil stabilisation (Vítková et al. 2017) and is mostly present in mixed stands (that is, there are not many pure *R. pseudoacacia* stands). *Robinia pseudoacacia* is considered as invasive across all of Switzerland, but especially in Ticino (Info Flora, 2013). The primary negative effects of *R. pseudoacacia* relate to habitat alterations and reduction of the native biodiversity (CABI, 2018), which results principally from changes in nutrient availability and light conditions (Vítková et al. 2017). Like many other invasive tree species (Zengeya et al. 2017), through having both negative ecological impacts and economic and cultural value, *R. pseudoacacia* generates conflicting opinions between different interest groups (Vítková et al. 2017), making it important to better understand its distribution, dynamics and spread to ensure efficient and effective management to reduce unnecessary costs and potentially improve benefits (Vítková et al. 2017).

To manage IAS, it is essential to know what factors facilitate successful invasions. For this reason, one aspect of invasion science focuses on the processes driving biological invasions and looks into factors such as traits of the invasive species or of the receiving community, and how this may facilitate invasive capacity and success (Rejmanek & Richardson, 1996; Richardson & Pysek, 2006). Community invasibility refers to the susceptibility of habitats to colonization, establishment and spread of IAS, and is often related to the biotic resistance hypothesis (e.g. Byers et al. 2003; Case, 1990; Law & Morton 1996), climate (e.g. Holmes et al. 2005; Vicente et al. 2010), management, disturbance and history of the introduction of IAS (having an effect on propagule pressure (Colautti et al. 2006; Richardson & Pysek, 2006; Theoharides & Dukes, 2007)). Similarly, invasiveness consists in the traits of IAS that help to facilitate their colonization, establishment and spread in the new environment (Goodwin et al. 1999), such as rapid juvenile growth, wide abiotic tolerance, effective dispersal, novel weapons, novel interactions, and high resource acquisition and competitive ability, between others (Richardson & Pysek, 2006; Theoharides & Dukes, 2007). Spread dynamics (Arim et

al. 2006) and mechanisms of impact on native communities and ecosystems have also been widely studied (e. g. Benesperi et al. 2012; Lazzaro et al. 2018; Ricciardi & Cohen, 2007; Vilà et al. 2011).

In the case of the study species, *R. pseudoacacia* has different traits that increase its invasiveness. It has a very wide abiotic tolerance concerning soils (Cierjacks et al. 2013) and it has weedy qualities, that is, it grows very rapidly, establishes well after disturbance, and can survive well during frosts and droughts (Vítková et al. 2017). Moreover, it has very few natural enemies and pathogens in the introduced range (Cierjacks et al. 2013). However, *R. pseudoacacia* does not establish well in low light conditions and it is not highly effective in long-distance dispersal and creation of new colonies (Vítková et al. 2017). Concerning invasibility the wide range of reasons for introduction and the multiple landscapes it was planted in has led to high propagule pressure but also shows it is a generalist (Vítková et al. 2017; Vítková et al. 2019).

It is important to consider that the primary drivers of plant invasion can change according to scale (Milbau et al. 2009; Stohlgren et al. 2006). For example, while climate is the universal driver that can predict invasion globally and at the level of continents or large regions, it remains important also at smaller regional and local extents. Climate is also the major filter during the colonization stage (Theoharides & Dukes, 2007). However, at regional and local levels, topography, landcover and land use, disturbance, biotic interactions and resource availability also become important factors facilitating or hindering invasions (Milbau et al. 2009). History of introduction, which can determine subsequent propagule pressure, can additionally be important at these levels (Donaldson et al. 2014). These factors work in a hierarchical manner, that is, small scale factors become important only when the conditions at larger scales are satisfied (Milbau et al. 2009), suggesting it is important to understand dynamics at different scales. Another important fact to consider is that these primary drivers of plant invasion also vary depending on the stage of invasion (Castro-Díez et al. 2011; Theoharides & Dukes, 2007). For instance, climate is the most important filter of invasion at the colonization stage, whereas disturbance regimes play an important role at the colonization and establishment stages. By contrast, biotic resistance is much more important at the establishment stage compared to the colonization stage (Theoharides & Dukes, 2007). Finally, propagule pressure which is determined by history of introduction and by reproductive capacity of the species, is important at the stage of transport and colonization primarily but can also have important and long-lasting effects at following stages (Donaldson et al. 2014; Theoharides & Dukes, 2007). For these reasons, disentangling the human and environmental factors that affect species distributions and

dynamics at different scales and stages of invasion is important for guiding management plans (Cabra-Rivas et al. 2016; Richardson & Whittaker 2010).

To understand these different invasion dynamics across different scales, different scientific tools and approaches can be used. Species distribution models (SDMs; Guisan & Thuiller, 2005) are one family of useful tools for understanding broad-scale requirements that facilitate invasions. SDMs relate georeferenced species occurrences with different human and environmental predictors variables through response curves, in order to better understand and/or predict their distribution (Guisan et al. 2017). Outputs from SDMs are useful for predicting new areas of invasion and this way support prevention, early detection and containment (Guisan et al. 2013). SDMs can also help understanding the importance of different drivers of invasion success for different alien species (Cabra-Rivas et al. 2012). Furthermore, combining a modelling approach with field-based studies can be useful when working at finer scales, to look at dynamics that are impossible or difficult to explore using SDMs or to validate the model outputs. In the case of invasions, field measurements are for instance particularly needed to look at the IAS impacts on receiving communities, or to look at IAS population growth and structure. In this case, climatic SDMs can guide sampling for the field-study and help afterwards in the analysis to look at importance of climate in explaining distribution of the invasive species.

Many studies have investigated the drivers and impacts of *R. pseudoacacia* invasions at local scales (e.g. Benesperi et al. 2012; Lazzaro et al. 2018; Cabra-Rivas et al. 2012), but the variability in invasion rates between and within different areas has been poorly studied (Vítková et al. 2019). In particular, while very different apparent levels of invasion were suspected between Switzerland and neighbouring countries, no obvious factor could be identified (R. Shackleton pers. obs.). For this reason, in this study we aimed to better understand the hierarchical dynamics of human and environmental factors in explaining different invasion rates of *R. pseudoacacia* in different countries in Europe using integrated methods. In particular, we wanted to understand the climatic and non-climatic (more local) drivers of invasion for this tree species. To do this, we compared the invasion dynamics in Switzerland and two of its neighbouring countries - France and Italy - with a combined modelling and fieldwork approach. We focused on localised areas in each country where the climate is similar but where invasion rates and dynamics seemed to differ (see table S1 in supplementary material). In particular, we aimed to answer the following questions: (1) Can we confirm the difference in invasion rates between the different countries? (2) Do different drivers of invasion have different importance, and do they vary among countries? (3) If *R. pseudoacacia* invasion rates

differ between neighbouring countries, do distinct environmental and anthropogenic factors drive this difference?

Materials and Methods

Study species

Robinia pseudoacacia is a deciduous thorny tree of the Fabaceae family. Its growth is rapid, and it can reach 30 m in height (Cierjacks et al. 2013). Thanks to *Rhizobium* bacteria communities in root nodules, *R. pseudoacacia* has a nitrogen fixing capacity allowing it to change soils (Cierjacks et al. 2013) and can promote further invasion by other alien species (D'Antonio et al. 1999). Flowers are white, borne in racemes, and are insect pollinated (Cierjacks et al. 2013). It reproduces both sexually and asexually through horizontal root elongation, the latter being its principal mode of reproduction. *R. pseudoacacia* can spread rapidly over short distances, especially through asexual reproduction (Kowarik 1996), but wind and water can sometimes facilitate long-distance dispersal of seed, although dispersal of more than 60 m is rare (Kowarik 2010; Morimoto et al. 2009). The establishment of new distant populations is not common, as the seeds are heavy, and the rate of germination is low (Cierjacks et al. 2013; Vítková et al. 2017). This means spread and new satellites of invasion normally establish thanks to human planting and disturbance.

R. pseudoacacia is native to North America in two disjunct areas along the eastern coast of the country. It is found with a wider range around the Appalachians mountains and with a smaller distribution between the states of Arkansas, Missouri and Oklahoma. In its native range, it occurs on limestone-derived soils with moist, temperate forests, often classified as humid or super-humid areas (Huntley, 1990). Nonetheless it has been introduced to many parts of the world in which the climate is different compared to its native range. This is likely due to the fact that it has a wide temperature tolerance, as it can tolerate temperatures as up as 40°C and as low as -12°C, but it remains limited by extreme frosts, long cold season and excessive shading (CABI, 2018; Sitzia et al. 2016; Vítková et al. 2017). This tree tolerates a wide range of soil pH, as well as pollution, infertile, saline, toxic and extremely dry soils, but does not do well in waterlogged and poorly drained soils (CABI, 2018; Vítková et al. 2017).

Study area

This study focuses on western central Europe (Figure 1 a)). For the vegetation surveys, two cross-border comparison sites were used: 1) Western Switzerland (namely Canton Vaud and Canton

Geneva at the west edge of the Swiss Alps) and neighbouring Eastern France (part of Haute-Savoie and Ain departments); and 2) South-Eastern Switzerland (Canton Ticino) and neighbouring North-Western Italy (Como, Varese and Verbano-Cusio-Ossola provinces) at the southern edge of the Swiss Alps, which is part of the Insubrian region (Figure 1 b). The first cross-border comparative site is characterised by a temperate and humid climate with cold, wet winters and abundant snowfall, with an annual mean temperature of about 9°C in the lowlands and mean annual total precipitations of about 1000mm (Kessler & Chambrud 1986; Météosuisse 2018; see Figure 1 c). The second study area is characterised by the Insubric climate with dry winters and wet springs and autumns. Annual mean temperature is between 11° and 12°C and mean annual total precipitations of about 2000 mm (Meteosvizzera 2012; see Figure 1d).

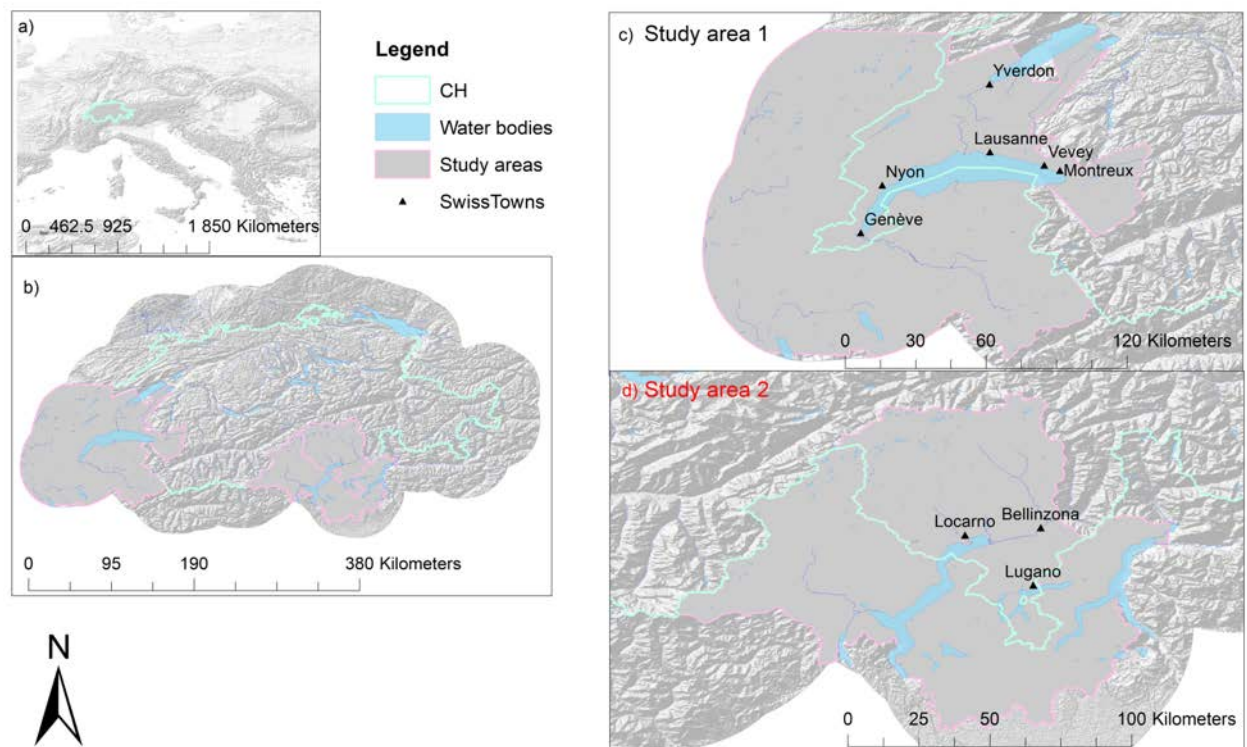


Fig. 3: Localization of the study areas. a) Localization of Switzerland within Europe in opaque grey and fair green borders. b) Switzerland with the localisation of the two study areas in opaque grey. c) The study area 1 is represented with the name of the major Swiss towns. d) the study area 2 is represented with the name of the major Swiss towns.

Species distribution modelling

Choice of data for modelling

A global species distribution model (SDM; Guisan & Thuiller, 2005) relating the species occurrence records from both the native and invaded range with climatic variables only was built, as climate is expected to have the greatest influence on species distribution at this scale (Woodward

1987; Guisan et al. 2006; Milbau et al. 2009). Furthermore, taking into account the occurrence records from both ranges allows capturing the complete climatic niche of the species and thus increases the model predictive power (Broennimann & Guisan, 2008; Verbruggen et al. 2013). Occurrence records for *R. pseudoacacia* were collected from the GBIF database for worldwide occurrences, from InfoFlora for Swiss occurrences, from TelaBotanica for French occurrences, and from Wikiplantbase for the Liguria and Toscana regions in Italy. Many occurrence records for Italy were not available on the internet, but records were collected through personal communications with the person responsible for the cartography of invasive species for each region (Passalacqua; Stinca; Bernardo; Martini; Bovio, Wilhalm; Alessandrini, pers. com.). Occurrences from before 1970 were removed because too old data do not match the time period used for the contemporary climate maps, and their locational accuracy was insufficient. This resulted in 31,677 presence points with a locational accuracy of 1000 m or finer. These points were spatially aggregated as revealed by the `ecospat.mantel.correlogram` test (in `ecospat` package, Broennimann et al. 2018) on RStudio (R Development CoreTeam, 2008), they were thus disaggregated to have only one point per cell of 1 km² (same as the climatic variables resolution, see below).

The 19 CHELSA bioclimatic variables from Karger et al. (2017; see table S2) at 1 km resolution (30 Arc seconds) were used as predictors. For the selection of the best predictors, and to avoid having highly correlated variables, a principal component analysis (PCA) and a correlation cluster were performed (see Figure S3 and S2 respectively). One or maximum two variables were then selected per cluster (see Table S2 for selected variables). Despite being correlated (see Figure S2) the variables `bio06` (min T° of coldest month) and `bio11` (mean T° of coldest quarter) were both used in the model as they were still clearly differentiated in the PCA (see Figure S3) and because in our case, as we predicted probability of presence in the same region as the sampled data, collinearity would have a limited impact on predictions (Dormann et al. 2013; Harrell, 2015). They were kept in order to evaluate the effect of extreme frosts in winter (Sitziá et al. 2016) and the effect of a long cold season (Vítková et al. 2017), as both mentioned as having substantial effect on *R. pseudoacacia* distribution in the literature.

Model fitting and evaluation

As modelling algorithms can have important effects on model outputs (Thuiller et al. 2004), and multiple technique exists for predicting species distribution each with their pros and cons (Elith et al. 2006), we chose to use an ensemble model combining different approaches (Araújo & New,

2007). This was conducted in RStudio using the package biomod2 (Thuiller et al. 2016). We applied five different modelling techniques: 1) a generalised linear model (GLM; McCullagh, 2019), 2) a generalised additive model (GAM) (Hastie & Tibshirani, 1990), 3) a generalised boosted model (GBM), (Ridgeway 1999), 4) a random forest (RF) (Breiman, 2001), and 5) a maximum entropy model (MAXENT) (Phillips et al. 2006). All these algorithms need a form of absence occurrence points to model the species distribution, thus, two sets of 30,000 pseudoabsences (PA; or background points) were randomly chosen in the spatial background. The choice of the PAs used to calibrate the model – and thus of the background within which they are selected – can have a big impact on the predictions (Thuiller et al. 2004; Barve et al. 2011). To avoid having PAs where *R. pseudoacacia* could not occur for environmental or accessibility reasons, the model was calibrated using only ecoregions (Olson et al. 2001) where the species is known to be present. Each single model algorithm was cross validated four times, with both PA sets. Models were calibrated using 70% of data available and evaluated with the remaining 30% (i.e. repeated split-sample cross-validation; Guisan et al. 2017), and variable importance was evaluated by permutations (i. e. resampling without replacement; Guisan et al. 2017). The Biomod2 package (Thuiller et al. 2016) gives response curves for each variable and modelling technique to help with evaluation (see Figure S6). Model performances were evaluated using two metrics: the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Hanley & McNeil, 1982) and the maximization approach (Guisan et al. 2017) of the true skill statistics (TSS; Allouche et al. 2006; i.e. maxTSS). Both of these metrics assess if the predictions given by the model differ from random predictions. AUC ranges from 0 to 1, with 0.5 indicating random predictions, whereas TSS ranges from -1 to 1, with 0 or less indicating predictions not different from random (Guisan et al. 2017). The ensemble model was built by weighted averaging, with the weights based on the repeated split-sample cross-validation performance. To decrease uncertainty and improve the overall accuracy of predictions, only individual models with a TSS score ≥ 0.8 were included in the ensemble model (Allouche et al. 2006; Shabani et al. 2018).

Spatial projections given by the ensemble model were transferred into ArcGIS v. 10.5.1 (ESRI Inc. 2011) and the continuous values of habitat suitability (between 0 and 1000) were reclassified in three suitability categories: low (0-333), medium (334-666) and high (667-1000) suitability.

Field study

Random-stratified sampling

A random-stratified balanced model-based sampling approach (Claridge, 2002; Guisan et al. 2006; Le Lay et al. 2010) was conducted. This approach allows for randomised sampling within prediction strata to be conducted, thus sampling a range of different environmental conditions for the species and can be useful to optimize the sampling effort while reducing error and bias (Guisan et al. 2017). The stratification was performed in RStudio and was based on three classes of climatic suitability (low, medium and high) from the previously prepared global model (see above), and aggregated landcover from CORINE 2012 v.20 (European Environment Agency (EEA)) (anthropogenic, 1; agricultural, 2; natural, 3; wet, 4 areas and water bodies, 5; see table S3). Water bodies were not eliminated because *R. pseudoacacia* can grow near lakes and rivers, and not taking into account the aggregated landcover water bodies would have eliminated all lake and river shores. To avoid having sampling points in the middle of the lake, only the pixels of category 5 that fell on shores were considered.

Each climatic suitability class was combined (whenever possible) with all the five landcover types, giving 15 strata. For high climatic suitability, five points were randomly chosen in each landcover type, except for the wet areas in Ticino because only four cells of this stratum exist. Points falling in medium and low climatic suitability combinations were chosen within a buffer of 5 km from the highly suitable points (at a minimum distance of 1 km, as for high climatic suitability) to avoid having too dispersed sampling locations. For medium climatic suitability, two points were randomly chosen in each landcover type, while only one point (whenever possible) was randomly chosen in each landcover type for low climatic suitability. Points were in the centre of a 1 km² cell. This stratification was chosen to allow comparing different landcover types and climatic suitability, and this way avoid having only few landcover types sampled (a risk with a simple random sampling). Fewer points were selected for medium and low suitability areas because the aim of the study is principally to compare highly suitable areas between countries, although they were needed to ensure that the sampling was not biased. The resulting sample comprised 181 locations with a 10 m x 10 m plots visited in each. This included: 39 plots in Italy and Ticino, 49 plots in Romandie and 54 plots in France (for the localisation of points in the habitat suitability map, see figure S5). When the target random sampling point was impossible to reach, another point was taken in the same cell or in another cell with the same value, in order to have a sampling as balanced as possible.

Sampling and data collection

The goal of the fieldwork was principally to investigate the role of ecological setting, disturbance and management in shaping the presence or absence, the density, age and height classes of *R. pseudoacacia*. To do this we collected the following information for each plot: presence-absence of the species, its density, height, breast height diameter (BHD), native tree species richness, soil cover, as well as the position of the plot in relation to the forest, evidence of management and disturbance. Bare soil or water; canopy tree cover; young tree cover; shrub cover; herb cover; adult robinia tree cover and young robinia tree cover was estimated as a percent of each 10 m x 10 m plot. In each plot we also assessed evidence of human management using five categories: none (=0); clear cut (=1); thinning (=2); just few trees cut (not systematic =3); mowing (=4); pasture (=5). Furthermore, at each plot, we also assessed disturbance using seven categories - none (=0); roadside (=1); railway side (=2); settlement (=3); dump (=4); agriculture (=5); natural disturbance (=6); two or more (=7) - that were recorded within 50 m from the limits of the plot, as seeds normally do not disperse at more than 60 m (Morimoto et al. 2009). This choice is conservative in order to be sure that that recorded disturbances could have an effect in the transport, establishment and survival of *R. pseudoacacia* seeds and growth. Position in relation to the forest was defined in three categories: inside (> 50 m from the forest edge); edge (< 50 m from the forest edge; Harper et al. 2005); non-forest (areas covered by trees of less than 50 m x 50 m). Classes of disturbance and management were defined following an exploratory fieldwork.

Mean BHD was used as a proxy to define a single age class for *R. pseudoacacia* in each plot with categories of: < 20 cm = young; 20-45 cm = middle; > 45 cm = old (classes taken from Staska et al. 2014). When there was more than one stem emerging for a single tree (after disturbance or by natural occurrence), only the biggest one was taken into account for categorising age class distributions. When different stems were growing from a clearly visible previously cut stem, the diameter was taken from cut trunk, and was therefore not at breast height. Because of frequent disturbance, and also very different ages within the same plot, it was difficult to assess an age class for certain plots. To complement the age classes, height classes were also assessed starting from *R. pseudoacacia* trees height within the plot. Height classes (classes taken from Vicente et al. 2019) are the following: < 0.5 m = A (seedling); 0.5-2 m = B (sapling); 2-5 m = C (small tree); 5-10 m = D (medium tree); > 10 m = E (big tree).

Furthermore, at each plot we included precise GPS points and the precise landcover type (not aggregated) from the raster CORINE 2012 landcover (EEA; see Table S3, 1st and 2nd columns), and

the habitat suitability given by the model in that point. To take the GPS measures in the centre of the plots the app Collector for ArcGIS (ESRI, 2019) was used, setting a minimum of 15 m horizontal precision (precision that was reachable in almost every location).

Statistical analyses of field data

Univariate analyses

First, field data were explored with univariate analyses to see if each predictor, among all those collected in the field, had an individual effect on *R. pseudoacacia* presence-absence, density, or age and height classes. GAMs with four smoothing terms ($k=4$; to uncover possible non-linear effects) were fitted to analyse the effect of habitat suitability and native tree species richness on presence-absence and tree density of *R. pseudoacacia* (the density variable was analysed with a negative binomial distribution, see S1: Choice of distribution). Chi-squared tests of independence, or Fisher's exact tests if one category had an expected frequency of less than 5, were used to analyse the differences between the different countries (France FR; Romandie CHfr (Cantons of Vaud and Geneva); Italy IT; Ticino TI) in *R. pseudoacacia*: presence-absence, height and age classes, disturbed/undisturbed sites, managed/unmanaged sites (the categories of management and disturbance were transformed into binary variables to simplify the analysis), land cover types (see table S3, 1st and 2nd columns), and positions in the forest (inside, edge/non-forest). The relationship between density and management, disturbance, country and land cover were analysed with Kruskal-Wallis non-parametric tests. Finally, variables that could not be controlled in the sampling design, that is, native tree species richness and disturbance, were analysed in relation to the country (Kruskal-Wallis test and chi-squared test of independence respectively) in order to rule out any significant difference among the countries. For all variables expected presences and absences in each category were calculated following the chi-squared test of independence formula (expected (theoretical) frequency if the response variable is independent from the explicative variable = (row total * column total) / grand total). All statistical analyses were computed in RStudio (v. 1.2.1335).

Multivariate analysis

To analyse the effects of predictors all together and understand their relative importance to explain presence-absence of *R. pseudoacacia*, Generalized Linear Mixed-Effects Models (GLMMs) from lme4 package (Bates, Maechler & Bolker, 2012) were fitted only with factors that showed a significant effect on probability of *R. pseudoacacia* presence in the univariate analyses. The GLMM

was used to analyse presence-absence of *R. pseudoacacia* in relation to habitat suitability, native tree species richness, disturbance, position in the forest and type of habitat (5 aggregated categories created from fieldwork results for this analysis: see table S3, 3rd column) as fixed effects. Continuous variables (that is, habitat suitability and native tree sp. richness) were scaled for the analysis. The region (Italy, Ticino, Romandie and France) was used as a random effect to account for its impact on the probability of presence. To assess the importance of each fixed effect in the model, one predictor was randomized at a time, and the mean R^2 (marginal and conditional) of 100 replicates was extracted and compared within each model and with the complete model. At the end, six models were built, one complete model with all predictors, one model with randomized “habitat suitability” variable, one with randomized “native tree species richness” variable, one with randomized “disturbance” variable, one with randomized “position in the forest” variable and finally one with randomized “landcover” variable.

Results

Species distribution modelling

Choice of data for modelling

Spatial autocorrelation (SAC) was not very high (about 0.25 at 1 km; see Figure S1) and disaggregation to completely eliminate SAC would have removed the majority of occurrence points. For this reason, the compromise to take only points at a minimum distance of one km from one each other was taken to optimise the number of occurrences in relation to SAC and resulted in 12,980 points with a SAC of about 0.25, from which coordinates were extracted to be used in the modelling.

Model evaluation, variables importance and suitability predictions

The model received high maxTSS and AUC scores and high sensitivity (see Table 1), signifying that it had a good match with the already existing presence points. Mean temperature of the coldest quarter (bio11) was the most important predictor for *R. pseudoacacia* distribution, followed by temperature seasonality (bio04; measure of temperature change during the year) and by the minimum temperature of the coldest month (bio06). Other predictors did not have a very high explanatory power (see Figure S4). Of these, precipitation of the warmest quarter was the most important (bio18; see Figure S4). From the suitability map it can be seen that all the lower lying plains in the three countries present ideal climatic conditions to sustain *R. pseudoacacia* populations

(Figure 2). Due to *R. pseudoacacia* short growing season and its sensitivity to the mean T° of coldest quarter of the year (see above), it can be seen that habitat suitability decreases very rapidly with altitude.

Table 3: Evaluation outputs for the global distribution ensemble model of *R. pseudoacacia* at 1 km resolution. The first column reports the names of the evaluation metrics and cutoffs, the second column (Emca) reports values for these metrics given by committee average, and the third column (Emwmean) reports the values given by weighted mean (used to build the ensemble model). Sensitivity and specificity are referred to the maxTSS and AUC cutoffs. Sen/spe thus give the % of presence-absence correctly predicted considering these cutoffs.

<i>Evaluation metric</i>	<i>Value (Emca)</i>	<i>Value (Emwmean)</i>
maxTSS	0.887	0.896
<i>maxTSS cutoff</i>	808	432
<i>sensitivity</i>	92.533	94.969
<i>specificity</i>	96.136	94.631
AUC (ROC)	0.987	0.989
<i>AUC cutoff</i>	808	437.5
<i>sensitivity</i>	92.533	94.828
<i>specificity</i>	96.136	94.83

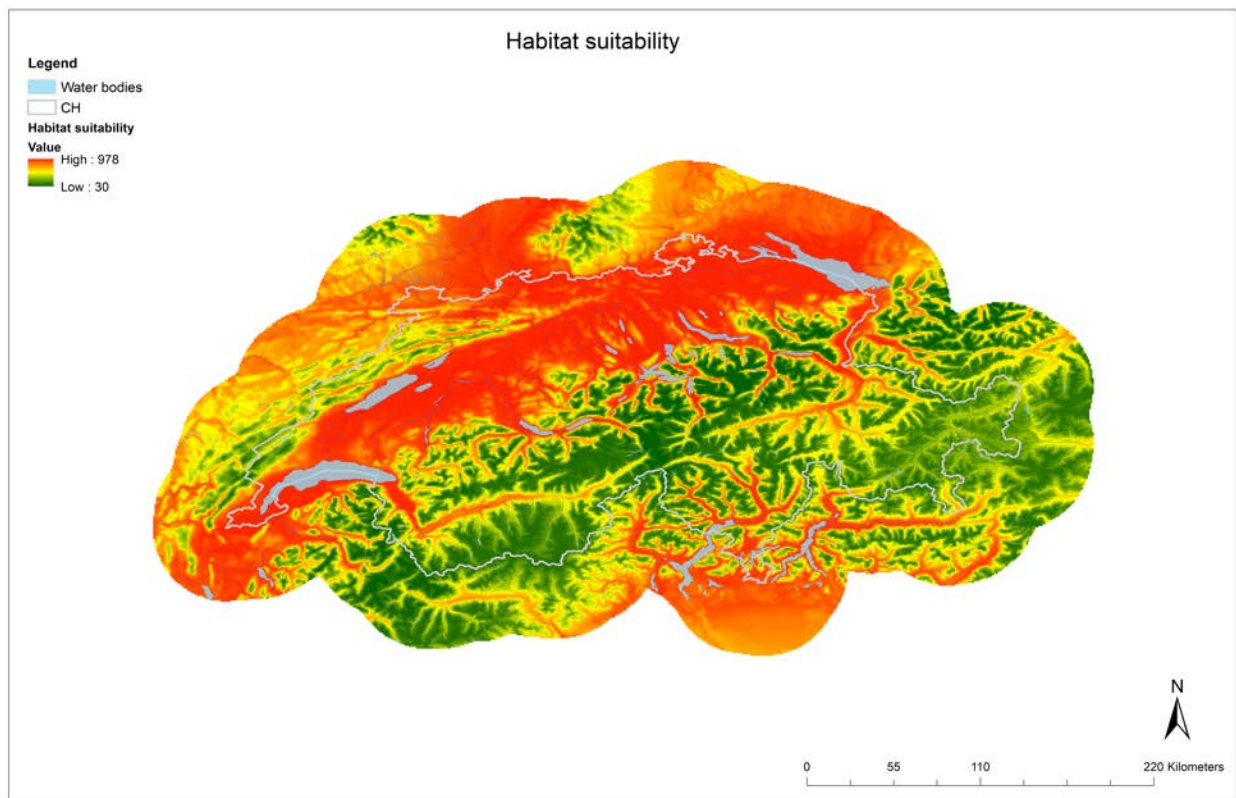


Fig. 4: Habitat suitability of *R. pseudoacacia* in Switzerland, and a buffer of 50 km outside the Swiss borders.

Human and ecological influences on *Robinia pseudoacacia* invasion dynamics

Univariate analyses

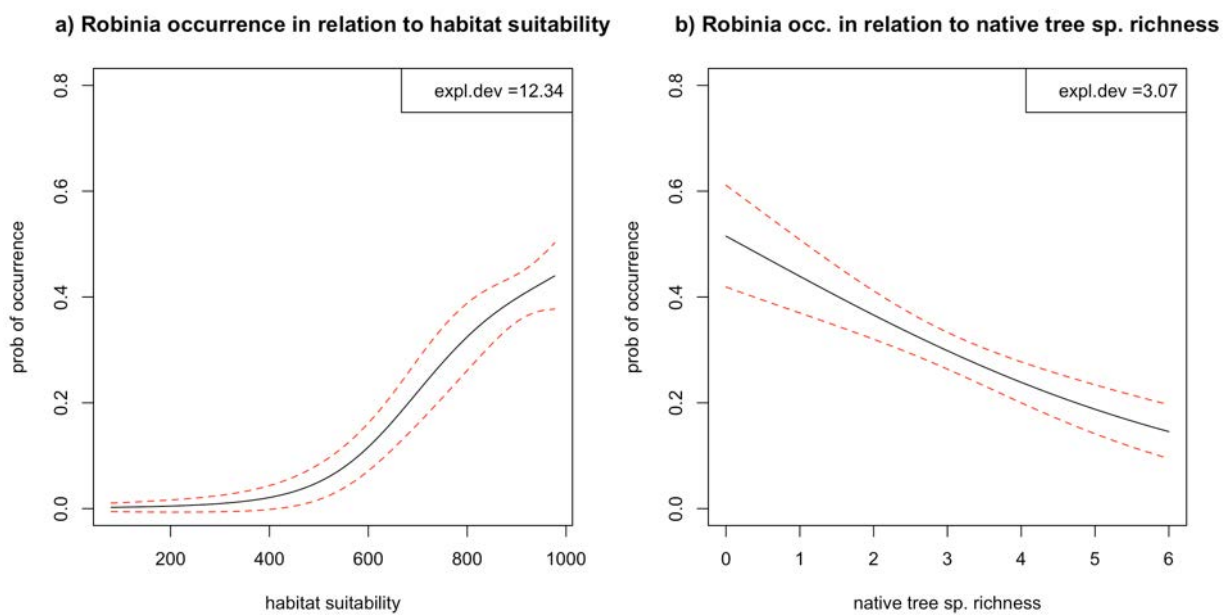
Presence of *R. pseudoacacia*, and its age classes (young and middle) were not independent from the country (presence: $\chi^2 = 17.159 \cdot df = 3 \cdot \text{Cramer's } V = 0.2537 \cdot p = 0.0006554$; Age class: $\chi^2 = 8.562 \cdot df = 3 \cdot \text{Cramer's } V = 0.3585 \cdot \text{Fisher's } p = 0.00012$; see Figure 2a, b and c). Concerning presence of *R. pseudoacacia*, in Ticino and Italy the percent of invaded plots (39% and 49% respectively) was more than three times higher than in Romandie (10%). Italy had almost the double the number of invaded plots compared to France (27%). Invasions in Switzerland remained less common than in the other two countries, even when Ticino (the most invaded canton in Switzerland), Vaud and Geneva Cantons were combined (23%). Concerning age classes, Switzerland (Ticino, Vaud and Geneva) had more middle-aged plots compared to France and Italy, which had more young-aged plots.

Across all countries, habitat suitability had a clear positive impact on occurrence of *R. pseudoacacia* (Chi.sq = 11.92 $\cdot df = 2.75186 \cdot p\text{-value} = 0.00238 \cdot R\text{-sq.}(adj) = 0.115$; see Figure 1a), increasing it of about 40% when it was at the maximum. *Robinia pseudoacacia* was, on the contrary, negatively affected by native tree species richness, with it being more likely to occur in areas with lower native tree species richness (Chi.sq = 6.423 $\cdot df = 2.000049 \cdot p\text{-value} = 0.0113 \cdot R\text{-sq.}(adj) = 0.0329$; see Figure 1b). Similarly, density of *R. pseudoacacia* decreased with an increasing richness of native species, but the relationship was more variable, also without taking into account three points that were considered as exceptions (with exceptions: Chi.sq = 17.06 $\cdot df = 3.627669 \cdot p\text{-value} = 0.000377 \cdot R\text{-sq.}(adj) = 0.225$; see Figure 1c; without exceptions: Chi.sq = 31.8 $\cdot df = 3.596629 \cdot p\text{-value} = 4.62e-07 \cdot R\text{-sq.}(adj) = 0.271$; see Figure 1d) than presence-absence. Density was not dependent on climatic suitability and was independent from any of the categorical variables.

Occurrence of *R. pseudoacacia* also differed according to placement in the forest, with it being more common at forest edges and outside forests ($\chi^2 = 11.248 \cdot df = 1 \cdot \phi = 0.251 \cdot p\text{-value} = 0.001$; Figure 2d) than elsewhere. Disturbed sites were more prone to *R. pseudoacacia* invasion than undisturbed ones ($\chi^2 = 10.676 \cdot df = 1 \cdot \phi = 0.257 \cdot p\text{-value} = 0.0004998$; see Figure 2e) and the presence of the species was not independent from the land cover category ($\chi^2 = 25.843 \cdot df = 16 \cdot \text{Cramer's } V = 0.3222 \cdot \text{Fisher's } p = 0.02199$; see Figure 2f). *Robinia pseudoacacia* was more common in discontinuous urban fabrics (residential areas), complex cultivation areas (mixed land uses), agricultural lands surrounded by natural vegetation (that is, not intensive agricultural land), broad-leaved forest and lake and river shores. On the contrary, mixed and coniferous forests hosted less *R. pseudoacacia*,

along with non-irrigated arable lands (intensive agriculture), pastures and marshes. Presence was not dependent on the evidence of management, and age classes were independent from all predictors except the “country”.

Native tree species richness and disturbance, which were not controlled by sampling design, were significantly different between the countries (native tree sp. richness: $\chi^2 = 24.822 \cdot df = 3 \cdot p\text{-value} = 1.682e-05$; disturbance: $\chi^2 = 9.0914 \cdot df = 3 \cdot \text{Cramer's } V = 0.06542 \cdot p\text{-value} = 0.0281$). Native tree species richness was the highest in Romandie (mean = 3.918367), followed by France (mean = 3.037037), Ticino (mean = 2.923077) and Italy (mean = 2.435897; see Figure 5 a)). Disturbance was slightly higher than expected in Romandie and France compared to Ticino where it was quite lower than expected and Italy where it was as expected by the chi-squared test of independence (see Figure 5 b)).



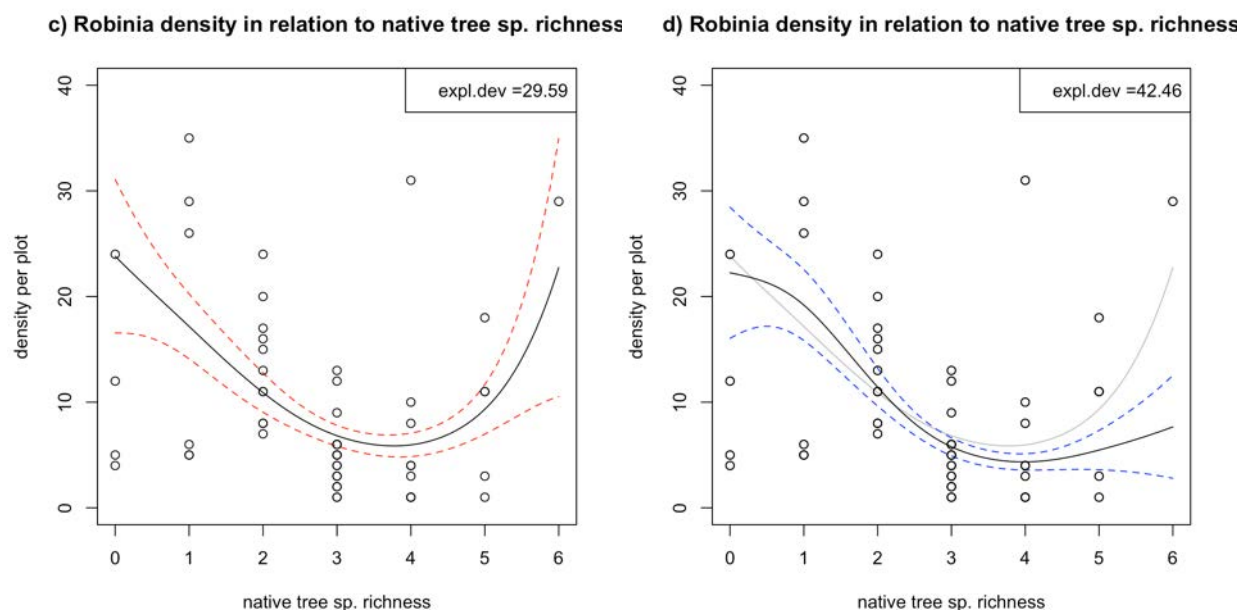
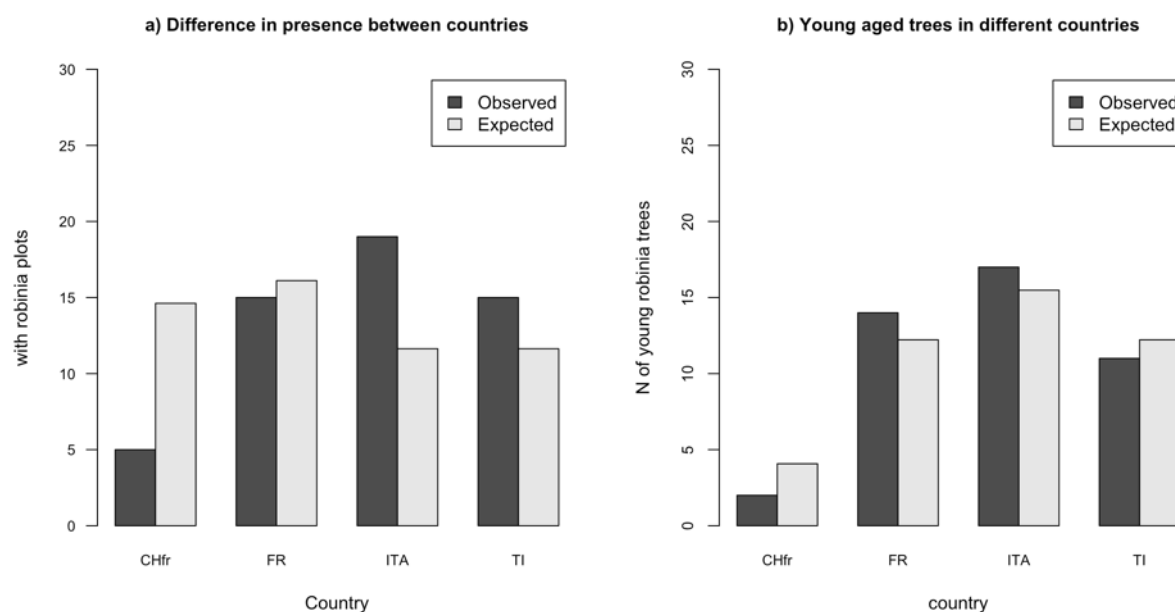


Fig. 3 Response functions generated by the plots of the univariate GAMs relating the species occurrence and density to two factors: **a)** occurrence in relation to habitat suitability (probability from 0 to 1 multiplied by 1000 in biomod2; **b)** occurrence in relation to native tree species richness; **c)** density in relation to native tree species richness; **d)** same as c), but without three outlier points considered as exceptions. In two of the three points *R. pseudoacacia* trees were just seedlings and saplings, for which survival was not sure; for the third point, *R. pseudoacacia* trees were quite old and there was a beginning of succession with small saplings of native trees of different species. Red and blue dashed lines represent the standard error, the points represent the data collected on the field.



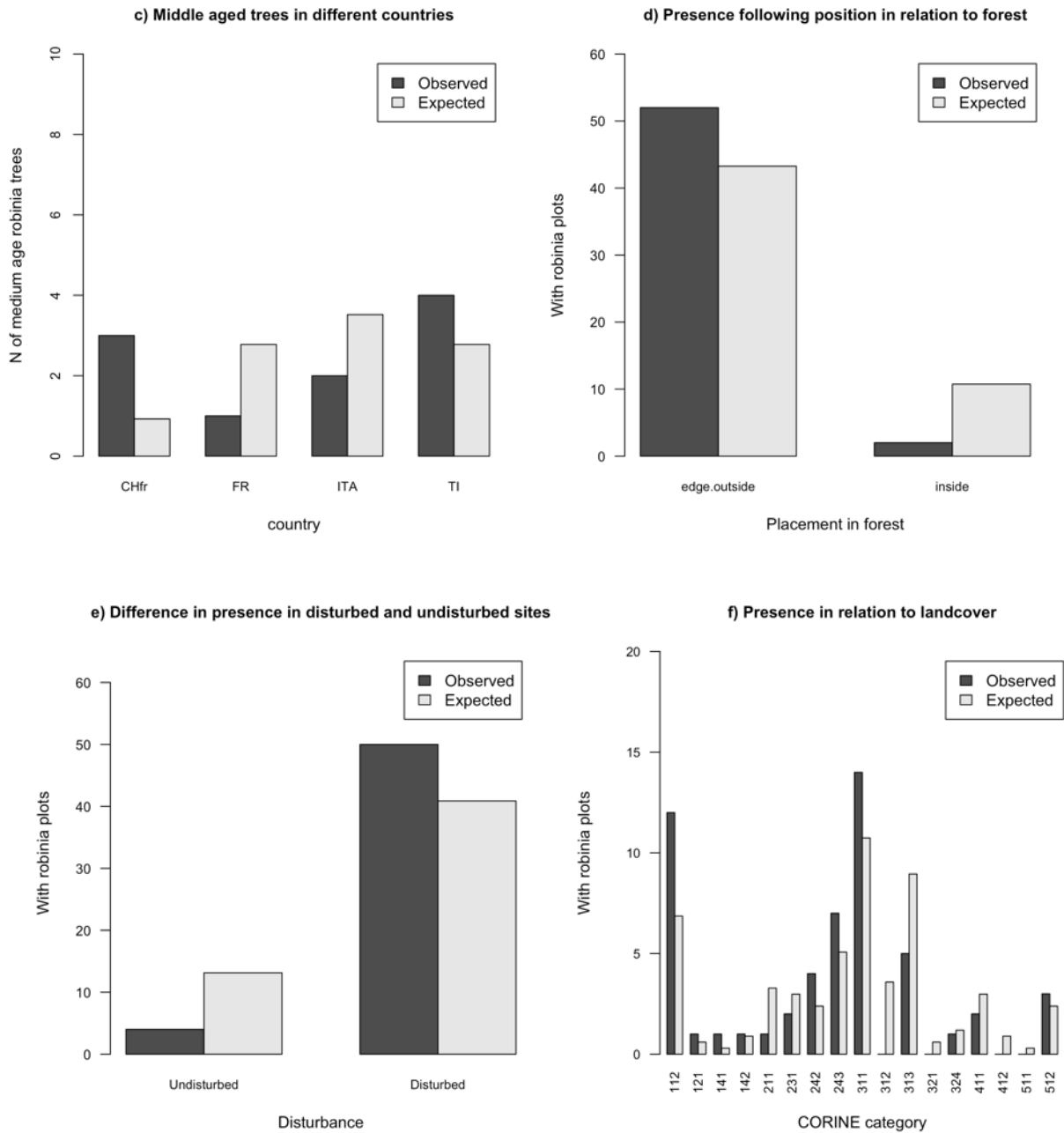


Fig. 4 Effect of categorical explicative variables on presence-absence and age classes of *R. pseudoacacia*. **a)** The number of plots with *R. pseudoacacia* in relation with the country in which the plots are located. **b)** Number of plots with average young-aged *R. pseudoacacia* trees and **c)** the number of plots with average middle-aged *R. pseudoacacia* trees, are presented in relation with the country in which the plots are located. **d)** Number of plots with *R. pseudoacacia* is presented in relation with the placement in the forest of the plots. **e)** The number of plots with *R. pseudoacacia* in relation to disturbance. **f)** The number of plots with *R. pseudoacacia* is presented in relation to landcover type. See M&M section for an explanation of the computation of the expected frequencies.

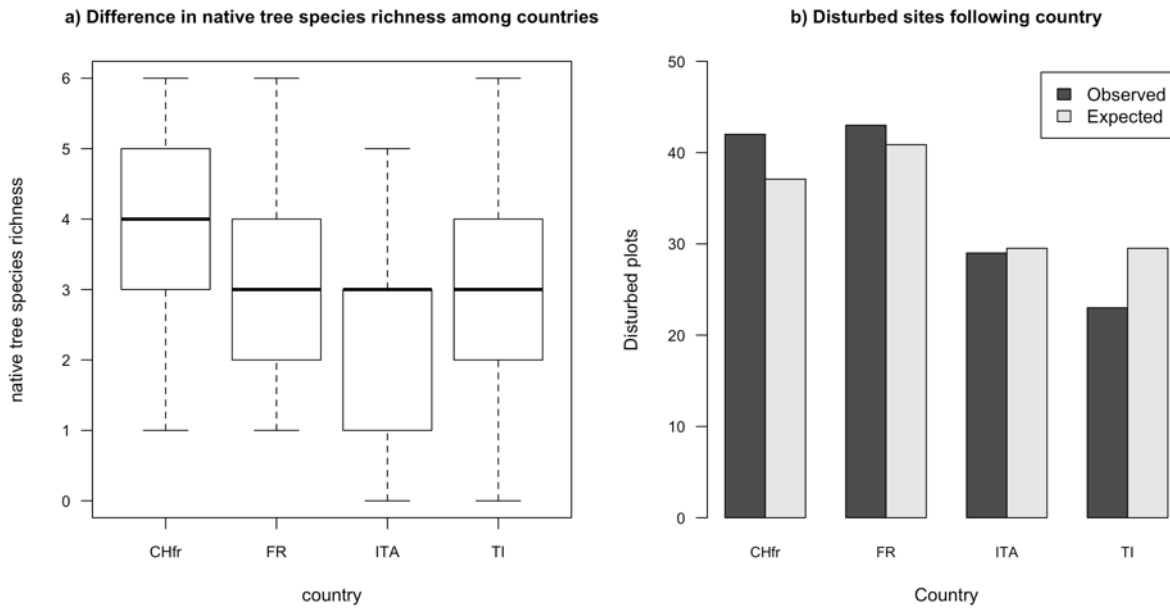


Fig. 5: Difference in variables that were not controlled by sampling design among countries. **a)** Difference in native tree species richness among countries is represented. the thick black line represents the median. **b)** Difference in disturbed plots between the different countries. See M&M section for an explanation of the computation of the expected frequencies.

Multivariate analyses

The most important predictor in the multivariate mixed model to explain the presence of *R. pseudoacacia* across the visited field plots was habitat suitability predicted by the ensemble SDM (see Figure 6). Disturbance was also seen to be an important predictor and higher disturbance had a significant positive effect on the occurrence of *R. pseudoacacia*. Higher native tree species richness and the position inside the forest (further in) had a negative effect *R. pseudoacacia* occurrence, but this effect was not significant. Finally, aggregated landcover did not have any negative nor positive effects on *R. pseudoacacia* occurrence, due to the fact that some land cover in the same aggregated category could promote invasion (e.g. extensive agriculture) and others rather hamper it (e.g. intensive farming). The random effect “country” in the mixed model explained ca. 10% of the total deviance in data in the full model, and this was consistent also in all the models with randomized variables (see Table 2 for statistic terms; see Figure 6).

Table 4: Coefficients and associated statistics for the complete multivariate mixed model. The first column lists all the predictors used in the modelling. Columns two to six provide the effects and associated statistics of predictors (fixed effects) on *R. pseudoacacia* presence-absence. The bottom rows (“Random effects”) show the effect of “country” as random factor.

Is_Robinia_there					
Predictors	Estimates	z value	Odds Ratios	CI	p

(Intercept)	-2.274351	-2.493	0.10	0.02 – 0.61	0.013
Habitat_suitability	1.539042	3.811	4.66	2.11 – 10.28	0.00014
native_trees_richness	-0.387269	-1.682	0.68	0.43 – 1.07	0.093
Dist_binary	1.362457	2.012	3.91	1.04 – 14.72	0.044
placement_inforest: inside	-1.456313	-1.697	0.23	0.04 – 1.25	0.090
Type_hab_simpl	0.006996	0.038	1.01	0.70 – 1.44	0.969
Random Effects					
σ^2	3.29				
τ_{00} country	1.04				
N _{country}	4				
Observations	181				
Marginal R ² / Conditional R ²	0.507 / 0.625				

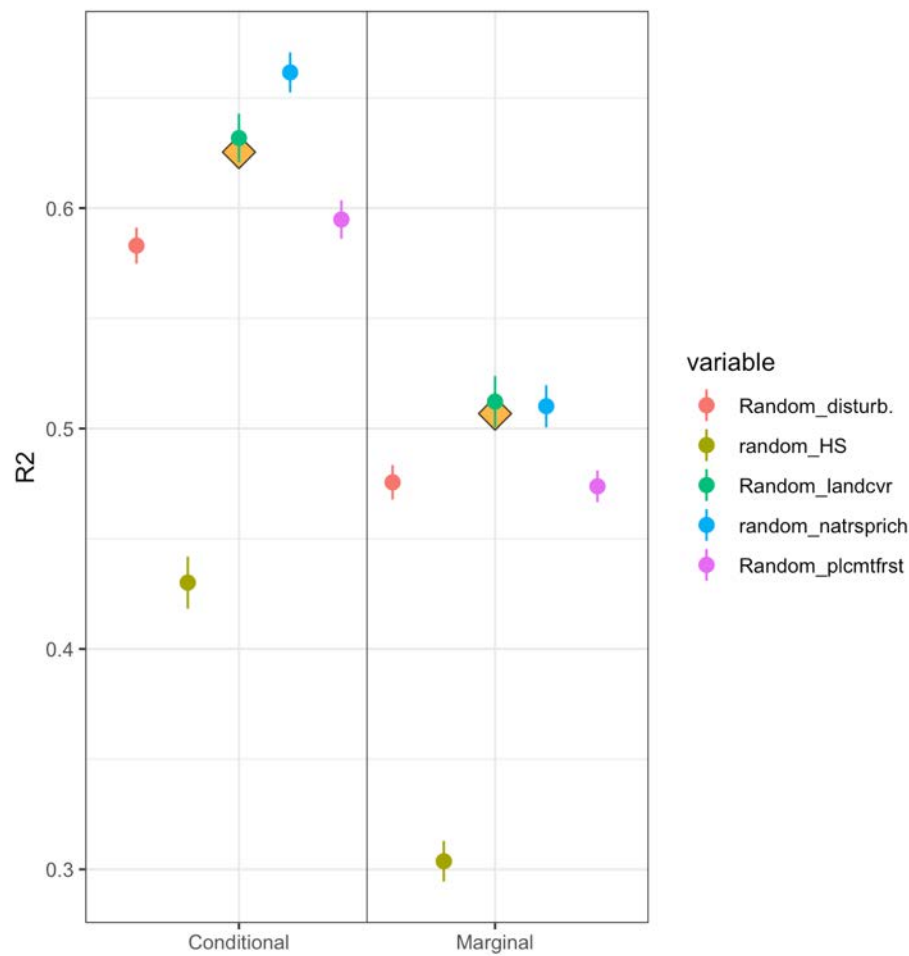


Fig. 6: The effects of multiple human-ecological factors on the presence of *R. pseudoacacia* based on the mixed models (GLMMs). The y axis shows the R^2 (deviance in probability of presence explained) of each model, the x axis presents on the left the conditional R^2 (models with random effect country included) and on the right the marginal R^2 (models with only fixed effects, that is without the “country” variable). The orange diamond in the centre represents the R^2 of the full model, whereas the points with the standard deviation represent the mean R^2 of models with randomized predictors (see M&M section for an explanation of the different models and how they were built).

Discussion

In this study, we aimed to better understand the anthropogenic and ecological factors that drive the invasion by a major IAS, the tree *R. pseudoacacia*. To do this we tried to explain the apparent difference in invasion rates that can be seen between three different countries: Switzerland, Italy and France, with two regions in Switzerland: Romandie, neighbouring France, and Ticino neighbouring Italy. In particular, we wanted to answer the following questions: (1) Can we confirm the difference in invasion rates between the different countries? (2) Do different drivers of invasion have different importance, and do they vary among countries? (3) If *R. pseudoacacia* invasion rates

differ between neighbouring countries, do distinct environmental and anthropogenic factors drive this difference? To answer these questions, we applied different methods: we modelled climatic suitability of *R. pseudoacacia* at a global level – to capture the full climatic niche - and then used it to conduct model-based fieldwork to assess presence-absence and population dynamics at a local level. We used ensemble models, univariate analyses (GAMs and chi-squared tests of independence) and multivariate mixed models (GLMMs) to analyse the data. The results reveal differences in invasion dynamics of *R. pseudoacacia* between the three countries and confirm what was indicated in the three countries' Forest Inventories (INFC 2007; IFN4 2009/13; IFN 2012): that is, Italy is the most invaded, followed by France and last Switzerland. The difference in invasion explained by country was not well explained by any of the anthropogenic-ecological factors we analysed, but individual factors across countries could be variably related to the invasion success. Finally, each predictor had a different importance in the models to explain the presence-absence and density of *R. pseudoacacia*, suggesting a hierarchical distribution of predictors at different scales and stages of invasion. Hereafter, we discuss each of these factors individually.

Is there a difference in invasion rates between countries?

The difference in invasion rates between the three countries was evident in the analysis (Figure 4 a). Italy was the most invaded of the countries followed by France and Switzerland (Ticino, Vaud and Geneva put together). These results were expected following the preliminary data collected from the forest inventories of the different countries (see Table S1), which is now confirmed by this study. Following our modelled habitat suitability (Figure 2), similar to the findings by Li et al. (2018), France, Italy and Switzerland have areas that are equally suitable in terms of climate for invasion by *R. pseudoacacia*, thus, climate cannot be the reason for the differences among countries. Four other factors analysed were investigated that could also explain these differences, but none of them seemed to explain well the difference alone. Another factor, not assessed quantitatively here, can also have a big importance on differential invasion rates: the introduction history and pathways that can affect propagule pressure; this factor will be discussed in detail below.

Do different drivers of invasion have different importance, and do they vary among countries?

Our analysis seems to confirm the hierarchy between predictors according to Milbau et al. (2009.) Climate suitability was the variable that contributed most in explaining *R. pseudoacacia* presence or absence in a certain area (Figure 6), according to previous studies (e.g. Milbau 2009; Szymura et al.

2018; Vicente et al. 2010). The second most important variable was disturbance, another well-known factor related to the facilitation of invasions (D'Antonio et al. 1999; McDougall & Turkington 2005; Szymura et al. 2018) through change in resource availability or landscape pattern (Theoharides & Dukes, 2007). Disturbance was followed by two predictors that did not show a significant effect on presence but seemed to play a role in it: position in the forest (being at the edge increased the probability of presence) and native tree species richness (i.e. a part of biotic resistance with competition of resident plants, herbivory by resident animals and soil fungal communities (Byers & Noonburg 2003; Levine et al. 2004), which seemed to decrease probability of presence). However, further investigation is needed here.

It is interesting to note that predictors seem to vary in importance also following the invasion stage at which the IAS is in a certain area. Climate and, in a smaller measure, disturbance seem to be two very important variables for evaluating whether the species can occur or not in a certain area, independently from the density it will reach. On another hand, climate and disturbance were not significant to predict density of this species among plots, whereas native trees richness (part of biotic resistance) was more important. That could mean that initial success does not predict necessarily successive establishment and spread, because drivers could differ among invasion stages, as sustained by Theoharides & Dukes (2007). Therefore, it seems that both anthropogenic and ecological factors are favouring *R. pseudoacacia* invasions, but with different dynamics depending on geographic and environmental contexts.

Finally, the predictors that could not be controlled with the sampling varied among countries: mean native tree species richness was different in the different countries, which could reflect biotic resistance and thus explain in part the difference in invasion rates between the different countries (see below). Disturbance was also slightly different between the countries, which could reflect land-use intensity. These differences will be further discussed below.

If R.pseudoacacia invasion rates differ between neighbouring countries, do distinct environmental and anthropogenic factors between regions drive this difference?

We observe that differences between countries exist, but this is not well explained by the explanatory variables we used. The richness in native tree species explains a small part of this difference (Figure 5 a; Figure 6; Table 2), which is in agreement with studies on biotic resistance to invasions (Levine et al. 2004), but it is not sufficient, and this relation between native trees richness and the presence of *R. pseudoacacia* could also represent the impact of invasive species on

massively invaded habitats (e.g. Vilà et al. 2011; some plots in Italy and Ticino were invaded by two or more alien species and there was not any native species), rather than biotic resistance to invasion. Another predictor that varied between the different countries was disturbance. However, as according to our index Romandie was the most disturbed (compared to the other regions, although the difference was slight), it was also the least invaded country, even though we saw from the mixed model that disturbance tends to promote invasion (see Table 2).

For this reason, our hypothesis is that the large part of the difference in invasion rates among countries, and thus the bulk of the remaining deviance in our model, could be explained by the history of introduction related to different cultural uses of *R. pseudoacacia* in the three different countries. This has likely caused a difference in propagule pressure in different habitats between countries, which had long-lasting effects on the distribution and spread of *R. pseudoacacia* invasions. In Switzerland *R. pseudoacacia* was initially introduced as small plantations, principally for honey production, and only secondarily for the creation of poles in vineyards and/or wine barrels and for landscaping and soil reclamation (i.e. restoring soil quality; Vítková et al. 2017), but it was never used for forestry purposes. In Italy, its major use was for soil reclamation after deforestation following World War Two (Ferraris et al. 2000; Maltoni et al. 2012) and stabilisation of slopes during road and railways construction (Alessandrini, pers. com.; Ferraris et al. 2000; Maltoni et al. 2012). Another use of *R. pseudoacacia* in Italy was for forestry practices (Ferraris et al. 2000; Maltoni et al. 2012; Regione Piemonte, 2014) leading to large plantations that contribute to high propagule pressure. Agricultural and field abandonment in the post-war period is also thought to have facilitated invasion by this species. In France, *R. pseudoacacia* was initially introduced for the creation of poles in vineyards and wine barrels. Later, in the 19th century it was used a lot for forestry practices (Ginter pers. com.; Ginter et al. 2018). Thus, Switzerland is, of the three countries, the one that introduced *R. pseudoacacia* least. Moreover, no recent plantation events exist in Switzerland (Vítková et al. 2017), whereas in Italy and France, its forestry qualities are still well regarded and as such the tree has been long promoted (Ferraris et al. 2000; Maltoni et al. 2012; Ginter et al. 2018). This is further suggested by the fact that, in Switzerland, we found older *R. pseudoacacia* trees in Ticino, Vaud and Geneva compared to France and Italy (Figure 4 b) and c)). All this confirms the findings by Vítková et al. (2019) that the number of uses in Central Europe (Switzerland is part of it) were less numerous than the number of uses in southern Europe (Italy and southern France are part of this area) and that difference in *R. pseudoacacia* presence between central Europe and southern Europe was given in a large part by the history of its introduction and its uses, leading to higher

propagule pressure in some places. Differences in use and the large number of propagules introduced increases the probability of establishment of seeds in the surrounding landscape and the further spread regardless of control efforts (Castro-Díez et al. 2011; Donaldson et al. 2013), thus supporting the role of history in the differences we observed between countries.

Concerning the difference between Ticino, Vaud and Geneva, our hypothesis is that this is again due to historical reasons related to introduction goals (and subsequent propagule pressure) and disturbance. In Ticino, *R. pseudacacia* was planted widely to stabilize slopes during the construction of the Gotthard railway (Delucchi, pers. com.): this likely created a high propagule pressure (Donaldson et al. 2013). Another important factor that likely promoted the spread of *R. pseudacacia* in both Ticino and Italy was the cortical cancer that affected chestnuts trees (*Castanea sativa* Miller) in the 60's (Delucchi, pers. com.): a vast number of chestnuts died or were cut, and *R. pseudoacacia* rapidly took this novel space and expanded considerably (Regione Piemonte, 2014; Delucchi, pers. com.). The other Swiss cantons are less steep so *R. pseudoacacia* was not used so much for soil stabilisation, chestnuts are much less frequent, and land use intensity is higher (agricultural principally), with likely less gaps for invasion. In particular, in the Vaud canton, the principal uses of *R. pseudoacacia* wood were for fence posts for carpentry uses (Daujat, pers. com.), which entailed only small plantations. The importance of human-dispersal and introduction in facilitating local invasions is key, as this species is a very good colonizer over short distances where already present but is a poor colonizer over long-distances, and thus with few natural colonies newly establishing far away (Vítková et al. 2017).

Other factors not considered in this study could be important to take into account for explaining the differences in invasion between countries. The first one is that some other factors could have been included in the model as predictors (e.g. soil type), that could improve the quantification of habitat suitability. However, in our opinion, this is not very likely because it is known that *R. pseudacacia* has a very wide abiotic tolerance (it is one of its major invasiveness traits) and can stand most soil types except very compacted and non-drained ones (Huntley, 1990; Vítková et al. 2017). Another factor could be the different solar radiation that distinguish the Canton Ticino from the Vaud and Geneva cantons (Météosuisse, 2018). *R. pseudoacacia* has been preferentially observed in sunny places (Cierjacks et al. 2013), and this could have an effect on its growth and spread velocity. Future studies should take this factor into account to assess whether it could have a role in the observed differences. Furthermore, including the German-speaking part of Switzerland into a similar study could help to further and more holistically identify interesting trends and

dynamics regarding invasions of *R. pseudoacacia*. Other factors that could be worth investigating in more details are approaches of the different countries to policies and management regarding *R. pseudoacacia*, looking into the history to better trace introduction pathways and goals for the species, and looking at soil seed banks to more properly assess propagule pressure. It could also be useful to better study the effects of different types of disturbance on *R. pseudoacacia* invasion dynamics, in order to account for different disturbances that could be either detrimental or positive, and to study the effects of native tree species richness and biotic resistance in general (which is quite debated in the literature; e. g. Herben et al. 2004), in order to better disentangle when native species richness acts as biotic resistance from when native species richness is impacted by the alien species, i.e., in which invasion stages is biotic resistance to invasion more effective. All these complementary analyses would be useful to better assess the proposed hypotheses.

Conclusion

Although it was not conclusive concerning the difference in invasion rates between the three countries, this study provides insights into invasion dynamics of *R. pseudoacacia*:

- Climate is further confirmed to be the most important predictor in explaining presence of *R. pseudoacacia*, and thus we can support the idea the climate is one of the major filters for invasion.
- Disturbance, in particular human-related, has an important role in explaining *R. pseudoacacia* presence.
- Native tree sp. richness seems to play a role in the difference in density reached by *R. pseudoacacia*, but further investigation is needed.
- None of the studied predictors can explain entirely the difference in invasion rates among countries.
- History of introduction (with its effect on propagule pressure), which is different in the three countries, could play a role in it but was not quantitatively tested in this study.
- Invasion dynamics depend on a vast number of human- and biology-related factors, each one with a different importance at different spatial scales and invasion stages. It is important to define the spatial scale and invasion stage that we want to consider, in order disentangle which factor is the most important in every specific situation, with the final aim to facilitate invasion management strategies.

Acknowledgements

I would like to thank Antoine Guisan for the direction of this project, for being always available to discuss about it and for helpful comments on a previous version of this paper. Many thanks also to Ross T. Shackleton for his supervision and stimulating discussions on all aspects of the project, and in particular for his invaluable help on the field. I am grateful to Olivier Broenniman for his suggestions in several parts of the project and, with Mathieu Chevalier, for their help in statistical analysis. I would also like to thank Simone Parisi for his support all along this project and for him being always available to help me with fieldwork. I thankfully acknowledge Alessandro Alessandrini, Liliana Bernardo, Maurizio Bovio, Emanuele Del Guacchio, Gabriele Galasso, Fabrizio Martini, Nicodemo G. Passalacqua, Anna Rampa, Adriano Stinca and Wilhalm Thomas for their courtesy in providing me with the occurrence data of the study species in Italy; Info Flora provided occurrence data for Switzerland and Tela Botanica for France. Thanks to Marco Delucchi and Mosè Cometta for the interesting and useful discussion on the study species; to Charline Daujat, Thomas Zumbunnen and Zoé Ginter for providing me with information on its introduction in Switzerland and France. I gratefully acknowledge Agassiz foundation for funding the study.

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**What drives the success of the invasive tree *Robinia pseudoacacia*:
climate suitability, disturbance or land management?**

Supplementary material

**Travail de Maîtrise universitaire ès Sciences en comportement, évolution et
conservation**
Master Thesis of Science in Behaviour, Evolution and Conservation

par

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**Directeur : Prof. Antoine Guisan
Superviseur : Dr. Ross T. Shackleton
Expert·e·s : Anonymous
Département d'Écologie et Évolution**

Janvier 2020

Table S1: Presence of *R. pseudoacacia* in forests of different European countries.

Presence in different countries			
	ha	% of forest surface	Source
CH (2013)	2'480	0.2	IFNS, 2013
I (2007)	233'553	2.3	INFC, 2007
F (2012)	200'000	1.2	IFNF, 2012
G	34'000	0.3	Vitkova et al. 2017
A	.	0.2	Vitkova et al. 2017

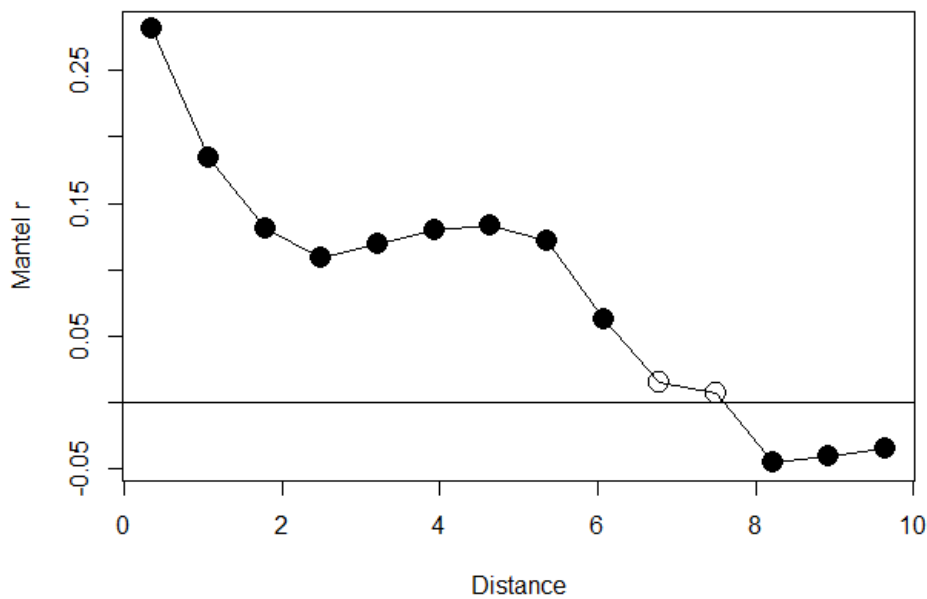


Figure S1: Spatial autocorrelation between the occurrence points (at 1 km resolution). The y axis shows the value of correlation found by the Mantel test, whereas the x axis shows the distance in decimal degrees (1 degree corresponds to about 78 km at 45N/S). It can be seen that SAC is eliminated only at 6 decimal degrees of distance (corresponding to about 470 km). For this reason, we decided to only take one point per cell of 1 km² as it is only correlated by a value of 0.25 at 1 km (about 0.001 degrees).

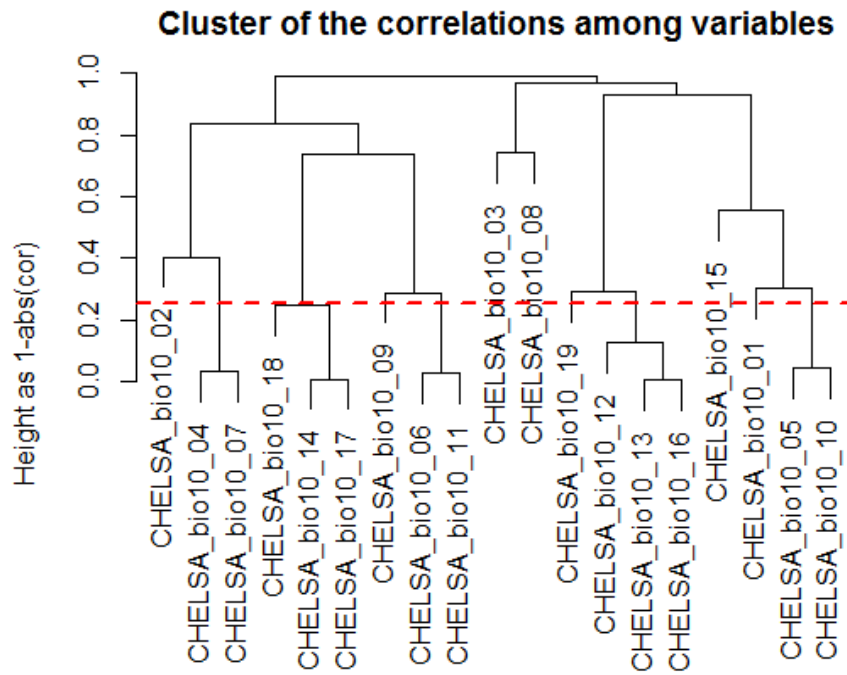


Fig. S2: Correlation among the CHELSA bioclimatic variables. The more the variables are next to each other in the phylogeny, the more they are correlated. For the model we tried to select one or maximum two variables per cluster, following what was known of the ecology of *R. pseudoacacia*. For the cluster containing bio15, bio01, bio 05 and bio10, none of the variables was selected because we wanted a maximum of six predictors to avoid overfitting. CHELSA_bio10_04 = bio04; CHELSA_bio10_06 = bio06; CHELSA_bio10_11 = bio11; CHELSA_bio10_19 = bio19; CHELSA_bio10_12 = bio12; CHELSA_bio10_18 = bio18. For a description of variable corresponding to the abbreviation see Table S4.

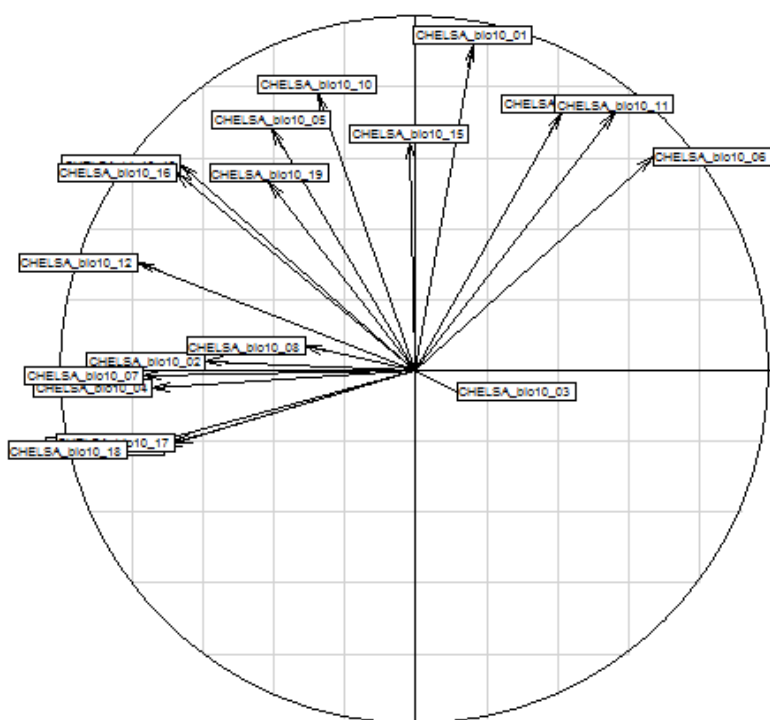


Fig. S3: PCA of CHELSA bioclimatic variables. Arrows that point in orthogonal directions are not correlated at all. The more the arrows point in the same direction, the more the variables are correlated. The length of the arrow represents the importance of the variable in explaining *R. pseudoacacia* distribution (the lengthier the more it explains).

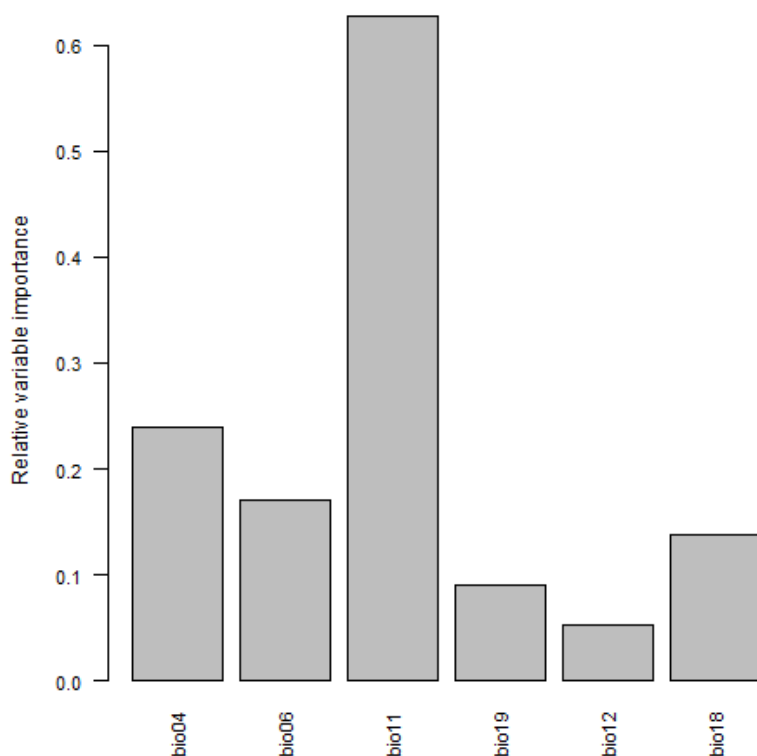


Figure S4: Importance of climatic variables included in the global distribution model for *R. pseudocacia*. The model was calibrated at the scale of global ecoregions.

Table S2: Predictors used for modelling *R. pseudoacacia* distribution.

Abbreviation	Variable	Unit	Source
Bio04	Temperature Seasonality (standard deviation *100)	°C * 100	Karger et al. (2017)
Bio06	Min Temperature of Coldest Month	°C	Karger et al. (2017)
Bio11	Mean Temperature of Coldest Quarter	°C	Karger et al. (2017)
Bio12	Annual Precipitation	mm	Karger et al. (2017)
Bio18	Precipitation of Warmest Quarter	mm	Karger et al. (2017)
Bio19	Precipitation of Coldest Quarter	mm	Karger et al. (2017)

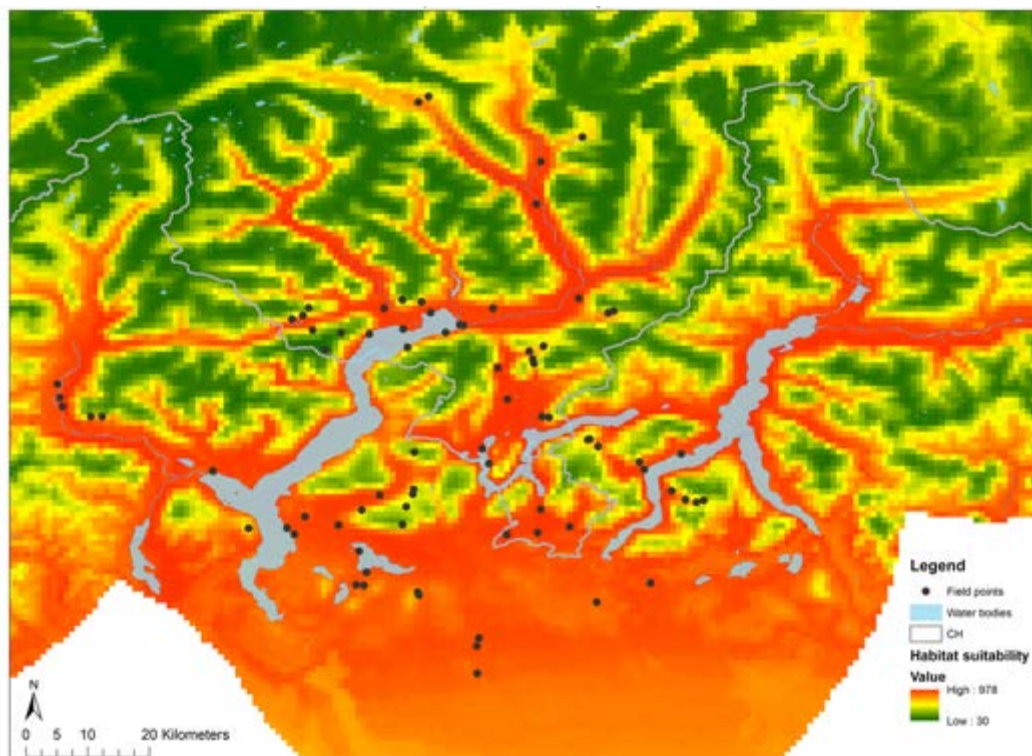
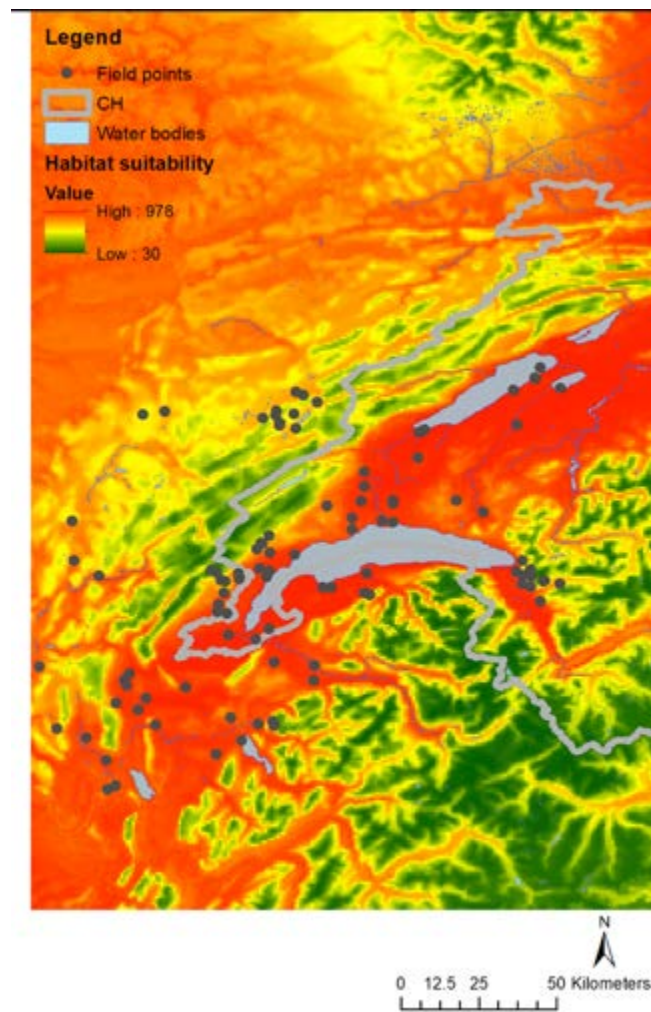


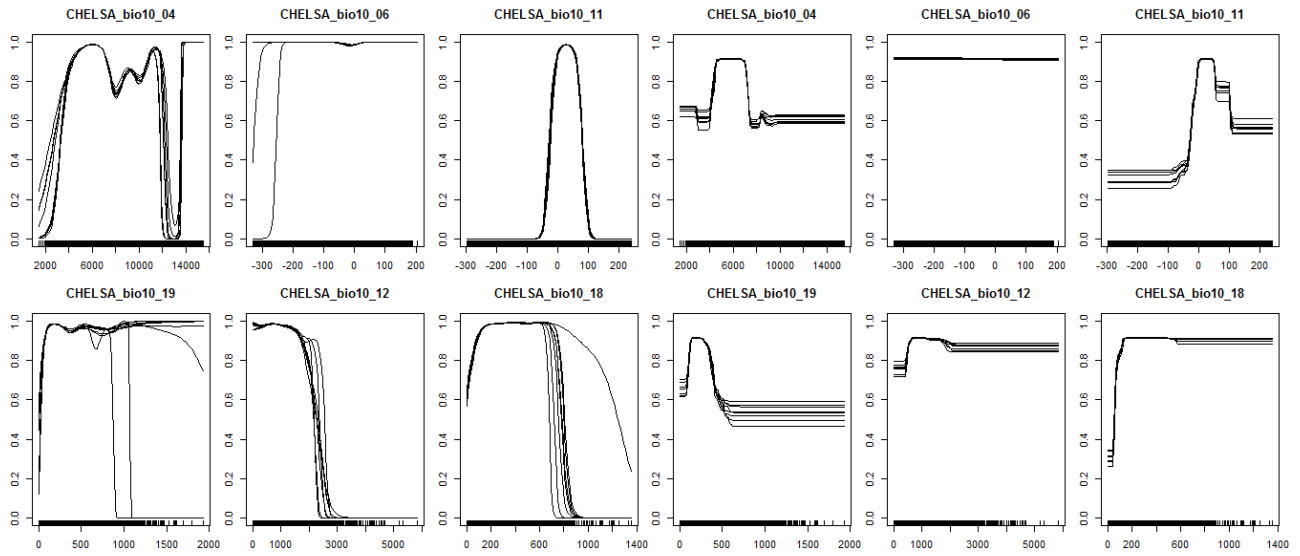
Fig. S5: Fieldwork points visited in the two study areas on the climatic suitability map.

Table S3: CORINE landcover categories. In the first three columns CORINE landcover types are represented with their code, name and reference. Fourth and Fifth columns represent the aggregated landcovers as we used them for fieldwork and analysis.

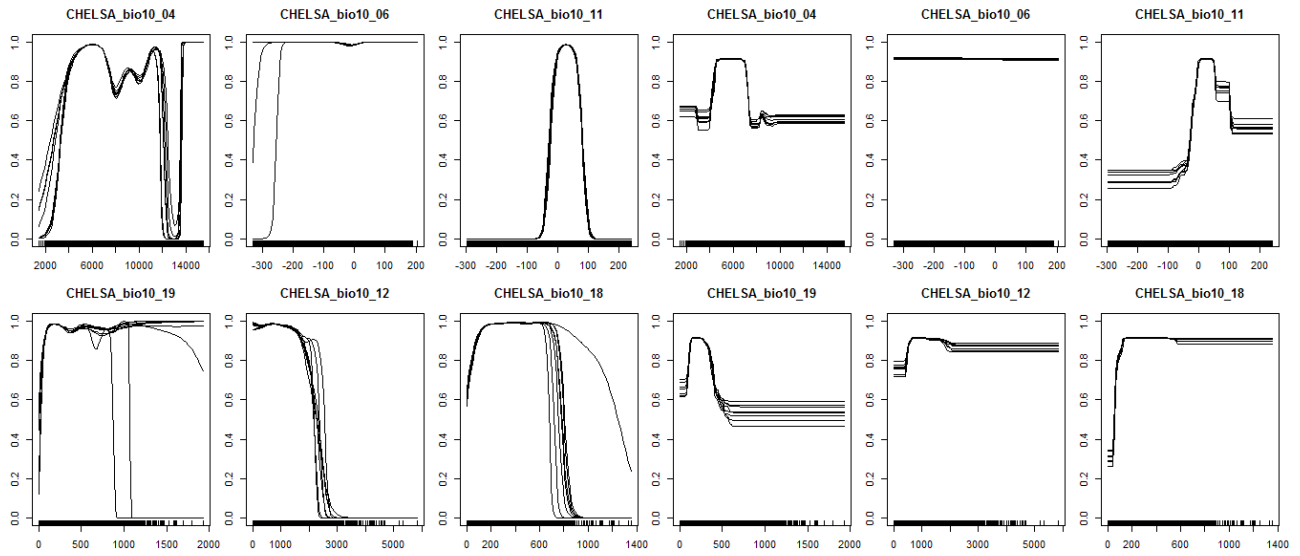
Value	Land cover type	Source	Aggregated landcover for fieldwork planification	Aggregated landcover for multivariate analysis
111	Continuous urban fabric	European Environment Agency (EEA)	Urban; 1	-
112	Discontinuous urban fabric		Urban; 1	Anthropic; 1
121	Industrial or commercial units		Urban; 1	Neutral or not enough data (<5 occurrences); 0
122	Road and rail networks and associated land		Urban; 1	-
123	Port areas		Urban; 1	-
124	Airports		Urban; 1	-
131	Mineral extraction sites		Urban; 1	-
132	Dump sites		Urban; 1	-
133	Construction sites		Urban; 1	-
141	Green urban areas		Urban; 1	Neutral or not enough data (<5 occurrences); 0
142	Sport and leisure facilities		Urban; 1	Neutral or not enough data (<5 occurrences); 0
211	Non-irrigated arable land		Agricultural; 2	Agricultural; 2
212	Permanently irrigated land		Agricultural; 2	-
213	Rice fields		Agricultural; 2	-
221	Vineyards		Agricultural; 2	-
222	Fruit trees and berry plantations		Agricultural; 2	-
223	Olive groves		Agricultural; 2	-
231	Pastures		Agricultural; 2	Agricultural; 2
241	Annual crops associated with permanent crops		Agricultural; 2	-
242	Complex cultivation patterns		Agricultural; 2	Agricultural; 2
243	Land principally occupied by agriculture, with significant areas of natural vegetation		Agricultural; 2	Agricultural; 2
244	Agro-forestry areas		Agricultural; 2	-
311	Broad-leaved forest		Natural; 3	Forest; 3

312	Coniferous forest		Natural; 3	Forest; 3
313	Mixed forest		Natural; 3	Forest; 3
321	Natural grasslands		Natural; 3	Neutral or not enough data (<5 occurrences); 0
322	Moors and heathland		Natural; 3	-
323	Sclerophyllous vegetation		Natural; 3	-
324	Transitional woodland-shrub		Natural; 3	Neutral or not enough data (<5 occurrences); 0
331	Beaches, dunes, sands		Natural; 3	-
332	Bare rocks		Natural; 3	-
333	Sparsely vegetated areas		Natural; 3	-
334	Burnt areas		Natural; 3	-
335	Glaciers and perpetual snow		Natural; 3	-
411	Inland marshes		Wet; 4	Humid and shores; 4
412	Peat bogs		Wet; 4	Neutral or not enough data (<5 occurrences); 0
421	Salt marshes		Wet; 4	-
422	Salines		Wet; 4	-
423	Intertidal flats		Wet; 4	-
511	Water courses		Water bodies; 5	Neutral or not enough data (<5 occurrences); 0
512	Water bodies		Water bodies; 5	Humid and shores; 4
521	Coastal lagoons		Water bodies; 5	-
522	Estuaries		Water bodies; 5	-
523	Sea and ocean		Water bodies; 5	-
999	NODATA		-	-

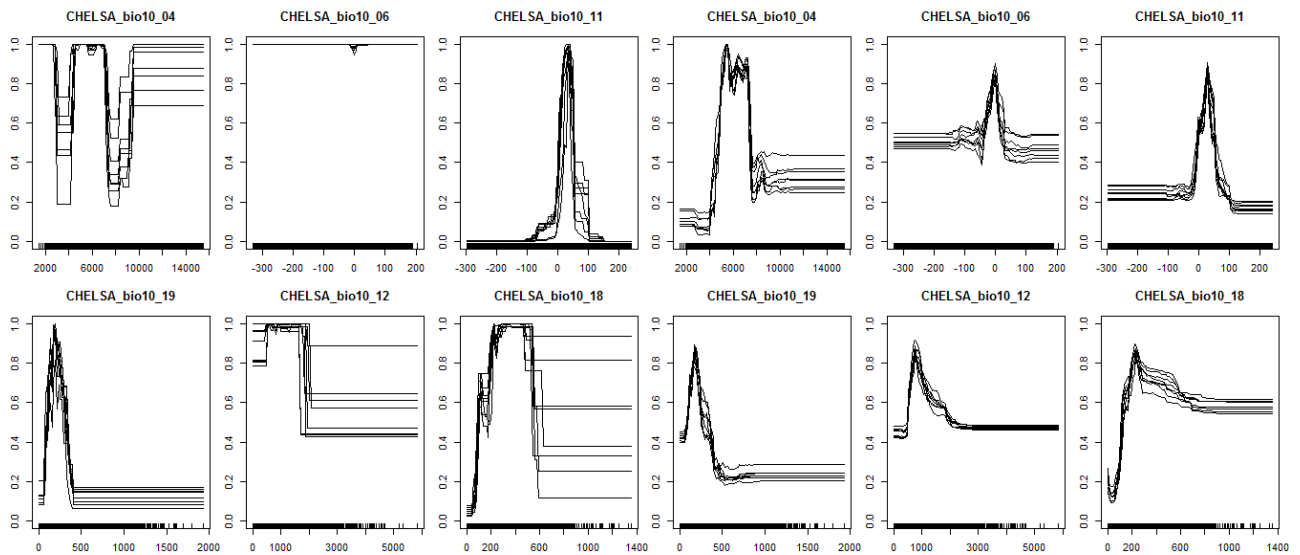
Response curves for *Robinia pseudoacacia*.fine's GAM



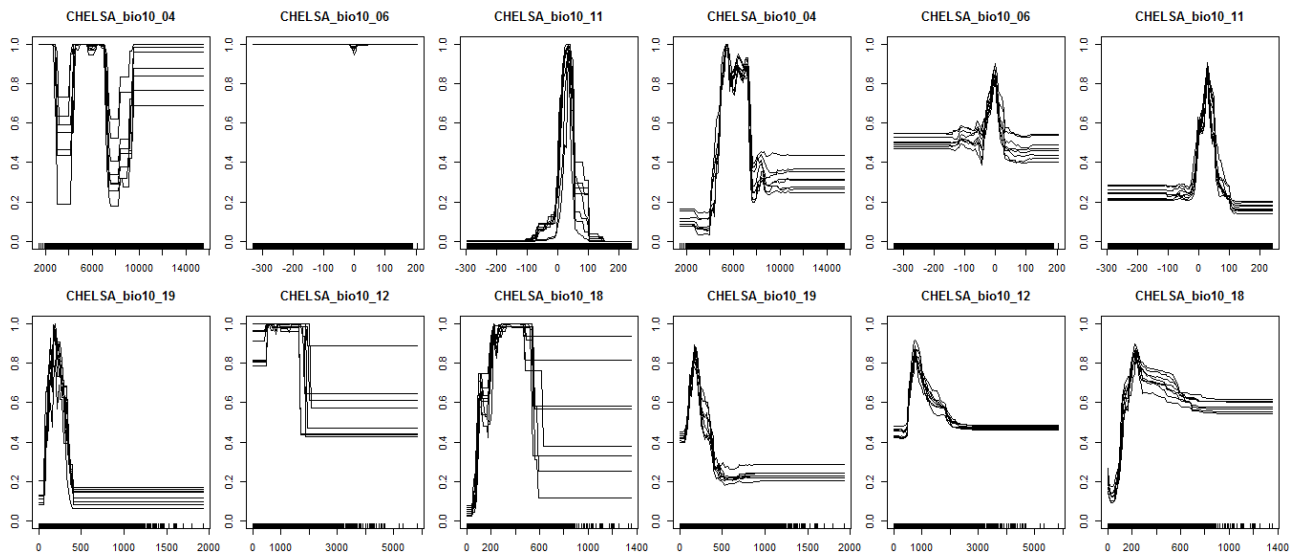
Response curves for *Robinia pseudoacacia*.fine's GBM



Response curves for *Robinia pseudoacacia*.fine's MAXENT.Phillips



Response curves for *Robinia pseudoacacia*.fine's RF



Response curves for *Robinia.pseudoacacia.fine*'s GLM

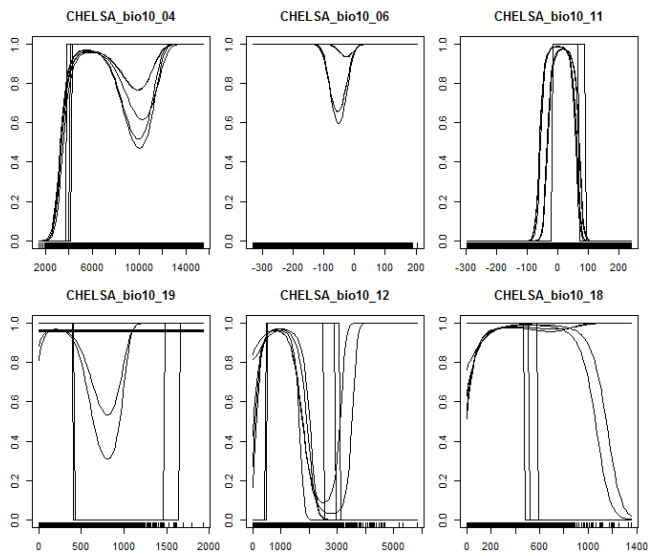


Fig. S6: Response curves of *R. pseudoacacia* for the six climatic variables included in the global model for the five modelling techniques. CHELSA_bio10_04 = bio04; CHELSA_bio10_06 = bio06; CHELSA_bio10_11 = bio11; CHELSA_bio10_19 = bio19; CHELSA_bio10_12 = bio12; CHELSA_bio10_18 = bio18. For a description of variable corresponding to the abbreviation see Table S4.

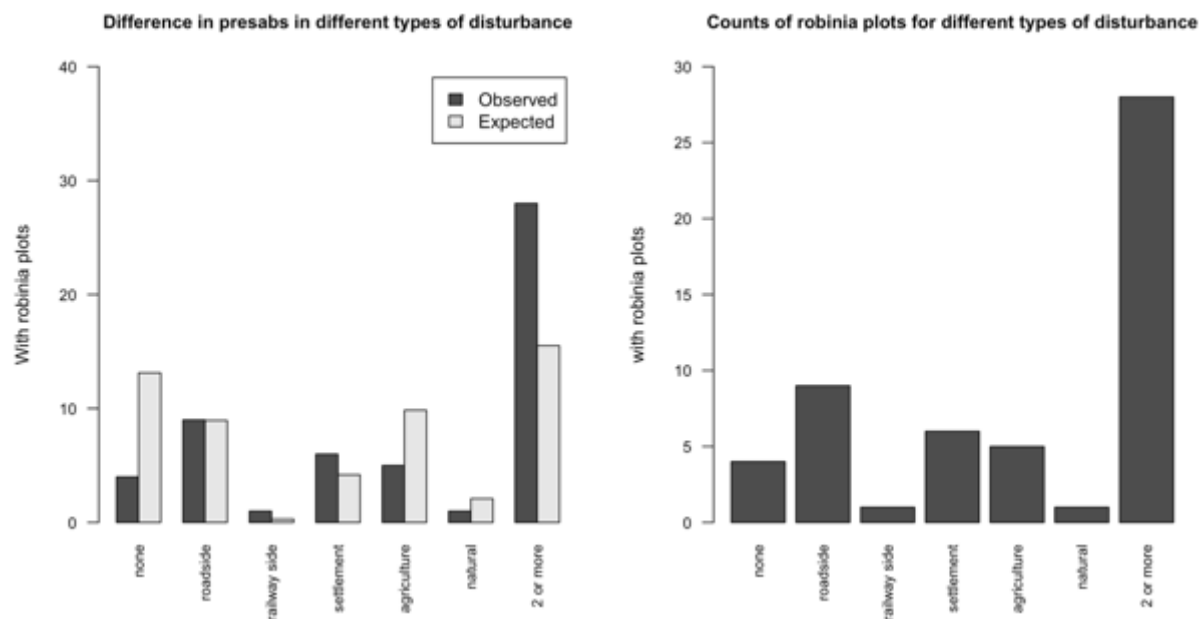


Fig. S7: Repartition of *R. pseudoacacia* presences in different disturbance types. On the left the proportion between expected and observed presences in a certain type of disturbance is presented, whereas at the right the number of plots containing the species in each type of disturbance is presented.

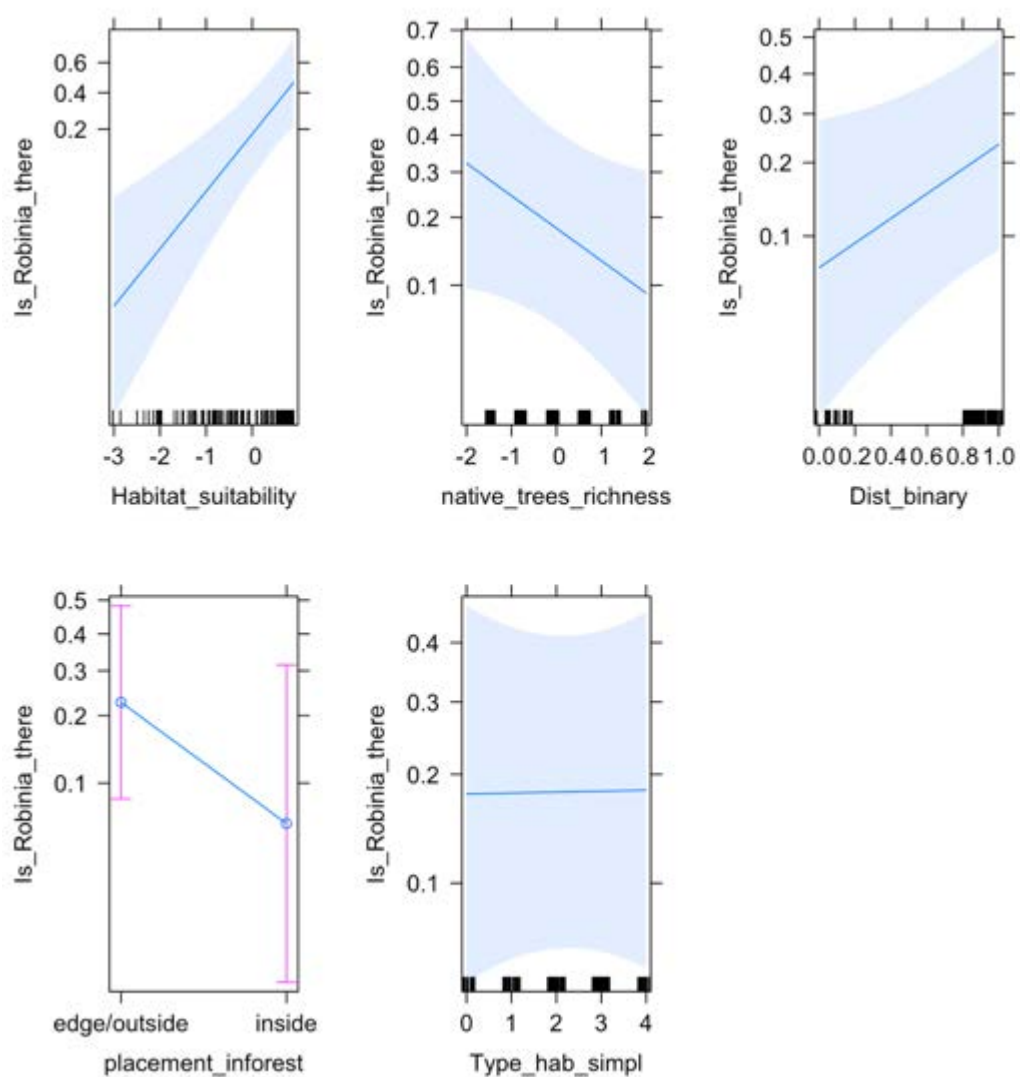


Fig. S8: Representation of the change in probability of presence of *R. pseudodacacia* in relation to the five explanatory variables of the mixed model. Pay attention to the fact that y axis has not always the same scale.

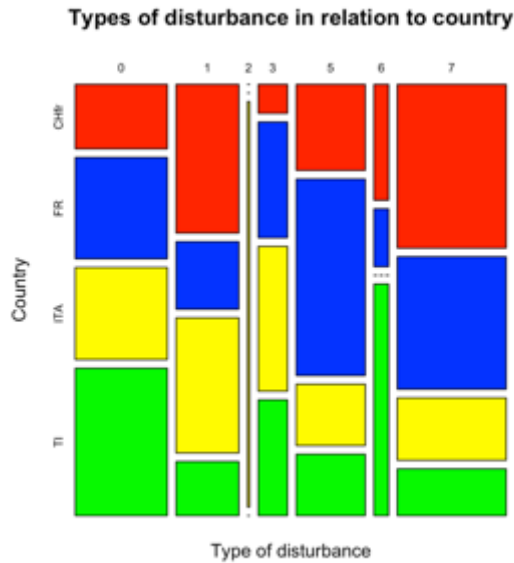


Fig. S9: The different types of disturbance collected in our field study are reported in relation to the country. The x axis represents the type of disturbance (for the correspondence of numbers with the disturbance type see the section M&M above), whereas the y axis represents the country (CHfr in red; FR in blue; ITA in yellow, TI in green). The height of the columns represents the proportion of the plots within each country on the total of the specific type of disturbance, whereas the width represents the proportion of that specific type of disturbance on the total of disturbed plots. Disturbance was analyzed as a binary variable because the categories were not precise, as for example the majority of plots had two or more types of disturbance, which entailed a loss of information.

S1: Choice of distribution

To analyse the effect of variables collected on density, a negative binomial family was chosen instead of a Poisson. This is due to the fact that the Poisson model was found to be over-dispersed by `P__dist` (package `msme`; dispersion = 7.77) and `dispersiontest` (package `AER`; alpha = 6.2, p-value = 0.008049) and the variance was much higher than the mean (one of Poisson's assumptions). Negative binomial family is surer to use when count data are over-dispersed (Rodriguez 2013), and the model was no more over-dispersed once negative binomial distribution was selected (dispersion = 1.18).

S2: Effect size

Given that any effect, no matter the magnitude, can produce small p-value or large p-value if the sample size is big or small enough and that identical or similar effects can have different p-values following the precision of the estimates, we decided to put effect size measures in the results of chi-squared tests of independence and in the results of the mixed model as a complement of information, because according to Iolongo (2016) effect size effect size takes into account the size

of the sample, whereas p-value does not take it into account, and when enlarging the sample, the probability of getting a small p-value increases also for very small effect that would not be recognized as significant with a smaller sample. Effect size measures that have been used in this paper are *phi* for 2x2 contingency tables, *Cramer's V* for tables with unequal number of columns and rows and *Odds ratio* for the probability of presence of *R. pseudoacacia* in the mixed model. These three effect sizes measure the effect as the variation between two or more variables observed between different groups. *Phi* and *Cramer's V* use the correlation to measure the effect, whereas Odds ratio represents the likelihood that an event occurs due to a certain factor and not due to chance (Ialongo, 2016).