Invasive potential of the Giant Hogweed (*Heracleum mantegazzianum*) in the Western Swiss Alps and implications for management

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ABSTRACT

The Giant Hogweed (*Heracleum mantegazzianum*), an invasive giant herb native from Caucasus, was first introduced in Switzerland (Geneva) in 1895 and cultivated in alpine botanical gardens because of its spectacular inflorescence. Since then, it escaped repeatedly from gardens, becoming invasive and leading to ecological, economical and health problems. In this study, we evaluated the invasion status of this alien invasive species in the Western Swiss Alps, by modelling its potential distribution and estimating current and future density and cost estimations. These assessment measures provide useful tools for an action plan in conservation biology. In the continuity of a previous study in 2004, we used a model-based sampling design to improve occurrences data and ultimately improve predictive models of the species distribution. Since we did not found as much occurrences as expected, different models were carrying out with different available data sets. The first predictive maps were based on naturalized occurrences versus all available presences and the second, on a set of absence sites stratified according to the strata of a previous available model. We tested two different estimations of the giant hogweed's population size: a design-based estimation and a model-based estimation. We first proceed to the Thompson design-based estimation through a random-stratified adaptive sampling. This estimation provided current population size of the focal species. The future potential population size of the focal species was achieved with the models resulting from the field sampling. For management cost, communes included in the study area were set as management units and assessed individually. A binary model using threshold value optimising ratio of omission to commission errors provided future potential costs. Finally, this filtered binomial model permits us to underline which communes should receive special attention for eradication.

INTRODUCTION

It has been widely recognized that alien invasive species consist in the second cause of biodiversity loss after habitat degradation (Wilcove & Chen 1998). In addition to ecological problems, such species could lead also to economical (e.g. *Impatiens glandulifera* or *Senecio inaquidens*) and health hazards (e.g. *Ambrosia artemisiifolia*). Worldwide, enhancement of transport for tourism and commercial exchanges through globalisation allows species displacements surmounting geographical barriers which could not be possible naturally.

According to the World Conservation Union (UICN) definitions, **"alien species"** means a species occurring outside its natural range and dispersal potential i.e. outside the range it occupies naturally or could not occupy without direct or indirect introduction or care by humans. Alien species are also called non-native, non-indigenous, introduced, foreign or exotic species. Some European authors also make a distinction between "archeophytes" and "neophytes" which are alien species introduced respectively before and after 1492 (Richardson *et al.* 2000). Among alien species some are defined as **"alien invasive species"**. Alien invasive, pest or noxious species means an alien species which becomes established in natural or semi-natural habitat, is an agent of change and threatens native biological diversity. Archeophytes are not considered as invasive species because they followed human migrations and do not cause biological problems (Revue Horticole Suisse 2005). In the case of plants, Richardson *et al.* (2000) defined **"naturalized plants"** as plants that reproduce consistently and sustain populations over many life cycles without intervention by humans or in spite of human intervention. They often recruit offspring freely, usually close to adult plants.

The Swiss flora is composed of 2943 species of which 350, about 10%, are alien species (Gigon & Weber 2005). Among these alien species, 10% could cause problems according to the ten's rules (Williamson 1996) quantifying transition probabilities. The Swiss Commission for Wild Plant Conservation CPS/SKEW had elaborate two lists of alien invasive plants. The first list, the Black List, indexes 20 alien invasive plants that

actually cause damages and have to been controlled. The second one, the Watch List, registers 20 species which have the potential to cause damages or already cause problems in neighbouring countries. Becker *et al.* (2005) underline that Swiss mountainous landscape is also subjected to invasion but the number of alien plants recorded decrease with elevation. In Switzerland, legal bases will still need to be completed to ensure prevention and fighting against these foreign organisms.

Prevention, early detection and efficient management are the most cost-effective means of reducing the problems caused by invasive plant species worldwide (Byers *et al.* 2002). In this case, niche-based Species Distribution Models (SDM, Guisan & Thuiller 2005) are useful to predict species future distribution allowing risk assessments (Welk 2004) and identifying regions where monitoring and management efforts would be most needed (Byers *et al.* 2002).

In case of alien invasive species modelling, there are two main limitations of such static and correlative models. First, the **pseudo-equilibrium assumption** (Franklin 1995) is violated. Indeed, invasive species are commonly still expanding in the invaded range (Peterson 2003) and according to the dispersal limitation theory (see Pulliam 2000), they have not yet colonized all suitable habitats, yielding commission errors in modelling invasive species (Guisan & Thuiller 2005). Actually, this consideration raises three relevant problems: i) Absences have not necessarily topo-climatic causes but in fact e.g. geographical ones and this is especially accentuated in the case of invasive species compared with common species leading to commission errors in the predictions (false positives). ii) Invasive field surveys may also lead to an incomplete sampling of occurrence sites resulting in bias in the predictions towards sampled habitats (omission errors) (Hulme 2003) and in underestimating species distribution (false negatives). iii) Finally, spatio-temporal autocorrelation is often observed because of source-sink dynamic especially for early colonisation phase where distribution might be more constrained by e.g. propagule availability than by climatic requirements (Rouget & Richardson 2003). In this latter case, independence data assumption needed for correlative models is not respected.

All these considerations generate weak predictions and to overcome all these problems, the solution might be to use the native range for model calibration. Despite the fact that sampling species' native distribution range is expensive and time consuming, projecting models from native range to invaded range may also violate the **niche conservatism assumption** (Peterson *et al.* 1999; Peterson 2003). Yet, one must be aware that climate match between native and host ranges is a primary condition for a successful establishment (Zalba *et al.* 2000; Thuiller *et al.* 2005) but, indeed, two main hypotheses might modulate the realized niche of non-native species: the enemy release hypothesis (Colautti *et al.* 2004) and the evolution of increased competitive ability hypothesis (Blossey & Notzold 1995; Sakai *et al.* 2001), like adaptations, hybridization, polyploidisation. These two hypotheses could explain why species became invasive and how they obtain their competitive superiority.

Scale (grain) and realism have an important role to play in modelling the spread of the distribution of invasive species. It is important to distinguish spatial prediction of potential establishment and spatial prediction of invasion, namely invasibility (Welk 2004). Potential establishment might be assessed at coarse resolution through climate-matching models based on native and invaded range's characteristics (e.g. Thuiller *et al.* 2005). This engenders an overestimation of species distribution and it fails to describe spatial structure of invasion (Hulme 2003). On the contrary, spatial prediction of invasibility needs to incorporate two additional ecological factors, namely resources fluctuation and disturbance (Inderjit 2005). These additional processes can be incorporate in correlative static models in an implicit manner e.g. including land use, human population density and land cover map (Fairbanks *et al.* 2000) to identify transformed habitats that are likely to be invaded first or e.g. geology and soil properties for a measure of resources fluctuations (Hulme 2003). The resulting models are more informative and more realistic but costly and time consuming to apply to large area.

In case of invasive species, most available data are presence-only leading to use **profile or envelope techniques** (see Pearce & Boyce 2005 and Guisan & Zimmermann 2000 for reviews), e.g. Environmental Niche Factor Analyses (ENFA, Hirzel *et al.* 2002,

e.g. Hausser 1995, Appendix 1). Another way consists in generating a pseudo-absence data set e.g. selected randomly (Ferrier & Watson 1997; Zaniewski *et al.* 2002) or using the presence of one species as evidence for the absence of the target species (e.g. Guisan *et al.* 2005) allowing **discrimination techniques** (Guisan & Zimmermann 2000; Guisan & Thuiller 2005). The mostly used presence/absence techniques are Generalized Linear Models (GLM, McCullagh & Nelder 1989) or Generalized Additive Models (GAM, Hastie & Tibshirani 1986; Appendix 1). Despite the modelling method, unknown biases are often associated with non-systematic presence-only data depending upon factors like distance to villages, accessibility and type of environment (Zaniewski 2002). Thus, Guisan & Zimmerman (2000) suggested that an optimal field sampling consists in a stratified survey to ensure a representative sampling of the whole environmental conditions in the study area and limit bias on data. Such design is costly and time consuming but generates a presence/absence data set allowing discrimination techniques to be efficiently used and providing the most interpretable and meaningful results.

More accurate estimates of population size are invaluable data for monitoring and managing alien invasive species as e.g. when eradication is attempted (see Craze *et al.* 2002). Thompson & Seber (1996) suggested using an adaptive sampling to estimate species population size in the case of sparse but highly clustered species. Even when non-indigenous species are widespread and occur locally at high abundance, they frequently are sparse when considering a whole landscape (Rew *et al.* 2005). Adaptive sampling requires a reiterative sampling process, generating networks of clusters with higher abundance. Indeed, when a part of a population is sampled, all the population is included in the resulting network (Appendix 2).

Guisan *et al.* (in press) proposed a model-based sampling design aimed at improving the data needed to fit a species distribution model while, at the same time, enhancing the chance to observe the species in the field. The present study built on previous works done by Benetollo & Monico (2003) and Benetollo (2005) on *Heracleum mantegazzianum*, in the same study area. A fitted model resulting from these previous studies was available. Here we aimed at continuing this model-based sampling design, by

conducting a second field campaign and a third step of this reiteration design. An improvement of the predictive distribution model should be expected. In addition, we used this model-based approach, combined with an adaptive cluster design in the field, to estimate the total population size of the focal species in the study area. This design-based estimation was then compared with a model-based design estimation. The last aim of the current study was to use a predictive model for setting-up possible plans in conservation biology in all communes included in the study area.

METHODS

Study species

The giant hogweed, *Heracleum mantegazzianum* Sommier & Levier is a monocarpic perennial giant herb with a thick tap-root, a tall single annual stout stem (200-500 cm), large pinnate deciduous leaves (up to 250-300 cm) and several compound umbels up to 80 cm across (Tiley *et al.* 1996). This Apiacea reproduces exclusively by seeds and one plant is able to produce over 50 000 seeds (Tiley *et al.* 1996). In the study area, flowering occurs in July and august (Swiss Commission for Wild Plant Conservation, CPS/SKEW).

The giant hogweed is native from west Caucasus where it occurs in the upper forest belt of the southern slopes, in meadows, clearings and forest margins (Pysek & Pysek 1995; Mladenova 1950). Some seeds were transported to Switzerland (Geneva) in 1890 by Sommier & Levier. The species was first planted by Henry Correvon in Geneva (Sommier & Levier 1900; Jeanmonod 1999) permitting Sommier and Levier to describe it in 1985. Then, H. Correvon scattered the species in alpine botanical gardens (Appendix 3). It was cultivated there as well as in private property (e.g. Saline Bex), because of its spectacular inflorescence. Since then, it escaped repeatedly from gardens spreading along watercourses, roadsides also promoted by wind and human mediated dispersal (Tiley *et al.* 1996). In the study area, seeds of *H. mantegazzianum* were largely distributed to beekeeper in the region of Ollon and Bex (Figure 1) because it is suspected to produce large amount of nectar (pers. com. Michel Marie). Other human mediated dispersal occurs like soil and umbels transport, e.g. for use in flower arrangements (Tiley *et al.* 1996).

Three main reasons are retained to justify eradication efforts in whole Europe. **i)** The species represents a human health hazard. Physical contact with its sap sensibilizes the skin to ultraviolet radiation causing irritation, inflammatory reaction and blistering (Tiley *et al.* 1996). Unusual hyperpigmentation also occurs on the exposed areas, which can last for years. **ii)** Giant hogweed's early spring germination outcompetes indigenous plants which play an important role in riverbank stability (Giant-alien Project 2002-2005; Caffrey 1999). **iii)** Its above-ground vegetation dies back each autumn (Tiley *et al.* 1996),

exposing the soil to erosion and leading to economical problems. In addition, washed soil induces indirectly accumulation of fine soil and silt particles on river's substrate and affects potentially salmonid reproduction (Wade *et al.* 1997).

Study Area

The study area encompasses all the Prealps of the "Canton de Vaud" in Western Switzerland, covering a surface of 704 km^2 (Figure 1). In the South-Western edge, the area comprises a part of the Rhone Valley with the lowest elevation, 372 m a.s.l. High elevations occur throughout most of the study area, with the highest peak being the Diablerets Sommit at 3209 m a.s.l.

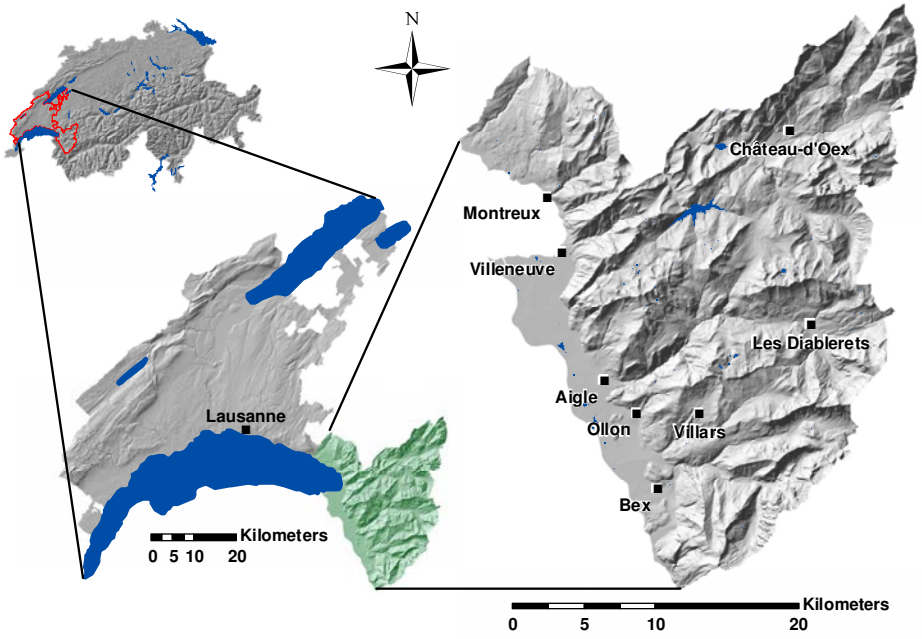

Figure 1: Situation of the study area: the Prealps of "Canton de Vaud" in Switzerland. Main localities are mentioned.

The calcareous Prealps are the first foothills of the Swiss Alps. Hence, they are subject to North Atlantic influences, bringing air loaded with humidity and precipitations (range from 1060 to 2400 mm per year). From south-east, continental influences ensure drier sunny conditions. Sun and rain alternate frequently. The average temperatures, elevation dependent, range between -3 and 10°C. Winter snowfalls are common and abundant (see Randin *et al.* in press).

Abundant wetness and radiations offer to *H. mantegazzianum* a suitable habitat. A good climate match with West Caucasus must be mentioned. Similarly with the study area, species native range is under influence of subtropical and continental climate with small daily temperature fluctuations, high air humidity, high solar radiation during summer and short vegetation period with annual rainfalls between 1000 and 2000mm leading to frequent snowfalls (Giant-alien Project 2002-2005; Pysek 1991; Ochsmann 1992; Mladenova 1950).

Environmental predictors

Thirteen quantitative environmental predictors (25 m resolution) including topographic, climatic, distances to rivers and to forest edges and vegetation productivity layers were used to build predictive models (Table 1). From the Digital Elevation Model *dem25*, provided by Swisstopo (Swiss Federal Office of Topography), topo-climatic variables (*precyy, sfroyy, sradyy, swb, taveyy, topo* and *twi25*) were calculated by N.E. Zimmermann at the WSL (Swiss Federal Institute for Forest, Snow and Landscape Research), following Zimmermann and Kienast (1999). The slope layer (*slp25)* and both quantitative distance predictors (*distriv* and *distlis*) were calculated with the ArcMap software (v.9 ESRI, Environmental Systems Research Institute 1992-99, Redlands, U.S.A) using respectively *dem25*, forests and rivers layers provided by Swisstopo. Two normalized difference vegetation index (NDVI) layers were derived following Rouse (1973) and Rouse *et al.* (1974) from Landsat TM, image from 10/2001 and 07/1999. The images were georeferenced in ArcMap.

Previous studies

In this study, we proposed to follow works of Benetollo & Monico (2003) and Benetollo (2005) where two different types of models (Appendix 1) were fitted on *H. mantegazzianum*, in the same study area. Firstly, an Ecological Niche Factor Analysis (ENFA, Hirzel *et al.* 2002) model was fitted at Swiss scale and at a 50m-resolution (ENFA 1 CH) with presence-only data initially available. On this latter model, focused on the Prealps of Canton de Vaud (ENFA 1), random sampling was conducted. The resulting presence/absence data set allowed fitting a Generalized Additive Model (GAM,

Hastie & Tibshirani 1986) at that regional scale, at a 25m-resolution. Hereafter, this GAM model will be referred to as GAM 2 because resulting from the second step of the reiteration design (Figure 2) proposed by Guisan *et al.* (in press).

GAM 2 obtained the best evaluation values compared to other models fitted respectively with a Generalized Linear Model (GLM, McCullagh & Nelder 1989) and an ENFA model. This model retained three predictors: slope (*slp25*), topographic position (*topo*) and distance to forest edges (*distils*) fitted with fourth order spline function.

Table 1: Quantitative environmental predictors selected for performing predictive models.

Abbreviation	Name	Unit	Source
dem25	Digital elevation model	[m]	swisstopo
precyy	Annual average of monthly mean precipitation sum (1961-1990)	[1/10mm/mth]	WSL
sfroyy	Annual average number of frost days during growing season	[day]*100	WSL
slp25	Slope	[deg]	calculated
sradyy	Annual average of daily average potential shortwave radiations per month	[KJ/day]	WSL
swb	Annual average site water balance accounting for soil properties	[1/mm/yr]	WSL
taveyy	Annual average of monthly average temperature (1961-1990)	[°C*100]	WSL
topo	Topographic position	unitless	WSL
twi25	Topographic wetness index	unitless	WSL
distriv	Distance to rivers	[m]	calculated
distlis	Distance to forest edges	[m]	calculated
ndvi1rectm	October normalized difference vegetation index	unitless	calculated
ndvi2rectm	July normalized difference vegetation index	unitless	calculated

Abbreviations, names, units and source of the environmental predictors used at a 25 m resolution. Swisstopo correspond to Swiss Federal Office of Topography; WSL means Swiss Federal Institute for Forest, Snow and Lanscape Research Institute and "calculated" are layers performed with ESRI (Environmental Systems Research Institute).

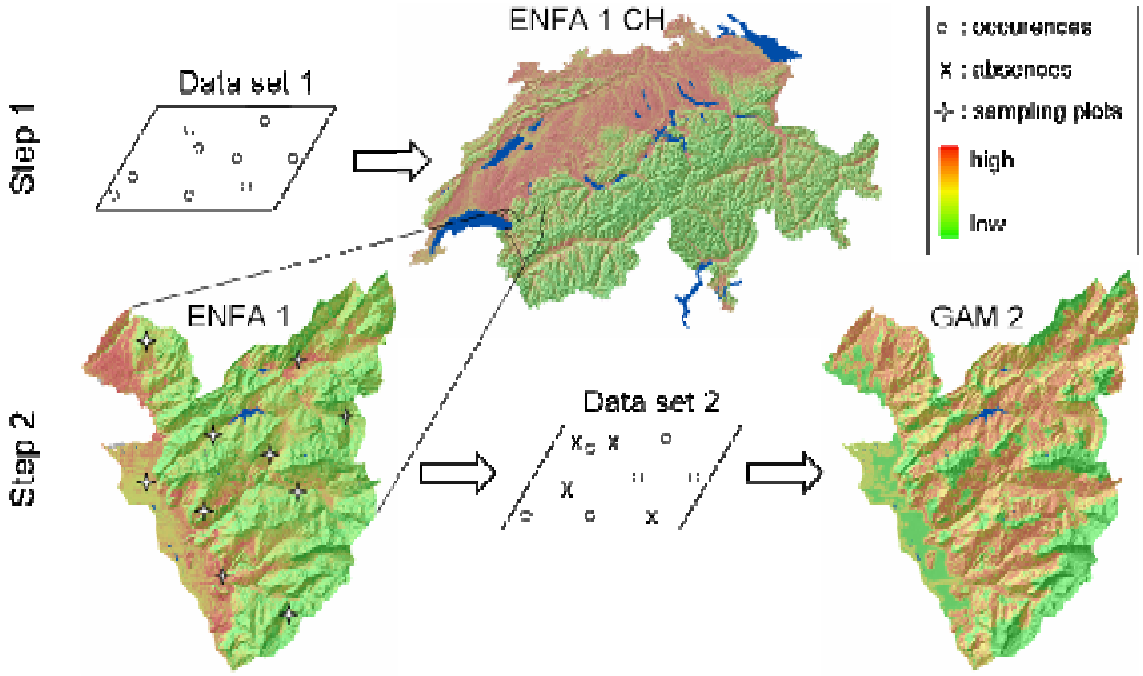

Figure 2: Reiteration design: Step 1 consisted in fitting an ENFA model at Swiss scale, at a 50 m resolution with presence-only data set initially available by CRSF database. Step 2 provided a presence-absence data set through a random-stratified sampling at regional scale based on the model fitted in step 1. This presence-absence data set allowed performing a GAM model at 25m-resolution in the Prealps of "Canton de Vaud". Colours represent establishment risks of *H. mantegazzianum.*

Cluster adaptive sampling

We conducted a random stratified adaptive sampling (Thompson & Seber 1996; Appendix 2) based on 10 strata corresponding to probability classes of GAM 2, an initial predictive model available for *H. mantegazzianum* (Benetollo 2005).

Hundred randomly defined sampling units (25 x 25 m) were visited in the entire study area i.e. 10 in each stratum. In each unit, we recorded the presence or absence of the target species, an estimation of abundance, fitness of the individuals through reproductive ability (number of flowering or fruiting plants) and sites' descriptions. The adaptive cluster design was applied to all sampling units. Additionally, non-stratified presence sites were also recorded when we encountered occurrences during the field work. For these latter, identical measures were preformed.

Additional data for modelling

Three available data sets were used to generate an additional absence data set for modelling.

- A set of 70 sampled sites was available from the **Ambrosia data set**. Random stratified adaptive sampling was performed in open areas especially at low and medium elevations (including Rhône Valley) during the same year and in the same area than the present study. The strata were defined by splitting a habitat suitability map for the invasive species *Ambrosia artemisiifolia* into 10 bins (see Appendix 4). The model was also based on an ENFA.
- Five hundred fifty exhaustive sampled sites in open areas from the lowest to the highest elevations were provided by the **MODIPLANT** database (ECOSPAT, Department of Ecology and Evolution, University of Lausanne). The MODIPLANT database was derived from a random stratified sampling in the same area but excluding the Rhône Valley, based on eight elevation strata, 4 slope strata and 4 aspect strata.

These two complementary data sets were joined and named **MODI-AMB**, covering the entire study area, including Rhône Valley.

- A set of 3074 forest plots were additionally available from the **PHYTO-VD** inventory, sampled systematically at each intersection of a grid covering the study area (every 400 m).

Predictive distribution models

Generalized Additive Models (GAM, Hastie and Tibshirani 1986) with a binomial probability distribution and logistic link function were performed using the SPLUS software (v. 2000, Mathsoft Inc., Seatle, WA, U.S.A). For each model, a weighting of the presence/absence was performed using the weight option and four degrees of freedom were allowed to determine the non-parametric smoothing spline function of the predictors.

Modelling framework

A first GAM model (**GAM 3.1**) considered only the unbiased presence/absence data resulting from random stratified sampling design (Figure 3).

A second GAM model (**GAM 3.2**) was fitted with the same presence/absence data used before but supplemented with non-random occurrences encountered during field survey. In order to limit spatial autocorrelation effects and respect independence data assumption for statistical models (Guisan & Thuiller 2005), we considered only occurrence sites distant of at least 150 m (Fischer 1994). However, an unknown sampling bias is associated with these additional occurrence sites (Zaniewski 2002). In these two models (GAM 3.1 & 3.2), the sampled data do not represent the whole study area proportionally.

A last GAM model was built by additionally considering a stratified-generated absence set, **GAM 3.3**. Generated absence sites were selected randomly from sites available in the AMB-MODI and PHYTO-VD data sets and stratified by the 10 strata of GAM 2 (see Cluster adaptive sampling). Three constrains were defined to generate this absence data set: i) already stratified absence sites used in the previous models were kept, ii) the total number of absences per strata is proportional to the surfaces' strata (Hirzel & Guisan 2002) and iii) the two data sets, MODI-AMB and PHYTO-VD, are equally represented in each strata of GAM 2. The second constrain takes sampling probability of absence sites into account according to the surface covered by the strata (Lehtonen and Pahkinen 2004). The third constrain limit bias due to two different data sampling design. Indeed, AMB-MODI represents open areas whereas PHYTO-VD represents forest habitats.

Invasive species could be maintained in unsuitable sites due to a source-sink dynamic (Pulliam 2000). Hence, we selected only naturalized occurrences to perform two additional models. The naturalized occurrences were combined either with presence/absence data resulting from random-stratified sampling (**GAM 3.4**) or with stratified-generated absence sites (**GAM 3.5**) (Figure 3). We defined three criteria to characterize naturalized populations. These must have: i) at least 30 individuals per 25 x 25 m square, ii) at least one adult plant (flowering or bearing seeds) and iii) no sites under

high human influences. These criteria are based on the definition of naturalized alien species (Richardson 2000; see Introduction).

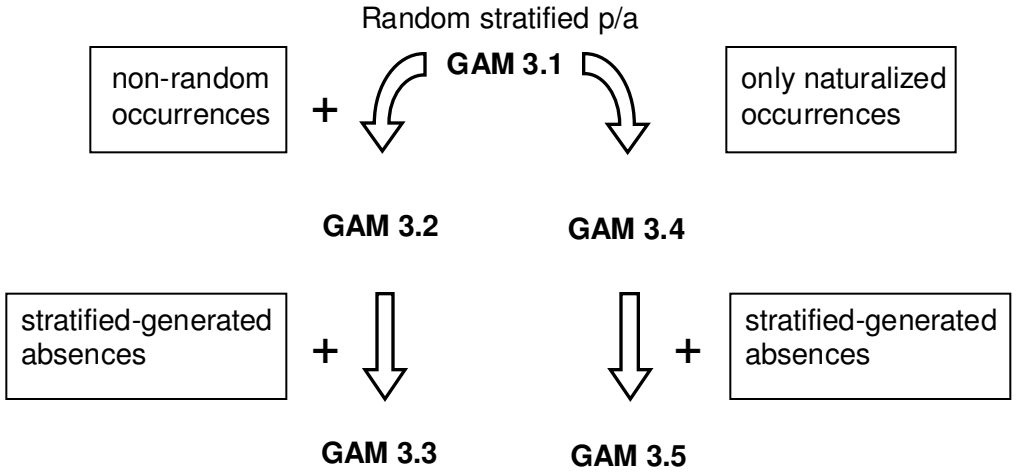

Figure 3: Modelling framework. Each Generalized Additive Models (GAM) was fitted with a different data set.

Model fitting

A stepwise procedure was used to select and incorporate in models only environmental predictors chosen according to the Akaike Information Criterion (AIC, Akaike 1973). Two main problems with stepwise procedures were underlined by Guisan *et al.* (2002) and therefore this technique implies a careful use. Small modifications of response data may lead to completely different predictor's subset. Moreover, two highly correlated predictors could both appear non-significant even though explaining individually a large part of data deviance. To avoid this collinearity problem, when correlation between two predictors was over rS=0.80 (Spearman rank correlation), only the predictor with the closest relationship with the focal species ecology is kept in the set of predictors. It consists in an expert choice step allowing a reduction of the predictor quantity. We characterized the fit of the models by examining the adjusted proportion of explained deviance (adj-D^2; ranging from 1 to 0; see Guisan & Zimmermann 2000).

Model evaluation

Our approach used the calibration data to evaluate, through a cross-validation procedure, the predictive power of the models (in Guisan & Zimmermann 2000), which has the advantage to allow using all available data to calibrate the model. The graphic ROC approach (Receiver Operating Chacarteristics plots; ROC-Plot; Fielding & Bell 1997) based on the relation of sensitivity to specificity offers a standard comparison technique between models. Sensitivity and specificity are defined as percentage of true positives correctly predicted, respectively, as the percentage of true negatives correctly predicted. From this method, the Area Under the Curve (AUC) can be derived, which ranges from 0.5 to 1. This measure is another way to express the model accuracy. AUC partitions measures were also obtained through cross-validation (CV) by separating data into 10-fold CV random partitions (CV-AUC evaluation value). The cross-validation process takes outliers' effects on models into account by generating pseudo-independent data partitions. All these evaluation measures were calculated in the SPLUSS software, using the ECOSPAT library functions (C. Randin and A. Guisan).

Spatial predictions

The potential distribution maps were generated from models using 'predict' function available in SPLUSS software and adapted for GAM models by C. Randin. The resulting maps indicate the probability of species occurrences in each 25 x 25 m plot of the study area.

Qualitative variables corresponding to *lakes*, *glaciers* and *rocks* were used afterwards to filter the prediction maps and improve model predictions (Guisan *et al.* in press). These three layers were provided by Swisstopo and represent unsuitable habitats for *H. mantegazzianum.*

In case of model-based estimation (see Density estimation), built-up area and intensive agricultural lowlands, where the giant hogweed might not become established in monospecific stands were also used as a filtered to make estimations more realistic. These two layers were also provided by Swisstopo.

Finally, probabilistic maps were transformed into presence-absence binary maps to distinguish suitable from unsuitable habitats for applications in conservation. The chosen threshold value used here corresponds to the intersection of the sensitivity and specificity curves that optimised the ratio of omission (false negative) and commission (false positive) errors (Fielding & Bell 1997).

Density estimation

Two different conceptual approaches were compared to estimate *H. mantegazzianum* total population size in the study area: a **design-based** and a **model-based estimation**. The first approach provided the actual population density estimation (Thompson & Seber 1996) whereas the second provided the future potential population density estimation in case of full invasion of the study area, i.e. species reaching its equilibrium in distribution.

The first estimation was based on the stratified adaptive sampling conducted during the field work and suggested by Thompson & Seber (1996). This sampling strategy is appropriate to estimate the actual total population size of sparse but highly clustered species, like *H. mantegazzianum*. Indeed, the giant hogweed is able to form monospecific stands in habitat reached by seed dispersal (Tiley *et al.* 1996). The mathematical calculations (Appendix 2) weight networks abundance estimations with the intersection probability of a clustered population with the set of random sites defined by the sampling design. The fact that a cluster might also overlay on two or more different strata was also taken into account.

The second approach was based on models performed and filtered after the field work. This latter estimation was largely dependent on the accuracy of the predictive model. It consisted in estimating the total population size of *H. mantegazzianum* in a study area where the species would be naturalized in each site according to the site invasion probability. The probability map was multiplied by the mean number of individuals found in naturalized squares 25 x 25 m. The resulting map ranged between 0 and this latter average. Finally, all the model values were cumulated and the total estimation corresponds to the sum of all the pixels of the study area.

Conservation biology applications

In a conservation context, we used a filtered potential distribution map (GAM 3.3) as a tool for setting-up possible conservation plans. The 25 communes located in the study area were set as management units and evaluated individually. For this part, we disposed of 25 additionally occurrences, not used before because their location was not enough precise. All occurrences resulting from adaptive sampling were also used.

We proposed to calculate, for each management unit, an **invasion status ratio** defined as the ratio of the number of recorded occurrences during field sampling to the total suitable surface (in square kilometres, km^2) predicted by a presence/absence binary map (see Spatial predictions). This ratio, potentially ranging from 0 to 1600, represented a measure of invasion status in each management unit. The maximum value of this ratio corresponds to the factor, which transform a number of pixel into a surface measure in square kilometres. Finally, this binary model permitted to underline which commune should receive special attention for eradication.

A minimum overall management **cost** for removing giant hogweeds from infested sites was calculated based on an estimation provided by Sampson (1994) and Hulme (2003), in the UK. A total of US$ 1'500 ha^{-1} was needed to eradicate the species but this estimation included only material and for a period of two years. In Swiss Francs it corresponds to 120 CHF per plot of 25 x 25 m. All recorded occurrences encountered during the field sampling were multiplied by the mean cost estimation to obtain a present minimum estimation cost. For the future potential cost in a hypothetically completely invaded area, the probability map was multiplied by the estimation value of costs for a square of 25 x 25 m and the pixel values were cumulated.

RESULTS

Field sampling

H. mantegazzianum was found in 6 out of the 100 random-stratified sites visited. Resulting networks were composed of 4 to 24 squares of 25 x 25 m. Abundances ranged from 1 to 355 individuals in the same square. In total, 188 absence sites and 61 occurrence sites were visited, totalizing 4'232 individuals.

In total, 93 occurrence sites (Figure 4) were including during the field work, non-random ones. The altitudinal distribution of giant hogweed ranged between 373 and 1967m a.s.l. These occurrences were found in different types of habitat, like sides of rivers, roads and railways, forest edges and clearings, meadows, dumps and gardens. More than 40% of all occurrences were situated near rivers (at 25 m distance). Three of them were located near the botanical garden of Pont de Nant above Bex (still active) and around ancient botanical gardens (see Appendix 3). Most populations were found in Villards-sur-Ollon and in Les Diablerets. Several large populations were also established in the region of Lac de l'Hongrin, in Nermont above Montreux and in the Rhône Valley on Rhône side in Yvorne.

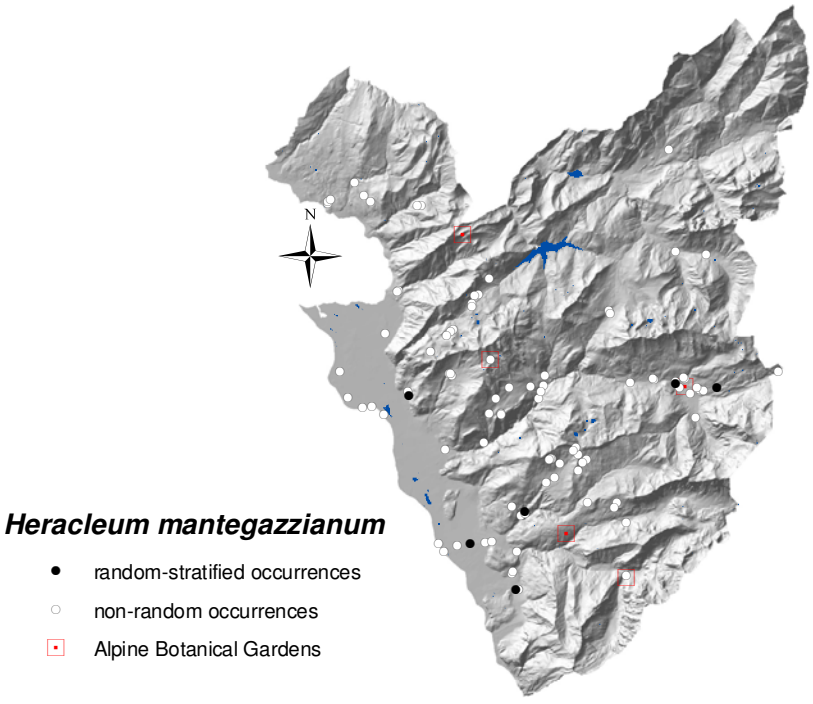

Figure 4: Random-stratified occurrences (black) and non-random occurrences (white) encountered during field work. Locations of different Alpine Botanical Garden are mentioned.

Predictive distribution models

Correlation values between environmental predictors were calculated (Appendix 5) showing that three predictors were highly correlated each other. Among three predictors (digital elevation model, *dem25*, temperature, *taveyy* and precipitations, *precyy*), we decided to use only precipitation (*precyy*) to fit the models.

The random-stratified sampling did not provide a sufficient number of occurrences to fit an acceptable potential predictive GAM model. All performed GAM retained a different subset of predictors. Slope was often selected as well as the two NDVI layers. Species response curves to predictors were quite constant except for NDVI indices which response curves were quite different depending on the data set used (Appendix 6). Proportion of explained deviance and evaluation values are summarized in Table 2. Potential distribution maps resulting from performed GAM models are represented in Appendix 7.

Table 2: Data, degree of freedom, proportion of explaining deviance and evaluation values (AUC and cv-AUC) of the five GAM models. The number of occurrences (occ.) and absences (abs.) and the number of degree of freedom (df) were different for fitting each model. Adj-D2 is the adjusted proportion of explained deviance; AUC is the Area Under the Curve derived with Receiver Operating Characteristics plots, ROC; cv-AUC is the AUC value obtained through 10-fold random partitions cross-validation. Ranges of different value are mentioned.

	occ.	**abs.**	**df**	**adj-D^2** [0; 1]	**AUC** [0.5; 1]	**cv-AUC** [0.5; 1]
GAM 3.1	13	181	2.8	0.331	0.788	0.722
GAM 3.2	90	181	5.7	0.175	0.766	0.741
GAM 3.3	90	600	14.3	0.318	0.853	0.778
GAM 3.4	53	181	5.7	0.172	0.752	0.671
GAM 3.5	53	600	11.7	0.309	0.846	0.746

GAM 3.1: The GAM based on the unbiased stratified data retained a unique predictor, annual average number of frost days during growing season (*sfroyy*). Response curve suggested that the target species prefers low values corresponding to low and medium elevation zones. The highest errors were obtained in high elevation values (Appendix 7). Evaluation with the ROC approach gave an AUC value of 0.78 and the AUC cross-validation value (cv-AUC) was calculated at 0.72. This model explained 33%

of the total deviance. The few number of stratified occurrence sites were not sufficient to create a satisfactory predictive model through AIC-stepwise selection.

GAM 3.2: This model, built with all occurrences encountered during field work, retained two different predictors, slope and the July NDVI layer. Response curves suggested optimal values for *H. mantegazzianum* on gentle slopes and high productivity sites. Highest error values were associated with high elevations corresponding to steep slopes and low productivity values (Appendix 7). AUC and cv-AUC were respectively of 0.76 and 0.74. The proportion of explained deviance was relatively low, with a value of 17%.

GAM 3.3: The model fitted with the 600 stratified absences retained five predictors: slope, solar radiation, distance to rivers and to forest edges and July's NDVI layer. Species occurrences were observed in gentle slopes with high solar radiations at low distances to rivers and forest edges and high productivity values (Appendix 7). The shape of the July's NDVI response curve was clearly unimodal compared with that of GAM 3.2. Oppositely the response curve for slope did not change. High errors in predictor curves were associated with very mountainous relief on steep slopes, on Northern exposure with low solar radiations, at high distances to rivers and forests and with low productivity values. This model obtained the best evaluation values. AUC and cv-AUC values were respectively of 0.85 and 0.77. The proportion of explained deviance was 31.8%.

GAM 3.4: The naturalized occurrences considered in GAM 3.4 obtained quite similar results as GAM 3.2. Slope was retained again, but NDVI layer of October was selected instead of that of July. Considerations about species optimal values were identical as for GAM 3.2. Errors were again associated with high elevations but also with high productivity values for October's NDVI (Appendix 7). Evaluations were quite similar to those of GAM 3.2, with value of 0.75 for AUC and 0.67 for cv-AUC. The model equally explained 17% of the total deviance.

GAM 3.5: The last model selected slope, solar radiation, distance to rivers and October's NDVI layer as predictors. Considerations concerning species' biology and errors along predictor response curves were the same as for GAM 3.3. The shapes of predictor response curves were similar to those obtained for GAM 3.3. Compared with GAM 3.4, the shape of the NDVI layer was significantly different. This model obtained similar evaluation values to GAM 3.3. AUC and cv-AUC values were of 0.84 and 0.74 respectively. The model explained 30.9% of the total deviance.

Correlation value between GAM 2 and selected model resulting by the new sampling year (GAM 3.3) is equal to 38%.

Density estimation

The design-based approach suggested by Thompson & Seber (1996) yielded an estimation of:

$$\hat{u}_{st} \cdot N = 3'316'215$$

with a variance of 8.6% corresponding to 287'341 individuals. *N* is defined as the number of pixels (squares of 25 x 25 m) in the study area.

The mean number of individuals in naturalized sites was 162 individuals in a surface of 25 square meters. In a hypothetic completely invaded study area, where each plot of 25 x 25 m would be naturalized, the estimation provides a total maximum number of individuals of:

$$162 \cdot N = 182'536'254$$

Thus, the design-based estimation corresponds here to 1.8% of the complete invasion.

We used the same mean number of individuals to calculate the model-based estimate. Using the fitted binomial GAM models, the predicted numbers of individuals in each square of 25 x 25 m were cumulated to yield the following results estimates (Table 3).

Table 3: Model-based estimation of total population size of *H. mantegazzianum* in case of a complete invasion scenario according to the invasion probability of each model. The value of the total population size (Pop. size) for each model is mentioned. The corresponding proportion (percent.) was obtained in calculating the ratio of the population size of each model to the total maximum number of individuals.

Model	Pop. size	Percent.
GAM 3.1	36'915'061	20.2%
GAM 3.2	57'977'265	31.8%
GAM 3.3	47'106'368	25.8%
GAM 3.4	62'098'374	34.0%
GAM 3.5	52'270'119	28.6%

Estimation values ranged from 36 to 62 mio of individuals with an average value at about 50 mio individuals corresponding to 25-30 % of a complete invasion of the study area. This value represented a study area where the species would be naturalized in each pixel, according to the invasion probability.

Conservation biology applications

The 25 communes, set as management units, were compared with surface (square kilometres and percentage compared to the whole area surface) and suitable surface for *H. mantegazzianum* (square kilometres and percentage compared to corresponding commune's surface) obtained from selected model (GAM 3.3) transformed in a binary map (Appendix 8) using the threshold optimising ratio of sensitivity to specificity (Appendix 9). We also inventoried number of occurrences in each management unit and derived invasive status ratio and minimum cost estimation (Table 4), respectively ranged from 0 to 5.47 and from 0 to 5'760 Swiss Francs for the most invaded communes, namely Rennaz concerning invasive status ratio and Ollon for the highest removing cost. The overall cost estimate for removing invasive plants varied greatly between communes but in general they provide very high values.

Table 4: Assessment of the present and potential invasion of *H. mantegazzianum* for all communes, set as management units in the study area and derived cost estimations.

Communes	Surface (%)	Surface (km^2)	Occurrences	Suitable surface (%)	Suitable surface (km^2)	Cost (CHF)	Overall cost estimation (CHF)	Invasive status ratio
Château-d'Oex	16.2%	113.9	3	22.5%	25.6	360	4'912'320	0.12
Bex	13.7%	96.7	19	11.9%	11.5	2'280	2'210'520	1.65
Ormont-Dessous	9.1%	63.9	10	34.5%	22.0	1200	4'230'000	0.45
Ormont-Dessus	8.7%	61.6	44	27.4%	16.9	5'280	3'237'240	2.61
Ollon	8.5%	59.6	48	28.7%	17.1	5'760	3'279'000	2.81
Rougemont	6.9%	48.6	0	27.8%	13.5	0	2'594'640	0
Montreux	4.8%	33.5	7	18.2%	6.1	840	1'172'520	1.15
Villeneuve	4.6%	32.1	6	13.5%	4.3	720	830'760	1.39
Rossinière	3.3%	23.3	0	12.3%	2.9	0	550'560	0
Corbeyrier	3.1%	21.9	10	23.1%	5.1	1'200	971'280	1.98
Leysin	2.6%	18.5	7	20.2%	3.7	840	716'880	1.87
Aigle	2.4%	16.6	5	19.9%	3.3	600	633'960	1.51
Blonay	2.3%	16.1	3	29.2%	4.7	360	901'800	0.64
Saint-Légier-La Chiésaz	2.1%	15.1	0	31.2%	4.7	0	906'480	0
Gryon	2.1%	15.1	3	34.0%	5.1	360	984'000	0.59
Lavey-Morcles	2.0%	14.2	0	6.2%	0.9	0	168'000	0
Yvorne	1.7%	12.3	13	20.1%	2.5	1'560	474'120	5.26
Noville	1.5%	10.4	0	56.8%	5.9	0	1'136'520	0
Corsier-sur-Vevey	1.0%	6.8	0	20.2%	1.4	0	263'520	0
Veytaux	0.9%	6.7	0	3.3%	0.2	0	42'600	0
Roche	0.9%	6.5	0	10.4%	0.7	0	129'480	0
Chessel	0.5%	3.5	2	31.2%	1.1	240	211'560	1.82
La-Tour-de-Peilz	0.5%	3.2	2	13.9%	0.5	240	86520	4.44
Vevey	0.3%	2.4	0	3.3%	0.1	0	14880	0
Rennaz	0.3%	2.2	2	16.7%	0.4	240	70200	5.47
Total		**704.7**	**184**		**160.0**	**22'080**	**30'729'360**	

Commune's surface (proportion, %, and square kilometres, km^2) were compared with suitable establishment surface (% and km^2) derived form giant hogweed binary GAM 3.3 model. Recorded occurrences were counted and an invasive status ratio was calculated. Invasive ratio corresponds to the ratio of the number of occurrences to the suitable surface (km^2) in each management unit. Present and future potential cost estimations were also calculated for each commune.

DISCUSSION

Several studies revealed the invasive spreading behaviour of the giant hogweed (*Heracleum mantegazzianum*) in Europe and North America (Tiley 1996, Giant-alien Project 2002-2005, see Appendix 10). In Switzerland, the species is known to be widely spread especially in the lowland (CPS/SKEW) but it is also present in Swiss Alps along mountain passes (Becker *et al.* 2005). In this study, we underlined the numerous infested sites found in the study area and modelled the spatial distribution of the species which was clearly related with localities where the giant hogweed has been first introduced (Jeanmonod 1999, Figure 4). The model-based sampling did not provide as much occurrences as expected. Then, several Generalized Additive Models (GAM) were performed using different data sets and one of them was chosen because obtaining the best evaluation values. We proposed also to calculate the population density of this invasive plant in the whole area and a method to evaluate individually management units concerning invasion and thus, its implications. In this perspective, we attempted to optimise a model for wildlife managers. The current study raised several relevant aspects for sampling and modelling invasive species.

Field sampling

During the field work, we verified all occurrence sites already known concerning *H. mantegazzianum* in the study area. We pointed out several identification errors. Ochsmann (1996) demonstrated that morphological characters used for species identification are highly variable, in the case of *Heracleum*. Moreover, the giant hogweed is very similar to another related indigenous and widely distributed hogweed namely *H. sphondylium* L. Therefore, hybrids between these two species are not unusual, and have been observed several times in locations where they occur simultaneously (Grace & Nelson 1981, Arora *et al.* 1982, Ochsmann 1996) making determinations more difficult. Some characters are powerful to distinguish these two species (Appendix 11). In our case, these considerations could explain the low correlation value between the model already available (GAM 2), on which sampling was built, and which selected (GAM 3.3).

Thus, we would expect improvement in predictive capacity of the models by improving the quality of the data.

In our sampling framework, the model-based sampling was not efficient. During the first sampling year, in 2004, 7 occurrences were provided from stratified sampling and we expected, with a new reiteration model-based sampling, to enhance the chance finding new populations. We found only 6 presences. Determination errors should have introduced bias in the model and its strata failing to describe species ecology. The low prevalence of invasive patchy species in a large landscape might also explain our results and should be reverse with an increasing colonisation time, leading to an increase in prediction precision.

Response variable

Binomial models were best performed in this study because, in case of invasive species, abundance is not necessary correlated with the site's characteristics. The abundance is closely linked to the colonisation time and the connectivity with a seed source upstream, in case of the giant hogweed. Indeed, Pysek & Pysek (1995) underlined that dispersal possibilities were the only significant factor affecting the magnitude of infestation, i.e. large stands were only formed if there was a good possibility of seed spread. Yet, abundance was also measured using an adaptive cluster sampling design to estimate population size.

We also used naturalized populations (see Introduction, Richardson *et al.* 2000) of giant hogweed because the focal species has the ability to postpone flowering if the site conditions are unsuitable (Giant-alien Project 2002-2005). An individual might also maintain itself in a microhabitat which was not revealed at our 25 m resolution. These latter considerations and the fact that we often recorded few individuals in occurrence sites justified using naturalized populations for modelling this alien invasive species, in accordance with Pulliam's (2000) source-sink theory.

Factors explaining the distribution of *H. mantegazzianum*

Several relevant species' ecology features emerged from predictor response curves. The most often retained predictors in the models were slope and one of the NDVI layers.

Firstly, slope (***slp25***) was retained in all models except GAM 3.1. This is an obvious variable underlying mechanical pressures on landscape, like e.g. erosion, accumulation of organic material, water and snow. *H. mantegazzianum* prefers deep (tap-root of 45-60cm) and rich soils, where moisture is maintained throughout the year (Tiley *et al.* 1996). These conditions are mainly found on gentle slopes, where accumulation of water and nutriments occur. Hence, it might be very useful to dispose of a more precise soil layers for this species. Under conditions of high mechanical load in winter time caused by snow accumulation, shrubs and trees are harmed and can hardly survive (Giant-alien Project 2002-2005). On contrary, the above-ground part of the giant hogweed's plant dies back each autumn and, in this way, snow accumulation could eliminate or decrease potential competition. Moreover, flowing water slows down with gentle slope values and seeds are able to reach the banks.

In each model, at least one NDVI layers (***ndvi1rectm*** & ***ndvi2rectm***) is retained, except for GAM 3.1. *H. mantegazzianum* occurs preferentially in productive habitats represented by large leave's plants. October's NDVI layer was always associated with the models considering the naturalized populations. At that period, seeds are already matures but younger plants may still grow. October productivity might allow longer accessibility to nutriments and a faster development into monospecific stands, characterizing naturalized populations. July's NDVI layers might evaluate the larger potential extent of invasion. An early spring NDVI layer could be very informative because the focal species germinates during this period but such satellite image was not available.

The solar radiations predictor (***sradyy***) was retained two times in models supplemented with additional absence (GAM 3.3 & GAM 3.5). These results matched the conditions in the native habitat of the species, Southern slopes, and in the native range, where radiations are high in summer. To overcome the quite shady habitats along rivers and forest edges (Tiley *et al.* 1996), the giant hogweed might need a high amount of radiations.

Rivers proximity (***distriv***) gave evidences of colonisation processes of *H. mantegazzianum*. Especially in mountains, linear habitats like water courses usually contribute to easier spread of invasive species through the landscape (Pysek & Prach 1994) and provide a good connectivity to a seed source located upstream, knowing that

first introductions happened at high and medium elevations (Figure 4). River banks are also very disturbed (destructive flooding) and sensible environment favourable to invasion, especially in plain where human pressure is greater in the study area. Nevertheless, the species might also tolerate other conditions and habitats. Actually, the predictor curve (Appendix 6) revealed that some populations were found up to 1000 m distance from a river. Riverbanks provide suitable habitats and nutriment conditions for seedling establishment and allowing subsequent colonisation (Pysek 1994).

According to the response curve (Appendix 6), most populations were found at a distance inferior to 300 m from a forest edge (***distlis***). In the native range, forest edges or glades are suitable habitats for the focal species. The reason might be that such transition environments are highly subjected to disturbance. This variable was only retained in the third model (GAM 3.3).

NDVI layers are variables describing implicitly resource fluctuations and distance to rivers and forest edges provide a kind of disturbance measure, allowing, when incorporated in models, to predict invasibility of *H. mantegazzianum* (Hulme 2003).

Can we model the distribution of *H. mantegazzianum*?

In our modelling framework, the model-based sampling proposed by Guisan *et al.* (in press) did not provide a sufficient number of occurrences to fit an acceptable potential predictive model (of a GAM type) in the study area after two sampling years. The first model with stratified presence-absence (GAM 3.1), retaining only number of frost days, may not be reliable according to occurrences encountered during field work and the fact that species niche could hardly be completely determined by a unique variable. For *H. mantegazzianum*, seeds' breaking of dormancy requires chilling (Tiley *et al.* 1996), but this latter might not explain why the variable number of frost days (*sfroyy*) was retained in this model, considering that we recorded additional occurrences ranging almost along the whole elevation gradient of the study area.

The second and the fourth models (GAM 3.2 and GAM 3.4), retaining only a topographic variable and a NDVI layer, were not persuasive enough because these two models obtained very low adjusted explained deviance values (adj-D^2). Thus, these two predictors might not be enough to predict the potential distribution of the focal species.

The model with all available presences supplemented by absence-generated data set (GAM 3.3) obtained the best evaluation values and retained predictors that seemed to be coherent with species ecology. Constancy in predictor selection was observed among this model and the fifth model (GAM 3.3 and GAM 3.5). Only forest edges distance was retained in addition in the third model (GAM 3.3) and it is important because such variable describes a native habitat of the focal species (Tiley *et al.* 1996). In naturalized populations, distance to river could be more relevant than forest edges because the proximity to a seed source could explain the magnitude of infestation in case of the giant hogweed (Pysek & Pysek 1995). It might explain why distance to rivers was retained instead of forest edges distance in the last model (GAM 3.5).

In general, results obtained with naturalized population demonstrate that predictor choice was not drastically different and seemed to be consistent. However, the supplemented generated-absence data set allowed fitting differently the response curves especially of NDVI layers (Appendix 6). In mountainous regions, environmental climatic conditions can change rapidly with the complex and heterogeneous gradients, like topography. Therefore, the absence data set additionally generated was also useful to sample all environmental conditions in some very large strata of the model used for sampling (GAM 2). Thus, the generated-absence data set sampled a larger number of environmental conditions compared with stratified absences resulting from two sampling years. A last advantageous of this additional large data set concerned setting weights clearly smaller for absences than those for presences, due to the presence/absence weighted. This is important in case of invasive species (non-equilibrium theory) to limit effect of false negatives on model calibration.

For further investigations in conservation applications, we choose the model fitted with all absences and the additionally absence-generated data set (GAM 3.3) to setting-up some conservation considerations concerning communes' status of invasion, because it showed the best evaluation. The value of adjusted explained deviance (adj-D^2) was not very high but it may be explained by the non-equilibrium theory, in the case of invasive species. For such species, a model can hardly discriminate among suitable and unsuitable absence sites leading to a large amount of unexplained deviance (residual deviance). This model used 14.7 degrees of freedom. The AIC criterion should limit overfitting effect in

taking number of parameters (predictors) and the number freedom degrees, used to fit each variable response curve, into account (Harrel 1996).

Comparison at the Swiss and regional scales

At the Swiss scale and at the resolution of the study area, ecology of *H. mantegazzianum* was found relatively similar in both models. At both resolutions, 92 and 90 presences were respectively available but the modelling method was different. In the Ecological Niche Factor Analyses model fit at the Swiss scale (ENFA 1), *H. mantegazzianum* preferred habitats near building and rivers, with weak slopes, high solar radiation, concave topographic position and near forest edges (Benetollo 2005). Except topographic position and distance to buildings, which were not taken into account in the current study, GAM 3.3 retained the predictors which obtained the highest scores in ENFA 1. Hence, the factors explaining species distribution appear similar at local and at coarse scales.

Density estimation

The **design-based estimation** proposed by Thompson & Seber (1996) provided the estimation of the actual population size of *H. mantegazzianum* in the study area. The design-based estimation is a non-biased approach directly based on the sampling. This sampling was stratified according to strata of a previous model (GAM 2; Benetollo 2005), which yielded an estimate of 3.3 mio of individuals in the Prealps of Canton Vaud. This value corresponded to 1.8% of a complete invasion scenario, obtained with the mean number of individuals in naturalized squares of 25 x 25m (162 individuals). Note that the mean density we found is very similar to the estimate of Wadsworth *et al.* (2000) in the same surface (156 individuals). The large strata, with low probability, might have more influence on the total estimation but here no occurrences were found in the larger strata. This method has also the advantage to be based on observed species data and to use them to weight the importance of strata (Thompson & Seber 1996).

Oppositely, the **model-based estimation** is largely dependent on the models' accuracy. Biases in the sampling or initial inappropriate variable choice might conduct to imprecision in the models and subsequently, biases in estimation. Indeed, absence of an

important predictor and failing in describing interactions between retained predictors might reduce precision in the total population size in case of a complete invasion scenario. This estimate was obtained by cumulating predicted number of individuals in each square of 25 x 25 m across the study area, by postulating that the species is in equilibrium with the environment. The dispersal limitation hypothesis (Pulliam 2000) renders this total estimation unrealistic because the species might not reach some parts of the study area, due to its limited dispersal capacity. The average value of all these estimates was around 50 mio individuals in a scenario of complete invasion of the study area, corresponding to 25-30 % of the whole surface area. These results have to be used with care, but nevertheless it strongly suggests that the species might still continue its expansion phase.

Conservation biology applications

If the aim of a management plan is to eradicate an alien invasive species, it is important to map its distribution and to identify regions with the highest invasion risks. To simplify decision making of wildlife managers, we decided to select a threshold to transform a probability map into a 0/1 binary map to optimise potential distribution models and simplifying their applicability. The chosen threshold, which optimised the ratio of omission (false negative) to commission (false positive) errors, must be carefully used for a conservation purpose. For management, false negative may lead to assign low priorities to regions with high risk of invasion (Robertson *et al.* 2004). In this case, the species will be detected too late, once it is well established, thus increasing management costs. To minimise this risk, the threshold might be chosen at very low values. On the other hand, by reducing the threshold value, we increase the surface where the species could potentially establish. Considering the amplitude of the task compared with the few involved managers, large extent of the area could remained unmanaged. This leads to a trade-off between increasing the predicted area and minimising the rate of omission errors.

Hereafter, we only discuss the invasive potential of some communes. The calculated "invasive status ratio", defined as the ratio of number of occurrences to focal species' suitable surface, appeared to be helpful in assessing individually invasion of

these management units. Château-d'Oex is the largest commune in the study area, but only few populations of giant hogweed were found there. Thus, the value of invasive status ratio for this unit is very low (0.1) and it might be explained by the intense agricultural activity occurring there and its relative isolation from introduction locations (Figure 4). The model suggested a high suitable surface for invasion, which have to be inspected. It is important to avoid some human-mediated long dispersal events to preserve this valley from invasion. Two communes, Ormont-Dessus and Ollon have similar results for their invasion status ratio. Actually, most populations were found in these two management units. A large part of their surface might be prone to invasion in the following years if nothing is done. Invasion processes might occur downstream from Ormont-Dessus to Ormont-Dessous and Aigle where suitable habitats seem to be present. Noville showed very suitable habitats for the species with more than half of its surface being predicted as prone to invasion. In this commune, the natural reserve "Les Grangettes" must be particularly preserved from invasion by giant hogweed, which was already observed in bogs and moist grassland (Pysek & Pysek 1998). Rennaz, Tour-de-Peilz and Yvorne had the highest invasive status ratio. For the first two communes, the high ratio should be explained by their low surfaces. In the case of Yvorne, the restricted surface and the numerous populations observed along the Rhône River require rapid conservation action.

The management cost of removing the species, we provide here, is probably a rough estimate of the real cost. However, our modelling analyses suggest that a large number of sites in the study area should be prone to future invasion. The magnitude of the invasion might probably reach 10 times the current state. Considering the discrepancy between actual costs to eradicate the species at present time and the potential costs in the case of a complete invasion in the future, we aim here to make local authorities aware of this increasing problem. In this respect, we believe that our analysis provides a direct and useful tool for monitoring and eradicating this noxious plant.

General considerations

The climate match between the study area and the native range, the high human-mediated dispersal through botanic or private gardens and the inexistent conservation

measures for removing giant hogweed populations might provide suitable conditions for this alien invasive species expected to continue its colonisation process. Two more considerations might also suggest the expansion phase of *H. mantegazzianum* in the study area. First of all, *H. mantegazzianum* is originally a mountain species (Pysek 1994). Giant hogweed's early flowering and fruiting phases ensures that it can survive a short vegetation period (Tiley *et al.* 1996), which is an advantageous trait for colonizing alpine habitats. According to Pysek *et al.* (1998), in high elevations, dispersal limitation probably occurs due to low human population density despite high habitat suitability. In Villars, a large population was observed in the upper forest belt illustrating the native habitat of the species in the Western Caucasus (Tiley *et al.* 1996). However, we recorded occurrence sites as well in the Rhône Valley (372 m a.s.l.) and at high elevations, but few populations were found above 1500 m a.s.l. The second consideration concerns the low affinity of *H. mantegazzianum* with riparian habitat, with only 10 % of occurrences found near rivers in the Czech Republic, where its spread had been well documented (Pysek 1994). Oppositely, in the study area, more than 40 % of the encountered occurrences were observed along river banks (at maximum 25 m distance). Our models thus suggest that rivers play an important role in predicting the species potential distribution in the Prealps of Canton de Vaud. Actually, for this species, Pysek and Prach (1993) pointed out that, in the Czech Republic, a period during spreading phase was considerably supported by rivers, restricting its distribution to this type of habitat. This should suggest a subsequent spread into the landscape of the study area, favoured by its competitive ability. Roads and railways serve as other alternative colonisation routes (Pysek & Prach 1993, Schmidt 1989).

In Switzerland, roads maintenance is frequent and might reduce spreading capacity of the focal species in mowing regularly this plant and reducing its seed production, but it did not lead to a long term control (Appendix 11). The Swiss mountainous area is intensively used in open areas by agriculture exploitation. Pasturing and mowing are especially frequent in the study area and giant hogweed is frequently grazed (Appendix 11). These considerations may considerably limit spreading of *H. mantegazzianum* and thus, confining suitable sites to riparian habitats. More field work to document its distribution would be necessary to answer this question.

CONCLUSION

H. mantegazzianum was observed in numerous sites and management units in the Western part of the Swiss Alps. Its expansion phase and the high surface predicted to be prone to invasion in the study area might suggest further ecological and health hazards induced by this alien invasive plant. Unpredictable human-mediated dispersal needs to be seriously avoided in drawing attention of people on such a problematic attractive weed. In the case of invasive species, potential predictive GAM models might be powerful for coordinating some eradication plan undertaken by communes. The chosen model should be used for assessing invasion risks in the study area and precision of such model needs to be enhanced iteratively allowing proper prediction and monitory of the spread of this invasive plant. Our aim was to map the potential distribution of *H. mantegazzianum* and to estimate population size and costs for removing of the focal species. The current study found convergent results concerning current and future density and cost estimations.

PERSPECTIVES

The communes will be informed of the results of the current work. In further studies, an adaptive sampling based on strata of the new model may be conduct again, enhancing chances to sampling unknown populations. A new sampling year should also provide more information on species' present distribution. For this latter, remote sensing through aerial photographs might be a useful tool for detecting new populations (Mullerova 2005) although restricted to open area because forests prevent detection. Dynamic models would be also able to simulate future colonisation scenario to assess the time needed to invade the whole area. A preliminary study of the plastid DNA variation in some populations of *H. mantegazzianum* was done (Appendix 12) revealing numerous variations. Genetics analyses should allow studying interesting evolutionary processes on population dynamic of the giant hogweed during its colonisation phase and underlining number of introduction locations.

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Centre de Lullier – Revue Horticole Suisse: www.lullier.ch

Giant-alien Project (2002-2005): www.giant-alien.dk financed by the European Commision within the 5th Framework Programme, Energy, Environment and Sustainable Development.

MODIPLANT project, ECOSPAT, Departement of Ecology and Evolution (DEE), University of Lausanne http://ecospat.unil.ch/index.pl/research

Swiss Commission for Wild Plant Conservation, CPS/SKEW: www.cps-skew.ch

Swiss Federal Office of Topography, Swisstopo: www.swisstopo.ch

Swiss Federal Institute for Forest, Snow and Landscape Research, WSL: www.wsl.ch

The International Union for the Conservation of Nature and Natural Resources, IUCN: www.iucn.org

APPENDIXES

Appendix 1: ENFA and GAM

The profile technique (presence-only) used in this study is Environmental Niche Factor Analyses (ENFA). This multivariate approach situates the environmental niche of the species within the environmental characteristics of all variables describing the study area. This method, similar to principal component analyses (PCA), transforms the multidimensional environmental space into unrelated axes, also called factors. The first factor is called marginality and is defined as the difference between the mean values of all predictors in the whole area and the mean value observed for the study species. The following factors are specialisation indices, defined as the ratio of the ecological variance measured for species niche to the variance in the whole area.

The discrimination technique performed in the current study is Generalized Additive Models (GAM), a non-parametric extension of Generalized Linear Models (GLM). Both allow selection, through stepwise selection, and incorporation of a predictor sub-set presumed closer to focal species ecology. The predictor response curves, in GAMs, are fitted with a smoothing function instead of linear or quadratic relationships as in GLMs. In some cases, species responses are better fitted using complex, non-parametric response (Bio *et al.* 1998).

Appendix 2:

A. Adaptive sampling

Adaptive sampling postulates that if the focal species is observed in one of the defined sampling square, the four neighbouring squares with adjacent boundaries are also investigated (Figure 5). This reiteration process is applied to each defined and neighbouring square where the species is occurring resulting in a cluster of squares representing all occurrence sampled squares.

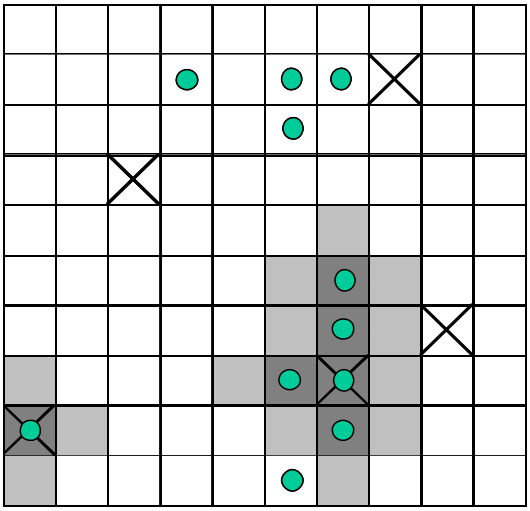

Figure 5: Illustration of adaptive sampling design used to estimate the population size of a focal species which distribution is represented with solid circles. Cross-marked squares defined the initial sampling squares usually chosen randomly. If the focal species is observed one of these latter (dark grey squares), all adjacent squares (light-grey) are investigated. The process is repeated if the species is observed again, resulting in networks, defined as cluster of occurrence sampled squares.

B. Design-based estimation

N units are partitioned into ***h*** strata with $\mathbf{N_h}$ unit per stratum. A simple random sampling of ***n*** units is performed in each stratum given in total ***h*n*** sampled units. Whenever a unit in the sample contains one or more individuals ***y*** of the target species, adjacent units are added to the sample through adaptive sampling. This leads to create ***k*** networks with associated the y-value $\boldsymbol{y_k}$ defined as the total number of individuals in the network. One network could eventually straddle a stratum boundary. So, $\boldsymbol{x_{hk}}$ define the number of units in stratum h that lie in network k. To simplify the equations writing we set h as 10 strata, n as 10 unit per stratum leading to 100 sampled units and also 100 networks.

The intersection probability α_k for each network must first be calculated:

$$\alpha_k = 1 - \left[\prod_{h=1}^{10} \binom{N_h - x_{hk}}{n} \Big/ \binom{N_h}{n} \right],$$

In other words, α_k corresponds to the probability that networks are included in the sample.

Then, the mean number of individuals per square $\hat{u}_{st}$ in the whole study area in case of stratified sampling is estimated as:

$$\hat{u}_{st} = \frac{1}{N}\sum_{k=1}^{100}\frac{y_k}{\alpha_k}$$

The variance is given by:

$$\mathrm{var}[\hat{u}_{st}] = \frac{1}{N^2}\sum_{k=1}^{100}\sum_{k'=1}^{100} y_k \cdot y_{k'}\left(\frac{\alpha_{kk'} - \alpha_k \cdot \alpha_{k'}}{\alpha_k \cdot \alpha_{k'}}\right),$$

where $\alpha_{kk'}$ define the probability that the initial sample intersects both networks k and k':

$$\alpha_{kk'} = 1-(1-\alpha_k)-(1-\alpha_{k'})+\left[\prod_{h=1}^{10}\binom{N_h - x_{hk} - x_{hk'}}{n}\Big/\binom{N_h}{n}\right]$$

Some simplifications were made compared with Thompson and Seber (1996) equations: the number of n primary unit per strata might be different per each stratum, e.g. proportional to the size of the strata. It could not be done in this study because 10 is considered as the statistically smaller number of primary units per strata and a proportional approach implies a total number of sampling units much greater than 100.

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Appendix 3: Alpine botanical gardens

Alpine Botanical Gardens	Date	Status	*Heracleum mantegazzianum*	Elevation	Source
La Linnea, Pont-de-Nant, Bex	1891	maintain	Cultivate, escaped from garden	1253	Botanical Garden of Lausanne
La Rambertsia, Rochers-de-Naye, Montreux	1896	maintain	Absent since 2001	1999	Botanical Garden of Lausanne
Les Diablerets village, Ormont-dessous	?	ancient	Escaped from garden	1155	Botanical Garden of Lausanne
Tour d'Aï, Leysin	~1950	ancient	Still present	1967	Botanical Garden of Lausanne
Gryon village, Gryon	?	ancient	?	~1100	H. Correvon Archives

Location, foundation date, status, elevation of alpine botanical garden in the study area with different information sources. Presence or absence of *H. mantegazzianum* is mentioned.

Appendix 4: AMBROSIA exploratory study and dataset

Introduction

The ragweed, *Ambrosia artemisiifolia* L., is an annual Astreracea native from North-America. It was introduced in Europe since the XVIIIth century as a ballast weed or associated with cereals transport (Dahl *et al.* 1999) and became an important cause of pollen allergy in Europe, still rare in Switzerland (Taramarcaz 2005).

Methods

We conducted in the same study area (Study area) an identical random-stratified adaptive sampling of 70 sites on 10 strata corresponded to probability classes of a habitat suitability map (ENFA I). This model was performed at Swiss scale using 204 occurrence sites available from CRSF database and 32 predictors describing each 50 x 50 m square of Switzerland (Table 5) . Then the suitability map was aggregate at 25 m.

The climatic layers provided by the WSL (Zimmermann and Kienast, unpublished). Principal component analysis (PCA) were performed to simplified monthly layers of solar radiation, precipitation, evaporation and moisture index by creating indexes of seasonality (Broennimann Diploma Thesis 2003) allowing reducing predictor quantity. An adequate number of principal components were retained in order to have a cumulate explained variance above 99% for each predictor. The first two principal components were kept for daily average of evaporation per month (*etptc1*, *etptc2*), the first three for monthly moisture index (*mindc1*, *mindc2*, *mindc3*), the first three for monthly precipitations sum (*precc1*, *precc2*, *precc3*), the first for daily average of potential diffuse shortwave radiation per month (*sdifc1*), the first two for daily average of potential direct shortwave radiation per month (*sdirc1, sdirc2*), the first two for monthly solar radiations (*sradc1, sradc2*) and finally the first for monthly temperatures average (*tavec1*). For these monthly layers series, we also calculated the average layers from May until October corresponding to the growing season of the focal species. Logarithmic distances to forest and rivers were also calculated using forests and rivers layers providing from Swisstopo. Environmental variables correlated with Spearman rank correlation value above 0.85

were avoided and variables with the closest relationship with the focal species ecology were kept.

Table 5: Selected quantitative environmental predictors.

Abbreviation	Name	Unity	Source
gams_t *	Continentality indices of Gams	unitless	WSL
ddeg300 *	Sum of annual degreedays with 3° threshold	[day·C°]	WSL
pday *	Number of precipitation days per growing season	[day]	WSL
slp *	Slope	[degree]	calculated
swb *	Soil water budget	[mm/yr]	WSL
sffroy *	Annual average number of frost days during growing season	[days]	WSL
sradmoy *	Average solar radiation from May until October	[KJ/m^2]	calculated
sradc1	Index of solar radiation	unitless	calculated
sradc2 *	Index of solar radiation	unitless	calculated
precmoy *	Average sum of precipitation from May until October	[mm]	calculated
precc1	Index of precipitation	unitless	calculated
precc2 *	Index of precipitation	unitless	calculated
precc3 *	Index of precipitation	unitless	calculated
etptmoy	Daily average of evaporation per month from May until October	[1/10mm/day]	calculated
etptc1	Index of evaporation	unitless	calculated
etptc2 *	Index of evaporation	unitless	calculated
mindmoy *	Average moisture index from May until October	[mm]	calculated
mindc1	Index of moisture	unitless	calculated
mindc2 *	Index of moisture	unitless	calculated
mindc3	Index of moisture	unitless	calculated
sdirmoy	Daily average of potential direct shortwave radiation per month from May until October	[KJ/day]	calculated
sdirc1	Index of potential direct shortwave radiation	unitless	calculated
sdirc2	Index of potential direct shortwave radiation	unitless	calculated
sdifmoy	Daily average of potential diffuse shortwave radiation per month from May until October	[KJ/day]	calculated
sdifc1	Index of potential diffuse shortwave radiation	unitless	calculated
tavemoy	Monthly average temperature from May until October	[°C·100]	calculated
tavec1	Index of temperature	unitless	calculated
twi *	Topographic witness index	unitless	WSL
norditude *	North-South exposition	[°]	calculated
estitude *	East-West exposition	[°]	calculated
dforest *	Distances to forests (ln transformation)	[m]	calculated
driver *	Distances to rivers (ln transformation)	[m]	calculated

Reteained predictors are marked with an asterisk (*) (see Environmental predictor of *H. mantegazzianum* study for further details).

Results

The 19 uncorrelated environmental predictors (Table 5; Table 7) were used to perform the ENFA model at Swiss scale, each explaining a different proportion of the first four factors (Table 6). For this analysis, the global coefficient of marginality was calculated at 1.87, the specialisation, 3.73. The broken-stick method selected the first five factors explaining 94% of total variance. The potential distribution map is showed in Figure 6.

Table 6: Coefficient of predictors in the ENFA. The first factor is defined as the marginality values and the others, specialisation indices.

Factor 1	**57%**	**Factor 2**	**14%**	**Factor 3**	**9%**	**Factor 4**	**5%**
gams_t	-0.48	*etptc2*	-0.55	*precmoy*	0.67	*mindmoy*	-0.65
pday	-0.41	*precc2*	-0.48	*mindmoy*	-0.63	*precc3*	-0.51
ddeg300	0.39	*precmoy*	0.40	*sradmoy*	-0.25	*pday*	0.30
slp	-0.32	*gams_t*	0.35	*gams_t*	0.18	*precmoy*	0.29
swb	-0.27	*sradmoy*	0.28	*precc2*	-0.17	*sradmoy*	-0.25
precc3	-0.23	*mindc2*	-0.22	*ddeg300*	0.13	*precc2*	0.19
sffroy	-0.22	*ddeg300*	0.20	*pday*	0.08	*ddeg300*	-0.14
etptc2	-0.21	*mindmoy*	0.09	*precc3*	-0.06	*mindc2*	0.12
mindmoy	-0.21	*sradc2*	0.09	*swb*	-0.03	*etptc2*	0.10
twi	0.17	*pday*	0.07	*dforest*	-0.03	*gams_t*	0.05
sradc2	0.14	*sffroy*	-0.06	*sradc2*	0.02	*dforest*	0.04
sradmoy	0.12	*dforest*	0.06	*twi*	-0.01	*slp*	0.02
precc2	0.10	*precc3*	-0.06	*etptc2*	0.01	*sffroy*	-0.02
mindc2	-0.10	*driver*	-0.02	*driver*	-0.01	*driver*	0.01
dforest	0.08	*swb*	0.01	*slp*	0.00	*sradc2*	0.01
precmoy	-0.06	*slp*	0.01	*estitude*	0.00	*twi*	0.01
driver	-0.04	*estitude*	0.00	*mindc2*	0.00	*estitude*	0.01
norditude	0.03	*norditude*	0.00	*norditude*	0.00	*swb*	0.00
estitude	0.00	*twi*	0.00	*sffroy*	0.00	*norditude*	0.00

In Switzerland, *A. artemisiifolia* prefers low value of continentality (-0.48), low number of precipitation days during growing season (-0.41), high values of degreedays (0.39), gentle slopes (-0.32), low soil water budget values, low index of precipitation (-0.23) and a low number of frost days (-0.22). The species mean values for average precipitations are close to the mean values in Swiss landscape. The second factor precised

that the focal species is little tolerant to greater or lower precipitations (-0.48 and 0.40) and for continentality (0.35).

The estimation of the total population density of *A. artemisiifolia* in the Prealps of Canton de Vaud, according to the random-stratified adaptive sampling was estimated at 17'801 individuals with variance of 14'934 individuals (80%).

Discussion

According with Lauber & Wagner (2000), *A. artemisiifolia* occurs in the hottest stations of Switzerland, in disturbed habitats with rich soils and a moderate dryness explaining the high score of the first three variables (*gams_t*, *pday* and *ddeg300*). Invasion of *A. artemisiifolia* in Switzerland had several origins. Well established in Italy and in France, the invasive ragweed follows main roads to colonize Swiss landscape through respectively Ticino and Geneva; one other in Basel coming from Germany is suspected. This could explain the high scores for contenentality index (*gams_t*), which is sensible to variation of topography, and slope (*slp*) both related with location of main roads in the landscape. For the population size estimation, the very high variance might be explained by the fact that only one occurrence was recorded. The main result here concerned the non-establishment of this alien invasive plant in the study area, which is very satisfactory in term of conservation biology and public health.

Conclusion

For *A. artemisiifolia,* the most unforeseeable invasion process provides from seed assemblages for wild birds infested by ragweed's seeds conferred to the species an unpredictable dispersal potential. Both colonized squares found during the field work were due to these seeds assemblages. If nothing is done to limit dispersal of the focal species, our model suggested that the lower altitudes of the study area will be progressively colonized in the following years.

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Lauber Wagner (2000) *FLORA HELVETICA: Flore illustrée de Suisse*, Ed. Paul Haupt, Berne, Stuttgart, Vienne.

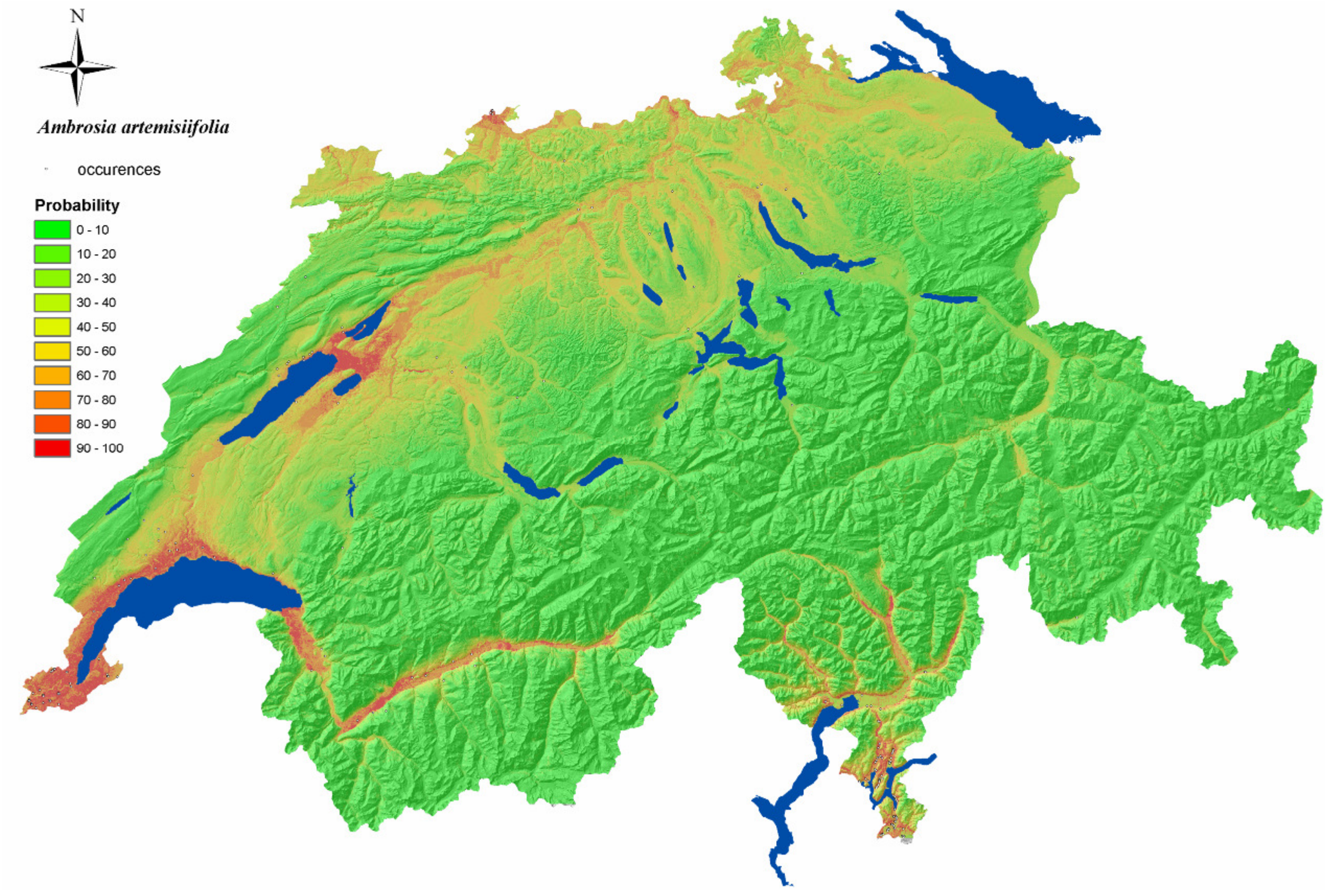
Taramarcaz, P., Lambelet, C., Clot, B., Keimer, C., Hauser (2005) Ragweed (Ambrosio) progression and its health risks: will Switzerland resist this invasion? *Swiss Medical Weekly*, **135**, 538-548.

Table 7: Correlation matrix of the 32 predictors selected for perform habitat suitability model for *Ambrosia artemisiifolia.*

	gams_t	ddeg300	pday	slp	swb	sffroy	sradmoy	sradc1	sradc2	precmoy	precc1	precc2	precc3	etptmoy	etptc1	etptc2	mindmoy	mindc1	mindc2	mindc3	sdirmoy	sdirc1	sdirc2	sdifmoy	sdifc1	tavemoy	tavec1	twi	norditude	estitude	dforest	driver
gams_t	*1*	-0.84	0.22	0.47	0.18	0.73	-0.21	-0.13	-0.27	-0.08	0.00	-0.21	-0.18	-0.77	-0.79	0.26	0.43	0.43	-0.18	0.02	-0.22	-0.14	-0.26	0.36	0.36	*-0.86*	*-0.86*	-0.28	-0.01	0.00	0.34	0.11
ddeg300	-0.84	*1*	-0.49	-0.58	-0.44	-0.81	0.25	0.16	0.34	-0.40	-0.50	0.18	0.12	*0.91*	*0.93*	-0.23	-0.79	-0.80	0.04	0.02	0.27	0.16	0.34	-0.47	-0.47	*0.99*	*0.99*	0.37	0.01	0.00	-0.42	-0.15
pday	0.22	-0.49	*1*	0.30	0.61	0.31	-0.12	-0.08	-0.13	0.59	0.60	-0.03	0.67	-0.43	-0.44	0.13	0.57	0.59	0.26	-0.67	-0.12	-0.08	-0.13	0.21	0.21	-0.49	-0.49	-0.22	0.00	0.00	0.16	0.00
slp	0.47	-0.58	0.30	*1*	0.43	0.42	-0.42	-0.25	-0.66	0.41	0.44	0.02	-0.11	-0.67	-0.68	0.11	0.65	0.65	-0.11	-0.09	-0.44	-0.25	-0.66	*0.86*	*0.86*	-0.61	-0.61	-0.63	-0.01	-0.01	-0.09	0.02
swb	0.18	-0.44	0.61	0.43	*1*	0.22	-0.24	-0.19	-0.14	0.71	0.63	0.29	0.30	-0.45	-0.47	0.25	0.70	0.69	-0.06	-0.33	-0.25	-0.19	-0.14	0.26	0.26	-0.46	-0.46	-0.31	-0.01	0.00	-0.06	-0.15
sffroy	0.73	-0.81	0.31	0.42	0.22	*1*	-0.19	-0.11	-0.26	0.23	0.32	-0.19	-0.17	-0.74	-0.76	0.14	0.60	0.60	-0.07	0.04	-0.19	-0.11	-0.25	0.35	0.35	-0.80	-0.81	-0.26	0.00	0.00	0.43	0.17
sradmoy	-0.21	0.25	-0.12	-0.42	-0.24	-0.19	*1*	*0.97*	0.08	-0.17	-0.18	-0.03	0.07	0.58	0.53	0.55	-0.44	-0.39	0.23	0.20	*1.00*	*0.97*	0.03	-0.45	-0.45	0.26	0.26	0.23	0.00	0.00	0.03	0.03
sradc1	-0.13	0.16	-0.08	-0.25	-0.19	-0.11	*0.97*	*1*	-0.12	-0.10	-0.10	-0.02	0.03	0.47	0.42	0.59	-0.33	-0.29	0.21	0.20	*0.97*	*1.00*	-0.17	-0.27	-0.27	0.16	0.16	0.13	0.00	0.00	0.03	0.05
sradc2	-0.27	0.34	-0.13	-0.66	-0.14	-0.26	0.08	-0.12	*1*	-0.22	-0.25	0.00	0.14	0.36	0.38	-0.08	-0.35	-0.36	0.07	0.04	0.09	-0.13	*1.00*	-0.75	-0.75	0.35	0.35	0.43	0.01	0.00	0.00	-0.11
precmoy	-0.08	-0.40	0.59	0.41	0.71	0.23	-0.17	-0.10	-0.22	*1*	*0.93*	0.36	0.16	-0.40	-0.42	0.13	0.82	0.82	-0.02	-0.19	-0.18	-0.10	-0.22	0.32	0.32	-0.40	-0.40	-0.28	-0.01	0.00	0.07	-0.03
precc1	0.00	-0.50	0.60	0.44	0.63	0.32	-0.18	-0.10	-0.25	*0.93*	*1*	-0.01	0.09	-0.49	-0.50	0.15	0.83	*0.87*	0.28	-0.06	-0.19	-0.11	-0.25	0.35	0.35	-0.50	-0.50	-0.30	-0.01	0.00	0.13	0.06
precc2	-0.21	0.18	-0.03	0.02	0.29	-0.19	-0.03	-0.02	0.00	0.36	-0.01	*1*	0.06	0.13	0.14	-0.03	0.15	0.02	-0.80	-0.21	-0.03	-0.02	0.00	0.01	0.01	0.18	0.18	-0.02	0.00	0.00	-0.13	-0.24
precc3	-0.18	0.12	0.67	-0.11	0.30	-0.17	0.07	0.03	0.14	0.16	0.09	0.06	*1*	0.16	0.16	0.08	-0.06	-0.05	0.30	*-0.90*	0.07	0.04	0.14	-0.15	-0.15	0.12	0.11	0.04	0.00	0.00	-0.13	-0.11
etptmoy	-0.77	*0.91*	-0.43	-0.67	-0.45	-0.74	0.58	0.47	0.36	-0.40	-0.49	0.13	0.16	*1*	*1.00*	0.03	-0.84	-0.83	0.15	0.06	0.59	0.48	0.34	-0.59	-0.59	*0.92*	*0.92*	0.41	0.01	0.00	-0.33	-0.11
etptc1	-0.79	*0.93*	-0.44	-0.68	-0.47	-0.76	0.53	0.42	0.38	-0.42	-0.50	0.14	0.16	*1.00*	*1*	-0.04	*-0.85*	-0.84	0.13	0.05	0.54	0.42	0.37	-0.59	-0.59	*0.94*	*0.94*	0.42	0.01	0.00	-0.34	-0.11
etptc2	0.26	-0.23	0.13	0.11	0.25	0.14	0.55	0.59	-0.08	0.13	0.15	-0.03	0.08	0.03	-0.04	*1*	0.07	0.14	0.24	0.17	0.53	0.58	-0.11	-0.06	-0.06	-0.28	-0.28	-0.08	-0.01	-0.01	-0.05	-0.08
mindmoy	0.43	-0.79	0.57	0.65	0.70	0.60	-0.44	-0.33	-0.35	0.82	0.83	0.15	-0.06	-0.84	*-0.85*	0.07	*1*	*0.99*	-0.13	-0.10	-0.45	-0.34	-0.34	0.54	0.54	-0.80	-0.80	-0.41	-0.01	0.00	0.25	0.05
mindc1	0.43	-0.80	0.59	0.65	0.69	0.60	-0.39	-0.29	-0.36	0.82	*0.87*	0.02	-0.05	-0.83	-0.84	0.14	*0.99*	*1*	0.01	-0.06	-0.40	-0.29	-0.35	0.53	0.53	-0.81	-0.81	-0.41	-0.01	0.00	0.24	0.07
mindc2	-0.18	0.04	0.26	-0.11	-0.06	-0.07	0.23	0.21	0.07	-0.02	0.28	-0.80	0.30	0.15	0.13	0.24	-0.13	0.01	*1*	-0.01	0.23	0.21	0.06	-0.14	-0.14	0.03	0.03	0.05	0.00	0.00	-0.08	0.14
mindc3	0.02	0.02	-0.67	-0.09	-0.33	0.04	0.20	0.20	0.04	-0.19	-0.06	-0.21	*-0.90*	0.06	0.05	0.17	-0.10	-0.06	-0.01	*1*	0.20	0.20	0.03	-0.09	-0.09	0.01	0.02	0.07	0.00	0.00	0.07	0.09
sdirmoy	-0.22	0.27	-0.12	-0.44	-0.25	-0.19	*1.00*	*0.97*	0.09	-0.18	-0.19	-0.03	0.07	0.59	0.54	0.53	-0.45	-0.40	0.23	0.20	*1*	*0.97*	0.04	-0.47	-0.47	0.28	0.28	0.25	0.00	0.00	0.03	0.03
sdirc1	-0.14	0.16	-0.08	-0.25	-0.19	-0.11	*0.97*	*1.00*	-0.13	-0.10	-0.11	-0.02	0.04	0.48	0.42	0.58	-0.34	-0.29	0.21	0.20	*0.97*	*1*	-0.18	-0.27	-0.27	0.17	0.17	0.13	0.00	0.00	0.03	0.05
sdirc2	-0.26	0.34	-0.13	-0.66	-0.14	-0.25	0.03	-0.17	*1.00*	-0.22	-0.25	0.00	0.14	0.34	0.37	-0.11	-0.34	-0.35	0.06	0.03	0.04	-0.18	*1*	-0.75	-0.75	0.35	0.35	0.42	0.01	0.00	0.00	-0.11
sdifmoy	0.36	-0.47	0.21	*0.86*	0.26	0.35	-0.45	-0.27	-0.75	0.32	0.35	0.01	-0.15	-0.59	-0.59	-0.06	0.54	0.53	-0.14	-0.09	-0.47	-0.27	-0.75	*1*	*1.00*	-0.49	-0.48	-0.55	-0.01	0.00	0.00	0.09
sdifc1	0.36	-0.47	0.21	*0.86*	0.26	0.35	-0.45	-0.27	-0.75	0.32	0.35	0.01	-0.15	-0.59	-0.59	-0.06	0.54	0.53	-0.14	-0.09	-0.47	-0.27	-0.75	*1.00*	*1*	-0.49	-0.48	-0.55	-0.01	0.00	0.00	0.09
tavemoy	*-0.86*	*0.99*	-0.49	-0.61	-0.46	-0.80	0.26	0.16	0.35	-0.40	-0.50	0.18	0.12	*0.92*	*0.94*	-0.28	-0.80	-0.81	0.03	0.01	0.28	0.17	0.35	-0.49	-0.49	*1*	*1.00*	0.38	0.01	0.01	-0.39	-0.14
tavec1	*-0.86*	*0.99*	-0.49	-0.61	-0.46	-0.81	0.26	0.16	0.35	-0.40	-0.50	0.18	0.11	*0.92*	*0.94*	-0.28	-0.80	-0.81	0.03	0.02	0.28	0.17	0.35	-0.48	-0.48	*1.00*	*1*	0.38	0.01	0.01	-0.39	-0.14
twi	-0.28	0.37	-0.22	-0.63	-0.31	-0.26	0.23	0.13	0.43	-0.28	-0.30	-0.02	0.04	0.41	0.42	-0.08	-0.41	-0.41	0.05	0.07	0.25	0.13	0.42	-0.55	-0.55	0.38	0.38	*1*	0.01	0.01	0.10	-0.05
norditude	-0.01	0.01	0.00	-0.01	-0.01	0.00	0.00	0.00	0.01	-0.01	-0.01	0.00	0.00	0.01	0.01	-0.01	-0.01	-0.01	0.00	0.00	0.00	0.00	0.01	-0.01	-0.01	0.01	0.01	0.01	*1*	0.00	0.00	0.00
estitude	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.00	*1*	0.00	0.00
dforest	0.34	-0.42	0.16	-0.09	-0.06	0.43	0.03	0.03	0.00	0.07	0.13	-0.13	-0.13	-0.33	-0.34	-0.05	0.25	0.24	-0.08	0.07	0.03	0.03	0.00	0.00	0.00	-0.39	-0.39	0.10	0.00	0.00	*1*	0.17
driver	0.11	-0.15	0.00	0.02	-0.15	0.17	0.03	0.05	-0.11	-0.03	0.06	-0.24	-0.11	-0.11	-0.11	-0.08	0.05	0.07	0.14	0.09	0.03	0.05	-0.11	0.09	0.09	-0.14	-0.14	-0.05	0.00	0.00	0.17	*1*

Legend: Predictors abbreviations are given in Table 5. In italic are mentioned correlation values above threshold of 0.85.

Figure 6: Potential distribution map of *Ambrosia artemisiifolia* at Swiss scale and at 50 m resolution. 204 occurrences were available from CRSF database to fit the model.

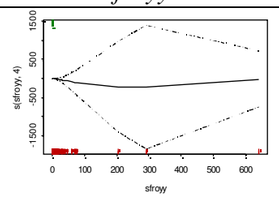
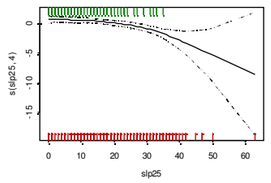
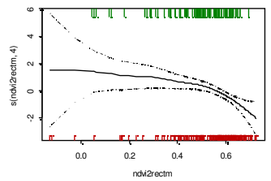
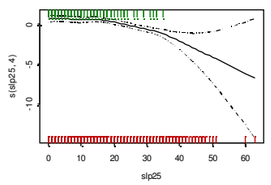
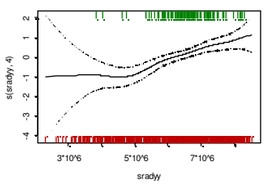
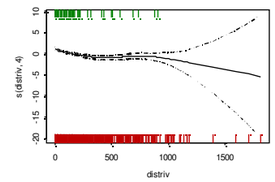
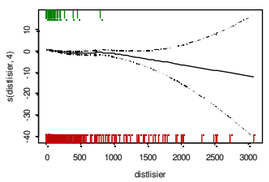
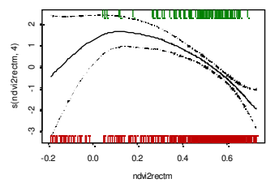
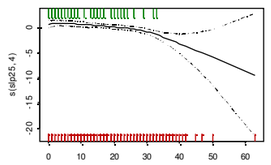
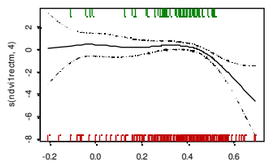
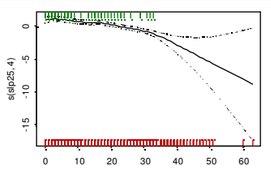
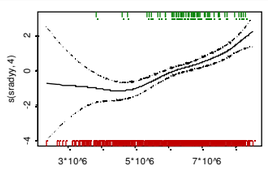
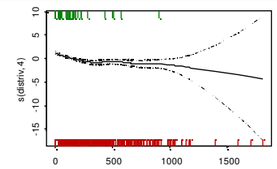
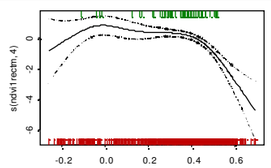


Appendix 5: Correlation matrix of the thirteen environmental variables (*H. mantegazzianum)*

	dem25	*preccy*	*sfroyy*	*slp25*	*sradyy*	*swb*	*taveyy*	*topo*	*twi25*	*distriv*	*distlis*	*ndvi1rectm*	*ndvi2rectm*
dem25	1	**0.940**	0.579	0.492	-0.205	0.612	**-0.996**	0.235	-0.346	0.225	0.447	-0.440	-0.177
preccy	**0.940**	1	0.563	0.476	-0.208	0.646	**-0.946**	0.218	-0.341	0.175	0.417	-0.415	-0.181
sfroyy	0.579	0.563	1	0.263	-0.183	0.078	-0.558	0.190	-0.164	0.346	0.672	-0.475	-0.513
slp25	0.492	0.476	0.263	1	-0.280	0.291	-0.492	0.151	-0.539	0.253	0.095	-0.303	-0.086
Sradyy	-0.205	-0.208	-0.183	-0.280	1	-0.221	0.194	0.076	0.112	-0.056	-0.133	0.576	0.230
Swb	0.612	0.646	0.078	0.291	-0.221	1	-0.636	0.030	-0.227	-0.137	-0.029	-0.105	0.213
Taveyy	**-0.996**	**-0.946**	-0.558	-0.492	0.194	-0.636	1	-0.236	0.350	-0.205	-0.421	0.421	0.155
Topo	0.235	0.218	0.190	0.151	0.076	0.030	-0.236	1	-0.328	0.248	0.070	-0.006	-0.019
twi25	-0.346	-0.341	-0.164	-0.539	0.112	-0.227	0.350	-0.328	1	-0.154	-0.045	0.085	-0.017
Distriv	0.225	0.175	0.346	0.253	-0.056	-0.137	-0.205	0.248	-0.154	1	0.366	-0.266	-0.300
Distlis	0.447	0.417	0.672	0.095	-0.133	-0.029	-0.421	0.070	-0.045	0.366	1	-0.435	-0.507
ndvi1rectm	-0.440	-0.415	-0.475	-0.303	0.576	-0.105	0.421	-0.006	0.085	-0.266	-0.435	1	0.632
ndvi2rectm	-0.177	-0.181	-0.513	-0.086	0.230	0.213	0.155	-0.019	-0.017	-0.300	-0.507	0.632	1

Legend: Abbreviations are given in Table 1. In bold characters are mentioned correlation values above threshold fixed at 0.8.

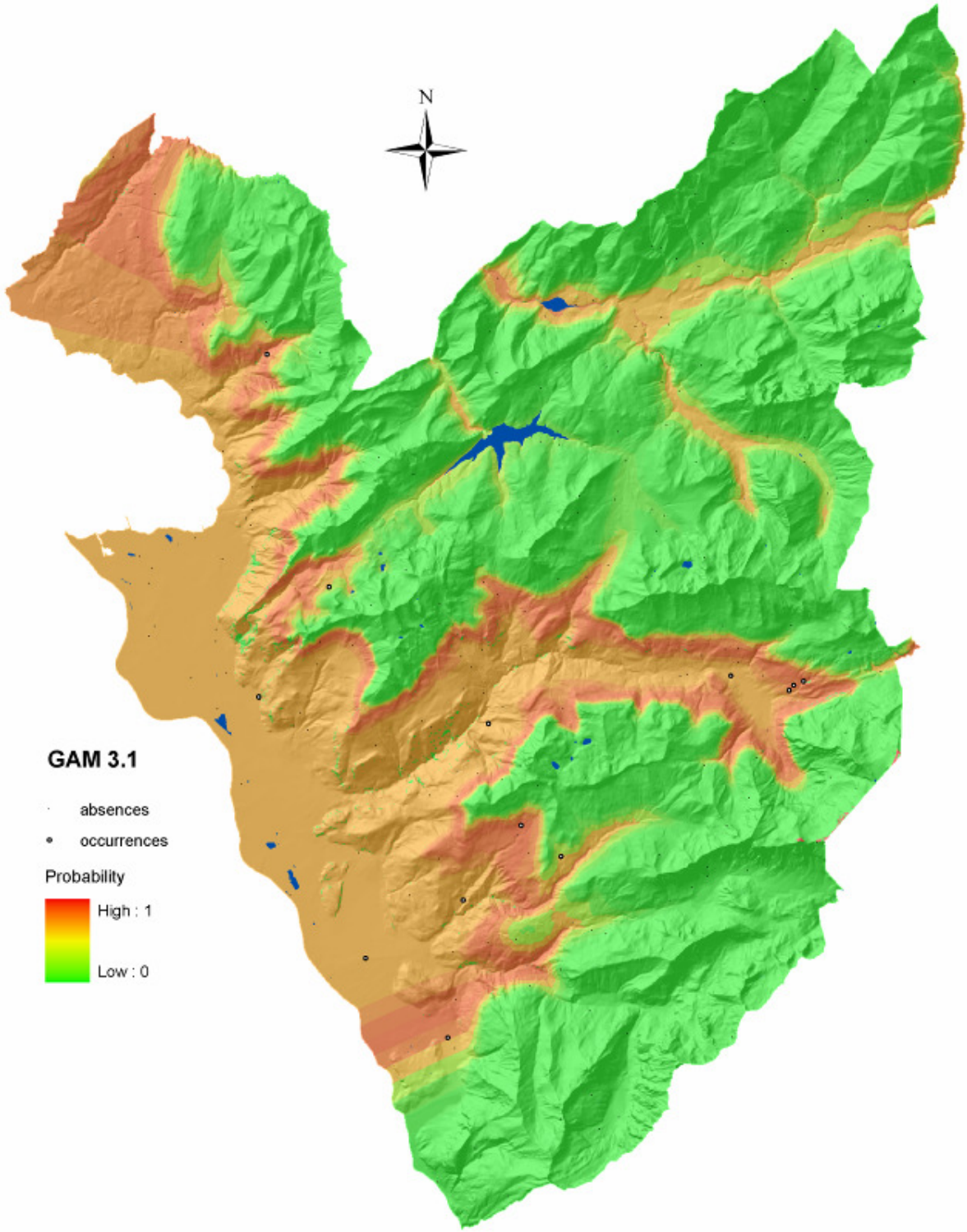
Appendix 6: Predictors' response curves of GAM models.

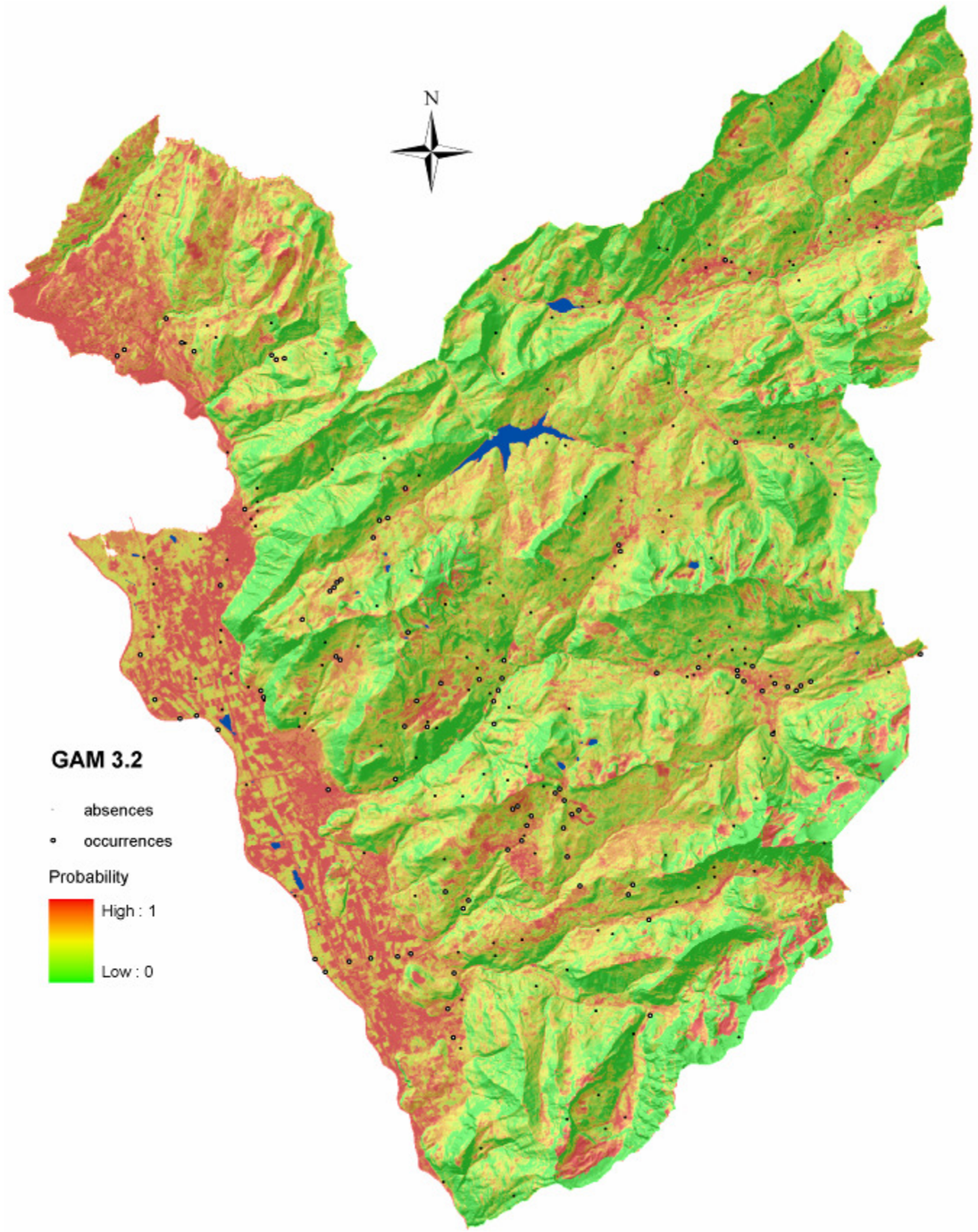
	sfroyy	*slp25*	*sradyy*	*distriv*	*distlis*	*ndvi1rectm*	*ndvi2rectm*
GAM 3.1 Df_{tot}: 2.8	 Df: 2.8						
GAM 3.2 Df_{tot}: 5.7		 Df: 2.8					 Df: 2.9
GAM 3.3 Df_{tot}: 14.3		 Df: 3.0	 Df: 2.9	 Df: 3.0	 Df: 2.6		 Df: 2.8
GAM 3.4 Df_{tot}: 5.7		 Df: 2.8				 Df: 2.9	
GAM 3.5 Df_{tot}: 11.7		 Df: 3.0	 Df: 2.9	 Df: 3.0		 Df: 2.8	

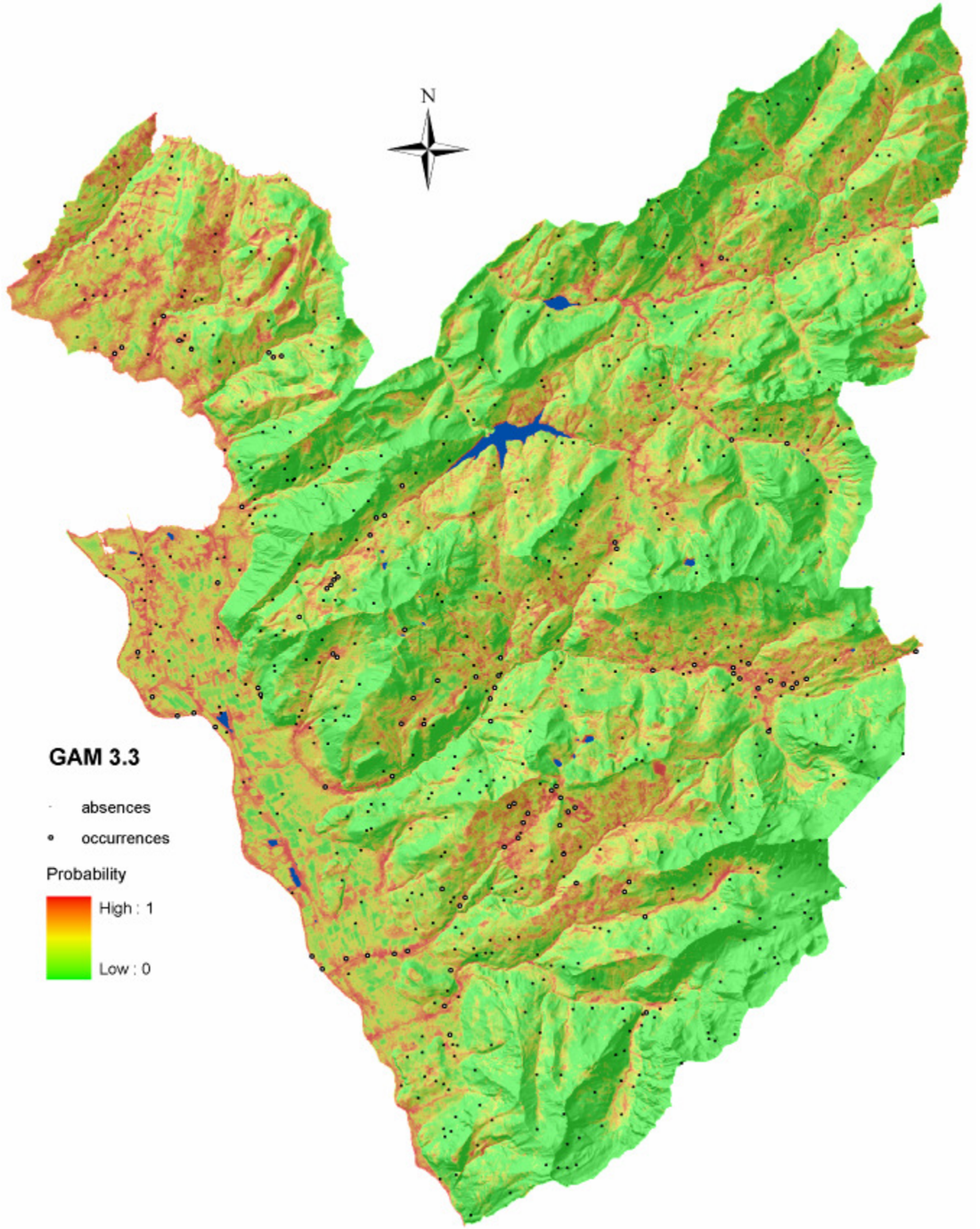
Degrees of freedom are mentioned for each predictor (Df) and for each model (Df_{tot}). Number of frost days (*sfroyy*), slope (*slp25*), solar radiations (*sradyy*), distances to rivers (*distlis*) and to forest edges (*dislis*) and two NDVI layers of October (*ndvi1rectm*) and July (*ndvi2rectm*). The green lines indicate occurrences' values of corresponding predictor and the red lines, absences' values. Standard errors are mentioned in dotted lines.

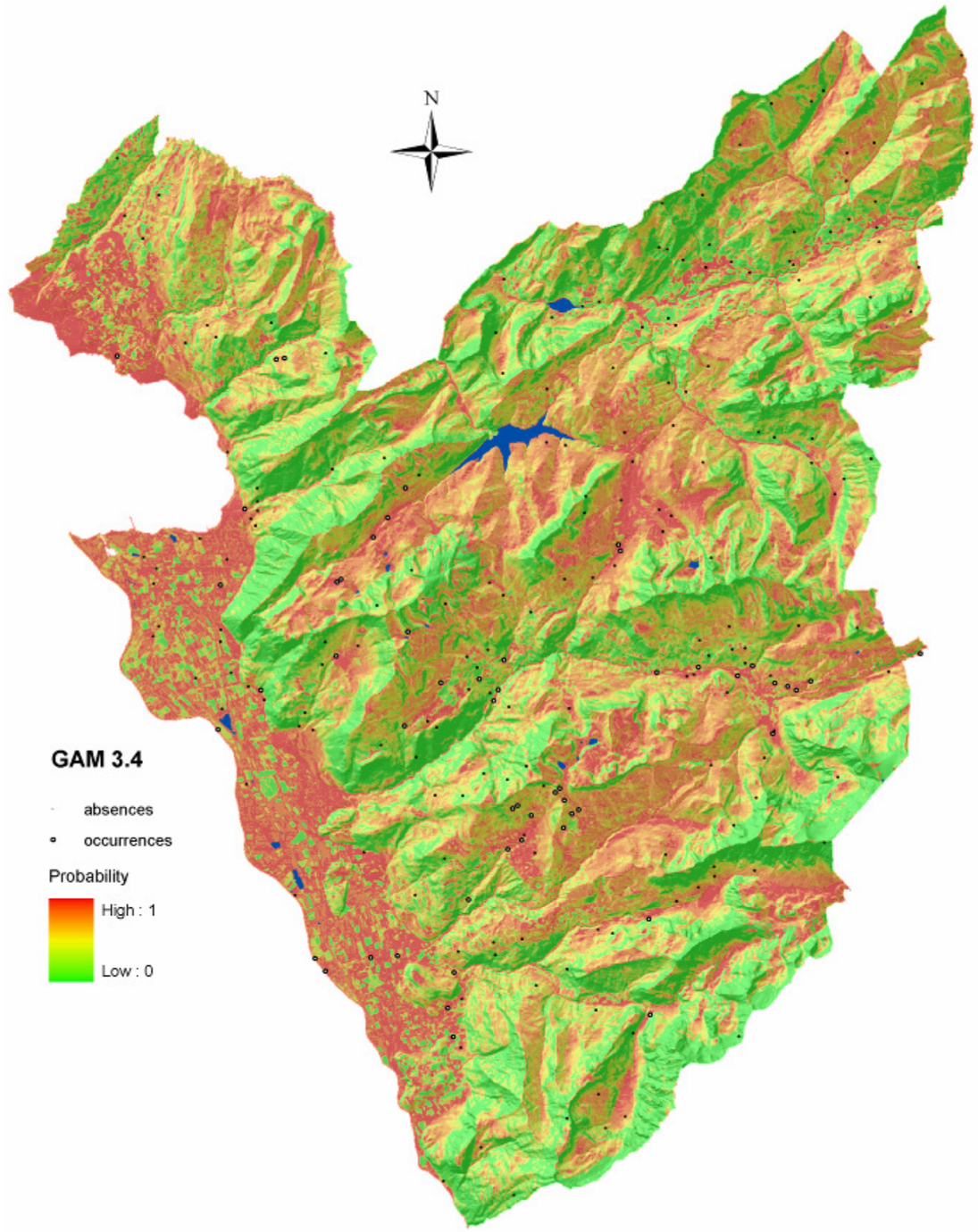
Appendix 7: Potential distribution maps of *H. mantegazzianum*.

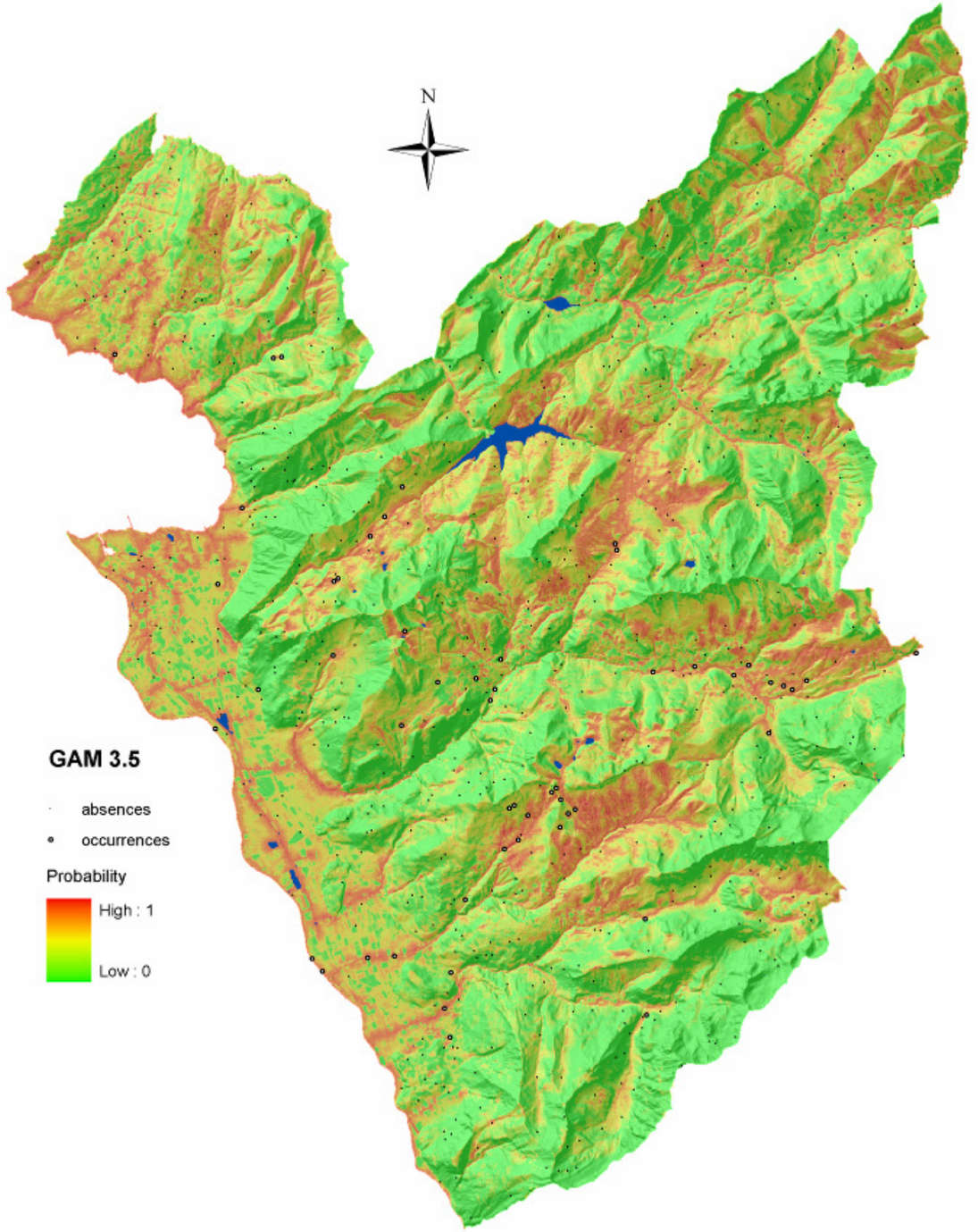
Potential distribution maps indicate probability of invasion by the giant hogweed with low value in green and high value in red. Data used to fit each model are show on the maps.




N
GAM 3.2
absences
occurrences
Probability
High : 1
Low : 0

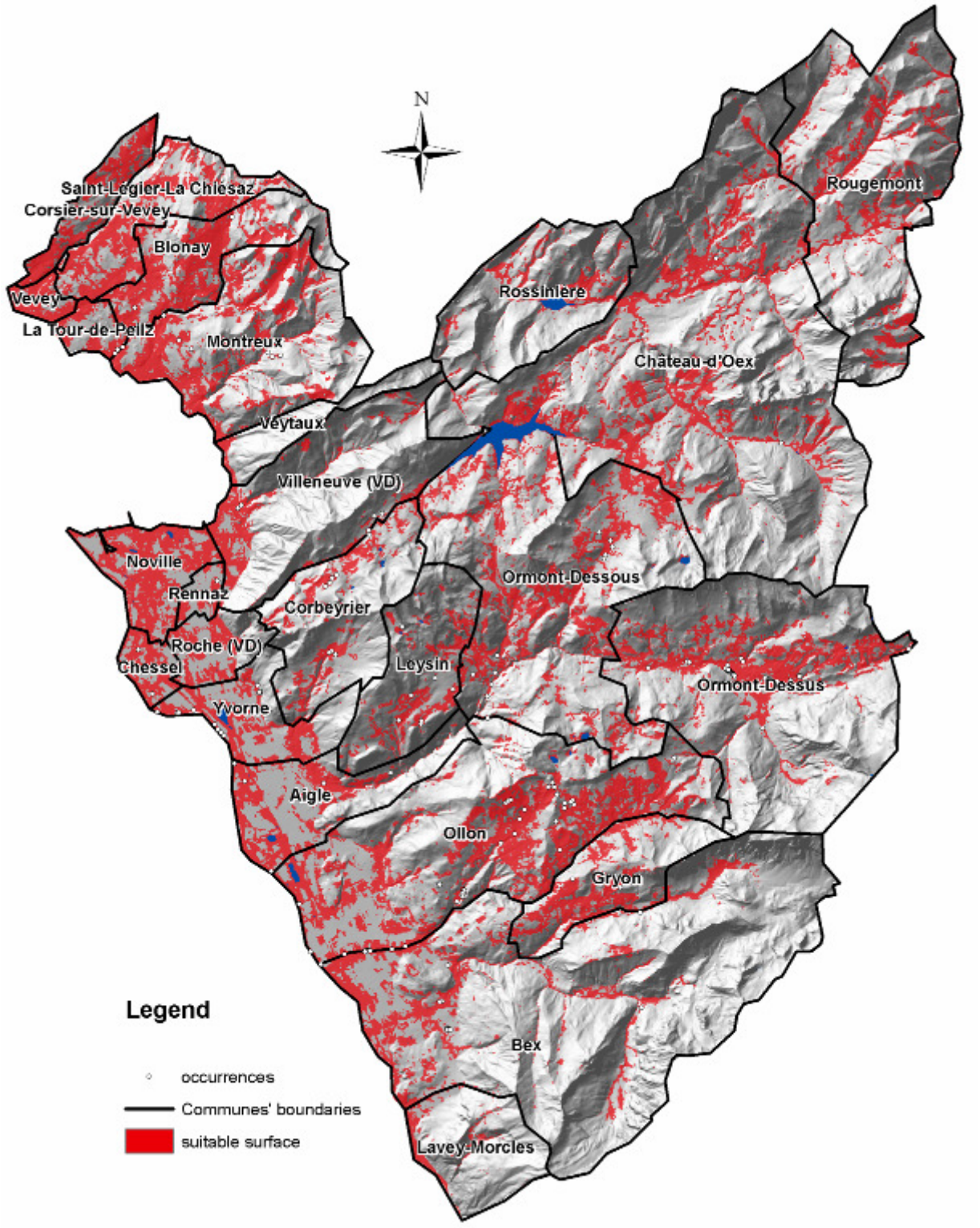

N
GAM 3.3
absences
occurrences
Probability
High : 1
Low : 0


N
GAM 3.4
absences
occurrences
Probability
High : 1
Low : 0


N
GAM 3.5
absences
occurrences
Probability
High : 1
Low : 0

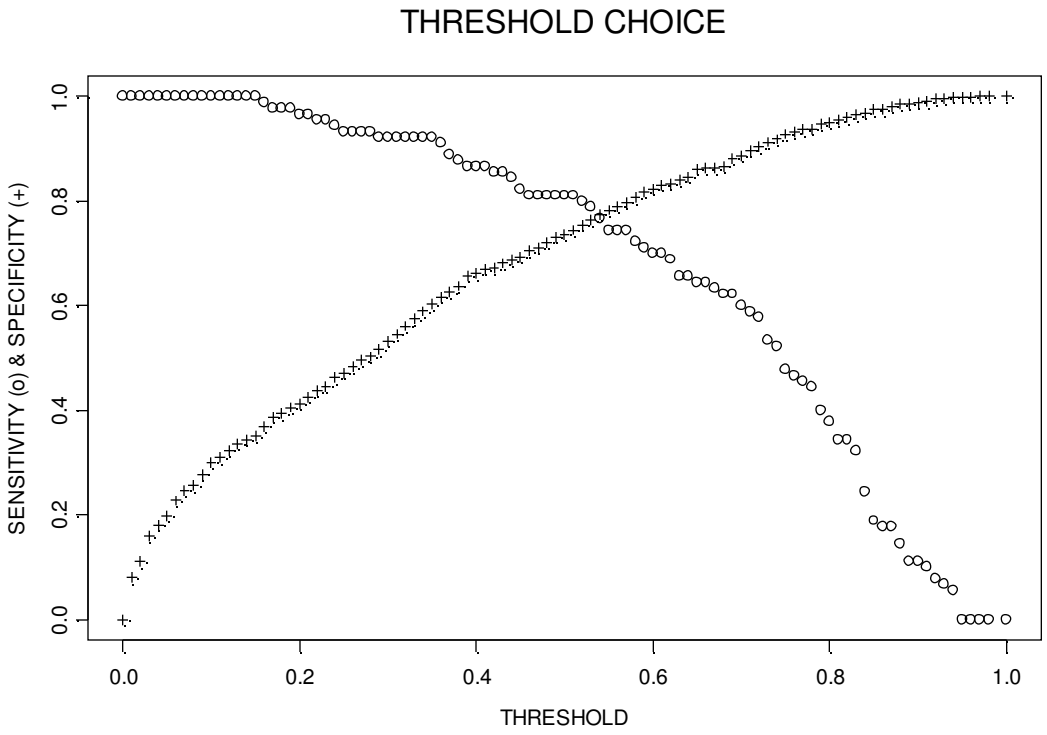
Appendix 8: Communes' map of the Prealps of the "Canton de Vaud"

Location of the 25 communes included in the study area, all occurrences (○) encountered during field work and the suitable surface for *H. mantegazzianum* (in red) obtained from GAM 3.3 model transformed into a binary map.



Appendix 9: Threshold choice

Intersection of sensitivity and specificity curves determines the threshold (0.535) optimising both measures.



Appendix 10: Morphological and invasive traits of *H. mantegazzianum* and management methods

Determination errors may annihilate any efforts of a conservation plan on alien invasive species. Indeed, *H. mantegazzianum* is very similar to *H. sphondylium*. *H. mantegazzianum* can be recognized by its tall adult shape, umbels disposition (with a main umbel in the top of the straight stem), high number of umbels' rays (50-150 rays), glabrous leaves. In contrary, *H. sphodylium* has a lot of ramifications and numerous umbels with no main straight stem, a lower number of umbels' rays (up to 45) and leaves with short and stiff hears (Aeschimann & Burdet 1994). Moreover, the giant hogweed has a specific strong odour (Hegi 1987) which we found useful for determination.

Several characteristics of *H. mantegazzianum* should be responsible for its ability to invade rapidly natural or semi-natural area. It is a hemicryptophyte which germinates in early spring outcompeting native vegetation (Caffrey 1999). It posses a high relative growth rate (Pysek & Pysek 1995), a high seed production, explaining the tendency of the species to form monospecific stands, and an efficient fruit dispersal by human activities, water and wind (Tiley *et al.* 1996). The giant hogweed flowers between the second and the fifth year of its life and then dies (Wadsworth *et al.* 2000). It has the ability to postpone flowering if grazing or unfavourable site conditions (Giant-alien Project 2002-2005). Because of early flowering and fructification time, seeds could already disperse in end of August (Caffrey 1999). Short vegetation period (4-5 months) allows the plant to grow in high elevations. Overlap of the male and female flowering phases allows self-fertilisation and producing viable self-pollinated seeds. One long-distance event enables the species to start an invasion (Giant-alien Project 2002-2005). The seeds have an extremely high percentage of germination (the majority within one year) and might float in water for up to three days (Tiley *et al.* 1996). Furanocoumarins containing in the sap have antimicrobial and antifungal properties (Tiley *et al.* 1996).

Attempting eradication an alien invasive species implies having good knowledge of its ecology. Mapping the current and potential distribution of *H. mantegazzianum* should be useful to orientate the eradication strategy. Management plans have to begin from upstream to downstream, especially at riversides. Long-term eradication of a species would be impossible if neighbouring sites act as seed sources (Wadsworth *et al.* 2000).

Eradication plan must be coordinate at regional scale and must be aimed at depleting seed bank in infested soils. Two different methods might be effective to eradicate giant hogweed's population: **physical** or **chemical action**. In Switzerland, the use of chemicals (herbicides) is forbidden along river, lake, road and railway sides and in forest and forest edges (Ordonnance sur la reduction des risques liés aux produits chimiques, ORRChim; RS 814.81) supporting the main habitats where the invasive species was observed in the Western Swiss Alps. Therefore, we encourage manager to respect this law for preserving native flora and fauna.

Concerning **physical action**, removing umbels, roots cutting, mowing and grazing are effective to stabilized population growth and eradicating the giant hogweed from infested area. Umbels should be removed, ideally, just after flowering, when seed are formed but not yet mature. Efficient regeneration (flowering) was observed after biomass removal (Giant-alien Project 2002-2005) and such technique need to be repeated frequently during flowering season and during several years until depletion of plant nutrient reserves leading finally to death. Root cutting is very effective, but expensive in time. Cutting should be done 10 cm below soil surface to kill the plant (Giant-alien Project 2002-2005). Deep ploughing of the soil (up to 24 cm) is also very effective. Mowing should be useful for larger population and must be repeated 2-3 times during the season. Mowing machine may enhance seed germination but may also spread seeds (Tiley *et al.* 1996). All cutting part of the plant must be removed from invaded area and destroyed. The large amount of organic material produced by the species could increase nutriment status in the ground making the conditions better for the species (Pysek & Pysek 1995). Repeated grazing and trampling with sheep, pigs, goats and cattle is a very efficient and cheap method (Anderson 1994). Young and small leaves are preferred. So, mature plants could survive (Tiley *et al.* 1996). Movement of animals especially cattle allows seed dispersal (Dawson and Holland 1999).

Large infested area or infrequently visited sites are best treated with **chemical** but physical management may be recommended only if frequent attention can be given through the growing season for cutting umbels (Dawson & Hollan 1999). The plant is susceptible to glyphosate: spray when plants are above 15cm because under this size,

young plants are less susceptible to spraying (5 l ha^{-1}) and therefore must be repeated several times during growing season.

Combined use of the methods should be a great strategy and continuing control until the population is eradicated. If fruiting is avoided, management could last 4-6 years. The most important care concerns seeds dispersal. Soil transport must be avoided. Motor cars, animals and human contribute to wide dispersal of giant hogweed.

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Wadsworth, R.A., Collingham, Y.C., Willis, S.G., Huntley, B., Hulme, P.E. (2005) Simulating the spread and management of alien riparian weeds: are they out of control? *Journal of Applied Ecology*, **37**, 28-38.

Appendix 11: Letter addressed to communes of the study area

We drew attention on local people in such a problematic species by sending them this letter.

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Mobile : 079 / 475.23.01
Secrétariat :
Tél. : +41 21 692 41 60

Greffe, Secrétariat communal
de la Commune de Aigle

Lausanne, le 24 août 2005

Concerne : Collecte de données et recherche scientifique sur la Berce du Caucase et l'Ambroisie

Madame, Monsieur,

Dans le cadre de mon travail de Master en Biologie de la Conservation à l'Université de Lausanne, je recherche des nouvelles populations de deux **plantes exotiques et invasives** qui posent des problèmes d'écologie et de santé dans les Préalpes vaudoises. La première espèce (la **Berce du Caucase** – *Heracleum mantegazzianum*) a été introduite dés la fin du XIX^{è} siècle par l'homme dans nombre de jardins botaniques ou jardins privés. Cette plante de grande taille provoque des brûlures et des cloques par la combinaison du soleil et d'un contact cutané avec une partie de sa tige ou des ses feuilles.
La deuxième espèce, l'**Ambroisie** (*Ambrosia artemisiifolia*), remonte actuellement la vallée du Rhône. Cette plante originaire d'Amérique du Sud cause, par son pollen, des allergies violentes qui peuvent conduire à une hospitalisation.

Ces deux plantes colonisent rapidement des milieux influencés par l'homme et dispersent leurs graines en grandes quantités le long des routes et des rivières. J'aimerais pouvoir répertorier les populations sources de ces deux espèces et ainsi retracer leur invasion. Ces informations permettront ainsi de dresser des cartes de répartition actuelles et potentielles de la distribution des ces deux plantes, de mieux comprendre leurs modes de colonisation et de proposer finalement un plan de gestion.

A cet effet, je vous serais très reconnaissant si vous pouviez me faire parvenir la localisation de lieux privés ou publiques hébergeant ces deux espèces sur le territoire de votre commune accompagnée, dans la mesure du possible, de la durée pendant laquelle elles ont été observées. Par ailleurs, la localisation de jardins botaniques connus, entretenus ou abandonnés, pourrait également constituer une aide supplémentaire dans mes recherches. Ces deux types d'informations seraient extrêmement utiles pour élaborer un éventuel programme d'éradication.

S'il n'est pas possible pour vous de me fournir ces informations, il me serait très utile d'obtenir une liste d'employés ou d'habitants de votre commune susceptibles de me fournir ce type de renseignements. Des renseignements nécessaires à l'identification de ces deux plantes sont en annexes avec des adresses de contact.
Il me sera aussi possible à la fin de l'été de vous fournir les emplacements des populations de ces deux espèces sur votre commune.

De plus, je me permets de vous demander l'autorisation de circuler sur vos routes communales normalement fermées au trafic, jusqu'à la mi-octobre.

J'espère que cette lettre saura retenir votre attention et dans l'attente d'une réponse de votre part, je vous adresse, Madame, Monsieur, l'expression de mes sentiments les meilleures.

Florian Dessimoz

Annexe : Adresses de contact et fiches descriptives des deux espèces concernées

Adresses de contact :

Nom	Antoine Guisan Professeur assistant	Olivier Broennimann Doctorant
Email	Antoine.Guisan@unil.ch	Olivier.Broennimann@unil.ch
Tel.	+41 21 692 42 54 +41 21 692 42 60	+41 21 692 42 69
Adresse	Université de Lausanne Département d'écologie et évolution Bâtiment de Biologie CH-1015 Lausanne	Université de Lausanne Département d'écologie et évolution Bâtiment de Biologie CH-1015 Lausanne

Berce du Caucase (*Heracleum mantegazzianum*) :

Ombellifère ornementale pouvant atteindre 3m50 de haut et dont les feuilles mesurent de 0.5 à 1m de longueur.

Attention : A ne pas confondre avec la Berce commune indigène, de taille inférieure.

Photo 1 : Berce du Caucase (*Heracleum mantegazzianum*), photo prise au lieu dit Pont Bourquin aux Diablerets cet été.

Ambroisie à feuilles d'armoise (*Ambrosia artemisiifolia*) nom commun herbe à poux :

Mauvaise herbe redoutée en agriculture à feuilles vertes sur les deux faces. Semences contenues dans mélange de graines pour oiseaux. Son pollen est très allergène !

Attention : A ne pas confondre avec l'Armoise vulgaire : feuilles vertes foncées dessus et blanches tomenteuses dessous.

Pour plus d'informations, consultez le site de la Commission suisse pour la conservation de plantes sauvages (CPS) :
http://www.cps-skew.ch/francais/info_plantes_envahissantes.htm

Le groupe de travail CPS a élaboré de brèves fiches pour les espèces de la liste Noire. Cette liste répertorie les néophytes envahissantes de Suisse, qui causent actuellement des **dommages au niveau de la diversité biologique, de la santé et/ou de l'économie**. L'expansion de ces espèces doit être empêchée.

Fiches descriptives individuelles :
Berce du Caucase : http://www.cps-skew.ch/francais/ambr_art_f.pdf
Ambroisie : http://www.cps-skew.ch/francais/hera_man_f.pdf

Photo 2 : Ambroisie à feuilles d'armoise (*Ambrosia artemisiifolia*)

Appendix 12: Preliminary study of the plastid DNA variation in *H. mantegazzianum* populations from Western Swiss Alps

Introduction

Studying genetic diversity and evolutionary changes of invasive species might allow better understanding basic population dynamic. Introductions of alien species widely occur due to worldwide enhancement of transport for tourism and economical exchanges. Such long-distance colonization events often permit few individuals to reach a new host range and may involve reducing genetic variation in new established populations through bottleneck process and genetic drift (Sakai *et al.* 2001). Thus, multiple introductions might increase probability of successful invasion. Evolution of increased competitive ability hypothesis (Blossey & Notzol 1995) might also be relevant to explain how a species become invasive. For this hypothesis, hybridization might justify such an increasing of fitness in introducing gene from native into invasive species (Ellstrand & Schierenbeck 2000).

In this preliminary study focused on the Giant Hogweed (*Heracleum mantegazzianum*), we aimed at revealing plastid DNA polymorphism for a following study.

Material and methods

Thirty-two individuals were sampled in eight invasive populations of *Heracleum mantegazzianum* (pop. no. 10, 42, 48, 49, 53, 66, 70 and 81; Figure 7). For each population, individuals, distant each other with at least 2 m, were sampled in a horizontal transect. For each individual, a single leaf was collected and desiccated in Silica gel. In addition, one individual (T1) suspected to be issued from hybridization between *H. mantegazzianum* and *H. sphondyllium* species was also analysed. Four individuals (Sp1-Sp4) belonging to *H. sphondylium* were lastly prospected on one site (Sp; Figure 7).

For each individual, DNAs were extracted using a CTAB method. All individuals were firstly characterized using two plastid DNA (ptDNA) microsatellite loci (ccmp5 and ccmp10; Weising and Gardner 1999) using the methodology described by Baali-Cherif and Besnard (2005). Two ptDNA spacers, *Trn*L-*Trn*F and *Trn*T-*Trn*L, were then sequenced for polymorphic haplotypes revealed in both *H. mantegazzianum* (individuals

10.4, 81.4 and T1) and *H. sphondylium* (Sp3 and Sp4). Based on these sequences, all individuals were characterized for three additional polymorphisms (del-1, del-2 and sub-2) in the *Trn*T-*Trn*L spacer. This characterization consisted by the PCR amplification of the *Trn*T-*Trn*L spacer followed by a restriction with the *Taq*I enzyme. Restriction fragments were separated on a 3.2% agarose gel.

A Reduced Median Network (Bandelt *et al.* 1999) was reconstructed to infer the phylogenetic relationships between the ptDNA haplotypes. This analysis was performed using the NETWORK software.

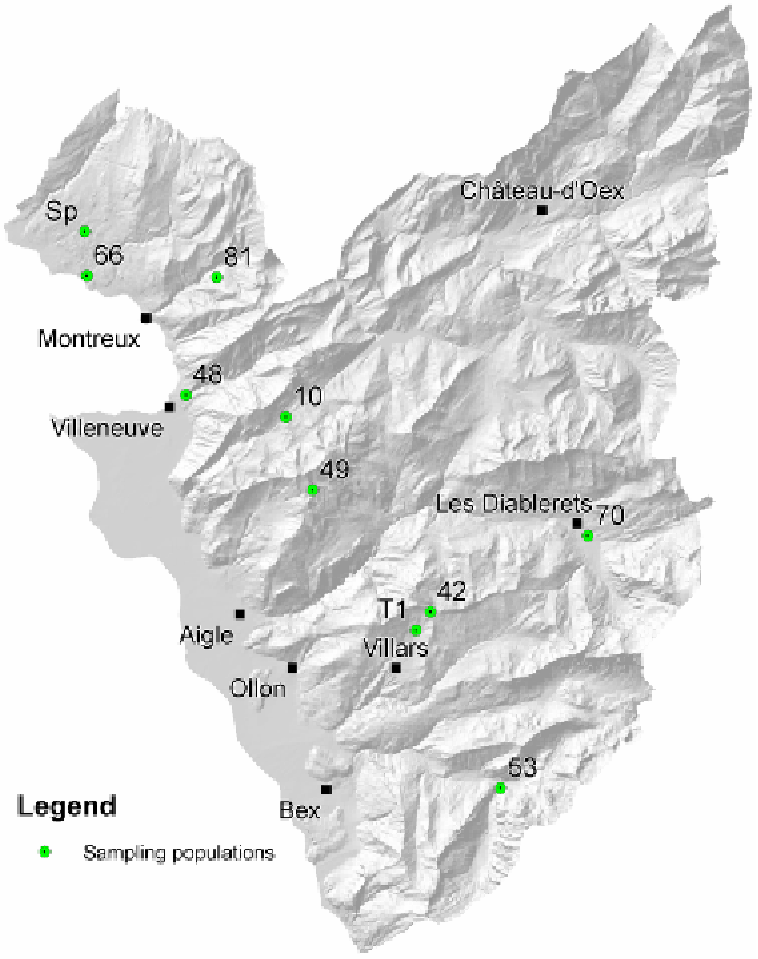

Figure 7: Locations of different sampled populations in the study area, the Western Swiss Alps in the "Canton the Vaud". Main localities are mentioned on the map.

Results

Both ccmp5 and ccmp10 rendered polymorphism in both *H. mantegazzianum* and *H. sphondyllium* (Table 8). Based on these loci, five distinct ptDNA haplotypes were revealed. Inter-genic spacer sequencing of these different haplotypes revealed six additional polymorphisms (two indels and four substitutions; Figure 8) in *Trn*T-*Trn*L, but no variation was found in *Trn*L-*Trn*F (data not shown). Using polymorphisms del-1, del-2 and sub-2 (Figure 8), five ptDNA haplotypes were finally revealed on the whole sample (Table 8). A reduced median network was reconstructed based on both microsatellites and *Trn*T-*Trn*L sequence data (Figure 9). Three distinct ptDNA haplotype lineages can be defined: the first one corresponds to the *H. sphondylium* haplotypes (HS.1 and HS.2); the second one to the *H. mantegazzianum* haplotypes HM.1 and HM.3; and the third one is only represented by the *H. mantegazzianum* haplotype HM.2.

Geographic distribution of ptDNA haplotypes are illustrated in Figure 10. The widely disperse haplotype is Hm.1. Haplotype Hm.2 was found in only three of the eight populations of *H. mantegazzianum*.

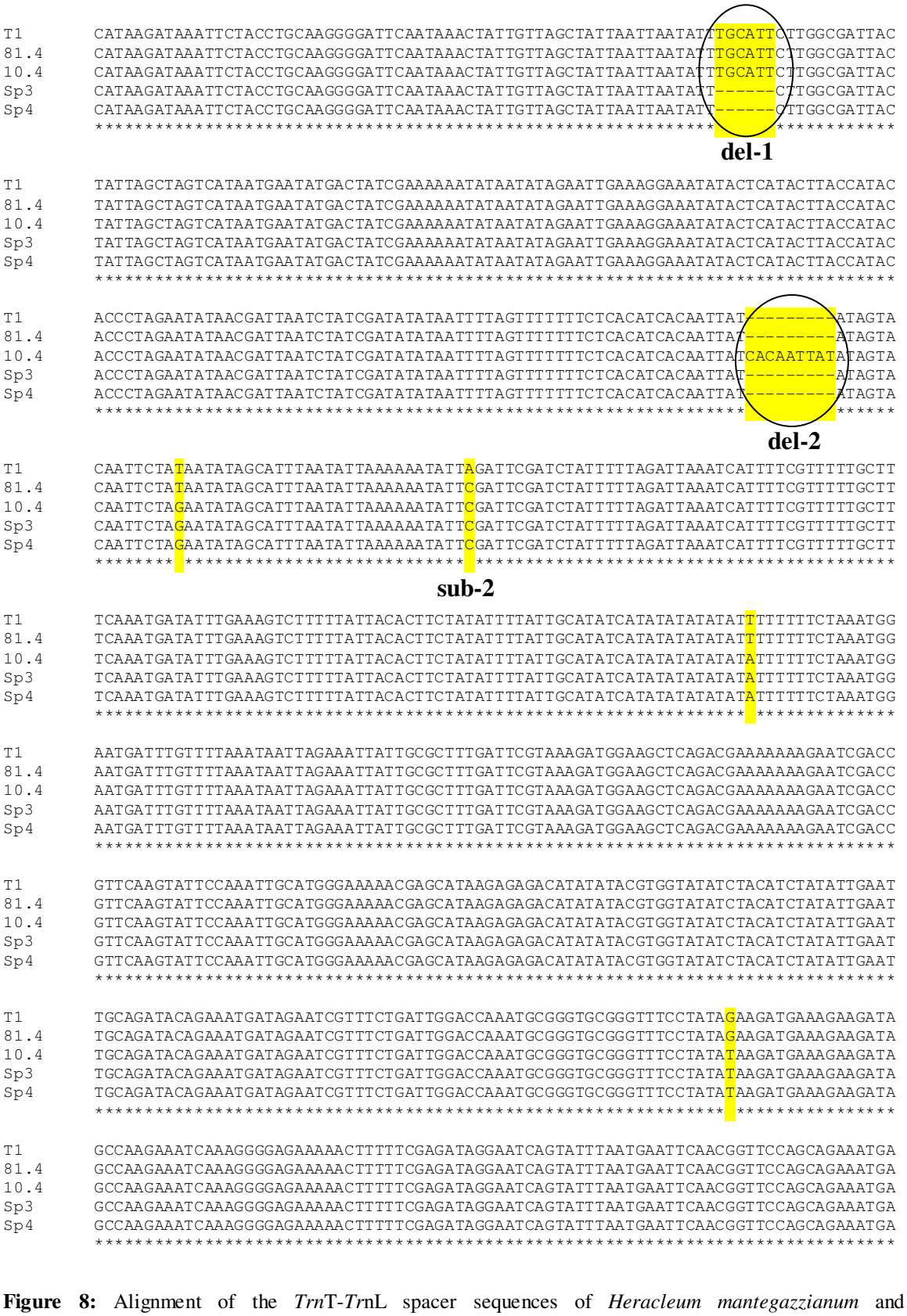

Figure 8: Alignment of the *Trn*T-*Trn*L spacer sequences of *Heracleum mantegazzianum* and *H. sphondylium*. Polymorphisms used to characterize all individuals are indicated (del-1, del-2 and sub-2).

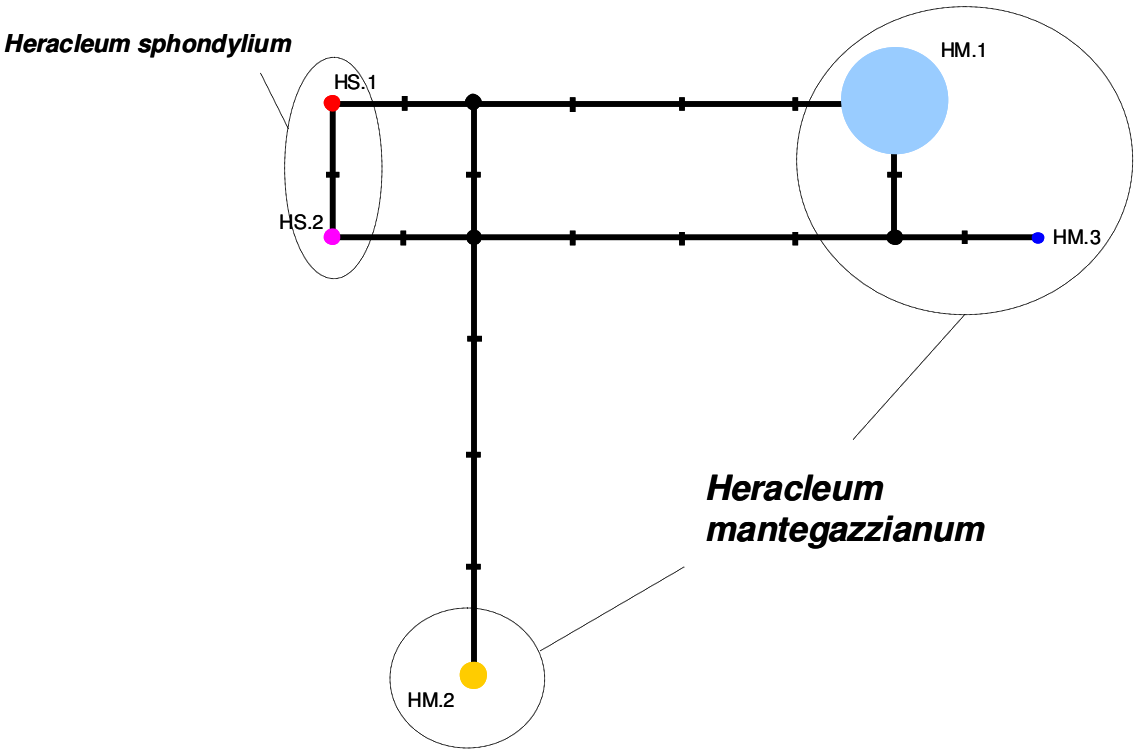

Figure 9: Reduced Median Network (Bandelt *et al.* 1999) representing phylogenetic relationships of the plastid DNA haplotypes revealed in *Heracleum mantegazzianum* (Hm.1, Hm.2 and Hm.3) and *H. sphondylium* (Hs.1 and Hs.2) in Western Switzerland. The circle size is proportional to the frequency of each haplotype. The network is based on both microsatellites and *Trn*T-*Trn*L sequence data.

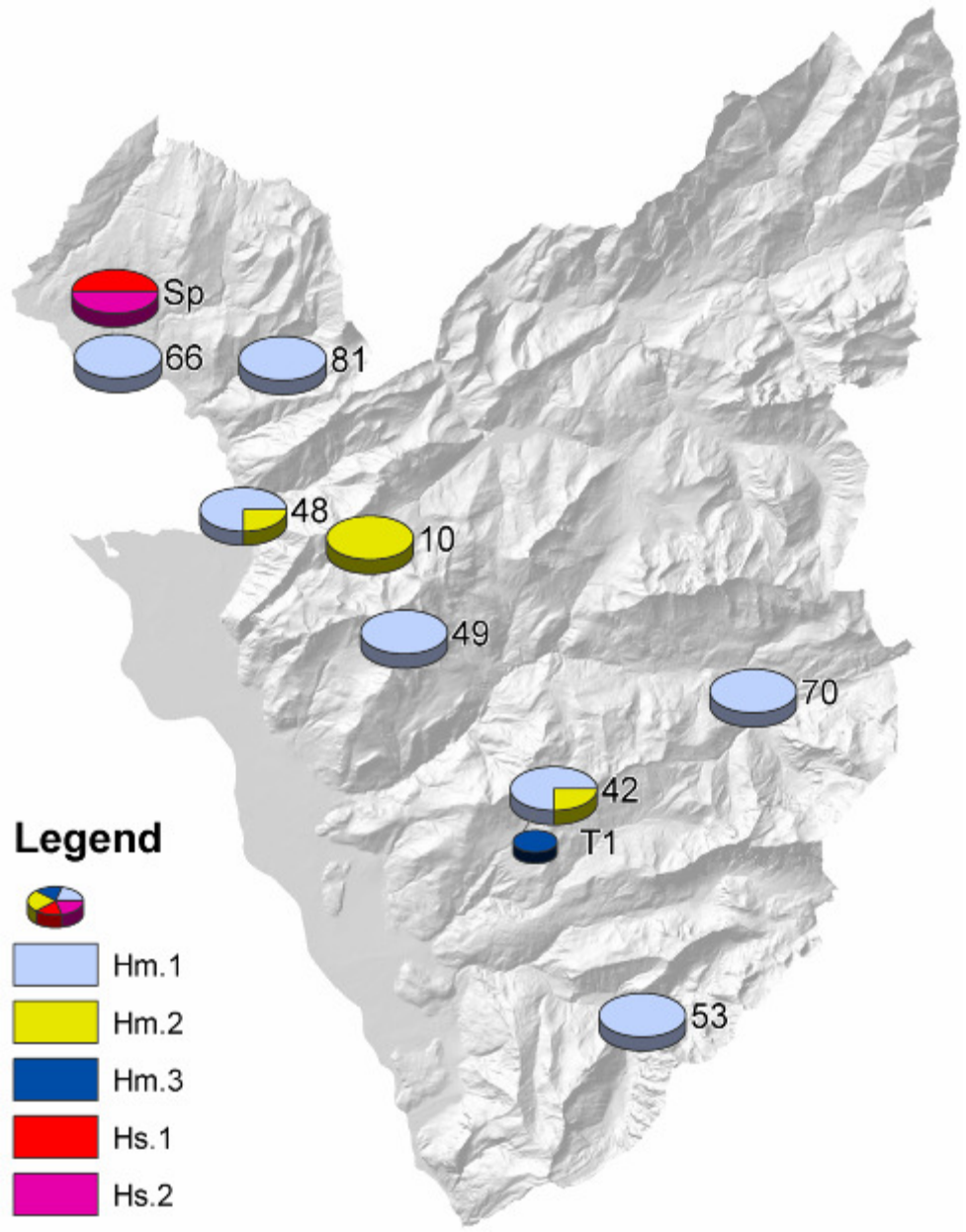

Figure 10: Geographical locations of ptDNA haplotypes. Names and colours of different haplotypes are the same as in Figure 9. Pies represent the proportion of different haplotypes in each sampled sites and their sizes are proportional to the sampled individuals.

Table 8: Plastid DNA profile of the 37 studied individuals. Allele size is given for ccmp5 and ccmp10, while absence (+) or presence (-) is indicated for restriction site and indels.

Individuals	*ccmp5*	*ccmp10*	*Trn*TL-*Taq*I	*Trn*TL-del1	*Trn*TL-del2
T1	105	98	+	-	+
10.1	106	99	-	-	-
10.2	106	99	-	-	-
10.3	106	99	-	-	-
10.4	106	99	-	-	-
42.1	104	98	-	-	+
42.2	106	99	-	-	-
42.3	104	98	-	-	+
42.4	104	98	-	-	+
48.1	106	99	-	-	-
48.2	104	98	-	-	+
48.3	104	98	-	-	+
48.4	104	98	-	-	+
49.1	104	98	-	-	+
49.2	104	98	-	-	+
49.3	104	98	-	-	+
49.4	104	98	-	-	+
53.1	104	98	-	-	+
53.2	104	98	-	-	+
53.3	104	98	-	-	+
53.4	104	98	-	-	+
66.1	104	98	-	-	+
66.2	104	98	-	-	+
66.3	104	98	-	-	+
66.4	104	98	-	-	+
70.1	104	98	-	-	+
70.2	104	98	-	-	+
70.3	104	98	-	-	+
70.4	104	98	-	-	+
81.1	104	98	-	-	+
81.2	104	98	-	-	+
81.3	104	98	-	-	+
81.4	104	98	-	-	+
Sp1	104	98	-	+	+
Sp2	105	98	-	+	+
Sp3	104	98	-	+	+
Sp4	105	98	-	+	+

Discussion

This study revealed relatively high genetic variations in plastid DNA of *H. mantegazzianum* in the sampled sites of the Western Swiss Alps where three different haplotypes were found.

High amount of morphological variation has been also observed on the field according to Ochsmann (1996). In our study, individuals displaying Hm.1 were not morphological distinguished to individuals displaying Hm.2. Moreover, individual belonging to Hm.3 haplotype had different morphological characteristics (i.e. hairy leaves). Our phylogenetic analyses clearly indicated that haplotypes Hm.1 and Hm.2 are very divergent. *H. mantegazzianum* is closely related to *H. sosnowski* and *H. persicum* (Giant-Alien project 2002). All these three species are considered as the Giant Hogweed group. Only the presence of *H. mantegazzianum* is confirmed in Switzerland but it is possible that previous gene flow between these taxa has occurred explaining the presence of highly divergent haplotypes in Swiss populations. Moreover, *H. persicum* is suspected to occur in the study area (in site 66) but genetic analyses could not confirm this hypothesis.

No evidences in plastid DNA variation confirmed the suspected hybrid (T1; Hm.3 haplotype) between *H. sphondyllium* and *H. mantegazzianum*. More individuals of *H. sphondyllium* will be analysed in the following study and nuclear markers (Walker *et al.* 2003) will also be investigated and may allow testing this hypothesis of hybridization between native and invasive *Heracleum* taxa.

No variation was found in the three populations found near or in Alpine Botanical Gardens where the species was introduced (corresponding to populations 49, 53 and 70) suggesting a single origin source of the species in these gardens.

This preliminary study aimed at revealing polymorphism of *H. mantegzzianum* will be followed in the current year and more analysed individuals might confirm some of our assumptions and underlying evolutionary processes on population dynamics of *H. mantegazzianum* during colonisation phase and retrace number of introduction events.

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NETWORK software: http://www.fluxus-engineering.com/sharenet.htm