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Modeling the invasive potential of Giant Hogweed (*Heracleum mantegazzianum*), investigating its impact on native species richness, and population monitoring in the Swiss Prealps

Master Thesis of Science in Behavior, Evolution and Conservation

by

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Modélisation du potentiel invasif de la Berce du Caucase, (*Heracleum mantegazzianum*), étude de son impact sur la richesse spécifique des communautés indigènes, et suivi des populations dans les Préalpes vaudoises

RÉSUMÉ

Les invasions biologiques sont une composante majeure du changement global, et un nombre croissant d'études ont eu pour but d'orienter les efforts de gestion. Anticiper la propagation et évaluer les risques pour la biodiversité indigène ainsi que les effets de la gestion sont d'une importance capitale dans ce contexte. La présente étude vise à répondre à de tels besoins concernant la berce du Caucase, *Heracleum mantegazzianum*, dans les Préalpes vaudoises, en s'appuyant sur des études antérieures dans cette zone d'étude et sur l'application de quatre méthodes: i) la calibration de modèles de distribution, à l'échelle mondiale et à l'échelle suisse, permettant ainsi l'évaluation de la répartition potentielle de l'espèce, ii) un échantillonnage adaptif aléatoire-stratifié basé sur le modèle, permettant d'estimer la densité de populations dans la zone d'étude ainsi qu'un éventuel changement d'invasion depuis la dernière estimation (2005), iii) des relevés de végétation, en mesurant l'effet de la berce du Caucase sur la richesse spécifique indigène dans les parcelles envahies, et iv) le suivi des populations enregistrées en 2005 afin d'évaluer l'efficacité des efforts de gestion entrepris. Les modèles prédisent que la distribution de l'espèce est associée à des hivers froids, à un climat continental ainsi qu'à des sols humides à l'échelle mondiale, et à une proximité aux lignes de transport et à de fortes variations de température à l'échelle régionale. Une seule grande population a été trouvée lors de l'échantillonnage aléatoire, ce qui n'a pas permis une estimation fiable de la densité dans la zone d'étude. Aucun effet de la berce du Caucase sur la richesse spécifique indigène n'a été détecté. Toutefois, puisque la majorité des parcelles envahies avaient un recouvrement bas de la berce du Caucase, nous ne pouvons pas exclure que celle-ci puisse causer des réductions significatives de la richesse spécifique à des recouvrements élevés. Le suivi des populations a montré que dans de nombreuses communes les populations ont diminué, mais dans d'autres elles ont demeuré constantes ou ont augmenté sur une période de huit ans (2005-2013). Cette étude donne un aperçu de la répartition potentielle de la berce du Caucase ainsi que de l'évolution temporelle des populations et souligne l'utilité des modèles de distribution d'espèces ainsi que le suivi continu des populations.

Modeling the invasive potential of Giant Hogweed (*Heracleum mantegazzianum*), investigating its impact on native species richness, and population monitoring in the Swiss Prealps

ABSTRACT

Biological invasions are a major component of global change, and growing research has aimed at guiding management efforts. Anticipating further spread and assessing the risks to native biodiversity and the effects of management are of key importance. We aim to meet such research needs concerning the giant hogweed, *Heracleum mantegazzianum*, in the Western Swiss Prealps, by building on previous works in the study area, and applying four methods: i) building species distribution models, at worldwide and Swiss scales, thus assessing species' potential distribution, ii) model-based random adaptive sampling in order to estimate population density in the study area and assess an eventual change of invasion status since the last such estimation (2005), iii) vegetation sampling and testing for an effect of giant hogweed on native species richness in invaded plots, and iv) monitoring of populations recorded in 2005 in order to assess the efficiency of management. Species distribution was predicted to be associated with cold winters, continental climates, and moist soils at a global scale, and proximity to transport lines and high temperature variation regionally. Random sampling resulted in only one large population occurrence, leading to an unreliable density estimate. No effect of giant hogweed on native species richness was detected, but we argue that since there was bias towards low giant hogweed covers in invaded plots, we cannot exclude that it may cause significant reductions of species richness at high covers. Monitoring showed that in many locations populations had decreased, but in others they had remained constant or increased over an eight-year period (2005-2013). This study provides insights into the potential distribution of giant hogweed and the temporal evolution of populations, and emphasizes the utility of species distribution models and continued population monitoring.

Keywords: invasive species, species distribution models, ecological impacts, monitoring, giant hogweed management

INTRODUCTION

Invasive alien species have been recognized as one of the biggest threats to global biodiversity, second only to habitat destruction and degradation among detrimental human activities (Wilcove et al. 1998; Clavero and García-Berthou 2005). Accordingly, the number of invasive species has been increasing over the past few centuries, due to the globalization of transport and trade, allowing species to cross natural biogeographic barriers and establish outside of their natural range (Lodge 1993; Hulme 2009). It is estimated that there are around 6'658 alien terrestrial plant species in Europe (www.europe-aliens.org), which often impact native biodiversity (Mooney and Cleland 2001; Vilà et al. 2011) and human health (Pyšek and Richardson 2010), and cause substantial economic losses (Pimentel et al. 2005).

Such invasion phenomena have prompted many research efforts concerning the biology of invasions, e.g. factors affecting invasion success (Rejmanek and Richardson 1996; Lloret et al. 2005) or dynamics of spread (Pyšek 1991; Müllerova et al. 2005), but also their practical implications: prediction of distribution (Thuiller et al. 2005), assessment of ecological (Ehrenfeld 2003; Brooks et al. 2004; Olden et al. 2004) and economic impacts (Vilà et al. 2010), and management planning in order to reduce these impacts (Pheloung et al. 1999; Zavaleta et al. 2001).

Predictive species distribution models (SDMs; Guisan and Thuiller 2005; Elith and Leathwick 2009) are proving to be powerful tools for such management and risk assessment studies (Thuiller et al. 2005; Vicente et al. 2011). In the case of invasive species, extracting bioclimatic variables from both native and invaded ranges (at global and more local scales) allows taking into account the largest possible range of conditions favorable to the study species (Broennimann and Guisan 2008). Matching these variables to a study area of interest then enables prediction of areas most favorable to the species, and thus most at risk of

57 invasion, in turn allowing the development of prevention measures and management plans
58 (Guisan et al. 2013).
59 Parallel to such predictive studies, which help anticipate further spread of alien species,
60 continued field monitoring is important, as it allows early detection of new invasions and
61 rapid response, which is more effective than mitigation and restoration after invasion (Pyšek
62 and Richardson 2010). Monitoring also assesses the efficiency of management once efforts
63 are under way, allowing for them to be improved and adapted upon to meet local needs
64 (Blossey 1999).
65 In addition, assessing the impacts of invasions allows identification of threats and
66 management planning. Although the issue of invasive species' impact on native communities
67 is often cited by ecologists, published studies that present particular measures of impact are
68 often lacking (Gordon 1998; Parker et al. 1999). Two main difficulties hinder the assessment
69 of ecological impacts of invasive species: first, the fact that biological invasions are identified
70 in a post-hoc manner (Müllerova et al. 2005), once the invasion is already under way, hence
71 the inability to observe ecological impacts as they happen in time, from entry to spread and
72 impact of the invader. Second, it is difficult to formulate a generalization of ecological
73 impacts of biological invasions, as they vary largely depending on the invader (Vilà et al.
74 2011), but also on the characteristics of the recipient community (Rejmánek 1989; Tilman
75 1999). Contrary to economic impact, there is no common currency for quantifying ecological
76 impact, leading to considerable difficulty in defining the nature and degree of these impacts
77 (Andersen et al. 2004).
78 Nevertheless, it remains important to define and quantify the impact of invasive species, and
79 to distinguish between those species with negligible and those with significant impacts on
80 native biodiversity, in order to prioritize management efforts (Byers et al. 2002). Terrestrial
81 plant invaders are among the taxa with the most species causing ecological impacts (Vilà et
82 al. 2010). However, while some directly impact native communities, through processes such

as allelopathy (*Acacia dealbata*, *Solidago canadensis*, Lorenzo et al. 2010; Zhang et al. 2009) or nitrogen fixation (*Robinia pseudoacacia*, Boring and Swank 1984), others, such as *Impatiens glandulifera*, may have more negligible impacts (Hejda and Pyšek 2006). Tall species that form dense monospecific stands, such as *Reynoutria japonica* or *Heracleum mantegazzianum*, tend to exclude native species simply by occupying large amounts of space in invaded habitats (Bímová et al. 2004; Hejda et al. 2009).

One way of assessing impacts of plant invaders on native species diversity is by comparing community characteristics of invaded and non-invaded plots of the same habitat type, an approach known as space-for-time substitution (Pickett 1989). This approach has been successfully applied in several invasion studies (Pyšek and Pyšek 1995; Bímová et al. 2004; Hejda and Pyšek 2006; Hejda et al. 2009), but despite its informative power, has remained infrequently conducted for such studies.

A prominent example of an invasive alien in Europe is the giant hogweed, *Heracleum mantegazzianum* Sommier & Levier. Native to the Greater Caucasus, it is now widespread throughout temperate Europe. This exceptionally tall forb (2-5 m) forms dense mono-specific stands and is a human health hazard, making it one of the species on the Black List of invasive species in Switzerland (www.infoflora.ch). Previous works on *Heracleum mantegazzianum* by Benetollo (2005) and Dessimoz (2006) in the Western Swiss Prealps of the canton of Vaud have focused on fitting species distribution models at the scales of Switzerland and of the Prealps, and conducting random-stratified adaptive sampling (Thompson and Seber 1996) in the study area. This sampling method is ideal for sparse but highly clustered species, as is the case for giant hogweed, and allows population density estimation in the sampled study area, which can be informative of current invasion status and therefore allow estimation of eradication costs. Dessimoz (2006) calculated such an estimate of giant hogweed population density in the study area, recorded abundances of all encountered populations during field work, estimated invasion status for communes of the

study area, and estimated the minimum cost of eradication for each commune. The present study builds on these earlier works on *Heracleum mantegazzianum* in the Western Swiss Prealps, aiming to meet further needs.

Focusing on four practical implications of giant hogweed invasion, we aim at:

i) Building species distribution models for giant hogweed, using a multi-scale approach (Gallien et al. 2012): by fitting models at both global (worldwide) and regional (Switzerland) scales, unlike in previous giant hogweed studies in the study area (Benetollo 2005, Dessimoz 2006), we aim to provide more informative insights into the species' potential distribution and ecology at these two scales.

ii) Estimating the density of giant hogweed in the study area: as done by Dessimoz in 2005, we aim to conduct adaptive sampling (Thompson and Seber 1996), based on the new model, and use the adaptive design to estimate the density of giant hogweed in the Western Swiss Prealps. The estimations from 2005 and 2013 can then be compared, in order to detect a possible change in estimated giant hogweed number over this eight-year period.

iii) Sampling of invaded plant communities along an altitudinal gradient in the study area and investigating the impact of giant hogweed on native species richness in invaded plots. Here we aimed at answering the following questions: Does giant hogweed presence and/or cover have an effect on native species richness? And if so, does this effect vary along the elevation gradient in the study area (i.e. among different communities found along this gradient)?

iv) Monitoring giant hogweed populations by revisiting those recorded by Dessimoz in 2005 and investigating their persistence and change in size; additionally, investigating whether new invaded sites were present in the study area.

METHODS

Study species

Heracleum mantegazzianum Sommier & Levier, the giant hogweed, is a monocarpic perennial forb of the Apiaceae family. In its native range, the Greater Caucasus, it occurs in clearings, meadows, and forest margins, often along streams, in montane areas (Mandenova 1950). It was first introduced to Europe as an ornamental in 1817, and is now widespread throughout temperate Europe, in at least 15 countries (Nielsen et al. 2005), as well as in North America (Page et al. 2006). The first record of giant hogweed in Switzerland dates to 1892, at the Botanical Gardens in Geneva. It was subsequently introduced to several alpine botanical gardens (including ones in the study area), from which it escaped repeatedly (Henry et al. 2009). Giant hogweed can reach up to 5 m in height, with several compound umbels, reaching up to 0.8 m in diameter. A single plant produces on average 20'000 seeds, but potentially up to 100'000 seeds (Tiley et al. 1996). Flowering occurs in July and August. The flowers are mostly pollinated by dipterans and hymenopterans, and plants are self-compatible (Tiley et al. 1996). Most seeds are dispersed close to the plant, but some can disperse much further, by water or human-mediated dispersal: dispersal is facilitated by roads and rivers, as the seeds can attach to car tires and be carried by road, or can float in water for up to three days and are often carried downstream (Wadsworth et al. 2000; Walker et al. 2003).

There are several problems linked to giant hogweed invasion in Europe. It often grows in dense stands and is dominant where it establishes, reducing native species diversity (Hejda et al. 2009). The exceptionally large leaves cause competition for light with other species. It can also hybridize with the native hogweed, *Heracleum sphondylium*, although hybridization rates appear to be very low where the two species co-occur (less than 0.1, Grace and Nelson 1981), and hybrids are virtually sterile (Weimarck et al. 1979). The plant often establishes along rivers, where it can cause increased erosion of the riverbank, as the above-ground vegetation

158 dies back each autumn, exposing bare soil (Roblin et al. 1994). It is also a human health
159 hazard, as the sap contains furanocoumarins, which, when in contact with the skin and
160 subsequently exposed to UV radiation, cause skin burning, which can be very painful and
161 leave life-long scars (Lagey et al. 1995). In Switzerland, giant hogweed is on the Black List of
162 invasive species (introduced species which pose a threat to native species, and/or to human
163 health; www.infoflora.ch).
164
165 **Study area**
166 The study area of the Prealps of the canton of Vaud, Switzerland (Fig. 1), is located at the
167 western edge of the Swiss Alps, covering a total area of 704 km^2. It is at the transition
168 between the Rhône Valley at the south-west edge and the foothills of the Alps to the east.
169 Elevations range from 372-3200 m asl. Dominant bedrock is calcareous. Annual mean
170 temperatures range from -3 to 10°C, depending on elevation, while mean total precipitation
171 ranges from 1060-2400 mm per year. Winters are cold and wet, with abundant snow fall.
172
173 **Species distribution modeling**
174 ***Multi-scale SDM framework***
175 We used a multi-scale modeling approach, in which SDMs were fitted at two scales: global
176 and regional (Gallien et al. 2012). First, a global SDM with worldwide species distribution,
177 using only climatic variables was built. This allows capturing the widest possible climatic
178 niche of the species (in both native and invaded ranges) and thus improving prediction power
179 (Broennimann and Guisan 2008). This global SDM based on the climatic niche was used in
180 two ways: (i) to predict the species' potential distribution in Switzerland; and (ii) to further
181 weigh pseudoabsences to be used in the regional SDM. For species for which the equilibrium
182 assumption does not hold (i.e. the species is not in equilibrium with its environment, as is the

183 case for invasive species), using the output of the global model in this way significantly
184 improves the predictive power of the regional model (Gallien et al. 2012).
185 The regional SDM was calibrated at a much finer resolution in Switzerland and included
186 climate but also disturbance and topographic variables affecting species distribution at a finer
187 scale (Guisan and Thuiller 2005; Lassueur et al. 2006).
188
189 *Global model*
190 Species occurrences were used for the widest possible range of giant hogweed. We extracted
191 coordinates of species occurrences from the GBIF database (www.gbif.org), providing data
192 points mostly for Central and Western Europe and North America (14'047 points total), and
193 from Info Flora (the Swiss national floristic database: www.infoflora.ch) for occurrences in
194 Switzerland (2'978 points). For the native range, population coordinates were taken from
195 Henry et al. 2009 (11 populations), as well as 42 population coordinates that were provided
196 by Pyšek (personal communication). Only occurrences with a precision higher than 1500 m,
197 or those which had coordinates of more than three numbers after the decimal were kept (9813
198 occurrences total). As the occurrence points were aggregated, occurrences were selected
199 randomly within each aggregate, by setting a 10 km minimal distance between occurrences,
200 thus reducing the effect of occurrence clusters in a way analogous to "occurrence thinning"
201 (Verbruggen et al. 2013). This resulted in 1617 occurrences after des-aggregation.
202 As the delimitation of the study area used to calibrate SDMs can have an important impact on
203 predictions (Barve et al. 2011), we tested three different calibration backgrounds using world,
204 biomes and ecoregions (Olson et al. 2001) where the species occurs as extents, and the
205 different model outcomes were compared. Within each of these extents, 10'000
206 pseudoabsences were randomly sampled.
207 Only climatic variables were considered for the global model, as they represent the most
208 important influences at this scale (Woodward 1987; Thuiller et al. 2004). The 19 bioclimatic

variables from Hijmans et al. (2005) and one soil water balance variable (www.cgiar-csi.org) were considered at a 30 Arc seconds (about 1 km) resolution. In order to select the best predictors for the global model and to avoid high correlation between predictors, the initial 20 predictors were clustered based on their correlation after extraction for each of the model calibration extents, and grouped into nine equidistant clusters (Fig. S1). One predictor in each group was then selected (from the ecoregions correlation clusters), based on it having the most direct ecological effect on the study species (Guisan and Zimmermann 2000; see Table 1 for selected variables).

Regional model

For the regional model, species occurrences for Switzerland were obtained from Info Flora, and those with a precision higher than 100 m were included. All data points recorded by Dessimoz (2006) for the Prealps study area were also included. This resulted in a total of 2361 occurrence points for Switzerland. Occurrences in Switzerland were des-aggregated, keeping a minimum distance of 250 m between occurrences, resulting in 1304 occurrence points after des-aggregation.

Two sets of 10’000 pseudoabsences were generated for the regional scale (Switzerland). A first set, to be used for model calibration, was biased towards areas in Switzerland predicted as unsuitable by the global ecoregions model (i.e. more pseudoabsences in unsuitable areas, Chefaoui and Lobo 2008, Gallien et al. 2012). A second pseudoabsence set for Switzerland was generated randomly, to be used for model evaluation. Both these pseudoabsence sets were sampled across all of Switzerland, but after exclusion of altitudes over 2’500 m asl (above which the species does not occur in Switzerland), as well as unsuitable primary surface categories such as lakes, glaciers, rock and scree (obtained from Swisstopo (www.swisstopo.ch); for included primary surface categories, see Table S1).

234 For predictor selection, the same method as for the global model was used for the regional
235 model. In total, 12 predictors were used at this scale (Table 2), at a 25 m resolution, out of an
236 initial 15 selected predictors (Fig. S1d). In addition to climatic predictors, topographic and
237 anthropogenic variables likely to influence distribution of the study species were included.
238
239 *Statistical analysis and spatial projections*
240 Models were developed in R CRAN (R Core Team, 2012), using the biomod2 package
241 (Thuiller et al. 2009), and fitted using three techniques: Generalized Linear Model (GLM,
242 Guisan et al. 2002), Generalized Boosted Model (GBM, Elith et al. 2008), and Maximum
243 Entropy model (MAXENT, Phillips and Dudik 2008). Model predictions and evaluations
244 were then averaged into a single ensemble model (Araújo and New 2007), in which all three
245 model techniques were given the same weight. This approach accounts for uncertainty of
246 individual models and leads to improvement of predictions compared to using a single
247 modeling technique (Thuiller et al. 2009). Biomod also assessed the importance of each
248 predictor variable through permutations, and provided response curves of the species for each
249 variable and modeling technique.
250 Models were evaluated using the Area Under the receiver operating characteristic Curve
251 (ROC AUC, Fielding and Bell 1997) and the True Skill Statistics (TSS, Allouche et al. 2006).
252 These two indices include both presences and absences in the evaluation. As biological
253 invasions are ongoing processes and all suitable area may not be colonized, we also computed
254 the Boyce index (Hirzel et al. 2006), a presence-only evaluator. Spatial projections were
255 mapped over the study area using ArcGIS (ESRI 2012). For the global model, predictions
256 were projected across the whole of Switzerland. For the regional model, projections were
257 made across the Prealps study area, after exclusion of altitudes over 2’500 m asl and
258 unsuitable primary surface categories (Table S1). The whole procedure (pseudoabsence
259 sampling, model calibration, evaluation and projection) was replicated ten times and values

(for model evaluation, variable importance and suitability) were averaged across the ten replicates. Mean suitability predictions of the global ecoregions model were converted into binary predictions (suitable or unsuitable) using the threshold corresponding to the maximum TSS (Freeman and Moisen 2008), in order to investigate the distribution of suitable pixels across the elevation gradient in Switzerland.

Field work

Random-stratified adaptive sampling

Following the work of Dessimoz (2006), random-stratified adaptive sampling was conducted (Thompson and Seber 1996). This approach allows for estimation of the species density and therefore of the total number of individuals in the study area. It is ideal for sparse but highly clustered species, as is the case for giant hogweed, which occurs in dense stands in locations reached by seed dispersal (Tiley et al. 1996). The sites to be visited were chosen based on a random-stratified design: ten strata were defined, corresponding to probability classes of the regional distribution model for giant hogweed in the Prealps study area, after exclusion of unsuitable primary surface categories (Table S1). In each stratum, ten points were randomly chosen, resulting in 100 sites to be visited (25 m x 25 m plots). If the species was present in one of the sites, the adaptive sampling method was carried out: the four neighboring plots were equally sampled, and the procedure repeated until the species was no longer found in neighboring plots, resulting in a network of plots which represent the whole population cluster (Fig. S2). For each visited site, we recorded a description of the site, as well as presence or absence of the study species, and if present, the number of individuals, their percent surface cover, and the presence of flowering individuals.

283 ***Community sampling***

284 For the community study, the goal was to investigate the impact of giant hogweed on species
285 richness in the study area by comparing invaded and non-invaded environmentally similar
286 plots. Complete vegetation inventories were carried out in 4 m x 4 m plots. The sites were
287 chosen once again based on a random-stratified design: four strata were defined across the
288 study area, this time based on the altitudinal gradient covered by known giant hogweed
289 populations in the study area (370-1'700 m asl). As plant communities change along
290 altitudinal gradients (McCain and Grytnes 2010), the effect of giant hogweed on communities
291 may also vary with altitude (since impacts of invasion vary depending on the recipient
292 community; Tilman 1999; Levine and Antonio 1999). By inventorying communities across an
293 elevation gradient, our aim was to have a sample of different habitat types, representative of
294 those found along the elevation gradient in the study area, and therefore investigate whether
295 giant hogweed effect varies with the altitude or habitat type of the community, or whether its
296 effect is independent of the altitude of the recipient community in the study area.

297 Four altitude strata were defined. Five invaded sites per altitude stratum were randomly
298 chosen among reported giant hogweed occurrences (resulting in 20 sites). Each time a site
299 where giant hogweed was present was inventoried (hereafter invaded site), a neighboring site
300 where the species was absent (hereafter non-invaded site) was also inventoried, resulting in 20
301 site pairs. These pairs were chosen so as to be of the same habitat type (Pyšek and Pyšek
302 1995). The invaded 4 m x 4 m plots were placed within the site so as to maximize the cover of
303 giant hogweed.

304 For both invaded and non-invaded sites, the complete list of vascular plants was recorded, and
305 the sampling was first done in a 1 m x 1 m plot, after which the plot surface was doubled by
306 sampling of an adjacent plot of equal surface area (Fig. S3). This process was then carried out
307 three more times, so as to result in a 4 m x 4 m plot. In this way, the effect of scale could be
308 investigated, as invasive species may have impacts that vary depending on the scale

considered (Sax and Gaines 2003), or that are detectable on multiple scales (Hejda et al. 2009). In addition, in the case of a significant effect of giant hogweed cover on species number, species-area curves between invaded and non-invaded plots could be compared, in order to visualize the effect of giant hogweed cover on the shape of the species-area curves in invaded plots. In each 1m x 1 m plot, the complete list of vascular plant species was recorded. In subsequent plots, only the new species present were recorded. In invaded plots, the number and percent coverage of giant hogweed and the number of flowering individuals was recorded for 2 m x 2 m and 4 m x 4 m plots.

Population monitoring

When revisiting a population that had been visited in 2005 and for which the abundance of giant hogweed stands was available from that year, we recorded whether the population had been found again in 2013, and if so we estimated whether the size of the population had increased, decreased or stayed constant since 2005, and recorded whether signs of eradication were visible (stems cut at the ground, leaves left over after mowing, withered individuals from herbicide injection).

Population coordinates obtained from Info Flora (www.infoflora.ch) upon request were also visited. For these points, no previous abundance data was available, so we merely recorded whether the population was found, and if not whether it was possible that giant hogweed had been confused with the native common hogweed, *Heracleum sphondylium* (Dessimoz (2006) had identified this as being the case with some reported occurrences).

Analysis of field data

Density estimation

Estimation of the actual giant hogweed population density in the study area, based on the random-stratified adaptive sampling conducted during field work, was carried out following

335 Thompson and Seber (1996), as done by Dessimoz in 2005 (refer to Supplementary Material
336 p.4, for details).
337
338 ***Invaded Communities***
339 We tested for an effect of giant hogweed presence and cover, and of the altitude strata, on
340 species number using a Generalized Linear Mixed Model (GLMM). The site (identical for
341 each plot pair), was set as a random factor. This was done for both 2 m x 2 m and 4 m x 4 m
342 plot sizes. We also tested whether average giant hogweed cover in invaded plots significantly
343 differed between the four altitude strata by one-way ANOVA.
344
345 ***Population monitoring***
346 We tested with a Chi-squared test whether the population status change from 2005-2013
347 (coded as either population size increase, decrease (including populations no longer found), or
348 remaining constant) differed across altitudes (coded as the four altitude strata used for the
349 community sampling), or across communes. For this, only communes with more than three
350 revisited occurrences were included.
351
352 **RESULTS**
353
354 **Predictive distribution models**
355 ***Model evaluation***
356 The models had high evaluation values, both at global and regional scales with AUC between
357 0.926 and 0.991, TSS between 0.725 and 0.928 and Boyce between 0.882 and 0.967 (Table
358 3).
359 Using larger calibration extents for the global model (world or biomes) produced higher AUC
360 and TSS values but lower Boyce index values than for the ecoregions model. Indeed, the

world model had the highest AUC and TSS values, but the lowest AUC threshold, TSS threshold and Boyce index values. The ecoregions model on the other hand, had the lowest AUC and TSS values, but the highest Boyce index (Table 3).

Variable importance

The most important variables for the global models were relatively consistent among the three different global models fitted. Maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), and temperature seasonality (bio4) were consistently among the four most important variables for the global models (Fig. 2 & Fig. S4). For two of the global models, those fitted at ecoregions and biomes scales, yearly soil water balance (sws2) was also among the four most important variables (Fig. 2 & Fig. S4B). Response curves for the ecoregions model indicate that giant hogweed distribution is limited by extreme maximum and minimum temperatures and extreme seasonality, and high aridity (i.e. low soil water balance; Fig. S5).

For the regional model, the most important variable was distance to roads, followed by number of frost days during growing season (sfroyy), annual temperature standard deviation (tvar) and number of precipitation days during growing season (pday) (Fig. 3). Response curves for regional predictors indicate that the species is found close to roads and in areas of high temperature variation (Fig. S6).

Suitability predictions

The suitability predictions of the global models, projected across Switzerland, were more refined for the model calibrated at the ecoregions level than at larger global extents (Fig. 4 & Fig. S7). After conversion into binary of the suitability predictions of the global ecoregions model projected in Switzerland, 68% of the country's surface was predicted as climatically suitable. Giant hogweed was predicted to avoid the high peaks of the Central Alps (Fig. 4),

and to prefer elevations under 2000 m (at colline, montane and subalpine altitude levels, with an optimum around 400-500 m; Fig. S8). This also holds for the Prealps, where the highest peaks were predicted as unsuitable (Fig. 5).

Field sampling and analysis

Stratified adaptive sampling

The stratified adaptive sampling resulted in one occurrence site for giant hogweed, out of the 100 sites visited. The resulting network, located at the Villars Golf Course, in the commune of Ollon, was composed of 44 plot squares in five probability strata, and a total of 6'570 individuals (Fig. S9).

Density estimation

The density estimation based on adaptive stratified sampling yielded an estimation of:

$\hat{u}_{st}$ x N = 949'972

individuals in the whole study area. $\hat{u}_{st}$ is the mean number of giant hogweed individuals per pixel, equal to 1.02, and N is the total number of pixels (25 m x 25 m plots) in the study area. Given that only one occurrence point was sampled, a measure of variance could not be calculated.

Invaded communities

Altitudes of sampled invaded communities ranged from 380-1494 m asl. Invaded habitat types were varied (for a description of sampled invaded sites, see Table S3). In lowlands, giant hogweed mostly invaded ruderal sites, and was found along forest or field edges, and along rivers and roads. At higher altitudes, communities of higher conservation interest were also invaded, such as wetland meadows (e.g. Calthion), and riparian and tall herb (megaphorb) communities. Species most often found alongside giant hogweed were common

and often nitrophilous or ruderal species (Table S4). Only 16% of total species found alongside giant hogweed in 4 m x 4 m plots were present in 30% or more of invaded sampled plots, illustrating the diversity of the latter. Cover of giant hogweed in invaded plots ranged from 1-97%, and tended to increase with altitude (Fig. S10), but this effect was not significant.

Impact on invaded plant communities

Giant hogweed presence and cover did not significantly affect species richness in invaded plots, in any of the altitude strata, and for both plot surfaces sizes tested (2 m x 2 m and 4 m x 4 m). On average species number in invaded plots was similar to that in non-invaded plots (Fig. S11).

Population monitoring

We visited 31 reported occurrence sites obtained from Info Flora. Of the latter sites, giant hogweed was found at only 17/31 sites, and for five sites, reported occurrences were likely identification errors, as native common hogweed, *Heracleum sphondylium*, was abundantly present, whereas no nearby giant hogweed populations were, the alien species being completely absent in the commune (e.g. in Rossinière). Hereafter, we focus on the populations reported by Dessimoz, as abundance data from 2005 was available for these populations, and as those taken from Info Flora are less reliable.

We visited 51 giant hogweed sites recorded by Dessimoz in 2005, out of 100 reported sites. Giant hogweed was found at 41 sites (80%). At 20/41 sites, giant hogweed abundance had decreased. At 14/41 sites, abundances remained about the same as in 2005, and at 7/41 sites, populations had grown larger. In addition, 15 new populations were recorded. Populations where giant hogweed number had decreased since 2005 were on average at lower altitudes (Fig. S12), but this effect was not significant. Population size changes did however differ

significantly among communes (p-value < 0.0001). Most population decreases had occurred in the communes of Corbeyrier and Montreux, while populations were mostly constant in Ormont-Dessous and Ormont-Dessus, and were constant or had increased in Ollon (Fig. S13). Populations were most frequently found in the communes of Ollon and Ormont-Dessus, as was the case in 2005. Populations found here were also the largest and often had many flowering individuals. Of the seven populations which had increased in size, six were in the commune of Ollon, as were 12 of the 15 new population occurrences (the rest being in Ormont-Dessous in both cases). The large population cluster sampled for density estimation was in Ollon, and five other populations of comparable size were found in this commune. In Ormont-Dessus and Ormont-Dessous, where the species was also highly present, populations were mainly found along the main road, and had mostly persisted since 2005 (Fig. S13).

In other communes, giant hogweed populations had decreased. In the commune of Yvorne and elsewhere along the Rhône River, where eradication efforts were evident (stems cut at the ground), giant hogweed had clearly declined since 2005, and was practically absent, apart from a few small specimens and leftovers from eradication. In Montreux, only one population was found (outside of the urban area, at higher elevation, along a hiking trail). All other populations visited in this commune were no longer found. In Corbeyrier, large populations were reported in 2005 along the roads of the Lac de l'Hongrin region. We found that although populations were still highly present along roads in this area, the number of stands had decreased, and individuals were small due to frequent mowing.

DISCUSSION

In this study, we applied four different methods to estimate the potential distribution, density, ecological impact and temporal evolution of giant hogweed populations in the Western Swiss Prealps. Predictive species distribution models, both at global and regional scales, were

informative of potential distribution, allowing anticipation of further spread, and having useful management applications. Population monitoring assessed the efficiency of management and identified areas where further efforts are needed. As for adaptive sampling and assessment of giant hogweed impact on native species richness, where the trends were non-significant, the limitations of these studies are discussed hereafter.

Predictive distribution model

Outputs of the global models confirmed the notion that calibration extents influence model outputs (Barve et al. 2011). In the present study, the global model calibrated at the scale of ecoregions produced the most refined spatial predictions, and had the highest Boyce index, suggesting that the ecoregions scale captured the global distribution of giant hogweed best. Ecoregions are built upon foundations of biogeography, and are nested within biomes, therefore providing more refined but still sufficiently global units to reflect species distribution (Olson et al. 2001).

The utility of the multi-scale approach is confirmed by the fact that the regional model, which took into account information from the global model, but used a different set of predictors and a finer calibration scale, produced more refined predictions for the study area compared with the global model (Fig. 4 & Fig. 5). Factors determining species distribution often act at multiple scales (Pearson et al. 2004; Guisan and Thuiller 2005). At the regional scale, we were able to additionally take into account variables that influence species distribution at a finer resolution than do gross climate features (Walter and Box 1976).

Factors explaining giant hogweed distribution at global scale

For the three different global models, three climate predictors were consistently among the most important, all relating to temperature: maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), and temperature seasonality (bio4),

491 with giant hogweed found in areas with intermediate maximum temperatures, low minimum
492 temperatures, and high temperature seasonality (Fig. S5). These climate preferences matched
493 climate conditions in the native range, the Greater Caucasus, where climate is predominantly
494 continental (Mandenova 1950).
495 The requirement of low winter temperatures is also confirmed by the species' biology, as
496 giant hogweed seeds need to undergo chilling in order to germinate (Tiley et al. 1996), and
497 confirms findings of previous studies in which giant hogweed distribution was also found to
498 be correlated with low winter temperatures (Pyšek et al. 1998; Nielsen et al. 2008). In
499 Switzerland, the species is found in mountainous areas (up to 2'000 m, Fig S8) where
500 minimum annual temperatures are low, although it avoids the highest alpine peaks, which
501 were predicted as unsuitable (Fig. 4). This avoidance of summits and their surrounding slopes
502 may partly be due to increased disturbance at low elevations, i.e. higher density of roads and
503 increased transport which allows seeds to be dispersed throughout lower elevations. In
504 addition, despite the species' need for cold winter temperatures, it generally finds its optimum
505 in high productivity habitats in montane zones (Thiele et al. 2007), where soils are of high
506 nutrient content (Landolt et al. 2009). Soils near summits are often thin and rocky, with low
507 nutrient content. Moreover, the alpine environment imposes many physiological constraints,
508 due to factors such as high wind and solar radiation, long lasting snow cover and short
509 growing seasons, favoring small species with early and rapid flowering (Billings 1974).
510 However, with global climate change such environments could become more suitable to
511 invasion, putting these fragile ecosystems at risk.
512 For two global models, those calibrated at ecoregions and biomes scales, yearly soil water
513 balance (sws2) was among the most important variables. The response curves indicate that the
514 species finds its optimum in areas with high soil water balance (Fig. S5), a finding that again
515 is consistent with the known species' biology. Indeed, giant hogweed prefers soils where

moisture is maintained throughout the year (Tiley et al. 1996, Landolt et al. 2009), and moisture is also required for seed germination (Tiley et al. 1996).

Factors explaining giant hogweed distribution at regional scale

The most important environmental predictors for the regional model, in order of average importance, were distance to transport lines, number of frost days during growing season (sfroyy), annual temperature standard deviation (tvar), and number of precipitation days per growing season (pday), with the species found close to roads and in areas with high temperature variation (Fig S6).

Proximity to transport lines was the most important predictor at the regional scale. For invasive species, as distribution is dependent on the introduction pathways resulting from human activities (Theoharides and Dukes 2007), and roads are known to be important dispersal means for invasive plant species (Parendes and Jones 2000; Pyšek, et al. 2007a; von der Lippe and Kowarik 2007), it is not surprising that this variable contributes significantly to determining species' distribution. The actual distribution of giant hogweed in Switzerland and in the Prealps is clearly related to the distribution of roads (Fig. S14), and the importance of this variable in predicting the species' distribution emphasizes that roads have been an efficient dispersal means for giant hogweed in Switzerland.

Watercourses are also known to be important dispersal vectors (Pyšek and Prach 1993), but in our model distance to watercourses was not as important in predicting regional distribution, suggesting that roads may take precedence as the main dispersal means for giant hogweed in Switzerland. Since giant hogweed is a short-lived monocarpic perennial that reproduces exclusively by seed (Pergl et al. 2006), this makes it dependant on habitat disturbance. Roads provide ideal dispersal and disturbance conditions for giant hogweed persistence and spread, achieving connectivity of individual metapopulations (Pergl et al. 2012).

The importance of the number of frost days during growing season in the regional model corroborates the seeds' requirement of chilling to undergo germination (Tiley et al. 1996), as mentioned above. Temperature variance throughout the year (tvar) was important also at the regional scale, as was temperature seasonality (bio4) at the global scale, supporting the preference for continental climates. The importance of the number of precipitation days during growing season (pday) at the regional scale is in agreement with the species' need for moisture for seed germination, and is consistent with the importance of high soil water balance (sws2) at the global scale, as well as with findings of Nielsen et al. (2008), where giant hogweed distribution was associated with spring precipitation. These findings thus confirm our knowledge of the species' ecology, but more importantly provide support to the use of species distribution models and spatial predictions for management purposes (Guisan et al. 2013).

Density estimation

The model-based field sampling did not provide a sufficient number of occurrences for a reliable estimation of population density. In 2005, Dessimoz found six occurrences using model-based sampling, and calculated an estimate of $\hat{u}_{st}$ x N = 3'316'215 ± 287'341 for the total number of individuals in the study area, a substantially higher estimate from the one in the present study ($\hat{u}_{st}$ x N = 949'972). This seems to indicate that globally the number of individuals has decreased since 2005. However, only one occurrence was found in our study, therefore the reliability of the estimate is uncertain, as a variance measure could not be calculated.

For the six occurrences found in 2005, networks were composed of four to 24 plot squares, adding up to 61 squares in total and 4'232 individuals. In 2013, we found a lower number of populations than Dessimoz (2005), but the one population found (44 plots and 6'570 individuals in total) was much larger than any encountered in 2005. This suggests that overall

567 eradication efforts have been carried out efficiently in the study area (therefore reducing the
568 number of populations), but that some remaining populations may have grown rapidly,
569 illustrating the expansion risk of non-controlled populations.
570 The fact that Dessimoz (2006) and others (Brown and Thomas 2000) applied the adaptive
571 sampling method successfully shows that it can be useful and informative. However, one of
572 the main challenges in applying it is planning for uncertainty of the final sample size (Smith
573 et al. 2004). Unlike conventional sampling designs in which sample size is fixed (i.e. 100
574 units to be sampled results in 100 sampled units), the final sample size in adaptive sampling
575 designs depends on what is found as the sampling is conducted (i.e. 100 units to be sampled
576 results in more than 100 sampled units if occurrences are found, since the neighboring units
577 are then also sampled). Smith et al. (2004) point out that final sample size will tend to be
578 highly variable in populations containing only a few large clusters, which seemed to be the
579 case in our study. If by chance the initial sample intersects a large cluster, many adaptive units
580 will be sampled; however, if a large cluster is not intercepted, the final sample size will be
581 equal to the initial sample size.
582 Here we sampled one such very large cluster. Brown (1994) proposes implementing stopping
583 rules (the sampling is stopped when a preset sample size is reached) in order to reduce the
584 maximum final sample size (by limiting the size of sampled clusters), but this may bias
585 results, and does not eliminate variation in final sample size. For the problem of finding only
586 one population cluster, the only solution remains increasing the initial sample size in order to
587 increase in turn the probability of intersecting occurrences.
588 In our sampling design, we excluded surfaces which were unfavorable to giant hogweed, such
589 as glaciers, agricultural lands and scree (Table S1). For a more efficient sampling, it would be
590 useful to also exclude forest layers. Forests represent the second largest primary surface
591 category in the study area, and many points fell within forest cover. However, giant hogweed
592 is rarely found within forested areas, and mostly remains along forest margins or in clearings

(Thiele et al. 2007). Keeping clear forest but excluding at least densely forested areas would therefore increase the chances of finding occurrences using random sampling.

Impacts on Invaded communities

We found no significant effect of giant hogweed presence or cover on species richness in invaded communities. In a similar study, Hejda et al. (2009) compared species richness between invaded and non-invaded plots in the Czech Republic, for 13 invasive species. Giant hogweed was one of the species with the largest impact on species richness, second only to *Reynoutria* species, causing reductions of 53% in plots with giant hogweed cover over 90%. This is to our knowledge the only other published study that directly investigated effects of giant hogweed on native communities.

In the present study, the main limitation to detecting an effect of giant hogweed presence was likely the fact that invaded plots of a large range of covers were included (covers ranged from 1-97%, compared to 90-100% in the study by Hejda et al.). At low covers, giant hogweed is unlikely to have an effect, as invaders mostly impact native communities only when they are dominant (Richardson et al. 1989; Pyšek and Pyšek 1995; Daehler 2003; Hejda et al. 2009). This may contribute to explaining the lack of effect of giant hogweed presence on species richness in invaded plots. Moreover, our sampling was biased towards low cover sites (Fig. S15). Indeed, 13 sites had giant hogweed covers equal to or under 30%, while seven had covers equal to or over 60%. Our altitude stratification was a constraint for cover, since we wanted to include sites distributed homogenously across the altitudinal range of the study area, but covers were not homogenously distributed across the altitudinal range. At low altitude strata, giant hogweed stands consisted of small and sparse individuals, and often evidence of management was found, leading to on average lower cover in plots (Fig. S10), although this effect was not significant. This trend could be due to the fact that eradication efforts were often carried out at lower elevations, where giant hogweed invasion decreases the

619 recreational value of highly frequented areas, such as river banks (the Rhône river banks are
620 frequented by walkers and cyclists) and urban areas (in the commune of Montreux), leading
621 to lower persistence in urban areas (Pergl et al. 2012). This is supported by the population
622 monitoring results, where we also found a trend of more population decreases at lower
623 altitudes (Fig. S12).
624 Our results may indicate that giant hogweed has no significant effect on species richness at
625 low covers, but it is likely that not enough high cover sites were included in order to detect an
626 effect at high covers. Based on previous evidence (Hejda et al. 2009), and on the biological
627 characteristics of the study species (dense covers and exceptionally large leaves which shade
628 light; Tiley et al. 1996), we cannot exclude the hypothesis that giant hogweed reduces species
629 richness at high covers.
630 It should also be noted that recording species abundances can provide valuable additional
631 information, and allow better identification of giant hogweed effects on native communities.
632 Indeed, in addition to reductions of species richness, Hejda et al. (2009) found negative
633 impacts of giant hogweed on Shannon diversity and community evenness. In fact, they
634 reported that impacts of invasion were generally weakest when measured as a decrease in
635 species richness, and stronger when measured as diversity and evenness. Invasive species may
636 favor some species while rendering others less abundant, an effect that would go unnoticed
637 when investigating species number alone. Therefore, measuring simply the number of species
638 lost due to invasion does not take into account possible modifications of community
639 composition (i.e. relative abundances of species in the community).
640
641 **Population monitoring and conservation biology application**
642 Monitoring the expansion or contraction of populations is of prime importance to assessing
643 the past and current invasion status of communes, which are the management units in
644 Switzerland for invasive species. Knowing the total distribution of the target species and

645 conducting regular evaluation of management projects are crucial to the projects' success
646 (Pyšek and Richardson 2010).
647 In the summer of 2005, Dessimoz reported the presence of 100 populations in the study area
648 (including the six found by adaptive sampling), adding up to 11'178 individuals. In 2013, we
649 counted 6'570 individuals in a single population for adaptive sampling (Fig. S9), while five
650 other populations of comparable size were found in the study area (all in the commune of
651 Ollon). The combined results of the adaptive sampling and population monitoring lead us to
652 think that giant hogweed presence has increased in the some locations of the Swiss Prealps
653 since 2005. Where conditions are favorable and no eradication measures are applied, giant
654 hogweed populations may rapidly increase, as illustrated by the large increases of some
655 populations over an eight-year period in the study area.
656 In 2005, Dessimoz reported that Yvorne was the commune having the second highest invasive
657 status ratio (number of occurrences over total suitable surface, equal to 5.26 for Yvorne in
658 2005), due to the high number of populations observed along the Rhône River, and the small
659 commune size. Eight years later, giant hogweed was practically absent from the Rhône river
660 banks, apart from a few small specimens that displayed evidence of eradication efforts. In the
661 commune of Montreux, populations were equally on the decline, as only one population was
662 found. Such successful management provides encouraging evidence that long-term
663 eradication measures are efficient in reducing the size and cover of plants (Nielsen et al.
664 2005), thus also reducing the risk of skin burning for humans, and avoiding seed production
665 and further spread.
666 On the other hand, in non-managed areas, giant hogweed populations may rapidly increase if
667 conditions are favorable (Nielsen et al. 2005). In 2005, most populations were found in the
668 communes of Ollon and Ormont-Dessus, which had the highest estimated eradication costs
669 and were among the communes with the highest invasive status ratios (2.81 and 2.61,
670 respectively). In 2013, populations of giant hogweed were again found most frequently in

671 these two communes, and were also the largest populations found in the study area, with
672 many flowering individuals. Most new populations encountered were in the commune of
673 Ollon, and six populations in the commune had increased in size since 2005.
674 Current invasion status was therefore mostly correlated with past invasion status in the study
675 area, with the most highly invaded communes remaining constant over the investigated time
676 period. The fact that population increases have taken place in areas that were already highly
677 invaded suggests an intermediate invasion stage, in which spread from neighboring suitable
678 habitats is important (Nielsen et al. 2008). The importance of transport lines as predictors of
679 species distribution in Switzerland also supports the hypothesis of an intermediate invasion
680 stage, in which spread is still highly dependent on human dispersal means (Pyšek et al.
681 2007a), resulting in species presence along such habitats with high disturbance. In later
682 phases of invasion, invasive species may establish in more natural habitats with less human
683 disturbance (Richardson et al. 2000). Such populations that are clustered within close
684 proximity (e.g. in the same commune) are more likely to persist (Pergl et al. 2012) and spread,
685 as the probability that an area will be colonized is a function of its distance from neighboring
686 populations (Pyšek et al. 2007b). Presence along roads also facilitates the persistence and
687 spread of populations.
688 Since large surfaces in highly invaded communes are predicted as favorable to giant hogweed
689 (Fig. S13), large areas may be prone to invasion in following years if no action is taken.
690 Moreover, highly invaded communes are at relatively high altitudes (compared to the Rhône
691 Valley at the western edge of the study area), meaning that giant hogweed populations present
692 there may act as source populations, dispersing seeds along tributary rivers (as can be seen
693 along La Gryonne) downstream to other communes, where conditions are equally (or more)
694 favorable.
695 Establishment of priority management areas should take into account such considerations, and
696 linear habitats which are good vectors for seed transport, such as riverbanks and roadsides

(Pyšek and Prach 1994; von der Lippe and Kowarik 2007), should be given management priority. The conservation value of an invaded community may also be taken into account, as giant hogweed invades a wide range of communities, some of which are of higher conservation interest (Hejda et al. 2009), and should also be given management priority. In an effort to provide useful information for management, the communes of the study area will be informed of the present work.

CONCLUSION

Although the density estimation and species' impact studies were not conclusive, due to the above-mentioned limitations, their successful application in other studies (Dessimoz 2006, Hejda et al. 2009), confirms their respective informative powers when applied successfully. The species distribution models provided informative insights into giant hogweed's ecology and potential distribution, and population monitoring assessed the current invasion status of giant hogweed in the Western Swiss Prealps, and its temporal evolution since 2005. Considering the large area and density occupied by giant hogweed stands and the fact that it is a human health hazard, it can be an important nuisance in the landscape. It is widely accepted that the impact of such invasions will increase in the future and taking immediate action allows mitigating future impacts and economic costs. The present study provides useful insights for management, allowing anticipation of further spread and assessment of areas where further management is needed, and emphasizes the utility of predictive distribution models and continued population monitoring in invasion studies.

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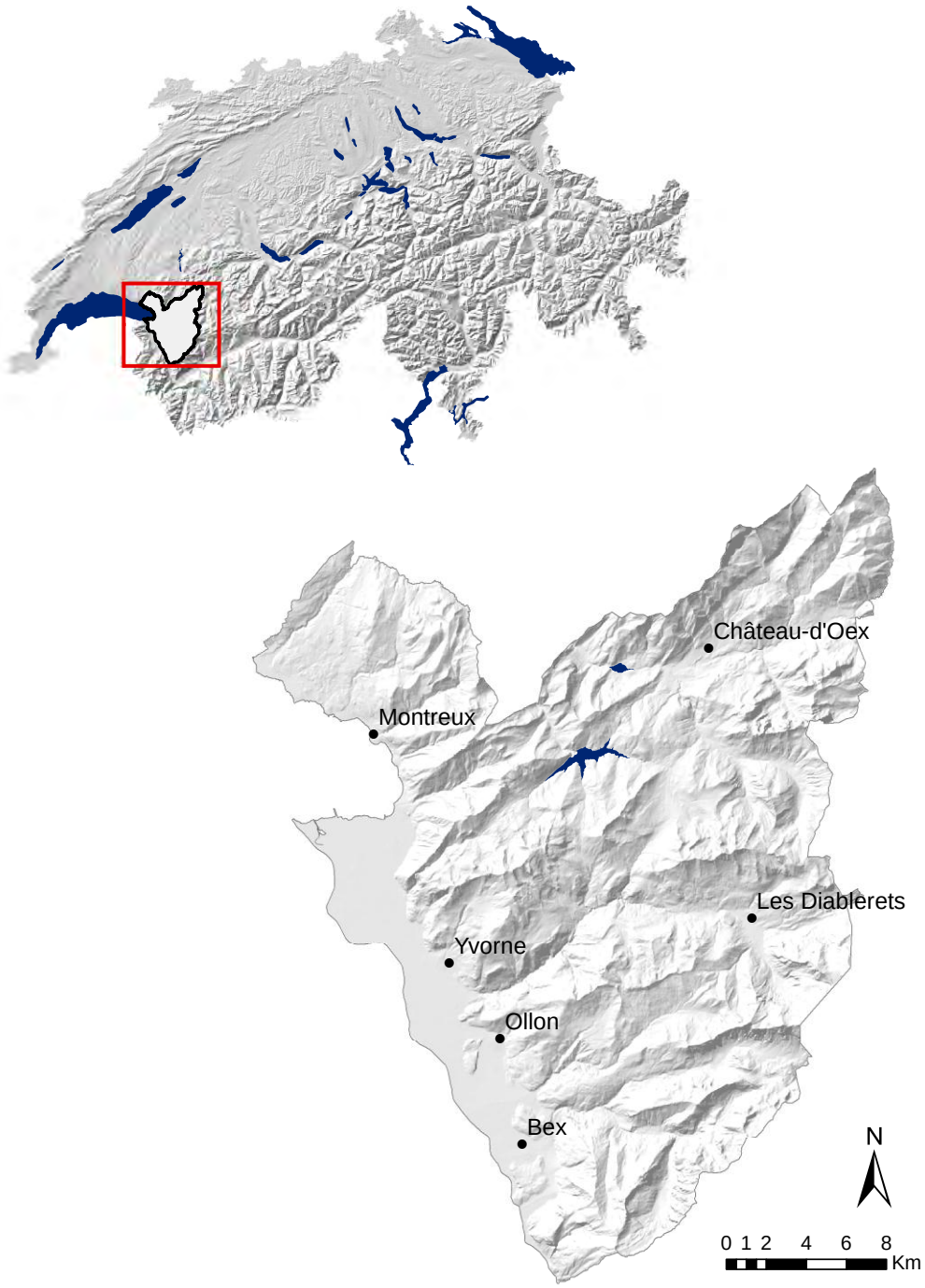


975 **Figure 1.** Localization within Switzerland of the study area of the Prealps of the canton of

976 Vaud, and close up of the focal area, with indication of some major towns.

Abbreviation	Predictor variable	Unit	Source
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	°C	Hijmans et al. 2005
bio3	Isothermality (mean diurnal range/annual range) (* 100)	°C*100	Hijmans et al. 2005
bio4	Temperature Seasonality (standard deviation *100)	°C*100	Hijmans et al. 2005
bio5	Maximum temperature of warmest month	°C	Hijmans et al. 2005
bio6	Minimum temperature of coldest month	°C	Hijmans et al. 2005
bio12	Annual precipitation	mm	Hijmans et al. 2005
bio15	Precipitation Seasonality (Coefficient of Variation)	mm^2	Hijmans et al. 2005
bio17	Precipitation of Driest Quarter	mm	Hijmans et al. 2005
sws2	Yearly soil water balance (effective precipitation + irrigation - actual evapotranspiration - soil runoff)	mm	Calculated from Monthly soil water balance, from CGIAR-CSI (www.cgiar-csi.org)

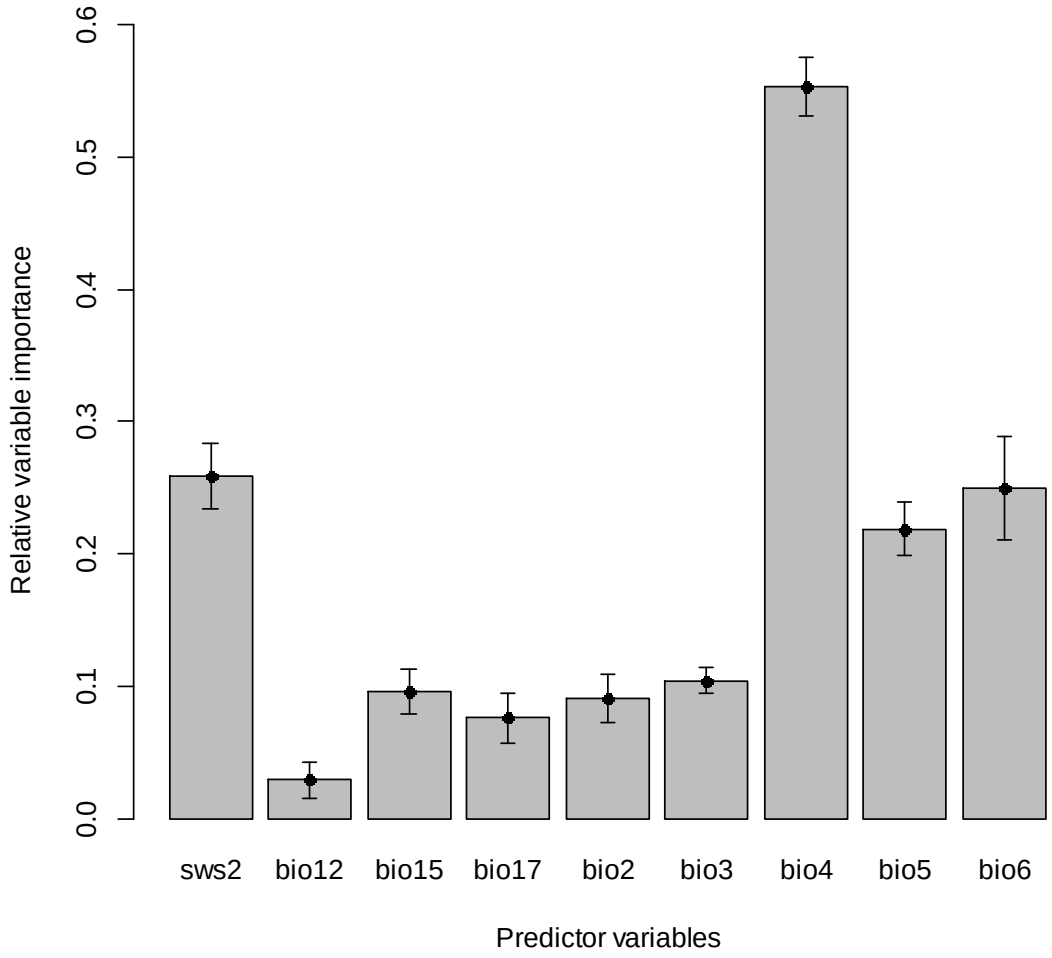
977 **Table 1.** Climate variables included in the global distribution models for giant hogweed
978 (calibrated at a global scale, and projected across Switzerland).

Abbreviation	Predictor variable	Unit	Source
tvar	Annual standard deviation of monthly mean of average temperature (1961-1990)	°C	Calculated from tave1-12 from Zimmermann and Kienast 1999
min_temp	Annual mean of monthly mean of minimum temperature (1961-1990)	°C	Calculated from tave1-12 from Zimmermann and Kienast 1999
sfroyy	Annual mean number of frost days during growing season	days	Zimmermann and Kienast 1999
sradyy	Annual mean of monthly global potential shortwave radiation	KJ	Zimmermann and Kienast 1999
pday	Annual mean number of precipitation days per growing season (1961-1990)	days	Zimmermann and Kienast 1999
pvar	Annual standard deviation of monthly mean precipitation sum (1961-1990)	mm	Calculated from prec1-12 from Zimmermann and Kienast 1999
mindyy	Annual mean of monthly moisture index (P - PET)	mm	Zimmermann and Kienast 1999
topo	Topographic position	unitless	Zimmermann and Kienast 1999
roads	Euclidean distance to roads and railway lines	m	Calculated from Swisstopo transport layers (1^{st}-3^{rd} category roads, highways and train tracks) in ArcGIS (Esri, 2008)
forest	Euclidean distance to forest edge	m	Calculated from vector25 (forest) from Swisstopo
geb	Density of buildings in 250m radius	unitless	Calculated from vector25 (geba) from Swisstopo
water	Euclidean distance to water (streams, rivers & lakes)	m	Calculated from Swisstopo water layers (lakes, rivers)

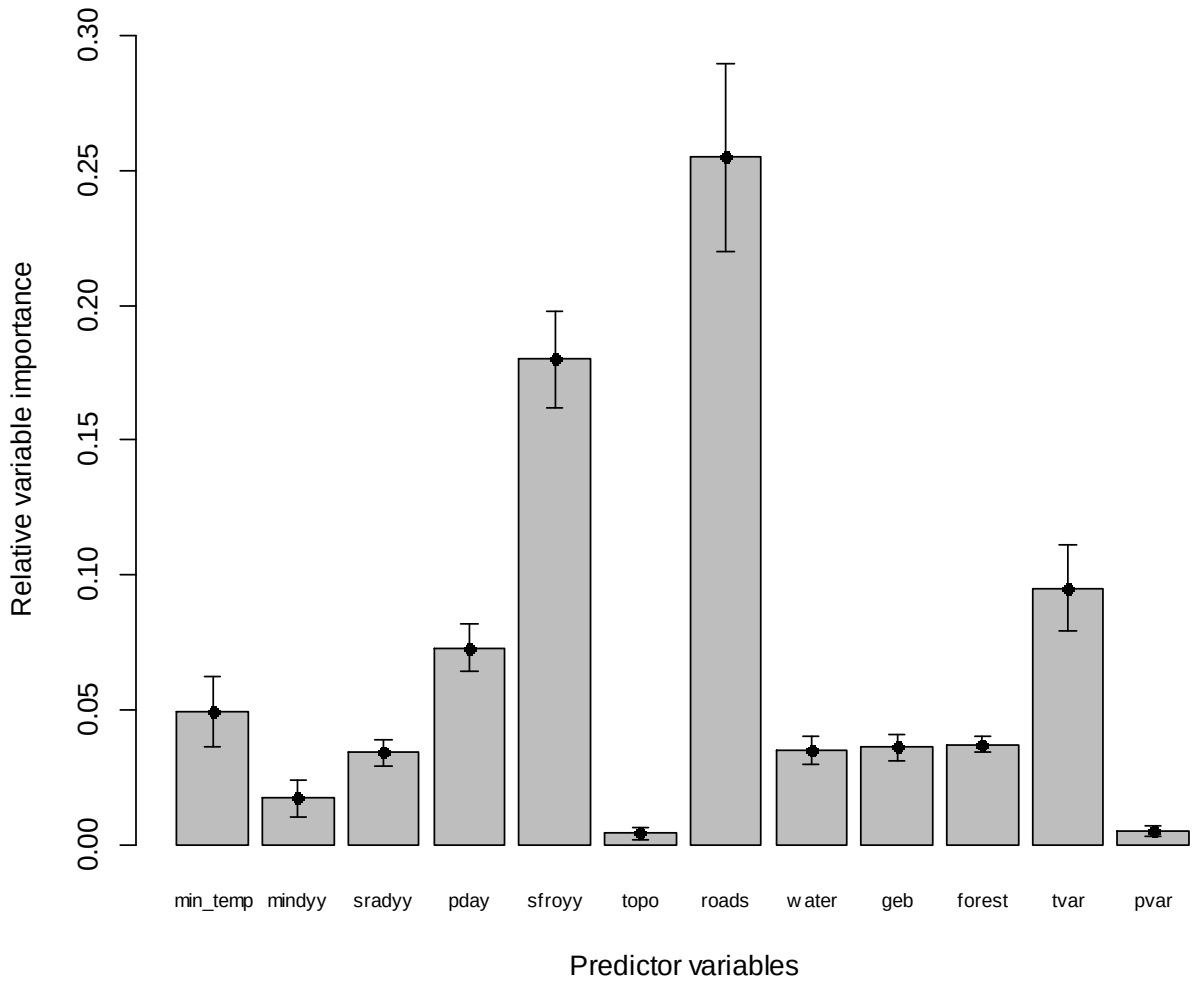
Table 2. Climatic, topographic and anthropogenic variables included in the regional distribution model for giant hogweed (calibrated at the scale of Switzerland, and projected across the study area of the Western Swiss Prealps).

Global models						Regional model	
A		B		C			
Evaluation metric	**Value**	**Evaluation metric**	**Value**	**Evaluation metric**	**Value**	**Evaluation metric**	**Value**
TSS	0.928	TSS	0.894	TSS	0.725	TSS	0.79
AUC	0.991	AUC	0.983	AUC	0.926	AUC	0.96
TSS threshold	437.6	TSS threshold	483.1	TSS threshold	481.5	TSS threshold	531
AUC threshold	434.7	AUC threshold	485.8	AUC threshold	480.1	AUC threshold	531.5
Boyce	0.882	Boyce	0.905	Boyce	0.967	Boyce	0.914

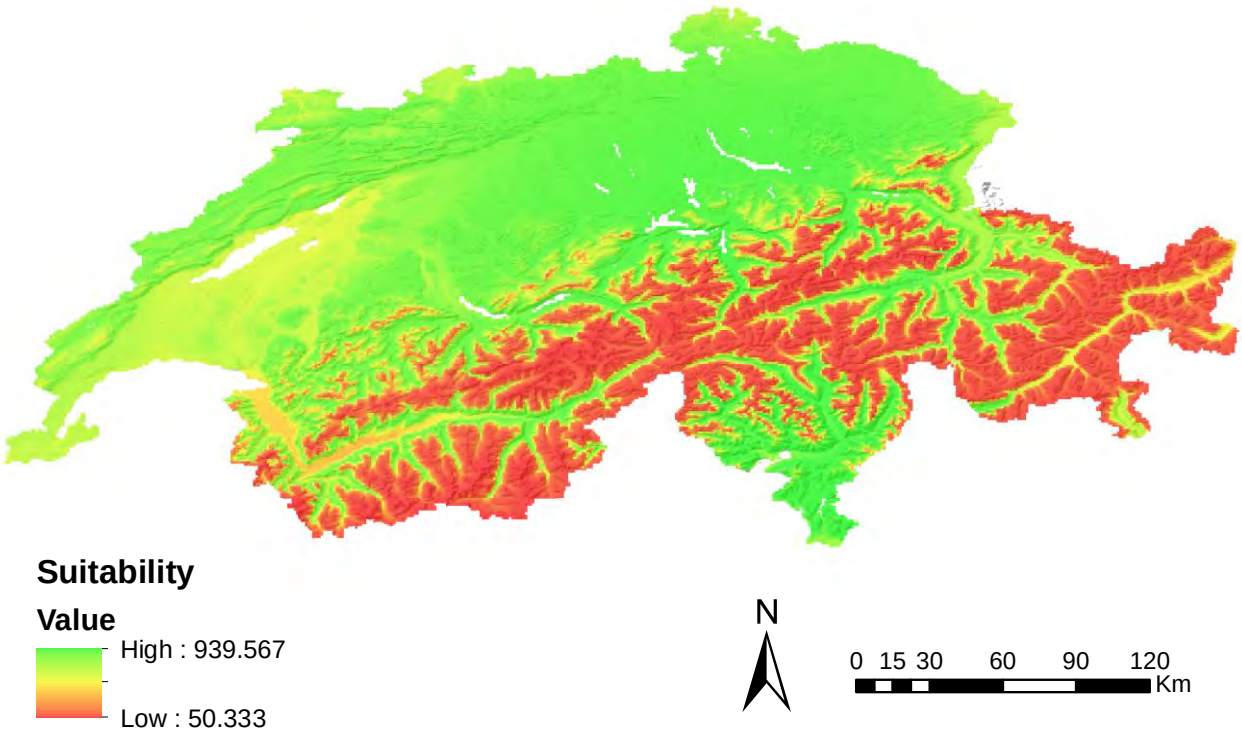
982 **Table 3.** Evaluation values for the global distribution models for giant hogweed (A to C:
983 calibrated at world, biomes and ecoregions scales, respectively), and for the regional model
984 (calibrated at the scale of Switzerland). Values are means across ten model replicates.



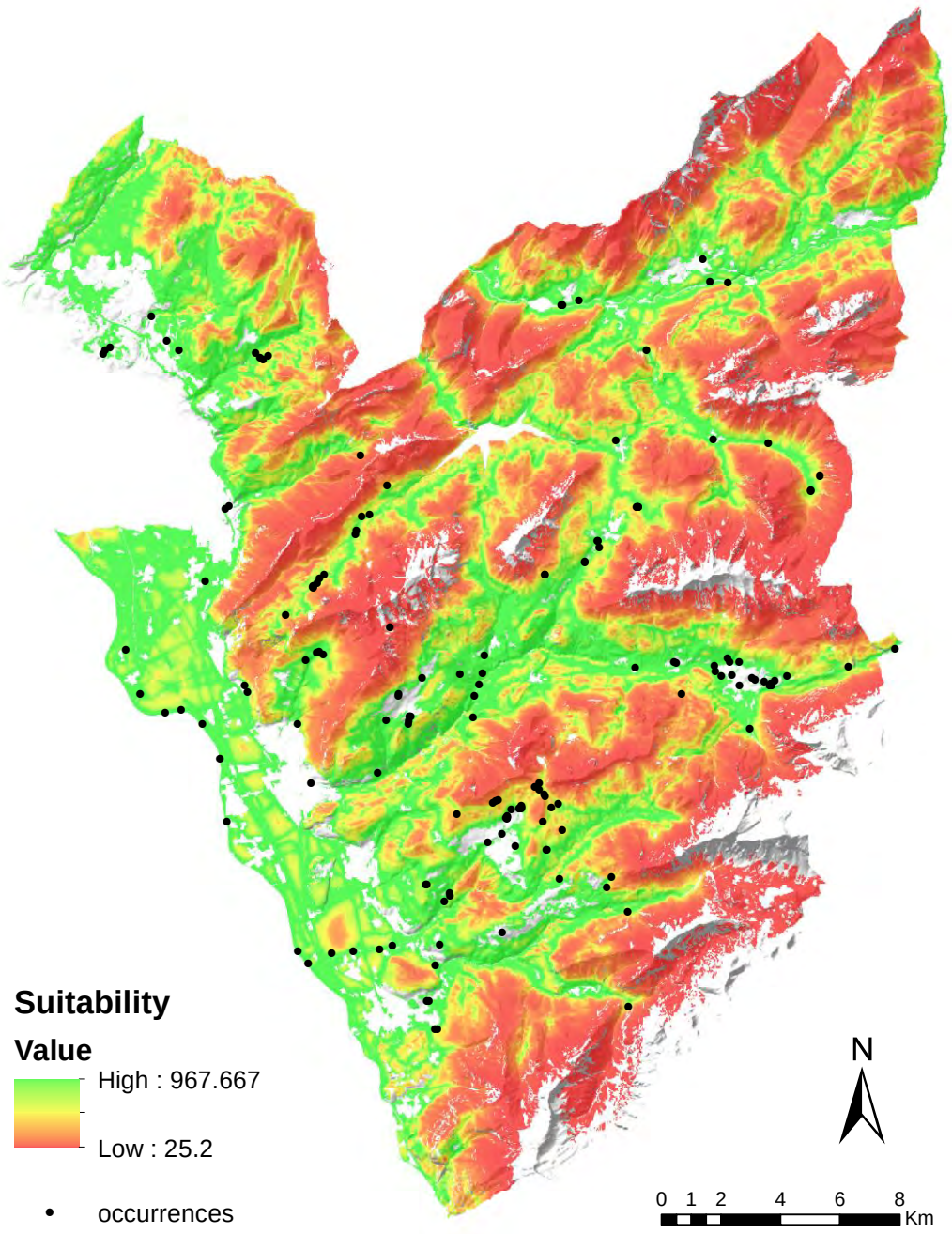
985 **Figure 2.** Importance of climatic variables included in the global ecoregions distribution
986 model for giant hogweed. The global model was calibrated at the scale of global ecoregions.
987 Variable importance was assessed through permutations, and values shown are means across
988 ten model replicates. For a description of variables corresponding to abbreviations, see Table
989 1.



990 **Figure 3.** Importance of predictor variables included in the regional distribution model for
991 giant hogweed. The regional model was calibrated at the scale of Switzerland. Variable
992 importance was assessed through permutations, and values shown are means across ten model
993 replicates. For a description of variables corresponding to abbreviations, see Table 2.



994 **Figure 4.** Suitability predictions of the global ecoregions distribution model for giant
995 hogweed (calibrated at the scale of global ecoregions, and projected across Switzerland).
996 Suitability values are means across ten model replicates.



997 **Figure 5.** Suitability predictions of the regional distribution model for giant hogweed
998 (calibrated at the scale of Switzerland, and projected across the study area of the Western
999 Swiss Prealps). Suitability values are means across ten model replicates. Previously available
1000 species occurrences in the study area are shown.

Modeling the invasive potential of giant hogweed (*Heracleum mantegazzianum*) in the Swiss Prealps, investigation of its impact on native species richness, and population monitoring

Supplementary Material

Master Thesis of Science in Behavior, Evolution and Conservation

Mila PAJKOVIC

Director: Prof. Antoine Guisan
Supervisor: Blaise Petitpierre
Department of Ecology and Evolution

January 2014

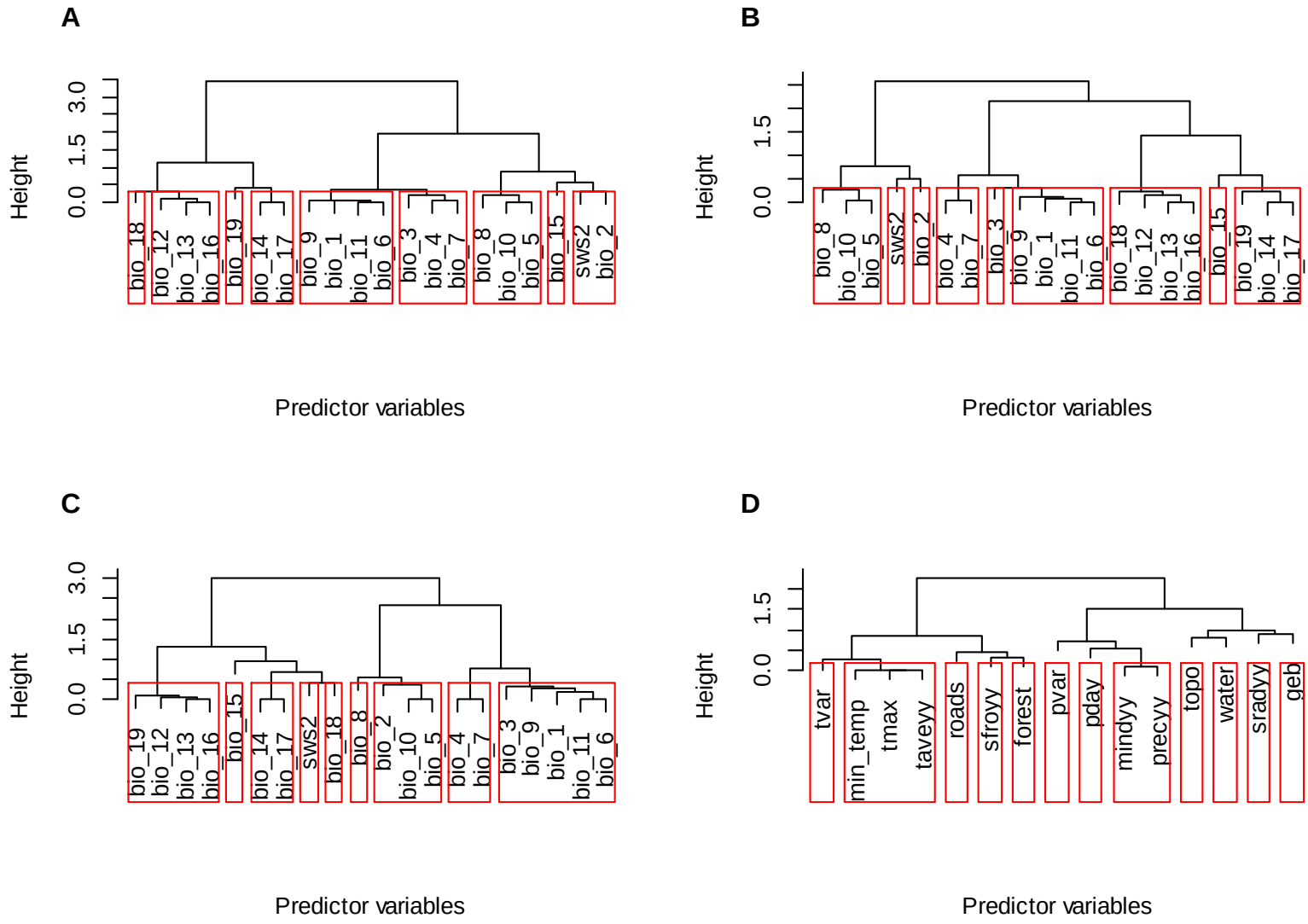


Figure S1. Correlation clusters for the predictor variables used in giant hogweed distribution models. A to C are variable correlations for the global models, at world, biomes and ecoregions scales, respectively, (nine climatic variables used in these models), and D is for the regional model calibrated at the scale of Switzerland (12 predictors used in this model; climatic, but also topographic and disturbance variables). In order to avoid high correlation between predictors, initial predictors were clustered based on their correlation and grouped into equidistant clusters (indicated by red boxes). One predictor in each of these groups was then selected based on it having the most direct ecological effect on the study species.

Abbreviation	Description (primary surface category)
Z_BaumS	Plant nursery
Z_Fels	Rock
Z_Fluss	River
Z_Gebue	Bushes
Z_GerGeb	Scree with bushes
Z_GerGle	Scree on glacier
Z_Geroel	Scree
Z_GerWa	Scree in forest
Z_GerWaO	Scree in clear forest
Z_Glet	Glacier
Z_GsPist	Track on grass
Z_HaPist	Track on hard coating
Z_KiGrub	Gravel pit
Z_LeGrub	Clay pit
Z_ObstAn	Orchard
Z_Reben	Grape vines
Z_See	Lake
Z_Siedl	Housing area
Z_StauDa	Retention dyke
Z_StauMa	Dam
Z_SteBru	Stone pit
Z_SumGeb	Marsh and bushes
Z_Sumpf	Marsh
Z_SumWa	Forest marsh
Z_SumWaO	Marsh in clear forest
Z_Uebrig	Other type of primary surface
Z_Wald	Forest
Z_WaldOf	Clear forest

Table S1. Primary surface categories included (in white) and excluded (in grey) for sampling of pseudoabsences in Switzerland, regional model projection and random-stratified adaptive sampling in the study area. Primary surface categories were taken from Swisstopo (www.swisstopo.ch), for all of Switzerland at a resolution of 25m.

Random-stratified adaptive sampling (extract from Dessimoz 2006)

Adaptive sampling postulates that if the focal species is observed in one of the defined sampling plots, the four neighboring plots with adjacent boundaries are also investigated (Figure S2). This reiteration process is applied to each randomly sampled and neighboring plot where the species occurs, resulting in a network of plots representing all sampled occurrence plots of a clustered population.

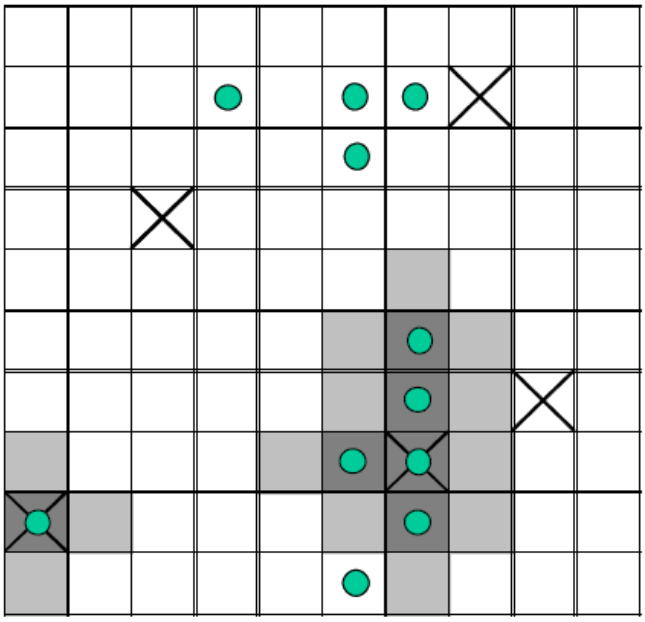


Figure S2. Illustration of adaptive sampling design used to estimate the population size of a focal species. The actual distribution of the species is represented with solid circles. Cross-marked plots define the initial plots chosen by random-stratified sampling design. If the focal species is observed in one of the latter plots (dark gray), all adjacent plots (light gray) are investigated. The process is repeated if the species is observed again, resulting in networks of sampled occurrence plots (figure from Dessimoz 2006, unpublished).

Density estimation (Appendix 2 from Dessimoz 2006)

Following the adaptive sampling, the density of the focal species can be estimated for the study area.

N units are partitioned into ***h*** strata with N_h units per stratum. A simple random sampling of ***n*** units is performed in each stratum, giving 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 ***k*** networks with the associated y-value y_k defined as the total number of individuals in the network. One network could eventually straddle a stratum boundary. Therefore, x_{hk} defines the number of units in stratum h that lie in network k. To simplify the writing of equations we set h as 10 strata and n as 10 units per stratum leading to 100 sampled units and also 100 networks.

The intersection probability α_k a 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 unit (pixel), $\hat{u}_{st}$, in the study area 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':

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

Reference: Thompson SK, Seber GAF (1996) Adaptive Sampling. Wiley, New York

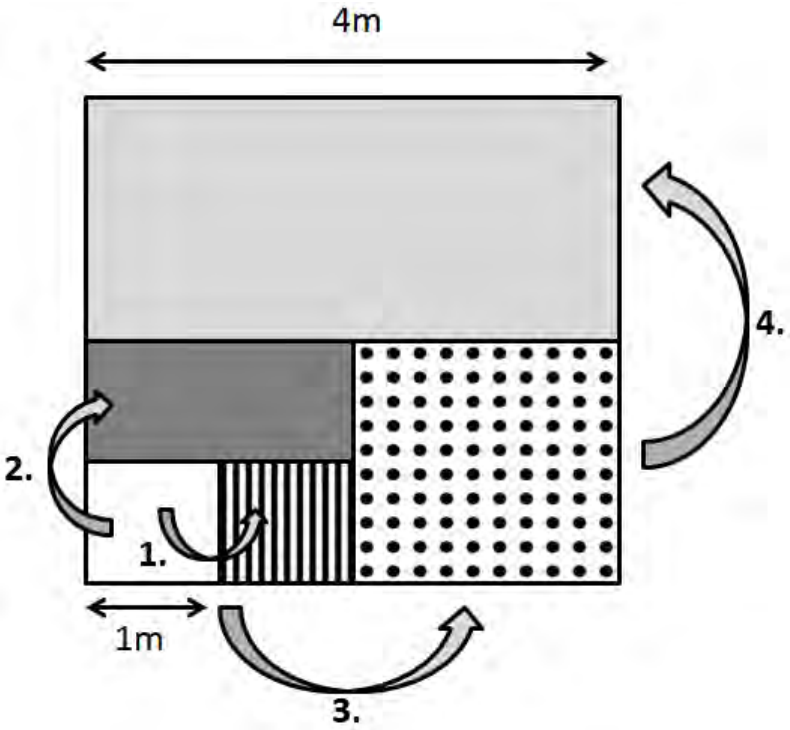


Figure S3. The progressive sampling design used for the community inventories. The sampling was first done in a 1 m x 1 m cell (white); the surface was then doubled by sampling of an adjacent cell of equal surface (lined cell); the new species found in this cell were recorded; this procedure was repeated three times (dark gray, dotted and light gray cells were added to the inventory), until the whole 4 m x 4 m cell was investigated.

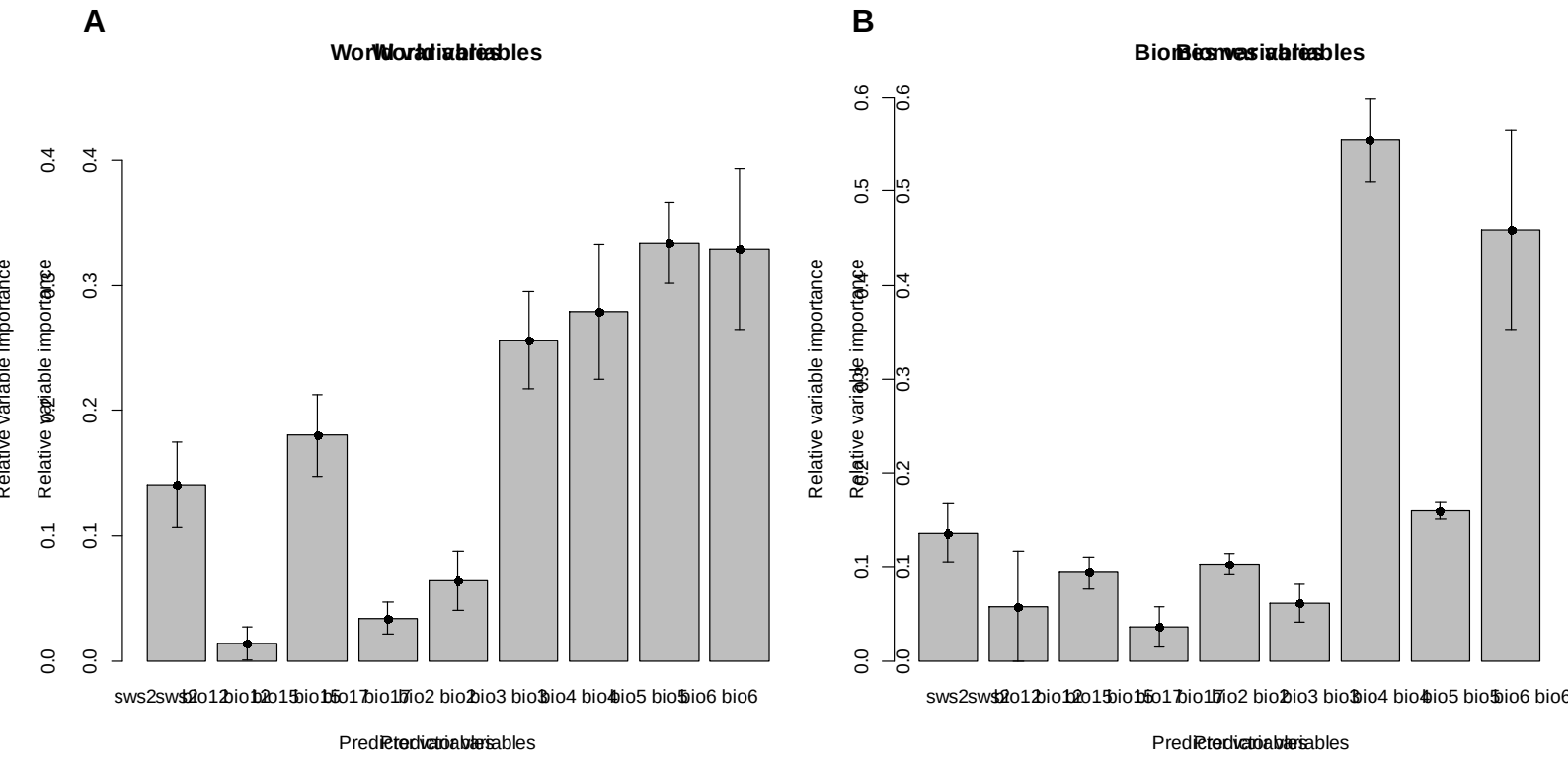


Figure S4. Importance of climatic variables in global giant hogweed distribution models, for models calibrated at world (A) and biomes (B) scales. Variable importance was assessed through permutations, and values shown are means across ten model replicates. For a description of variables corresponding to abbreviations, see Table 1.

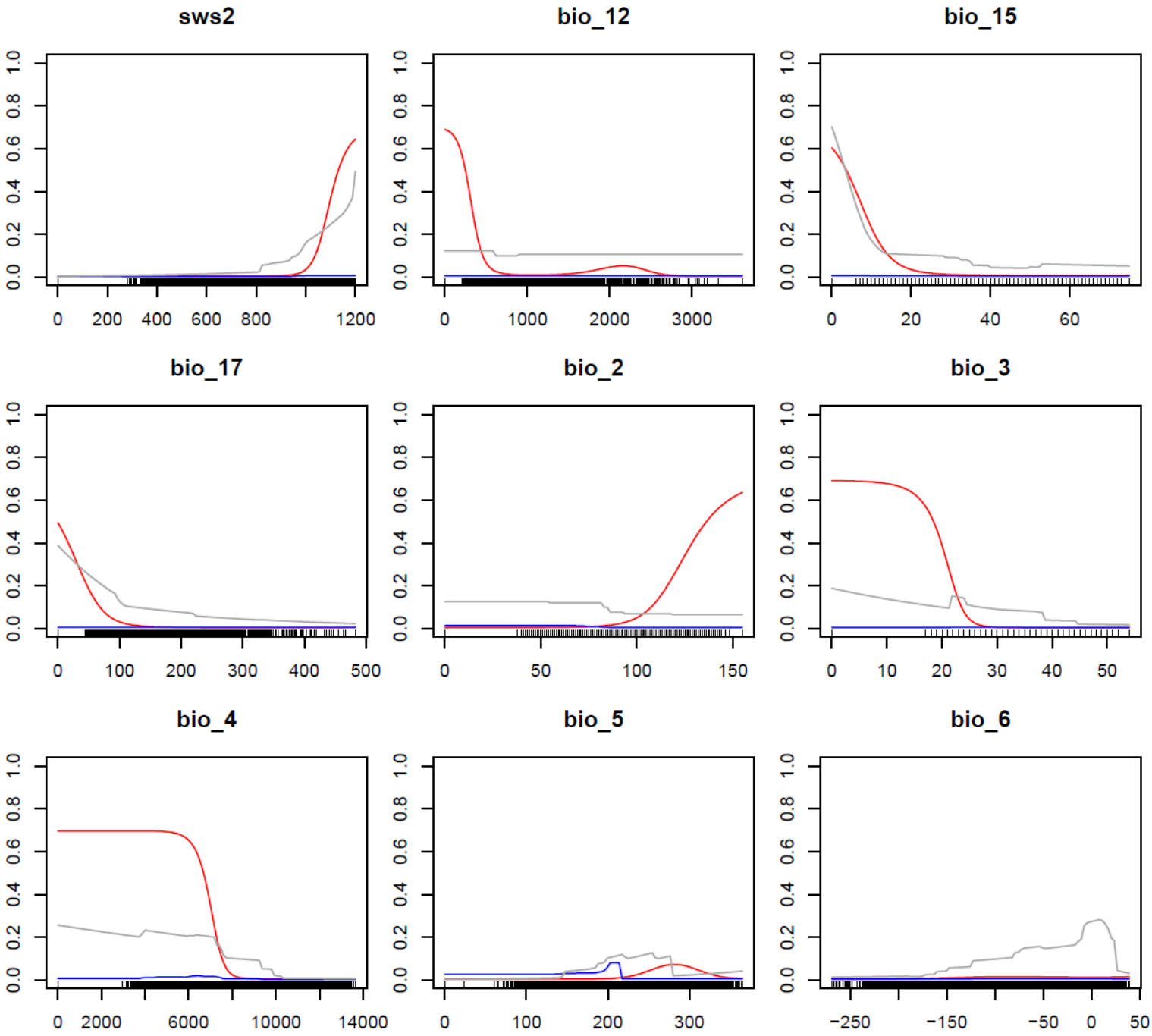


Figure S5. Response curves for giant hogweed, for the nine climatic variables included in the global model, calibrated at the scale of ecoregions, for three different modeling techniques: GLM in red, GBM in blue, MAXENT in gray. For a description of variables corresponding to abbreviations, see Table 1.

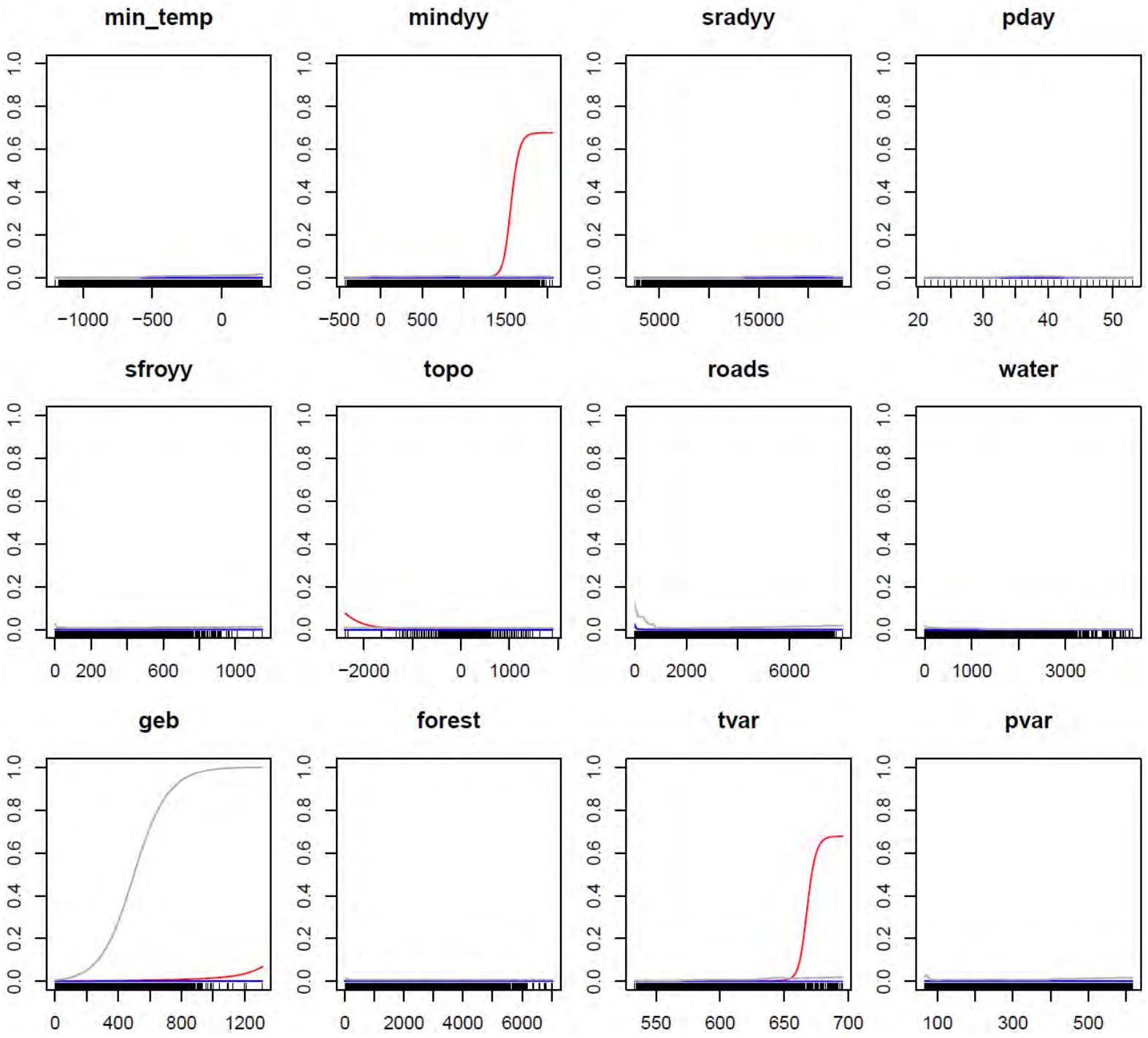


Figure S6. Response curves for giant hogweed for the 12 predictor variables included in the regional model, calibrated at the scale of Switzerland, for three different modeling techniques: GLM in red, GBM in blue, MAXENT in gray. For a description of variables corresponding to abbreviations, see Table 2.

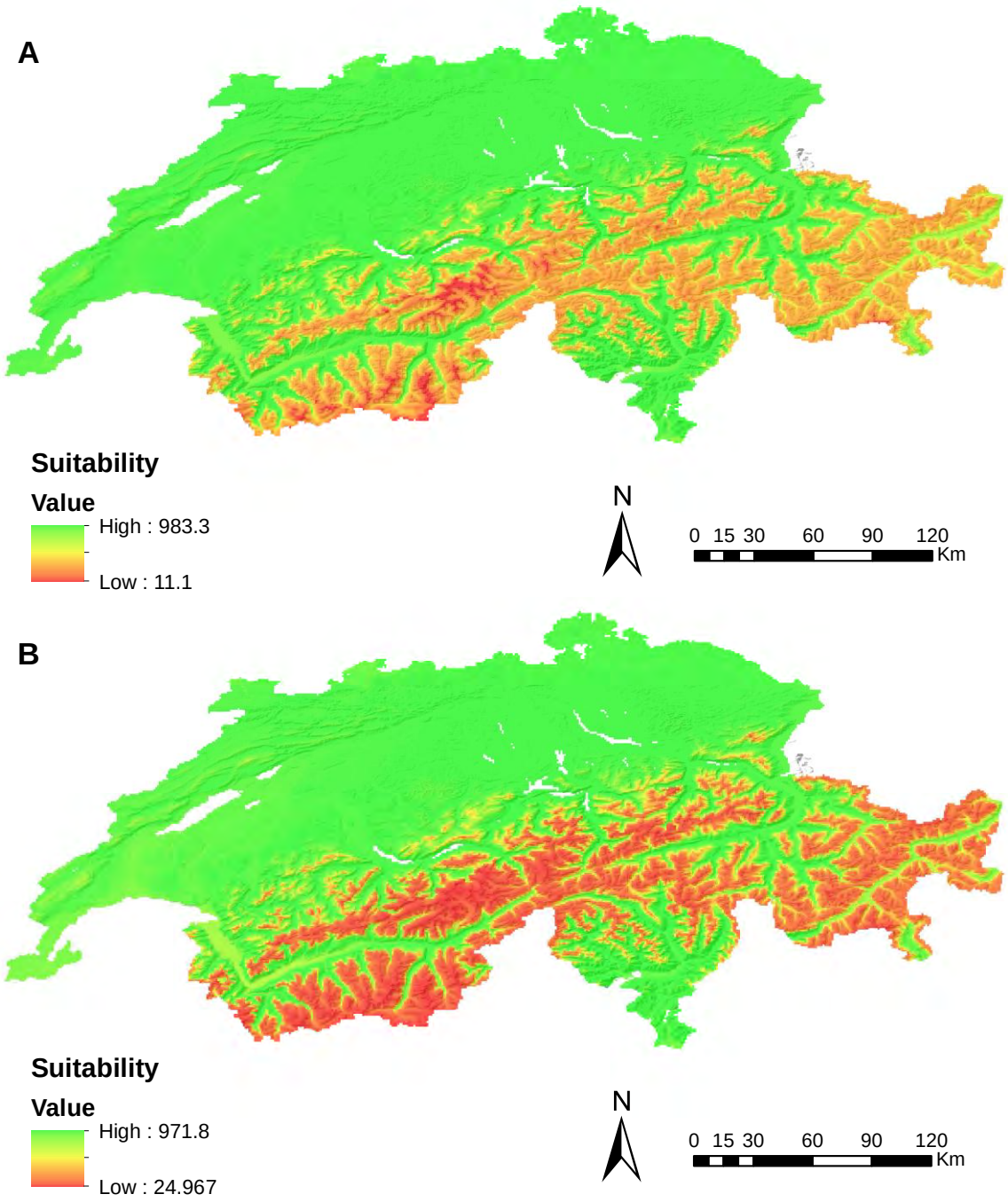


Figure S7. Suitability predictions of the global distribution models for giant hogweed, calibrated at world (A) and biomes (B) scales, and projected across Switzerland. Suitability values are means across ten model replicates.

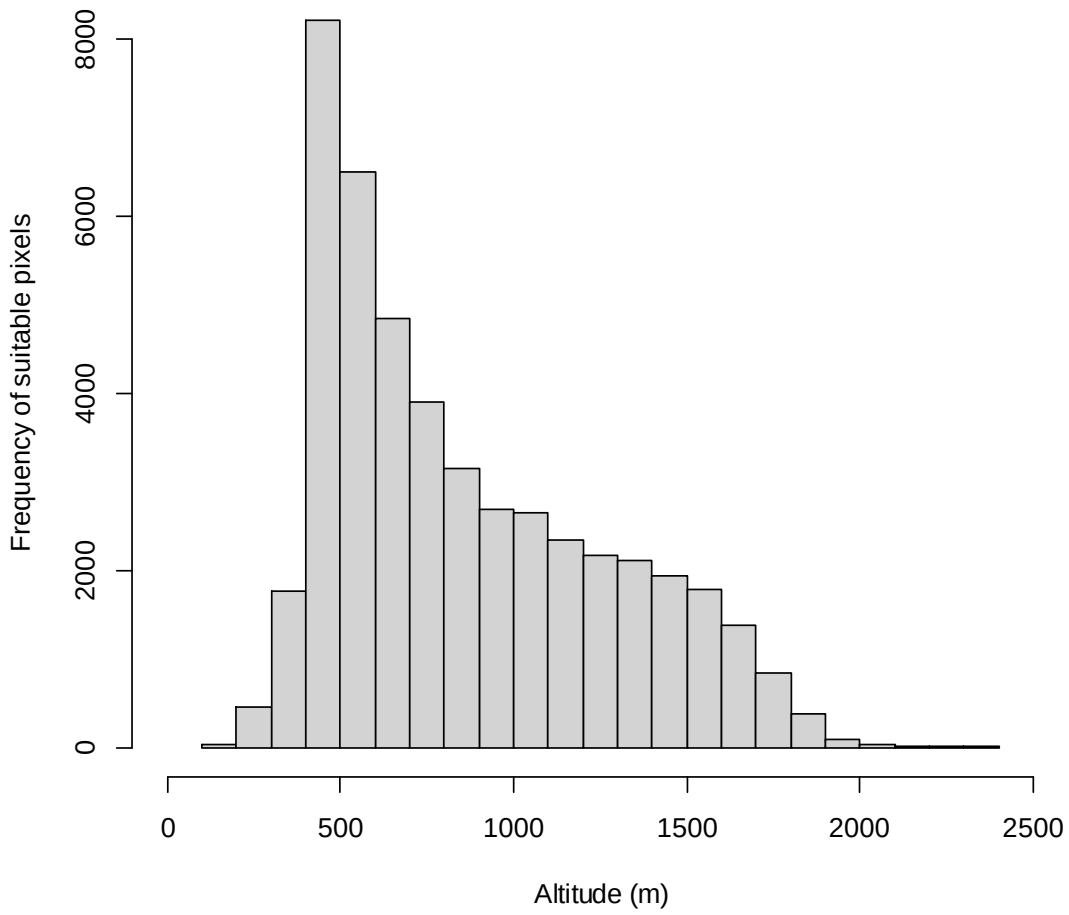


Figure S8. Distribution of suitable pixels for giant hogweed along the altitudinal gradient in Switzerland, as predicted by the global ecoregions model (calibrated at the scale of ecoregions), and converted into binary predictions (suitable or unsuitable) using the threshold corresponding to the maximum TSS (presented in Table 3).

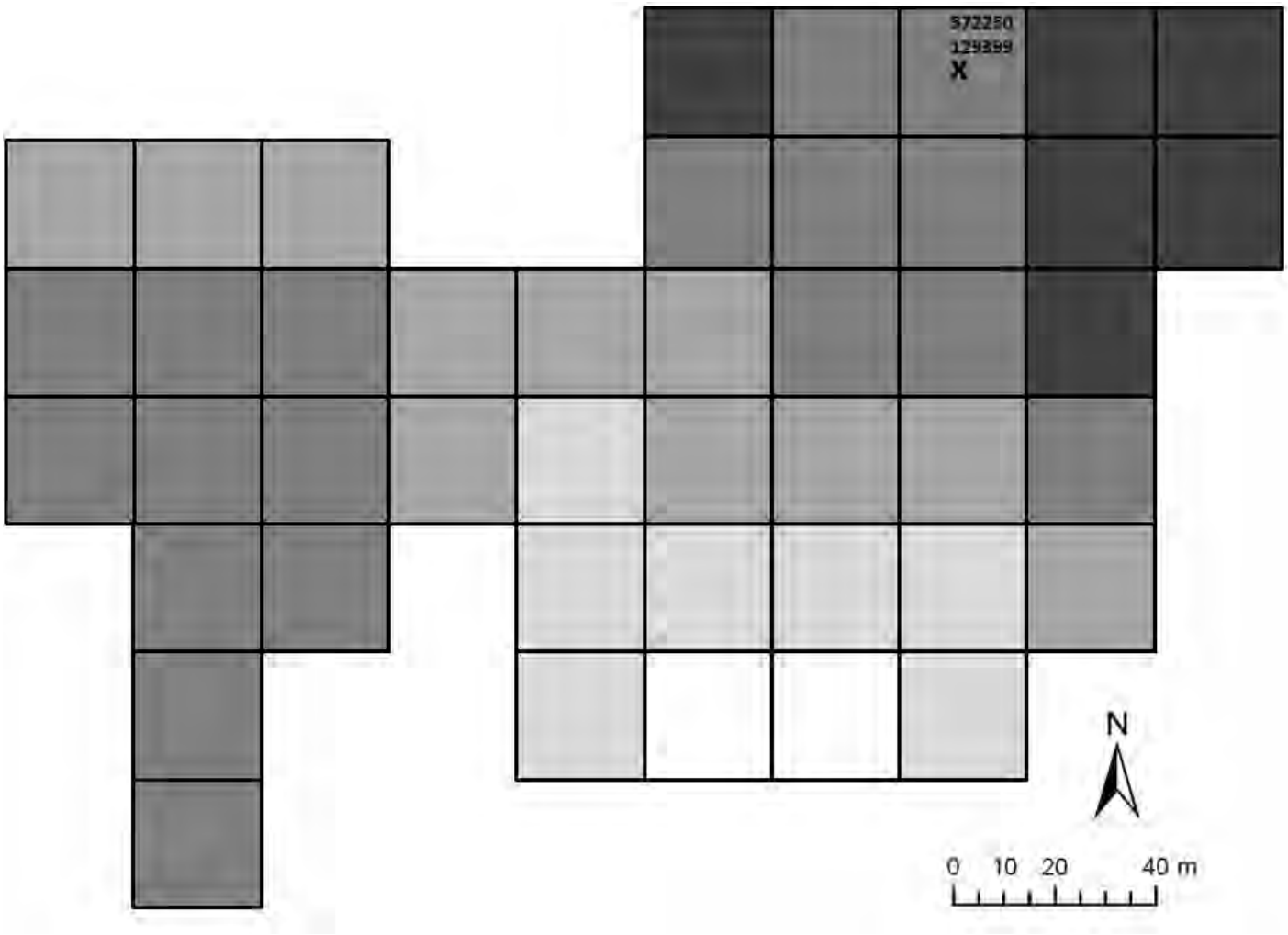


Figure S9. The network of giant hogweed plots sampled for adaptive-stratified density estimation, in the commune of Ollon. The cross with geographic coordinates indicates the initial site, obtained by random-stratified sampling according to the probability strata of the regional species distribution model. Each square indicates the subsequently sampled sites where giant hogweed was present, totaling 44 squares, and each measuring 25 m x 25 m. The sampled network squares fall into five probability strata, shown by the square colors: strata 2 to 6 are indicated from darkest to lightest, in decreasing order of suitability (stratum 1 being predicted as most favorable to the study species). The network contains in total 6’570 individuals.

ID	x	y	Altitude (m)	Number of giant hogweed stands	Giant hogweed cover (%)	Commune	Site description
2	559149	132143	380	1	1	Yvorne	Meadow on the edge of pedestrian path along the Rhône River (Arrhenatherion).
13	557077	144200	388.8	3	7	La Tour-de-Peilz	Stream edge, close to houses.
3	563621	124150	391.4	4	2.5	Ollon	Ruderal site along the Rhône River and pedestrian path.
4	564756	124070	406.4	11	5	Ollon	In agricultural meadow, along the edge of a path and of forest.
5	568212	121532	460.3	22	80	Bex	Next to cultivated field, close to houses; very dense patch of giant hogweed and bramble.
7	568541	125792	697.4	3	10	Ollon	Forest; close to river and along a hiking trail.
6	568534	125830	706.8	4	17	Ollon	Forest; close to river and along a hiking trail.
8	569550	132714	808.8	8	70	Ormont-Dessous	River's edge, close to construction site.
10	578060	146600	915.1	1	3	Chateau-D'Oex	Ruderal community along river’s edge.
9	569883	134077	952.4	11	10	Ormont-Dessous	Along a stream and a pedestrain trail, next to the main road toward Les Mosses.
11	567911	126392	989.4	25	30	Ollon	Clear forest, along road edge.
1	562643	144148	1045.6	11	25	Montreux	Clear forest, along road edge.
15	577633	133557	1143.9	19	70	Ormont-Dessus	Field and forest edge, next to river.
12	564246	134172	1188	4	2.5	Corbeyrier	Meadow along road edge to one side and forest edge to the other.
16	579527	133101	1293.6	43	85	Ormont-Dessus	Forest along the road.
14	570647	128621	1360.9	110	97	Ollon	Along a pedestrain trail, close to a stream and a residential area (Villars-sur-Ollon).
20	573548	137499	1390.7	14	60	Ormont-Dessous	Wetland meadow; Calthion. Along a stream.
17	573686	137914	1416	20	65	Ormont-Dessous	Wetland meadow; Calthion. Along a stream.
19	565540	138108	1444.3	8	17	Corbeyrier	Stream's edge along the road. Eradication efforts in most of the area.
18	564261	136535	1493.6	1	3	Corbeyrier	Pasture along road's edge.

Table S3. Information concerning the 20 sampled invaded giant hogweed sites. Geographic coordinates and characteristics correspond to invaded 4 m x 4 m plots.

Species	Frequency (%)
Fraxinus excelsior	65
Urtica dioica	65
Dactylis glomerata	60
Taraxacum officinale aggr.	60
Glechoma hederacea aggr.	55
Vicia sepium	55
Geum urbanum	45
Poa trivialis	45
Ranunculus acris aggr.	45
Rubus idaeus	45
Geranium robertianum	40
Lamium galeobdolon subsp. montanum	40
Ranunculus repens	40
Rubus fruticosus aggr.	40
Stachys sylvatica	40
Chaerophyllum hirsutum aggr.	35
Cirsium oleraceum	35
Filipendula ulmaria	35
Fragaria vesca	35
Heracleum sphondylium aggr.	35
Veronica chamaedrys	35
Arrhenatherum elatius	30
Epilobium montanum	30
Galeopsis tetrahit	30
Galium album	30
Geranium sylvaticum	30
Trifolium pratense	30

Table S4. Most common species found alongside giant hogweed (in the same 4 m x 4 m plot). Only species found in 30% or more of the plots surveyed (20 plots in total) are shown, corresponding to 16% of total species recorded in invaded plots.

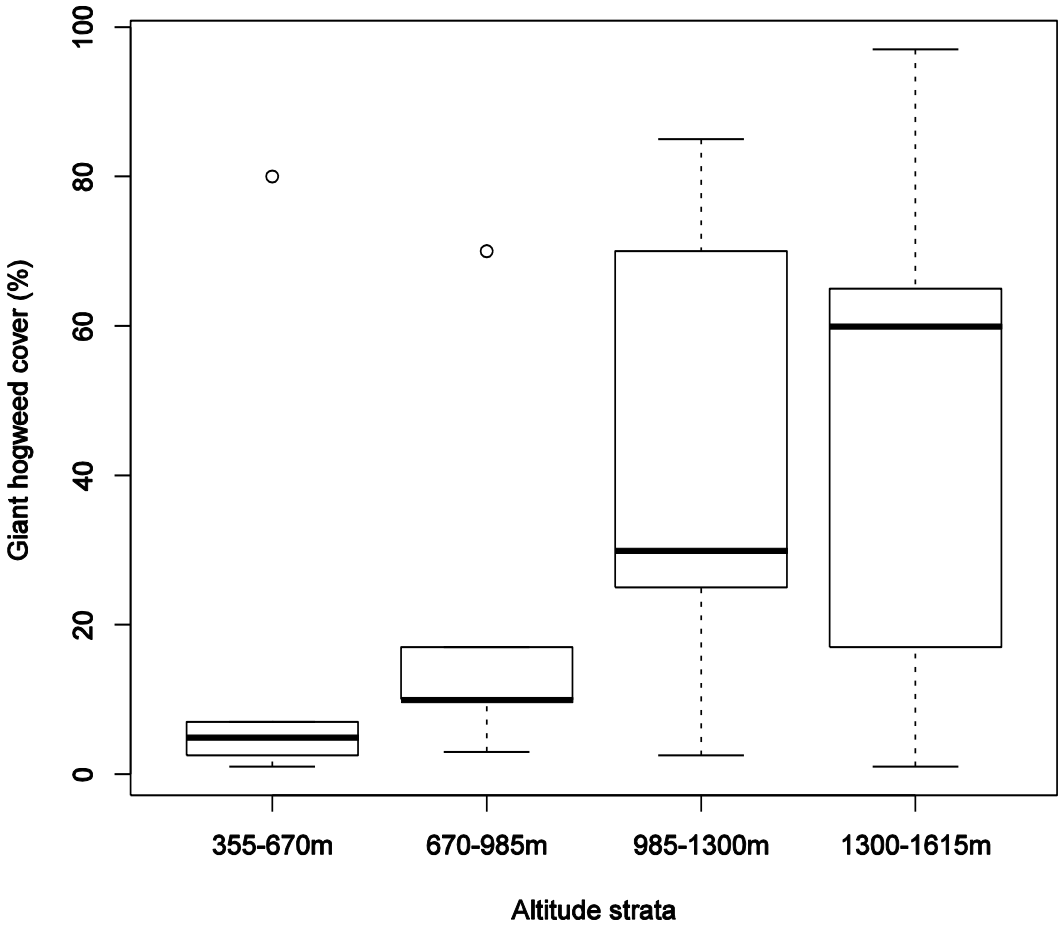


Figure S10. Giant hogweed cover in invaded 4 m x 4 m plots, sampled within four altitude strata in the study area (five sites per stratum).

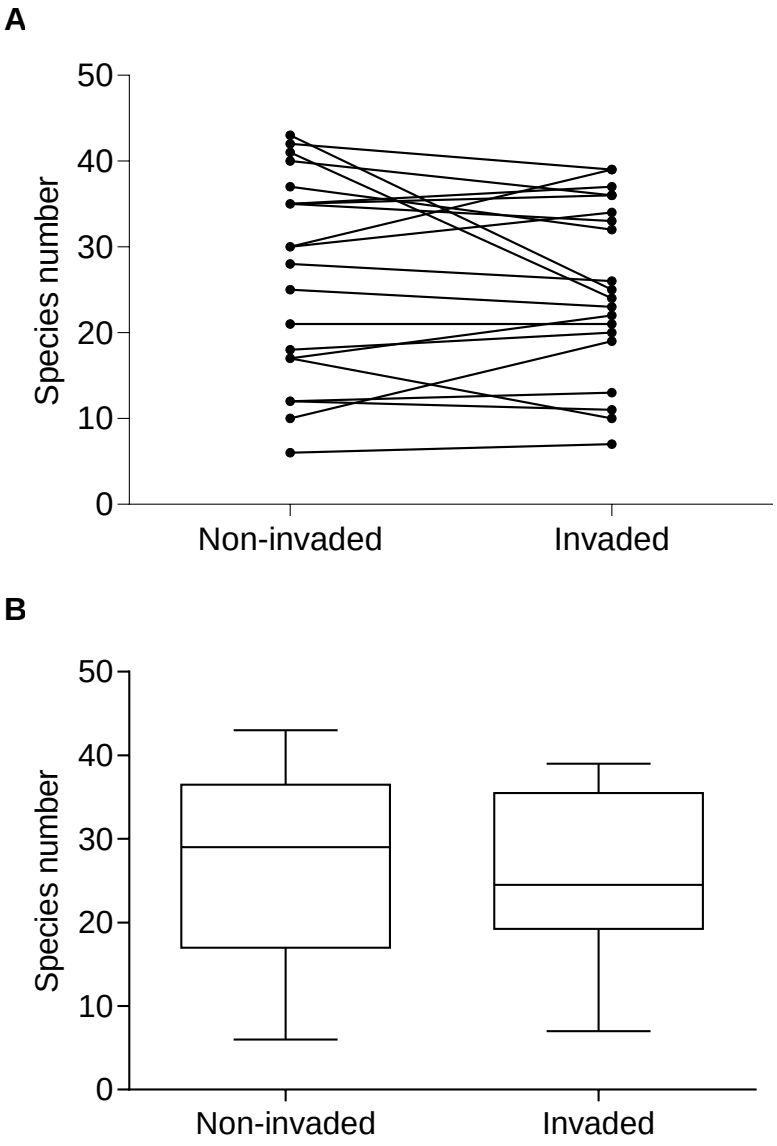


Figure S11. Comparison of species number in invaded and non-invaded 4 m x 4 m plot pairs (A) and boxplots (B) of species number in invaded and non-invaded plots.

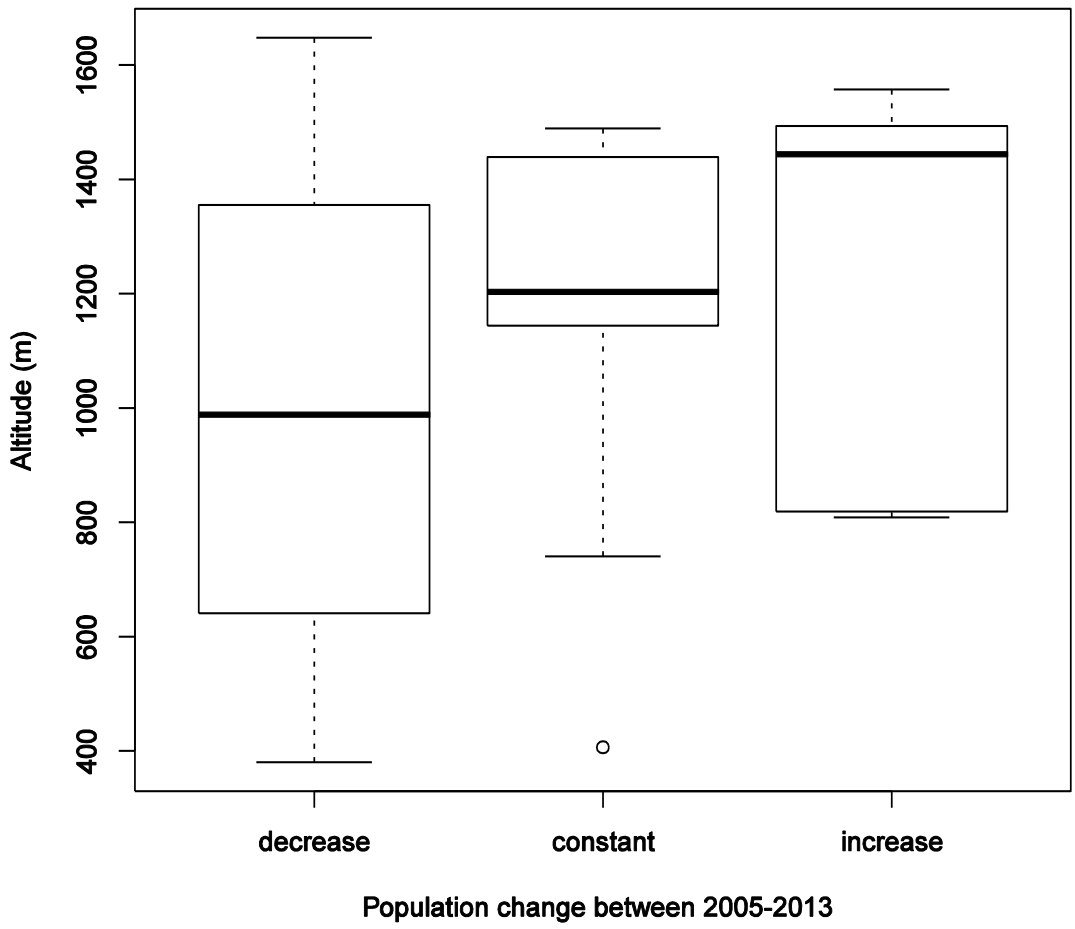


Figure S12. Altitudes of giant hogweed populations recorded by Dessimoz in 2005 and revisited in 2013, grouped according to their change in size over this eight-year period.

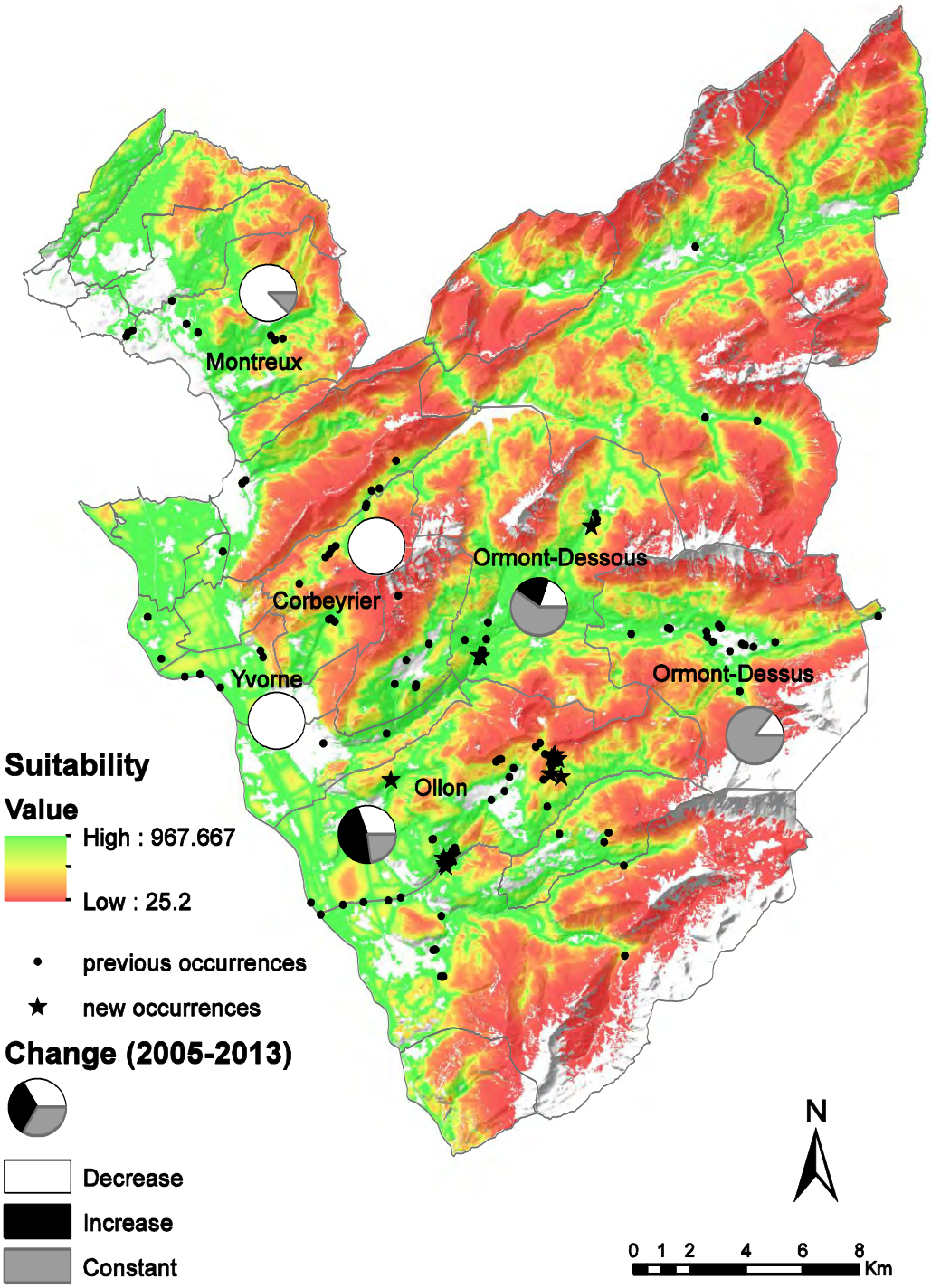


Figure S13. Suitability predictions of the regional model, calibrated at the scale of Switzerland, and projected across the study area of the Western Swiss Prealps. Occurrences recorded by Dessimoz in 2005 and new occurrences recorded in 2013 are shown, along with mentioned communes in the study area. Pie charts represent proportions of revisited populations which had remained constant, decreased or increased in size over the eight-year period (2005-2013) in each mentioned commune.

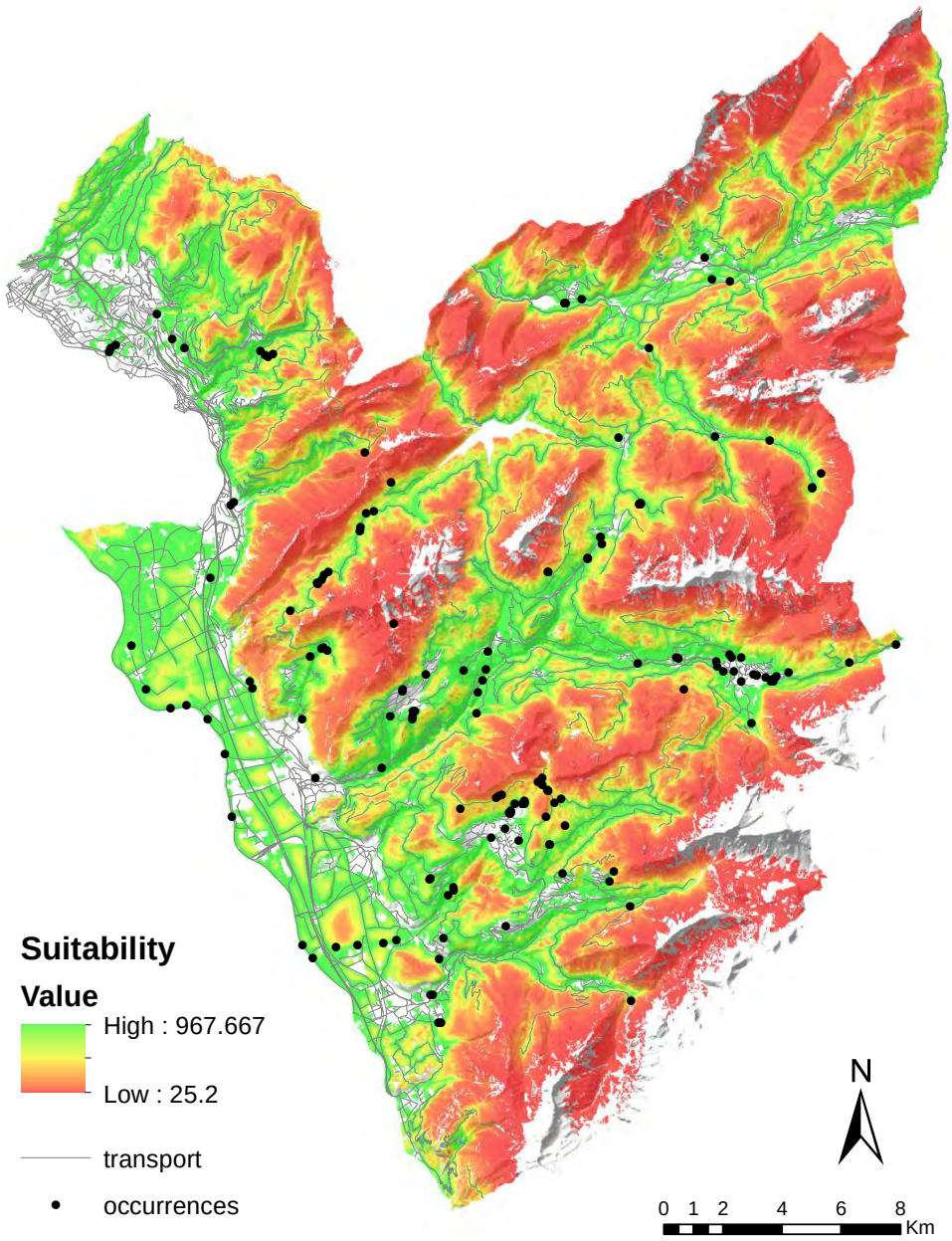


Figure S14. Suitability for giant hogweed, as predicted by the regional distribution model (calibrated at the scale of Switzerland), with known giant hogweed occurrences and transport lines (highways, main roads and railway tracks), in the study area of the Western Swiss Prealps.

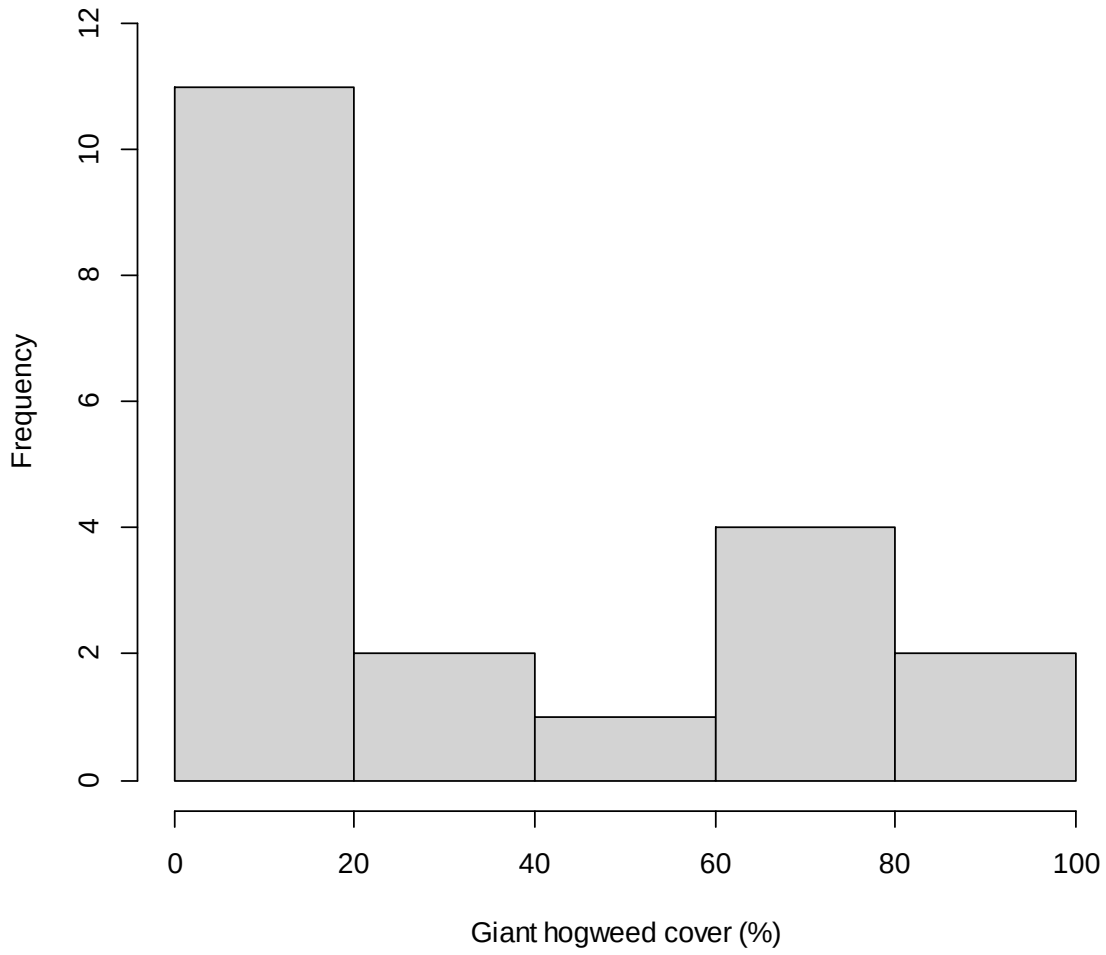


Figure S15. Distribution of giant hogweed covers within sampled 4 m x 4 m invaded sites (20 sites in total).