serval
serveur académique lausannois

Unil
UNIL | Université de Lausanne
Faculté de biologie
et de médecine

1   **Running head: More neophytes in hotter mountains?**

2   **Title: Will climate change increase the risk of plant invasions into mountains?**

3

4   Blaise Petitpierre[1], Keith McDougall[2], Tim Seipel[3], Olivier Broennimann[1], Antoine Guisan[1, 4]*,

5   Christoph Kueffer[5]*

6

7   [1] Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland.

8   [2] Department of Environmental Management and Ecology, La Trobe University, Wodonga,

9   Australia.

10   [3] Department of Land Resources and Environmental Sciences, Montana State University,

11   Bozeman, MT, USA.

12   [4] Institute of Earth Surface Dynamics, University of Lausanne, 1015 Lausanne, Switzerland.

13   [5] Institute of Integrative Biology, Department of Environmental Systems Science, ETH Zurich,

14   Switzerland.

15

16   [*] Shared last authorship

17

18   Corresponding author: Blaise Petitpierre, blaise.petitpierre@unil.ch, tel +41 21 692 42 79, fax

19   +41 21 692 41 65

20

21   Paper type: article

1 **Abstract**

2 Mountain ecosystems have been less adversely affected by invasions of non-native plants than

3 most other ecosystems, partially because most invasive plants in the lowlands are limited by

4 climate and cannot grow under harsher high-elevation conditions. However, with ongoing

5 climate change, invasive species may rapidly move upwards and threaten mid, and then high

6 elevation mountain ecosystems. We evaluated this threat by modeling the current and future

7 habitat suitability for 48 invasive plant species in Switzerland and New South Wales, Australia.

8 Both regions had contrasting climate interactions with elevation, resulting in possible different

9 responses of species distributions to climate change. Using a species distribution modeling

10 approach that combines data from two spatial scales, we built high-resolution species distribution

11 models (≤ 250 m) that account for the global climatic niche of species and also finer variables

12 depicting local climate and disturbances. We found that different environmental drivers limit the

13 elevation range of invasive species in each of the two regions, leading to region-specific species

14 responses to climate change. The optimal suitability for plant invaders is predicted to markedly

15 shift from the lowland to the montane or subalpine zone in Switzerland, whereas the upward shift

16 is far less pronounced in New South Wales where montane and subalpine elevations are already

17 suitable. The results suggest that species most likely to invade high elevations in Switzerland

18 will be cold-tolerant, whereas species with an affinity to moist soils are most likely to invade

19 higher elevations in Australia. Other plant traits were only marginally associated with elevation

20 limits. These results demonstrate that a more systematic consideration of future distributions of

21 invasive species is required in conservation plans of not yet invaded mountainous ecosystems.

22 **Keywords**: Australian Alps, elevation limits, environmental gradients, invasive plants, multi-

23 scale approach, plant traits, species distribution models, Switzerland

1   **Introduction**

2   Non-native plant species richness is generally low in mountainous areas, especially at high

3   elevations (McDougall *et al.*, 2011a, Seipel *et al.*, 2012), where few non-native species occur and

4   these rarely become abundant or negatively affect ecosystems and biodiversity (McDougall *et*

5   *al.*, 2011b, Kueffer *et al.*, 2014). Several possible explanations have been proposed for this

6   pattern, which contrasts strongly with most non-mountain biomes (Pauchard *et al.*, 2009). First,

7   less intensive land use and reduced human activity at high elevations reduce invasion

8   opportunities due to the greater resistance of undisturbed habitats to invasion (Pauchard &

9   Alaback, 2004, Parks *et al.*, 2005, Marini *et al.*, 2009, Jakobs *et al.*, 2010, Kueffer *et al.*, 2014).

10   Additionally, it has been proposed that introductions of non-native species have predominantly

11   occurred at low elevations in mountains, resulting in a lower propagule pressure and delayed

12   invasions at high elevations (Becker *et al.*, 2005, Alexander *et al.*, 2011). Time-lags may also be

13   partly related to a need for adaptive evolution (Dietz & Edwards, 2006, Haider *et al.*, 2012).

14   Such a preponderance of introduction of lowland species to mountain regions also means that

15   only non-native species with a broad climatic niche that can grow both in lowland and higher

16   elevation climates can reach alpine ecosystems ('directional ecological filtering', Alexander *et*

17   *al.*, 2011). Indeed, species pre-adapted to a mountain climate are conspicuously lacking from

18   high elevation non-native floras worldwide (McDougall *et al.*, 2011a). Furthermore, non-native

19   richness patterns might be shaped by the same abiotic factors (i.e. area, climate, productivity and

20   water availability) that explain a decline of native species richness with elevation (Rahbek, 1995,

21   McCain, 2007, Romdal & Grytnes, 2007, Jakobs *et al.*, 2010, Alexander *et al.*, 2011). Although

22   many factors may affect the spread of non-native species from lowlands to high elevations in

1   mountains, climate is clearly important (Marini *et al.*, 2009, Jakobs *et al.*, 2010, Trtikova *et al.*,

2   2010, Kueffer *et al.*, 2014, Seipel *et al.*, 2015).

3   The rate of invasion into higher elevations is likely to increase in the future. First, propagule

4   pressure and habitat disturbances may increase in mountainous regions due to economic

5   development, leading to the exchange of climatically pre-adapted mountain species between

6   mountainous regions (e.g. tourism; McDougall *et al.*, 2005, McDougall *et al.*, 2011b). Second,

7   climate change might reduce the climatic limitation of current non-native species distributions

8   and facilitate invasions into mountains (Pauchard *et al.*, 2009, Walther *et al.*, 2009, Barni *et al.*,

9   2012). There is evidence that human, animal and plant diseases are currently moving toward

10 higher elevations with climate change, posing a new threat to mountain livelihoods, ecosystems,

11 and biodiversity (Benning *et al.*, 2002, Hay *et al.*, 2002, Kurz *et al.*, 2008, Walther *et al.*, 2009,

12 Siraj *et al.*, 2014). To our knowledge, however, whether plant invasion risks will increase in

13 mountain areas with climate change has not been systematically and quantitatively investigated,

14 although the resulting impacts on ecosystems and economy might be as important as direct

15 consequences from climate change (Scholes *et al.*, 2014).

16 In particular, it is not clear whether climate change will lead to the same invasion risks in

17 different mountainous regions. Different climate factors might interact in shaping species

18 distribution limits along the elevation gradients, and their importance might differ depending on

19 climatic distances between lowlands and the top of the gradient. For instance, aridity, more than

20 temperature, seems to act as a limiting factor for the invasion of non-native species in dry, higher

21 elevation areas (e.g. in Hawaii; Jakobs *et al.*, 2010, Juvik *et al.*, 2011), and non-climatic habitat

22 factors can also restrict expansion of non-native species into higher elevations (Haider *et al.*,

23 2010). Thus, depending on the limiting factors, species distributions might respond differently to

1 climate change because not all climate factors will change with the same magnitude and

2 direction (Crimmins *et al.*, 2011, McCain & Colwell, 2011). Further, impacts of climate change

3 will not be homogenous around the world and some mountain ranges will be more affected than

4 others (Engler *et al.*, 2011). Models including all these parameters are needed to understand and

5 anticipate how invasive species will react to climate change in mountainous areas.

6 Preventing biological invasions is considered to be more efficient than control and eradication

7 efforts following introduction (Leung *et al.*, 2002). Accordingly, reliable anticipation of

8 invasions is critical for conservation management of mountain biodiversity hotspots, especially

9 given the island-like nature of mountains that makes mountainous ecosystems more vulnerable to

10 biological invasions. To do this, species distribution models (SDMs; Guisan & Thuiller, 2005)

11 based on environmental niche quantification can identify potential suitable habitats for non-

12 native species in geographic space (identified as species potential distributions, Thuiller *et al.*,

13 2005, Guisan *et al.*, 2014) and support conservation decisions (Guisan *et al.*, 2013). SDMs relate

14 species distribution in space to environmental variables (generally available as GIS layers) based

15 on a statistical characterization of the Hutchinsonian realized species niche (*sensu* Soberon,

16 2007; i.e. assuming implicitly biotic interactions but also dispersal limitations). When climate

17 change scenarios are available, SDMs can be used to assess the potential responses of plant

18 distributions to climate change (e.g. Engler *et al.*, 2011).

19 Distribution and climate data across the complete environmental range of a species are typically

20 required to identify the niche (Thuiller *et al.*, 2004, Guisan *et al.*, 2014). For this purpose, the

21 most exhaustive geographical species distribution is needed. Coarse resolution data typically

22 available over large geographic extents may however not reflect the fine-scale environmental

23 heterogeneity that drives local to regional species distributions. In the case of complex

1   topographies, such as in mountainous landscapes, spatial extent and resolution strongly matter

2   for building SDMs and deriving projections (Randin *et al.*, 2009a, Seipel *et al.*, 2012, Franklin *et*

3   *al.*, 2013). Therefore large-scale SDMs and predictions may differ substantially from those

4   calibrated at a finer, local or regional scale, and they may for instance overestimate (Trivedi *et*

5   *al.*, 2008, Franklin *et al.*, 2013) or underestimate (Randin *et al.*, 2009a) species persistence in

6   mountainous landscapes. In turn, SDMs fitted over small extents may result in truncated climatic

7   niches and project biased distributions under present and future climates (Thuiller *et al.*, 2004).

8   This is why modeling approaches that combine local and global scale analyses (e.g. Pearson *et*

9   *al.*, 2004, Gallien *et al.*, 2012) are particularly needed to provide robust predictions in

10   heterogeneous mountain landscapes.

11   In this paper, we assess whether mountainous areas will be at increased risk of plant invasions

12   under climate change in two mountainous areas where climatic gradients interact differently with

13   the elevation gradient. We used a combined approach linking coarser data models at a global

14   scale with finer distribution data and environmental maps available for particular local mountain

15   ranges. Because species response to climate change along elevation gradient can be different

16   among mountain ranges (e.g. Engler *et al.*, 2011), we modeled potential distributions for invasive

17   plant species using SDMs in two study areas. In Switzerland (CH; including the Swiss Alps and

18   Jura mountains) temperature is assumed to be the major limiting factor determining the upper

19   distribution of non-native species because of the broad elevation gradient. In the Australian Alps

20   in New South Wales (NSW), which has a narrower elevation gradient, aridity may play relatively

21   a more important role in shaping species distributions. Data were obtained for 48 species in total,

22   24 from CH, and 29 from NSW; 5 species were common to both study areas. We assessed the

23   magnitude of the elevation shift for invasive plant species in these mountains using the

1   predictions of SDMs under six climate change scenarios. Because species that share the same

2   ecological traits may exhibit similar responses to climate change (Thuiller *et al.*, 2005), we then

3   tested the hypothesis that shared species traits and other biogeographical characteristics are

4   associated with species upper elevation limit. With this we aim to get a better understanding of

5   whether responses of different types of invasive plants to future climates differ according to their

6   properties.

7   The specific questions we addressed in this paper were:

8   1) Will the risk of plant invasions at high elevations in mountains increase with climate change?

9   2) Will climate change influence non-native species potential distribution in the same way in two

10   contrasted mountain ranges?

11   3) To what type of non-native species will the upper reaches of mountains be vulnerable in a

12   future climate?

13

14   **Methods**

15   *Study areas*

16   Switzerland (CH, total area 41,285 km2) is characterized by a mountainous landscape with a

17   large elevation gradient (between 192 and 4634 m asl, Fig. 1a). The Alps are the most important

18   mountain range occupying 60% of the area of the country. In the northwest, the Jura is smaller

19   and less elevated (10% of the country area with a maximal elevation of 1680 m asl). Western

20   European broadleaf forests and European-Mediterranean montane forests are the two ecoregions

21   found in CH (Olson et al., 2001). We classified CH into 4 elevation zones: lowland (192 - 800 m

22   asl), montane (801 - 1500 m asl), subalpine (1501 - 2200 m asl) and alpine (2201 - 3100 m asl),

1   representing ecological units structured by the elevation (Ozenda *et al.*, 1988). Higher elevations

2   were not included in the analyses because environmental conditions become hostile for virtually

3   all plant species.

4   New South Wales (NSW, total area 809,444 km^2) is located in southeastern Australia and

5   contains portions of the Australian Alps. New South Wales is characterized by a strong gradient

6   of increasing precipitation from west to east. Six ecoregions have been identified: Eastern-

7   Southeast Australia temperate forests, Australian Alps montane grasslands, Eastern Australian

8   temperate forests, Southeast Australia temperate savanna, Murray-Darling woodlands and mallee

9   and Eastern Australia mulga shrublands (Olson *et al.*, 2001). NSW is considered a hotspot of

10 invasive plants in Australia (O'Donnell *et al.*, 2011). We classified NSW into 5 elevation zones

11 corresponding to the same ecological units as in CH and subdivided the lowest zone into dry and

12 wet parts due to a strong aridity gradient (Fig. 1b): dry lowland (0 - 700 m asl and current annual

13 precipitation < 500 mm), wet lowland (0 - 700 m asl and current annual precipitation > 500 mm),

14 montane (701 - 1400 m asl), subalpine (1401 - 1800 m asl) and alpine (1801 - 2228 m asl). We

15 did not include the Simpson Desert ecoregion in the analyses because no study species had more

16 than five occurrences.

17 On average, CH is colder and wetter than NSW. Climate change scenarios predict a higher

18 increase of temperature and a stronger decrease of wetness in CH. However, this highly depends

19 on the different scenarios (Tables S5 to S8) and the decrease of wetness in regards to the

20 proportion of the average value, is similar. Temperature and precipitation differences between

21 CH and NSW along elevation gradients are shown in Fig. S1.

22

23 *Species data*

1   For both CH and NSW, only terrestrial plant species with precise-enough georeferenced

2   occurrence data at both local and worldwide scale were selected (minimum number of

3   occurrences N = 18, Tables S1 and S2). In CH, it resulted in a selection of 24 major invasive

4   species (out of the 36 of national concern; www.infoflora.ch; last accessed 26 May 2014). We

5   used occurrence data from the info flora database (www.infoflora.ch) and from the Mountain

6   Invasion Research Network dataset (MIREN; Becker *et al.*, 2005, Seipel, 2011).

7   Data for NSW invaders were obtained from relevés stored in the Atlas of NSW Wildlife

8   (http://www.bionet.nsw.gov.au; accessed 5 October, 2013). Because there are more invasive

9   plant species in NSW than CH, we selected only 24 species that occurred in or close to the

10   Australian Alps and had sufficient records for building robust SDMs. There was no prior reason

11   to expect that any of them would respond to climate change in a particular way. We additionally

12   selected five species, which occurred both in CH and NSW and had sufficient records for SDMs,

13   to allow direct comparisons of species behavior in different climates (*Ailanthus altissima,*

14   *Ambrosia artemisiifolia, Lonicera japonica, Prunus laurocerasus and Robinia pseudoacacia*,

15   Tables S3 and S4 and Fig. S2 and S5). For both CH and NSW, these data were collected during a

16   wide temporal window (from the first reported observation until 2010).

17   In addition to datasets from both regions we also gathered occurrence data from the Global

18   Biodiversity Information Facility (*data.gbif.org*, accessed between August and September 2012)

19   for use in construction of the SDMs at a global scale. We retained occurrences when location

20   accuracy was greater than 2.5 km and 250 m for global and local SDMs a compromise between

21   occurrence accuracy and occurrence number. Despite this small locational uncertainty SDMs

22   remain robust (Graham *et al.*, 2008).

23

1   *Multi-scale SDMs framework*

2   To combine the widest species niche (including the widest species distribution) and finer topo-

3   climatic variation typically characterizing mountainous landscapes, we fitted SDMs at two

4   scales: global and local. First, global SDMs were built based on worldwide species distributions

5   and coarser climatic variables. We included occurrences from both the native and multiple

6   invaded ranges to capture the most complete climatic niche of species, and to diminish the risk of

7   under-predicting the range of the potential distribution in the invaded ranges due to enemy

8   release (Broennimann & Guisan, 2008, Beaumont *et al.*, 2009). These global climatic SDMs

9   were used in two ways: (i) to predict the current and future distribution for different climate

10   change scenarios; and (ii) to select the pseudo-absences to be used in the local SDMs (Gallien *et*

11   *al.*, 2012). The local SDMs were calibrated at a much finer resolution and included climate but

12   also disturbance variables that can affect species distribution at a local scale.

13

14   *Global SDMs*

15   Eight climatic variables, known to optimize the geographic transferability of SDMs, were used at

16   the global scale (Petitpierre, 2014). Precipitation and temperature data at 30 arc seconds

17   resolution (about 1km at the equator) were obtained from the Worldclim database (Hijmans *et*

18   *al.*, 2005). Aridity and aridity seasonality data (variance of monthly aridity means) were obtained

19   from the Global Aridity and PET database (http://www.cgiar-csi.org) at the same resolution.

20   These data represent the yearly average between 1950 and 2000. Potential mismatches between

21   the timeframes of the climate data and the species observation should not impact the results for

22   higher elevation because the majority of the species were first introduced to lowland areas then

23   spreading to higher elevations. In addition, all occurrences collected in NSW are post-1950.

1   Thus, only the oldest species observation in the lowland in CH, which might not match the

2   timeframe of the climatic data, are not distributed at higher elevation. Observations at the upper

3   elevation of the species were observed within the timeframe of the climate data. The next step

4   was to define an ecologically-relevant study background to calibrate the SDMs and select

5   pseudo-absences, because inadequate extents may result in over-optimistic evaluations (Guisan

6   & Thuiller, 2005, Chefaoui & Lobo, 2008, Barve *et al.*, 2011, Acevedo *et al.*, 2012). We

7   defined the study background for each species as the ecoregions covered by the species

8   distribution. Ecoregions are geographical units characterized by homogeneity between climates,

9   geology, fauna and flora (Olson *et al.*, 2001).

10

11 *Local SDMs*

12 For each study area (CH and NSW) and species, we used georeferenced data from local

13 databases and defined the extent in the same way as for the global SDMs. Within this extent,

14 pseudo-absences were selected inversely proportional to the suitability provided by the global

15 SDMs for the same species (as in Gallien *et al.*, 2012, but with a linear weight). At a finer local

16 scale, other factors than climate can be important in driving invasive species distribution (Guisan

17 *et al.*, 2014). Because some of our species were intimately linked to water streams and invasive

18 species are known to be promoted by human disturbances (Marini *et al.*, 2009, Nobis *et al.*,

19 2009, Jakobs *et al.*, 2010), we used two disturbance variables (distance to the closest river, lake

20 or shore and density of urban area), combined with three climatic variables at a resolution of 100

21 m and 250 m for CH and NSW, respectively (Table 1). For CH, climate variables (yearly

22 average between 1961 and 1990) were taken from Zimmermann & Kienast (1999), whereas for

1   NSW they were provided by the NSW Office of Environment and Heritage (for the year 1990,

2   Christopher Simpson, personal communication).

3

4   *Modeling techniques*

5   For both global and local SDMs, we randomly sampled 10,000 pseudo-absences in the study

6   background of each species, weighted to reach an equal prevalence with presences. To reduce

7   spatial autocorrelation due to sampling bias, occurrences were disaggregated to keep a 10 km

8   minimal distance between two occurrences in the global SDMs and 1 km in the local SDMs.

9   Data were split into calibration (70%) and evaluation (30%) datasets. We applied an

10 ENSEMBLE modeling approach by averaging three modeling techniques: generalized linear

11 models (GLM) with polynomial quadratic coefficients preceded by a stepwise selection based on

12 the Bayesian Information Criteria (BIC, McCullagh & Nelder, 1983); generalized boosted

13 regression models (GBM) with 5000 trees and 7 degrees of interaction depth (Friedman *et al.*,

14 2000); and MAXENT with default parameters (Phillips *et al.*, 2006). The BIOMOD package was

15 used for GLM and GBM (Thuiller *et al.*, 2009) and the dismo package for MAXENT (Hijmans

16 *et al.*, 2005), implemented in R software (R, 2012). The whole procedure was replicated 10 times

17 per species and averaged. The same large set of down-weighted pseudo-absences was used here

18 with all modelling techniques to ensure a common modelling framework (but see Barbet-Massin

19 *et al.*, 2012 for different pseudo-absence selection strategies for different modeling techniques).

20 To estimate the contribution of variables, SDMs were run with each variable randomized 5 times

21 separately and the obtained predictions are correlated with the unrandomized SDMs. A high

22 correlation means that the randomized variable is not important whereas a low correlation

23 indicates the randomized variable is crucial in the depiction of the species potential distribution

1   (Thuiller *et al.*, 2009). Suitability and variable contributions were averaged across techniques

2   and iterations. The resulting averaged suitability predictions were evaluated with the Area Under

3   the Curve of a Receiver Operating Characteristics (Roc AUC, Zweig & Campbell, 1993) and the

4   True Skill Statistics (TSS, also known as corrected Kappa, Allouche *et al.*, 2006). This

5   represents the standard procedure for such ENSEMBLE modeling procedure using BIOMOD

6   (e.g. Marmion *et al.*, 2009). Additionally, we used two "presence-only" evaluators, the Boyce

7   index (B; Hirzel *et al.*, 2006) and the sensitivity rate, which is the rate of correctly predicted

8   presences when the prediction is made binary. Presence-only evaluators are particularly relevant

9   in the case of invasive species because invasions are ongoing processes, and observed

10   distributions may not reflect the distributional equilibrium. Absences may thus not be reliable for

11   model evaluation. For clarity, we only present AUC and Boyce in the manuscript (but see Tables

12   S1 - S4 for the other evaluators). Continuous probabilities of spatial projections were binarized

13   using the threshold providing the best TSS. The spatial projections were done at the same

14   resolution as the environmental layers and associated with a digital elevation model of the mean

15   elevation within each pixel. For each species, we removed the ten highest elevated predicted sites

16   to lower the possible effects of outliers on the upper elevation limit. For each species, we

17   assessed the proportion of the study area covered by the potential distribution within each

18   elevation zone and measured the highest potential elevation.

19   Because extrapolating SDM predictions to non-analog climate may provide spurious and thus

20   unreliable results (Fitzpatrick & Hargrove, 2009, Mandle *et al.*, 2010, Peterson, 2011, Webber *et*

21   *al.*, 2011, Guisan *et al.*, 2014), we removed sites presenting such novel climate from the analysis,

22   using the Multivariate Environmental Similarity Surfaces (MESS, Elith *et al.*, 2010) but see Fig.

23   S5 for results including non-analog climates).

1

2 *Spatial projections under future climate*

3 Scenarios for global SDMs were available from the Research Program on Climate Change,

4 Agriculture and Food Security (http://www.CCAFS-climate.org, Ramirez & Jarvis, 2008).

5 Climate change scenarios for variables G7 and G8 (Table 1) were derived following Zomer *et al.*

6 (2008) using bioclimatic variables of Worldclim. For both the global and local scale analyses, we

7 used predictions for two years (2030 and 2070) derived from six different climate change

8 scenarios representing two emission scenarios of IPCC's 4th assessment report (A1B and A2,

9 IPCC, 2007) and based on three Global Circulation Models (GCMs): HadCM3, ECHAM5 and

10 Ccsm3 (Tables S5 to S8). For local SDMs in CH, Regional Circulation Models (RCMs) were

11 available at a 1 km resolution (N.E. Zimmermann, WSL, personal communication). Climate

12 anomaly was bilinearly interpolated at a 100 m resolution. For NSW, RCMs were available at a

13 250 m resolution (C. Simpson, NSW Office of Environment and Heritage, pers. com.).

14

15 *Species traits and biogeographical characteristics*

16 For each species, we collected a number of traits and characteristics (Table S9) to (i) determine if

17 the species had different ecological characteristics between CH and NSW, and (ii) to test traits

18 are associated with the elevation pattern of predicted species distributions (Thuiller *et al.*, 2005).

19 These traits were gathered from two databases, Flora Indicativa (Landolt *et al.*, 2010, based on

20 expert knowledge) and Biolflor (Kühn *et al.*, 2004). Flora indicativa provided indicator values

21 assigned to each species for their optima along various environmental variables and information

22 on the species ecology. We additionally considered Grime's C-S-R classification system for

1   interpreting species ecological strategies (Grime, 1979). We used a two-sided randomization test

2   to compare the distribution of traits among species in CH and NSW when variables were

3   quantitative or semi-quantitative (e.g. Landolt's indices); for qualitative traits we performed non-

4   parametric Chi-Square tests.

5   Further, we modeled the association between the traits of a species and three variables related to

6   the upper distribution limit: 1) current observed maximal elevation, 2) current predicted maximal

7   elevation and 3) shift between predicted maximal elevation under current conditions and

8   predicted maximal elevation under climate conditions in A1 2070 scenarios. Future maximal

9   predicted elevations were averaged for the two A1 2070 scenarios (scenarios 6 and 7 in Tables

10   S1 to S4). In the model of predicted elevation shifts, we included the *elevation potential*, i.e. the

11   difference between the current predicted maximal elevation for each species and the maximal

12   elevation of the gradient in the region, as an explanatory factor. For both NSW and CH species

13   pools, we tested these associations based on predictions from global and local SDMs. Because

14   the number of species traits was high in relation to the number of species, we used a hierarchical

15   approach to select important ones and avoid model over-parameterization. First, for each trait we

16   built a univariate GLM and compared the Bayesian Information Criterion (BIC; more restrictive

17   than AIC) of the obtained model to a model with only the intercept (null model). If the model

18   including the trait did not have a better BIC than the null model, the trait was not considered

19   further. After this first selection, all combinations of the retained traits were examined and the

20   combination providing the best BIC was used as the final model. Multimodel inference and

21   variable selection were done in R using the library MuMIn (Barton, 2012)

22

23   **Results**

1   *Evaluation of SDMs*

2   In CH, SDMs had high evaluation scores when fitted at both global (AUC = 0.88 ± 0.05; B = 0.8

3   ± 0.07; Table S1) and local (AUC = 0.91 ± 0.06; B = 0.72 ± 0.22; Table S2) scales. The same

4   overall good performances were found in NSW at global (AUC = 0.89 ± 0.04; B = 0.95 ± 0.05;

5   Table S3) and local (AUC = 0.95 ± 0.05; B = 0.76 ± 0.04; Table S4) scales. Only the local SDMs

6   for *P. laurocerasus* in NSW had a poor B (-0.19).

7

8   *Species distribution under current climate*

9   Equivalent elevations in CH and NSW are not equivalent for climate variables (Fig. 2 and S1)

10   but we report species distribution along the elevation gradient to better answer our initial

11   questions about invasions and elevation in mountains. Climatic differences between CH and

12   NSW are discussed in the discussion section.

13   In CH, invasive plant species are on average currently observed up to the montane zone (1317 ±

14   497 m). This was not significantly different from the maximal elevation predicted by local SDMs

15   (1331 ± 473 m) but differed significantly from the one predicted by global SDMs, where on

16   average, species were predicted to reach the subalpine area (1843 ± 473 m, t-test P < 0.001, Fig.

17   2). Indeed, global SDMs predicted more suitability in general, and also at more elevated areas

18   (84 ± 22%, 57 ± 35%, 17 ± 23% and 3 ± 6% of the total area in lowland, montane, subalpine and

19   alpine zones, respectively) compared to local SDMs (37 ± 19%, 4 ± 6%, 1 ± 4% and 0 ± 0%;

20   Fig. 3 and 4). For global SDMs in CH, the most important variables were temperature variability,

21   temperature of the coldest quarter and aridity index (Fig. 5a), while average temperature was the

22   most important variable for local SDMs (Fig. 5b). Species traits explained between 51% and

1   70% of the variance of the current upper elevation limit in CH (both observed and predicted),

2   with a positive association with species resistance to cold, presence of rosette, diploidy and the

3   ability to be competitive on nutrient rich soils (Table 2, Fig. S6).

4   In NSW, the selected species are currently observed at a similar maximal average elevation to

5   CH (1287 ± 292 m). However, SDMs predicted a significantly higher elevation limit when fitted

6   at both global (1789 ± 271 m; t-test P < 0.001) and local (1628 ± 447 m; t-test P = 0.001; Fig. 2)

7   scales. On average, SDMs predicted more suitable area for invasive species at higher elevation

8   than in CH, including for the species occurring in both CH and NSW (Fig. 4 and S4). The

9   montane and subalpine areas were predicted to be the most suitable by both global (with 6 ±

10 11%, 33 ± 26%, 61 ± 30%, 63 ± 38% and 40 ± 42% of the total area at dry lowland, wet lowland,

11 montane, subalpine and alpine zones respectively) and local SDMs (2 ± 5%, 18 ± 15%, 43±

12 32%, 35 ± 39% and 28 ± 40%; Fig. 3 and 4). For the global SDMs (Fig. 5a), the most important

13 variables were the same as for CH except that temperature seasonality was more important for

14 species in NSW than in CH (t-test P < 0.001, Fig. 5). When calibrated at the local scale, the most

15 important variables in determining species distributions in NSW were temperature, precipitation

16 and temperature variability (Fig. 5b), which were all significantly different from the CH local

17 SDMs (Fig. 5). Disturbance variables contributed substantially less than climate variables in both

18 NSW and CH (Fig. 5b)

19 We also found significant differences between CH and NSW for the following species traits:

20 Landolt's indices of temperature (4.27 vs 3.85; t-test P = 0.040), soil moisture (1.92 vs 1.42; t-

21 test P = 0.027), life strategies (CH species are more competitive, Chi-square test P = 0.019),

22 number of occurrences used to calibrate the SDMs (227 vs 1318; t-test P < 0.001) and the

23 number of species present in southern temperate areas (15 vs 20 species, Chi-square test P =

1   0.044). The other traits tested did not show significant differences between CH and NSW (see all

2   p-values in table S9). In NSW, traits related to the maximal elevation explained between 25%

3   and 86% of the variation in species maximal elevations (observed or predicted, Table 2, Fig. S6),

4   and were different from CH (Table 2). In NSW, species maximal elevation was associated with

5   various traits, but not with Landolt's temperature, while index of soil moisture predicted the

6   observed maximal elevation. Global SDMs, predicted that stress-tolerant competitors (*sensu*

7   Grime, 1979) had lower maximal elevations (Table 2).

8

9   *Species distribution under future climate*

10   In CH, both global and local SDMs predicted an increase of suitability at higher elevation (Fig. 3

11   and 4). Based on global SDMs, climate change scenarios indicate a decrease of potential

12   suitability in the lowland, no change in the montane zone, and an increase in the subalpine and

13   alpine zones, whereas local SDMs predicted that lowland and montane zones will experience the

14   most dramatic increases in suitability in the future (Fig. 4 and 5). However, in the most extreme

15   climate change scenarios, suitability was predicted to decrease at the lowland zone. For local

16   SDMs, this decrease can be attributed to the exclusion of non-analog climates, which removed

17   large areas of the lowland zone (but see Fig. S2 when SDMs are extrapolated to novel climates),

18   whereas only up to 7 species will experience non-analog climates in the lowland based on global

19   SDMs (Fig. S7). For both global and local SDMs, climate change scenarios had a significant

20   effect on the maximal predicted elevation of distributions (Kruskall-test, $P < 0.001$), reaching a

21   maximum of 2430 ± 474 m and 2170 ± 340 respectively for scenario HadCM1 A1B 2070 (Fig.

22   2). When results from both A1b scenarios were averaged, the difference between current and

23   future potential elevation varied between -79 m for *Lonicera japonica* and 995 m for *Prunus*

1 *laurocerasus* with an average of 579 ± 286 m in global SDMs (Table S1), and between 252 m

2 for *Sedum spurium* and 979 m for *Bunias orientalis* with local SDMs (Table S2). The average

3 Spearman correlation between local and global SDMs predictions of the highest elevations under

4 the current conditions and the six climate change scenarios was 0.57 ± 0.13. In CH, only species

5 *elevation potential* was significantly associated with this shift of the maximal elevation,

6 explaining 32% and 51% of this elevational response for local and global SDMs respectively

7 (Table 2). Spatial projections are available for each species and each climatic scenario in Fig. S8

8 and S9.

9 In NSW, although SDMs predicted some elevation shift, these predictions differed substantially

10 from the ones in CH. Climate change scenarios predicted a decrease of suitability at lowland and

11 montane zones but the predictions differed between global and local SDMs for the upper

12 elevation. While global SDMs predicted an increase of suitability at subalpine and alpine zones,

13 local SDMs showed a slight increase of suitability at subalpine zone, and no changes of the

14 global suitability at the alpine zone (Fig. 3 and 4). This difference remained when testing the

15 effect of climate change scenarios on the upper elevation limits. It was significant for the global

16 SDMs (Kruskall-test, $P < 0.001$), reaching an average of 1969 ± 190 m with scenario ECHAM5

17 A2 2070 (Fig. 2), whereas there was no effect on local SDM predictions (Kruskall-test, $P = 0.98$,

18 Fig. 2), reaching a maximum of 1720 ± 353 m with the scenario HadCM3 A2 2070. When

19 results from both A1b 2070 scenarios were averaged, the difference between future and current

20 predicted elevation varied between -70 m for *Chondrilla juncea* and 432 m for *Ambrosia*

21 *artemisiifolia* (Table S3) and between -979 m for *I. aquifolium* and 523 m for *A. artemisiifolia*

22 for global and local SDMs respectively. In NSW, 25% of the variation in elevation shift was

23 explained by growth strategy (with competitive ruderal strategists *sensu* Grime, 1979) and by

1   species with wider elevation potential (see methods; Table 2 and S10). In contrast, 44% of the

2   variation of the shift in predicted maximal elevation by local SDMs was explained by the species

3   ability to keep their leaves in winter (wintergreen species).

4

5   **Discussion**

6   We assessed the difference between current and future potential distribution of a selection of

7   plant invaders in two disparate mountainous areas. Our SDMs predict an upward shift of the

8   upper elevational distribution limit for most modelled invasive plant species. Across all climate

9   change scenarios and models, an upward shift of up to 500 m for local SDMs, and of 1000 m for

10   global SDMs, is predicted. The montane, subalpine and alpine zones will be at high risk of plant

11   invasion in a future climate. However, the magnitude of this upward shift in response to climate

12   change strongly depends on the study area, with a less pronounced shift in New South Wales

13   (NSW) than in Switzerland (CH). These Ecological and environmental differences between the

14   regions may explain the different changes in the predicted distributions of invasive plant species.

15   In the following sections, we discuss possible causes for these contrasting patterns and the

16   implications of distributional shifts of invasive plant species towards higher elevations for

17   mountain ecosystems and their conservation.

18

19   *Interplay of temperature and aridity along the elevation gradient*

20   Due to the topographic configuration of the Australian Alps, the upper distribution limits of the

21   studied invasive species are closer to the upper limit of the elevation gradient in NSW than in

22   CH, which reduces the potential for a further upward shift of their distribution under climate

1 change. In other words, for most species a large part of the coldest conditions available in NSW

2 are already suitable under current climatic conditions, while this is not the case in CH (see

3 appendix S1). As a result, suitable areas are predicted to decrease in NSW because montane to

4 alpine areas are a small proportion of total land area, while in CH a reduction in suitable area at

5 low elevation is compensated with an increase in suitable habitat at higher elevation (Fig. 3 and

6 4). Thus, the most important factor associated with species distributional response to climate

7 change is the *elevation potential* of the species (see Methods). Species with lower current

8 predicted elevation are further from the top of the elevation gradient and have greater predicted

9 elevation expansion in both NSW and CH (Table 2 and S6). The importance of the elevation

10 potential is more difficult to explain in CH because the elevation gradient is not limiting, but

11 only a few species are predicted to reach the highest elevation of the gradient in the future

12 (Tables S1 and S2). A possible explanation might be that the magnitude of the distributional

13 response of species to climate change can change along the elevation gradient (Engler *et al.*,

14 2011), with species at lower elevation shifting more strongly than species located at higher

15 elevation. Overall, our results corroborate published analyses that show mountains with larger

16 elevation gradients, combined with species positioned lower along elevation gradients, offer

17 more opportunity for upward range shifts (Engler *et al.*, 2011).

18 Compared to CH, the studied invasive species in NSW are adapted to colder environments, as

19 indicated by their lower indicator values for temperature (T; Landolt *et al.*, 2010). Additionally,

20 at comparable elevation the temperature is higher in NSW (Fig. S1). This can explain why non-

21 native species are currently predicted at a higher position along the elevation gradient in NSW

22 (i.e. maximal suitability is found in the montane-subalpine elevation zones in NSW while in

23 lowland-montane zones in CH). Other factors might also explain the different responses between

1 NSW and CH. For example, local SDMs show that the alpine zone is not currently highly

2 suitable for most species in NSW and will not become more suitable with climate change. This is

3 because cold temperatures alone are not the primary limiting factor in NSW. The potential

4 distributions of species in NSW are primarily shaped by temperature seasonality and

5 precipitation, and only secondarily by annual mean temperature (L1 on Fig. 5). Consequently in

6 NSW changes in temperature seasonality and precipitation patterns in the future will influence

7 species distributions. In particular, the stress-tolerant species in NSW are predicted by global

8 SDMs to lower their elevation limit (negative coefficient for CSS species in table S10),

9 suggesting that the coldest temperatures at the top of the gradient do not represent the most

10 stressful factor in NSW. Such a downwards shift with climate change due to changing aridity

11 conditions has also been shown for some plants species in California (Crimmins *et al.*, 2011), in

12 Europe (Lenoir *et al.*, 2010), and for vertebrates in different mountain ranges around the world

13 (McCain & Colwell, 2011).

14

15 *The interplay of species traits and elevation limits*

16 Species traits associated with the observed or predicted upper elevation limits differ markedly

17 between CH and NSW, according to the strongest abiotic gradient prevailing in each of the two

18 regions, i.e. precipitation in NSW and temperature in CH (Fig. S1). Preference for moister soils

19 characterizes species that are predicted to reach higher elevations in NSW, whereas in CH

20 elevation limit is related to cold tolerant species. In NSW, only anthropochory is negatively

21 correlated with elevation (Table 2). This may reflect the lower impact of anthropogenic activities

22 in the wilder higher elevation areas of the Australian Alps, where tourism has burgeoned only

23 since the 1970s (Scherrer & Pickering, 2010), bringing fewer non-native species there than to

1   lowlands (Pauchard *et al.*, 2009). Among morphological and genetic traits, species forming

2   rosettes or having a diploid cytotype have higher predicted elevation limits in CH (Table 2).

3   Rosettes are typical of alpine plant communities and are an adaptation to cold conditions, light

4   availability, nutrient storage, and herbivory and characterize the plant traits of many alpine areas

5   in the Swiss Alps (Billings, 1974, Körner, 2003, Choler, 2005, De Bello *et al.*, 2005).

6   Distribution of ploidy along an elevation gradient is a debated topic (e.g. Kearney, 2005) but

7   diploid cytotypes among native flora have been shown for some species to occur more frequently

8   in cold conditions at high elevation (Gauthier *et al.*, 1998, Treier *et al.*, 2009, Martin &

9   Husband, 2013). Among biogeographical origins, only the few species of subtropical areas, and

10   thus adapted to hot and dry conditions, are predicted with a lower elevation limit in NSW under

11   current conditions (Table 2).

12

13   *Implications for mid to high elevation ecosystems*

14   Our results show that with climate change most plant invaders that are currently found in

15   lowland areas will have a high potential to colonize mountain ecosystems. High-elevation

16   ecosystems in the European Alps represent some of the last relatively undisturbed ecosystems

17   with a large and unique native biodiversity (Nagy *et al.*, 2003, Price, 2010). Very few non-native

18   plant species currently occur in these ecosystems and only few pose a problem (Kueffer, 2010).

19   Consequently, awareness among mountain conservation managers is low and limited

20   management capacity is in place (McDougall *et al.*, 2011b). With climate change the situation

21   might rapidly change. First, previous studies reported that climate change will negatively affect

22   native plant communities in mountainous areas (Engler *et al.*, 2011, Hughes, 2011, Düllinger *et*

23   *al.*, 2012), our results suggest that invasions by non-native species may amplify such negative

1   effects. Many of the most problematic invasive plant species have already established high

2   population densities in mountain valleys and dispersal distances to alpine ecosystems are short

3   once climatic barriers are removed, possibly contributing to the decline of species at risk of

4   extinction (Düllinger *et al.*, 2012, e.g. if non-native species invade micro-habitats serving as

5   climate refugia for native species Scherrer & Körner, 2011).

6   In Australia, although the selected species in NSW were predicted to be less likely to invade

7   higher elevations than the species in CH, many species were still predicted to extend their range

8   into the alpine zone, which is currently largely free of invasive species outside of disturbed areas

9   (McDougall et al. 2005). These results confirm findings by Duursma *et al.* (2013) who identified

10   subalpine grasslands as the most favorable habitat in Australia for novel potential invaders under

11   a future climate. Further, in response to climate change, new types of non-native plants might be

12   introduced as part of human mitigation or adaptation strategies, posing novel invasion risks

13   (Kueffer, 2010). Indeed, for the Australian Alps it has been shown that adaptation of the tourism

14   industry to climate change by promoting summer activities has already led to the introduction of

15   non-native horticultural plants that are in the process of invading protected areas (McDougall *et*

16   *al.*, 2011a).

17

18   *Limitations and perspectives*

19   Our results may overestimate the suitability for invasive species for several reasons. First, our

20   approach neither modeled the demography of metapopulation nor the dispersal rate because these

21   parameters were not available for all the considered species. Invasive species are by definition

22   dispersing such as it is difficult to model the niche with "true" absences. Apparent absences may

23   simply be sites that are not yet colonized. It has been shown that SDMs using pseudo-absences

1   rather than "true" absences could over predict potential distributions of species (Vaclavik &

2   Meentemeyer, 2009). Dispersal limitation may also explain why predicted highest elevation is

3   higher than the observed highest observed elevation for most of the species (Fig. 5, Table S1 to

4   S4). Invasive plant dispersal could be limited to human and disturbed pathways (i.e. roadsides,

5   railways, rivers Pysek & Richardson, 2007). For natural or semi-natural habitats, the unlimited-

6   dispersal assumption may not hold. While the unlimited dispersal scenario used in this study is

7   over-simplistic, it was shown to be closer to reality than the "no-dispersal" scenario in

8   mountainous areas (Engler *et al.*, 2009). Finally, our approach did not include any soil or land-

9   use variables. Although these variables have limited impact for fine scale predictions in

10   mountainous landscape (Randin *et al.*, 2009b), soil variables may be confounded with climatic

11   variables, thus biasing and possibly overestimating future spatial predictions (Bertrand *et al.*,

12   2012). On the other hand, our approach does not include human demographical scenarios for

13   future projections. In CH, the human demography and thus human disturbances is assumed to

14   increase, which should favor invasive plant species (Nobis *et al.*, 2009). Our approach may

15   underestimate the human impact in mountainous areas in the future but as our models and

16   previous ones reveal, non-climatic variables have much less relative importance in the depiction

17   of potential distribution of invasive plant species (Nobis *et al.*, 2009). Eventually, it should be

18   noted that our approach stacking binarized prediction maps provides an overestimation of the

19   number of species (Dubuis *et al.*, 2011, Pottier *et al.*, 2013, Calabrese *et al.*, 2014) and should be

20   rather considered as a suitability index for invasive plant species rather than an actual number of

21   species. Macroecological models (MEM) depicting spatial distribution of species richness are

22   known to be less biased (because taking into account biotic interactions) but individual species

23   responses to climate change are lost (Guisan & Rahbek, 2011, Dubuis *et al.*, 2011). Previous

1   MEM have been applied regionally in CH at a 1 km^2 resolution and provided a very similar

2   picture of invasive plants "richness" under current conditions in CH (Nobis *et al.*, 2009).

3   Including soil variables, dispersal rates, metapopulations demography and more scenarios for

4   non-climatic variable is desirable, in particular for conservation plan working at the species level

5   and requiring fine scale modeling and knowledge of population demographics.

6

7   **Conclusions**

8   Our results identify three key findings that address our initial questions. First, the risk of plant

9   invasions toward higher elevations in mountain areas is predicted to increase with climate

10 change. Currently the highest elevation vegetation zones in mountains are not yet

11 environmentally suitable for most invasive plant species, but these will become increasingly

12 suitable with climate change. Second, climate change will not influence invasive species

13 distributions in the same way in different mountain ranges. The magnitude of invasive species

14 distributional shifts will depend on distinct climatic factors affecting invader plants. Whereas

15 mountain susceptibility to invasions is predicted to increase sharply from the lowland to the

16 subalpine zone in Switzerland, where the elevation gradient is wide and species distributions are

17 mainly limited by cold temperatures, it is only predicted to increase slightly up to the alpine zone

18 or remain bound to the same maximal elevation in the Australian Alps, where the elevation

19 gradient is narrower, precipitation is an important factor shaping species distributions and many

20 species already reach the montane and subalpine zones. Third, non-native species that invade the

21 upper reaches of mountains in a future climate scenario are cold-tolerant species in the Swiss

22 Alps but species that prefer moister soils in the Australian Alps., Other traits are more marginally

23 associated with elevation limits include anthropochory for the lower limit in Australia, rosette

1 and ploidy level for the highest limits in Switzerland. These distributional shifts of non-native

2 species will likely represent a supplementary threat on native mountainous biodiversity already

3 affected by climate and land use changes. Consideration of invasive species in conservation

4 plans of sensitive mountain areas and systematic risk assessments are clearly required. In this

5 regard, we showed that SDMs can be useful for anticipating risks of future invasions (and see

6 Guisan *et al.*, 2013).

7

Acknowledgments

20

21

1   **References**

2   Acevedo P, Jiménez-Valverde A, Lobo JM, Real R (2012) Delimiting the geographical

3   background in species distribution modelling. *Journal of Biogeography,* **39**, 1383-1390.

4   Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium

5   (2011) Assembly of nonnative floras along elevational gradients explained by directional

6   ecological filtering. *Proceedings of the National Academy of Sciences,* **108**, 656-661.

7   Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models:

8   prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,* **43**, 1223-

9   1232.

10   Barbet-Massin M, Jiguet F, Albert CH, Thuiller W (2012) Selecting pseudo-absences for species

11   distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 1-

12   12.

13   Barni E, Bacaro G, Falzoi S, Spanna F, Siniscalco C (2012) Establishing climatic constraints

14   shaping the distribution of alien plant species along the elevation gradient in the Alps.

15   *Plant Ecology,* **213**, 757-767.

16   Barton K (2012) MuMIn: Multi-model inference, 1.7.11. Model selection and model averaging

17   based on information criteria (AICc and alike). CRAN Repository. http://CRAN.R-

18   project.org/package=MuMIn.

19   Barve N, Barve V, Jimenez-Valverde A *et al.* (2011) The crucial role of the accessible area in

20   ecological niche modeling and species distribution modeling. *Ecological Modelling,* **222**,

21   1810-1819.

1 Beaumont LJ, Gallagher RV, Thuiller W, Downey PO, Leishman MR, Hughes L (2009)

2   Different climatic envelopes among invasive populations may lead to underestimations of

3   current and future biological invasions. *Diversity and Distributions,* **15**, 409-420.

4 Becker T, Dietz H, Billeter R, Buschmann H, Edwards PJ (2005) Altitudinal distribution of alien

5   plant species in the Swiss Alps. *Perspectives in Plant Ecology Evolution and Systematics,*

6   **7**, 173-183.

7 Benning TL, Lapointe D, Atkinson CT, Vitousek PM (2002) Interactions of climate change with

8   biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic

9   birds using a geographic information system. *Proceedings of the National Academy of*

10   *Sciences,* **99**, 14246-14249.

11 Bertrand R, Perez V, Gégout JC (2012). Disregarding the edaphic dimension in species

12   distribution models leads to the omission of crucial spatial information under climate

13   change: the case of *Quercus pubescens* in France. *Global Change Biology,* **18**, 2648-

14   2660.

15 Billings WD (1974) Adaptations and origins of alpine plants. *Arctic and Alpine Research,* **6**,

16   129-142.

17 Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native

18   and invaded ranges matter. *Biology Letters,* **4**, 585-589.

19 Calabrese J M, Certain G, Kraan C, Dormann C F (2014). Stacking species distribution models

20   and adjusting bias by linking them to macroecological models. *Global Ecology and*

21   *Biogeography,* **23**, 99-112.

22 Chefaoui RM, Lobo JM (2008) Assessing the effects of pseudo-absences on predictive

23   distribution model performance. *Ecological Modelling,* **210**, 478-486.

1 Choler P (2005) Consistent shifts in alpine plant traits along a mesotopographical gradient.

2   *Arctic, Antarctic, and Alpine Research,* **37**, 444-453.

3 Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR (2011) Changes in

4   climatic water balance drive downhill shifts in plant species optimum elevations. *Science,*

5   **331**, 324-327.

6 De Bello F, Leps J, Sebastia MT (2005) Predictive value of plant traits to grazing along a

7   climatic gradient in the Mediterranean. *Journal of Applied Ecology,* **42**, 824-833.

8 Dietz H, Edwards PJ (2006) Recognition that causal processes change during plant invasion

9   helps explain conflicts in evidence. *Ecology,* **87**, 1359-1367.

10 Dubuis A, Pottier J, Rion V, Pellissier L, Theurillat JP, Guisan A (2011). Predicting spatial

11   patterns of plant species richness: a comparison of direct macroecological and species

12   stacking modelling approaches. *Diversity and Distributions,* **17**, 1122-1131.

13 Düllinger S, Gattringer A, Thuiller W *et al.* (2012) Extinction debt of high-mountain plants

14   under twenty-first-century climate change. *Nature Climate Change,* **2**, 619-622.

15 Duursma DE, Gallagher RV, Roger E, Hughes L, Downey PO, Leishman MR (2013) Next-

16   Generation Invaders? Hotspots for Naturalised Sleeper Weeds in Australia under Future

17   Climates. *Plos One,* **8**, e84222.

18 Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods in*

19   *Ecology and Evolution,* **1**, 330-342.

20 Engler R, Randin CF, Vittoz P *et al.* (2009). Predicting future distributions of mountain plants

21   under climate change: does dispersal capacity matter? *Ecography,* **32**, 34-45.

22 Engler R, Randin CF, Thuiller W *et al.* (2011) 21st century climate change threatens mountain

23   flora unequally across Europe. *Global Change Biology,* **17**, 2330-2341.

1   Fitzpatrick MC, Hargrove WW (2009) The projection of species distribution models and the

2   problem of non-analog climate. *Biodiversity and Conservation,* **18**, 2255-2261.

3   Franklin J, Davis FW, Ikegami M, Syphard AD, Flint LE, Flint AL, Hannah L (2013). Modeling

4   plant species distributions under future climates: how fine scale do climate projections

5   need to be? *Global Change Biology,* **19**, 473-483.

6   Friedman JH, Hastie TJ, Tibshirani R (2000) Additive logistic regression: a statistical view of

7   boosting. *Annals of Statistics,* **28**, 337-374.

8   Gallien L, Douzet R, Pratte S, Zimmermann NE, Thuiller W (2012) Invasive species distribution

9   models - how violating the equilibrium assumption can create new insights? *Global*

10   *Ecology and Biogeography,* **21**, 1126-1136.

11 Gauthier P, Lumaret R, Bédécarrats A (1998) Genetic variation and gene flow in Alpine diploid

12   and tetraploid populations of *Lotus* (*L. alpinus* (D.C.) Schleicher/*L. corniculatus* L.). I.

13   Insights from morphological and allozyme markers. *Heredity,* **80**, 683-693.

14 Graham CH, Elith J, Hijmans RJ, Guisan A, Peterson AT, Loiselle BA (2008) The influence of

15   spatial errors in species occurrence data used in distribution models. *Journal of Applied*

16   *Ecology,* **45**, 239-247.

17 Grime JP (1979) *Plant strategies and vegetation processes,* New York, John Wiley and Sons.

18 Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift

19   studies: insights from biological invasions. *Trends in Ecology & Evolution,* **29**, 260-269.

20 Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat

21   models. *Ecology Letters,* **8**, 993-1009.

22 Guisan A, Tingley R, Baumgartner JB *et al.* (2013) Predicting species distributions for

23   conservation decisions. *Ecology Letters,* **16**, 1424-1435.

1   Guisan A, Rahbek C (2011). SESAM–a new framework integrating macroecological and species

2   distribution models for predicting spatio-temporal patterns of species assemblages.

3   *Journal of Biogeography,* **38**, 1433-1444.

4   Haider S, Alexander J, Dietz H, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic

5   origin, residence time and habitat context in shaping non-native plant distributions along

6   an altitudinal gradient. *Biological Invasions,* **12**, 4003-4018.

7   Haider S, Kueffer C, Edwards PJ, Alexander JM (2012) Genetically based differentiation in

8   growth of multiple non-native plant species along a steep environmental gradient.

9   *Oecologia,* **170**, 89-99.

10   Hay SI, Cox J, Rogers DJ *et al.* (2002) Climate change and the resurgence of malaria in the East

11   African highlands. *Nature,* **415**, 905-909.

12   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated

13   climate surfaces for global land areas. *International Journal of Climatology,* **25**, 1965-

14   1978.

15   Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat

16   suitability models to predict species presences. *Ecological Modelling,* **199**, 142-152.

17   Hughes L (2011) Climate change and Australia: key vulnerable regions. *Regional Environmental*

18   *Change,* **11**, 189-195.

19   IPCC (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group*

20   *I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change,*

21   Cambridge, UK and New York, NY, USA, Cambridge University Press.

1　Jakobs G, Kueffer C, Daehler C (2010) Introduced weed richness across altitudinal gradients in

2　　　　Hawaii: humps, humans and water-energy dynamics. *Biological Invasions,* **12**, 4019-

3　　　　4031.

4　Juvik JO, Rodomsky BT, Price JP, Hansen EW, Kueffer C (2011) The upper limits of vegetation

5　　　　on Mauna Loa, Hawaii: a 50th-anniversary reassessment. *Ecology,* **92**, 518-525.

6　Kearney M (2005) Hybridization, glaciation and geographical parthenogenesis. *Trends in*

7　　　　*Ecology & Evolution,* **20**, 495–502.

8　Körner C (2003) *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystem,* New

9　　　　York, Springer.

10　Kueffer C (2010) Alien plants in the Alps: status and future invasion risks. In: *Europe's*

11　　　　*ecological backbone: recognising the true value of our mountains.* (ed Price E) pp 153-

12　　　　154. Copenhagen, European Environment Agency (EEA).

13　Kueffer C, McDougall K, Alexander J *et al.* (2014) Plant invasions into mountain protected

14　　　　areas: assessment, prevention and control at multiple spatial scales. In: *Plant invasions in*

15　　　　*protected areas: patterns, problems and challenges.* (eds Foxcroft LC, Pyšek P,

16　　　　Richardson DM, Genovesi P) pp 153-154, Dordrecht, Springer.

17　Kühn I, Durka W, Klotz S (2004) BiolFlor - a new plant-trait database as a tool for plant

18　　　　invasion ecology. *Diversity and Distributions,* **10**, 363-365.

19　Kurz WA, Dymond CC, Stinson G *et al.* (2008) Mountain pine beetle and forest carbon feedback

20　　　　to climate change. *Nature,* **452**, 987-990.

21　Landolt E, Bäumler B, Erhardt A *et al.* (2010) *Flora indicativa: Ecological indicator values and*

22　　　　*Biological attributes of flora of Switzerland and the Alps,* Bern, Haupt.

1 Lenoir J, Gegout JC, Guisan A *et al.* (2010) Going against the flow: potential mechanisms for

2   unexpected downslope range shifts in a warming climate. *Ecography,* **33**, 295-303.

3 Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of

4   prevention or a pound of cure: bioeconomic risk analysis of invasive species.

5   *Proceedings of the Royal Society of London Series B-Biological Sciences,* **269**, 2407-

6   2413.

7 Mandle L, Warren DL, Hoffmann MH, Peterson AT, Schmitt J, Von Wettberg EJ (2010)

8   Conclusions about Niche Expansion in Introduced *Impatiens walleriana* Populations

9   Depend on Method of Analysis. *Plos One,* **5**, e15297.

10 Marmion M, Parviaine M, Luoto M, Heikkinen RK, Thuiller W (2009). Evaluation of consensus

11   methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59-

12   69.

13 Marini L, Gaston KJ, Prosser F, Hulme PE (2009) Contrasting response of native and alien plant

14   species richness to environmental energy and human impact along alpine elevation

15   gradients. *Global Ecology and Biogeography,* **18**, 652-661.

16 Martin SL, Husband BC (2013) Adaptation of diploid and tetraploid *Chamerion angustifolium* to

17   elevation but not to local environment *Evolution,* **67**, 1780-1791.

18 McCain CM (2007) Could temperature and water availability drive elevational species richness

19   patterns? A global case study for bats. *Global Ecology and Biogeography,* **16**, 1-13.

20 McCain CM, Colwell RK (2011) Assessing the threat to montane biodiversity from discordant

21   shifts in temperature and precipitation in a changing climate. *Ecology Letters,* **14**, 1236-

22   1245.

1   McCullagh P, Nelder JA (1983) *Generalized Linear Models: First Edition,* London, New-York,

2   Chapman and Hall.

3   McDougall KL, Alexander JM, Haider S, Pauchard A, Walsh NG, Kueffer C (2011a) Alien flora

4   of mountains: global comparisons for the development of local preventive measures

5   against plant invasions. *Diversity and Distributions,* **17**, 103-111.

6   McDougall KL, Khuroo AA, Loope LL *et al.* (2011b) Plant Invasions in Mountains: Global

7   Lessons for Better Management. *Mountain Research and Development,* **31**, 380-387.

8   McDougall KL, Morgan JW, Walsh NG, Williams RJ (2005) Plant invasions in treeless

9   vegetation of the Australian Alps. *Perspectives in Plant Ecology, Evolution and*

10   *Systematics,* **7**, 159-171.

11 Nagy L, Grabherr G, Körner C, Thompson DBA (eds) (2003) *Alpine Biodiversity in Europe,*

12   Stuttgart, Springer.

13 Nobis M P, Jaeger JA, Zimmermann N E (2009). Neophyte species richness at the landscape

14   scale under urban sprawl and climate warming. *Diversity and Distributions,* **15**, 928-939.

15 O'Donnell J, Gallagher RV, Wilson PD, Downey PO, Hughes L, Leishman MR (2011) Invasion

16   hotspots for non-native plants in Australia under current and future climates. *Global*

17   *Change Biology,* **18**, 617-629.

18 Olson DM, Dinerstein E, Wikramanayake ED *et al.* (2001) Terrestrial ecoregions of the worlds:

19   A new map of life on Earth. *Bioscience,* **51**, 933-938.

20 Ozenda P, Mayer H, Zirnig A (1988) *Die Vegetation der Alpen im europäischen Gebirgsraum,*

21   Stuttgart, Fischer.

Parks CG, Radosevich SR, Endress BA *et al.* (2005) Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. *Perspectives in Plant Ecology, Evolution and Systematics,* **7**, 137-158.

Pauchard A, Alaback PB (2004) Influence of elevation, land use, and landscape context on patterns of alien plant invasions along roadsides in protected areas of south-central Chile. *Conservation Biology,* **18**, 238-248.

Pauchard A, Kueffer C, Dietz H *et al.* (2009) Ain't no mountain high enough: Plant invasions reaching high elevations. *Frontiers in Ecology and the Environment,* **7**, 479-486.

Pearson RG, Dawson TP, Liu C (2004) Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography,* **27**, 285-298.

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography,* **38**, 817-827.

Petitpierre B (2014) Using environmental niche modelling to understand biological invasions in a changing world. Unpublished PhD University of Lausanne, Lausanne.

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* **190**, 231-259.

Pottier J, Dubuis A, Pellissier L *et al.* (2013). The accuracy of plant assemblage prediction from species distribution models varies along environmental gradients. *Global Ecology and Biogeography,* **22**, 52-63.

Price MF (2010) Europe's ecological backbone: recognising the true value of our mountains. Copenhagen, European Environment Agency.

Pyšek, P., & Richardson, D. M. (2007). Traits associated with invasiveness in alien plants: where do we stand? In *Biological invasions* (pp. 97-125). Springer Berlin Heidelberg.

1 R (2012) *R: A language and environment for statistical computing. Version 2.15.1,* Vienna,

2   Austria, R Foundation for Statistical Computing.

3 Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? *Ecography,* **18**,

4   200-205.

5 Ramirez J, Jarvis A (2008) High Resolution Statistically Downscaled Future Climate Surfaces.

6   International Center for Tropical Agriculture (CIAT). CGIAR Research Program on

7   Climate Change, Agriculture and Food Security (CCAFS). Cali, Colombia.

8 Randin CF, Engler R, Normand S *et al.* (2009a) Climate change and plant distribution: local

9   models predict high-elevation persistence. *Global Change Biology,* **15**, 1557-1569.

10 Randin CF, Jaccard H, Vittoz P, Yoccoz NG, Guisan A (2009b). Land use improves spatial

11   predictions of mountain plant abundance but not presence-absence. *Journal of Vegetation*

12   *Science,* **20**, 996-1008.

13 Romdal TS, Grytnes J-A (2007) An indirect area effect on elevational species richness patterns.

14   *Ecography,* **30**, 440-448.

15 Scherrer D, Korner C (2011) Topographically controlled thermal-habitat differentiation buffers

16   alpine plant diversity against climate warming. *Journal of Biogeography,* **38**, 406-416.

17 Scherrer P, Pickering CM (2010) The Australian Alps: opportunities and challenges for

18   geotourism. In: *Geotourism: the tourism of geology and landscape.* (eds Newsome D,

19   Dowling R) pp 77–87. Goodfellows Publishers, London.

20 Scholes R, Settele J, Betts R *et al.* (2014) Chapter 4. Terrestrial and Inland Water Systems. In:

21   *Climate Change 2014: Impacts, Adaptation, and Vulnerability (IPCC Working Group II).*

22   (eds Field CB, Et Al.).

23

1

2 Seipel TF (2011) Distribution and demographics of non-native plants in mountainous regions.

3   ETH. http://dx.doi.org/10.3929/ethz-a-006961752

4 Seipel T, Alexander JM, Daehler CC *et al.* (2015) Performance of the herb *Verbascum thapsus*

5   along environmental gradients in its native and non-native ranges. *Journal of*

6   *Biogeography* **42**, 132-143.

7 Seipel T, Kueffer C, Rew LJ *et al.* (2012) Processes at multiple scales affect richness and

8   similarity of non-native plant species in mountains around the world. *Global Ecology and*

9   *Biogeography,* **21**, 236-246.

10 Siraj AS, Santos-Vega M, Bouma MJ, Yadeta D, Carrascal DR, Pascual M (2014) Altitudinal

11   changes in malaria incidence in highlands of Ethiopia and Colombia. *Science,* **343**, 1154-

12   1158.

13 Soberon J (2007) Grinnellian and Eltonian niches and geographic distributions of species.

14   *Ecology Letters,* **10**, 1115-1123.

15 Thuiller W, Brotons L, Araújo MB, Lavorel S (2004) Effects of restricting environmental range

16   of data to project current and future species distributions. *Ecography,* **27**, 165-172.

17 Thuiller W, Lafourcade B, Engler R, Araujo MB (2009) BIOMOD - a platform for ensemble

18   forecasting of species distributions. *Ecography,* **32**, 369-373.

19 Thuiller W, Lavorel S, Araújo MB (2005) Niche properties and geographical extent as predictors

20   of species sensitivity to climate change. *Global Ecology and Biogeography,* **14**, 347-357.

21 Treier UA, Broennimann O, Normand S, Guisan A, Schaffner U, Steinger T, Mueller-Schaerer H

22   (2009) Shift in cytotype frequency and niche space in the invasive plant *Centaurea*

23   *maculosa*. *Ecology,* **90**, 1366-1377.

1   Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate

2   model projections of climate change impacts on mountain plants. *Global Change*

3   *Biology,* **14**, 1089-1103.

4   Trtikova M, Edwards PJ, Güsewell S (2010) No adaptation to altitude in the invasive plant

5   *Erigeron annuus* in the Swiss Alps. *Ecography,* **33**, 556-564.

6   Vaclavik T, Meentemeyer RK (2009) Invasive species distribution modeling (iSDM): Are

7   absence data and dispersal constraints needed to predict actual distributions? *Ecological*

8   *Modelling,* **220**, 3248-3258.

9   Walther G-R, Roques A, Hulme PE *et al.* (2009) Alien species in a warmer world: risks and

10   opportunities. *Trends in Ecology & Evolution,* **24**, 686-693.

11 Webber BL, Yates CJ, Le Maitre DC *et al.* (2011) Modelling horses for novel climate courses:

12   Insights from projecting potential distributions of native and alien Australian acacias with

13   correlative and mechanistic models. *Diversity and Distributions,* **17**, 978-1000.

14 Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland:

15   Species versus community approach. *Journal of Vegetation Science,* **10**, 469-482.

16 Zomer RJ, Trabucco A, Bossio DA, Van Straaten O, Verchot LV (2008) Climate Change

17   Mitigation: A Spatial Analysis of Global Land Suitability for Clean Development

18   Mechanism Afforestation and Reforestation. *Agriculture, Ecosystems & Environment,*

19   **126**, 67 - 80.

20 Zweig MH, Campbell G (1993) Receiver operating characteristic (ROC plots) - a fundamental

21   evaluation tool in clinical medicine. *Clinical Chemistry,* **39**, 1589-1589.

22

1   **Short description of Ecological Archives material**

2   The supporting information contains descriptions of current and future climate in CH and NSW

3   (Fig. S1, Tables S5 to S8), the results for the five species invading both CH and NSW (Fig. S2 to

4   S4), the impact of climate analogy (Fig. S5 and S7), traits analysis material (Fig. S6, Tables S9

5   and S10) and individual species results (Fig. S8 and S9, Tables S1 to S4)

6

1 **Tables and captions.**

2 **Table 1**: Variables used in SDMs.

Abbreviation	Scale	Variable description
G1	Global	Annual Mean Temperature
G2	Global	Temperature Seasonality
G3	Global	Mean Temperature of Warmest Quarter
G4	Global	Mean Temperature of Coldest Quarter
G5	Global	Precipitation Seasonality
G6	Global	Precipitation of Warmest Quarter
G7	Global	Aridity
G8	Global	Aridity Seasonality
L1	Local	Annual Mean Temperature
L2	Local	Temperature Seasonality
L3	Local	Annual Precipitation
L4	Local	Density of Urban Area
L5	Local	Distance to the Closest River, Lake or Shore

3

4

1

Table 2: GLMs assessing the relationship between elevation limits and species traits: observed

maximal elevation, predicted maximal elevation by SDMs and difference (i.e. shift) between

current and future (A1 2070) predicted elevation limit. The species traits retained after variable

selection (with its relationship with the response variables given in brackets) and the explained

deviance (R^2) of the models are indicated. See Table S9 for more details on species traits and

Table S10 for the exact coefficients of the models. The *elevation potential* variable was only

included in the GLMs modeling the shift in current vs future maximal elevation.

Extent	Response	SDMs	Species traits after stepwise selection	R^2
CH	Current observed maximal elevation	-	Temperature (-)	0.53
	Current predicted maximal elevation	Global	Temperature (-); Soil nutrients (+)	0.51
	Shift in current vs. future predicted maximal elevation	Global	*Elevation potential* (+)	0.32
	Current predicted maximal elevation	Local	Temperature (-); Rosette (+); ploidy (-)	0.70
	Shift in current vs. future predicted maximal elevation	Local	*Elevation potential* (+)	0.51
NSW	Current observed maximal elevation	-	Soil moisture (+); Anthropochory (-)	0.59
	Current predicted maximal	Global	Subtropical (-)	0.25

	elevation			
	Shift in current vs. future predicted maximal elevation	Global	Life strategies (see table S10); *Elevation potential* (+)	0.83
	Current predicted maximal elevation	Local	Subtropical (-); Soil moisture (+); Woody (-); Zoochory (+)	0.86
	Shift in current vs. future predicted maximal elevation	Local	Leaf duration (-)	0.44

1

2

1   **Figure legends**

2

3   **Figure 1**: Study area and distribution of elevation zones in Switzerland (CH, a) and New South

4   Wales (NSW, b). The elevation gradient was divided into lowland (192 - 800 m asl. in CH, 0 -

5   700 m asl. in NSW), montane (801 - 1500 m in CH, 701 - 1400 in NSW), subalpine (1501 - 2200

6   m in CH, 1401 - 1800 m in NSW) and alpine zones (2201 - 3100 m in CH, 1801 - 2228 m in

7   NSW). Note that areas with extreme climatic conditions were removed from the study and that

8   lowland in NSW was split into wet (> 500 mm of annual precipitation) and dry areas (< 500 mm

9   of annual precipitation).

10

11   **Figure 2**: Highest observed (Obs) and predicted elevation under current conditions and the six

12   climate change scenarios (labeled 1 to 7, as in tables S1 to S4) predicted by local (black) and

13   global (grey) models in Switzerland (a) and New South Wales (b). Yearly average temperature

14   (T) and precipitation (P) are plotted along the elevation gradient to inform about the climatic

15   conditions along the elevation gradients in the two study area.

16

17   **Figure 3**: Stacking of species binary potential distributions provided by local and global SDMs

18   in Switzerland and New South Wales under seven different climatic conditions (see table S6 to

19   S9 for a detailed description of the scenarios). Colors represent the potential number of species

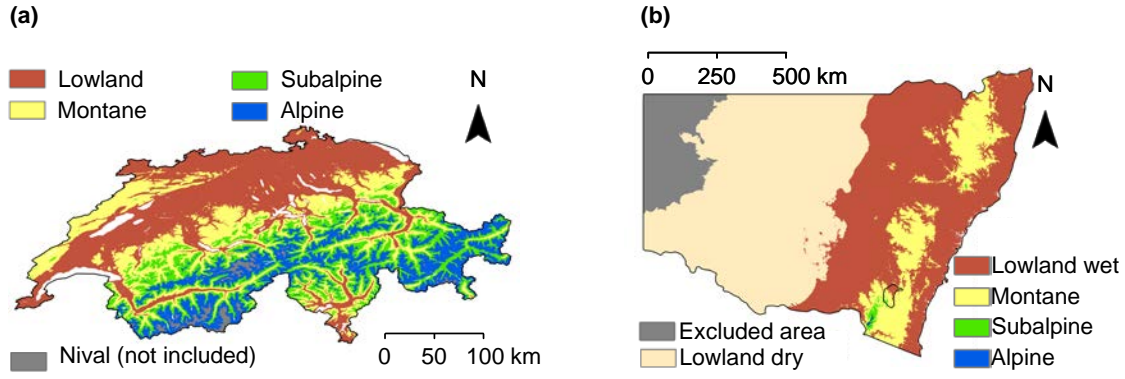20   (# species). Non-analog climate is depicted in grey.

21

1 **Figure 4**: Proportion of suitable area predicted by global and local SDMs for the current

2 conditions and the six climate change scenarios (labeled 1 to 7, as in tables S6 to S9) in each

3 vegetation zone (lowland dry, lowland wet, montane, subalpine and alpine) in Switzerland (a)

4 and New South Wales (b). The stars show the significance of the difference between the average

5 predicted elevation between the global and the local SDMs assessed with a t-test (*** means p-

6 val < 0.001, ** 0.001> p-val < 0.01, * 0.01> p-val < 0.05).

7

8 **Figure 5**: Variable importance (assessed by the ENSEMBLE modeling) for invasive species in

9 New South Wales (black) and Switzerland (grey) in global (a) and local (b) SDMs. For the

10 global SDMs, annual mean temperature, temperature seasonality, mean temperature of the

11 warmest quarter, mean temperature of the coldest quarter, precipitation seasonality, precipitation

12 of the warmest quarter aridity and aridity seasonality are abbreviated G1 to G8 respectively,

13 whereas annual mean temperature, temperature seasonality, annual precipitations, density of

14 urban areas and distance the closest water course are abbreviated L1 to L5 for the local SDMs, as

15 in table 1. Stars represent the significance of the difference between CH and NSW values for

16 each variable assessed with a t-test (*** means p-val < 0.001, ** 0.001> p-val < 0.01, * 0.01> p-
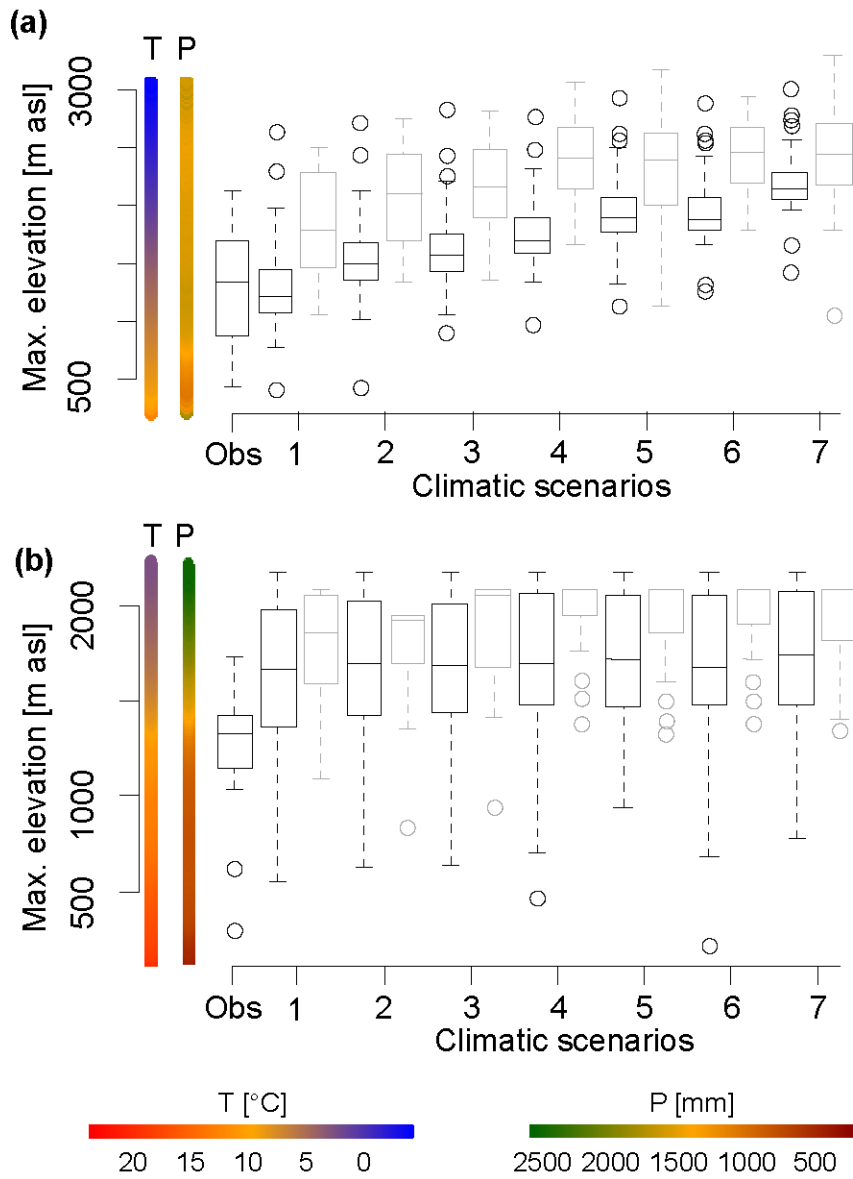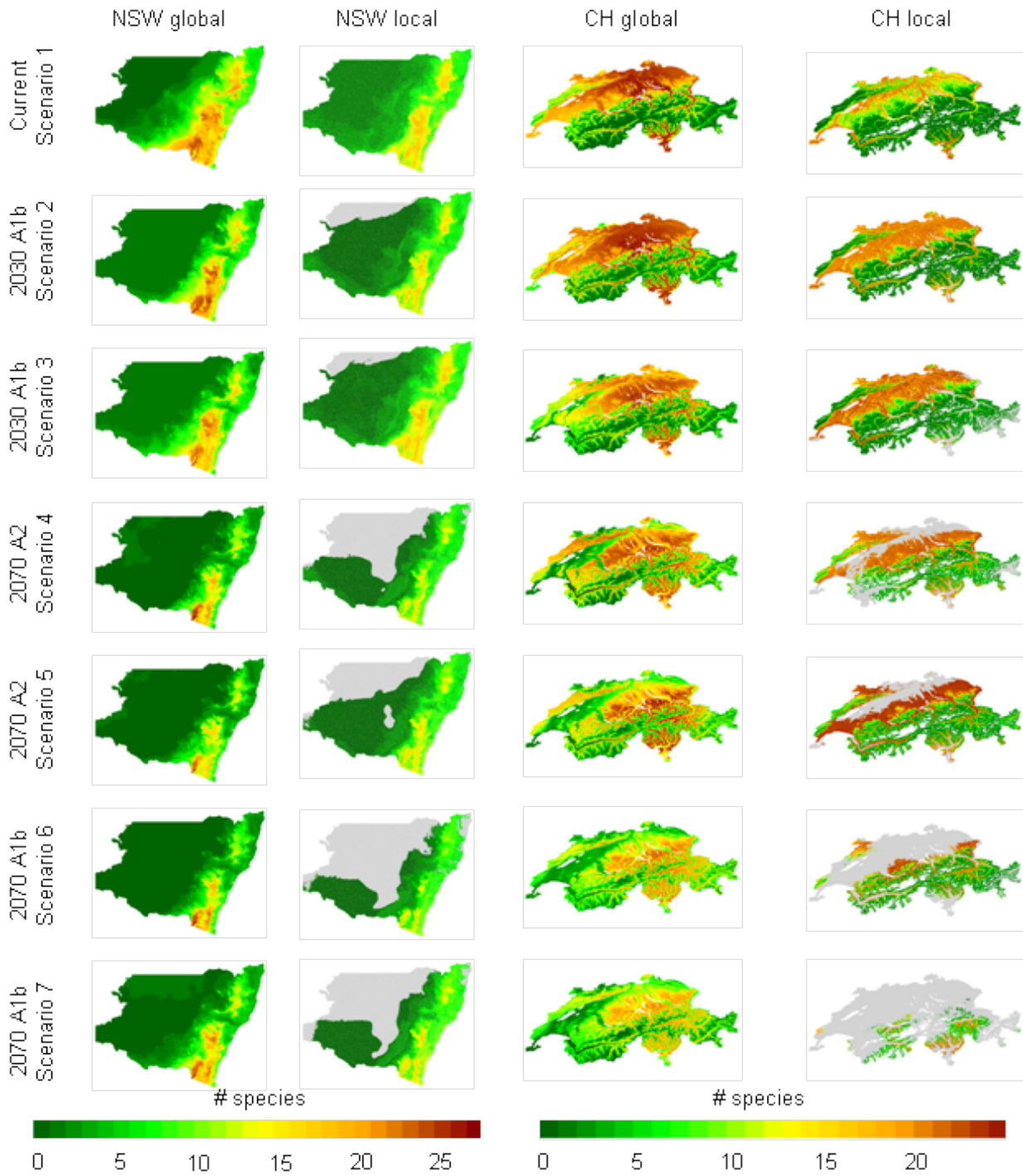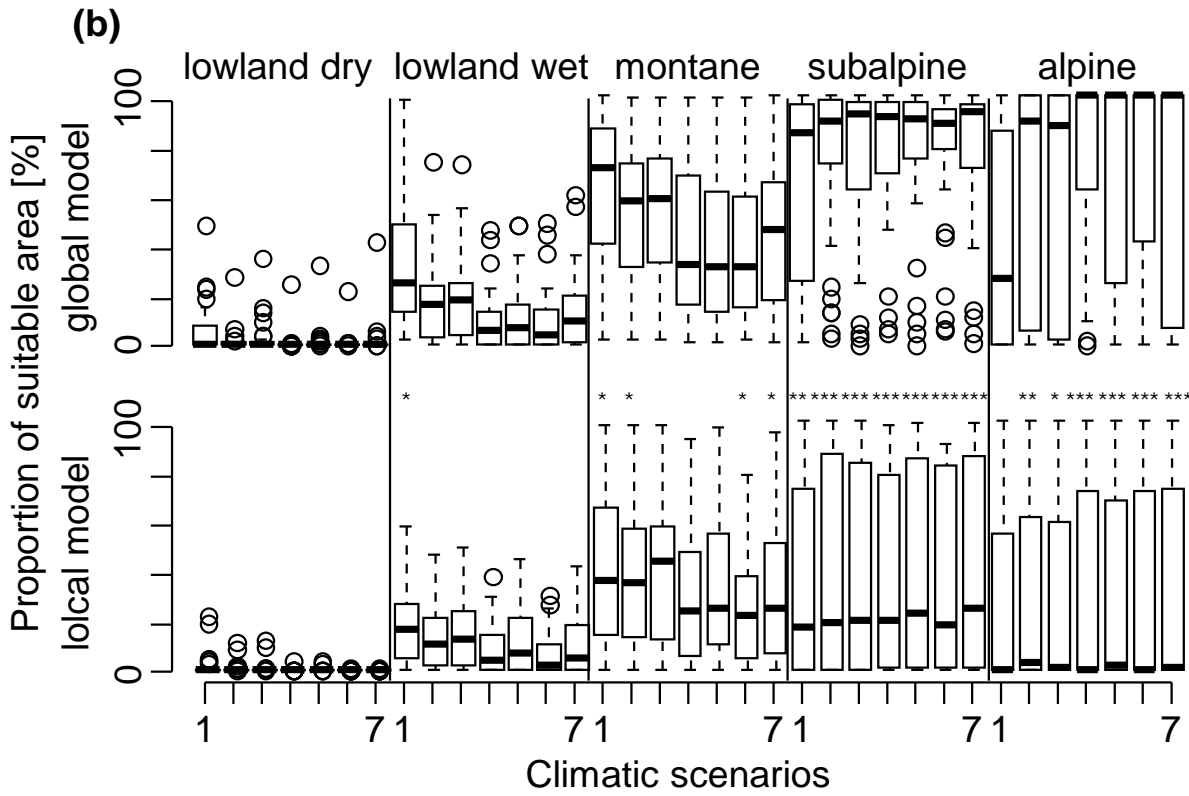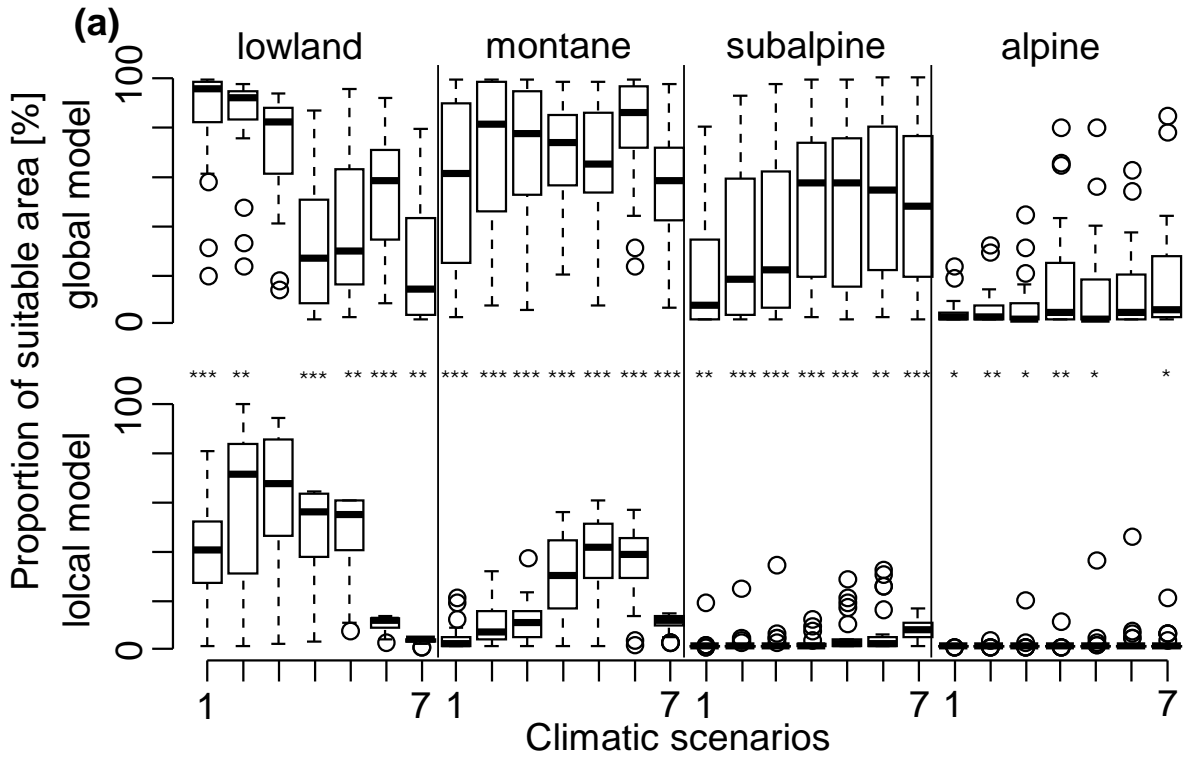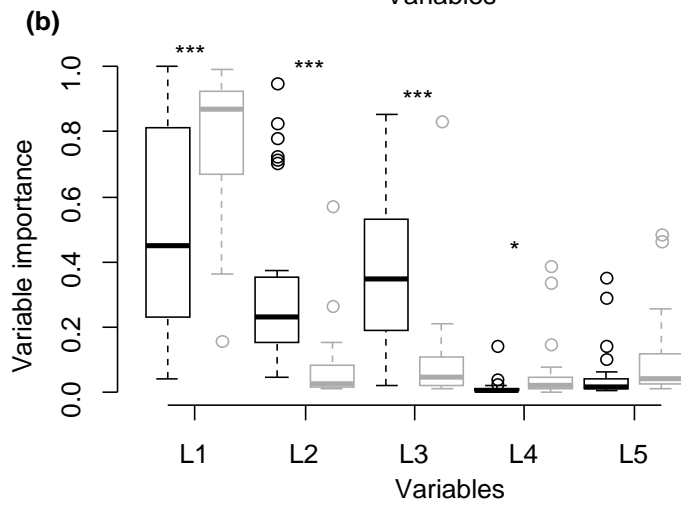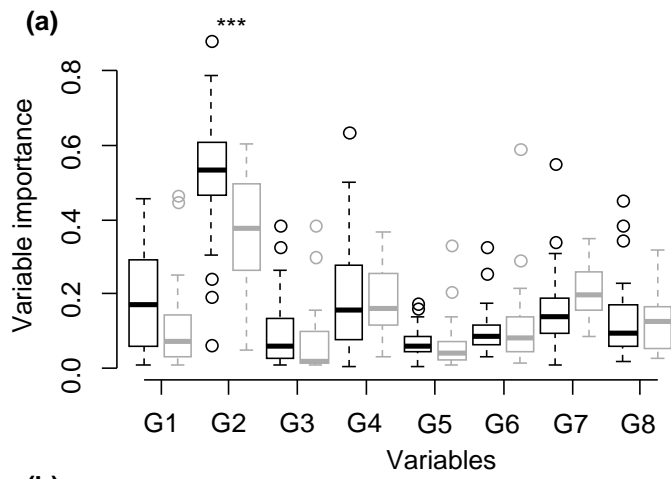
17 val < 0.05).

18

1   **Figures**

2

3   Fig. 1

4

1   Fig. 2.

2

1   Fig. 3.

2

3

1 Fig. 5.

2