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Faculty of Biology and Medicine Publication

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Journal: Ecological applications : a publication of the Ecological Society of America

Year: 2016 Mar

Volume: 26

Issue: 2

Pages: 530-44

Running head: More neophytes in hotter mountains?

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

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Paper type: article

Abstract

Mountain ecosystems have been less adversely affected by invasions of non-native plants than most other ecosystems, partially because most invasive plants in the lowlands are limited by climate and cannot grow under harsher high-elevation conditions. However, with ongoing climate change, invasive species may rapidly move upwards and threaten mid, and then high elevation mountain ecosystems. We evaluated this threat by modeling the current and future habitat suitability for 48 invasive plant species in Switzerland and New South Wales, Australia. Both regions had contrasting climate interactions with elevation, resulting in possible different responses of species distributions to climate change. Using a species distribution modeling approach that combines data from two spatial scales, we built high-resolution species distribution models (≤ 250 m) that account for the global climatic niche of species and also finer variables depicting local climate and disturbances. We found that different environmental drivers limit the elevation range of invasive species in each of the two regions, leading to region-specific species responses to climate change. The optimal suitability for plant invaders is predicted to markedly shift from the lowland to the montane or subalpine zone in Switzerland, whereas the upward shift is far less pronounced in New South Wales where montane and subalpine elevations are already suitable. The results suggest that species most likely to invade high elevations in Switzerland will be cold-tolerant, whereas species with an affinity to moist soils are most likely to invade higher elevations in Australia. Other plant traits were only marginally associated with elevation limits. These results demonstrate that a more systematic consideration of future distributions of invasive species is required in conservation plans of not yet invaded mountainous ecosystems.

Keywords: Australian Alps, elevation limits, environmental gradients, invasive plants, multi-scale approach, plant traits, species distribution models, Switzerland

Introduction

Non-native plant species richness is generally low in mountainous areas, especially at high elevations (McDougall *et al.*, 2011a, Seipel *et al.*, 2012), where few non-native species occur and these rarely become abundant or negatively affect ecosystems and biodiversity (McDougall *et al.*, 2011b, Kueffer *et al.*, 2014). Several possible explanations have been proposed for this pattern, which contrasts strongly with most non-mountain biomes (Pauchard *et al.*, 2009). First, less intensive land use and reduced human activity at high elevations reduce invasion opportunities due to the greater resistance of undisturbed habitats to invasion (Pauchard & Alaback, 2004, Parks *et al.*, 2005, Marini *et al.*, 2009, Jakobs *et al.*, 2010, Kueffer *et al.*, 2014). Additionally, it has been proposed that introductions of non-native species have predominantly occurred at low elevations in mountains, resulting in a lower propagule pressure and delayed invasions at high elevations (Becker *et al.*, 2005, Alexander *et al.*, 2011). Time-lags may also be partly related to a need for adaptive evolution (Dietz & Edwards, 2006, Haider *et al.*, 2012). Such a preponderance of introduction of lowland species to mountain regions also means that only non-native species with a broad climatic niche that can grow both in lowland and higher elevation climates can reach alpine ecosystems (‘directional ecological filtering’, Alexander *et al.*, 2011). Indeed, species pre-adapted to a mountain climate are conspicuously lacking from high elevation non-native floras worldwide (McDougall *et al.*, 2011a). Furthermore, non-native richness patterns might be shaped by the same abiotic factors (i.e. area, climate, productivity and water availability) that explain a decline of native species richness with elevation (Rahbek, 1995, McCain, 2007, Romdal & Grytnes, 2007, Jakobs *et al.*, 2010, Alexander *et al.*, 2011). Although many factors may affect the spread of non-native species from lowlands to high elevations in mountains, climate is clearly important (Marini *et al.*, 2009, Jakobs *et al.*, 2010, Trtikova *et al.*, 2010, Kueffer *et al.*, 2014, Seipel *et al.*, 2015).

The rate of invasion into higher elevations is likely to increase in the future. First, propagule pressure and habitat disturbances may increase in mountainous regions due to economic development, leading to the exchange of climatically pre-adapted mountain species between mountainous regions (e.g. tourism; McDougall *et al.*, 2005, McDougall *et al.*, 2011b). Second, climate change might reduce the climatic limitation of current non-native species distributions and facilitate invasions into mountains (Pauchard *et al.*, 2009, Walther *et al.*, 2009, Barni *et al.*, 2012). There is evidence that human, animal and plant diseases are currently moving toward higher elevations with climate change, posing a new threat to mountain livelihoods, ecosystems, and biodiversity (Benning *et al.*, 2002, Hay *et al.*, 2002, Kurz *et al.*, 2008, Walther *et al.*, 2009, Siraj *et al.*, 2014). To our knowledge, however, whether plant invasion risks will increase in mountain areas with climate change has not been systematically and quantitatively investigated, although the resulting impacts on ecosystems and economy might be as important as direct consequences from climate change (Scholes *et al.*, 2014).

In particular, it is not clear whether climate change will lead to the same invasion risks in different mountainous regions. Different climate factors might interact in shaping species distribution limits along the elevation gradients, and their importance might differ depending on climatic distances between lowlands and the top of the gradient. For instance, aridity, more than temperature, seems to act as a limiting factor for the invasion of non-native species in dry, higher elevation areas (e.g. in Hawaii; Jakobs *et al.*, 2010, Juvik *et al.*, 2011), and non-climatic habitat factors can also restrict expansion of non-native species into higher elevations (Haider *et al.*, 2010). Thus, depending on the limiting factors, species distributions might respond differently to climate change because not all climate factors will change with the same magnitude and direction (Crimmins *et al.*, 2011, McCain & Colwell, 2011). Further, impacts of climate change will not be homogenous around the world and some mountain ranges will be more affected than others (Engler *et al.*, 2011). Models including all these parameters are needed to understand and anticipate how invasive species will react to climate change in mountainous areas.

Preventing biological invasions is considered to be more efficient than control and eradication efforts following introduction (Leung *et al.*, 2002). Accordingly, reliable anticipation of invasions is critical for conservation management of mountain biodiversity hotspots, especially given the island-like nature of mountains that makes mountainous ecosystems more vulnerable to biological invasions. To do this, species distribution models (SDMs; Guisan & Thuiller, 2005) based on environmental niche quantification can identify potential suitable habitats for non-native species in geographic space (identified as species potential distributions, Thuiller *et al.*, 2005, Guisan *et al.*, 2014) and support conservation decisions (Guisan *et al.*, 2013). SDMs relate species distribution in space to environmental variables (generally available as GIS layers) based on a statistical characterization of the Hutchinsonian realized species niche (*sensu* Soberon, 2007; i.e. assuming implicitly biotic interactions but also dispersal limitations). When climate change scenarios are available, SDMs can be used to assess the potential responses of plant distributions to climate change (e.g. Engler *et al.*, 2011).

Distribution and climate data across the complete environmental range of a species are typically required to identify the niche (Thuiller *et al.*, 2004, Guisan *et al.*, 2014). For this purpose, the most exhaustive geographical species distribution is needed. Coarse resolution data typically available over large geographic extents may however not reflect the fine-scale environmental heterogeneity that drives local to regional species distributions. In the case of complex topographies, such as in mountainous landscapes, spatial extent and resolution strongly matter for building SDMs and deriving projections (Randin *et al.*, 2009a, Seipel *et al.*, 2012, Franklin *et al.*, 2013). Therefore large-scale SDMs and predictions may differ substantially from those calibrated at a finer, local or regional scale, and they may for instance overestimate (Trivedi *et al.*, 2008, Franklin *et al.*, 2013) or underestimate (Randin *et al.*, 2009a) species persistence in mountainous landscapes. In turn, SDMs fitted over small extents may result in truncated climatic niches and project biased distributions under present and future climates (Thuiller *et al.*, 2004). This is why modeling approaches that combine local and global scale analyses (e.g. Pearson *et al.*, 2004, Gallien *et al.*, 2012) are particularly needed to provide robust predictions in heterogeneous mountain landscapes.

In this paper, we assess whether mountainous areas will be at increased risk of plant invasions under climate change in two mountainous areas where climatic gradients interact differently with the elevation gradient. We used a combined approach linking coarser data models at a global scale with finer distribution data and environmental maps available for particular local mountain ranges. Because species response to climate change along elevation gradient can be different among mountain ranges (e.g. Engler *et al.*, 2011), we modeled potential distributions for invasive plant species using SDMs in two study areas. In Switzerland (CH; including the Swiss Alps and Jura mountains) temperature is assumed to be the major limiting factor determining the upper distribution of non-native species because of the broad elevation gradient. In the Australian Alps in New South Wales (NSW), which has a narrower elevation gradient, aridity may play relatively a more important role in shaping species distributions. Data were obtained for 48 species in total, 24 from CH, and 29 from NSW; 5 species were common to both study areas. We assessed the magnitude of the elevation shift for invasive plant species in these mountains using the predictions of SDMs under six climate change scenarios. Because species that share the same ecological traits may exhibit similar responses to climate change (Thuiller *et al.*, 2005), we then tested the hypothesis that shared species traits and other biogeographical characteristics are associated with species upper elevation limit. With this we aim to get a better understanding of whether responses of different types of invasive plants to future climates differ according to their properties.

The specific questions we addressed in this paper were:

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

2) Will climate change influence non-native species potential distribution in the same way in two contrasted mountain ranges?

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

Methods

Study areas

Switzerland (CH, total area 41,285 km2) is characterized by a mountainous landscape with a large elevation gradient (between 192 and 4634 m asl, Fig. 1a). The Alps are the most important mountain range occupying 60% of the area of the country. In the northwest, the Jura is smaller and less elevated (10% of the country area with a maximal elevation of 1680 m asl). Western European broadleaf forests and European-Mediterranean montane forests are the two ecoregions found in CH (Olson et al., 2001). We classified CH into 4 elevation zones: lowland (192 - 800 m asl), montane (801 - 1500 m asl), subalpine (1501 - 2200 m asl) and alpine (2201 - 3100 m asl), representing ecological units structured by the elevation (Ozenda *et al.*, 1988). Higher elevations were not included in the analyses because environmental conditions become hostile for virtually all plant species.

New South Wales (NSW, total area 809,444 km^2) is located in southeastern Australia and contains portions of the Australian Alps. New South Wales is characterized by a strong gradient of increasing precipitation from west to east. Six ecoregions have been identified: Eastern-Southeast Australia temperate forests, Australian Alps montane grasslands, Eastern Australian temperate forests, Southeast Australia temperate savanna, Murray-Darling woodlands and mallee and Eastern Australia mulga shrublands (Olson *et al.*, 2001). NSW is considered a hotspot of invasive plants in Australia (O'Donnell *et al.*, 2011). We classified NSW into 5 elevation zones corresponding to the same ecological units as in CH and subdivided the lowest zone into dry and wet parts due to a strong aridity gradient (Fig. 1b): dry lowland (0 - 700 m asl and current annual precipitation < 500 mm), wet lowland (0 - 700 m asl and current annual precipitation > 500 mm), montane (701 - 1400 m asl), subalpine (1401 - 1800 m asl) and alpine (1801 - 2228 m asl). We did not include the Simpson Desert ecoregion in the analyses because no study species had more than five occurrences.

On average, CH is colder and wetter than NSW. Climate change scenarios predict a higher increase of temperature and a stronger decrease of wetness in CH. However, this highly depends on the different scenarios (Tables S5 to S8) and the decrease of wetness in regards to the proportion of the average value, is similar. Temperature and precipitation differences between CH and NSW along elevation gradients are shown in Fig. S1.

Species data

For both CH and NSW, only terrestrial plant species with precise-enough georeferenced occurrence data at both local and worldwide scale were selected (minimum number of occurrences N = 18, Tables S1 and S2). In CH, it resulted in a selection of 24 major invasive species (out of the 36 of national concern; www.infoflora.ch; last accessed 26 May 2014). We used occurrence data from the info flora database (www.infoflora.ch) and from the Mountain Invasion Research Network dataset (MIREN; Becker *et al.*, 2005, Seipel, 2011).

Data for NSW invaders were obtained from relevés stored in the Atlas of NSW Wildlife (http://www.bionet.nsw.gov.au; accessed 5 October, 2013). Because there are more invasive plant species in NSW than CH, we selected only 24 species that occurred in or close to the Australian Alps and had sufficient records for building robust SDMs. There was no prior reason to expect that any of them would respond to climate change in a particular way. We additionally selected five species, which occurred both in CH and NSW and had sufficient records for SDMs, to allow direct comparisons of species behavior in different climates (*Ailanthus altissima, Ambrosia artemisiifolia, Lonicera japonica, Prunus laurocerasus and Robinia pseudoacacia*, Tables S3 and S4 and Fig. S2 and S5). For both CH and NSW, these data were collected during a wide temporal window (from the first reported observation until 2010).

In addition to datasets from both regions we also gathered occurrence data from the Global Biodiversity Information Facility (*data.gbif.org*, accessed between August and September 2012) for use in construction of the SDMs at a global scale. We retained occurrences when location accuracy was greater than 2.5 km and 250 m for global and local SDMs a compromise between occurrence accuracy and occurrence number. Despite this small locational uncertainty SDMs remain robust (Graham *et al.*, 2008).

Multi-scale SDMs framework

To combine the widest species niche (including the widest species distribution) and finer topo-climatic variation typically characterizing mountainous landscapes, we fitted SDMs at two scales: global and local. First, global SDMs were built based on worldwide species distributions and coarser climatic variables. We included occurrences from both the native and multiple invaded ranges to capture the most complete climatic niche of species, and to diminish the risk of under-predicting the range of the potential distribution in the invaded ranges due to enemy release (Broennimann & Guisan, 2008, Beaumont *et al.*, 2009). These global climatic SDMs were used in two ways: (i) to predict the current and future distribution for different climate change scenarios; and (ii) to select the pseudo-absences to be used in the local SDMs (Gallien *et al.*, 2012). The local SDMs were calibrated at a much finer resolution and included climate but also disturbance variables that can affect species distribution at a local scale.

Global SDMs

Eight climatic variables, known to optimize the geographic transferability of SDMs, were used at the global scale (Petitpierre, 2014). Precipitation and temperature data at 30 arc seconds resolution (about 1km at the equator) were obtained from the Worldclim database (Hijmans *et al.*, 2005). Aridity and aridity seasonality data (variance of monthly aridity means) were obtained from the Global Aridity and PET database (http://www.cgiar-csi.org) at the same resolution. These data represent the yearly average between 1950 and 2000. Potential mismatches between the timeframes of the climate data and the species observation should not impact the results for higher elevation because the majority of the species were first introduced to lowland areas then spreading to higher elevations. In addition, all occurrences collected in NSW are post-1950.

Thus, only the oldest species observation in the lowland in CH, which might not match the timeframe of the climatic data, are not distributed at higher elevation. Observations at the upper elevation of the species were observed within the timeframe of the climate data. The next step was to define an ecologically-relevant study background to calibrate the SDMs and select pseudo-absences, because inadequate extents may result in over-optimistic evaluations (Guisan & Thuiller, 2005, Chefaoui & Lobo, 2008, Barve *et al.*, 2011, Acevedo *et al.*, 2012). We defined the study background for each species as the ecoregions covered by the species distribution. Ecoregions are geographical units characterized by homogeneity between climates, geology, fauna and flora (Olson *et al.*, 2001).

Local SDMs

For each study area (CH and NSW) and species, we used georeferenced data from local databases and defined the extent in the same way as for the global SDMs. Within this extent, pseudo-absences were selected inversely proportional to the suitability provided by the global SDMs for the same species (as in Gallien *et al.*, 2012, but with a linear weight). At a finer local scale, other factors than climate can be important in driving invasive species distribution (Guisan *et al.*, 2014). Because some of our species were intimately linked to water streams and invasive species are known to be promoted by human disturbances (Marini *et al.*, 2009, Nobis *et al.*, 2009, Jakobs *et al.*, 2010), we used two disturbance variables (distance to the closest river, lake or shore and density of urban area), combined with three climatic variables at a resolution of 100 m and 250 m for CH and NSW, respectively (Table 1). For CH, climate variables (yearly average between 1961 and 1990) were taken from Zimmermann & Kienast (1999), whereas for

NSW they were provided by the NSW Office of Environment and Heritage (for the year 1990, Christopher Simpson, personal communication).

Modeling techniques

For both global and local SDMs, we randomly sampled 10,000 pseudo-absences in the study background of each species, weighted to reach an equal prevalence with presences. To reduce spatial autocorrelation due to sampling bias, occurrences were disaggregated to keep a 10 km minimal distance between two occurrences in the global SDMs and 1 km in the local SDMs. Data were split into calibration (70%) and evaluation (30%) datasets. We applied an ENSEMBLE modeling approach by averaging three modeling techniques: generalized linear models (GLM) with polynomial quadratic coefficients preceded by a stepwise selection based on the Bayesian Information Criteria (BIC, McCullagh & Nelder, 1983); generalized boosted regression models (GBM) with 5000 trees and 7 degrees of interaction depth (Friedman *et al.*, 2000); and MAXENT with default parameters (Phillips *et al.*, 2006). The BIOMOD package was used for GLM and GBM (Thuiller *et al.*, 2009) and the dismo package for MAXENT (Hijmans *et al.*, 2005), implemented in R software (R, 2012). The whole procedure was replicated 10 times per species and averaged. The same large set of down-weighted pseudo-absences was used here with all modelling techniques to ensure a common modelling framework (but see Barbet-Massin *et al.*, 2012 for different pseudo-absence selection strategies for different modeling techniques). To estimate the contribution of variables, SDMs were run with each variable randomized 5 times separately and the obtained predictions are correlated with the unrandomized SDMs. A high correlation means that the randomized variable is not important whereas a low correlation indicates the randomized variable is crucial in the depiction of the species potential distribution

(Thuiller *et al.*, 2009). Suitability and variable contributions were averaged across techniques and iterations. The resulting averaged suitability predictions were evaluated with the Area Under the Curve of a Receiver Operating Characteristics (Roc AUC, Zweig & Campbell, 1993) and the True Skill Statistics (TSS, also known as corrected Kappa, Allouche *et al.*, 2006). This represents the standard procedure for such ENSEMBLE modeling procedure using BIOMOD (e.g. Marmion *et al.*, 2009). Additionally, we used two "presence-only" evaluators, the Boyce index (B; Hirzel *et al.*, 2006) and the sensitivity rate, which is the rate of correctly predicted presences when the prediction is made binary. Presence-only evaluators are particularly relevant in the case of invasive species because invasions are ongoing processes, and observed distributions may not reflect the distributional equilibrium. Absences may thus not be reliable for model evaluation. For clarity, we only present AUC and Boyce in the manuscript (but see Tables S1 - S4 for the other evaluators). Continuous probabilities of spatial projections were binarized using the threshold providing the best TSS. The spatial projections were done at the same resolution as the environmental layers and associated with a digital elevation model of the mean elevation within each pixel. For each species, we removed the ten highest elevated predicted sites to lower the possible effects of outliers on the upper elevation limit. For each species, we assessed the proportion of the study area covered by the potential distribution within each elevation zone and measured the highest potential elevation.

Because extrapolating SDM predictions to non-analog climate may provide spurious and thus unreliable results (Fitzpatrick & Hargrove, 2009, Mandle *et al.*, 2010, Peterson, 2011, Webber *et al.*, 2011, Guisan *et al.*, 2014), we removed sites presenting such novel climate from the analysis, using the Multivariate Environmental Similarity Surfaces (MESS, Elith *et al.*, 2010) but see Fig. S5 for results including non-analog climates).

Spatial projections under future climate

Scenarios for global SDMs were available from the Research Program on Climate Change, Agriculture and Food Security (http://www.CCAFS-climate.org, Ramirez & Jarvis, 2008). Climate change scenarios for variables G7 and G8 (Table 1) were derived following Zomer *et al.* (2008) using bioclimatic variables of Worldclim. For both the global and local scale analyses, we used predictions for two years (2030 and 2070) derived from six different climate change scenarios representing two emission scenarios of IPCC's 4th assessment report (A1B and A2, IPCC, 2007) and based on three Global Circulation Models (GCMs): HadCM3, ECHAM5 and Ccsm3 (Tables S5 to S8). For local SDMs in CH, Regional Circulation Models (RCMs) were available at a 1 km resolution (N.E. Zimmermann, WSL, personal communication). Climate anomaly was bilinearly interpolated at a 100 m resolution. For NSW, RCMs were available at a 250 m resolution (C. Simpson, NSW Office of Environment and Heritage, pers. com.).

Species traits and biogeographical characteristics

For each species, we collected a number of traits and characteristics (Table S9) to (i) determine if the species had different ecological characteristics between CH and NSW, and (ii) to test traits are associated with the elevation pattern of predicted species distributions (Thuiller *et al.*, 2005). These traits were gathered from two databases, Flora Indicativa (Landolt *et al.*, 2010, based on expert knowledge) and Biolflor (Kühn *et al.*, 2004). Flora indicativa provided indicator values assigned to each species for their optima along various environmental variables and information on the species ecology. We additionally considered Grime's C-S-R classification system for interpreting species ecological strategies (Grime, 1979). We used a two-sided randomization test to compare the distribution of traits among species in CH and NSW when variables were quantitative or semi-quantitative (e.g. Landolt's indices); for qualitative traits we performed non-parametric Chi-Square tests.

Further, we modeled the association between the traits of a species and three variables related to the upper distribution limit: 1) current observed maximal elevation, 2) current predicted maximal elevation and 3) shift between predicted maximal elevation under current conditions and predicted maximal elevation under climate conditions in A1 2070 scenarios. Future maximal predicted elevations were averaged for the two A1 2070 scenarios (scenarios 6 and 7 in Tables S1 to S4). In the model of predicted elevation shifts, we included the *elevation potential*, i.e. the difference between the current predicted maximal elevation for each species and the maximal elevation of the gradient in the region, as an explanatory factor. For both NSW and CH species pools, we tested these associations based on predictions from global and local SDMs. Because the number of species traits was high in relation to the number of species, we used a hierarchical approach to select important ones and avoid model over-parameterization. First, for each trait we built a univariate GLM and compared the Bayesian Information Criterion (BIC; more restrictive than AIC) of the obtained model to a model with only the intercept (null model). If the model including the trait did not have a better BIC than the null model, the trait was not considered further. After this first selection, all combinations of the retained traits were examined and the combination providing the best BIC was used as the final model. Multimodel inference and variable selection were done in R using the library MuMIn (Barton, 2012)

Results

Evaluation of SDMs

In CH, SDMs had high evaluation scores when fitted at both global (AUC = 0.88 ± 0.05; B = 0.8 ± 0.07; Table S1) and local (AUC = 0.91 ± 0.06; B = 0.72 ± 0.22; Table S2) scales. The same overall good performances were found in NSW at global (AUC = 0.89 ± 0.04; B = 0.95 ± 0.05; Table S3) and local (AUC = 0.95 ± 0.05; B = 0.76 ± 0.04; Table S4) scales. Only the local SDMs for *P. laurocerasus* in NSW had a poor B (-0.19).

Species distribution under current climate

Equivalent elevations in CH and NSW are not equivalent for climate variables (Fig. 2 and S1) but we report species distribution along the elevation gradient to better answer our initial questions about invasions and elevation in mountains. Climatic differences between CH and NSW are discussed in the discussion section.

In CH, invasive plant species are on average currently observed up to the montane zone (1317 ± 497 m). This was not significantly different from the maximal elevation predicted by local SDMs (1331 ± 473 m) but differed significantly from the one predicted by global SDMs, where on average, species were predicted to reach the subalpine area (1843 ± 473 m, t-test $P < 0.001$, Fig. 2). Indeed, global SDMs predicted more suitability in general, and also at more elevated areas (84 ± 22%, 57 ± 35%, 17 ± 23% and 3 ± 6% of the total area in lowland, montane, subalpine and alpine zones, respectively) compared to local SDMs (37 ± 19%, 4 ± 6%, 1 ± 4% and 0 ± 0%; Fig. 3 and 4). For global SDMs in CH, the most important variables were temperature variability, temperature of the coldest quarter and aridity index (Fig. 5a), while average temperature was the most important variable for local SDMs (Fig. 5b). Species traits explained between 51% and

70% of the variance of the current upper elevation limit in CH (both observed and predicted), with a positive association with species resistance to cold, presence of rosette, diploidy and the ability to be competitive on nutrient rich soils (Table 2, Fig. S6).

In NSW, the selected species are currently observed at a similar maximal average elevation to CH (1287 ± 292 m). However, SDMs predicted a significantly higher elevation limit when fitted at both global (1789 ± 271 m; t-test $P < 0.001$) and local (1628 ± 447 m; t-test $P = 0.001$; Fig. 2) scales. On average, SDMs predicted more suitable area for invasive species at higher elevation than in CH, including for the species occurring in both CH and NSW (Fig. 4 and S4). The montane and subalpine areas were predicted to be the most suitable by both global (with 6 ± 11%, 33 ± 26%, 61 ± 30%, 63 ± 38% and 40 ± 42% of the total area at dry lowland, wet lowland, montane, subalpine and alpine zones respectively) and local SDMs (2 ± 5%, 18 ± 15%, 43± 32%, 35 ± 39% and 28 ± 40%; Fig. 3 and 4). For the global SDMs (Fig. 5a), the most important variables were the same as for CH except that temperature seasonality was more important for species in NSW than in CH (t-test $P < 0.001$, Fig. 5). When calibrated at the local scale, the most important variables in determining species distributions in NSW were temperature, precipitation and temperature variability (Fig. 5b), which were all significantly different from the CH local SDMs (Fig. 5). Disturbance variables contributed substantially less than climate variables in both NSW and CH (Fig. 5b)

We also found significant differences between CH and NSW for the following species traits: Landolt’s indices of temperature (4.27 vs 3.85; t-test $P = 0.040$), soil moisture (1.92 vs 1.42; t-test $P = 0.027$), life strategies (CH species are more competitive, Chi-square test $P = 0.019$), number of occurrences used to calibrate the SDMs (227 vs 1318; t-test $P < 0.001$) and the number of species present in southern temperate areas (15 vs 20 species, Chi-square test P =

0.044). The other traits tested did not show significant differences between CH and NSW (see all p-values in table S9). In NSW, traits related to the maximal elevation explained between 25% and 86% of the variation in species maximal elevations (observed or predicted, Table 2, Fig. S6), and were different from CH (Table 2). In NSW, species maximal elevation was associated with various traits, but not with Landolt's temperature, while index of soil moisture predicted the observed maximal elevation. Global SDMs, predicted that stress-tolerant competitors (*sensu* Grime, 1979) had lower maximal elevations (Table 2).

Species distribution under future climate

In CH, both global and local SDMs predicted an increase of suitability at higher elevation (Fig. 3 and 4). Based on global SDMs, climate change scenarios indicate a decrease of potential suitability in the lowland, no change in the montane zone, and an increase in the subalpine and alpine zones, whereas local SDMs predicted that lowland and montane zones will experience the most dramatic increases in suitability in the future (Fig. 4 and 5). However, in the most extreme climate change scenarios, suitability was predicted to decrease at the lowland zone. For local SDMs, this decrease can be attributed to the exclusion of non-analog climates, which removed large areas of the lowland zone (but see Fig. S2 when SDMs are extrapolated to novel climates), whereas only up to 7 species will experience non-analog climates in the lowland based on global SDMs (Fig. S7). For both global and local SDMs, climate change scenarios had a significant effect on the maximal predicted elevation of distributions (Kruskall-test, $P < 0.001$), reaching a maximum of 2430 ± 474 m and 2170 ± 340 respectively for scenario HadCM1 A1B 2070 (Fig. 2). When results from both A1b scenarios were averaged, the difference between current and future potential elevation varied between -79 m for *Lonicera japonica* and 995 m for *Prunus* *laurocerasus* with an average of 579 ± 286 m in global SDMs (Table S1), and between 252 m for *Sedum spurium* and 979 m for *Bunias orientalis* with local SDMs (Table S2). The average Spearman correlation between local and global SDMs predictions of the highest elevations under the current conditions and the six climate change scenarios was 0.57 ± 0.13. In CH, only species *elevation potential* was significantly associated with this shift of the maximal elevation, explaining 32% and 51% of this elevational response for local and global SDMs respectively (Table 2). Spatial projections are available for each species and each climatic scenario in Fig. S8 and S9.

In NSW, although SDMs predicted some elevation shift, these predictions differed substantially from the ones in CH. Climate change scenarios predicted a decrease of suitability at lowland and montane zones but the predictions differed between global and local SDMs for the upper elevation. While global SDMs predicted an increase of suitability at subalpine and alpine zones, local SDMs showed a slight increase of suitability at subalpine zone, and no changes of the global suitability at the alpine zone (Fig. 3 and 4). This difference remained when testing the effect of climate change scenarios on the upper elevation limits. It was significant for the global SDMs (Kruskall-test, $P < 0.001$), reaching an average of 1969 ± 190 m with scenario ECHAM5 A2 2070 (Fig. 2), whereas there was no effect on local SDM predictions (Kruskall-test, $P = 0.98$, Fig. 2), reaching a maximum of 1720 ± 353 m with the scenario HadCM3 A2 2070. When results from both A1b 2070 scenarios were averaged, the difference between future and current predicted elevation varied between -70 m for *Chondrilla juncea* and 432 m for *Ambrosia artemisiifolia* (Table S3) and between -979 m for *I. aquifolium* and 523 m for *A. artemisiifolia* for global and local SDMs respectively. In NSW, 25% of the variation in elevation shift was explained by growth strategy (with competitive ruderal strategists *sensu* Grime, 1979) and by species with wider elevation potential (see methods; Table 2 and S10). In contrast, 44% of the variation of the shift in predicted maximal elevation by local SDMs was explained by the species ability to keep their leaves in winter (wintergreen species).

Discussion

We assessed the difference between current and future potential distribution of a selection of plant invaders in two disparate mountainous areas. Our SDMs predict an upward shift of the upper elevational distribution limit for most modelled invasive plant species. Across all climate change scenarios and models, an upward shift of up to 500 m for local SDMs, and of 1000 m for global SDMs, is predicted. The montane, subalpine and alpine zones will be at high risk of plant invasion in a future climate. However, the magnitude of this upward shift in response to climate change strongly depends on the study area, with a less pronounced shift in New South Wales (NSW) than in Switzerland (CH). These Ecological and environmental differences between the regions may explain the different changes in the predicted distributions of invasive plant species. In the following sections, we discuss possible causes for these contrasting patterns and the implications of distributional shifts of invasive plant species towards higher elevations for mountain ecosystems and their conservation.

Interplay of temperature and aridity along the elevation gradient

Due to the topographic configuration of the Australian Alps, the upper distribution limits of the studied invasive species are closer to the upper limit of the elevation gradient in NSW than in CH, which reduces the potential for a further upward shift of their distribution under climate change. In other words, for most species a large part of the coldest conditions available in NSW are already suitable under current climatic conditions, while this is not the case in CH (see appendix S1). As a result, suitable areas are predicted to decrease in NSW because montane to alpine areas are a small proportion of total land area, while in CH a reduction in suitable area at low elevation is compensated with an increase in suitable habitat at higher elevation (Fig. 3 and 4). Thus, the most important factor associated with species distributional response to climate change is the *elevation potential* of the species (see Methods). Species with lower current predicted elevation are further from the top of the elevation gradient and have greater predicted elevation expansion in both NSW and CH (Table 2 and S6). The importance of the elevation potential is more difficult to explain in CH because the elevation gradient is not limiting, but only a few species are predicted to reach the highest elevation of the gradient in the future (Tables S1 and S2). A possible explanation might be that the magnitude of the distributional response of species to climate change can change along the elevation gradient (Engler *et al.*, 2011), with species at lower elevation shifting more strongly than species located at higher elevation. Overall, our results corroborate published analyses that show mountains with larger elevation gradients, combined with species positioned lower along elevation gradients, offer more opportunity for upward range shifts (Engler *et al.*, 2011).

Compared to CH, the studied invasive species in NSW are adapted to colder environments, as indicated by their lower indicator values for temperature (T; Landolt *et al.*, 2010). Additionally, at comparable elevation the temperature is higher in NSW (Fig. S1). This can explain why non-native species are currently predicted at a higher position along the elevation gradient in NSW (i.e. maximal suitability is found in the montane-subalpine elevation zones in NSW while in lowland-montane zones in CH). Other factors might also explain the different responses between

NSW and CH. For example, local SDMs show that the alpine zone is not currently highly suitable for most species in NSW and will not become more suitable with climate change. This is because cold temperatures alone are not the primary limiting factor in NSW. The potential distributions of species in NSW are primarily shaped by temperature seasonality and precipitation, and only secondarily by annual mean temperature (L1 on Fig. 5). Consequently in NSW changes in temperature seasonality and precipitation patterns in the future will influence species distributions. In particular, the stress-tolerant species in NSW are predicted by global SDMs to lower their elevation limit (negative coefficient for CSS species in table S10), suggesting that the coldest temperatures at the top of the gradient do not represent the most stressful factor in NSW. Such a downwards shift with climate change due to changing aridity conditions has also been shown for some plants species in California (Crimmins *et al.*, 2011), in Europe (Lenoir *et al.*, 2010), and for vertebrates in different mountain ranges around the world (McCain & Colwell, 2011).

The interplay of species traits and elevation limits

Species traits associated with the observed or predicted upper elevation limits differ markedly between CH and NSW, according to the strongest abiotic gradient prevailing in each of the two regions, i.e. precipitation in NSW and temperature in CH (Fig. S1). Preference for moister soils characterizes species that are predicted to reach higher elevations in NSW, whereas in CH elevation limit is related to cold tolerant species. In NSW, only anthropochory is negatively correlated with elevation (Table 2). This may reflect the lower impact of anthropogenic activities in the wilder higher elevation areas of the Australian Alps, where tourism has burgeoned only since the 1970s (Scherrer & Pickering, 2010), bringing fewer non-native species there than to lowlands (Pauchard *et al.*, 2009). Among morphological and genetic traits, species forming rosettes or having a diploid cytotype have higher predicted elevation limits in CH (Table 2). Rosettes are typical of alpine plant communities and are an adaptation to cold conditions, light availability, nutrient storage, and herbivory and characterize the plant traits of many alpine areas in the Swiss Alps (Billings, 1974, Körner, 2003, Choler, 2005, De Bello *et al.*, 2005). Distribution of ploidy along an elevation gradient is a debated topic (e.g. Kearney, 2005) but diploid cytotypes among native flora have been shown for some species to occur more frequently in cold conditions at high elevation (Gauthier *et al.*, 1998, Treier *et al.*, 2009, Martin & Husband, 2013). Among biogeographical origins, only the few species of subtropical areas, and thus adapted to hot and dry conditions, are predicted with a lower elevation limit in NSW under current conditions (Table 2).

Implications for mid to high elevation ecosystems

Our results show that with climate change most plant invaders that are currently found in lowland areas will have a high potential to colonize mountain ecosystems. High-elevation ecosystems in the European Alps represent some of the last relatively undisturbed ecosystems with a large and unique native biodiversity (Nagy *et al.*, 2003, Price, 2010). Very few non-native plant species currently occur in these ecosystems and only few pose a problem (Kueffer, 2010). Consequently, awareness among mountain conservation managers is low and limited management capacity is in place (McDougall *et al.*, 2011b). With climate change the situation might rapidly change. First, previous studies reported that climate change will negatively affect native plant communities in mountainous areas (Engler *et al.*, 2011, Hughes, 2011, Düllinger *et al.*, 2012), our results suggest that invasions by non-native species may amplify such negative effects. Many of the most problematic invasive plant species have already established high population densities in mountain valleys and dispersal distances to alpine ecosystems are short once climatic barriers are removed, possibly contributing to the decline of species at risk of extinction (Düllinger *et al.*, 2012, e.g. if non-native species invade micro-habitats serving as climate refugia for native species Scherrer & Körner, 2011).

In Australia, although the selected species in NSW were predicted to be less likely to invade higher elevations than the species in CH, many species were still predicted to extend their range into the alpine zone, which is currently largely free of invasive species outside of disturbed areas (McDougall et al. 2005). These results confirm findings by Duursma *et al.* (2013) who identified subalpine grasslands as the most favorable habitat in Australia for novel potential invaders under a future climate. Further, in response to climate change, new types of non-native plants might be introduced as part of human mitigation or adaptation strategies, posing novel invasion risks (Kueffer, 2010). Indeed, for the Australian Alps it has been shown that adaptation of the tourism industry to climate change by promoting summer activities has already led to the introduction of non-native horticultural plants that are in the process of invading protected areas (McDougall *et al.*, 2011a).

Limitations and perspectives

Our results may overestimate the suitability for invasive species for several reasons. First, our approach neither modeled the demography of metapopulation nor the dispersal rate because these parameters were not available for all the considered species. Invasive species are by definition dispersing such as it is difficult to model the niche with “true” absences. Apparent absences may simply be sites that are not yet colonized. It has been shown that SDMs using pseudo-absences rather than “true” absences could over predict potential distributions of species (Vaclavik & Meentemeyer, 2009). Dispersal limitation may also explain why predicted highest elevation is higher than the observed highest observed elevation for most of the species (Fig. 5, Table S1 to S4). Invasive plant dispersal could be limited to human and disturbed pathways (i.e. roadsides, railways, rivers Pysek & Richardson, 2007). For natural or semi-natural habitats, the unlimited-dispersal assumption may not hold. While the unlimited dispersal scenario used in this study is over-simplistic, it was shown to be closer to reality than the “no-dispersal” scenario in mountainous areas (Engler *et al.*, 2009). Finally, our approach did not include any soil or land-use variables. Although these variables have limited impact for fine scale predictions in mountainous landscape (Randin *et al.*, 2009b), soil variables may be confounded with climatic variables, thus biasing and possibly overestimating future spatial predictions (Bertrand *et al.*, 2012). On the other hand, our approach does not include human demographical scenarios for future projections. In CH, the human demography and thus human disturbances is assumed to increase, which should favor invasive plant species (Nobis *et al.*, 2009). Our approach may underestimate the human impact in mountainous areas in the future but as our models and previous ones reveal, non-climatic variables have much less relative importance in the depiction of potential distribution of invasive plant species (Nobis *et al.*, 2009). Eventually, it should be noted that our approach stacking binarized prediction maps provides an overestimation of the number of species (Dubuis *et al.*, 2011, Pottier *et al.*, 2013, Calabrese *et al.*, 2014) and should be rather considered as a suitability index for invasive plant species rather than an actual number of species. Macroecological models (MEM) depicting spatial distribution of species richness are known to be less biased (because taking into account biotic interactions) but individual species responses to climate change are lost (Guisan & Rahbek, 2011, Dubuis *et al.*, 2011). Previous

MEM have been applied regionally in CH at a 1 km^2 resolution and provided a very similar picture of invasive plants “richness” under current conditions in CH (Nobis *et al.*, 2009).

Including soil variables, dispersal rates, metapopulations demography and more scenarios for non-climatic variable is desirable, in particular for conservation plan working at the species level and requiring fine scale modeling and knowledge of population demographics.

Conclusions

Our results identify three key findings that address our initial questions. First, the risk of plant invasions toward higher elevations in mountain areas is predicted to increase with climate change. Currently the highest elevation vegetation zones in mountains are not yet environmentally suitable for most invasive plant species, but these will become increasingly suitable with climate change. Second, climate change will not influence invasive species distributions in the same way in different mountain ranges. The magnitude of invasive species distributional shifts will depend on distinct climatic factors affecting invader plants. Whereas mountain susceptibility to invasions is predicted to increase sharply from the lowland to the subalpine zone in Switzerland, where the elevation gradient is wide and species distributions are mainly limited by cold temperatures, it is only predicted to increase slightly up to the alpine zone or remain bound to the same maximal elevation in the Australian Alps, where the elevation gradient is narrower, precipitation is an important factor shaping species distributions and many species already reach the montane and subalpine zones. Third, non-native species that invade the upper reaches of mountains in a future climate scenario are cold-tolerant species in the Swiss Alps but species that prefer moister soils in the Australian Alps., Other traits are more marginally associated with elevation limits include anthropochory for the lower limit in Australia, rosette and ploidy level for the highest limits in Switzerland. These distributional shifts of non-native species will likely represent a supplementary threat on native mountainous biodiversity already affected by climate and land use changes. Consideration of invasive species in conservation plans of sensitive mountain areas and systematic risk assessments are clearly required. In this regard, we showed that SDMs can be useful for anticipating risks of future invasions (and see Guisan *et al.*, 2013).

Acknowledgments

Climatic scenarios data for local SDMs in CH were provided by Achilleas Psomas, Dirk Schmarz and Niklaus E. Zimmermann (WSL institute). Climatic scenario data for local SDMs in NSW were provided by Christopher Simpson (NSW Office of Environment and Heritage). These latter layers were developed in an ARC Linkage project (LP0989537) on climate change, supported in part by GER. The computations were performed at the Vital-IT (http://www.vital-it.ch) Center for high-performance computing of the SIB Swiss Institute of Bioinformatics. AG, OB and BP received support at the earlier stages of the study from the Swiss National Center of Competences in Research 'Plant Survival' (granted by the Swiss National Science Foundation), and CK from USDA National Institute of Food and Agriculture, Biology of Weedy and Invasive Species Program grant no. 2006-35320-17360 (to Curtis Daehler). We thank two anonymous reviewers for their constructive comments on the manuscript.

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Short description of Ecological Archives material

The supporting information contains descriptions of current and future climate in CH and NSW (Fig. S1, Tables S5 to S8), the results for the five species invading both CH and NSW (Fig. S2 to S4), the impact of climate analogy (Fig. S5 and S7), traits analysis material (Fig. S6, Tables S9 and S10) and individual species results (Fig. S8 and S9, Tables S1 to S4)

Tables and captions.

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

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**	$\mathbf{R^2}$
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

Figure legends

Figure 1: Study area and distribution of elevation zones in Switzerland (CH, a) and New South Wales (NSW, b). The elevation gradient was divided into lowland (192 - 800 m asl. in CH, 0 - 700 m asl. in NSW), montane (801 - 1500 m in CH, 701 - 1400 in NSW), subalpine (1501 - 2200 m in CH, 1401 - 1800 m in NSW) and alpine zones (2201 - 3100 m in CH, 1801 - 2228 m in NSW). Note that areas with extreme climatic conditions were removed from the study and that lowland in NSW was split into wet (> 500 mm of annual precipitation) and dry areas (< 500 mm of annual precipitation).

Figure 2: Highest observed (Obs) and predicted elevation under current conditions and the six climate change scenarios (labeled 1 to 7, as in tables S1 to S4) predicted by local (black) and global (grey) models in Switzerland (a) and New South Wales (b). Yearly average temperature (T) and precipitation (P) are plotted along the elevation gradient to inform about the climatic conditions along the elevation gradients in the two study area.

Figure 3: Stacking of species binary potential distributions provided by local and global SDMs in Switzerland and New South Wales under seven different climatic conditions (see table S6 to S9 for a detailed description of the scenarios). Colors represent the potential number of species (# species). Non-analog climate is depicted in grey.

Figure 4: Proportion of suitable area predicted by global and local SDMs for the current conditions and the six climate change scenarios (labeled 1 to 7, as in tables S6 to S9) in each vegetation zone (lowland dry, lowland wet, montane, subalpine and alpine) in Switzerland (a) and New South Wales (b). The stars show the significance of the difference between the average predicted elevation between the global and the local SDMs assessed with a t-test (*** means p-val < 0.001, ** 0.001> p-val < 0.01, * 0.01> p-val < 0.05).

Figure 5: Variable importance (assessed by the ENSEMBLE modeling) for invasive species in New South Wales (black) and Switzerland (grey) in global (a) and local (b) SDMs. For the global SDMs, annual mean temperature, temperature seasonality, mean temperature of the warmest quarter, mean temperature of the coldest quarter, precipitation seasonality, precipitation of the warmest quarter aridity and aridity seasonality are abbreviated G1 to G8 respectively, whereas annual mean temperature, temperature seasonality, annual precipitations, density of urban areas and distance the closest water course are abbreviated L1 to L5 for the local SDMs, as in table 1. Stars represent the significance of the difference between CH and NSW values for each variable assessed with a t-test (*** means p-val < 0.001, ** 0.001> p-val < 0.01, * 0.01> p-val < 0.05).

Figures

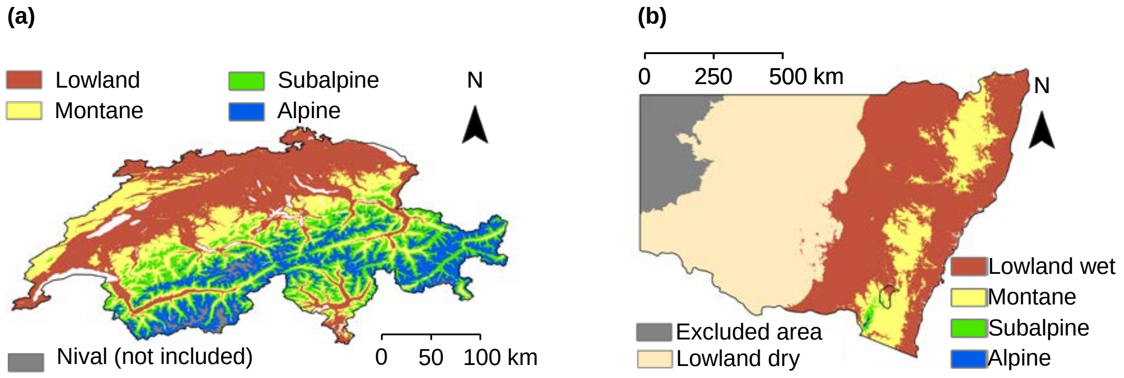


Fig. 1

Fig. 2.

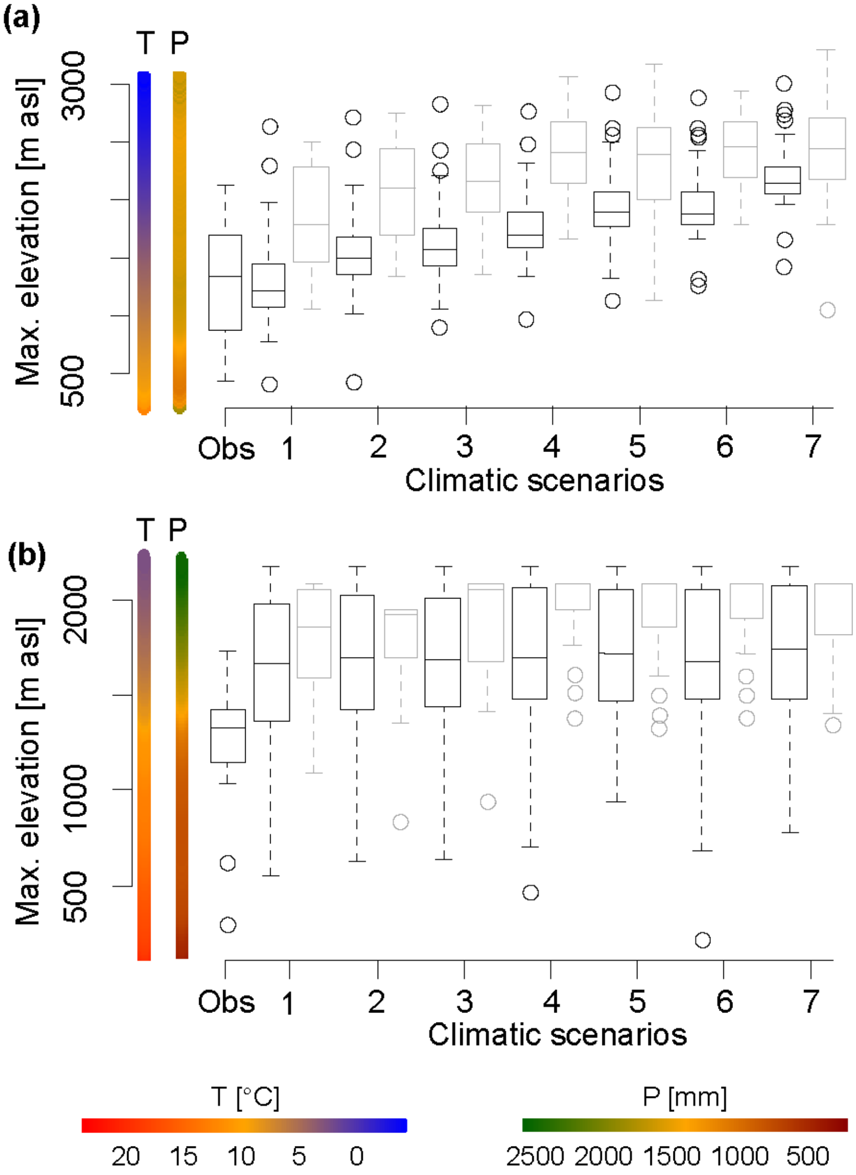

(a)
T
P
Max. elevation [m asl]
3000
500
Obs
1
2
3
4
5
6
7
Climatic scenarios
(b)
T
P
Max. elevation [m asl]
2000
1000
500
Obs
1
2
3
4
5
6
7
Climatic scenarios
T [°C]
20
15
10
5
0
P [mm]
2500
2000
1500
1000
500

Fig. 3.

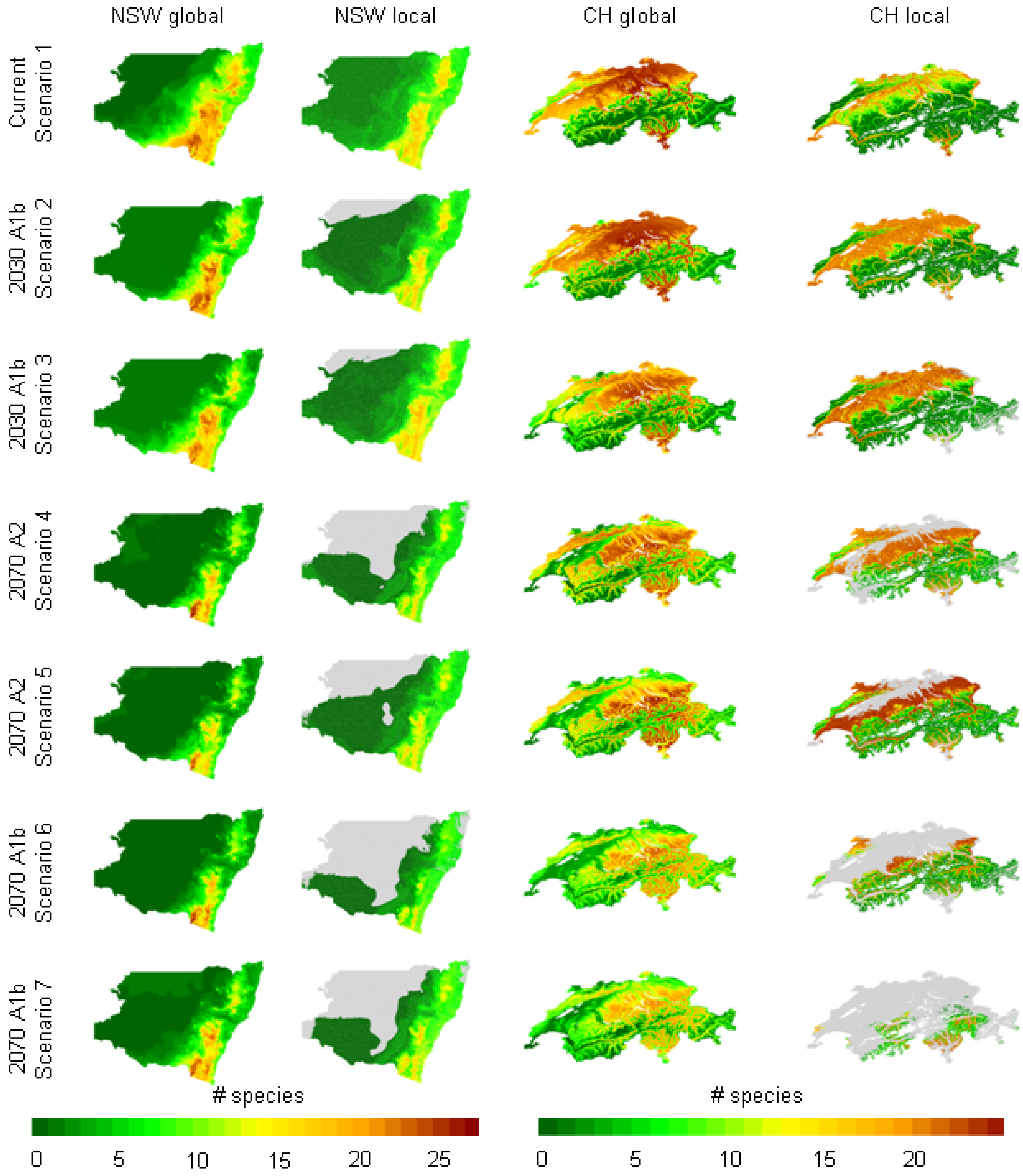

NSW global
NSW local
CH global
CH local
Current
Scenario 1
2030 A1b
Scenario 2
2030 A1b
Scenario 3
2070 A2
Scenario 4
2070 A2
Scenario 5
2070 A1b
Scenario 6
2070 A1b
Scenario 7
species
0
5
10
15
20
25
species
0
5
10
15
20

Fig. 4.

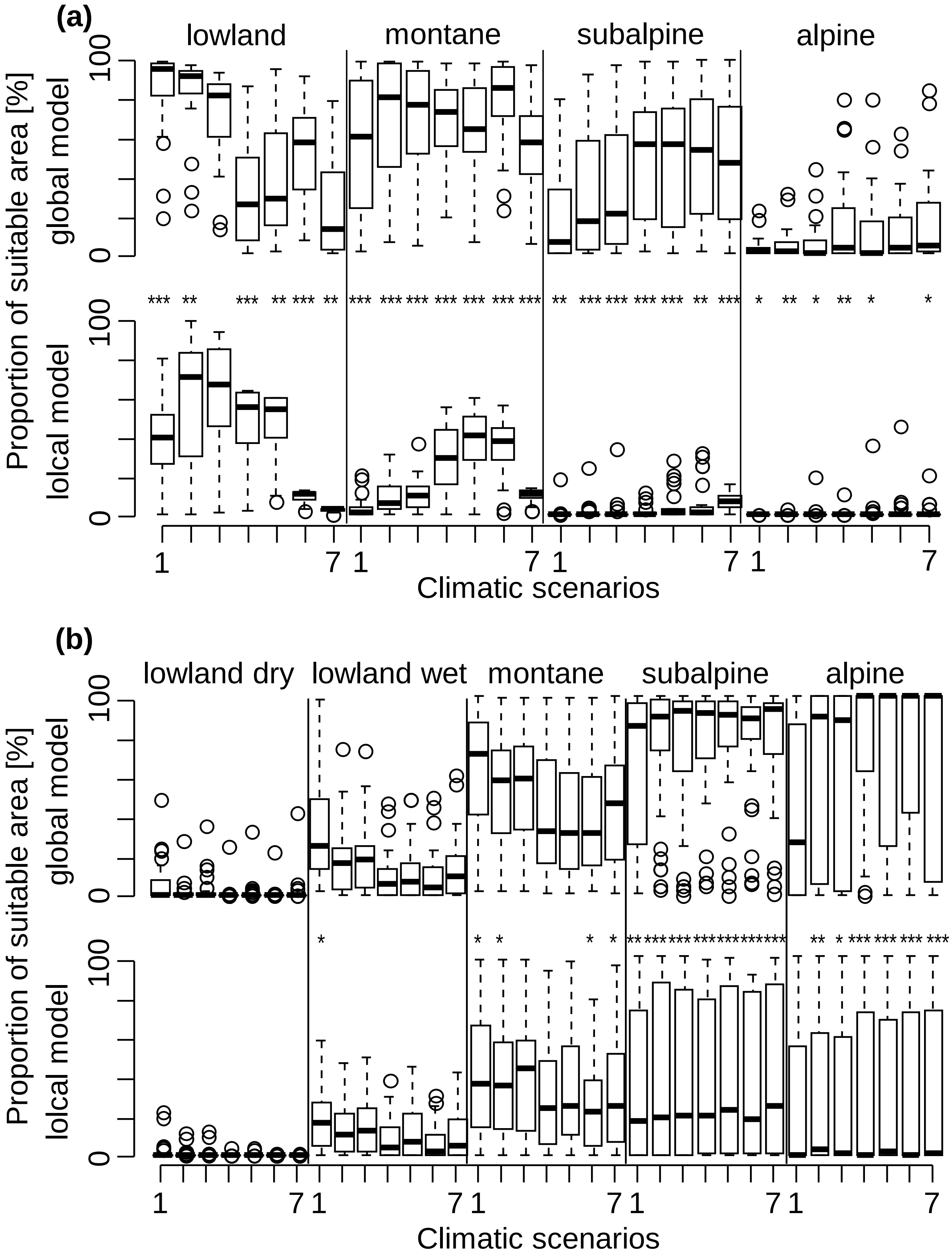
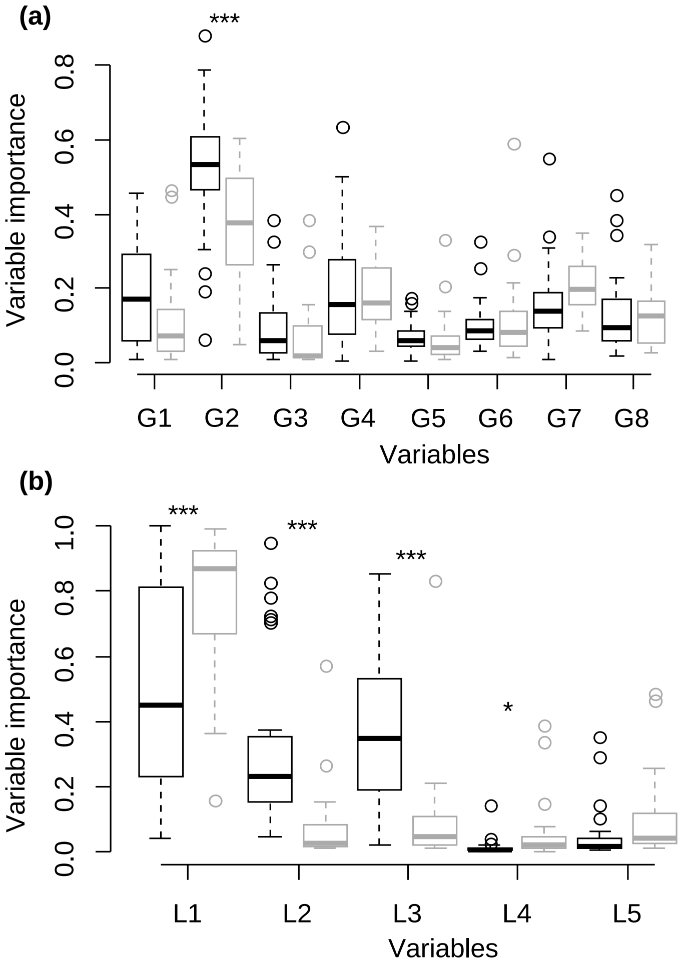

(a)
lowland
montane
subalpine
alpine
Proportion of suitable area [%]
global model
lolcal model
0
100
1
7
Climatic scenarios
(b)
lowland dry
lowland wet
montane
subalpine
alpine
Proportion of suitable area [%]
global model
lolcal model
0
100
1
7
Climatic scenarios

Fig. 5.


(a)
***
Variable importance
0.0
0.2
0.4
0.6
0.8
G1
G2
G3
G4
G5
G6
G7
G8
Variables
(b)
***
***
***
*
Variable importance
0.0
0.2
0.4
0.6
0.8
1.0
L1
L2
L3
L4
L5
Variables