

21st century climate change threatens mountain flora unequally across Europe

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Abstract

Continental-scale assessments of 21st century global impacts of climate change on biodiversity have forecasted range contractions for many species. These coarse resolution studies are, however, of limited relevance for projecting risks to biodiversity in mountain systems, where pronounced microclimatic variation could allow species to persist locally, and are ill-suited for assessment of species-specific threat in particular regions. Here, we assess the impacts of climate change on 2632 plant species across all major European mountain ranges, using high-resolution (ca. 100 m) species samples and data expressing four future climate scenarios. Projected habitat loss is greater for species distributed at higher elevations; depending on the climate scenario, we find 36–55% of alpine species, 31–51% of subalpine species and 19–46% of montane species lose more than 80% of their suitable habitat by 2070–2100. While our high-resolution analyses consistently indicate marked levels of threat to cold-adapted mountain floras across Europe, they also reveal unequal distribution of this threat across the various mountain ranges. Impacts on floras from regions projected to undergo increased warming accompanied by decreased precipitation, such as the Pyrenees and the Eastern Austrian Alps, will likely be greater than on floras in regions where the increase in temperature is less pronounced and rainfall increases concomitantly, such as in the Norwegian Scandes and the Scottish Highlands. This suggests that change in precipitation, not only warming, plays an important role in determining the potential impacts of climate change on vegetation.

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Introduction

Among the world's ecosystems, mountains and their unique biota are disproportionately exposed to climate change (Beniston *et al.*, 1996; Theurillat & Guisan, 2001; Nogués-Bravo *et al.*, 2007). Effects of ongoing climate warming on plant species, generally in the form of an upward shift in distribution, have already been detected across Europe (Lenoir *et al.*, 2008), and particularly in a number of mountain ranges, including the Alps (e.g. Walther *et al.*, 2005; Pauli *et al.*, 2007; Parolo & Rossi, 2008; Vittoz *et al.*, 2008), the Norwegian Scandes (Klanderud & Birks, 2003) and several Iberian mountain ranges (Peñuelas & Boada, 2003; Sanz-Elorza *et al.*, 2003). This is of concern as mountain ecosystems represent invaluable resources, both in terms of biodiversity and the ecosystem services they provide (Körner, 2003; Viviroli & Weingartner, 2004).

In order to assess the potential impacts of climate change on plant distributions, a commonly employed method is the use of species distribution models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). These models relate species observations (presence/absence or abundance) to a series of environmental variables, often of topo-climatic nature, in order to model a species' realized niche and its associated potential distribution in the landscape. Under the assumption of niche conservatism (i.e. the tendency of the realized niche of a species to remain unchanged over time; Pearman *et al.*, 2008), models can then be projected under future climatic scenarios in order to infer a species' future potential distribution. This also assumes that biotic interactions, such as competition or facilitation, are unaffected by altered environmental conditions.

Using these tools, models forecasting changes in species distributions as functions of climate scenarios for the 21st century predict a massive reduction of plant diversity and high community turnover (Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Randin *et al.*, 2009; Dirnböck *et al.*, 2011). However, these forecasts are of limited relevance for continent-wide assessment of climate change impacts on mountain biota. This is because they either (i) use coarse spatial resolution data (e.g. 50 or 15 km, Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005) that impede accurate species-specific assessments in mountain areas (Akçakaya *et al.*, 2006) and potentially overestimate suitable habitat loss by not capturing microclimatic conditions that can represent climatically suitable refugia for species (Randin *et al.*, 2009) or (ii) involve analyses of limited geographic extents that restricts

inference to individual mountain areas (e.g. Dirnböck *et al.*, 2003, 2011; Engler *et al.*, 2009; Randin *et al.*, 2009), and use a variety of methods that complicate direct comparison among studies. To our knowledge, there is currently no study that encompasses a large geographic extent while being conducted at a fine spatial resolution and with standardized methods, thereby allowing for a comprehensive continent-wide assessment of the potential impacts of climate change on mountain plants.

Here we use high-resolution environmental data (100 m, and sometimes 1 km), a suite of five different modeling techniques combined in an ensemble forecasting approach (Guisan & Thuiller, 2005; Araújo & New, 2007), four IPCC-based climate change scenarios (Nakicenovic & Swart, 2000) and standardized methods to assess comprehensively the possible effects of climate change on the potential distributions of 2632 plant species by the end of the 21st century (2070–2100 time period average) in 12 target areas (Table 1), spanning all major European mountain ranges. These include the Alps, Pyrenees, Carpathians, Apennines, Scandes and Scottish Highlands. Taken together our study areas cover 130 000 km², representing ~5% of the European mountain surface as defined by the World Mountain Map of the United Nations Environment Programme (<http://www.unep-wcmc.org/habitats/mountains/statistics.htm>) and represent, to our knowledge, the largest European-wide fine-scale assessment of potential climate change impacts on vegetation to date.

To assess the levels of potential threat to species from climate change, we computed the net proportion of potentially suitable habitat from our baseline period (1960–1990 average) that is projected to become lost or gained under the four climate change scenarios. Results were analyzed for each one of the five modeling techniques as well as for the consensus distributions derived by averaging species projected distributions across the ensemble of models. We hypothesize that estimation of suitable habitat loss based on high spatial resolution data is likely to be lower than former estimations from coarse-grained studies, and that mountain ranges across Europe exhibit different sensitivity as a function of projected climate change.

Methods

Study areas and species datasets

We prepared species presence–absence datasets for 12 study areas distributed across the major European mountain ranges (the Alps, Pyrenees, Carpathians, Apennines, Scandes and the

Table 1 Number of species, vegetation plots and physical attributes of the different datasets

Study area name	No. of species	No. of veg. plots	Data collection period	Area (km ²)	Spatial resolution (m)	Altitude (m a.s.l.) min–max	Elevation range (m)
Eastern Austrian Alps	269	987	1994–2001	741	100	495–2265	1770
South-East Carpathians	116	968	1934–2005	38 157	1000	135–2390	2255
French Alps 1	597	2083	1960–2005	57 496	100	0–4785	4785
French Alps 2	114	274	1995–1997	63	100	1485–3185	1700
Central Apennines	10	278	2002–2004	59	100	1495–2280	785
Norwegian Scandes	90	608	1997–2002	18 366	100	0–2445	2445
Spanish Pyrenees 1	1118	8902	1960–2005	8996	1000	400–3135	2735
Spanish Pyrenees 2	5	113	2002–2005	5206	100	465–2880	2415
Scottish Highlands	124	608	2002–2005	438	100	100–1200	1100
Swiss inner Alps 1	265	1511	1971–1995	243	100	1505–4595	3090
Swiss inner Alps 2	100	458	1993–1995	19	100	1875–3490	1615
Swiss Western Alps	287	550	2002–2004	704	100	370–3125	2755

Scottish Highlands; Table 1, Fig. 1 and Supporting Information, Appendix S1) by deriving more than 8000 presence-absence records from vegetation surveys. To prevent poor model calibration, species with less than 20 occurrence records within a dataset were discarded, leaving a total of 3095 species (2961 angiosperms, 36 gymnosperms, 52 pteridophytes, 11 lycophytes and 35 bryophytes – details for each study area are given in Supporting Information, Appendix S1), some of which occurred in several study areas. Spatial accuracy of the vegetation plots is of 100 m or better for 10 study areas and of 1 km or better for the remaining two datasets (South-East Carpathians and Spanish Pyrenees 1). The spatial accuracy of the vegetation plots dictated the resolution at which spatial projection and analyses were carried out for each study area.

Environmental variables

The following eight topo-climatic variables were used for model calibration: mean annual temperature, mean temperature of the coldest month, annual, summer (July–September) and winter (January–March) sum of precipitations, annual, summer and winter moisture index (see Supporting Information, Appendix S2 for full details of environmental variable preparation). These are known to represent physiological requirements of plant species (Prentice *et al.*, 1992). The moisture index was calculated as the difference between precipitation and potential evapotranspiration, expressing the amount of water that is potentially available at a site. Potential evapotranspiration (Jensen–Haise formula) was itself computed by accounting for elevation, slope, aspect, shadowing, cloud cover, latitude, longitude, direct and diffuse potential radiation. All variables were derived from long-term (1960–1990 average) monthly means for average temperature, sum of precipitations and average cloudiness, combined with data from digital elevation models. Variables were prepared identically for all study areas and at a spatial resolution matching the one of the records of the species datasets (see Table 1).

In some cases, species tolerance to warmer temperatures may be slightly under-estimated when the vegetation data of a

study area (Table 1) was collected more recently than the baseline climatic data (averaged from 1960 to 1990). Climate has warmed since 1960–1990 and the temperature values associated to sampling locations visited after this date are thus lower than they really are. This could lead to slight over-estimation of habitat loss from climate change.

Climate change scenarios

We used four different climate projections developed by the UK Met Office Hadley Centre for Climate Prediction and Research (Mitchell *et al.*, 2004; Mitchell & Jones, 2005) that we averaged over the 2070–2100 time period. These were derived from a global circulation model (HadCM3; Mitchell *et al.*, 1998; Gordon *et al.*, 2000), are based on four different socio-economic scenarios – A1FI, A2, B1 and B2 – proposed by the Intergovernmental Panel on Climate Change (Nakicenovic & Swart, 2000), and are used in its fourth and latest assessment report (IPCC, 2007). These projections were available in the form of 10' (~15 km in Europe) grids of monthly average temperatures, monthly sums of precipitations and monthly average cloudiness. Projections were averaged over the 2070–2100 time period and downscaled using bilinear interpolation to match the spatial resolution of the considered study area (see also Supporting Information, Appendix S2). With a projected average warming of +5.6 °C over western and central Europe by 2070–2100, the A1FI projections represents the most extreme climate change scenario. B1 is the mildest (+3.0 °C), A2 (+4.5 °C) and B2 (+3.3 °C) are intermediate.

Species distribution modeling

For each species in each mountain range where it was recorded, potential distribution was modeled using five different techniques: generalized linear models (GLM; McCullagh & Nelder, 1989), generalized additive models (GAM; Hastie & Tibshirani, 1986), boosted regression trees (GBM; Ridgeway, 1999), random forest (Breiman, 2001) and multivariate adaptive regression splines (MARS; Friedman, 1991). GLMs and GAMs were calibrated using a binomial distribution and a

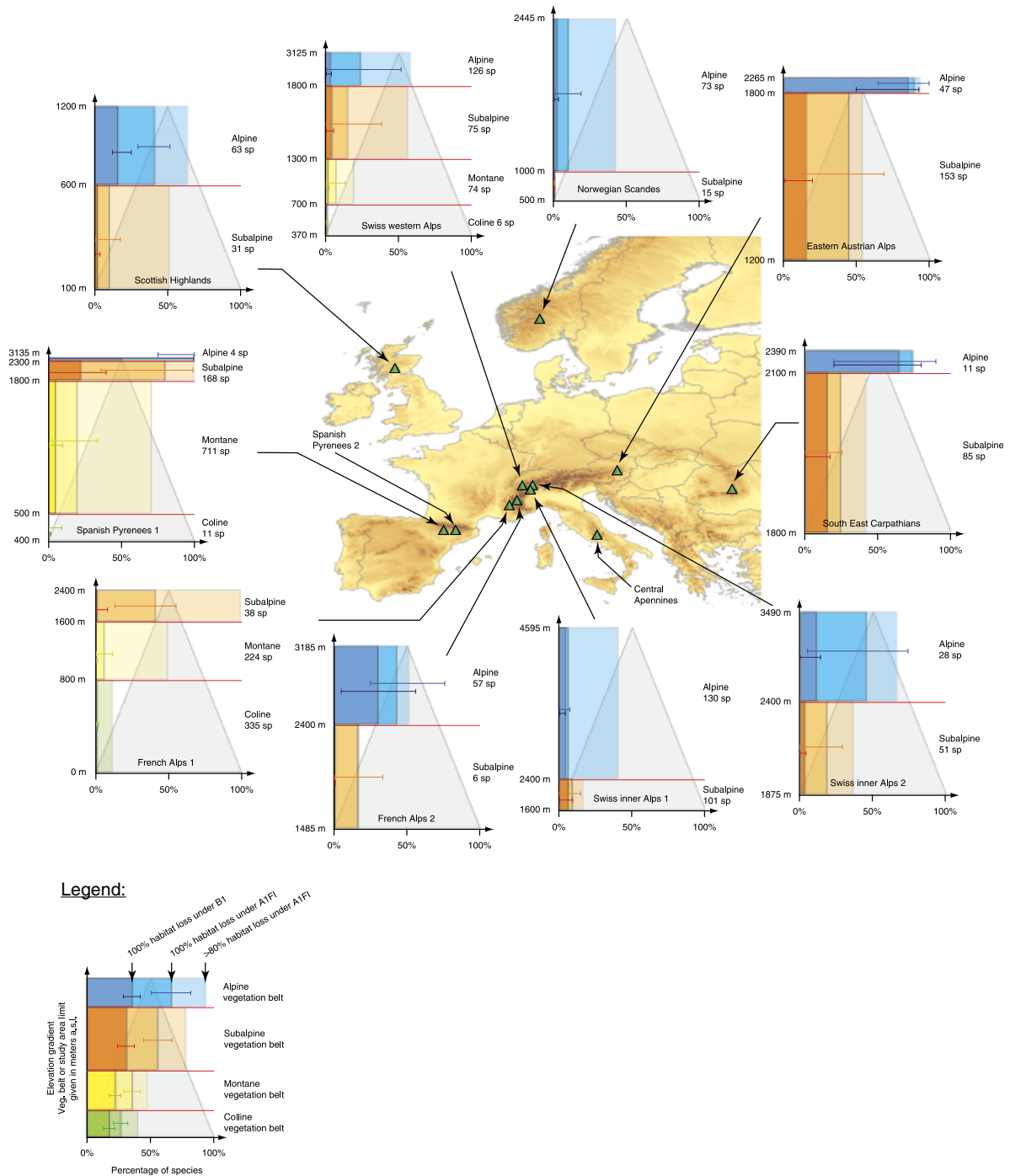


Fig. 1 Proportion of species with projected high loss of suitable habitats by 2070–2100. Proportion of species projected to lose 100% or >80% of their habitats under A1FI (most extreme) and B1 (least extreme) climate change scenarios by 2070–2100. Results are given by study area and vegetation belt, with the height of each vegetation belt in the drawing being proportional to its surface extent in the study area. Grey translucent triangles in the background of each graph only illustrate a mountain’s shape, helping to visualize the elevation gradient – they do not carry any additional information. Medium and dark shaded polygons represent the proportions of species projected to lose all of their suitable habitats under, respectively, A1FI and B1 climate change scenarios. Values are derived from the consensus projections (see ‘Methods’) and error bars indicate the range of values observed in 80% of the individual models (i.e. all but the two most outlying models). Error bars for A1FI are always above error bars for B1. Light shaded polygons indicate the percentages of species whose potential habitat is projected to decrease >80% under A1FI, no error bar is given for this value. Results for the central Apennines and Spanish Pyrenees 2 datasets are not given due to their small number of species.

logistic link function. A bi-directional stepwise procedure was used for explanatory variable selection, based on the Akaike information criterion (Akaike, 1974). Up to second-order polynomials (linear and quadratic terms) were allowed for each explanatory variable in the GLMs. GBMs were calibrated with a maximum number of trees set to 3000, fivefold cross-validation procedure to select the optimal numbers of trees to be kept and a value of 5 as maximum depth of variable interactions. Random forest models were fitted by growing 750 trees with half the numbers of available predictors sampled for splitting at each node. MARS models were fitted with a maximum interaction degree equal to 2. All models were calibrated using the *Biomod* package (Thuiller *et al.*, 2009) in R (R Development Core Team, 2009).

The predictive power of each individual model was evaluated through a repeated data-splitting procedure (for details, see Thuiller *et al.*, 2009). A model was trained on 70% of the data and evaluated on the remaining 30% using two measures that assess the agreement between predicted and observed values: the area under the receiver–operating characteristic curve (AUC; Hanley & McNeil, 1982) and the true skill statistic (TSS; Allouche *et al.*, 2006). The AUC evaluation value varies from 0.5 for a model whose predictions are no better than random, to 1 for a model achieving perfect agreement with the observed data. The TSS evaluation value varies between 0 (random model) and 1 (perfect agreement).

This data-splitting procedure was repeated 50 times and the evaluation values averaged. Note that, while model evaluation was carried out using the above-mentioned data-splitting procedure, the final models used for spatial projections were calibrated using 100% of the data for a species in a given study area, thereby allowing to take advantage of all available data.

To avoid working with poorly calibrated models, only projections from models with AUC > 0.7 and TSS > 0.4 were considered in all subsequent analyses. These values represent the minimum evaluation score for a model to be considered useful (Araújo *et al.*, 2005, adapted from Swets, 1988). Data-splitting in the evaluation procedure was performed randomly while maintaining the original prevalence of a species' presences and absences in the data.

Model averaging was performed by weighting the individual model's projections, respectively, by their AUC or TSS scores (see Supporting Information, Appendix S3) and averaging the result, a method shown to be particularly robust (Marmion *et al.*, 2009). The final results, as presented in the figures and the text, are means of the results from the AUC and TSS model averaging projections.

Spatial projections

To produce maps of potentially suitable habitat, we reclassified the probabilistic projections of each model into binary values, representing either suitable or unsuitable habitat. This conversion required the selection of a threshold above which a pixel was reclassified as potentially suitable and unsuitable below. We tested two different thresholds: (i) maximizing jointly the percentage of presences and absences correctly predicted, i.e. the probability where sensitivity = specificity

(Liu *et al.*, 2005). This threshold is thereafter referred to as 'AUC-based threshold'. (ii) maximizing the value of the TSS evaluation value, thereafter referred to as 'TSS-based threshold'. Each individual model and their weighted average (i.e. consensus model) thus yielded two different projections of potential current and future distribution for a given species in a given study area. Altogether, we obtained 12 different projections for each species in each study area (five modeling techniques plus the weighted average, multiplied by the two reclassification thresholds) for each set of climatic conditions (Current, A1FI, A2, B1, B2).

We subsequently applied a mask representing heavily anthropized areas (e.g. urban areas) and water bodies to avoid projections at locations that are unsuitable regardless of climate. Finally, projections were further restricted to three broad land cover classes (forests, grasslands, bare rock and glaciers) in which a species was observed at least once (e.g. a grassland species could not be projected to occur in forested areas). Glaciers were combined with bare rock for the reason that expected glacier retreat (Zemp *et al.*, 2006) might open these habitats for plant colonization in the future. As a given species was generally associated fairly easily with a land cover class (Supporting Information, Appendix S1 – Table S1.2), this filtering procedure was not very strict, its purpose being mainly to avoid very coarse mistakes, e.g. projecting grassland specialists to forests, or vice versa. Details of the surface covered by each land cover class can be found in Supporting Information, Appendix S1.

Species were assumed to have unlimited dispersal capability, thus occupying all pixels projected to become potentially suitable as a result of climate change. This assumption might be optimistic, but was shown to provide good estimates of species habitat loss levels for mountain areas (Engler *et al.*, 2009), where the ground velocity of temperature change is generally low (Loarie *et al.*, 2009).

Data analysis

In order to analyze potential climate change impacts by altitudinal zones, each study area was divided into one or more of four vegetation belts: alpine, subalpine, montane and colline. These were defined separately for each study area based on expert knowledge (see Supporting Information, Appendix S4 for details). Each species in each study area was in turn associated to the vegetation belt where the majority of its field observations fell into.

For each mountain range and vegetation belt, the proportion of species projected to decrease in distribution by 100% and >80% by 2070–2100, as compared with the projections obtained for the baseline time period (1960–1990), were computed. Percentages obtained from datasets and individual vegetation belts with too few species (Spanish Pyrenees 2 and central Apennines datasets) were not considered when computing averages as they did not provide reliable values.

Since the individual study areas differ in terms of size (surface extent), elevation range and species composition, their projected suitable habitat loss levels might not be directly

comparable. For instance, a study area with a larger elevation range offers more room for upwards migration of species. In order to assess the effect that these three factors may have on projected species habitat loss levels, we fitted ordinary and logistic regressions (GLMs) relating the proportion of species projected to lose 100% or >80% of their suitable habitat by 2070–2100 to a study area's elevation range, surface extent and position of species along the altitudinal gradient (see Supporting Information, Appendix S5 for details). The ordinary linear regressions were fitted with one explanatory variable at a time while logistic regressions were fitted both with one variable at a time (to see their individual explanatory power) and using all three explanatory variables together. Residuals of the multivariate logistic regressions were then used as indicator of the relative sensitivity of a given study area to climate change compared with the other European mountain ranges.

Results

Unless otherwise specified, all values presented in the figures and text are derived from the consensus projections, i.e. the ensemble forecasting based on the five individual modeling techniques and the two reclassification thresholds.

Model performance

After removing species for which the models had insufficient predictive power (i.e. $AUC < 0.7$ or $TSS < 0.4$), 2632 of the initial 3095 species were left (2527 angiosperms, 34 gymnosperms, 39 pteridophytes, eight lycophytes and 24 bryophytes – details for each study area are given in Supporting Information, Appendix S1). Only these 2632 species were used in all further analyses. Full details and analyses of model performance are given in Supporting Information, Appendix S6.

Change in species potential habitat by 2070–2100

Across our 12 mountain areas, the percentage of species projected to lose 100% of their suitable habitat by 2070–2100 varies from 5% to 55% (mean = 25 ± 16 , 1 SD) for the most extreme A1FI scenario, 1–47% (mean = 20 ± 15) for the A2 scenario and 0–35% (mean = 11 ± 11) under B1 and B2 (Fig. 1 and Supporting Information, Table S1). Compared with the number of species that are at risk of losing all their suitable habitat, the number of species projected to undergo >80% habitat loss are roughly doubled for the A1FI and A2 scenarios, and tripled for the B1 and B2 scenarios (Supporting Information, Table S1).

Breaking down these numbers by altitudinal vegetation belts (from highest to lowest: alpine, subalpine, montane, colline), the projected effects of climate

change on the loss of plant habitat are greatest at high elevation across all studied mountain ranges. Alpine species projected to lose all of their suitable habitats total $41 \pm 29\%$ (mean across all study areas ± 1 SD) under A1FI, $37 \pm 30\%$ under A2 and $26 \pm 31\%$ under B1 and B2 scenarios (Fig. 1 and Supporting Information, Table S2). Concordantly, pooling all species by vegetation belt reveals that, on average and depending on the climate change scenario considered, suitable climatic habitats decrease by >80% for 36–55% of all alpine species, 31–51% of all subalpine species and 19–46% of all montane species (Fig. 2, Supporting Information, Table S3). While the majority of alpine, subalpine and montane species potentially lose substantial proportions of their suitable habitat, the potential habitat of most colline species is, in contrast, projected to increase (Fig. 2). Note, however, that among the species projected to importantly increase their suitable habitats, part of the increase in distribution may result from truncated response curves, in which case the projected distribution of these species is likely to be overestimated (see 'Discussion').

Relative sensitivity of floras between mountain ranges

The univariate ordinary and logistic regressions showed that a study area's elevation range and the position of its species along the altitudinal gradient are the two variables that best explain the differences in projected habitat loss levels by 2070–2100 between mountain ranges (supplementary material, Appendix S5 – Tables S5.2, S5.3 and Fig. S5.1). In univariate logistic regressions, depending on the climate change scenario, study area elevation range explained between 25% and 49% (mean = 39%) of the differences in proportions of species projected to lose 100% and >80% of their suitable habitats (Supporting Information, Table S5.3). Species position along the elevation gradient explained between 10% and 58% (mean = 40%). These two variables always explained a significant proportion of the variance in both ordinary and logistic regressions (P -value < 0.001 , ANOVA χ^2 -test, $N = 10$). Difference in study area surface extent had low explanatory power in ordinary regressions (Adj. R^2 between -0.05 and 0.13) but still explained a significant amount of deviance in the logistic regressions (7–22%, mean = 15%). Taken together, a study area's elevation range, surface extent, and the position of its species along the altitudinal gradient explained 64–88% (mean = 80%) and 24–58% (mean = 46%) of the among-mountain variation in the proportion of species projected to, respectively, lose 100% and >80% of their suitable habitat depending on the climate change scenario. All factors did generally explain a highly significant proportion

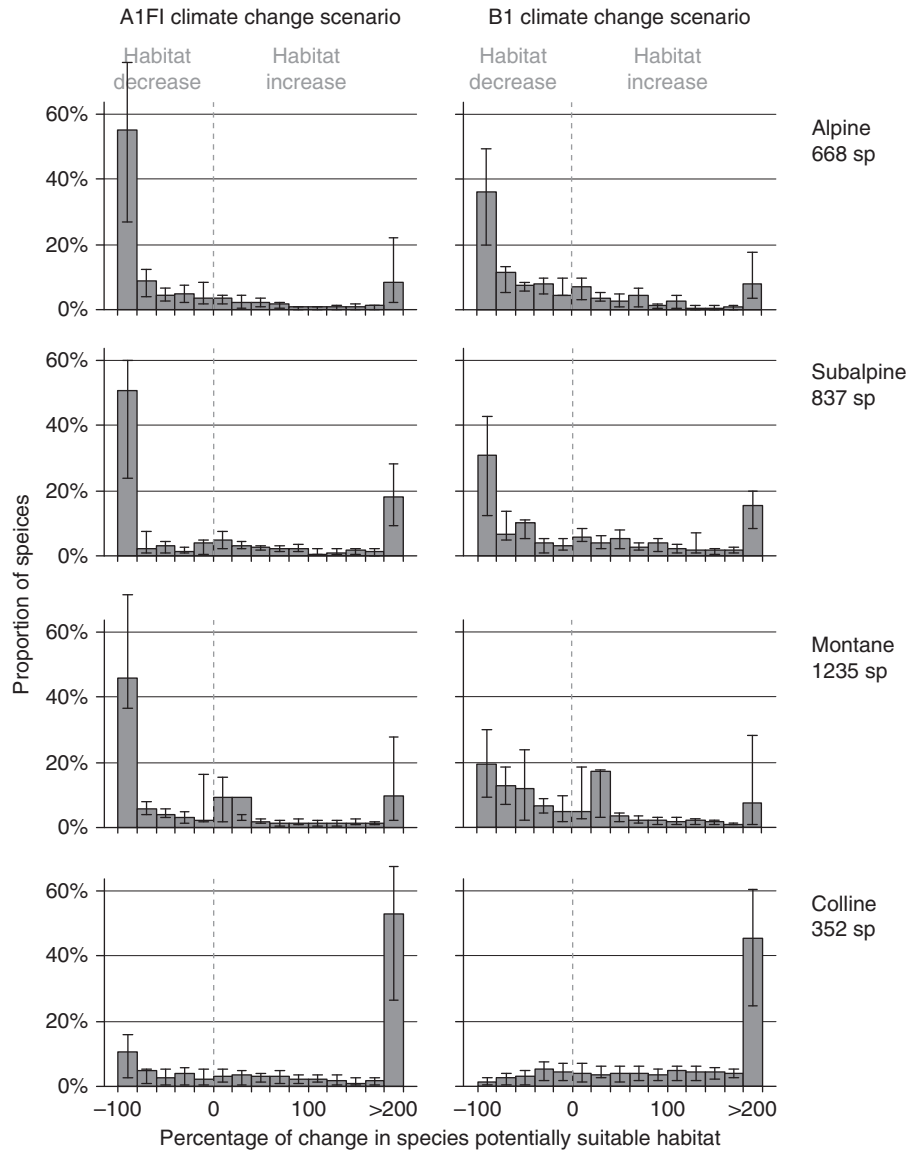


Fig. 2 Change in species potential distribution by vegetation belt for 2070–2100. Average distribution of the percentage of suitable habitat loss (negative values) or gain (positive values) relative to a species' initial distribution per vegetation belt for all species of all study areas under A1FI (left panels) and B1 (right panels) climate change scenarios by 2070–2100. Values are derived from the consensus projections (see methods) and error bars indicate the range of values observed in 80% of the individual models (i.e. all but the two most outlying models). The vertical dashed lines indicate the separation between species projected to decrease (negative values) or increase (positive values) in distribution. Values were weighted so that all mountain ranges had equal importance. Note that among the species projected to importantly increase their suitable habitats, part of the increase in distribution is likely to be linked to truncated response curves, and the projected distribution of these species is thus likely to be overestimated (see 'Discussion').

of variance in the data (P -value < 0.001 , ANOVA χ^2 -test, $N = 10$). Full details of the ordinary and logistic regressions are given in Supporting Information, Appendix S5.

The residuals from those regressions, used as indicators of relative sensitivity of a given study area's flora to climate change, indicate that floras of the Spanish Pyrenees and Eastern Austrian Alps appear relatively

more sensitive to climate change, the Swiss inner Alps, French Alps and Carpathians floras are at average, and the Scottish Highlands, Norwegian Scandes and Swiss Western Alps floras appear less sensitive (Fig. 3a). These differences in floras sensitivities generally reflect the distribution of temperature and precipitation anomalies projected by the climate change scenarios we considered (Fig. 3b and c).

Discussion

A coarse resolution, pan-European study (Thuiller *et al.*, 2005) projects that a maximum of ~60% of plant species of European mountain areas could lose their entire suitable habitat by 2051–2080 under the A1FI climate change scenario (+5.6 °C by 2070–2100). In contrast, our results forecast a lower degree of threat to mountain floras, with a maximum of 5–55%

(average = $25 \pm 16\%$ SD) of species projected to lose their entire suitable habitat by 2070–2100 under the same climate change scenario, depending on the study area. Although differing species pools might play a role, the difference between these results likely owes to the divergent spatial resolutions of the two studies. Using a resolution of ~15 km to assess the potential impacts of climate change, Thuiller *et al.* (2005) likely overestimates habitat loss for mountain flora. This is because fine-

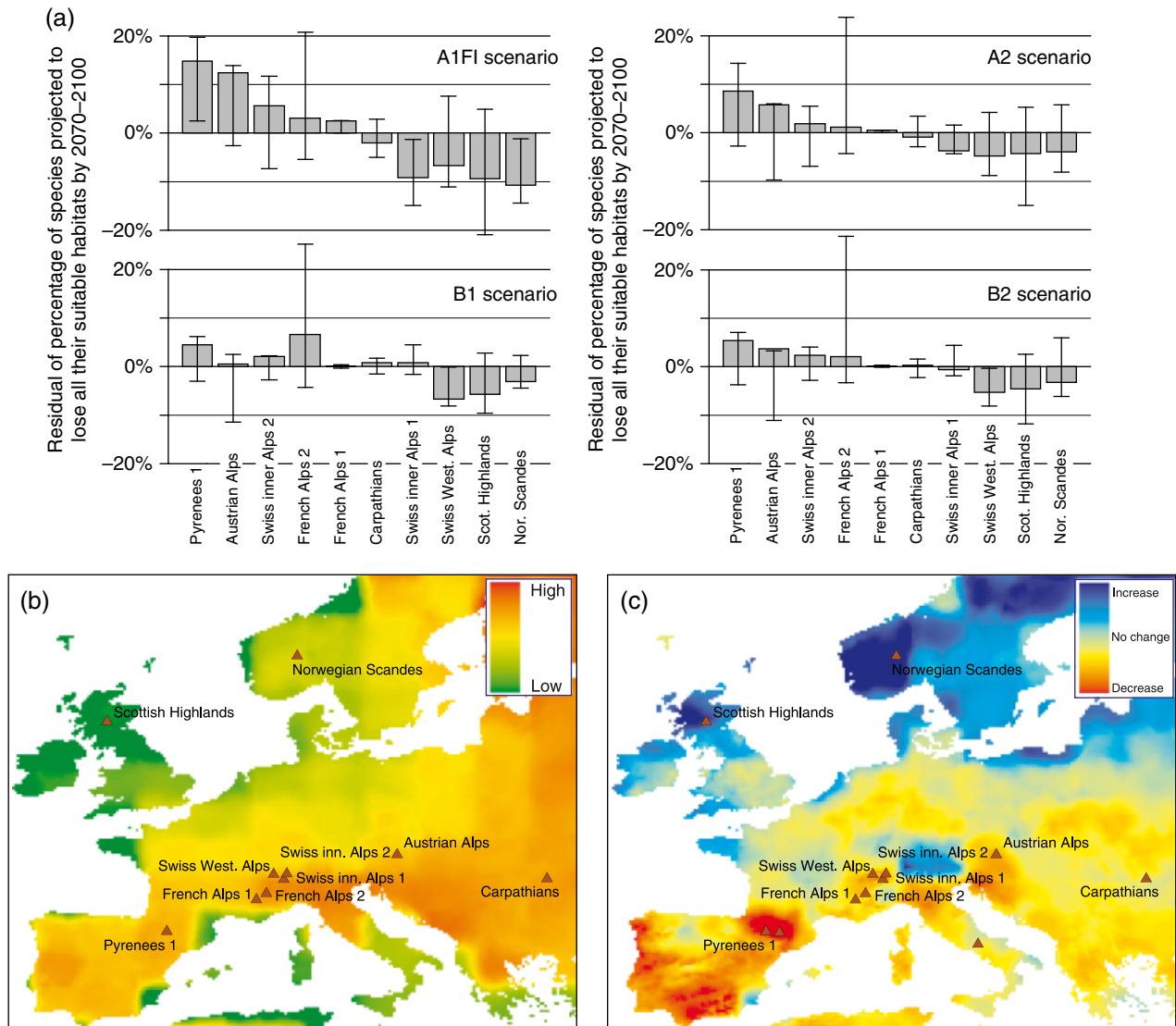


Fig. 3 Relative sensitivity of floras between European mountain ranges. (a) Logistic regression residuals of rates of species complete habitat loss under four different climate change scenarios (A1FI, A2, B1, B2) as a function of study area elevation range, surface extent and species position along the elevation gradient. Values are derived from the consensus projections (see 'Methods') and error bars indicate the range of values observed in 80% of the individual models (i.e. all but the two most outlying models). (b) Map of projected temperature increase by 2070–2100 under A1FI climate change projection. (c) Map of the first axis of a principal component analysis of the projected change in annual, summer and winter sum of precipitation by 2070–2100 under A1FI climate projection. Blue areas are projected to receive increased precipitation, red areas decreased precipitation.

scale topographic variation that provides suitable habitats for species is not expressed in such coarse resolution data (Randin *et al.*, 2009).

Notwithstanding, a number of other factors, not assessable from empirical distribution data, could influence levels of habitat loss projected in both this study and Thuiller *et al.* (2005). One source of uncertainty arises from the fact that, as calibrated in this study, distribution models only account implicitly for biotic interactions such as competition or facilitation. This is because they model the realized niche of species, which at least partly incorporates these interactions. For instance, models for high-elevation species indicate low-elevation areas as unsuitable habitats because they are too warm. But 'too warm' should here often be interpreted as 'with too much competition' rather than 'physiologically too warm', because, in the absence of competitors, many alpine species would be able to withstand these warmer conditions, as shown by transplantation experiments (e.g. Hautier *et al.*, 2009). While this is a desirable property that simplifies model calibration, its corollary is that models provide a static representation of biotic interactions. This becomes a source of uncertainty if the interactions between species are altered, as might occur with climate change (Davis *et al.*, 1998; Brooker, 2006; Memmott *et al.*, 2007; Suttle *et al.*, 2007). Our projections for high elevation species might not be highly susceptible to this effect because the realized niche of these species is already heavily limited through competition at lower elevations under current climatic conditions. This is not the case for species inhabiting the lower parts of the elevation gradient, which are likely to have new competitors entering their habitat. Therefore projections for low elevation species likely bear more uncertainty than those for high elevation species and their future distribution may be more restricted than we forecast here. The severity of this bias also depends on the type of species that is modeled: Pearman *et al.* (2008) illustrate for instance that dominant species show greater conservatism in their realized niche than others. Delay in migration of competing species might also temporarily limit the competition intensity and allow persistence of species for a longer period of time than projected by the models. Although efforts to explicitly (rather than implicitly) integrate biotic interactions into distribution models are on-going, generally by using the distribution of competing species as additional explanatory variables (e.g. Leathwick & Austin, 2001; Heikkinen *et al.*, 2007), this method is difficult to apply to a large number of species and the issue of forecasting how these interactions will evolve under future environmental conditions remains unsolved.

Another source of uncertainty in projections from species distribution models derives from our inability

to forecast how species might genetically adapt or express phenotypic plasticity to changing environmental conditions (Theurillat & Guisan, 2001). While some studies have shown evidence of rapid evolutionary change (Thomas *et al.*, 2001), others have found niche conservatism over several millions of years (Peterson *et al.*, 1999; see Pearman *et al.*, 2008, for a review) or rates of evolutionary change much slower than required for species to evolve necessary adaptations in the face of climate change (Davis & Shaw, 2001; Etterson & Shaw, 2001). Such contradictory evidence again suggests that niche conservatism depends on the species considered. For instance, long-lived species and species with limited dispersal abilities are thought to have higher conservatism of their realized niche (Pearson & Dawson, 2003).

Changes in land cover also represent a source of uncertainty because we assume that our three broad categories of land cover (forests, grasslands, bare rock and glaciers) will remain unchanged by 2070–2100. While this could potentially lead our projections to under-estimate species habitat loss (see de Chazal & Rounsevell, 2009, for a review), integrating land cover changes at a fine resolution remains a challenging task due to the inherent uncertainty associated with land cover change models that are highly sensitive to socio-economic 'storylines' (e.g. Schröter *et al.*, 2005; Verburg *et al.*, 2010). In alpine and subalpine environments, where the tree-line is often maintained artificially low by human activities, preservation of traditional land use such as pasturing can decrease habitat loss for open-habitat species that would become excluded through upward shift of trees and reforestation of areas already suitable for forests under current climatic conditions (Theurillat & Guisan, 2001; Dirnböck *et al.*, 2003, 2011).

Finally, the particular case of the species projected to increase importantly in distribution (>100% and especially by >200%, see Fig. 2) must be considered with care. At least for some of these species, the projected suitable habitat is overestimated due to truncated response curves, i.e. part of the species' ecological niche is missing for model calibration because it is located outside of the study area (Guisan & Theurillat 2000; Thuiller *et al.*, 2004). When projected under new environmental conditions that are outside of the calibration range (typically warmer temperatures), such truncated response curves may wrongly predict the new conditions as suitable, effectively ignoring the fact that these new conditions (warmer temperatures in our case) could either be physiologically unsuitable, or – and this is more likely – create favorable conditions for superior competitors. Slow migration rates might also impede some species from reaching all their newly suitable habitats (Engler *et al.*, 2009). Thus, while those species

projected to increase substantially in distribution are unlikely to be threatened in the future, their projected distribution is most likely overestimated.

The trend in our analysis is that higher elevation vegetation is more exposed to habitat loss from climate-change than species at lower elevations and this is consistent across all mountain ranges. However, our results also reveal important among-range variability. For instance, depending on the climate change scenario, 85–90% of the alpine species in the Eastern Austrian Alps are projected to experience 100% habitat loss compared with only 1–10% in the Norwegian Scandes. The majority of this variability in projected habitat loss between study areas arises from the pronounced differences in elevation range and species pools among mountain ranges. While study area surface extent also explains some of the variation, it has less influence than the elevation range and species pool of a study area.

Together these three factors (study area elevation range, surface extent and position of species along the altitudinal gradient) explain between 64% and 88% (depending on the climate change scenarios) of the among-mountain variation in the proportion of species projected to lose 100% of their suitable habitats. Mountains with larger elevation gradients and, especially, greater elevation extent above the lower limit of the alpine belt, present a lower degree of species sensitivity to climate change on average than do other mountains because of greater opportunity for the upward migration of species. Further, species positioned lower along elevation gradients are less sensitive to climate change because these species have more opportunity for upward range shift. This result highlights the fact that assessments of florae sensitivity to climate change heavily depend on the geography of the particular study area, as well as on the species pool being analyzed. These factors need consideration during interpretation of the results, even for studies involving a single study area.

Estimating the relative sensitivity of the flora of each region to climate change after accounting for differences in elevation range, surface extent and position of species along the elevation gradient, reveals that florae of the Spanish Pyrenees and Eastern Austrian Alps are projected to be relatively more sensitive to climate change than average, whereas the florae from the Scottish Highlands, the Norwegian Scandes and the Swiss Western Alps are projected to be less sensitive. This trend corroborates results from coarser scale projections (Thuiller *et al.*, 2005). Mountains ranges where our models project florae to be particularly at risk from climate change (Eastern Austrian Alps and Spanish Pyrenees) are characterized by substantial temperature increase (Fig. 3b) and concomitant rainfall decrease (Fig.

3c, red areas). Conversely, the Scottish Highlands and the Norwegian Scandes, the two ranges whose florae are projected as least exposed to climate change, have the smallest increase in mean annual temperature under the A1FI climate change scenario (+3.7 and +5.0 °C, respectively) and the smallest and third smallest increase under B1 (+2.1 and +2.8 °C, respectively). These two ranges also contrast with the others in that projected future rainfall increases rather than decreases (Fig. 3c, blue areas). Our results thus suggest that change in precipitation, not only warming, plays an important role in determining the potential impacts of climate change on vegetation.

Given the broad geographical coverage and high spatial resolution of our study, the results likely represent comprehensively the potential impacts of climate change on the European mountain florae. The use of fine-resolution modeling reduces the magnitude of projected habitat loss from climate change when compared with projections from coarse resolution models. Nonetheless, we forecast substantial loss of potential habitat for a majority of alpine plant species, supporting the view that mountains are where great losses of species will likely occur, but that these losses will be unequally distributed across the various mountain ranges in Europe. This is of notable concern because mountain ecosystems provide invaluable resources, not only in terms of their flora and fauna (a third to half of the total European flora, Theurillat, 1995), but also in terms of the ecosystem services that mountains provide to human society (detailed in Körner, 2003). Actions to mitigate the effects of climate change on mountain florae (e.g. Berry, 2009) should be taken now, before many mountain species become critically endangered.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Projected decrease in species distributions by study area.

Table S2. Projected decrease in species distributions by study area and vegetation belt.

Table S3. Projected decrease in species distributions by vegetation belt (all species pooled).

Appendix S1. Study areas and sampling units (vegetation plots) geographical position, details of study area land cover and number of species per taxonomic group.

Appendix S2. Environmental variables preparation methodology.

Appendix S3. Ensemble modeling (ensemble forecasting) methodology.

Appendix S4. Vegetation belt definition and species classification.

Appendix S5. Ordinary and logistic regressions of species suitable habitat loss against study area elevation range, surface extent, and species distribution along the elevation gradient.

Appendix S6. Details of model evaluation and comparison.

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