

Climate change and plant distribution: local models predict high-elevation persistence

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Abstract

Mountain ecosystems will likely be affected by global warming during the 21st century, with substantial biodiversity loss predicted by species distribution models (SDMs). Depending on the geographic extent, elevation range, and spatial resolution of data used in making these models, different rates of habitat loss have been predicted, with associated risk of species extinction. Few coordinated across-scale comparisons have been made using data of different resolutions and geographic extents. Here, we assess whether climate change-induced habitat losses predicted at the European scale ($10 \times 10'$ grid cells) are also predicted from local-scale data and modeling ($25 \text{ m} \times 25 \text{ m}$ grid cells) in two regions of the Swiss Alps. We show that local-scale models predict persistence of suitable habitats in up to 100% of species that were predicted by a European-scale model to lose all their suitable habitats in the area. Proportion of habitat loss depends on climate change scenario and study area. We find good agreement between the mismatch in predictions between scales and the fine-grain elevation range within $10 \times 10'$ cells. The greatest prediction discrepancy for alpine species occurs in the area with the largest nival zone. Our results suggest elevation range as the main driver for the observed prediction discrepancies. Local-scale projections may better reflect the possibility for species to track their climatic requirement toward higher elevations.

Keywords: climate change, Europe, mountain region, species distribution model, Swiss Alps

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Introduction

Mountain ecosystems are likely sensitive to global warming owing to the reduction in area with increasing elevation (Guisan *et al.*, 1995; Theurillat *et al.*, 1998; Diaz *et al.*, 2003; Beniston, 2006). A recent global assessment of the impacts of climate change on these ecosystems suggests that they should experience unprecedented rates of warming during the 21st century, two to three times greater than observed during the 20th century (Nogués-Bravo *et al.*, 2006). These rapid changes in temperature and other climate parameters at high elevations are expected to have strong effects on plant

communities (Guisan *et al.*, 1995; Beniston *et al.*, 1996; Guisan & Theurillat, 2000; Walther, 2003). The first biological impacts of past and ongoing global warming are already visible in the Alps, and include the upward shift of treelines (Gehrig-Fasel, 2007) and the upward shift and range reduction in alpine and nival plant species (Braun-Blanquet, 1957; Hofer, 1992; Grabherr *et al.*, 1994; Pauli *et al.*, 1996, 2007; Walther *et al.*, 2005; Vittoz *et al.*, 2006).

In the last decade, species distribution models (SDMs; Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) have become important tools to evaluate the potential impacts of climate change on plant distributions (Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005). These tools statistically relate multiple abiotic habitat characteristics (*sensu* Kearney & Porter, 2004)

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with observed occurrences of a species, thus fitting the original definition of the Hutchinsonian (Hutchinson, 1957) environmental niche (Kearney & Porter, 2004; i.e. without explicitly requiring a mechanistic link between environmental gradients and population fitness (see also Guisan & Thuiller, 2005; Araujo & Guisan, 2006). Hereafter, we will simply refer to the *realized niche* for this initial definition of the niche.

Using these tools, models of climate change impacts on biodiversity have been developed at several scales (but see Davis *et al.*, 1998; Bahn & Körner, 2003; Hampe, 2004; Dormann, 2007). At the extent of western Europe, Thuiller *et al.* (2005) forecasted that the plant diversity of some European mountain ranges (e.g. mid-elevation Alps) could be disproportionately sensitive to climate change, with up to 60% species loss per 10' grid cell. This study modeled the distribution of 1350 species using data from the Atlas Florae Europaeae (AFE; Lahti & Lampinen, 1999). Similarly, a local-scale study of 85 subalpine and alpine nonwoody plants of open habitat was conducted at high resolution (20 m × 20 m) in the Austrian Alps (Dirnböck *et al.*, 2003). The authors predicted that up to 40–50% of the plant species could potentially become extinct owing to climate change. Finally, in a study of 62 alpine and nival plants, Guisan & Theurillat (2000) predicted relatively low rates of total habitat loss, between 2% and 5%, but nearly 40% of the species were nevertheless predicted to lose more than 90% of their suitable habitat. These SDM results suggest that alpine and nival plants, in particular, may lose much of their suitable climatic habitats, owing to the decrease in suitable habitat area with increasing elevation (Guisan & Theurillat, 2000). Nonetheless, still few studies have used SDMs to assess the possible impacts of climate change on plant species in mountain environments (e.g. Dirnböck *et al.*, 2003).

Although SDM studies consistently predict substantial impacts on plant diversity in mountains, the rates of predicted habitat loss vary among studies, which themselves vary in study area extent, data resolution, and species composition. In spite of this and of variation in the results of the studies, very few comparisons of predictions across resolutions in a single region have been attempted (e.g. Trivedi *et al.*, 2008). This is potentially an important deficiency because coarse-resolution predictions based on SDMs are commonly used in the preparation of reports by the Intergovernmental Panel on Climate Change (IPCC; <http://www.ipcc.ch>). These reports are then of potential use to conservation planners, managers, and other decision makers to anticipate biodiversity losses in alpine and other systems across local, regional, and larger scales. Thus, an assessment is needed as to whether studies conducted at different scales yield comparable and consistent predictions.

A particular aspect that needs to be assessed is whether studies conducted at different spatial resolutions in a common study area and pool of species lead to different predictions of climate impacts. Such a discrepancy might, for instance, arise because different resolutions can reflect and represent topography, habitat, and climate variation differently. The relationship between certain environmental variables and species occurrence can differ when calculated at local or European scales (Guisan & Thuiller, 2005). For example, the mean temperature interpolated from local stations at a 20 m resolution (Dirnböck *et al.*, 2003) contains more variability than expressed by the mean temperature within a 50 km × 50 km grid cell in which variation in elevation is poorly represented (Thuiller *et al.*, 2005). Such differences in resolution and study area size might produce differences among SDMs in regard to the estimated minimal annual temperature tolerated by a species. This could happen when models are fitted with temperature data coming from relatively large cell sizes over a large area (e.g. Europe) that do not represent well substantial temperature variation with elevation. This, in turn, could result in underprediction of species distributions in areas at the cold end of the temperature gradient. In contrast, models fitted at a local scale and fine resolution could predict the persistence of suitable thermal habitat at high elevations within coarser resolution cells predicted overall to be unsuitable from models fitted at larger scale (e.g. from Thuiller *et al.*, 2005).

Here, we examine this 'local high-elevation habitat persistence hypothesis.' We estimate, with fine-resolution (local-scale) models, the proportion of suitable habitat remaining for each species after climate change within cells predicted by coarse-resolution (European-scale) models to become overall unsuitable. We further investigate whether such predicted local habitat persistence results from (1) the particular topographic configuration in the local study areas; (2) the differences in estimated climatic niche of species when measured at both scales by determining whether the curves of probability of species presence along climatic gradients are truncated when fitted with local-scale data; (3) the choice of modeling techniques; and (4) difference in performance of models that are fitted under current conditions using data at the two extents and resolutions.

Methods

Study areas

We fitted SDMs for Western Europe (34°N–72°N, 11°W–32°E; 5.7×10^6 km²) and for two local study areas in the

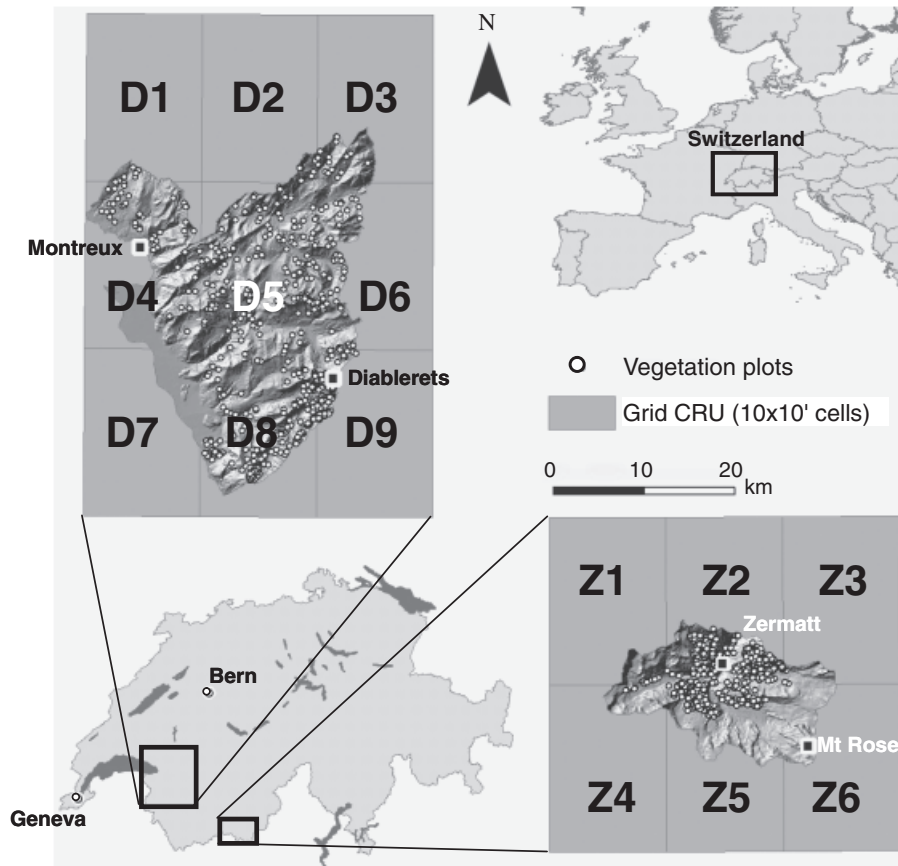


Fig. 1 Location of the Diablerets and Zermatt study areas. $10 \times 10'$ pixels used for projections at the European scale are indicated for each study area.

Western Alps: Diablerets and Zermatt (Fig. 1). The Diablerets study area (Fig. 1) covers nearly all mountain massifs of the Western Alps of the Canton de Vaud (Swiss state, $6^{\circ}50' - 7^{\circ}10'E$, $46^{\circ}10' - 46^{\circ}30'N$, $>700 \text{ km}^2$). The elevation ranges from 375 m in Montreux to 3210 m on the top of the Diablerets massif. The annual mean temperature and total precipitation vary, respectively, from 8°C and 1200 mm at 600 m elevation to -5°C and 2600 mm at 3000 m elevation (Bouët, 1985).

The Zermatt study area is located in the Central Alps of the Canton of Valais (Switzerland; $7^{\circ}58' - 7^{\circ}91'E$, $45^{\circ}92' - 46^{\circ}06'N$, 243 km^2) at the end of the Matter valley. Its elevation varies from 1480 m at the bottom of the valley near the village of Zermatt to 4634 m on the top of the Mt Rose massif. The climate conditions in the Matter valley have a continental character with low precipitation and high-radiation budgets. The annual mean temperature and total precipitation range, respectively, from 3.5°C and 612 mm at 1638 m elevation to -6.5°C and 680 mm at 3130 m elevation (MeteoSwiss). This area also holds glaciers that currently comprise 43% of the study area.

Species data

Data on the distributions of species in Europe were extracted from the AFE (Lahti & Lampinen, 1999), which uses a mapping grid of $50 \text{ km} \times 50 \text{ km}$ cells (hereafter called 'AFE cells') based on the Universal Transverse Mercator (UTM) projection and the Military Grid Reference. Our sample included 2089 AFE cells. Species distributions data at the local scale were based on 550 64 m^2 vegetation plots in the Diablerets area and 1511 vegetation plots between 10 and 30 m^2 in the Zermatt area. Plots were restricted to open nonwoody vegetation (grassland, meadow, rock, and scree vegetation).

We developed models for 78 species that occur in more than 19 AFE cells and in at least one of the two local study areas. Of these species, 42 occur in the Diablerets and 51 in Zermatt (see Supporting information Appendix S1).

Climatic predictors

We used seven climatically derived variables expected to have a major direct ecophysiological impact on plant

species (see Prentice *et al.*, 1992 for examples of variables; see Körner, 2003 for autoecology of alpine plants): growing degree days ($GDD > 5^{\circ}\text{C}$), mean annual temperature, minimum temperature of the coldest month, mean annual, winter and summer precipitation, and potential evapotranspiration. For the European scale, these climatic variables were obtained from the Climatic Research Unit (<http://www.cru.uea.ac.uk>) at a $10'$ resolution. Mean values were averaged for the standard period 1961–1990. These $10 \times 10'$ maps were then aggregated to $50 \text{ km} \times 50 \text{ km}$ resolution to match the AFE species data and allow fitting the models, which were then projected back on the $10 \times 10'$ maps. The Diablerets and the Zermatt study areas were captured by nine and six $10 \times 10'$ cells, respectively (Fig. 1).

We generated an identical set of environmental predictors for the Diablerets and Zermatt study areas at a local-scale resolution of 25 m (hereafter called '25 m \times 25 m cells'). We first calculated linear lapse rates (i.e. rate of change along elevation) for long-term (1961–1990) monthly mean temperature and monthly rainfall taken from the national meteorological networks of Switzerland (MeteoSwiss). Next, we normalized the monthly values to sea level (0 m a.s.l.), using the regression lapse rates fitted along the elevation gradient, and interpolated the 0 m data to the whole surface of both study areas using inverse distance weighted interpolations (IDW). Finally, the spatially interpolated values (representing locally adjusted regression intercepts) were re-projected to actual elevations using a 25 m DEM (Digital Elevation Model) and the regression lapse rates (for details, see Zimmermann & Kienast, 1999). Additionally, the spatially distributed hydrological model PREVAH (Gurtz *et al.*, 1999; Randin *et al.*, 2006) was used to obtain a physically based predictor for potential evapotranspiration in both study areas, taking into account the effect of local topography.

Climate change scenarios

Spatial climate change projections were derived on the European scale for the 2080 time period ($10 \times 10'$ climatic grids; averages for 2070–2099) from the general circulation model (GCM) provided by the UK Hadley Center for Climate Prediction and Research (HadCM3; Carson, 1999), for which output from four different socioeconomic storylines (A1FI, A2, B1, B2) provided by the IPCC (Nakicenovic & Swart, 2000) were available. With an average increase of $+6.3 \pm 0.3^{\circ}\text{C}$ in the two study areas for the period 2070–2099, the A1FI climate change scenario is the most extreme. B1 is mildest ($+3.2 \pm 0.2^{\circ}\text{C}$), and A2 ($+4.9 \pm 0.3^{\circ}\text{C}$) and B2 ($+3.5 \pm 0.2^{\circ}\text{C}$) are intermediate.

Climate change projections at the local scale were obtained for temperature and precipitation and the four IPCC scenarios by calculating monthly mean anomalies between the standard period 1961–1990 and the future time period 2070–2099 based on the $10 \times 10'$ climatic grids. These anomalies were then downscaled to the 25 m resolution of local models using bilinear interpolation and added to the local-scale climatic predictors.

SDMs and their projections

We calibrated and projected SDMs (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) at both European and local scales using the latest version of the BIOMOD package (Thuiller, 2003), so as to follow as closely as possible the methods of Thuiller *et al.* (2005). For each species, generalized linear models (GLM), generalized additive models (GAM), and gradient boosting machine (GBM) were calibrated on a random sample of 70% of the initial observation data and evaluated on the remaining 30% dataset (but see Araujo *et al.*, 2005b) using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Fielding & Bell, 1997). We selected for each species and each scale the modeling technique that gives the best AUC value [best modeling technique approach – see Thuiller (2003)].

The most commonly used models for predicting species distribution so far are GLMs (e.g. Hill & Caswell, 1999; Bakkenes *et al.*, 2002; Guisan *et al.*, 2002) and GAMs are increasingly used (Yee & Mitchell, 1991; Frescino *et al.*, 2001; Guisan *et al.*, 2002; Thuiller *et al.*, 2006a), whereas GBM (Friedman *et al.*, 2000) has only recently been used (Leathwick *et al.*, 2006; Broennimann *et al.*, 2007; Pearman *et al.*, 2008) and implemented in BIOMOD (Leathwick *et al.*, 2006; Thuiller *et al.*, 2006b). GBM was ranked as the best performing techniques in a recent large comparative analysis by Elith *et al.* (2006).

Models for 78 species were fitted at the European scale using the AFE distribution data at a resolution of $50 \text{ km} \times 50 \text{ km}$. These models were then used to predict current and future species' occurrence within the $10 \times 10'$ cells overlaying the two study areas, following the procedure proposed by Araujo *et al.* (2005a). Although we agree that this downscaling procedure can generate additional uncertainty, and thus should be used with caution, we used it for sake of comparability with previous studies at the European scale. At the local scale, models were fitted and species distributions were predicted for 42 species in the Diablerets and for 51 species in Zermatt using the $25 \text{ m} \times 25 \text{ m}$ resolution climatic maps of the two study areas. Masks based on forests, lakes, urbanized areas, roads, and rivers were subsequently applied at the local scale to avoid spurious projections at locations that were not suitable

for reasons other than climate. Finally, species predictions were further restricted to landcover categories (grassland, meadow rock, and scree) on which the species was at least observed once.

For each species, we derived presence–absence predictions by using a threshold probability of presence that maximized the percentage of presences and absences correctly predicted in the training dataset (Pearce & Ferrier, 2000; Thuiller, 2003).

Calculating the persistence rate at local scale

A species would likely become extinct when predicted to lose 100% of its suitable habitat. However, because the link between habitat loss and extinction formally requires a population viability analysis (PVA) in addition to predictions of the spatial distribution of habitat (Botkin *et al.*, 2007), we only discuss here our projections in terms of habitat loss. Four situations are possible when comparing predicted habitat suitability under current and future climatic conditions at the two scales (i.e. the four cells of a two-way contingency table). First, a $10 \times 10'$ cell might be suitable under the European-scale model and also contains suitable $25 \text{ m} \times 25 \text{ m}$ cells predicted by the local model. Second, a $10 \times 10'$ cell might be predicted suitable but have no suitable $25 \text{ m} \times 25 \text{ m}$ cell predicted within it. Third, a $10 \times 10'$ cell might be predicted unsuitable but one or more $25 \text{ m} \times 25 \text{ m}$ cells are predicted suitable within it. Finally, a $10 \times 10'$ cell might be predicted unsuitable and does not contain any suitable $25 \text{ m} \times 25 \text{ m}$ cells. Cases 2 and 3 represent mismatch in the modeling outcome at the two scales. Furthermore, loss of suitable habitat only occurs when a cell predicted suitable under current climate becomes unsuitable after climate change. Because our study areas only partially overlap with each $10 \times 10'$ cell, we can only quantify the third case here, allowing us to test the local scale 'refugia' hypothesis.

We examine how frequently local persistence is predicted to occur by calculating a coefficient across the s species predicted to be extinct within the $10 \times 10'$ cells. Let l_i be the total number of $10 \times 10'$ cells predicted to become unsuitable in the future for species i by the European model. Let then p_i be the number of times the local model predicts the persistence of at least one suitable $25 \text{ m} \times 25 \text{ m}$ cell for species i among the l_i $10 \times 10'$ cells. We calculated a local persistence coefficient P within each $10 \times 10'$ cell considered (cell-specific P) or for each of the s species separately considering all the $10 \times 10'$ cells they occurred initially (species-specific P) as follows:

$$P = \frac{\sum_{i=1}^s p_i}{\sum_{i=1}^s l_i}. \quad (1)$$

The local persistence coefficient reaches a maximum value of 100 when all species within the $10 \times 10'$ cells are predicted by local models to have sufficient habitat to persist.

Sensitivity analysis of the P coefficient

In order to discuss the potential errors generated by considering a minimum of 1 pixel in the P coefficient (e.g. the pixel may be a false-positive), P was calculated for a set of different minimum numbers of $25 \text{ m} \times 25 \text{ m}$ cells with suitable habitat remaining (1, 10, 50, 100, 200, 500, 1000, and 2000 $25 \text{ m} \times 25 \text{ m}$ cells).

Possible causes of habitat persistence at the local scale

We calculated several metrics to assess reasons for possible habitat persistence at the local scale. Predicted local persistence could result from differences in the elevation ranges represented in $10 \times 10'$ cells or from the divergence between the estimates of climatic conditions at the two scales. In the first step, we examined the temperature distribution of the $25 \text{ m} \times 25 \text{ m}$ cells within each $10 \times 10'$ cell. We then controlled whether a relationship existed between the persistence coefficient and (i) the percent overlay between the study area and the $10 \times 10'$ cells and (ii) the minimum, mean, maximum elevation, and range of elevation of $25 \text{ m} \times 25 \text{ m}$ cells within the $10 \times 10'$ cell and study area (i.e. the intersection). In the second step, we measured for each $10 \times 10'$ cell the agreement between the estimates of mean annual temperature and precipitation based on the low- and high-resolution climatic data available at the European and local scales, respectively. For this set of analysis, P was calculated separately for each $10 \times 10'$ cell by pooling the species (cell-specific P). For all following analyses, P was calculated separately for each species predicted extinct within the $10 \times 10'$ cells by pooling the $10 \times 10'$ cells (species-specific P).

Local persistence of habitat may also result from differences in species' elevation optimum, as high-elevation species mostly are expected to be negatively affected by climate change. To test this, we derived an index of elevation optimum for the 78 species as follows. A species was first assigned one of three possible values for its association (VA) with each elevation belt (EB from low to high: 1 = colline, 2 = montane, 3 = sub-alpine, 4 = alpine, 5 = nival), based on data from the Atlas Flora Alpina (Aeschimann *et al.*, 2005). Values for VA are as follows: 0 if absent, 1 if not frequent, and 2 if commonly present within the corresponding elevation belt. The elevation optimum index was then calculated as

$$\text{Index} = \sum \frac{\text{EB} \times \text{VA}}{\sum \text{VA}}. \quad (2)$$

It resulted in four categories: $1 < \text{montane} \leq 2$; $2 < \text{subalpine} \leq 3$; $3 < \text{alpine} \leq 4$; $4 < \text{nival} \leq 5$. Because of the low number of nival species, these species were pooled with alpine species. We then examined the frequency with which species habitat persisted within each of these categories.

Likewise, local habitat persistence could depend on the position of species' optimum along climatic gradients. We therefore calculated the position of the environmental optimum of each species at both scales. Training data were concatenated, centered, and scaled for the seven climatic variables, so that the multidimensional space defined by the environmental variables was the same at the two scales. Finally, a principal component analysis (PCA) was applied to the difference between the centroids of the species' position at local and European scales (Pearman *et al.*, 2008). The relationship between this difference and the persistence coefficient was tested with linear regressions under the four climate change scenarios.

Furthermore, truncated response curves may result in spurious future predictions of species' distributions (Thuiller *et al.*, 2004). Therefore, we estimated the number of species with truncated response curves at local and European scales using Huisman–Olf–Fresco models (HOF models; Huisman *et al.*, 1993; Oksanen & Minchin, 2002). HOF models include a hierarchical set of five models of increasing complexity: (I) flat curve with no response, (II) monotone increasing curve, (III) monotone increasing curve reaching a 'plateau,' (IV) symmetric unimodal curve, and (V) skewed unimodal response curve. Models I–III represent truncated responses, while models IV–V represent symmetric or skewed unimodal responses. We assessed the effect of a truncated response curve along the local and European temperature gradients on the persistence coefficient by testing whether species with truncated response curves along the local and/or European climatic gradients had a persistence rate different from that of species without truncated response curves (Wilcoxon's signed-rank tests).

Finally, we assessed the difference in model evaluation (AUC) for each species between the local and European scales. The relationship between the species' local persistence and the difference in AUC was estimated by a linear regression.

Results

Models performance

Models obtained on average a fair evaluation at the local scale (mean AUC = 0.84, SD = 0.08 for species in the Diablerets, Appendix S1-a; and mean AUC = 0.81,

Table 1 Percentage of species predicted to become extinct within $10 \times 10'$ cells (C1–C15) at the European scales (ES) under the four climate change scenarios

$10 \times 10'$ cell	A1FI ES	A2 ES	B1 ES	B2 ES
C1	76.2	38.1	19.0	26.2
C2	61.9	26.2	9.5	23.8
C3	42.9	16.7	11.9	14.3
C4	83.3	47.6	31.0	28.6
C5	38.1	16.7	11.9	11.9
C6	38.1	16.7	11.9	14.3
C7	64.3	28.6	16.7	11.9
C8	38.1	11.9	11.9	14.3
C9	35.7	11.9	7.1	9.5
C10	52.3	6.8	13.6	4.5
C11	54.2	10.4	12.5	6.3
C12	40.5	2.4	11.9	2.4
C13	52.2	10.9	15.2	6.5
C14	45.5	2.3	13.6	2.3
C15	54.2	12.5	18.8	8.3
Mean	51.8	17.3	14.4	12.3
Standard deviation	14.5	12.8	5.6	8.3

SD = 0.07 for species in Zermatt, Appendix S1-b) and a good evaluation at the European scale (mean AUC = 0.94, SD = 0.04 for species in the Diablerets, Appendix S1-a; and mean AUC = 0.96, SD = 0.04 for species in Zermatt, Appendix S1-b), making them useful for deriving future projections.

Predicted species loss at the European scale

Predictions of species loss per $10 \times 10'$ cells at the European scale (Table 1) are within the same order as those predicted previously (Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005). Depending on which $10 \times 10'$ cell is considered, maximum percent loss at the European scale was between 35.7% and 83.3% for the A1FI warming scenario and lowest rates between 2.3% and 28.6% for the B2 warming scenario (see also Supporting information Appendix S3).

Local persistence rate and its potential causes

Our results showed considerable variability in the temperature represented by $25 \text{ m} \times 25 \text{ m}$ cells within each $10 \times 10'$ cell (Fig. 2). For all $10 \times 10'$ cells, the temperature at the European scale reflects the mean conditions at the local scale. However, low-temperature regions that represent potential refuges for plants are not captured at the coarse resolution of the European-scale data.

Local habitat persistence coefficients were high, ranging between 69% (A1FI) and 74% (B2) for the Diablerets area and 100% for the Zermatt area (Fig. 3; see also Supporting information Appendix S3). Difference in

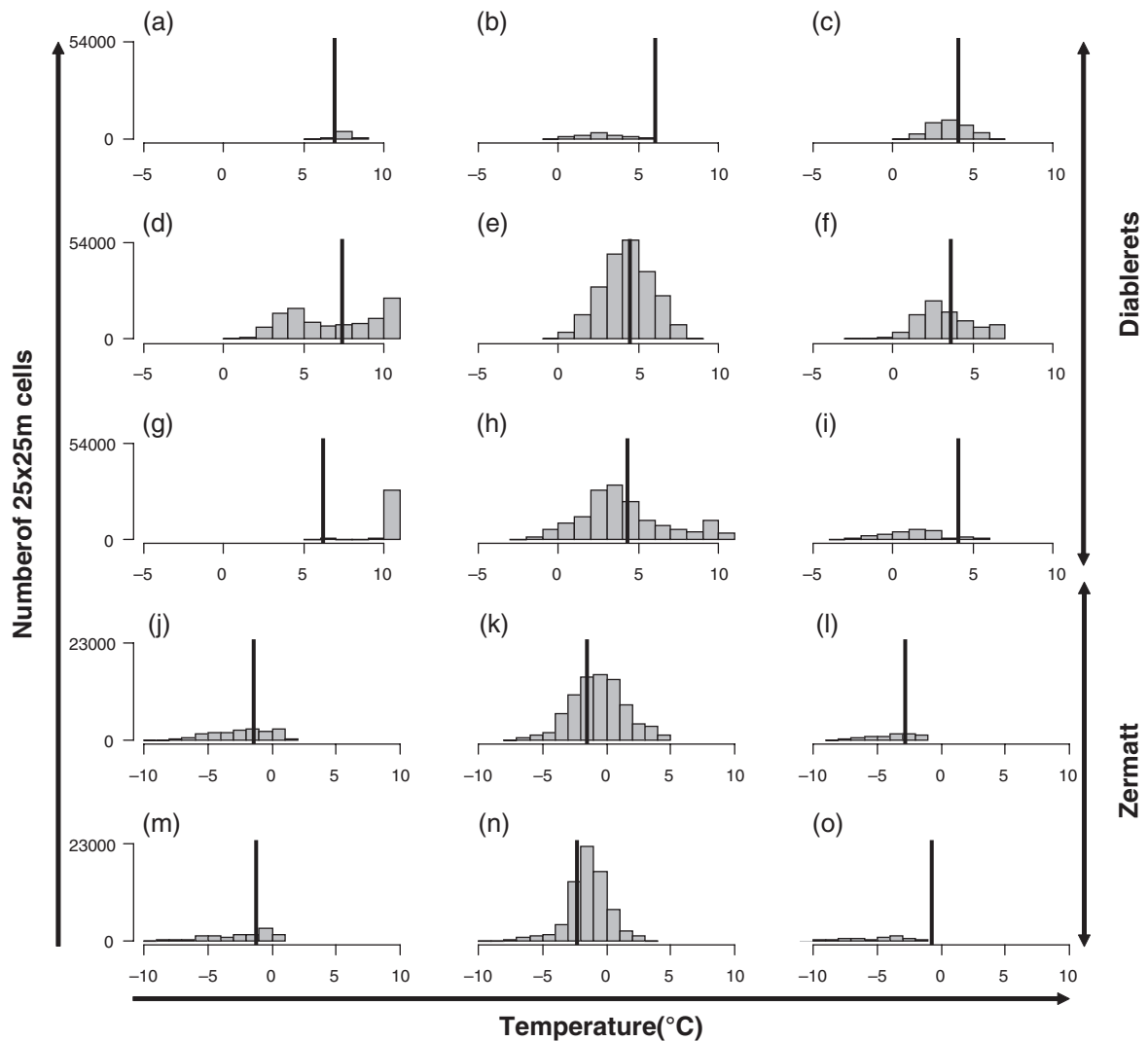


Fig. 2 Frequency distribution of the mean annual temperature (1°C intervals) for the $25\text{ m} \times 25\text{ m}$ cells within each $10 \times 10'$ cell of Diablerets (a to i: D1 to D9) and Zermatt (j to o: Z1 to Z6). The distribution of temperature reflects the local climatic variation within each $10 \times 10'$ cell. The vertical lines indicate the mean annual temperature of $10 \times 10'$ cells.

elevation range within $10 \times 10'$ cells was correlated with predicted local persistence. We found a strong and significant relationship between persistence rate and elevation range within $10 \times 10'$ cell under the four climate change scenarios (Fig. 4). The warmer the future climatic conditions, the higher the level of significance of the correlation. However, linear regressions showed no significant relationships between persistence rate and any other elevation attribute of $10 \times 10'$ cells (surface, minimum, mean, and maximum elevation; all P -values > 0.05). In addition, the rate of habitat persistence per elevation belt was in general high for species with optima in the subalpine and alpine zones in both study areas (Table 2) but was the highest overall in Zermatt.

Finally, no significant relationship (P -value > 0.05) was observed for any scenario between habitat persis-

tence locally and any of the other factors tested: (i) difference in niche position, (ii) truncated response curves along temperature on one or both scales, (iii) model quality between the two scales, (iv) modeling techniques, and (v) model evaluation (AUC).

Sensitivity analysis of the P coefficient

When increasing the minimum number of remaining $25\text{ m} \times 25\text{ m}$ cells from 1 to 2000, the P coefficient decreased by 19.9% and 19.1% under A1 for Diablerets and Zermatt, respectively (Fig. 5; see also Supporting information Appendix S4). The decrease under B2 was 3.1% for Diablerets, whereas the P coefficient remained stable in Zermatt.

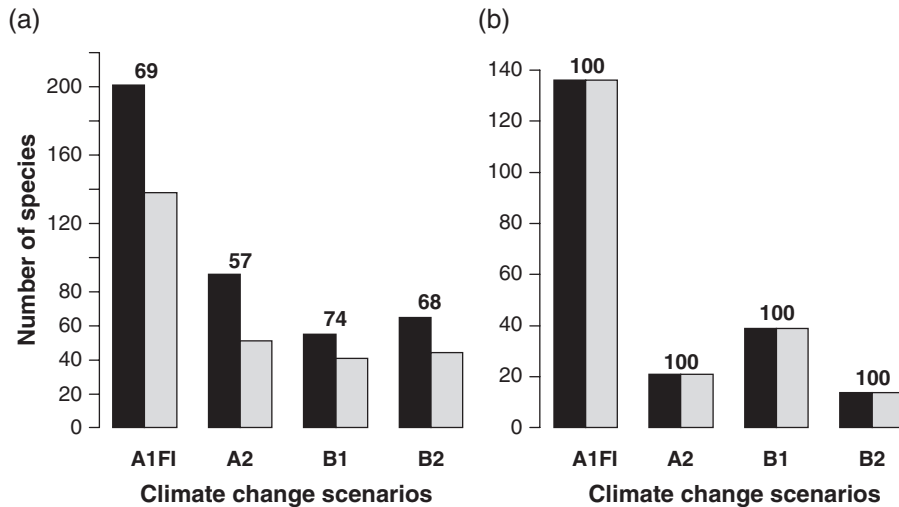


Fig. 3 Number of cases where a 10 × 10' cell becomes unsuitable for a species (black) compared with the number of cases where suitable habitat persists for these species in a 10 × 10' when modeled at the local (25 m × 25 m cells) scale (gray) for Diablerets (a) and Zermatt (b). The local persistence coefficient is indicated on the top of each bar. All 10 × 10' cells in each study area are pooled.

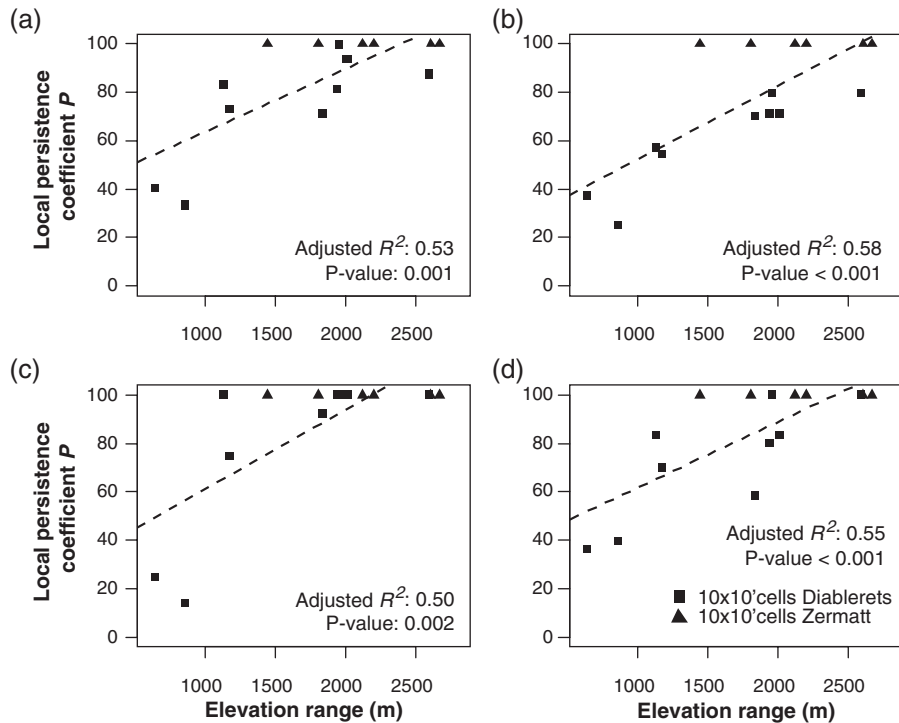


Fig. 4 Relationship between the local coefficient of persistence P and the elevation range of 25 m × 25 m cells within a 10 × 10' cell under the four climate change scenarios (a: A1FI, b: A2, c: B1, d: B2). The P coefficient has been calculated for each 10 × 10' cell individually (cell-specific P). The dashed lines represent regression trends.

Discussion

In this study, we assessed the 'local high-elevation persistence hypothesis' for 78 mountain species modeled at both European and local scales. We found that local models predicted persistence of some habitat of a

number of species in 10 × 10' cells that were predicted by models fitted at the European scale to contain no habitat. Persistence rates of habitat were especially high when considering the most severe warming scenario A1FI and were also greater in the Zermatt study area than in the Diablerets area owing to the presence of

higher elevations in the Zermatt area. Finally, the divergence between scales remained of ca. 50% when considering a minimum surface of ca. 1 km² for species to persist under the future climate conditions. Hence, our results give support to the persistence high-elevation habitat hypothesis, but too many limitations affecting the comparison between scales still prevent a formal testing of this hypothesis. Furthermore, it is impossible without data on future plant distributions to know if local projections are better than global ones.

Overall, we observed a strong relationship between the proportion of species with persisting habitat and the

observed elevation range calculated from fine-grained data within 10 × 10' cells. Greater habitat persistence also occurred in alpine species in Zermatt than in the Diablerets, suggesting that elevation range is the main driver for the predicted local-scale habitat persistence. None of the other relationships we explored showed a significant relationship with the proportion of species with persisting habitat.

Our results highlight the importance of assessing the potential impacts of climate change on species distributions at several scales, especially at local scale in mountain areas where the rugged topography requires fine mapping of environmental predictors. Possible high-elevation refuges for alpine and nival plants are likely better captured at a 25 m × 25 m resolution than at a 10 × 10' resolution, as the latter corresponds to 16 km × 16 km cells in the Swiss Alps. This contrast between scales might help to explain the quaternary conundrum, i.e. why fewer species than expected went extinct during glacial periods when models predict so many extinctions with similar amplitude of climate change (Botkin *et al.*, 2007).

However, local predictions are also entailed with a major weakness compared with predictions at the extent of Europe: the full realized niche of species may be captured incompletely at local scale owing to the limited geographic – and therefore environmental – extent

Table 2 Persistence coefficient (*P*) per optimum of elevation

	Diablerets			Zermatt	
	M	S	A	S	A
A1FI	100	68	61	100	100
A2	68	73	17	100	100
B1	100	78	50	100	100
B2	77	81	23	100	100

The climate change scenarios are represented for each study area and 10 × 10' cells in each study area are pooled (cell-specific *P*).

M, montane; S, subalpine; A, alpine.

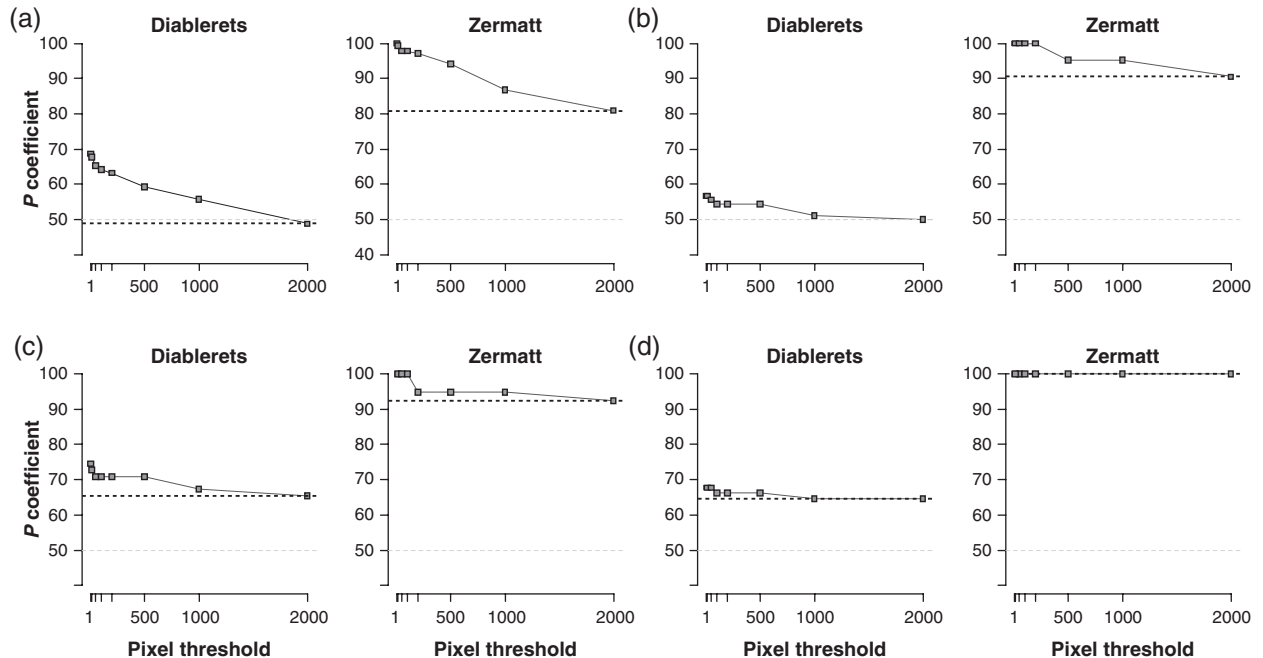


Fig. 5 Habitat persistence coefficient (*P*) calculated as the number of 25 m × 25 m cells with suitable habitat remaining for each species (1, 10, 50, 100, 200, 500, 1000, and 2000 25 m × 25 m cells) for each climate change scenario (a: A1FI, b: A2, c: B1 and d: B2) and for Diablerets and Zermatt (cell-specific *P* grouped by study area). The red dotted horizontal line represents the value of *P* when calculated with a minimum number of 25 m × 25 m cells necessary for a species to persist set to 2000, and the gray dotted horizontal line represents a *P* of 50 (50% of divergence between scales).

considered. In this case, truncated response curves may result for some species (especially low-elevation ones), and contribute to spurious predictions of future species distributions. If no distribution limit is established at both ends of the temperature gradient, species could potentially be predicted to either migrate indefinitely to higher elevations or remain present at the lowest elevation, even under climate change (Van Horn, 2002; Thuiller *et al.*, 2004). Indeed, although we did not observe any relationship between truncation of these curves and habitat persistence in our study, truncation can have effects on projections of species future distributions (e.g. Thuiller *et al.*, 2004) and thus deserves further investigation.

Some further limitations are also associated with local models. In our study, the set of local predictor variables may have not covered the full range of ecological requirements of the species, because it did not include process-based geomorphic predictors such as snow accumulation, rockfall, avalanche paths, or human-induced perturbations such as land use practices, which further contribute to limit species distributions (Dirnböck *et al.*, 2003; Dirnböck & Dullinger, 2004). However, we did not consider the retreat of glaciers in Zermatt, which in turn could contribute to increase available space for high-elevation species, and thus to further increase the divergence between scales. Absences may also not be comparable between the two scales. At local scale, absences may be due to a number of nonclimate-related factors, such as competitive exclusion, demographic processes, or environmental stochasticity, whereas climate is more likely to drive absences at the European scale.

Overall, the main reason for habitat persistence under the local scenario seems to be the importance of the length of elevation gradient, and probably the associated local topographic diversity, expressed within each large $10 \times 10'$ cell. Climatic differences along elevation gradients, as apparent at $25 \text{ m} \times 25 \text{ m}$ resolution (Fig. 2; see also Supporting information Appendix S2), allow plant species to find suitable climatic conditions at higher elevation under climate change. In contrast, models at a $10 \times 10'$ resolution reflect the mean climatic conditions within the cell, and thus provide imprecise values of the probability of occurrence of species along a thermal gradient. Global circulation models, from which some European-scale predictors were derived, likely do not express hygric continentality from the precipitation regime. This is suggested by precipitation being over- or underestimated in both study areas (results not shown, see Supporting information Appendix S2), thus contributing to the discrepancies between predictions at the two scales.

Continentality is an important climatic driver in mountain systems (Beniston, 2006). Inaccurate estima-

tion of it by global or regional circulation models will hamper the prediction of species distributions in response to climate change. As highlighted by Nogués-Bravo *et al.* (2006), the coarse spatial resolution of GCMs/RCMs used at the European scale does not enable to capture the complex, topographically driven spatial patterning of temperature and other regional climate features at local scale. We thus propose a combination of GCM/RCM anomaly mapping downscaled and combined with finer scale present day climate maps, in order to better reflect local patterns of climate change within individual mountain ranges. Subalpine and alpine species in Zermatt were predicted to be less threatened by climate change – and thus show a higher persistence rate – than in the Diablerets. This result further highlights the importance of assessing the impact of climate change locally and independently for distinct mountain regions.

Local persistence may also result in local adaptations of species regarding their environment (e.g. ecotypes) and to local changes in biotic interactions that may result in changes of a species' realized niche. This may affect comparisons between European- and local-scale models and projections (Randin *et al.*, 2006).

Several new developments may contribute to the improvement of local models. First, our predictions were made assuming unlimited dispersal from present to future conditions found at higher elevations. Considering dynamic dispersal as climate changes progressively – and possibly nonlinearly over time – is an important constraint that needs to be added to static projections from SDMs (Thuiller *et al.*, 2008). So far, such examples only exist for few species (Carey, 1996; Dullinger *et al.*, 2004).

Second, the set of climatic predictors used in our study may be further improved to better express the true habitat requirements of species. Although our set of predictors was chosen to reflect as much as possible the known physiological requirements of species, deriving even more proximal predictors would allow a finer and ecologically more meaningful characterization of the species' realized niche (Guisan & Zimmermann, 2000; Austin, 2002). This should improve local projections of future species' distributions (Guisan & Thuiller, 2005).

Third, improved projections are likely to be obtained by combining the strength of models fitted at the two scales, by fitting the full realized climatic niche of a species from large-scale data picturing the whole species' range (e.g. AFE data at the European scale), and then refining the part of the niche where projections have to be made with finer scale data and local predictors. Such hierarchical approach of environmental drivers of species distributions (Pearson & Dawson, 2004) is worth further development and should be specifically tested for deriving improved projections of

future species distributions. Models could also be improved by considering additional techniques in an ensemble modeling approach (Araujo & New, 2007), like random forest (Prasad *et al.*, 2006), support vector machine (Drake *et al.*, 2006) or maxent (Phillips *et al.*, 2006), which showed promising results in other modeling studies of species distribution.

Fourth and the last, the rough projections obtained from niche-based models could be used in conducting PVA for species in the study areas. Currently, this step cannot be made because we lack an adequate procedure to estimate extinction risks from the area predicted to remain suitable for a species under future climatic conditions (Botkin *et al.*, 2007). In this study, we considered that a species could persist at the local scale if only one 25 m × 25 m cell persisted. Long-term persistence of species in only one such cell is ecologically questionable. However, even when considering a minimum viable surface of more than 1 km² for persistence (i.e. 2000 25 m × 25 m cells), the habitat persistence coefficient remained large (i.e. over 50%; see Supporting information Appendix S4). Adding a PVA requires, at least, information on (i) the degree of occupancy of suitable habitat by each species under current condition, (ii) the degree of contiguity of the remaining habitat, and (iii) the minimum absolute number of suitable cells a species requires to maintain positive population growth. This is a challenging, yet feasible, task (Morris & Doak, 2003).

Interestingly, a recent cross-scale comparison study found results opposite to ours (Trivedi *et al.*, 2008). Projections of European-scale model (50 km × 50 km) predicted the persistence of 10 species in a mountain range of Scotland, while local models (50 m × 50 m) predicted the extinction of nine of them. The authors discuss that European models overestimated species' thermal tolerances, because the input coarse-resolution climate data were biased against the cold, high-altitude habitats of mountain plants. Further studies are thus required to assess, across a larger number of mountain ranges, whether local predictions over- or underpredict species extinctions compared with large-scale projections.

Conclusion

Our study yielded two main conclusions. First, local-scale models can predict persistent species habitat at high elevations within large cells that are predicted by coarse-resolution, European-scale models to become unsuitable (the 'local high-elevation refuge hypothesis'). Hence, European-wide projections might overestimate extinction risks for alpine species. Yet, for some species, local habitat persistence often owed to very few suitable 25 m × 25 m cells, suggesting a tenuous connec-

tion of habitat persistence with species persistence. Thus, for these species, predictions based on the European-scale data and resolutions remain plausible. These results require further testing. Secondly, models fitted at both scales examined here have strengths and drawbacks. In future studies, we suggest combining their strengths in a hierarchical approach that can estimate the full realized climatic niche of species while benefiting from finer environmental predictors locally.

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Supporting Information

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

Appendix S1. Species found in either (a) the Diablerets or (b) Zermatt dataset and are in the Atlas Florae Europaeae (AFE). The best modeling technique used for spatial projection and its area under the curve (AUC) value are indicated for each species and each scale. The elevation index (EI) is the last column. See separated Excel files for (a) the Diablerets and (b) Zermatt.

Appendix S2. Relationships between (a) projections of the mean annual temperature at the local scale (x -axis) and within the $10 \times 10'$ cells at the European scale (y -axis) and (b) projections of the mean annual precipitation at the local scale (x -axis) and within the $10 \times 10'$ cells at the European scale (y -axis). The mean temperature and mean precipitation at the local scale are calculated by averaging the values of all $25 \text{ m} \times 25 \text{ m}$ cells of one of the study areas within a $10 \times 10'$ cell. The diagonal represents a perfect agreement between scales and the dashed lines are regressions lines.

Appendix S3. Number of $25 \text{ m} \times 25 \text{ m}$ (LS) and $10 \times 10'$ (ES) cells remaining for each species under the four climate change scenarios for (a) the Diablerets (D1 to D9) and (b) Zermatt (Z1 to Z6). See separated Excel files for (a) the Diablerets and (b) Zermatt.

Appendix S4. Habitat persistence coefficient (P) calculated as the number of $25 \text{ m} \times 25 \text{ m}$ cells with suitable habitat remaining for each species (1, 10, 50, 100, 200, 500, 1000, and 2000 $25 \text{ m} \times 25 \text{ m}$ cells) for each climate change scenario.

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