nature climate change

LETTERS

Extinction debt of high-mountain plants under twenty-first-century climate change

Stefan Dullinger[1,2]*, Andreas Gattringer[1], Wilfried Thuiller[3], Dietmar Moser[1], Niklaus E. Zimmermann[4], Antoine Guisan[5], Wolfgang Willner[1], Christoph Plutzar[1,6], Michael Leitner[7,8], Thomas Mang[1,2], Marco Caccianiga[9], Thomas Dirnböck[10], Siegrun Ertl[2], Anton Fischer[11], Jonathan Lenoir[12,13], Jens-Christian Svenning[12], Achilleas Psomas[4], Dirk R. Schmatz[4], Urban Silc[14], Pascal Vittoz[5] and Karl Hülber[1]

Quantitative estimates of the range loss of mountain plants under climate change have so far mostly relied on static geographical projections of species' habitat shifts[1–3]. Here, we use a hybrid model[4] that combines such projections with simulations of demography and seed dispersal to forecast the climate-driven spatio-temporal dynamics of 150 high-mountain plant species across the European Alps. This model predicts average range size reductions of 44–50% by the end of the twenty-first century, which is similar to projections from the most 'optimistic' static model (49%). However, the hybrid model also indicates that population dynamics will lag behind climatic trends and that an average of 40% of the range still occupied at the end of the twenty-first century will have become climatically unsuitable for the respective species, creating an extinction debt[5,6]. Alarmingly, species endemic to the Alps seem to face the highest range losses. These results caution against optimistic conclusions from moderate range size reductions observed during the twenty-first century as they are likely to belie more severe longer-term effects of climate warming on mountain plants.

Many plant and animal species have already been shifting their ranges in response to the past century's climatic trends[7–9]. In mountains, owing to the altitudinal temperature gradient, species should primarily move upslope under warming, as has indeed been frequently documented during the recent decades[10,11] as well as in the palaeorecord[12,13]. As mountains usually have conical shapes, upslope movement inevitably results in range loss and may even lead to 'mountain-top extinctions'[14] in extreme cases. However, previous predictions of the magnitude of such range and biodiversity losses during the twenty-first century have been criticized[4,15] for relying on static 'niche-based' modelling approaches[16], which disregard several processes crucial to range shifts, notably: propagule dispersal; the establishment and growth of populations at newly available sites; and the potential (transient) persistence of declining remnant populations under deteriorating conditions[17,18]. The mistakes that might result from neglecting these antagonizing processes are not obvious a priori: on the one hand, dispersal limitation may prevent species from keeping track with moving climates and hence niche-based predictions might underestimate real range loss[19,20]; on the other hand, remnant dynamics may actually retard extinction processes, and range contractions observed during the next decades may thus be less pronounced than expected from niche-based models[15].

To evaluate the possible effects of these processes on the range dynamics of mountain plants, here we use a so-called hybrid model[4], which couples niche-based projections of geographical habitat shifts with mechanistic simulations of local demography and seed dispersal. The model has a cellular-automaton-type structure: it represents the study area as a regular grid of sites and simulates changes in local (that is, per grid cell) species abundance forced by an annual climatic time series. We applied this model to forecast the twenty-first-century range shifts of a sample of 150 high-mountain herb, graminoid and dwarf shrub species at a fine spatial grain (100 m) across the entire European Alps (Supplementary Table S1), that is, over an area of about 20 million cells (that is, sites). Temperature and precipitation time series for the twenty-first century, predicted by a regional circulation model under the Intergovernmental Panel on Climate Change A1B scenario, were used as climatic drivers of these dynamics (Supplementary Methods; we did not explore further climatic scenarios because of the extremely high computational demands of the hybrid model simulations). To account for uncertainties in species-specific parameter values of dispersal and demography, we ran the hybrid model with two different sets of parameter values per species, one representing the lower, and one the upper edge of a plausible interval (Supplementary Table S1 and Methods). We then compared the simulated range

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[1]Vienna Institute for Nature Conservation and Analyses, Giessergasse 6/7, A-1090 Vienna, Austria, [2]Faculty Centre of Biodiversity, University of Vienna, Rennweg 14, A-1030 Vienna, Austria, [3]Université Grenoble I, CNRS, Laboratoire d'Ecologie Alpine, UMR 5553, BP 53, 38041 Grenoble Cedex 9, France, [4]Landscape Dynamics Unit, Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland, [5]Department of Ecology and Evolution, University of Lausanne, Bâtiment Biophore, CH-1015 Lausanne, Switzerland, [6]Institute of Social Ecology Vienna (SEC), Alpen-Adria-University, Schottenfeldgasse 29, A-1070 Vienna, Austria, [7]Faculty of Physics, University of Vienna, Strudlhofgasse 4, A-1090 Vienna, Austria, [8]FRM II, Technical University of Munich, Lichtenbergstraße 1, 85747 Garching, Germany, [9]Department of Biology, Università degli Studi di Milano, Via Celoria 26, I-20133 Milan, Italy, [10]Environment Agency Austria, Department for Ecosystem Research & Monitoring, Spittelauer Lände 5, 1090 Vienna, Austria, [11]Geobotany, Center of Life and Food Sciences, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, D-85354 Freising, Germany, [12]Ecoinformatics & Biodiversity Group, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus, Denmark, [13]Ecologie et Dynamique des Systèmes Anthropisés (EA4698), Université de Picardie Jules Verne, 1 rue des Louvels, F-80037 Amiens Cedex, France, [14]Institute of Biology Zrc Sazu, Novi trg 2, SI-1000 Ljubljana, Slovenia. *e-mail: stefan.dullinger@univie.ac.at.

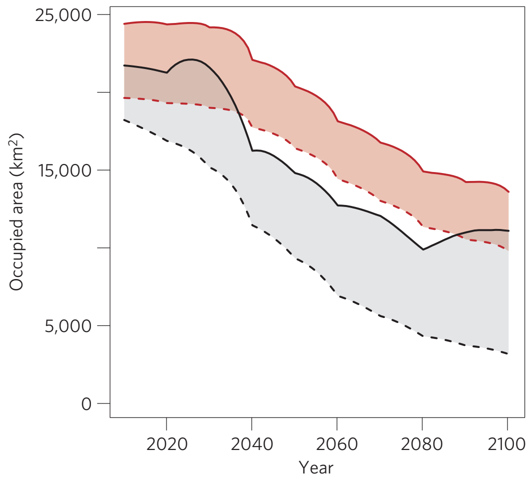

Figure 1 | Predicted average range size reduction of 150 mountain plant species of the European Alps during the twenty-first century. The red lines represent results of hybrid model simulations, the black lines niche-based projections. Shaded polygons illustrate possible model outcomes within the extremes set by hybrid models with low (dashed) or high (solid) demographic and dispersal parameter values; or by niche-based models under a no-dispersal (dashed) or under an unlimited-dispersal (solid) scenario. Differences in model predictions for the year 2010 result from a 20-year model burn-in period.

dynamics with two alternative predictions of niche-based models that assume either that species instantaneously adapt their ranges to any change in the distribution of suitable sites (‘unlimited dispersal’ scenario), or that they are unable to move beyond the initially occupied sites (‘no dispersal’ scenario). Unrealistic as they are, these two scenarios are commonly assumed to delimit the extremes of possible climate-change-driven range size reductions[4].

Averaged across all 150 species, hybrid model simulations indicate that by the end of the twenty-first century these high-mountain plants will have lost 44–50% of their present alpine ranges under high and low values of demographic and dispersal parameters, respectively (Fig. 1). Importantly, these predictions are not midway between the static niche-based projections under unlimited (49%) or no-dispersal (82%) assumptions, but close to or even lower than the former. However, in parallel with these surprisingly moderate range contractions, the hybrid model simulates a rising spatial mismatch between climatically suitable and occupied sites: the proportion of climatically unsuitable sites among those occupied by the species will strongly increase during the next decades (Fig. 2), owing to delayed local extinctions of the mostly clonal high-mountain plants (Supplementary Table S1 and Fig. S1). Simultaneously, the proportion of climatically suitable sites among those unoccupied by the species will also steadily increase (Fig. 2) because seed dispersal capacities are limited and do not allow ‘emigrants’ from existing populations to colonize all sites that will have become suitable as a result of the changing climate. When restricting range calculations to the subset of climatically suitable sites, the hybrid model hence makes a much less optimistic forecast with an average range size reduction of 57–66% until the year 2100. These figures are actually in the middle of the two extremes set by static model predictions, although still slightly closer to the unlimited-dispersal scenario.

Range loss will affect species unequally. To quantify this variation, we also calculated the proportions of species expected to lose, or gain, a certain percentage of their present range sizes until the end of the twenty-first century[1,3]. Moreover, we divided the species set into a subalpine (98 sp.) and an alpine (52 sp.) group; as well as into species endemic to the alpine chain (25 sp.) and more widely distributed species (125 sp.; ref. 21). We then computed range loss separately for each group. Under the given climatic scenario, static niche-based models predict that by the year 2100, 34% and 73% of the species will have lost >80% of their suitable area under the unlimited or no-dispersal assumptions, respectively (Fig. 3 and Supplementary Fig. S2). As with average range contractions, the hybrid model predicts lower such percentages than even the unlimited-dispersal static model if range loss calculations are based on all occupied sites (25–31% of the species, see Fig. 3), but higher percentages if calculations account for the climatically suitable sites alone (38–52%). In line with previous findings[3], the hybrid model also predicts that more alpine than subalpine species will lose >80% of their range, but differences in expected range loss are still more pronounced between endemic (72–76%) and non-endemic (39–48%) species. Predictions of complete range loss generally varied in a similar way: the hybrid model forecasts that 6–8% of the full set of species, 5–6% of the subalpine species, 8–12% of the alpine species, 3–4% of the non-endemic species and 20–28% of the endemic species will no longer occupy any climatically suitable sites by 2100. Hybrid model

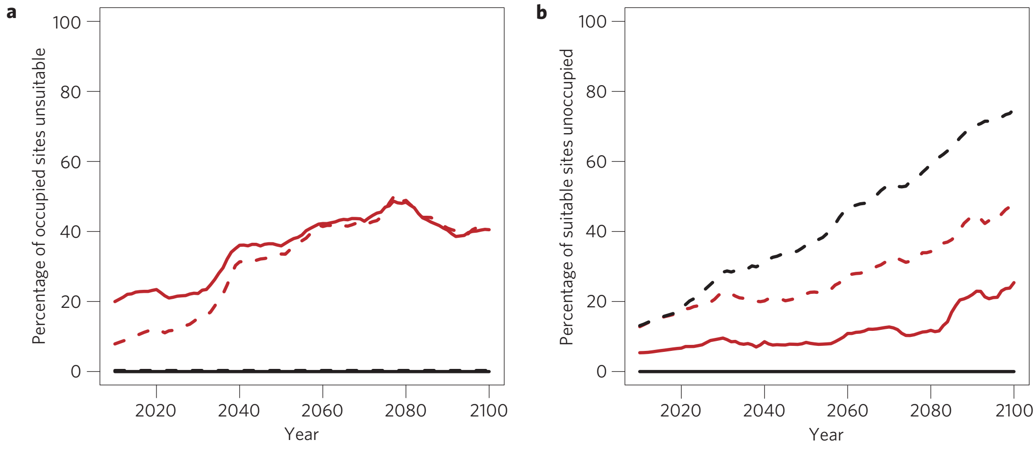

Figure 2 | Spatial mismatch between sites predicted to be occupied and sites predicted to be suitable. a, Percentage of unsuitable sites among those predicted to be occupied. **b**, Percentage of suitable sites predicted to remain unoccupied. Sites are 100 m × 100 m cells in a regular grid spanning the European Alps. Red lines represent hybrid model results with demographic and dispersal parameters set to high (solid) and low (dashed) values, respectively, the black lines niche-model projections under an unrestricted-dispersal (solid) and a no-dispersal (dashed) scenario. Values are averages across 150 model species. Suitability was measured by the projections of niche-based models for each species and year.

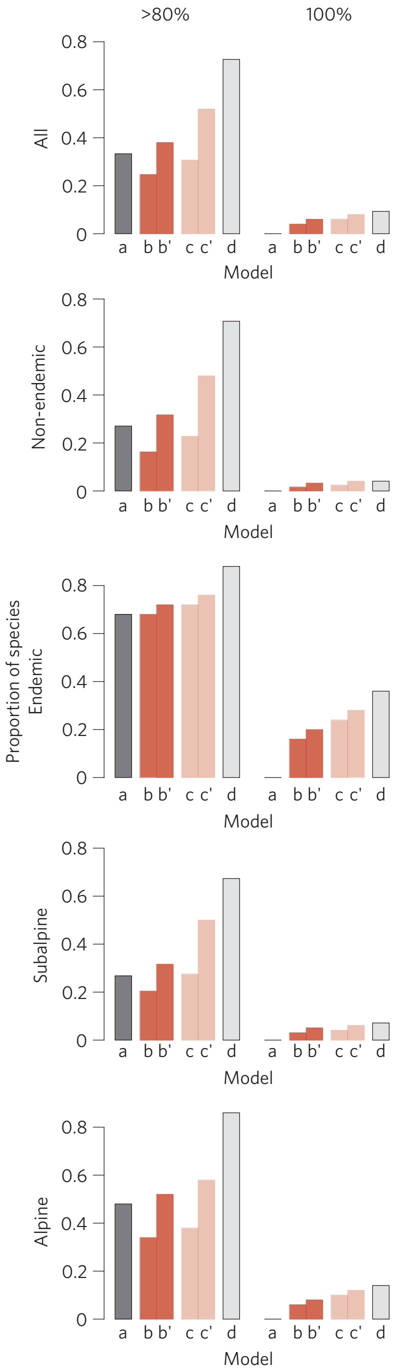

Figure 3 | Proportion of species predicted to have lost >80% or 100% of their range by the end of the twenty-first century. Red bars represent results from hybrid models with demographic and dispersal parameters set to high (b, b′) and low (c, c′) values, respectively. Bars b and c refer to loss calculations based on the number of sites predicted to be occupied, bars b′ and c′ to loss calculations based on the number of sites predicted to be both occupied and still climatically suitable to the species. Grey bars represent results of niche-based projections under unlimited-dispersal (a) or no-dispersal (d) assumptions.

predictions for sites occupied irrespective of climatic suitability are less severe (Fig. 3 and Supplementary Fig. S2), whereas static niche-based models under the no-dispersal assumption always forecast higher such percentages. Under an unlimited-dispersal assumption, however, static models predict that some suitable areas will remain for each one of the 150 species (Fig. 3). Only with respect to the number of species predicted to lose their entire Alpine range, niche models under an unlimited-dispersal assumption hence provide the expected ‘most optimistic’ forecast.

The hybrid model indicates that the opposing effects of delayed local population extinctions and lagged migration rates will result in less severe twenty-first-century range reductions of alpine plants than expected from static, niche-based model predictions. However, these apparently ‘optimistic’ forecasts include a large proportion of remnant populations under already unsuitable climatic conditions. The persistence of such remnant populations creates an extinction debt that will have to be paid later unless species manage to adapt phenotypically or genetically to the changing climate[22] and to the likely associated alterations in their biotic environments[23]. Our simulations indicate that such repayment will take several decades, on average, and might extend to several centuries for some species and/or populations (Supplementary Fig. S1). Furthermore, recent evidence of frequent postglacial migration lags among alpine plants[24] strongly indicates that the complementary ‘immigration credit’[25]—represented by the accumulating number of suitable, but uncolonized sites—will not become fully realized for a long time into the future. This is particularly likely for endemics, which—despite having often large climatically suitable ranges available[24]—are often restricted to those marginal chains of the Alps that had served as refugia during Pleistocene glaciations[26]. Worryingly, most of these marginal chains have relatively low summit heights, making their alpine plant populations particularly vulnerable to mountain-top extinctions[27]. As indicated by hybrid model simulations, this paucity of local cold-climate refugia at high altitudes, combined with low mobility[24], puts alpine endemics disproportionally at risk under climate warming.

Our hybrid model represents considerable progress over purely static projections of range shifts, and over previous hybrid models that include only dispersal simulations[20], by providing insights into the transient dynamics that are likely to dominate the range responses of plants to climate warming over the next century. Still, it is by necessity based on simplifying assumptions and coarse parameter estimates, and also neglects potentially important factors such as microscale climatic variation[28], extreme climatic events[29], differential climatic sensitivity among individual life-history stages, wind-speed changes and their dispersal effects[30] and interactions among migrating plant species[23]. Despite these caveats, by using two widely contrasting sets of parameter values our simulations provide a plausible estimate of the span of twenty-first-century range dynamics of alpine plants. Most importantly, our results consistently caution against drawing over-optimistic conclusions from relatively modest range contractions observed during the coming decades, as these are likely to mask more severe longer-term warming effects on mountain plant distribution.

Methods

We fitted niche models[16] for 150 plant species by relating occurrence data from 14,040 vegetation plots to one soil and five bioclimatic variables downscaled to a 100 m spatial resolution. We then projected changing suitability surfaces until the end of the twenty-first century based on an annual climatic series for the Intergovernmental Panel on Climate Change A1B scenario (Supplementary Methods). Initial species distributions for hybrid model simulations were set by suitability projections under present climatic conditions, converted to presence/absence using prevalence as threshold. To correct for model predictions outside the realized range, these projections were filtered by maps of actual species occurrence in 55 alpine regions[23].

Populations of particular 100 × 100 m sites were represented by stage-(seeds, juveniles, adults) structured cohorts. Population dynamics was driven by demographic rates (germination, seed bank persistence, juvenile survival, maturation, fecundity, clonal growth, adult survival). We collected species-specific data on these rates from databases and literature (Supplementary Table S1). Owing to remaining parameter uncertainties, we defined for each species and parameter a low and high value along a credible range (see Supplementary Table S1 and Fig. S3 for a sensitivity analysis). Finally, we assigned species-specific demographic rate values to each site of the study area assuming that the rates are functions of site suitability (Supplementary Methods).

We used mechanistic models to construct wind, exo- and endozoochorous seed dispersal kernels. For combining the contributions of the three kernels to overall seed shadows, we assumed either a high (1–5%) or low (0.1–0.5%) share of the more fat-tailed zoochorous kernels.

Simulated range dynamics finally resulted from the impact of climate-driven site suitability changes on demographic rates and the consequent growth or decline of populations, eventual extinction or dispersal-mediated establishment in hitherto uncolonized sites.

Received 17 November 2011; accepted 2 April 2012;
published online 6 May 2012

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Acknowledgements

This research was financially supported by the EU 6th Framework Programme for Research, Technological Development and Demonstration (project ECOCHANGE, GOCE-CT-2007-036866) as well as by the Danish Council for Independent Research—Natural Sciences (grant 272-07-0242 to J-C.S.) and the ANR Diversitalp project (ANR-2007-BDIV-014). We thank the Vienna Scientific Cluster (http://vsc.ac.at/) for granting access to its computational resources. Niche-based models were performed using the CIMENT infrastructure (https://ciment.ujf-grenoble.fr), supported by the Rhône-Alpes region (GRANT CPER07-13 CIRA). Thanks to S. Rechnitzer for improving the English.

Author contributions

S.D., W.T., N.E.Z., A. Guisan and K.H. designed the study. N.E.Z., A.P. and D.R.S. processed the climatic data, and W.W. prepared the soil map. S.D., W.T., N.E.Z., A. Guisan, W.W., M.C., T.D., A.F., J.L., J-C.S., U.S. and P.V. contributed vegetation plot data. W.W. and J.L. compiled the plot database. W.T. calibrated and fitted all niche-based models. S.E., S.D. and K.H. collected plant seeds and S.E. measured seed traits. T.M. and M.L. implemented dispersal models and S.D. calibrated dispersal kernels. S.D., A. Gattringer, K.H. and M.L. designed the hybrid model, A. Gattringer translated it into C code and ran the code on the Vienna Scientific Cluster. K.H. and S.D. analysed the simulation results. D.M. and C.P. did all geographic information system work. S.D. wrote the paper, with substantial help from all co-authors.

Additional information

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