



Predicting future distributions of mountain plants under climate change: does dispersal capacity matter?

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Many studies have investigated the potential impacts of climate change on the distribution of plant species, but few have attempted to constrain projections through plant dispersal limitations. Instead, most studies published so far have simplified dispersal as either unlimited or null. However, depending on the dispersal capacity of a species, landscape fragmentation, and the rate of climatic change, these assumptions can lead to serious over- or underestimation of the future distribution of plant species.

To quantify the discrepancies between simulations accounting for dispersal or not, we carried out projections of future distribution over the 21st century for 287 mountain plant species in a study area of the western Swiss Alps. For each species, simulations were run for four dispersal scenarios (unlimited dispersal, no dispersal, realistic dispersal, and realistic dispersal with long-distance dispersal events) and under four climate change scenarios.

Although simulations accounting for realistic dispersal limitations did significantly differ from those considering dispersal as unlimited or null in terms of projected future distribution, the unlimited dispersal simplification did nevertheless provide good approximations for species extinctions under more moderate climate change scenarios. Overall, simulations accounting for dispersal limitations produced, for our mountainous study area, results that were significantly closer to unlimited dispersal than to no dispersal. Finally, analysis of the temporal pattern of species extinctions over the entire 21st century revealed that important species extinctions for our study area might not occur before the 2080–2100 period, due to the possibility of a large number of species shifting their distribution to higher elevation.

During the last three decades, strong evidence has emerged suggesting that increased atmospheric concentration of greenhouse gases, particularly carbon dioxide and methane linked to human activities, have already begun to modify the global climate (IPCC 2007). On average, global surface temperature increased by 0.61 ($\pm 0.18^\circ\text{C}$) between 1861 and 2000 (Folland et al. 2001).

Evidence from palynology and fossil records have shown that, in the past, plant species have successfully responded to environmental change by 1) remaining within the modified climate by tolerance or adaptation, 2) migrating to track suitable conditions, or most likely a combination of both (Davis and Shaw 2001, Jump and Peuelas 2005). However, due to its high magnitude and fast rate, it is

uncertain whether plants will be able to withstand the climate change forecasted for the 21st century by tolerance and adaptation solely (Davis and Shaw 2001, Etterson and Shaw 2001, Jump and Peuelas 2005). The ability of plants to migrate and keep pace with the shift of their suitable habitats is thus likely to be of prime importance for their survival, although this might sometimes require migration rates much higher than those observed from pollen reconstructions (Davis and Shaw 2001, Malcolm et al. 2002). In addition to the rapidity of climate change, a further challenge to plant migration is the human-driven habitat fragmentation that renders the landscape increasingly impassable (Pitelka et al. 1997), and hampers both seed dispersal and gene flow between populations (Davis and Shaw 2001). Finally, natural barriers to dispersal, such as rivers, lakes, forests, or valleys and mountain ranges at a

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larger scale, represent yet another set of potential obstacles to successful migration.

If a species can neither adapt to the modified environmental conditions nor migrate fast enough, then drastic range reduction or even local extinction – or quasi-extinction – is to be expected. Quasi-extinction indicates that a species could still persist in a few small and scattered locations in the form of relict populations (Eriksson 2000), but these remaining individuals may be very vulnerable to any further disturbances. Reductions in distribution or extinction are particularly expected for species with weak dispersal capacity, long maturation time (i.e. time before the production of propagules), and/or slow growth rate.

A widespread method to assess the impact of future climate change on plants has been the utilization of species distribution models (Guisan and Zimmermann 2000, Guisan and Thuiller 2005). A broad range of projections have already been carried out to forecast future plant species distributions, at large geographical scales with coarse resolution (e.g. at continental scale, Bakkenes et al. 2002, Thuiller et al. 2005), and also at regional or local scales with high resolution data (Guisan and Theurillat 2000, Dirnböck et al. 2003). Importantly, these models assume that a species is in equilibrium with its environment, and therefore, do not consider possible adaptations or tolerance to climate change. Another limitation of species distribution models, at least in their basic implementation, is that they ignore dispersal restrictions. Thus far, most studies have been based on the assumption of universal dispersal (i.e. a species has unlimited dispersal, its future distribution being the entire area projected by the model; Thomas et al. 2004). While this hypothesis might provide good approximations for plants that are human-dispersed or have high dispersal ability, it is likely overestimating the future distribution of many other species for the previously mentioned reasons, namely the fast rate of the forecasted climate change and habitat fragmentation. As the unlimited dispersal assumption represents an optimistic “best case” scenario, some studies have also provided a “worst case” no-dispersal scenario (Thuiller et al. 2005, Loarie et al. 2008), to provide a lower bound for their projections. However, the difference between these extreme projections can yield large uncertainties (Thuiller et al. 2004).

Reducing these uncertainties requires taking dispersal processes into account more directly. While some studies have already included dispersal limitation when projecting species distribution under climate change scenarios (e.g. Dullinger et al. 2004, Iverson et al. 2004), none has done it for a large number of species at a fine spatial scale.

Using the MigClim cellular automaton (Engler and Guisan 2009), which allows for implementation of plant dispersal constraints into projections of future species distribution, we here 1) project potential future distribution and assess the extinction risk over the 21st century for 287 plant species of the western Swiss Alps while accounting for realistic dispersal limitations and, 2) compare these results to those from unlimited and no-dispersal projections. More specifically, this study aims to address the following: 1) are simulations implementing realistic dispersal limitations

close to projections assuming no dispersal, unlimited dispersal or neither of these? 2) How much does the inclusion of long-distance dispersal events affect the projections? 3) What is the temporal pattern of plant species extinctions during the 21st century in our study area? 4) Does the predicted range reduction and extinction risk estimated with different dispersal simulations relate to species migration capacity and altitudinal optimum? For each species, simulations were performed under four climate change and four dispersal scenarios: realistic dispersal distance with and without long-distance dispersal events, no dispersal, and unlimited dispersal.

Materials and methods

Study area

The Diablerets study area (Fig. 1a–b) is located in the western Swiss Alps (6°50′–7°15′E; 46°10′–46°30′N) and covers 700 km². Elevation ranges from 375 m in Montreux to 3210 m at the top of the Diablerets massif. Mean annual temperature and yearly precipitation sum vary from 8°C and 1200 mm at 600 m to –5°C and 2600 mm at 3000 m (Bouët 1985). The soil parent material is mainly calcareous. Vegetation has been and is still influenced by human activity: pasture is commonly observed from the bottom of the Rhone valley to the subalpine and lower alpine zones. Meadows with varying levels of human management intensity are mainly found at lower elevations.

Species dataset

During the summers of 2002–2004, 550 vegetation plots were sampled following a random-stratified sampling design restricted to non-woody vegetation (pastures and meadows below the timberline, grassland, rock, and scree above the line; Fig. 1a). Stratification included elevation, slope, aspect, and simplified classes of geology and land cover (Supplementary material Appendix S1). A minimum distance of 200 m was set between plots to minimize the effect of spatial auto-correlation when calibrating the models. Each plot had a 64 m² surface (8 × 8 m) in which the presence of all species was recorded. Species with <20 presence points were removed to prevent loss of robustness in distribution models, leaving a total of 287 species.

Topographic and climatic predictors

Climate data were derived from long-term (1961–1990) monthly means for average temperature (°C) and sum of precipitation (mm) provided by the Swiss national meteorological station network at different altitudes. Methods for computation and description of the variables are summarized in Zimmermann and Kienast (1999). In this study, we employed three climatic and two topographic variables at a 25 m resolution (Table 1). These variables are thought to best represent the physiological requirements of species,

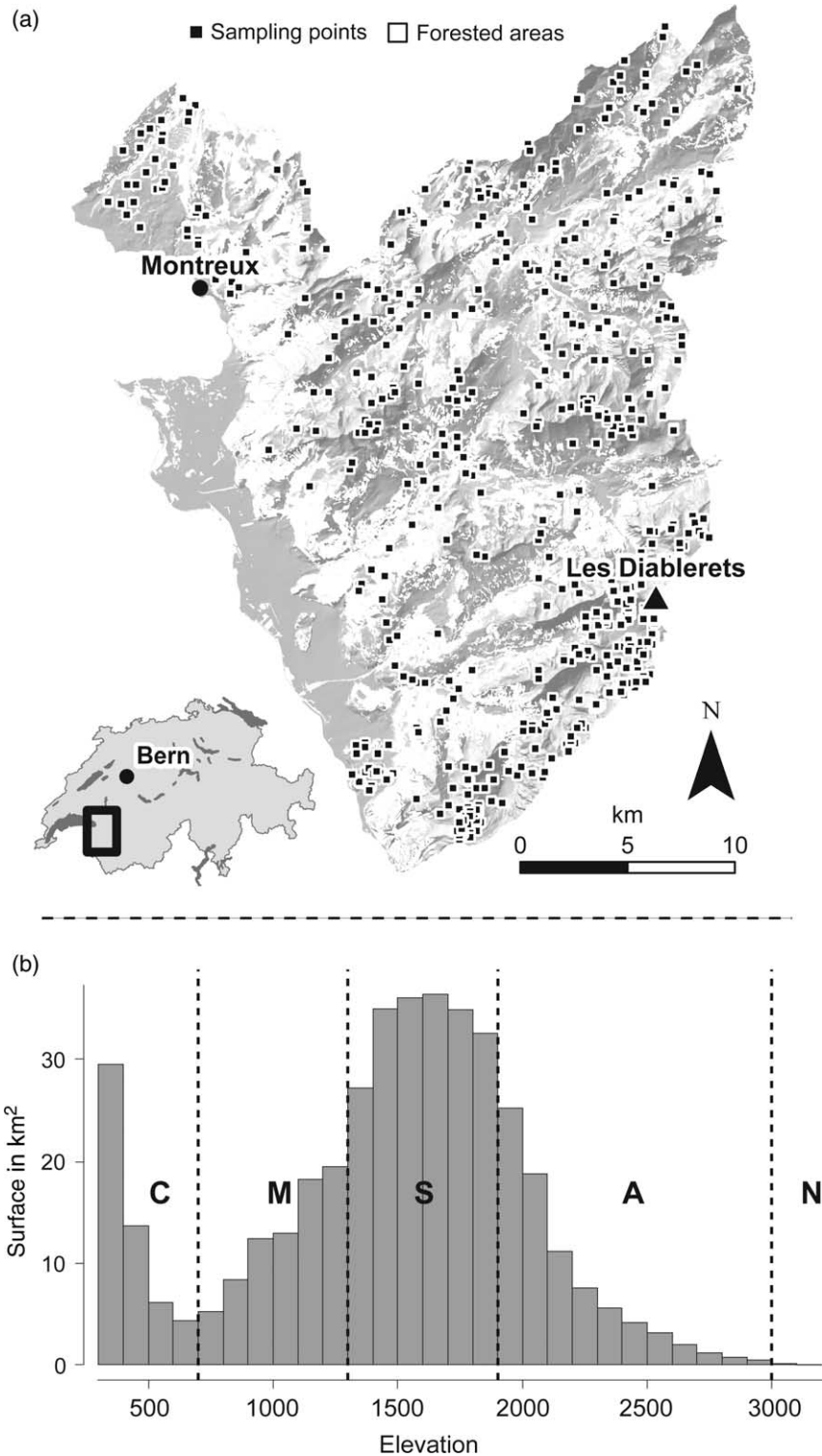


Figure 1. (a) The Diablerets study area and its location in Switzerland. Areas in white were not used in spatial projection. (b) Frequency distribution of elevation with limits of vegetation zones: C = colline; M = montane; S = subalpine; A = alpine; N = nival.

i.e. energy, water, and nutrients (Pearson et al. 2002, Körner 2003). Degree-days of the growing season (threshold of 0°C) were derived from interpolated monthly temperatures. The moisture index was calculated as the difference between precipitation and potential evapotranspiration, expressing the amount of soil water that is

potentially available at a site. The sum of mean daily values for the months of June, July, and August were used, since these represent the warmest and driest months of the year. The potential global solar radiation was calculated over the year. Topographic position and slope were derived from a 25 m resolution elevation model. Positive values of

Table 1. Topographic and climatic variables used to model species distributions.

Variables	Units	Details	References
Temperature degree days	$^{\circ}\text{C} \times \text{d} \times \text{yr}^{-1}$	Sum of days multiplied by temperature $>0^{\circ}\text{C}$	Zimmermann and Kienast (1999)
Moisture index (average of monthly values June–August)	$\text{mm} \times \text{d}^{-1}$	Monthly average of daily atmospheric H_2O balance	Zimmermann and Kienast (1999)
Global solar radiation (sum over the year)	$\text{kJ} \times \text{m}^{-2} \times \text{yr}^{-1}$	Sum of monthly average of daily global solar radiation	Zimmermann et al. (2007)
Slope	Degrees	Slope inclination	ArcGIS Spatial Analyst extension
Topographic position	Unitless	Integration of topographic features (ridge, slope, toe slope) at various spatial scales	Zimmermann et al. (2007)

topographic position express relative ridges, tops, and exposed sites, while negative values indicate sinks, valleys, or toe slopes.

Climate change scenarios

We used four different climate projections for the 2001–2100 time period developed by the UK Hadley Center for Climate Prediction and Research. These were derived from a global circulation model (HadCM3; Carson 1999), and are based on four different socio-economic scenarios: A1FI (hereafter referred to as “A1”), A2, B1, and B2 of the IPCC (Intergovernmental Panel on Climate Change; Nakicenovic and Swart 2000).

The climate change projections, in the form of $10'$ (~ 15 km in Switzerland) grids, were used to calculate monthly mean temperature and precipitation anomalies for our study area between the standard period of 1961–1990 and 20 five-year periods from 2001 to 2100. These anomalies were then downscaled to 25 m resolution using bilinear interpolation and added to current monthly precipitations and temperatures. Thereafter, we calculated the derived environmental predictors for the study area under future climatic conditions. With an average increase of $+7.6^{\circ}\text{C}$ in our study area by 2100, the A1 climate change scenario is the most extreme. B1 is most modest ($+3.9^{\circ}\text{C}$), while A2 ($+6.2^{\circ}\text{C}$) and B2 ($+4.4^{\circ}\text{C}$) are intermediate scenarios.

Species distribution models

For each species, generalized linear models (GLM; McCullagh and Nelder 1989), generalized additive models (GAM; Hastie and Tibshirani 1986), gradient boosting machines (GBM; Friedman et al. 2000), and Random Forests (RF; Breiman 2001) were fitted using species presence-absence as the response variable and climatic and topographic variables as predictors (i.e. explanatory variables). GLMs and GAMs were calibrated using a binomial distribution and a logistic link function (i.e. logistic regression). A stepwise procedure in both directions was used for predictor selection, based on the Akaike information criterion (AIC; Akaike 1973). Up to second-order polynomials (linear and quadratic terms) were allowed for each predictor, with the linear term being forced into the model each time the quadratic term was retained.

The accuracy of each model was evaluated by 10-fold cross-validation (van Houwelingen and Le Cessie 1990) on the training data set. In the cross-validation procedure, the original prevalence of the species presences and absences in the data set was maintained in each fold. Comparisons of predicted (probabilistic scale) and observed (presence-absence) values were based on the area under the curve (AUC) of a receiver-operating characteristic plot (ROC; Fielding and Bell 1997).

Spatial projections

The modeling technique that produced, on average, the highest AUC values over the entire species dataset was selected to carry out spatial projections. Spatial projections of GLM were reclassified into presence-absence using a ROC – optimized threshold maximizing jointly the percentage of presences and absences correctly predicted (i.e. the probability where sensitivity = specificity; Liu et al. 2005).

Masks based on forests, lakes, urbanized areas, roads, and rivers were subsequently applied on the raw projections to avoid spurious projections at locations unsuitable for reasons other than climate. Finally, projections were further restricted to land cover classes (grasslands, rock, and scree) for which a species was observed at least once.

Dynamic simulation using the MigClim cellular automaton

MigClim (Engler and Guisan 2009) is a cellular automaton that allows simulation of the dispersal of plant species in the landscape, while implementing a climate change scenario at the same time. The MigClim model allows distinguishing between regular dispersal (hereafter, referred to as short-distance dispersal), where most of the seeds (e.g. 99%) are distributed with a predictable pattern, and long-distance dispersal (LDD), which affects only a small number of seeds and relies on more stochastic means of dispersal. Further MigClim parameters that were used in the present study were generation time, resilience time to unfavorable conditions, and barriers to dispersal.

Because of the high number of species modeled in our study (i.e. 287), it is difficult to obtain very accurate data to calibrate the dispersal behavior of each species. In fact, such data does not exist for the large majority, if not all, of the species considered in our study. To overcome this lack of

Table 2. Parameters used in the MigClim model for each dispersal category (1–7).

	Dispersal categories						
	1	2	3	4	5	6	7
Max disp. dist.	1 m	5 m	15 m	150 m	500 m	1500 m	5000 m
MaxLDD disp. dist.	1 km	1 km	1 km	1 km	5 km	5 km	10 km
LDD frequency*	0.002	0.002	0.0004	0.01	0.04	0.04	0.04
Disp. event freq.**	5 yr	5 yr	1 yr	1 yr	1 yr	1 yr	1 yr
Generation time	Parameter set individually for each species (Supplementary material Appendix S3)						
Resilience time	Parameter set individually for each species (Supplementary material Appendix S3)						
Barriers	Forests or nothing						
Filters	Urban areas, lakes, rivers, glaciers+grassland and/or rock and/or scree						
No. of species	53	10	55	21	24	83	41
Pixel size	5 m	5 m	5 m	25 m	50 m	50 m	50 m
No. of pixels	30 000 000			4 800 000		1 200 000	

*Variations in LDD event frequencies reflect the corrections applied for pixel size and dispersal event frequency to maintain the 0.01 frequency assigned to 25 m pixels constant over all categories.

**Dispersal event frequency indicates the time between two successive dispersal events.

accurate data, we assigned each of our species to one of the seven dispersal types defined in Vittoz and Engler (2007) (Table 2, Supplementary material Appendix S2 and S3), based on morphological and seed dispersal traits found in Müller-Schneider (1986). This allowed to derive dispersal distances for each species that can be expected to lie within an accuracy of one order of magnitude, which is sufficient to achieve significant improvement over models that ignore dispersal (Engler and Guisan 2009). Each category was also assigned a maximum dispersal distance for LDD events between 1 and 10 km (Table 2), which corresponds to values commonly found in previous studies (Nathan 2005 and references therein).

The decrease in colonization probability with distance from a source pixel was chosen to reflect a negative exponential seed dispersal kernel, a common shape (Willson 1993), although many others exist (Clark et al. 1999, Nathan and Muller-Landau 2000, Powell and Zimmermann 2004). This negative exponential kernel was used only to model regular seed dispersal, as LDD events were modeled as an additional, separate component.

Details regarding the calibration of colonization probabilities are given in Supplementary material Appendix S4, and further explanation of the MigClim model can be found in Engler and Guisan (2009).

Species generation time (i.e. the time required before a newly colonized pixel can act as a seed source) and resilience to unfavorable environmental conditions (i.e. the time a pixel remains occupied even though its habitat has become unsuitable) were set individually for each species based on expert knowledge (Supplementary material Appendix S3). Landscape fragmentation was represented by forested areas that were used as “barriers” (i.e. pixels that impede dispersal across them, except for LDD events) as well as lakes, urbanized areas, roads and rivers that were considered “permanently unsuitable habitats” (i.e. pixels that are permanently unsuitable for the species, but allow dispersal across these areas).

For each species, four dispersal scenarios were run: no dispersal (=ND), realistic dispersal distance without LDD (=SDD for “short distance dispersal”), realistic dispersal distance with LDD (=LDD), and unlimited dispersal (=UD). All simulations were performed for the 100-yr period of 2001–2100 and under each of the four IPCC

climate change scenarios (A1, A2, B1, B2). The initial distribution of a species was defined as its potential habitat under current climatic conditions, i.e. 1961–1990 average. Changes in habitat suitability reflecting climate change were implemented every fifth year. Dispersal was simulated each year, except for categories 1 and 2 (Table 2), as these species have dispersal distances that are too short to be modeled on a yearly basis, even on a grid with 5 m resolution. Therefore, the dispersal distances of these categories were multiplied by five and dispersal was simulated every fifth year, which assumes a conservative best-case approximation, where spread rate = generation time \times dispersal distance. Finally, because each simulation included some randomness, all simulations were repeated five times and results were averaged.

Species extinctions by 2100 and throughout the 21st century

We first calculated the percentage of species predicted to become extinct and quasi-extinct by 2100 for each combination of dispersal (i.e. ND, SDD, LDD and UD) and climate change scenario (i.e. A1, A2, B1, and B2). Extinction and quasi-extinctions were defined, respectively, as a decrease of 100 or 90% in potential distribution as compared to a species’ initial area of occupancy. To examine the temporal pattern of extinctions, the percentage of species going extinct (100% threshold) was also computed for every five-year time period, from 2005 to 2100.

Relationship between species extinction risk, migration capacity, and altitudinal optimum

The relationship between a decrease in the distribution of a species by 2100 (expressed as a percentage of its initial distribution) and two biological traits (i.e. migration capacity and altitudinal distribution optimum) was assessed using univariate linear regressions. Only species with a decreasing distribution were considered for these analyses.

Migration capacity was expressed through a migration rate index (eq. 1):

$$\text{Migration rate index} = \log_{10} \left(\frac{\text{MaxDispersal}_{99\% \text{ of Seeds}}}{\text{Generation Time}} \right) + 1 \quad (1)$$

where $\text{MaxDispersal}_{99\% \text{ of Seeds}}$ is the maximum dispersal distance for 99% of the seeds (i.e. the short dispersal distance), and Generation Time is the number of years required for a species to start producing seeds.

An index was derived for each species to express altitudinal distribution optima. First, we assigned one of three possible frequency values (VA: 0 = absent, 1 = rare, 2 = commonly present) for each association of a species with an elevation belt (EB: 1 = colline, 2 = montane, 3 = subalpine, 4 = alpine, 5 = nival), using data from the Atlas Flora Alpina (Aeschimann et al. 2005). The elevation optimum index was then calculated as (eq. 2):

$$\text{Elevation optimum index} = \frac{\sum \text{EB} \times \text{VA}}{\sum \text{VA}} \quad (2)$$

This resulted in four categories: $1 < \text{montane} \leq 2$; $2 < \text{subalpine} \leq 3$; $3 < \text{alpine} \leq 4$; $4 < \text{nival} \leq 5$. Due to the low number of nival species, these were pooled with alpine species.

Results

Species distribution model performance

AUC values showed that overall, GLM performed slightly better than GAM, GBM, and RF (Supplementary material Appendix S5). A Wilcoxon signed-rank test (samples grouped by species AUCs) also confirmed that AUC values were significantly higher for GLM than for GAM, GBM, and RF (p value < 0.001).

Projected distributions and species extinctions by 2100

Among our pool of 287 species, the percentage of those going extinct in the study area (Fig. 2; 100% threshold) varied from 0.3% (UD under B1) up to 52.6% (ND under A1). Results from simulations with realistic dispersal distances (i.e. SDD and LDD) yielded extinction rates ranging from $\sim 1\%$ under B1 to $\sim 20\%$ under A1. These extinction rates were always closer to those of UD than ND simulations.

Quasi-extinction rates (i.e. species with over a 90% decrease in distribution; Fig. 2), values reached up to 89% (ND under A1) and were never below 23% (UD under B1). SDD and LDD simulations produced fairly similar results, with quasi-extinction rates of approximately 70% under A1 (most extreme) and 30% under B1 (least extreme).

Consideration of changes in potential spatial distribution rather than species extinctions or quasi-extinction reveals that at least 70% of the investigated species will likely decrease in distribution by the end of the 21st century (Fig. 3). For instance, even under B1 climate change scenario with unlimited-dispersal, a highly optimistic combination, 198 species out of 287 are forecasted to decrease in distribution. For over 50% of these species, the total area of occupancy decreases by at least 60% compared

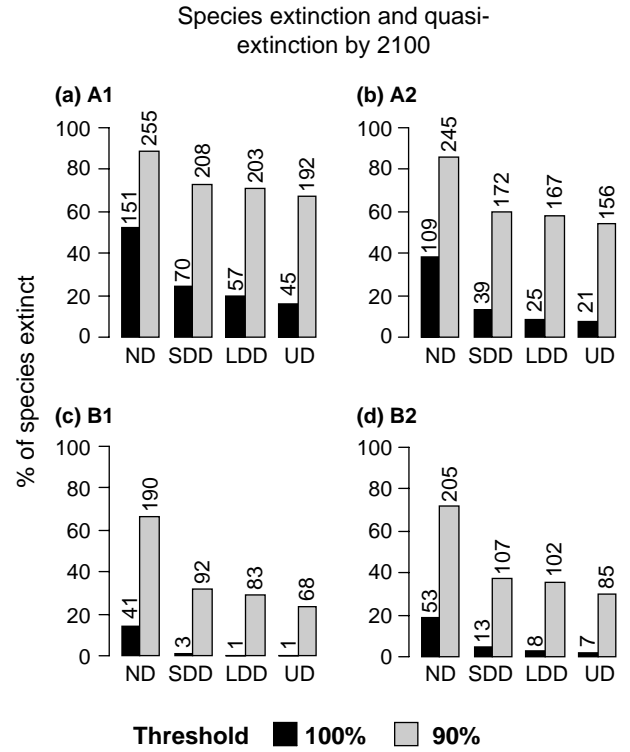


Figure 2. (a–d) Percentages and absolute numbers (above histogram bars) of species predicted to become extinct (100% threshold) or quasi-extinct (90% threshold) by 2100 under the four climate changes (A1, A2, B1, B2) and dispersal scenarios (ND, SDD, LDD, UD). ND = no dispersal, SDD = short distance dispersal, LDD = long-distance dispersal, UD = unlimited dispersal.

to their initial distribution (Fig. 3k, small arrow indicates the median value). Nevertheless, some species are predicted to significantly increase in spatial distribution (up to 500% of their initial area of occupancy). Comparison of the differences between ND, SDD, LDD, and UD simulations in terms of projected distribution surface for 2100 reveals that this difference is much larger for species with increases in potentially suitable habitat than those experiencing decreases (Fig. 3e–g, i–n; compare mean values for “L” and “G”). For instance, under the A1 climate change scenario, the mean difference in surface between ND and SDD projections is 7% for species with decreasing suitable habitat and 132% for species with increasing suitable habitat (Fig. 3e). Interestingly, the differences between ND and SDD/LDD are larger under milder climate change scenarios, while the differences between UD and SDD/LDD are larger under stronger climate change scenarios. Finally, similarly to extinction rates, the projections are generally closer to the UD than to the ND scenario, in terms of surface.

Projected species extinctions throughout the 21st century

The graphs of cumulative species extinctions during the 21st century (Fig. 4) show that extinctions are expected to start occurring from about 2040 onwards under the A1 climate change scenario, and from 2080 to 2090 under the A2, B1, and B2 scenarios (except for ND scenarios where

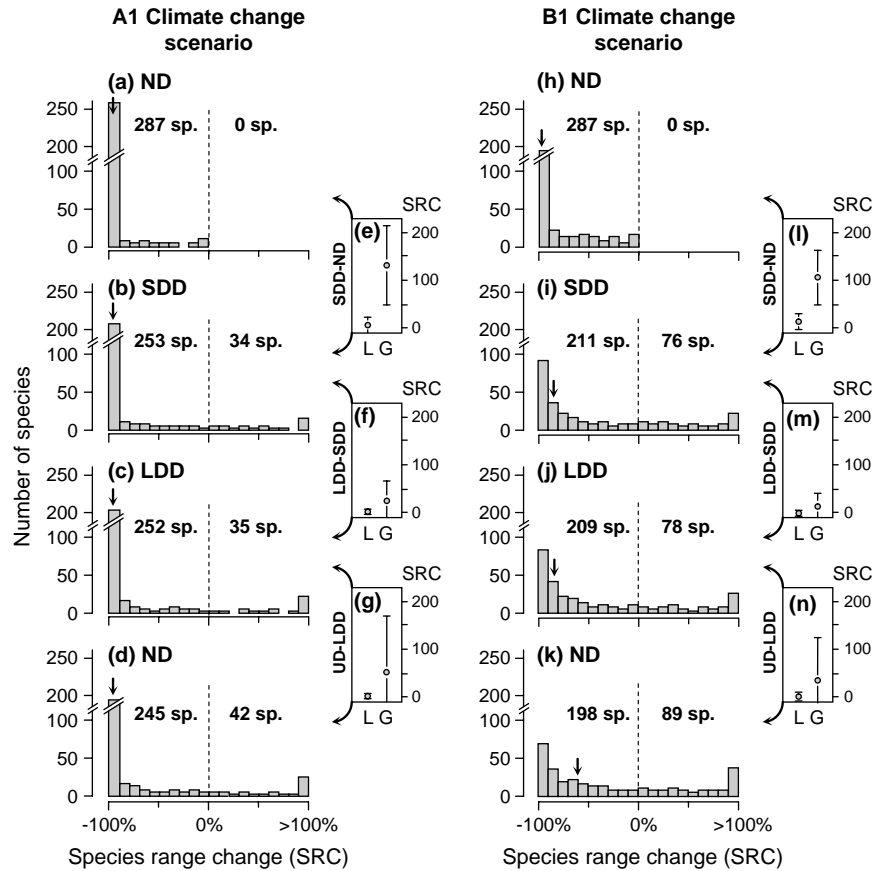


Figure 3. (a–d) and (h–k): frequency histograms of species range change (SRC) for 2100 under A1 (most extreme; left panels) and B1 (least extreme; right panels) climate change scenarios. SRC is the change in distribution surface expressed as a percentage of a species' initially occupied area. Negative values indicate species that are projected to decrease in potential distribution and positive values species projected to increase in potential distribution. For instance, a value of -50% means that the predicted distribution by 2100 has, in terms of surface, decreased of 50% as compared to the species' initial distribution. The numbers given in each graph indicate the number of species losing (SRC < 0; left number) or gaining (SRC > 0; right number) potential distribution. The small black arrow indicates the median value for all species. (e–g) and (l–n): Mean and standard deviation of the difference in SRC between ND and SDD (e, l), SDD and LDD (f, m), and LDD and UD (g, n) scenarios differentiated between potential species decreasing in distribution ("L" for "loss") and species increasing in distribution ("G" for "gain").

extinctions always start occurring already after 2040). In all scenarios, the large majority of extinctions are expected to occur between 2080 and 2100. The cumulative extinctions based on SDD and LDD simulations are always significantly lower than those obtained through the ND scenario (paired Wilcoxon signed-rank test, $p < 0.01$). Cumulative extinctions are also significantly different ($p < 0.05$) from each other under all climate change scenarios, except under B1 (the mildest), and are generally not significantly different from UD, except under A1 (the strongest).

Relationship between forecasted decrease in distribution and species traits

Significant negative relationships exist between the migration index and decrease in potential distribution (Fig. 5a–b and Supplementary material Appendix S6), indicating that species with higher dispersal capacity appear less affected by climate change. These relationships between migration index and decrease in potential distribution are strongest for LDD and SDD simulations, but an important disper-

sion of observations along the linear trend was observed under all scenarios (adjusted $R^2 = 0.14$ at the most; SDD B1 scenario).

Under all climate change and dispersal scenarios, a significant positive relationship exists between the elevation optimum index and decrease in projected spatial distribution (Supplementary material Appendix S6). This relationship is stronger (higher adjusted R^2) for SDD, LDD, and UD than for ND simulations. This trend also appears in the distribution of extinctions within different elevation optima (Fig. 6): a higher proportion of subalpine than montane, and alpine than subalpine, species are predicted to go extinct.

Discussion

In this study we projected the spatial distribution of 287 plants over the 21st century under four climate change scenarios in order to compare the results obtained from simulations with realistic dispersal limitations (SDD and LDD) to those assuming no or unlimited dispersal (ND and UD).

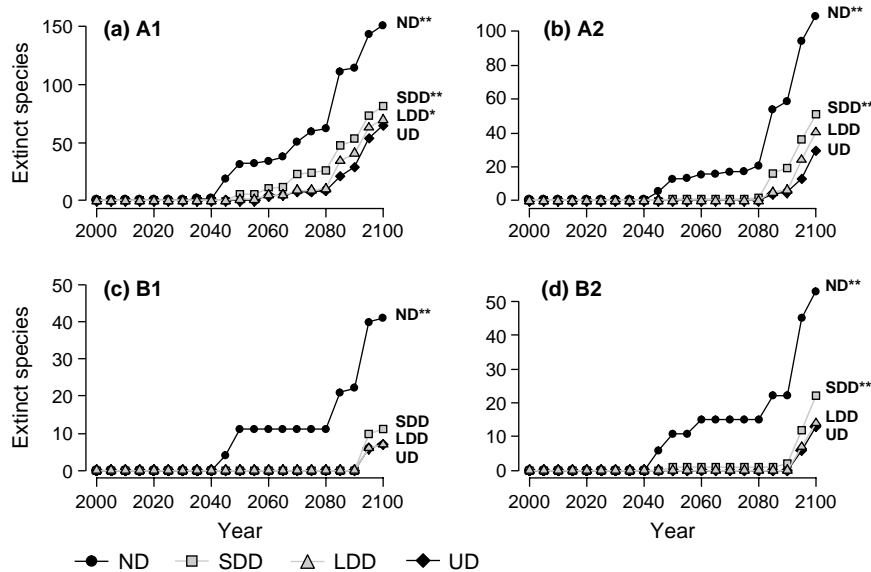


Figure 4. Cumulative number of species going extinct from 2000 to 2100 under the four climate change and four dispersal scenarios. ** = series is significantly different from the series immediately below with $p < 0.01$, * = series is significantly different from the series immediately below with $p < 0.05$. Abbreviations as in Fig. 2.

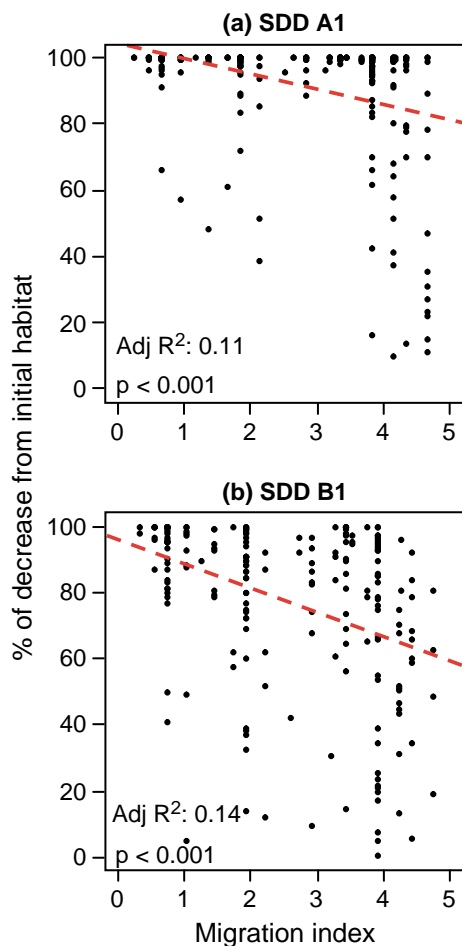


Figure 5. Relationship between migration rate index and decrease in projected distribution by 2100 shown for SDD simulations under A1 (a) and B1 (b) climate change scenarios. Explained variance (Adj. R^2) and significance of the regression slope (p-value) are given in each graph.

Are simulations accounting for dispersal limitations close to projections assuming no dispersal, unlimited dispersal, or neither?

Projections of SDD and LDD simulations were generally closer to UD than to ND, both in terms of species extinctions (Fig. 2) and surface of spatial distribution (Fig. 3). However, this does not necessarily indicate that UD is always a good approximation.

Considering the surface of future distribution, there is an important difference between those species for which suitable habitat is increasing as a result of climate change and those for which it is decreasing (Fig. 3e–g, i–n; compare mean values for “L” and “G”). For the latter category, UD simulations generally provide fairly good approximations, with an average difference between SDD or LDD and UD of $< 5\%$. But for species whose suitable habitat increases, neither UD nor ND provided good approximations on average.

In terms of species extinctions, the difference between SDD or LDD and UD simulations can also remain important. For example, the extinction rate predicted by SDD simulations is $\sim 24\%$ under the A1 climate change scenario, but this value is only $\sim 15\%$ with the UD scenario (Fig. 2a). However, under milder climate change scenario (B1, B2), the difference between SDD or LDD and UD is small and the UD simplification can thus provide a relatively safe estimation of species extinctions. These results indicate that previous assessments of species extinctions performed under similar conditions (i.e. mountain area, local or regional scale, and fine pixel size), but assuming unlimited dispersal (Guisan and Theurillat 2000, Dirnböck et al. 2003), may have provided fairly correct – although slightly too low – estimates. For future studies in mountain environments at local or regional scales, indications that the unlimited dispersal simplification provides good estimations of species extinctions under moderate climate change scenario could save considerable time (i.e. accounting for

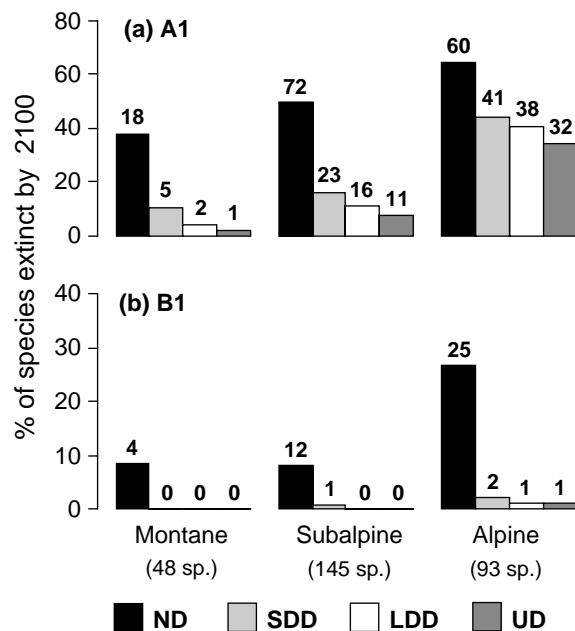


Figure 6. Percentage and absolute number (indicated above histogram bars) of species going extinct per altitudinal optimum for the A1 and B1 climate change scenarios. Abbreviations as in Fig. 2.

dispersal limitations involves a significant amount of additional work).

Our results demonstrating that simulations accounting for dispersal limitations are closer overall to the unlimited-dispersal than to the no-dispersal scenario are most likely strongly linked to the fact that our study area is mountainous: for instance, Midgley et al. (2006) found very different, almost opposite, results when modeling Proteaceae of the Cape Floristic Region. The explanation for such differing results lies in the generally steeper climatic gradients of mountain regions, like our study area. Steeper gradients reduce the shift in suitable habitat when projected under climate change, and thus decrease the migration distance required to track those shifts. For this reason, we expect differences between SDD or LDD and UD scenarios to be much larger in non-mountainous areas than in our results. Furthermore, species in mountain habitats are more likely to experience a decrease in potentially suitable habitat over time rather than a shift or increase. In such cases, limitations in dispersal capacity have less impact on the projections, since there are not many new pixels to potentially colonize in the given study area.

How much do long-distance dispersal (LDD) events affect projected distributions?

The importance of LDD in plant migration remains a debated topic (Pearson 2006). On the one hand, several studies have shown that LDD can be important for determining plant dispersal rates (Higgins et al. 2003, Pearson and Dawson 2005, Soons and Ozinga 2005), and particularly to explain previous fast plant migrations (Clark 1998, Nathan and Muller-Landau 2000, Higgins et al.

2003, Powell and Zimmermann 2004). On the other hand, late-glacial refugia and molecular data indicate that migration rates might not have been as high as initially thought (see Pearson 2006 for a review), at least not in the Alps where mountains may have prevented expansions (Taberlet et al. 1998).

In our study, addition of LDD events to our simulations resulted in species extinction rates to decrease almost to the level of UD simulations (Fig. 2, 4). While extinction rate differences between SDD and LDD simulations were sometimes significant, they were never very large. This can be explained by the study area configuration and the nature of the investigated species pool. First, the study area might be too small for LDD to have a high impact. Simulations made at a larger geographical scale are likely to exhibit greater differences between SDD and LDD scenarios. Second, most of our species undergo a decrease in potential spatial distribution. Thus, even if these species are given the possibility of longer dispersal distances, there is relatively modest suitable surface available. Note that for species that increase in distribution, including LDD can have a non-negligible impact. The mean increase in distribution surface due to LDD is between ~ 15 and $\sim 25\%$, depending on the climate change scenario (Fig. 3f, m).

What temporal patterns of extinctions are projected for the 21st century?

Projections of species distribution models are most often performed for environmental conditions of one or occasionally two future time periods, which are typically averages for several decades (Bakkenes et al. 2002, Dirnböck et al. 2003, Thomas et al. 2004, Thuiller et al. 2005). By projecting species extinctions for every five year period (Fig. 4) we are able to identify critical periods of expected extinctions within our study area over the 21st century. In our projections, species losses occur from 2050 onwards for the most pessimistic scenario (A1), and after 2080 for the three other climatic scenarios, except for ND simulations where species extinctions start at ~ 2040 . This inertia in species extinctions has two explanations: either a species has the possibility to move upwards to higher elevation, thereby postponing extinction, or its initial distribution covers a wide altitudinal range, making it adapted to a broader range of environmental conditions, and therefore, more resilient to changes in these conditions. Clearly, the dates of 2040–2050 and 2080 can only be considered valid for our study area and species pool, and should not be extrapolated to other areas, although some inertia in species extinction is very likely to occur for other mountain areas too.

Temporally explicit projections, such as in this study, are important for conservation planning. For instance, the identification of areas where extinction is predicted to occur by 2040 and 2080 may be preserved from direct land use impacts in order to reduce future threats. It also highlights the fact that an absence of observed extinctions during the next 40–80 yr should not be interpreted as an absence of the threat to species extinction in the longer term.

Does extinction risk and reduction in potential spatial distribution relate to species migration capacity and elevation optima?

We found significant relationships between the decrease in predicted distribution by 2100 and the species' migration capacity and altitudinal optimum (Fig. 5, 6, Supplementary material Appendix S6). Overall, alpine plants and species with dispersal distances <20 m appear to be particularly vulnerable to complete extinction by the end of the 21st century. This corroborates results from previous modeling studies (Guisan and Theurillat 2000, Dirnböck et al. 2003), and also from field-observations. For instance, Klanderud and Birks (2003) compared species compositions on Norwegian summits between 1930 and 1998, and reported that high elevation species had disappeared from lower elevation sites, with climate change as the most plausible explanation. In another study in the Italian Central Alps, Parolo and Rossi (2008) found that alpine species with larger seed weight and morphology less favorable for dispersal, migrated more slowly than other species over a 50 yr period, suggesting that such species might be at greater risk under rapid climate change. Finally, Vittoz et al. (in press) also identified that there were more species with efficient dispersal modes among good colonizers of several alpine summits than among weak colonizers.

Projection limitations and other sources of uncertainty

Since our habitat suitability projections were generated using GLMs, all limitations that are inherent to these models when used for climate change impact projections (e.g. truncated response curves, non-equilibrium of species with environment, see Guisan and Zimmermann 2000, Guisan and Thuiller 2005 for more details) also apply to our results. For instance, we need to be aware that our projections of extinction rates include some uncertainty, since the realized, and not the fundamental niche, of a given species was calibrated. Thus, if the realized and the fundamental niche of a target species differ clearly regarding the relevant changing climate factors, then our target species might actually be more tolerant than expected to predicted climate change over the shorter term. Over the longer term, we would – however – expect that this species is slowly out-competed by stronger competitors if the climate changes to low suitability of the realized niche. Future changes in land use (Vittoz et al. 2009) are a further source of uncertainty.

Furthermore, one should also keep in mind that the MigClim model and the data used herein for calibration remain a simplification compared to models that include more complex population dynamics and seed dispersal kernels (Dullinger et al. 2004, Powell and Zimmermann 2004, Pearson and Dawson 2005) or physiological response curves (Humphries et al. 1996). However, given that calibrating such complex models for hundreds of species is nearly impossible simply because accurate data on population dynamics and seed probability distribution functions are not easily available for the large majority of

species, our approach seems to represent a good balance between accuracy and use of available data.

Another point worth mentioning is that, although accounting for dispersal limitations potentially reduces uncertainty in projections (i.e. as compared to the unlimited dispersal – no dispersal simplifications), the part of uncertainty related to the magnitude of climate change or the criteria chosen to declare a species threatened (e.g. 90 or 100% thresholds of surface loss) remains very significant (e.g. Fig. 2).

Finally, because dynamic simulations accounting for dispersal limitations depend on a large number of local parameters (e.g. habitat fragmentation, species migration rates) the results provided by such models are necessarily site-specific, making their extrapolation to other study areas difficult.

Conclusion

In our study, simulations accounting for realistic dispersal limitations yielded extinction rates between ~1% (B1) and 25% (A1), and decreases in distribution for ~70% (B1) to 90% (A1) of the 287 species by the year 2100. Furthermore, we identified the following trends in our results: 1) restricting projections of future plant distribution through realistic dispersal limitations produced results that were generally closer to unlimited dispersal than to no dispersal. 2) In terms of species extinctions, using the unlimited dispersal simplification provided a good approximation of the results obtained while accounting for dispersal limitations. This is especially true under less extreme climate change scenarios (B1, B2). 3) In terms of projected distribution surface, the unlimited dispersal simplification provided fair approximations for species with decreasing distributions, but not for those whose distribution is increasing. 4) Including long-distance dispersal (LDD) events into the simulations generally produced extinction rates that were very close to those of the unlimited dispersal scenario. 5) The pattern of cumulative species extinction over time did not exhibit a linear increase. In simulations accounting for dispersal limitations, important numbers of extinctions are expected to start occurring for our study area during the 2080–2100 period. 6) High elevation and/or slow dispersing species are the most at risk in the face of climate change.

Although our results are based on a fairly large number of species, they nevertheless remain very dependent on the species considered and on the study area. Therefore, generalizing our results to other areas should be done cautiously. While these results can probably be generalized to other mountainous study areas of similar size and shape, they cannot be extrapolated as such to larger and flatter landscapes. In fact, running such simulations at a continental scale or in larger and flatter study areas is likely to produce very different results. The influence of introducing migration limitations into the projections of species distribution under climate change in such environments remains to be tested.

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