

MIGCLIM: Predicting plant distribution and dispersal in a changing climate

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ABSTRACT

Aim Many studies have forecasted the possible impact of climate change on plant distributions using models based on ecological niche theory, but most of them have ignored dispersal-limitations, assuming dispersal to be either unlimited or null. Depending on the rate of climatic change, the landscape fragmentation and the dispersal capabilities of individual species, these assumptions are likely to prove inaccurate, leading to under- or overestimation of future species distributions and yielding large uncertainty between these two extremes. As a result, the concepts of ‘potentially suitable’ and ‘potentially colonizable’ habitat are expected to differ significantly. To quantify to what extent these two concepts can differ, we developed MIGCLIM, a model simulating plant dispersal under climate change and landscape fragmentation scenarios. MIGCLIM implements various parameters, such as dispersal distance, increase in reproductive potential over time, landscape fragmentation or long-distance dispersal.

Location Western Swiss Alps.

Methods Using our MIGCLIM model, several simulations were run for two virtual species by varying dispersal distance and other parameters. Each simulation covered the 100-year period 2001–2100 and three different IPCC-based temperature warming scenarios were considered. Results of dispersal-limited projections were compared with unlimited and no-dispersal projections.

Results Our simulations indicate that: (1) using realistic parameter values, the future potential distributions generated using MIGCLIM can differ significantly (up to more than 95% difference in colonized surface) from those that ignore dispersal; (2) this divergence increases under more extreme climate warming scenarios and over longer time periods; and (3) the uncertainty associated with the warming scenario can be as large as the one related to dispersal parameters.

Main conclusions Accounting for dispersal, even roughly, can importantly reduce uncertainty in projections of species distribution under climate change scenarios.

Keywords

Cellular automaton, climate change, dispersal modelling, dynamic niche-based models, GLM, plant species distribution.

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INTRODUCTION

Assessing the potential impact of predicted global climate change (+1.8 to +4 K by 2100; IPCC, 2007) on vegetation is a pressing matter. A broad range of projections of future plant species distributions have already been made using niche-based species distribution models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) at large scales (e.g. Bakkenes *et al.*,

2002; Thuiller *et al.*, 2005) and at more local scales (e.g. in alpine landscapes; Gottfried *et al.*, 1999; Dirnbock *et al.*, 2003). Yet, most of these studies have assumed that dispersal is unlimited (or ‘universal’), where a species is allowed to disperse freely with its future distribution becoming the entire area projected as suitable by the model (Thomas *et al.*, 2004). As ‘unlimited dispersal’ represents an unrealistic best case scenario, some authors (e.g. Thomas *et al.*, 2004; Thuiller

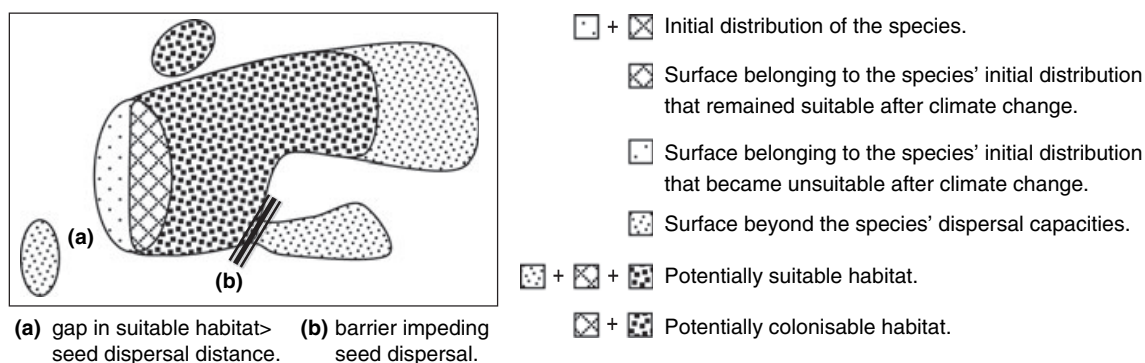


Figure 1 Schematic representation of a species distribution under climate change to explain the concepts of potentially *suitable* and potentially *colonizable* habitat.

et al., 2005) have also provided a worst case 'no-dispersal' scenario to give a lower bound to their projections. However, the difference between these extreme projections can yield large uncertainties (e.g. Thuiller, 2004).

While the unlimited dispersal assumption might provide good approximations for plants that are human-dispersed or have high dispersal ability, it probably overestimates the future distribution of many other species because: (1) human-driven habitat fragmentation makes it increasingly difficult for many species to migrate (Pitelka *et al.*, 1997); and (2) the speed of the expected global warming is predicted to be rapid – one or more orders of magnitude faster than past climate change events (Etterson & Shaw, 2001). Certain species may thus require migration rates much faster than those observed during post-glacial times (Malcolm *et al.*, 2002) and could fail to keep pace with rapid climate change. Compounded with this is the possibility that rapid climate change may not allow many species to evolve the necessary adaptations (Davis & Shaw, 2001; Etterson & Shaw, 2001).

Even though the need for including dispersal limitations into models has been raised repeatedly (Pitelka *et al.*, 1997; Woodward & Beerling, 1997; Cain *et al.*, 1998; Davis *et al.*, 1998; Nathan & Muller-Landau, 2000; Ronce, 2001; Araujo & Guisan, 2006; Midgley *et al.*, 2007; Thuiller *et al.*, 2008), so far relatively few niche-based climate change modelling studies have considered it (e.g. Carey, 1996; Ostendorf *et al.*, 2001; Dullinger *et al.*, 2004; Iverson *et al.*, 2004). Accounting or not for dispersal is equivalent to making a distinction between 'potentially *suitable* habitat' and 'potentially *colonizable* habitat'. Potentially suitable habitat is the area a species could occupy given unlimited dispersal ability, whereas potentially colonizable habitat accounts for dispersal constraints such as limited seed dispersal distance, time to reach reproductive maturity, gaps in suitable habitat or barriers to dispersal, e.g. rivers, mountain ranges or dense urban areas (Fig. 1).

Refining the projections from potentially *suitable* to potentially *colonizable* habitat requires transition from a static to a more dynamic approach of modelling species distributions. One way to achieve this is to use a cellular automaton, which can be briefly described as a grid of cells with values that evolve

over time according to rules that are affected by neighbouring cells (Sarkar, 2000). Cellular automata have already been widely used in ecology, for instance, to simulate vegetation succession (Yemshanov & Perera, 2002; Scheller *et al.*, 2007), competition between plants (Silvertown *et al.*, 1992), spread of invasive species (Higgins *et al.*, 2000) or plant migration (Collingham *et al.*, 1996; Pearson & Dawson, 2005). Yet, only a few studies have employed them to simulate species migrations when predicting future distributions under climate change (e.g. Carey, 1996; Ostendorf *et al.*, 2001; Dullinger *et al.*, 2004) and even fewer have derived projections for many species (e.g. Iverson *et al.*, 2004).

To investigate how dispersal limitations can modify projections of future plant distributions, we developed a model – MIGCLIM – capable of simulating plant migration under climate change and landscape fragmentation scenarios. Our MIGCLIM model couples predictive distribution maps, representing a species' habitat suitability as a function of evolving climate, with a cellular automaton that simulates dispersal, colonization, growth and extinction of the species in the landscape. A number of specific parameters can be defined, such as dispersal distance, barriers to dispersal, landscape fragmentation, stochastic long-distance dispersal (LDD) or increase in reproductive potential over time. Our objective when developing MIGCLIM was to provide a flexible tool that could be used to obtain refined projections of climate change impact for numerous plant species at various spatial scales. Although dispersal models exist based on more advanced population dynamics (e.g. Lischke *et al.*, 2006), they are usually restricted to trees and require advanced knowledge of a species' population dynamics, which is not available for most species. Hence, from the perspective of niche-based species distribution models, MIGCLIM represents an important step forward, because it allows more realistic projections of future distributions to be made for many species in a relatively simple way.

Using MIGCLIM, we illustrate how dispersal limitations can affect projections of future plant distributions under climate change compared to unlimited and no-dispersal scenarios. We do this by running different simulations for two virtual species under three temperature warming scenarios for the period

2005–2100 in a study area of the western Swiss Alps. Our study assesses: (1) the possible discrepancies between ‘potentially suitable’ versus ‘potentially colonizable’ habitats; and (2) the factors that may be responsible for these differences.

METHODS

The MigCLIM model

MigCLIM is a cellular automaton implemented within the ArcGIS® software (ESRI Inc., Redlands, CA, USA). The cells (hereafter pixels) are square and record various values such as pixel occupancy status, habitat suitability, reproductive potential or when it was last colonized. To simulate dispersal under climate change, MigCLIM requires the following inputs: a map defining the species’ initial distribution, maps picturing landscape fragmentation (i.e. barriers to dispersal and permanent unfavourable locations), the species’ dispersal parameters and a series of maps indicating how the distribution of potentially suitable habitats evolves as climate changes. Dispersal is simulated through a number of decisions that are taken, for each pixel, during each dispersal event (see also flowchart of Appendix S1 in Supporting Information).

1. Does the target pixel represent a suitable habitat? Is it unoccupied?
2. If point 1 is answered positively, the number n of source pixels within the specified dispersal distance is computed. Source pixels are already occupied pixels that can act as seed sources to colonize a target pixel. Optionally, a barrier layer can be given to prevent dispersal through those pixels being part of the barrier. If a barrier pixel is found between the target and a source pixel, the source pixel is ignored. Barriers can be used, e.g. to prevent a strictly grassland species to disperse through forests.
3. If $n > 0$, the target pixel becomes colonized with the combined probability P_{Col} (equation 1):

$$P_{\text{Col}} = 1 - \prod_{i=1}^n (1 - P_{\text{Disp}_i} \times P_{\text{Mat}_i}), \quad (1)$$

where P_{Disp_i} is a probability function of the distance between the target pixel and source pixel i and reflects the fact that colonization probability decreases over distance. P_{Mat_i} is a probability that is function of the time as the source pixel i became occupied and represents the increase in reproductive potential of source pixel i over time. P_{Mat} can be used to represent time for individuals to reach reproductive maturity and, more globally, the increase of a population’s reproductive potential due to an increase in the number of individual plants within a pixel over time. P_{Disp} and P_{Mat} are implemented as discrete functions and can easily be modified to fit any shape of seed dispersal curve and increase of reproductive potential over time.

4. Optionally, LDD and stochastic extinction events can be added to the simulation. LDD events are generated from source pixels with a probability $P_{\text{LDD}} \times P_{\text{Mat}}$ in a random direction and at a random distance within a user-defined range. If the pixel reached by the long dispersing seed is

potentially suitable (satisfying point 1), it becomes colonized. LDD events are not affected by barriers. Stochastic extinctions with probability P_{Ext} can also be defined to simulate random extinction of colonized pixels.

5. Steps 1–4 are repeated a number of times (n_{Disp}), typically set so that each repetition corresponds to 1 year.

6. Pixels that are no longer suitable due to changes in environmental conditions have their values reset to zero. Pixels that become unsuitable are reset only after the dispersion stage occurred (steps 1–5), because it is assumed that the change of a habitat from suitable to unsuitable is not a discrete but a continuous process. Thus, organisms inhabiting a pixel still have the potential to disperse during the step when the pixel turns unsuitable.

7. Steps 1–6 are repeated n_{HSmep} times. In each repetition, the habitat suitability is updated to reflect environmental change (e.g. climate change). Simulations without environmental change can be performed by setting $n_{\text{HSmep}} = 1$.

Additional parameters available in MigCLIM include vegetative and seed bank resilience time, post-dispersal survival and/or habitat invasibility, anisotropic dispersal to simulate dominant winds or slope, as well as specific dispersal along certain features, such as roads and rivers. These options were not used in the present study.

As the smallest modelling unit in the model is a population in a pixel, parameter values must represent values for a whole population, not for a single individual (see also Discussion for more details on model parameterization). All parameters can be modified to fit best the known dispersal characteristics of the modelled species.

Simulations using MigCLIM

Sensitivity analyses were run for two virtual species in a real landscape (the western Swiss Alps). To mirror ecological reality, the potential distributions under current and future climate conditions of the two virtual species were derived from those of two real species – *Arrhenatherum elatius* L. and *Lolium perenne* L. Therefore, we refer to our virtual species hereafter as ARELA and LOPER. For each species, several simulations were run by varying the dispersal parameters within a range of realistic values (Table 1). These were chosen to represent various plant functional types and are based on a thorough review of literature (Vittoz & Engler, 2007). As no accurate data could be found for LDD, these were set to 20 times the regular dispersal distance for 5–500 m simulations and to 10 times the regular dispersal distance for 1000 m simulations. This resulted in LDD distances ranging from 100 m to 10 km (Table 1), which corresponds to values commonly found in the literature (Nathan, 2005 and references therein). Two different rates of increase in pixel reproductive potential (P_{Mat}) were also tested; these resembled rates for herbs and trees respectively. In ‘Herb-type’ simulations, the reproductive potential of a pixel followed a sigmoid increase from 1 to 5 years, whereas in ‘Tree-type’, it started at 10 years and reached its maximum at 40 years. Some Tree-type simulations were not run for low dispersal distances because these were

Table 1 Dispersal parameters of the different ARELA and LOPER simulations. 'H' and 'T' in the simulation name stand for 'Herb-type' and 'Tree-type' and refer to the increase in pixel reproductive potential over time that reflects either a herb-like or tree-like life cycle.

Simulation name	5 m H	25 m H	100 m H	500 m H	1000 m H	100 m T	500 m T	1000 m T
Pixel size (m)	5	5	12.5	25	25	12.5	25	25
Disp. event freq. (years)*	5	1	1	1	1	1	1	1
Dispersal distance (DispDist) (m)	5	25	100	500	1000	100	500	1000
Max LDD distance (m)	100	500	2000	10,000	10,000	2000	10,000	10,000
LDD freq.†	0.002	0.0004	0.0025	0.01	0.01	0.0025	0.01	0.01
Pix. reprod. pot.‡	Sigmoid increase from 1 to 5 years					Sigmoid increase from 11 to 40 years		
Barriers	Yes (forests)					No		
Filter	Urban areas and lakes					No		
No. pixels	30,000,000		4,800,000		1,200,000		4,800,000	

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

†Variations in long-distance dispersal (LDD) event frequencies between simulations reflect the corrections applied for cell size and dispersal event frequency to maintain the 0.01 frequency assigned to 25-m pixels constant over all categories.

‡Pixel reproductive potential indicates how the probability of a colonized pixel to be a source pixel increases over time.

not considered realistic for trees. The spatial resolution (i.e. pixel size) at which the simulations were run was of either 25, 12.5 or 5 m, depending upon the maximum dispersal distance of the simulation (see Table 1).

The decrease in colonization probability with increasing distance from a source cell (P_{Disp}) was based on a negative exponential seed dispersal probability distribution function (equation 2; Ward *et al.*, 2004; Scheller *et al.*, 2007):

$$P_{\text{seed}}(x) = e^{(x - \text{pixelsize}) \cdot \left(\frac{\ln(1-k)}{\text{DispDist}}\right)} - e^{x \cdot \left(\frac{\ln(1-k)}{\text{DispDist}}\right)} \quad (2)$$

which can be simplified into the more conventional simple negative exponential form (equation 3):

$$P_{\text{seed}}(x) = \left(1 - k\right)^{\frac{\text{pixelsize}}{\text{DispDist}} - 1} \cdot e^{x \cdot \left(\frac{\ln(1-k)}{\text{DispDist}}\right)}, \quad (3)$$

where P_{seed} is the probability of a seed reaching distance $x \geq \text{pixelsize}$, pixelsize is the one-dimensional size of a pixel and DispDist is the dispersal distance reached by the proportion k of the seeds. Here we set $k = 0.99$, DispDist thus represents the regular dispersal distance for seeds, i.e. LDD events excluded (these were here modelled as a separate process). As the surface composed of pixels located at distance j from a source cell increases with distance from that source cell, the probability of a pixel to receive a seed is computed as (equation 4):

$$P_{\text{seed}}(\text{pixel}_j) = \frac{P_{\text{seed}}(x)}{\text{Surface}_j}, \quad (4)$$

where Surface_j is the surface covered by all pixels belonging to a same distance class. Assuming that the distribution of successful seeds (i.e. seeds leading a pixel to become colonized) is proportional to the overall distribution of seeds (P_{seed}), P_{Disp} is computed as (equation 5):

$$P_{\text{Disp}}(\text{pixel}_j) = 1 - (1 - P_{\text{seed}}(\text{pixel}_j))^{\text{Successful Seeds}}, \quad (5)$$

where P_{Disp} is the probability of colonization for a target pixel with distance j from a source pixel and *Successful Seeds* the number of successful seeds produced by a fully mature source

pixel. As the value of *Successful Seeds* was unknown for our virtual species (as is the case for most species), it was set so that $P_{\text{Disp}} = 0.99$ for a pixel immediately adjacent to a source pixel at 25-m resolution. Using this conservative (i.e. optimistic) calibration method led to average spread rates, for fully mature pixels, between 45 and 85% of DispDist , depending on the number of source pixels in the neighbourhood (tests run on homogenous landscapes). When running simulations at smaller pixels sizes (i.e. 12.5 and 5 m), the values of P_{Disp} were recomputed to ensure that the production of *Successful Seeds* per surface unit remained constant. In other words, the number of *Successful Seeds* was always proportional to pixel size, 5- and 12.5-m pixel producing respectively 25 and 4 times less successful seeds than 25-m pixels. This ensured that the species had always the same seed production per surface unit and thus that their spread rate was independent of the cell size at which simulations were run. Details of all dispersal kernels used in the different simulations are given in Appendix S2.

A negative exponential kernel shape as used here for P_{Seed} (equation 3) is common for seed dispersal (Willson, 1993), but many alternatives exist (e.g. Clark *et al.*, 1999; Nathan & Muller-Landau, 2000; Greene *et al.*, 2004) that could be used in MIGCLIM. While negative exponential kernels were found to approximate reasonably different seed dispersal types in previous studies (Bleher *et al.*, 2002; Bischoff, 2005; Clark *et al.*, 2005), one shortcoming is their underestimation of LDD events (Bullock & Clarke, 2000; Nathan *et al.*, 2008). In our simulations, however, LDD events were modelled as an additional, separate, process (this is an option in MIGCLIM). Hence, the negative exponential curve remains a reasonable approximation for regular dispersal (i.e. LDD excluded). Furthermore, while MIGCLIM can accommodate any shape of dispersal kernel, it can only be as refined as the pixel resolution allows. For instance, at a 5-m pixel resolution, a dispersal distance of 20 m can only be approximated by a dispersal kernel with four knots. Increasing pixel resolution, as done here for simulation with shorter dispersal distances (Table 1),

would theoretically allow infinite refinement of the dispersal kernel. In practice, however, computing power limits the minimal pixel size that can be used for a given study area. In our case, 5-m resolution was the smallest we could use, resulting in more than 30 million pixels for our study area.

For each species, all simulations listed in Table 1 were run for three temperature warming scenarios (three levels; Appendix S3) and both with and without LDD events (two levels). Each of these runs was replicated 30 times. The temperature increase scenarios represent the maximum ('max', +5.8 K), intermediate ('med', +3.6 K) and minimum ('min', +1.4 K) warming scenarios for 2100 of the intergovernmental panel on climate change third assessment report (Houghton *et al.*, 2001). The change in habitat suitability was modelled every fifth year from 2005 to 2100. The initial distribution of the species was set to their potentially suitable habitat under current climate conditions. Dispersal was simulated on a yearly basis, except for the 5 m Herb-type simulations where dispersal was simulated every fifth year and the dispersal distance multiplied by five (this assumes a conservative 'best case' approximation where spread rate = generation time \times dispersal distance). This was done because current computing power did not allow for a finer grid size than 5 m for our entire study area. No- and unlimited-dispersal simulations were also carried out for each climate change scenario to provide lower and upper bounds to the projections.

Study area and virtual species

The study area is a 700-km² subset of the western Swiss Alps (Fig. 2), with altitudes ranging from 400 to 3200 m a.s.l. *Arrhenatherum elatius* and *Lolium perenne*, the two grass

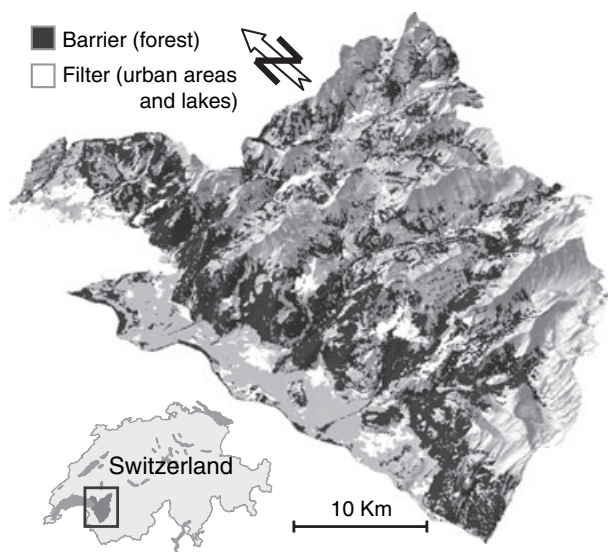


Figure 2 View of the Swiss western Alps study area showing forests (used as a 'barrier' feature in 'Herb-type' simulations) as well as urban areas and lakes (used as 'filter' features in all simulations).

species from which we derived the virtual species' distributions, are dominant in the study area and therefore are good indicators of possible change in the vegetation. ARELA illustrates the case of a species whose potentially suitable habitats are purely expanding (i.e. no habitat becomes unsuitable as climate changes), while LOPER illustrates the case where suitable habitat is shifted upwards in elevation.

Habitat suitability modelling

Generalized linear models (GLM; McCullagh & Nelder, 1989) were used to relate statistically presence-absence data to a set of topo-climatic environmental variables. The species distribution data originated from a dataset of 550 vegetation plots, sampled in a random-stratified way (Randin *et al.*, 2006). The set of initial environmental variables is given in Appendix S4. After backward stepwise selection, the final variables retained in the models were: mean annual temperature, mean annual daily solar radiation (this accounts for topographical overshadowing, slope and aspect values) and slope. The calibrated GLMs were then projected for current climatic conditions (1961–90 averages) and for every 5-year period from 2005 to 2100 to produce probabilistic habitat suitability predictions, which were reclassified into binary presence/absence maps (1 or 0) using an optimized-Kappa threshold (Engler *et al.*, 2004).

Environmental variables were available at a spatial resolution of 25 m, therefore also defining the resolution of the habitat suitability maps. To enable finer dispersal kernel modelling for the simulations with shorter dispersal distances, the resolution of habitat suitability maps was increased (when needed; see Table 1) to 12.5 or 5 m by dividing the original 25-m pixels into 4 or 25 smaller pixels.

RESULTS

All values presented are means of 30 repetitions. Standard deviations are not shown as they never exceeded 0.5 and 1.6% of the mean values obtained for the simulations with and without LDD. The initial distribution and an example of future distribution by 2100 of ARELA and LOPER are given in Appendix S5.

Comparing the projected distributions for 2100 of ARELA and LOPER to their initial distribution reveals that ARELA always increases its distribution as a result of climate change (Fig. 3a, all values $\geq 100\%$), whereas LOPER either loses or gains distribution surface, depending on the scenarios' dispersal distance (Fig. 3a: simulations with short dispersal distances have values $< 100\%$, those with longer dispersal distances values $> 100\%$). Comparing dispersal-limited to unlimited dispersal projections (Fig. 3b) by 2100 allows assessing the over-estimation made when using the unlimited dispersal modelling approach. This over-estimation varies from $< 20\%$ when using dispersal distances of 500 m or more, up to about 75% (ARELA) or 95% (LOPER) for 5 m Herb-type

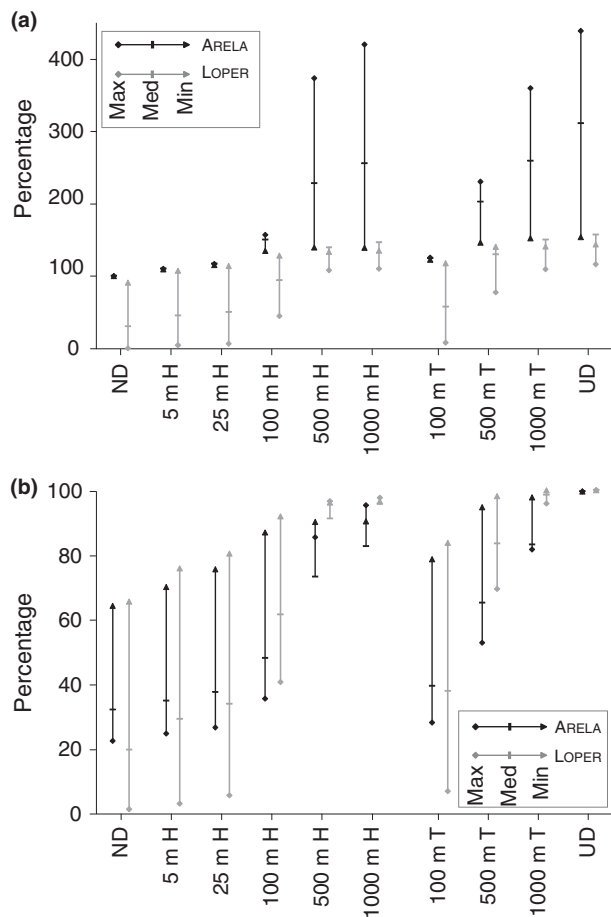


Figure 3 Potentially colonizable habitat (PCH) by 2100 for ARELA and LOPER simulations without long-distance dispersal (LDD) events for the three temperature warming scenarios (max, med, min). (a) PCH expressed as a percentage of the area initially occupied by a species. (b) PCH as a percentage of the unlimited dispersal scenario, which equals the total potentially suitable habitat. ND, no-dispersal; UD, unlimited dispersal; simulation names refer to those given in Table 1.

25 m Herb-type and 100 m Tree-type simulations under maximum climate change.

The impact of dispersal constraints and warming scenarios on distribution projections is modulated by the interaction between change in habitat suitability and landscape configuration. As a result, the importance of the impact of a given climate change scenario is not always the same for each dispersal distance scenario. For instance, the difference in surface between dispersal-limited and unlimited dispersal projections is usually more important under the maximum than under the medium climate change scenario, but exceptions exist (e.g. 500 m Herb-type simulations, Fig. 3b).

Comparing each simulation with LDD to its counterpart without LDD shows that the increase in projected distribution due to LDD remains on average below 50% (i.e. values smaller than 150% in Fig. 4), but can occasionally reach values far > 100% (e.g. 360% for LOPER 100 m Tree-type simulation; Fig. 4).

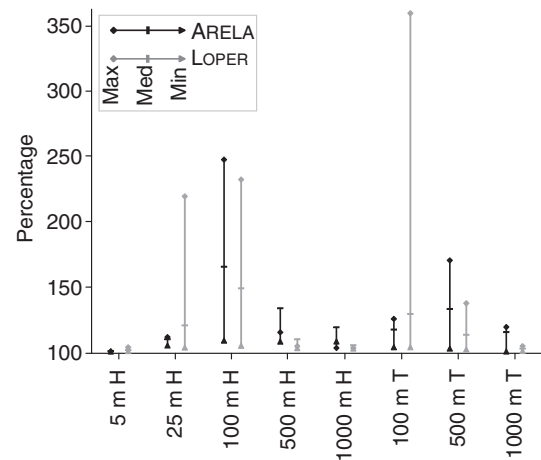


Figure 4 Relative increase in potentially colonizable habitat (PCH) by 2100 for ARELA and LOPER simulations when introducing long-distance dispersal (LDD) events into the simulations for the three temperature warming scenarios (max, med, min). Names of simulations refer to those given in Table 1.

The difference between projections obtained using the different dispersal scenarios is not constant and can increase considerably over time. This is illustrated for LOPER under maximum warming scenario (Fig. 5): while the difference in distribution between the different dispersal scenarios does not exceed 20% of the species' initial distribution in 2020, it becomes larger than 100% by 2100. The abrupt change in projected distributions around 2040 results from the geographical configuration of the study area, with the large flat area of the Rhone valley (western part of the study area, Fig. 2) becoming unsuitable for LOPER around 2040.

DISCUSSION

Impact of dispersal limitations on future distribution projections

Results of our simulations illustrate that depending on the warming scenario and the dispersal parameter values, taking dispersal into account can lead to strikingly different predictions from those obtained when dispersal is assumed to be either unlimited or null. For instance, in 5 m Herb-type and 100 m Tree-type simulations under maximum warming scenario (+5.8 K by 2100), the potentially colonizable habitat predicted for 2100 is about four times smaller than the potentially suitable habitat for ARELA and more than 15 times smaller for LOPER. In other words, predictions made by considering dispersal as unlimited would result in a 4-fold or more than 15-fold over-estimation of the species' future distribution. For the unlimited dispersal scenario to be a good approximation (< 5% difference between potentially *suitable* and potentially *colonizable* habitat), both species would need to have a regular seed dispersal distance (i.e. LDD excluded) reaching at least 1000 m or sometimes 500 m, if implementing LDD. Most species in our study area likely have regular

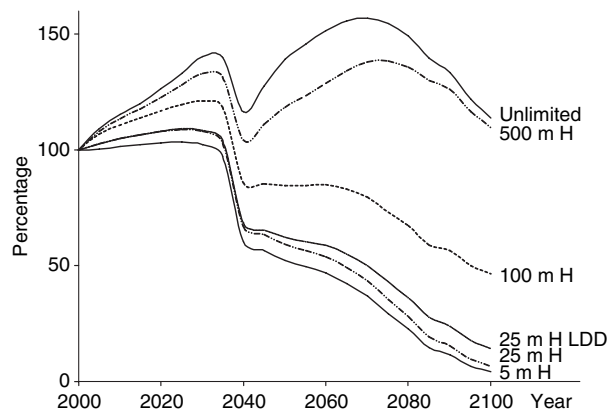


Figure 5 Evolution of the potentially colonizable habitat (PCH) over time for LOPER Herb-type simulations under maximum temperature warming scenario. PCH surface is given as a percentage of the species' initial distribution. Names of simulations refer to those given in Table 1.

dispersal distances much smaller than 1000 m (Vittoz & Engler, 2007) and are therefore likely to have future distributions significantly smaller than predicted by unlimited dispersal scenarios.

Not surprisingly, results obtained under the maximum warming scenario lead to the highest discrepancy between dispersal-restricted and unlimited dispersal projections, with surface differences up to about 75% for ARELA and 95% for LOPER. Yet, even under the medium (+3.6 K) or minimum (+1.4 K) warming scenarios, this discrepancy still reached about 60–70% (medium scenario) and 20–30% (minimum scenario) for both ARELA and LOPER (5 m Herb-type or 100 m Tree-type simulations, Fig. 3b).

For most species, as no accurate data are available on dispersal distances, only rough estimates can be obtained or derived from the literature, by considering species dispersal characteristics (dispersal vector, seed weight, etc.; Vittoz & Engler, 2007). *Arrhenatherum elatius* and *Lolium perenne*, the two species used to derive the virtual species (ARELA and LOPER), are mainly anemochorous (Müller-Schneider, 1986), suggesting a seed dispersal distance (LDD excluded) of about 20 m (Vittoz & Engler, 2007). This estimate is consistent with dispersal distances measured for other grass species (e.g. 20 m for *Bromus sterilis*; Howard *et al.*, 1991) and is also within the range of distances generally found for non-tree species (10–80 m; Bullock & Clarke, 2000, and references therein). Hence, the 25 m and 100 m Herb-type simulations are likely to cover a realistic range of dispersal distances for these species and provide a reasonable estimate of discrepancies between projections accounting for dispersal restrictions and those considering dispersal as unlimited or null.

Our results also illustrate how using rough estimates (e.g. dispersal distance between 20 and 100 m, as discussed above) rather than the no-dispersal and unlimited dispersal bounds can strongly reduce uncertainty in projections, even when the exact dispersal distance of the species remains unknown. When

considering the maximum warming scenario for ARELA, the ratio in projected distribution surface between unlimited dispersal and no-dispersal is 4.4 (meaning that the surface predicted by unlimited dispersal is 4.4 times larger than that of no-dispersal), but is reduced to 1.3 between 25 m and 100 m simulations. For LOPER, this ratio is reduced from 71.2 to 7.5. Comparable changes, although of a smaller magnitude, are observed for the medium (3.1–1.3 for ARELA and 5.1–1.8 for LOPER) and minimum (1.5–1.1 for both ARELA and LOPER) warming scenarios.

Effect of long-distance dispersal

Introducing LDD events in our simulations led to various relative rates of increase in projected distributions (Fig. 4) ranging from no or very little increase (e.g. 5 m and 1000 m simulations) up to 360% (LOPER 100 m Tree-type simulations under maximum warming). While the maximum LDD distance is obviously an important factor determining whether including LDD will have a large effect on projections (e.g. 5 m simulations show little increase in potentially colonizable habitat because LDD distance is too short), another aspect is the availability of suitable but unoccupied pixels in the study area. For instance, the 1000 m simulations show little increase in potentially colonizable habitat when adding LDD because they already fill almost their entire suitable habitat without LDD. These empty suitable sites can result from either: (1) the species not migrating fast enough to keep with climate change (explaining why the increase in distribution when introducing LDD is usually highest in the maximum warming scenario) or (2) the presence of barriers or gaps in suitable habitat that impedes the species from occupying all its potentially suitable habitats (Fig. 1). Therefore, although LDD can already have an important effect on projections made at a local scale, its impact should be even greater at larger, e.g. continental, scales. Our results also illustrate how anticipating the impact of dispersal parameters such as LDD can be difficult, further supporting the need for tools such as MIGCLIM for running sensitivity analyses.

Importance of climate change scenario

Along with dispersal distance, the intensity of the warming scenario proved to be a key factor in determining the level of uncertainty in future projections. In our simulations, variation in predicted future distributions always increased under more severe warming scenarios (Figs 3 & 4). The uncertainty in projections also increased over time (Fig. 5). As a result, ignoring dispersal or using incorrect dispersal parameters can lead to larger errors when simulations are made for higher temperature warming scenarios or over longer time periods. The variation in projected future distribution related to the temperature warming scenarios is also strongly dependent on the dispersal parameter values: it can be as important as – or even greater than – the variation due to dispersal parameters (e.g. Fig. 3, ARELA 500 m or 1000 m simulations), but it can

also be very small (e.g. Fig. 3, ARELA 5 m or 25 m simulations). For instance, even if the ARELA seed dispersal distance was identified to be precisely 500 m, a large amount of uncertainty would remain associated with the projections because of the warming scenarios. On the other hand, if one could show that this species only disperses seeds at 5 or 25 m, more accurate predictions could be achieved even though the climate change scenarios remain uncertain.

Generalizing our results

Results of projections for our two virtual species for 2100 showed that differences between potentially *suitable* and potentially *colonizable* habitat could vary from < 5% to more than 95%, depending on the dispersal distance and warming scenario that were used. The impact of a particular parameter on projections is dependent on: (1) the geographical configuration of the study area, (2) the initial distribution of the species, and (3) how the distribution of the potentially suitable habitats evolves as environmental conditions change. For these reasons, caution is recommended before generalizing our results to other areas or to other plant species. How frequent and important the overestimations are remains to be determined, but predictions for slow-dispersing species or made in fragmented landscapes should benefit from constraining projections through dispersal limitations. Furthermore, because our study area is mountainous, the distances required to keep track of suitable climate conditions are likely much shorter than in a flatter landscape (i.e. less Euclidian distance separates current and forecasted future distribution ranges due to the generally steeper climatic gradient found in mountains, e.g. Midgley *et al.*, 2003). Therefore, the differences found here between potentially *suitable* and potentially *colonizable* habitat (Fig. 3) may well constitute a conservative baseline, with greater differences to be expected when applying MIGCLIM to flatter and larger areas (as found e.g. by Midgley *et al.* (2006) on Proteaceae of the Cape Floristic Region).

Calibration, current limitations and perspectives of MIGCLIM

The higher complexity of dispersal models can also be a potential weakness, as they require a deeper knowledge of the modelled organism and its dispersal characteristics, for which data are often difficult to obtain (see Higgins *et al.*, 2003, for a review). For instance, although methods to estimate LDD events exist (Nathan *et al.*, 2003) and significant improvements have been made in LDD modelling (e.g. Takenberg, 2003; Soons *et al.*, 2004; Nathan *et al.*, 2005), accurately integrating them into spatially explicit models of species distribution and dispersal remains challenging. In fact, due to the inherent unpredictability of LDD, accurate predictions might not even be possible (Clark *et al.*, 2003).

To achieve accurate forecasts, the calibration of dispersal parameters must be made with care, especially when working with more extreme climate change scenarios and over long time periods. Ideally, this choice should be based on experimental or historical data (e.g. Iverson *et al.*, 1999), but in practice, these are scarce. Nonetheless, our results demonstrate that rough estimates can already significantly reduce uncertainty when compared to the large interval defined by the unlimited and no-dispersal scenarios. Below are some points of guidance for calibrating MIGCLIM's parameter:

Calibration of P_{Disp} (probability of a pixel to be colonized given its distance to a source pixel)

While accurately fitting a dispersal kernel can be difficult, estimating $DispDist$ (i.e. the maximum regular dispersal distance, LDD excluded) is usually possible (see e.g. the methodology proposed in Vittoz & Engler, 2007). In the simplest case, P_{Disp} can be set to 1 for all distances within $DispDist$. While this is a somewhat simplistic option, as it ignores the fact that P_{Disp} decreases with increasing distance from a source pixel, this setting can still be justified as being an optimistic best case approach. The alternative requires defining a seed dispersal kernel (P_{Seed}) and a link function relating P_{Seed} to P_{Disp} . Here we set the link function by assuming that the dispersal of successful seeds follows the same distribution as the dispersal of any seed (this might not be fully correct due to possible density-dependent seed mortality) and calibrated it by setting equation 5 equal 0.99 for pixels immediately adjacent to a source cell at 25-m pixel resolution. Although this calibration already leads to significant dispersal limitations, it remains an approximation and might produce overly optimistic dispersal rates. This calibration approach could, nevertheless, be improved if more data were available: for instance, knowing the number of seeds produced per surface unit and the rate with which these seeds survive to become mature individuals would allow computing more accurate values of P_{Disp} using equation 5. Another approach for calibrating the link between P_{Seed} and P_{Disp} would be to choose it so that the average spread rate corresponds to historical (e.g. as in Iverson *et al.*, 1999) or recent (e.g. Takahashi & Kamitani, 2004) measures for the species or a species with similar dispersal strategy. Finally, using more complex models (e.g. Pearson & Dawson, 2005) could also be a possible way of exploring and improving the link between P_{Seed} and P_{Disp} .

Calibration of long-distance dispersal

For computational efficiency reasons, we modelled LDD events as a separate process from regular dispersal. Ideally however, and this remains possible in MIGCLIM, both regular and LDD should be modelled in a single kernel. In such case, the choice of the dispersal kernel becomes extremely important: choosing a fat-tailed kernel will result in several magnitudes more LDD events than a negative exponential kernel (Nathan *et al.*, 2008).

Calibration of P_{Mat} (probability of a pixel to act as source pixel given the time since it became colonized)

As illustrated by our results (Fig. 3, comparing Tree-type and Herb-type simulation results), P_{Mat} has an important effect on the projections and can significantly slow down a species' progression. One simple way to calibrate this parameter is matching it to the values of an individual plant, setting it equal 0 before an individual starts producing seeds, and equal 1 from then on. Again, this is not fully realistic, but represents a best case approach that can already greatly impact predictions, especially, for organisms such as trees that need many years before producing seeds. If more detailed knowledge is available, this information can obviously be reflected in P_{Mat} .

Initial species distribution

In our simulations, the initial distributions of ARELA and LOPER were set to their entire potentially suitable habitat under current climatic conditions. While it would be preferable to use the true distribution of a species as starting point, this information is rarely known. A case where the initial distribution might be pretty well known is for invasive species: MIGCLIM could thus use the area of introduction of an invasive species to model its potential spread through the landscape.

Choice of pixel resolution

One obvious point is that pixel size should be much smaller than DispDist (here we always used a pixel size at least five times smaller than DispDist). Another issue that should be borne in mind is that the calibration of P_{Disp} (equation 5) is dependent on the pixel size at which a simulation is run (i.e. for a same species, larger pixels should produce more seeds than smaller ones). In this study, we developed kernels of P_{Disp} for 12.5- and 5-m pixel sizes so that the density of produced seeds per surface unit remained the same than for 25-m pixel sizes. This ensured that our species had a spread rate that was independent of the pixel size. Another possibility to keep constant spread rate across different pixel sizes is to use an optional MIGCLIM parameter that allows correcting the values of P_{Disp} when used with a different pixel size from the one it was calibrated for (see Appendix S6 for more details on this correction factor).

Habitat suitability

In our simulations, habitat suitability was treated as a binary variable, pixels being either suitable or not. In reality, habitat suitability is obviously a more continuous variable. This is an important consideration because habitat suitability does, in our model, implicitly represent post-dispersal seed-to-adult survival probability, which is a critical, yet often overlooked, parameter in species dispersal (Nathan, 2006). Using continuous rather than binary habitat suitability values is available as an optional parameter in the MIGCLIM model. The same

parameter can also be used to integrate a measure of habitat invasibility (e.g. Dullinger *et al.*, 2004).

The objective while developing MIGCLIM was to provide a flexible tool that can be used to obtain refined projections for many species, for which information available on dispersal characteristics is basic or can only be roughly estimated. Therefore, the model must necessarily sacrifice some accuracy for generality and cannot include as many parameters as other models developed for a single species (e.g. Dullinger *et al.*, 2004) or for addressing more theoretical insights (e.g. Pearson & Dawson, 2005). In its current state, MIGCLIM does not include explicit population dynamic parameters, such as number of individuals per pixel or number of seeds per individual. However, calibrating such parameters requires more complex population dynamic data, which are simply not available for most species.

CONCLUSION

This study illustrates to which extent 'potentially suitable habitat' and 'potentially colonizable habitat' can considerably differ when addressing the issue of plant distributions under climate change. Our results further support the view of dispersal being a key factor in this context (Pitelka *et al.*, 1997; Woodward & Beerling, 1997; Davis *et al.*, 1998; Cain *et al.*, 2000; Ronce, 2001).

A main limitation of dispersal models remains their requirement for deeper ecological knowledge to calibrate them for a given species. Nonetheless, approximations of these parameters can be obtained (e.g. Vittoz & Engler, 2007) and used to achieve refined projections for a large number of species. Additionally, as illustrated here, sensitivity analyses performed by varying dispersal parameters along a range of realistic values allows generating complementary uncertainty estimates around existing projections (e.g. Thuiller, 2004; Thuiller *et al.*, 2005).

MIGCLIM is available at <http://www.unil.ch/ecospat>.

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SUPPORTING INFORMATION

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

Appendix S1 Flow-chart view of the MIGCLIM model.

Appendix S2 Detail of P_{Disp} and P_{Mat} values used in the different simulations.

Appendix S3 IPCC-based temperature increase scenarios used in this study.

Appendix S4 Initial set of environmental variables used as input for the GLM stepwise selection procedure.

Appendix S5 Initial distribution and examples of predictions obtained for year 2100 for ARELA and LOPER.

Appendix S6 Explanation and justification of the optional pixel-size correction factor.

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