

# Modelling species' range shifts in a changing climate: The impacts of biotic interactions, dispersal distance and the rate of climate change

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## Abstract

There is an urgent need for accurate prediction of climate change impacts on species ranges. Current reliance on bioclimatic envelope approaches ignores important biological processes such as interactions and dispersal. Although much debated, it is unclear how such processes might influence range shifting. Using individual-based modelling we show that interspecific interactions and dispersal ability interact with the rate of climate change to determine range-shifting dynamics in a simulated community with two growth forms—mutualists and competitors. Interactions determine spatial arrangements of species prior to the onset of rapid climate change. These lead to space-occupancy effects that limit the rate of expansion of the fast-growing competitors but which can be overcome by increased long-distance dispersal. As the rate of climate change increases, lower levels of long-distance dispersal can drive the mutualists to extinction, demonstrating the potential for subtle process balances, non-linear dynamics and abrupt changes from species coexistence to species loss during climate change.

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## 1. Introduction

Climate change is already having detectable impacts on global biodiversity (Parmesan and Yohe, 2003) and may be as great a long-term threat to species survival as land use change (Thomas et al., 2004). The biodiversity impacts of climate change are manifest for example in altered phenology, population density and community structure (Edwards and Richardson, 2004; Parmesan and Yohe, 2003; Root et al., 2003; Walther et al., 2002). Changes in species ranges have also been detected (Beauprand et al., 2002; Thomas and Lennon, 1999; Walther et al., 2005), and are not unexpected given that species have temperature optima and dispersal processes enable species to track environmental conditions through space.

Predicting changes in the distribution of species as a result of climate change has now become a major goal for ecologists, not least because it greatly aids the development of adaptation and mitigation strategies for biodiversity conservation (CBD, 2003; EEA, 2004; Thomas et al., 2004). Manipulation experiments (Chapin et al., 1995; Emmett et al., 2004; Press et al., 1998) and long-term monitoring (Richardson and Schoeman, 2004; Root et al., 2003; Warren et al., 2001) provide some indication as to the current and potential future responses of species and ecosystems, but these approaches are limited either in terms of their spatial or temporal scope. Modelling has therefore become an important additional tool.

Climate envelope modelling in particular has been utilized to develop species response scenarios that cover large geographic areas and multiple future species generations (Bakkenes et al., 2002; Walther et al., 2005). However, the accuracy of this type of modelling has been

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the cause of recent debate. It has been proposed that climate envelope models might provide, at best, a rough approximation of the response of species' ranges to climate as the models do not include the impact of important processes such as dispersal ability and biotic interactions (Hampe, 2004; Pearson and Dawson, 2003). Such processes might severely restrict the ability of species to track climatic conditions through space and to establish within a new habitat (Guisan and Thuiller, 2005; Hiscock et al., 2004; Lortie et al., 2004; Brooker 2006). Incorporating such processes into climate envelope modelling, and understanding how they will interact with each other and the rate of climate change, will be crucial for producing the more accurate and detailed predictions of biodiversity responses that are required by the policy-making community (CBD, 2003; EEA, 2004; Message from Malahide, 2004).

In this paper, we begin to address these issues by incorporating key biotic processes into a highly simplified, strategic model simulating range shifting during climate change. We utilize a spatially explicit modelling approach to explore the potential impacts of both dispersal ability and the interactions between individuals on species range shifting. Our model is in part motivated by our desire to eventually predict the response of hypothetical arctic/alpine plants to climate change, focussing on the response of plants with two strategies: competitors and mutualists.

We use this hypothetical model system because: (1) positive interactions play an important role within arctic and alpine plant communities (Brooker and Callaghan, 1998; Callaway et al., 2002; Choler et al., 2001), (2) arctic and alpine environments are predicted to be highly vulnerable to climate change (ACIA, 2004; CBD, 2003; Houghton et al., 2001). In addition, clear links have been demonstrated between abiotic environmental conditions (e.g. growing season temperature) and the dominant type of interaction within plant communities, including arctic and alpine systems (Bertness and Ewanchuk, 2002; Callaway et al., 2002; Kikvidze et al., 2005). Consequently climate change impacts are likely to involve changes in the dominant type of interactions occurring within a system and using this type of model helps to understand these processes. Moreover, individuals engaging in positive interactions in the model can be seen as directly analogous to an arctic/alpine stress tolerant growth strategy—their species traits mean that they reproduce more slowly but are able to survive in more severe environments (Grime, 1977). This combination of factors makes such modelling directly relevant to understanding the response of threatened arctic/alpine biodiversity to climate change. Additionally, our model is likely to be of general relevance to many other natural assemblages that are held together by a mix of both positive and negative interspecific interactions.

We demonstrate that biotic interactions, which regulate spatial arrangement of species and space occupancy effects, and the level of long range dispersal, both of which are key biotic processes, determine the response of species to a changing climate, and that they interact with the rate of

climate change to produce non-linear responses and sudden species extinction.

## 2. The model

Here, we use an individual-based spatial model to explore the range shifting dynamics of a 'toy' assemblage comprising species engaging in both positive and negative interactions. Our model builds on recent work that sought to understand the role of positive interspecific interactions in the setting of species biogeographic ranges (Travis et al., 2005, 2006), and relates closely to several other recent theoretical studies in the field (Boza and Scheuring, 2004; Doebeli and Knowlton, 1998; Yamamura et al., 2004). Our previous work (Travis et al., 2005, 2006) was found to realistically simulate the spatial arrangement of mutualist and competitor strategies along static severity gradients. In this study, we take the same model and impose a changing "climate" by gradually reducing the severity of the environment through time along the whole range of the severity gradient, thus mimicking (in a very simplified manner) the impact of climate change in high latitude or high altitude environments.

As described in greater detail elsewhere (Travis et al., 2006), the model comprises a two-dimensional landscape of cells and two species. Each cell can be either empty or occupied by an individual of one or both species. Individuals of each species are either mutualists or competitors. This characteristic does not change over time and is passed to any offspring of that individual. Two parameters,  $r_{max}$  and  $r_{min}$ , determine the reproduction rate at the rich and poor extremes of the lattice, respectively. Depending on their horizontal position in the lattice, individuals are assigned a basic reproduction rate  $r$ . Lone competitors reproduce at a rate  $r$ , lone mutualists at a rate  $r-c$  ( $c$  being the cost of facilitation). An individual of any type in a cell with a mutualist has a benefit  $b$  to their particular reproduction rate. Reproduction occurs by replication of the individual into one of the four neighbouring cells (Von Neuman neighbourhood) or, in the case of long-distance dispersal, into any randomly chosen cell in the lattice. Reproduction is only successful if a propagule arrives at a cell currently unoccupied by that species. Every individual has a constant mortality rate  $d$ .

The lattice used is  $500 \times 100$  cells. Other than for production of Fig. 1, parameter values at the start of each simulation are as follows:  $r_{max} = 0.2$ ,  $r_{min} = -0.08$ ,  $d = 0.07$ ,  $c = 0.05$ ,  $b = 0.3$ . Before each period of climate change the model is run for 3000 generations under constant conditions to allow the populations to reach an equilibrium distribution. To simulate rapid climate change at the end of the stabilization period,  $r_{max}$  and  $r_{min}$  are incremented at the end of each generation by a certain amount. This reduces the severity across the full range of the environmental gradient, and effectively moves the species' "climate envelope" (defined by the range of reproduction rates within which a population can persist)

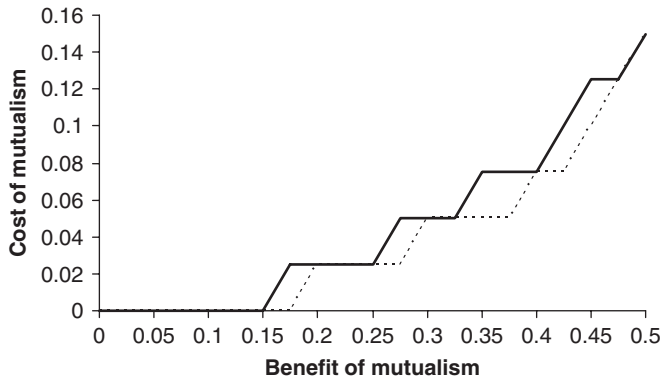


Fig. 1. Persistence of mutualists within a static environment (no climate change) with either no long-distance dispersal (solid line) or 1% long-distance dispersal (dashed line). The area beneath the lines shows the combinations of costs and benefits of mutualism where mutualists are able to persist. The models were run for 3000 generations; between runs the cost and benefits of mutualism were varied in increments of 0.025 units and the lines join the lowest benefits for which mutualists persisted.

to the right. The magnitude of the increase to  $r_{max}$  and  $r_{min}$  each generation determines the “speed” of climate change.

To understand the impacts and interactive effects of biotic interactions, dispersal ability and the rate of climate change on the ability of our model species to track their climate window, the modelling is undertaken in a number of discrete stages. Initially, we explore very simply the characteristics of the model by plotting the parameter space within a static environment within which co-existence of both mutualists and competitors can occur, both with and without long-distance dispersal. We then examine how populations of each growth form respond to a changing climate or long-distance dispersal in isolation. Finally we place both growth forms into the same model grid and allow the community to reach an equilibrium state before simulating climate change. We then systematically change both the rate of climate change and level of long-distance dispersal to examine the impact of these factors on species range shifting.

### 3. Results

In a static environment, the exact combination of costs and benefits of mutualism determine whether mutualists persist within the model, as demonstrated previously by Travis et al. (2005, 2006; Fig. 1). When the cost of mutualism = 0 mutualists will always persist, and if the model is run for long enough the benefit of mutualism can give an advantage such that mutualists can exclude competitors. Introducing even a small proportion of long distance dispersal into the model acts to reduce the area of parameter space in which mutualists persist (Fig. 1), and this highlights the importance of local spatial structure for the mutualists. In simulations investigating the response of the species to climate change we choose parameter space for which both mutualists and competitors persist when the climate is static.

In climate change simulations with species in isolation (i.e. when the model was run with either only competitors or only mutualists), we find that the competitors and mutualists increase in abundance and undergo similar amounts of range expansion, regardless of the rate of climate change (Fig. 2a, Table 1). The mutualists have overall a larger population size at any position in time and under all rates of climate because they are able to exploit more of the model space (i.e. they are able to survive in harsher conditions than their competitors as a consequence of their facilitative strategy), and they therefore have a lower proportional population increase (Table 1). When the species are in isolation, introducing 1% long-distance dispersal simply increases the rate at which both species can respond to climate change, especially the faster rates of climate change (Fig. 2b).

When mutualists and competitors co-occur (when both species are put into the model)—but in the absence of long-distance dispersal—the population size of the mutualists is reduced; their comparatively low reproductive rate and facilitative strategy mean that they are displaced by the competitors from the most productive part of the model space and only persist in harsher environmental conditions (Fig. 2c). Combining the two species in the same model also impacts upon population growth during climate change, but this effect is dependent on the rate of climate change. The expansion of the competitor population is restricted by the presence of the mutualist population at the faster rates of climate change (Table 1; Fig. 2a and c). In comparison the rate of population increase of the mutualists is less affected by the presence of the competitors. In fact, although the absolute increase in mutualist population size is reduced when the species are combined, the relative increase in mutualist population size is greater because their initial population size is less, and this effect is stronger with faster rates of climate change (Table 1). This indicates that availability of space rather than initial population size is controlling the rate of population change. The expanding range margin of the competitors is moving into space already occupied by the mutualists (and range expansion is therefore governed by biotic interactions as well as climate), whereas that of the mutualists is moving into unoccupied space (and is therefore only governed by environmental conditions).

Addition of 1% long-distance dispersal to the two-species model causes further declines in the size of the mutualist population (Fig. 2d). The negative effect of long-distance dispersal on mutualist population survival becomes stronger with an increasing rate of climate change, and the mutualists no longer limit the expansion of the competitors—in fact the expansion of the competitors drives the mutualists to extinction. There appears to be a subtle balance between the level of long-distance dispersal and the rate of climate change in determining the model’s dynamics, as further explored in Fig. 3.

At low rates of climate change and when the model has only 0.1% long-distance dispersal (Fig. 3b), the competitors

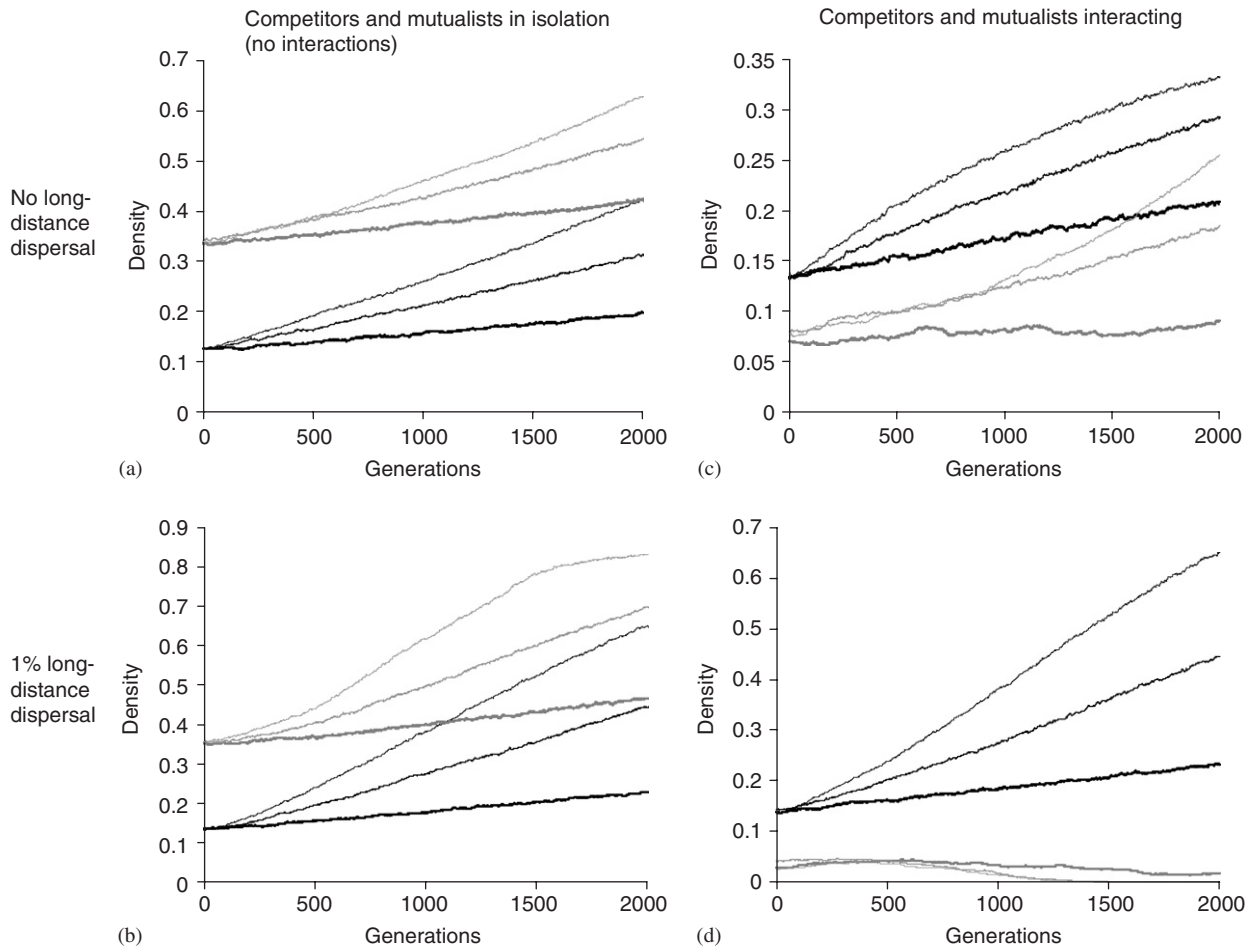


Fig. 2. Change through time in the populations of competitors (black) and mutualists (grey) under three rates of climate change: slow (thickest line), medium (intermediate thickness line) and fast (thin line). Figures (a)–(d) show the four possible combinations of model outputs with (a) two levels of interaction (mutualists and competitors in isolation vs. interacting) and (b) two levels of long-distance dispersal (no long-distance dispersal vs. 1% long-distance dispersal).

Table 1

Impact of the rate of climate change on population dynamics in models containing either the species in isolation or in models containing both competitors and mutualists over 2000 generations of climate change

| Species                               | Rate of climate change | Population size at $t = 1$ | Population size at $t = 2000$ | Net change in population size | Change in population size/initial population size |
|---------------------------------------|------------------------|----------------------------|-------------------------------|-------------------------------|---|
| <i>Species in isolation (Fig. 2a)</i> |                        |                            |                               |                               |   |
| Competitor                            | Slow                   | 0.13                       | 0.20                          | 0.07                          | 0.56  |
| Mutualist                             | Slow                   | 0.34                       | 0.42                          | 0.08                          | 0.25  |
| Competitor                            | Fast                   | 0.13                       | 0.43                          | 0.30                          | 2.35  |
| Mutualist                             | Fast                   | 0.34                       | 0.63                          | 0.29                          | 0.85  |
| <i>Species interacting (Fig. 2c)</i>  |                        |                            |                               |                               |   |
| Competitor                            | Slow                   | 0.13                       | 0.21                          | 0.08                          | 0.56  |
| Mutualist                             | Slow                   | 0.07                       | 0.09                          | 0.02                          | 0.29  |
| Competitor                            | Fast                   | 0.14                       | 0.33                          | 0.19                          | 1.40  |
| Mutualist                             | Fast                   | 0.08                       | 0.25                          | 0.18                          | 2.28  |

Model outputs are shown graphically in Figs. 2a and c.

are unable to establish a foothold beyond the mutualist population, and the outcome is effectively the same as when there is no long-distance dispersal (Fig. 3a). However, when 1% long-distance dispersal is introduced into the model (Fig. 3c), competitors can “leap-frog” the mutualists,

occupying the space into which the mutualists would have expanded. Mutualists do not benefit from relatively rare long-distance dispersal as their establishment and persistence in a new area relies on the presence of other individuals engaging in positive interactions, and the likelihood of this is

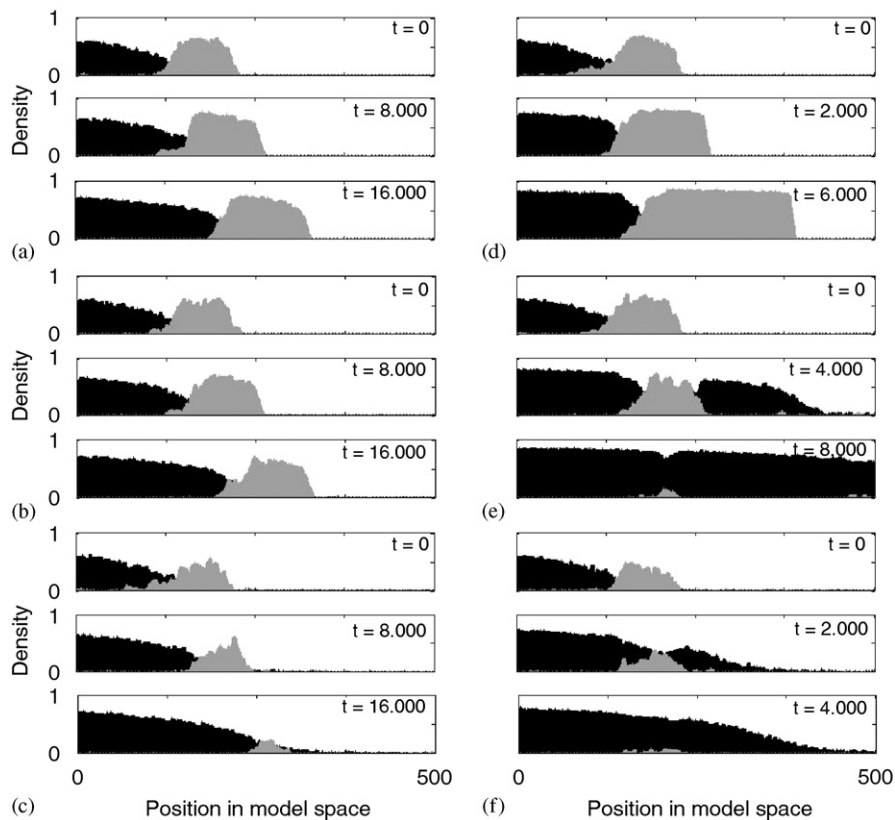


Fig. 3. Spatial distribution of competitors (black) and mutualists (grey) along an environmental gradient (0 least severe, 500 most severe) at various periods of time during slow climate change (a–c) and fast climate change (d–f). a, d, no long-distance dispersal. b, e, 0.1% long-distance dispersal. c, f, 1% long-distance dispersal. All figures were produced by averaging the density of individuals at a particular point along the severity gradient over 100 generations. Time slices shown best illustrate model dynamics. In all simulations, we checked that the mutualists' climate window remained within model space. This is the case in all the results shown except for Fig. 2e where the mutualist zone is no longer contained in the lattice. For this set of parameters we repeated the scenario with an enlarged lattice—this confirmed that mutualists were indeed unable to migrate to their climate envelope and became extinct.

low even with a comparatively high level of dispersal. Competitors do not suffer this Allee effect.

Mutualists are able to tolerate a greater total amount of climate change when the climate change occurs less rapidly; for example, when the climate change occurs at a rate of 0.00025 the mutualists survive as long as total climate change causes values of  $r$  to increase by  $<0.08$ , when it occurs at a rate of 0.00060 they survive if total change results in  $r$  increasing by  $<0.06$ , and when the rate is 0.000095 they only survive if the total change  $<0.02$ . At higher rates of climate change, the loss of mutualists from the system occurs at a lower level of long-distance dispersal, i.e. with 0.1% long-distance dispersal mutualists are lost from the system whereas they had previously survived (Fig. 3b and e). The climate envelope of the competitors moves sufficiently far and reproductive rates beyond the mutualists increase sufficiently that even 0.1% long-distance dispersal enables a viable population of competitors to establish and prevent the mutualists' range from shifting.

#### 4. Discussion

The response of a simple simulated community to climate change is dependent on the nature of interspecific

interactions, dispersal ability and the rate of climate change. Our simulated community obeys very simple rules, yet demonstrates the significant (and interactive) impact of these factors; ignoring them would result in incorrect predictions of the response of species to climate change. Essentially all ecological communities will involve considerably more complexity than is represented within our model, yet predictions are frequently made regarding future species ranges without considering any ecological processes, let alone potentially complex synergistic effects. The explicit inclusion of interactions in this model produces outcomes that would not have been observed with a classic climate-envelope approach. Although simplistic, such modelling of species responses to climate change is, to the best of our knowledge, entirely novel.

Prior to climate change being imposed on the model, interactions, in combination with physiological tolerances, play an important role by setting the spatial arrangement of species: the mutualists form a band between the competitors and the most severe environmental conditions. This result has been discussed previously (Travis et al., 2005) and mirrors the spatial arrangement of competitive and facilitative interactions found along alpine environmental severity gradients (Callaway et al., 2002; Choler

et al., 2001; Kikvidze et al. 2005). It is also analogous to the capacity of stress-tolerant species to survive in severe environments but with the associated costs of low growth rates and relatively lower competitive ability (Grime, 1977). However, although based upon concepts from alpine and arctic environments the output of this model provides a widely applicable demonstration of the interactive effects of the rate of climate change and biotic processes.

The initial spatial arrangement of species is critical, as space occupancy may limit the expansion of a species' range. In our model even though the mutualists are less competitive once occupying a site they are able to obstruct the influx of competitors. A similar space occupancy effect was found by Takenaka (2005) using a spatially-explicit tree-based model: migration of model tree species was retarded by remnant populations that had developed in a site prior to simulated warming. In real ecosystems, this is also likely to be an important process limiting the potential rate of range shifting through a landscape. Space occupancy is known to inhibit establishment and regulate diversity (Casado et al., 2004) and range expansion (Arrontes, 2002). Under climate change, although species may be dispersing into an area that has acquired climatic conditions to which they are now suited, they need space for establishment. For example Dullinger et al. (2003) showed that the expansion of subalpine *Pinus mugo* shrub following either land abandonment or climate change was strongly dependent on the type of vegetation that already dominated within the zone of potential colonization. The effect of space occupancy is also likely to be dependent upon the rate of turnover in the existing vegetation, which will itself depend both upon the longevity of individuals and the frequency of disturbance processes. The degree of lag in range shifting that this could cause may vary between growth forms. Short-lived species of disturbed habitats, for example farmland weed species, may suffer less from this occupancy lag than long-lived species such as trees, which may occupy a site for many years even in conditions that would inhibit their establishment. Importantly, climate change will impact upon the frequency of disturbance events, for example fires in woodlands (McCoy and Burn, 2005; Thornley and Cannell, 2004) and may alter the capacity for species to invade a landscape, although Takenaka (2005) demonstrated that processes other than disturbance, for example temporal variability in seed production in the case of trees, might also alter the rate of range shifting. One question we might now ask is whether space occupancy is already restricting the response of species to climate change. Perhaps we can already consider landscapes to be "under tension"—it is possible that climate is already exerting a pressure in favour of range shifting that will only be released following turnover and disturbance of existing vegetation. If so, then regulated disturbances might promote species range shifting during climate change.

The level of long-distance dispersal is critical. Even in a static environment it can determine whether particular

mutualist cost-benefit ratios allow long-term persistence of both species. Under climate change it enables species to overcome existing limiting patterns of space occupancy (the competitors "leap-frog" of the mutualists) and determines future patterns of space occupancy and species survival. Importantly however, although the role of dispersal has been raised previously (Guisan and Thuiller, 2005; Hampe, 2004; Travis 2003; Warren et al., 2001), we show here how it might interact with the rate of climate change. At a given level of long-distance dispersal we see either species co-existence or the extinction of one of the species depending upon the rate of climate change. The subtlety of this relationship is problematic for the production of scenarios for the impact of climate change on biodiversity: potentially complex interactions between the rate of climate change and biotic processes might determine whether species will continue to coexist, or whether there is a catastrophic collapse of populations.

## 5. Conclusion

The surprising, but logical, responses of our model system, which are dependent upon the explicit inclusion of interactions and their effects on reproductive rates and the spatial arrangement of species, support current calls for the integration of biotic processes such as dispersal ability and interactions into range modelling (Guisan and Thuiller, 2005; Hampe, 2004; Takenaka, 2005). In addition further strategic modelling is required to improve our theoretical understanding of how different ecological and evolutionary processes will influence species responses to climate change. That a model community as simple as that described here can exhibit such a complex range of responses to climate change, suggests that predicting future biogeographic ranges is likely to be fraught with difficulties. However, there is currently a will to make these types of predictions and efforts now need to be directed towards integrating the sophisticated statistical methods used to predict where suitable climate will be found in the future with spatial ecological and evolutionary modelling.

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