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LOCAL ADAPTATION AND THE EVOLUTION OF  
2 SPECIES RANGES UNDER CLIMATE CHANGE

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### Abstract

6           The potential impact of climate change on biodiversity is well documented. A well  
developed range of statistical methods currently exists that projects the possible fu-  
8           ture habitat of a species directly from the current climate and a species distribution.  
However, studies incorporating ecological and evolutionary processes remain limited.  
10          Here, we focus on the potential role that local adaptation to climate may play in  
driving the range dynamics of sessile organisms. Incorporating environmental adap-  
12          tation into a stochastic simulation yields several new insights. Counter-intuitively,  
our simulation results suggest that species with broader ranges are not necessarily  
14          more robust to climate change. Instead, species with broader ranges can be more  
susceptible to extinction as locally adapted genotypes are often blocked from range  
16          shifting by the presence of cooler adapted genotypes that persist even when their  
optimum climate has left them behind. Interestingly, our results also suggest that it  
18          will not always be the cold-adapted phenotypes that drive polewards range expan-  
sion. Instead, range shifts may be driven by phenotypes conferring adaptation to  
20          conditions prevalent towards the centre of a species' equilibrium distribution. This  
may have important consequences for the conservation method termed predictive  
22          provenancing. These initial results highlight the potential importance of local adap-  
tation in determining how species will respond to climate change and we argue that  
24          this is an area requiring urgent theoretical and empirical attention.

Keywords: local density dependence; environmental gradient; environmental  
26          niche; extinction, species' range.

## Introduction

28 The threat that climate change poses to biodiversity is well documented (Parme-  
san and Yohe, 2003; Pearson et al., 2002; Peterson et al., 2002; Thomas et al., 2004;  
30 Walther et al., 2002). Many species have already exhibited responses to the changing  
environment; in a meta-analysis Parmesan and Yohe (2003) found that 434 species  
32 out of 893 had shifted in distribution and/or abundance. A key question is whether  
climate change increases the risk that species will become extinct, and initial results  
34 from a study by Thomas et al. (2004) are alarming. Even for a best-case scenario,  
using the minimum expected climate change and ignoring the potential for dispersal  
36 limitation, the authors predict a 9-13% loss in species abundance. Using the worst  
climate scenario and with extreme dispersal limitation this figure rises to a staggering  
38 38-52%. Whilst this study represents a useful exercise, not least in terms of focussing  
minds on the problem at hand, it simultaneously highlights some important deficien-  
40 cies that it shares with the many bioclimate envelope models (BEMs), widely used  
to predict future ranges (Hampe, 2004). There is an urgent need for the development  
42 of a new generation of models to make this type of prediction. However, this goal is  
hindered by a basic lack of understanding of the likely consequences of key ecological  
44 and evolutionary processes for range dynamics under climate change. Local adapta-  
tion is a good example of one of these processes: many species comprise collections of  
46 populations each adapted to local climatic conditions. However, there has been little  
formal consideration of the impact the degree of local adaptation present within a  
48 species might have on range dynamics (Polechová et al., 2009), and no attempt to

incorporate these processes into predictive modelling. It is likely that two aspects of  
50 a species' adaptation will be important. First, the steepness with which an individual's  
fitness declines as it is moved from its optimal climate and second, the total  
52 range of environmental conditions under which a species, as a whole, can survive.  
In this contribution, we take a first step and develop a relatively simple simulation  
54 model to explore the issue of how local adaptation influences a species ability to track  
changing climate.

56 A plethora of studies have used bioclimate envelope modelling to predict the  
future biogeographic ranges of species (Bakkenes et al., 2002; Broennimann et al.,  
58 2006; Peterson et al., 2002; Schwarz et al., 2006; Thuiller et al., 2005). Refined  
methods are being developed that entail the use of increasingly sophisticated statistics  
60 (e.g. Gavin and Hu (2005)), genetic algorithms (e.g. Termansen et al. (2006)) and  
neural networks (e.g. Pearson and Dawson (2003)), and it has even been argued  
62 that the optimal approach should use a combination of these approaches in order  
to look for concordance between them (Araujo et al., 2005). Intense activity in this  
64 field has provided a suite of methods that obtain a relationship between the climate  
and a species range prior to environmental change: thus defining the 'climate space'  
66 occupied by the species. Utilising future climate scenarios, these methods predict the  
future climate space for the species. However, there is a growing realisation that this  
68 correlational approach alone is ill-equipped to predict future species ranges (Davis  
et al., 2005; Hampe, 2004; Lawton, 2000; Woodward and Beerling, 1997).

70 The dynamics of a species' range during a period of climate change will be dependent  
upon the existence and interplay of various ecological and evolutionary pro-

72 cesses. Dispersal is perhaps the most obvious of these and it is anticipated that  
species with greater dispersal ability will be better able to track a changing climate  
74 (Travis and Dytham, 2002; Travis et al., 2009). Midgley et al. (2002) incorporate  
simple dispersal functions into a model predicting future ranges of Cape Proteaceae.  
76 The description of the spatial population dynamics used in this model is relatively  
crude but, in linking a model of ecological dynamics with a BEM, Midgley et al.  
78 (2002) take an important step in the right direction.

Theoretical studies, often focussing on invasion biology rather than range dynam-  
80 ics under climate change, have considered a range of evolutionary dynamics during  
expansions: Garcia-Ramos and Rodriguez (2002) demonstrate the interacting roles  
82 played by local adaptation and habitat heterogeneity in determining spread rate;  
several theoretical studies have now demonstrated that range expansion might be  
84 accelerated by the evolution of increased dispersal propensity at expanding fronts  
(e.g. Travis and Dytham, 2002; Burton et al., 2010) and recent empirical evidence  
86 confirms that this is an important effect (Phillips et al., 2006); Klopstein et al. (2006)  
demonstrate that neutral mutations arising on the edge of a range expansion some-  
88 times ‘surf’ on the wave of advance and can thus reach a wider spatial distribution  
and higher frequency than would be expected in a stationary population. Klopstein  
90 et al. (2006) suggest that this surfing phenomenon may increase the rate of evolution  
of spatially expanding populations. More recent extensions to this work have demon-  
92 strated that this surfing dynamic can be important for non-neutral mutations. Even  
deleterious mutations can sometimes attain high abundance at an expanding front  
94 (Burton and Travis, 2008a; Excoffier and Ray, 2008; Travis et al., 2007) and this effect

can substantially modify evolutionary dynamics where fitness landscapes are rugged  
96 (Burton and Travis, 2008b). In this paper we concentrate on local adaptation, an  
important evolutionary process that, to date, has rather surprisingly received little  
98 attention in terms of its potential role in range expansions and determining a species  
dynamics during an episode of climate change.

100 Considerable empirical evidence indicates that locally adapted phenotypes are  
commonplace within many species (Lambrechts et al., 1996; McNeilly and Antonovic,  
102 1968; Riihimaki et al., 2005; Santamaria et al., 2003). For example, it has long  
been known that many plant species show genetic differentiation in the timing of  
104 flowering (McNeilly and Antonovic (1968); this variation is frequently clinal with  
northern populations consistently different from southern counterparts (Riihimaki  
106 et al., 2005). Occurrence of a genotype outside of its usual range may result in  
suboptimal flowering time and a corresponding reduction in fitness. Similar patterns  
108 have been described for a bird species: across Europe, blue tits exhibit adaptive  
differences in photoresponsiveness that results in laying dates coinciding with local  
110 caterpillar availability (Lambrechts et al., 1996). These two examples both involve the  
timing of key events being optimally aligned to seasonal environmental conditions,  
112 but there are other ways in which local adaptation may be manifest. It is likely  
that within many species there is variability in thermal tolerances with individuals  
114 towards warmer parts of the range adapted to function better in the heat while  
directional selection will have resulted in individuals found in cooler regions having  
116 a physiology that equips them to function efficiently in the cold (e.g. fish (Feminella  
and Matthews, 1984), amphibians (Olsson and Uller, 2003) and insects (Ayres and



118 Scriber, 1994)).

120 There is now recognition that local adaptation is likely to be an important de-  
terminant of species' responses to climate change and an interdisciplinary treatment  
122 of this issue, linking evolution and ecology, has already been called for (Pertoldi and  
Bach, 2007). We establish how local adaptation drives the dynamics of biogeographic  
124 ranges during and following a period of climate change. We utilise a spatially ex-  
plicit individual based simulation to model the impact of climate change on a single  
126 species. This model uses both stochastic demographic parameters and allows inclu-  
sion of local density dependent rates for survival of individuals. In our discussion we  
128 emphasise the potential implications of our results for conservation biology and high-  
light where we believe future effort is required to develop improved theory related to  
the evolutionary ecology of range shifting.

## 130      **The Model**

132      There has been considerable recent interest in modelling the ecological and evolu-  
134      tionary dynamics of spatially structured populations that live along environmental  
136      gradients (e.g. Alleaume-Benharira et al., 2006; Travis et al., 2006; Dytham, 2009)  
138      and some studies have extended this approach to consider the range shifting of pop-  
    ulations structured in this way (e.g. Brooker et al., 2007; Mustin et al., 2009). We  
    adopt a similar approach in this contribution and below we describe, in turn, the  
    structure of the landscape, the ecological and evolutionary features of the model,  
    and the simulation experiments that we conduct.

## **The Environment**

140      Individuals of the single species inhabit a two-dimensional landscape that, unless  
    specified otherwise, has dimensions 200 rows ( $x$  value) columns by 200 columns ( $y$   
142      value), which are ordered from the bottom left hand corner (i.e. increasing an in-  
    dividual's  $x$  location would move the individual up the grid, whilst increasing its  $y$   
144      location would move it to the right of the grid). A value of  $(x,y)$  determines an indi-  
    vidual's location. We assume that environmental conditions vary latitudinally (i.e.  
146      different rows have different conditions, for example due to variation in climate) and  
    the parameter,  $\theta(x)$ , is used to denote this condition. We assume a linear gradient,  
148       $b$ , in environmental conditions (i.e. for every value of  $y$ , the condition at  $x$ ,  $\theta(x)$  is  
     $bx$ ). An optimal environmental location,  $J$ , is defined as the climate under which  
150      the highest potential population growth rates are obtained. Potential growth rate

declines with distance from this optimum location.  $J$  is defined as a row value,  $x$ , on  
152 the grid. In all our simulations, we allow populations to first establish under stable  
environmental conditions and in these periods the environmental conditions within  
154 each row remains constant through time. To simulate environmental change (e.g. cli-  
mate warming), we increase  $\theta(x)$  for each row,  $x$  and increase  $J$  by  $\nu$  each year. The  
156 period of climate change lasts for  $T$  years. An example of an environmental condi-  
tion changing latitudinally could be a warming climate, where the local temperature  
158 increases in all locations over time. *Local* adaptation to this condition would allow  
individuals to reside in the climate in which they are adapted. An optimal location,  
160  $J$ , corresponds to a position where it is always favourable to be near, e.g. Pease et al.  
(1989) give the example of an advancing glacier, from which there exists an optimal  
162 place to reside. In the case of a warming climate, this optimal location could be any  
number of things e.g. a moving front of adverse weather conditions, the moving range  
164 of a quick-to-adapt parasite vector or food stuff in response to the changing climate.  
*Global* adaptation would allow individuals to reside near to this optimal location.

## 166 **The Ecology**

We assume that each cell on the lattice can support no more than one individual (i.e.  
168 we are using a patch occupancy model). In each year we simulate, in turn, reproduc-  
tion, dispersal of offspring and mortality. All individuals first have the opportunity  
170 to reproduce. To avoid potential biases towards particular locations or individuals,  
the order in which individuals are given the opportunity for reproduction is ran-  
172 domised. The probability that an individual reproduces depends upon its fitness (see

Local Adaptation and Evolution, below). A single offspring is born to a reproducing adult and this offspring immediately disperses. This once-in-a-lifetime dispersal event occurs via a uniformly distributed Moore neighbourhood (nearest eight cells). Offspring that disperse to an unoccupied cell automatically establish. In most simulations, dispersal to an occupied cell results in automatic death and there is thus a strong priority effect in relation to space occupancy. However, in some simulations we relax this assumption and allow offspring to displace established individuals with probability,  $p$ . We always assume reflective boundary conditions as a way of maintaining the current population size if the individuals are able to find space. After all individuals have had an opportunity to reproduce, and offspring have dispersed, we simulate mortality. All individuals are subject to stochastic mortality with probability,  $\mu$ . Mortality is independent of both the condition of the environment and an individual's phenotype.

## Local Adaptation and Evolution

Each individual carries two alleles. These are represented as integer values and their mean determines the environmental condition to which the individual is adapted. For example, an individual possessing two alleles with values 24 and 28, has phenotype,  $z=26$  (and is optimally adapted to the conditions in a row  $x$  such that  $\theta(x) = 26$ ). The probability that an individual reproduces in any given year depends upon both where the individual is located in relation to the environmental location with highest potential productivity,  $J$ , and the degree to which the individual is adapted to its local environment,  $\theta(x)$ . Formally, the probability of reproducing is given by the

following expression:

$$\exp [((\theta(x) - z)^2/2V_s) + ((J - x)^2/2W_s)]$$

196 where, the first term accounts for the degree to which the individual is locally  
 adapted and the second accounts for the proximity of the individual to the location  
 198 with highest potential productivity.  $V_s$  determines the steepness of decline in an  
 individual's fitness as it is moved further from the conditions to which it is best  
 200 adapted, while  $W_s$  determines the rate at which maximum potential reproduction  
 declines with distance from  $J$ . Note that  $W_s$  is akin to the notion of environmental  
 202 tolerance as described in Pease et al. (1989).

It is worth emphasising the distinction between  $W_s$  and  $V_s$  and the need for both  
 204 parameters in our model using a simple illustrative example. Consider first two  
 individuals, one of which is perfectly adapted to the conditions at location  $J$  while  
 206 the other is perfectly adapted to conditions found 10 rows higher on the lattice than  
 $J$ . Initially we will assume both are located in the environments to which they are  
 208 adapted. Despite the fact that both are optimally adapted, their reproductive fitness  
 will not be the same as the first individual (at location  $J$ ) is in the inherently more  
 210 productive environment. Our parameter  $W_s$  determines just how much lower the  
 reproductive fitness is of the individual found 10 rows away from  $J$ . Next consider  
 212 the case that these same two individuals are both located at the position 10 rows away  
 from  $J$ . Now the first individual will have the lower reproductive fitness because,  
 214 while both are in the same environment, the first is not optimally adapted to that

environment. The amount that the first individual's fitness is reduced due to it being  
216 less well-adapted is determined by  $V_s$ .

When a birth event occurs the offspring inherits two alleles: a copy of one of its  
218 parent's alleles (chosen randomly from the set of 2 with equal probability) and a copy  
from an individual, selected at random, in the vicinity of its parent. This vicinity can  
220 be considered as the pollen dispersal neighbourhood and we term it  $h$ . If the vicinity  
contains no individuals then the offspring inherits both alleles from its parent (this  
222 is akin to 'selfing'). During the copying of alleles that ensues, mutation occurs at  
each locus with a probability of  $\beta$ . When a mutation occurs, the value of the allele  
224 is modified by an amount randomly drawn from the discrete uniform distribution,  
(-10, 10).

## 226 **Simulation Experiments**

We have conducted a number of simulation experiments to explore the dynamics  
228 of the model. In the first set, we run the model under a stable climate (i.e. main-  
taining a constant position of maximum potential reproduction,  $J$ ). We run the  
230 model for a range of parameter values and, in particular, vary both  $V_s$  and  $W_s$ . We  
output population abundance and mean phenotype across the environmental gradi-  
232 ent. Subsequently, we run a large number of simulations where we initially allow the  
population to obtain quasidequilibrium under stable environmental conditions before  
234 simulating a period of climate change. In these simulations we are most interested  
in the probability that a population survives an episode of climate change. We run  
236 sensitivity analyses to ask, in turn, how this depends upon  $V_s$  and  $W_s$ , the strength

of the priority effect ( $p$ ), the rate ( $\nu$ ) and duration of climate change ( $T$ ), and the  
238 rate and size of mutations. In the final set of simulations we vary the probability of  
mortality ( $\beta$ ), the landscape width (by altering the number of columns on the grid),  
240 and the dispersal neighbourhood for pollen ( $h$ ). In all the sensitivity analyses, we  
run 50 replicate simulations for each parameter combination.

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## 242 Results

Under stable environmental conditions, population distributions establish as one  
244 would expect. For smaller  $W_s$  (corresponding to a steeper decline in maximum  
potential reproductive rate with distance from  $J$ ), smaller ranges emerge (Figures  
246 1a,1b and 1c). The corresponding mean phenotype is shown in Figures 1d, 1e and  
1f. For smaller  $W_s$ , there is a greater mismatch between the local environment and  
248 the mean phenotype away from  $J$  (in these figures  $J=140$ ).

Most of our results relate to range dynamics under climate change. Figure 2 il-  
250 lustrates typical dynamics showing snapshots at various stages in the climate change  
period. Initially, we allow the population to obtain quasiequilibrium under stable  
252 climate and this is what is shown in Figure 2a. At this stage, we define a ‘climate  
envelope’ for our simulated species. We establish the range of environmental condi-  
254 tions within which 99% of the individuals are found. We show the location of this  
climate envelope during the period of environmental change to illustrate how well  
256 the population’s range responds. In the example given in Figure 2, as the environ-  
ment changes, the population’s range lags behind its climate envelope. This is most  
258 marked at the expanding front, with the leading edge of the range advance falling a  
substantial distance behind the shifting climate window. However, it is also apparent  
260 that at the trailing edge some individuals are found well behind what we defined as  
the species’ climate envelope.

262 Running the simulation model for a wide range of parameter combinations re-  
vealed a rich range of behaviours. We illustrate some of the most important features



264 in Figure 3a which shows mean phenotypes across the environmental gradient on  
one axis, and how this distribution of phenotypes changes during and subsequent to  
266 a period of climate change (see Figure 3). For most runs of the model where the  
population survives the episode of climate change we observe that the range width  
268 following climate change is narrower (Figures 3a, 3b and 3d). This is a consequence  
of the loss of phenotypes adapted to the warmest and coolest extremes that were  
270 occupied by the population prior to the onset environmental change. Ultimately  
phenotypic variation is recovered and the range expands to reoccupy its original  
272 niche but this can take many thousands of generations. A common feature of the  
results is the initial expansion of the cold-adapted phenotypes (shown in green in  
274 Figure 3a) after the onset of change, but this is followed by a rapid collapse of these  
phenotypes (Figures 3b, 3c and 3d) and, in some cases, a rapid collapse of the whole  
276 population (Figure 3c). Figure 3c illustrates an important result: even when there  
is a considerable overlap between the range of a species prior to climate change and  
278 the climate envelope of the species following change (shown by the white lines in  
Figure 3) extinction can still occur. Finally, we sometimes observe dynamics where  
280 the population splits into distinct subpopulations comprising individuals with quite  
distinct phenotypes. Because they are adapted to quite different climates, these sub-  
282 populations can remain spatially disjunct for quite lengthy periods following climate  
change (see Figure 3d).

284 Figures 4 to 6 show the results of our sensitivity analyses, conducted to establish to  
roles of the different model parameters in determining the likelihood that a population  
286 is able to survive a period of climate change. Unsurprisingly, steeper declines in

individuals' reproductive fitness as they are moved away from their own optima  
288 (i.e. small  $V_s$ ), lead to reduced probabilities of populations surviving climate change  
(Figure 4a). However, for the sensitivity analysis around  $W_s$ , the results are a little  
290 less expected. Higher probabilities of extinction are observed when the fundamental  
environment niche of the species is broader (i.e. the chance of extinction is greater  
292 for higher  $W_s$  - see Figure 4b).

Perhaps our most important result is illustrated in Figure 5. This figure shows  
294 the results of simulations conducted to establish the role of  $p$  in determining the  
likelihood that species survive an episode of climate change. Recall that  $p$  determines  
296 the probability that an offspring is able to displace an already established individual  
from the site to which it disperses. The counterintuitive result shown in Figure 4b  
298 was obtained for  $p = 0.0$  (i.e. there is an absolute priority effect). When the opposite  
is assumed, and offspring always displace existing occupants (i.e.  $p = 1.0$ ), we find  
300 that species that have broader fundamental niches (higher  $W_s$ ) are now more likely to  
survive than those with narrower niches (lower  $W_s$ ). Interestingly, when we assume  
302 an offspring has a 50% chance of displacing an existing occupant ( $p = 0.5$ ), we find  
that the initial result holds and extinction risk is higher for higher  $W_s$ .

304 We find that the probability that a species' range survives a period of climate  
change is far more sensitive to some of the model's parameters than others. In  
306 general we find that the results are largely insensitive to the mutation parameters,  
neither the mutation rate nor the effect size of a single mutation have noticeable  
308 impacts (results not shown). However, the scale of pollen dispersal, the length of the  
period of climate change, the extrinsic probability of mortality and the width of the

310 landscape all have major effects. In general, extinction risk is higher when pollen  
disperses shorter distances (Figure 6a), the period of climate change is longer (Figure  
312 6b), the probability of extrinsic mortality is lower (Figure 6c) and the landscape is  
broader (Figure 6d).

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## 314 Discussion

316 In this contribution, we have presented results from a simulation model that inte-  
318 grates key features from similar models exploring species' dynamics in response to  
320 environmental change (Brooker et al., 2007; Dytham, 2009; Mustin et al., 2009, e.g.)  
322 and from previous analytical theory exploring local adaptation on environmental gra-  
dients (Kirkpatrick and Barton, 1997; Pease et al., 1989). We establish that local  
adaptation can play a major role in determining the dynamics of range shifting un-  
der climate change, and suggest that this is likely to have important implications for  
predictions of the impact of environmental change on both future species ranges and  
the rates of extinction.

324 Two results from our work clearly highlight how local adaptation can alter the  
nature of range shifting. First, a species may fail to survive a period of climate change,  
326 even when there is an overlap between its range prior to climate change and the area  
where climate is predicted to be suitable following climate change. Second, we find  
328 that often a range begins to expand in the direction of climate change before rapidly  
collapsing to extinction. Both these results have important applied implications.  
330 The first suggests that any predictions based upon treating the species as a single  
homogenous unit may be flawed and that, for this reason, simple extensions of the  
332 bioclimate envelope approach are likely to be inadequate. The second implies that we  
need to be extremely cautious before inferring that species that are already expanding  
334 their ranges in the direction of climate change will continue to do so.

In our initial simulations, we found that species occupying broader niches more

336 at risk of extinction due to climate change. This counterintuitive result required  
further investigation, and the key assumption driving this difference turned out to  
338 be local density dependence in the form of space occupancy. In the initial simula-  
tion model, individuals occupy a patch until they die and are never displaced by a  
340 newborn individual. When we alter the priority effect within the simulations, such  
that established individuals are no longer invulnerable to displacement by newborn  
342 individuals, we find that species with broader ranges in a stable climate are better  
able to survive a period of environmental change. Pease et al. (1989) concluded that  
344 without local density dependence, a species with a broader range was less likely to  
become extinct during an episode of climate change. This is agreement with our  
346 findings.

Examining the original distributions of the population before climate change in  
348 the simulation, it becomes clear why the result has been obtained. The individuals  
at the periphery of the range (those lying on the lines at the extrema of the current  
350 climate) are lower in density and will necessarily have a lower birth rate than those to-  
wards the centre of the distribution (given the same local adaptation). The offspring  
352 of these individuals will however be able to establish more readily since the density  
of individuals decreases away from the globally optimal location. Thus, we note that  
354 the absolute gradient of the density of individuals away from this global optimum  
increases with decreasing  $W_s$ . As a result, we see that decreasing  $W_s$  increases the  
356 availability of patches surrounding the optimum location, into which offspring can be  
born. Therefore as the climate starts to shift and the optimal location moves upwards,  
358 the high frequency of better adapted individuals with higher birth rates around the

centre of the distribution have more space to move forward in the range and the  
360 individuals at the front of the distribution are soon optimally located, making them  
more fecund (despite being less locally adapted) but with fewer density dependent  
362 effects limiting their birth rate. This then creates a faster turnover of new individ-  
uals, on which selection can act. When  $W_s$  is large, this movement and selection of  
364 phenotypes is much impaired leading to an overall reduction in the adaptability of  
the population and an increased chance of extinction. The local density-dependence  
366 effects have a much more striking effect on extinction probability than mutation rate  
or mutation size, which do not ameliorate extinction probability if density dependent  
368 effects are present.

The important role played by local density dependence, mediated through space  
370 occupancy effects, has recently been demonstrated for species assemblages and our  
results clearly demonstrate that it can also be important within a species. Takenaka  
372 (2004) uses simulation modelling to explore the distributions of coexisting tree species  
as they shift their ranges due to climate change. Takenaka's work shows that the  
374 replacement of one species by another better adapted to the new climatic conditions  
can be dramatically slowed if mature individuals continue to block space for lengthy  
376 periods even though the climate no longer suits them. Brooker et al. (2007) also  
described a similar space blocking effect in a simulation model describing the range  
378 dynamics of an assemblage comprising species arranged along an environmental stress  
gradient. The authors highlighted that the longevity of an organism would determine  
380 the strength of the effect. Our work highlights that these effects are not limited to  
interspecific interactions; prolonged space occupancy beyond the point at which an

382 individual is well adapted to local conditions can similarly limit the range shifting  
of locally adapted phenotypes within a single species. An important determinant  
384 of species' extinction, both within and between species, will be the relative rates  
at which fecundity and mortality are impacted as the climate shifts. If fecundity  
386 declines relatively rapidly, space occupancy effects will be greater, while if mortality  
increases more rapidly, when environmental conditions are displaced from those to  
388 which an individual is adapted, the effect will be weaker. Additionally, higher rates  
of fitness-independent mortality will reduce the strength of the space blocking effect  
390 and allow more successful range shifting (see Figure 6c for an example). In future  
work, it will be interesting to explore how the partitioning of local adaptation within  
392 and between species may influence the spatial dynamics of a species guild under  
climate change scenarios.

394 An interesting feature of our results is that a species can become extinct even  
when the climate envelopes before and after climate change overlap. The realisa-  
396 tion of the simulation model illustrated in Figure 3c shows this effect very clearly.  
Representation of a species as a single unit, as is the case in the statistical pattern  
398 matching methods used in bioclimate envelope modelling (Bakkenes et al., 2002;  
Broennimann et al., 2006; Schwarz et al., 2006; Thuiller et al., 2005) neglects this  
400 potentially crucial effect. There is an urgent need for a careful consideration of the  
taxonomic resolution at which we should be modelling the response of biodiversity  
402 to climate change. As further information becomes available on the extent to which  
populations within species are differentially adapted to local conditions, a critical  
404 appraisal of the importance of this evolutionary process will be required.

406 This question of the organisational level at which species are represented also  
needs addressing within the community using dynamic vegetation models to pre-  
408 dict both changes in ecological and biogeochemical processes during climate change  
(Cramer et al., 2001; Morales et al., 2005). Many of these models do not even work  
410 at the resolution of the species, instead they group species into functional types and  
assume that all members of a functional type share an identical environmental niche.  
412 In reality, species (or populations) towards the cooler end of the environmental space  
that can be occupied by the functional type will not function in warmer conditions as  
effectively as those species (or populations) that have adapted to the heat, and vice  
414 versa. This may have important consequences not only for the projections of future  
patterns of biodiversity made by this type of model but also for their projections of  
416 future biogeochemical cycles and balances.

418 A new generation of models is required that takes the best parts from bioclimate  
modelling and incorporates ecological and evolutionary dynamics. The results pre-  
sented in this paper make a strong case for the inclusion of local adaptation as a  
420 matter of urgency. One conservation management option to mitigate some of the ef-  
fects described in this paper would be the translocation of genotypes within a species  
422 range. Our simulations tend to show that the phenotypes adapted to the local condi-  
tions found in the core of the range tend to be the most important for range shifting,  
424 and from this we would suggest that a potential strategy would be to translocate  
individuals (for plants, pollen might suffice) from core areas to populations located  
426 towards the expanding front. A model parameterised with species-specific informa-  
tion on dispersal distance and the genetics of local adaptation would be an invaluable



428 aid in developing this type of strategy, and could be used to provide recommendations  
430 on the optimal amount and frequency of translocation.

430 The model considered in this paper has much in common with a model used  
432 to explore the dynamics of speciation along environmental gradients (Doebeli and  
434 Dieckmann, 2003). Interestingly, we have observed that in some regions of parameter  
436 space we find that disruptive selection can result in two (or more) spatially distinct  
438 species arising in our simulation model. This is not the main topic of this paper,  
440 however we note that both during and following a period of climate change a species'  
442 range tends to become fragmented (see Figures 2 and 3d). In some cases this spatial  
444 separation can last for a considerable period following the stabilisation of climate  
446 (Figure 3d) and it is interesting to speculate that in some cases this may act to  
448 promote speciation. It would certainly be worthwhile extending recent speciation  
450 models (Artzy-Randrup and Kondrashov, 2006; Bolnick, 2006; Yukilevich and True,  
2006) to consider the potential impacts of environmental change.

442 Understanding the response of biodiversity at different organisational levels un-  
444 der a period of rapid environmental change represents the greatest challenge faced  
446 by ecologists today. Here, we have considered how local adaptation within a sessile  
448 species' range can impact on that species dynamics during climate change. By apply-  
450 ing ideas and methods that are already well developed in the ecological literature we  
have obtained several new insights that we believe have important consequences for  
how we should go about both predicting and also managing changes in biodiversity  
under climate change. We hope that the results from theoretical studies such as this  
one make a persuasive case for a closer integration between the statistical modelling

that currently dominates the climate impacts literature and dynamic spatial models  
452 incorporating biological processes.

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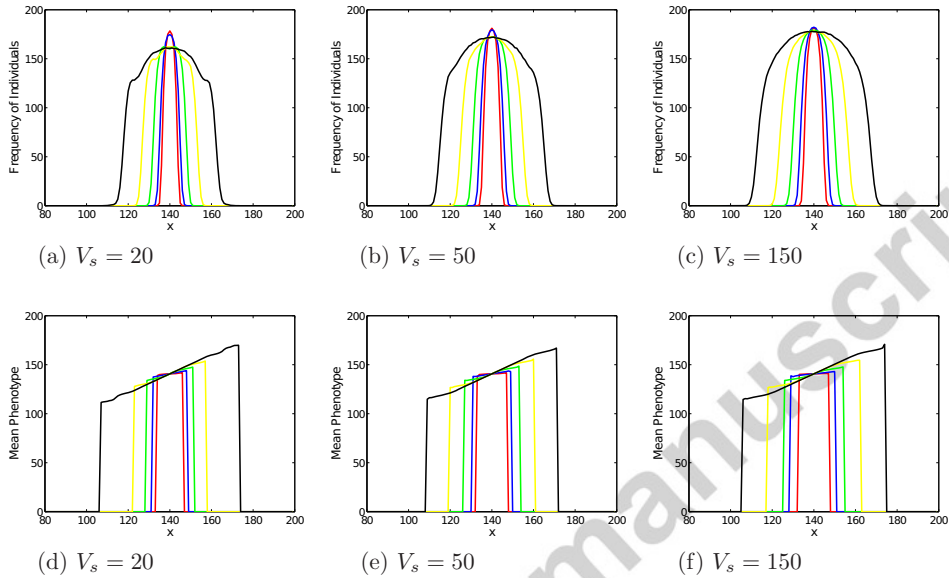


Figure 1: Frequency distributions for population size and trait value for the equilibrium in a constant environment, where the environment changes with  $x$ . The results were averaged over 50 realisations of the model. A set of simulations were run for a different values of  $2\ln W_s$ , given on the graph by different colours (red-2, blue-3, green-4, yellow-5, black-6). An increasing value of  $W_s$  relates to an increased environmental niche range, seen in Figures (a), (b) and (c). In Figures (d), (e) and (f) the mean phenotype is an average of all allele values (2 per individual) existing on the environmentally invariant line  $y = const$ . In the case of zero density, the mean phenotype is given a value 0.

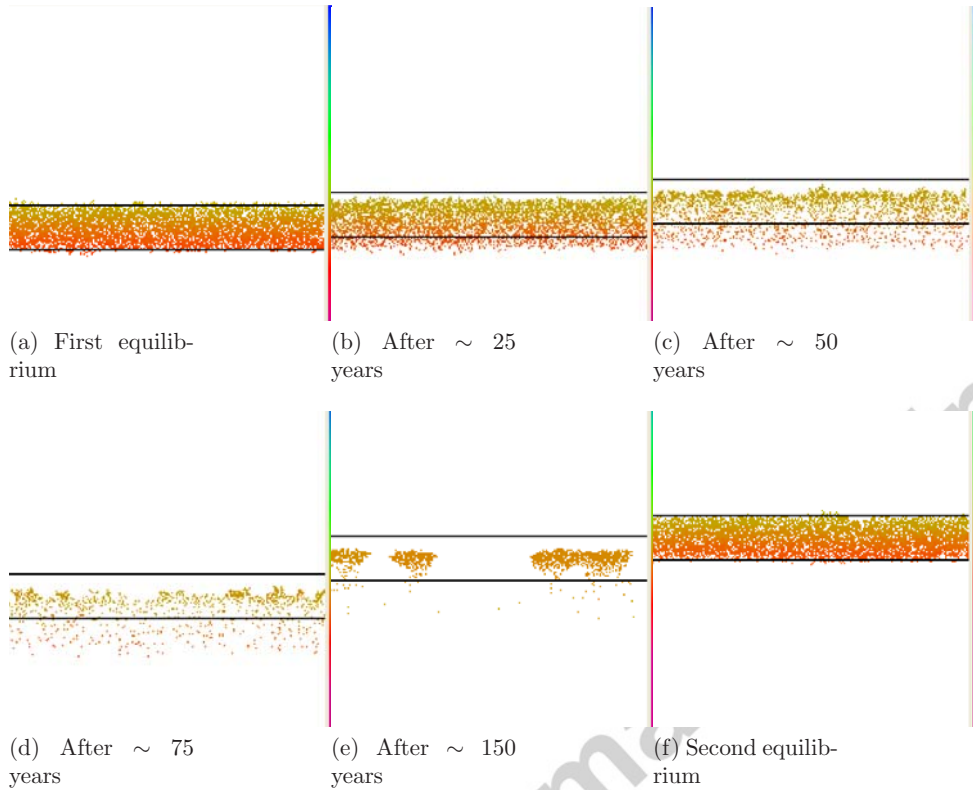


Figure 2: Snapshots of one realisation of the model showing population inhabiting the 2d lattice landscape. The grid corresponds to the individuals on the grid with the invariant environment of each row and changing environmental gradient through each column. The colour grid shows the optimal trait value for each location,  $\theta(x)$ , running from hot (red) to cool (blue). Individual patch colour shows trait value to which the individual is adapted,  $z$ . The climate envelope (shown by black lines) indicates the area holding approximately 98% of the population at pre-climate change equilibrium, with the median at the optimal. (a) shows the equilibrium in a constant environment before any climate change has occurred; (b), (c), (d) and (e) show the population at a specified time after change onset and (f) shows final distribution after climate change. Illustrative parameters are chosen as  $W_s = \exp(5)/2$  and  $V_s = 25$ , under a climate change rate of  $\nu = 0.3$  over  $T = 200$  years to emphasise the range shift. During the climate shift this envelope tracks the environmental optimal for the population. The population splits into clusters before combining once the shift ends.

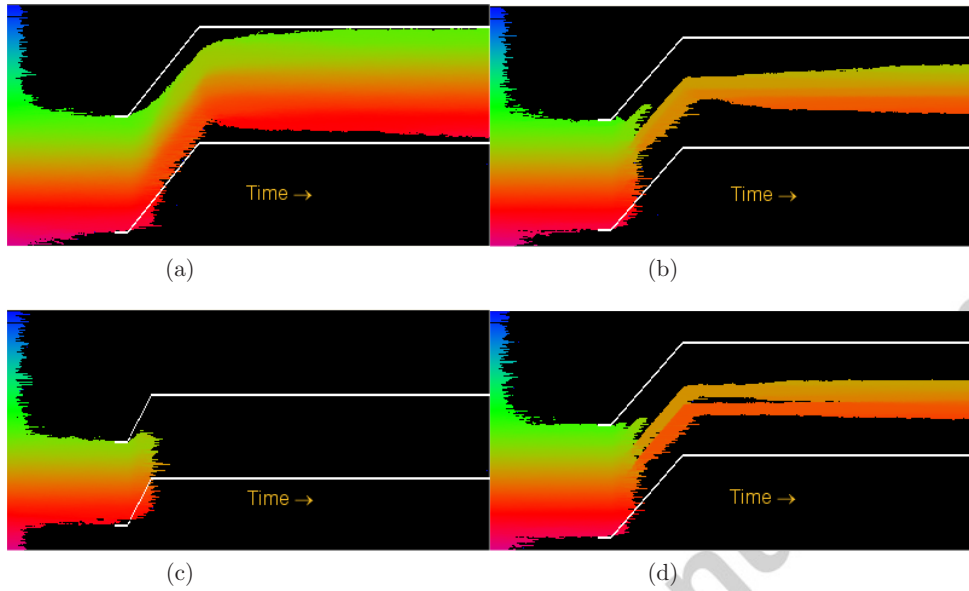


Figure 3: Four realisations of the model through a period of climate change. The colours show the population and its local adaptation,  $z$  (blue through to red). (a) shows population persistence with the majority of individuals tracking the climate;  $T=300, V_s=100, W_s=500, \nu=25$  leading to the subpopulation at the rear and very front of the range being lost but population persisting due to the middle third of the pre shift population moving. (b) shows population persistence through climate change with only a small subpopulation tracking the climate;  $T=300, V_s=10, W_s=500, \nu=23$  allowing population movement due to the middle of the front half of the range shifting, although front margin does show signs of initial movement. (c) shows population extinction during climate change;  $T=100, V_s=50, W_s=250, \nu=40$  produces a climate shift too fast for adaptation. (d) shows population persistence with two small subpopulations tracking the climate;  $T=300, V_s=7.5, W_s=500, \nu=23$  produces similar subpopulation shifting its range as seen in (b) but shift occurs in two geographically distinct subpopulations, which eventually rejoin for good on reaching the new equilibrium.

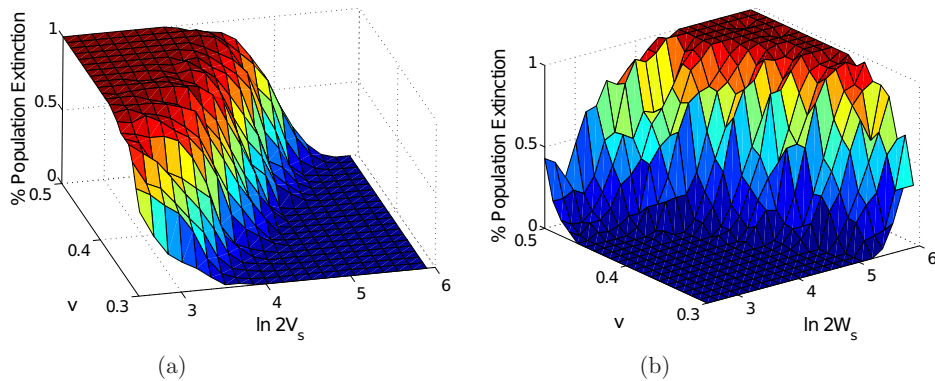


Figure 4: Sensitivity analysis for variance revealing both population variances ( $V_s$  and  $W_s$ ) having opposite effects on extinction probability in the model with (a) showing the effect of variance around local optimal adaptation and (b) the effect of variance around the optimal location. The extinction probability for any population can be noted as a non-decreasing function of the rate of climate change,  $\nu$ . Notice that an increase in the environmental niche (an increase in  $W_s$ ) leads to a increase, or no change, in the extinction probability.

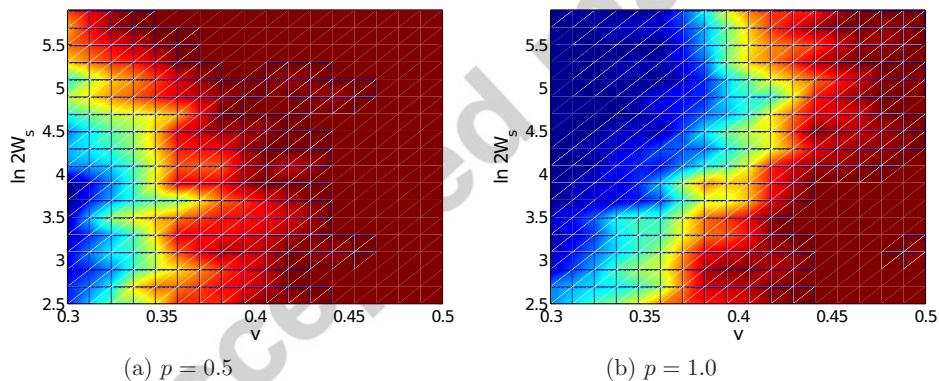


Figure 5: The effect of decreased density dependent effects on proportion of populations extinct under climate change. Red to Blue scale corresponds as before to 100% to 0% of populations extinct after climate shift. Note the qualitative difference in the two trends: in (a) where  $p=0.5$ , a large range width corresponds to a higher extinction probability, whereas in (b) a large range width allows better population persistence.

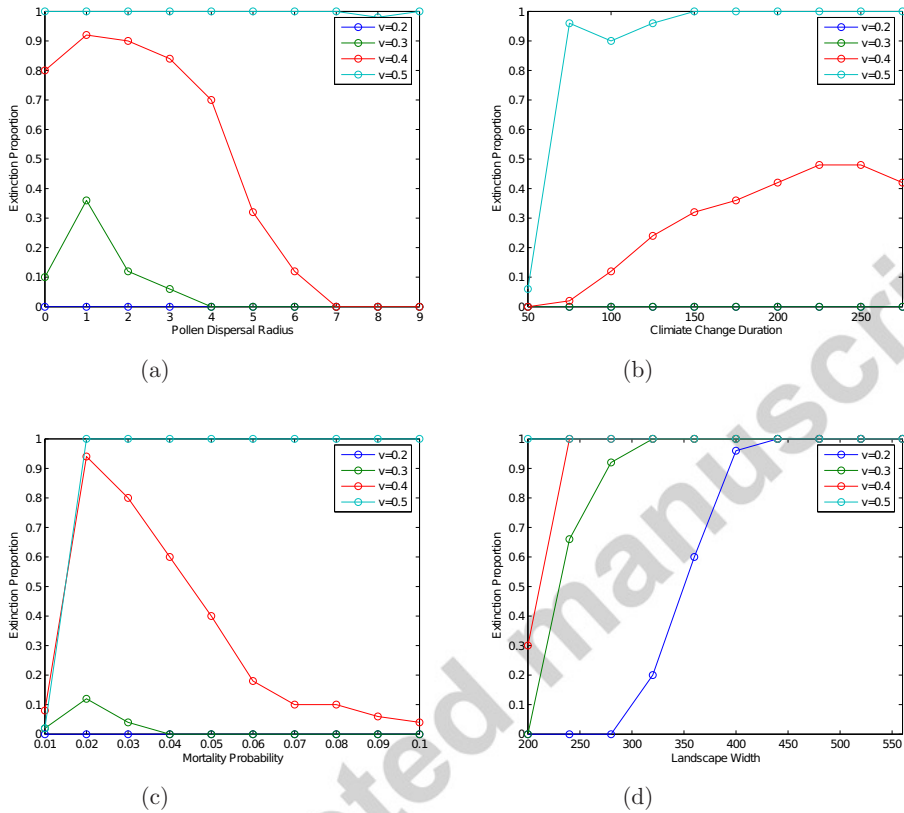


Figure 6: The effect of different parameters on species extinction. The plots show the proportion of realisations (out of a total of 50) where the species became extinct with varying rates of climate change. In all cases,  $W_s = 150$  and unless otherwise varied, parameter values are kept constant at  $N = 200$ ,  $T = 200$ ,  $V_s = 50$ ,  $\mu = 0.005$ ,  $\sigma = 1.207$  and maximum mutation size is set at 10.