



Changes in species' distributions during and after environmental change: which eco-evolutionary processes matter more?

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Improving our capacity for predicting range shifts requires improved theory exploring the interplay between ecological and evolutionary processes and the (changing) environment. We introduce an individual-based model incorporating simple stage structure and genetically determined resource allocation rules. Population dynamics are mediated by the resources available and the individual's genetics, and density dependence emerges solely as a consequence of resource levels decreasing as population density increases. Running the model for a set of stylised range-expansion scenarios reveals the extent to which eco-evolutionary processes can matter: spatial assortment of individuals possessing effective range expansion strategies (higher dispersal propensity, semelparity rather than iteroparity) can substantially accelerate range advance, and this is more important than the contribution of novel mutations arising during range expansion. In simulations of range expansion there is a greater risk of extinction when all individuals are given the mean strategy evolved in a stationary range. Additionally, our results demonstrate that the erosion of inter-individual variability during a range-shift can depress population abundance for lengthy periods, even after the climate has stabilised. Our theoretical results highlight the importance of accounting for inter-individual variability in future predictive modelling of species' responses to environmental change.

The century to 2006 saw a global warming of 0.76 degrees Celsius (Solomon et al. 2007). With projections of climate, for a range of scenarios, to warm another 0.3–6.4 degrees by the end of this century (Solomon et al. 2007) it might be expected that the distributional ranges of organisms will shift, perhaps by considerable distances. These distributional shifts are expected to track the most beneficial climatic environment, with species generally expected to move polewards (Parmesan 2006), or alternatively, and where it may be possible, species may track climate up an altitudinal gradient (Wilson et al. 2005).

Understanding the way that species may respond to environmental change is important not only for predicting the impact on biodiversity, but also in enabling the development of more effective conservation instruments to mitigate the potential loss of species (Dawson et al. 2011, Weeks et al. 2011, Hodgson et al. 2012).

The great majority of existing predictive modelling has relied on the 'climate envelope' approach (Berry et al. 2002, Araujo et al. 2005, Beaumont et al. 2005). This statistical

method takes a current species' distribution, identifies the climatic variables that correlate most strongly with the distribution, and then predicts the climate envelope under scenarios of climate change. The simplest assumption is then that the change in species distribution equates to the change in location of the climate envelope. However, such an approach is only likely to have limited success for a number of reasons. One such reason is that in addition to climate change, organisms are likely to face increasing habitat degradation and fragmentation. For example, some 38% of global (non-ocean) surface is currently under some form of agriculture (FAO 2007), and there is a risk that pressure on land will increase considerably, either through conversion or intensification of existing land (Foresight 2011, Tilman et al. 2011). For many species, this land use change will directly result in a reduction of range extent and global population abundance through the direct impact of a reduction in suitable habitat available. However, land use change is also likely to strongly interact with climate change in determining future distributions as the amount and pattern of available habitat will determine how rapidly species may track climate envelopes in space (Travis 2003, McInerney et al. 2007, Hodgson et al. 2012).

Improved understanding of how species will respond to environmental changes, including warming climate and intensification of farming, requires models that incorporate

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eco-evolutionary processes. This realisation has resulted in a rapid recent increase in theoretical and conservation interest on the effects of habitat heterogeneity, spatial demography and life history characteristics on range dynamics, species distribution and persistence under climate change (Mustin et al. 2008, Anderson et al. 2009, Wiens et al. 2009). As a simple example, if species have restricted dispersal abilities, and the environment is changing rapidly, they may be unable to track the available habitat as it moves geographically (Trakhtenbrot et al. 2005). Projections of species' future distributions are now beginning to incorporate some of the ecological processes that existing theory has indicated should be important and, to date, the primary focus has been on including dispersal (Engler and Guisan 2009, Willis et al. 2009, Midgley et al. 2010, Nathan et al. 2011). Not surprisingly, projections made by models incorporating dispersal often differ substantially from the basic climate envelope models (Zurell et al. 2012).

The way a species responds to changes in the environment is determined by the response of its individuals (such as by changes in their survival, growth, reproduction and dispersal) (Burton et al. 2010, Phillips et al. 2010a) and additionally the stage/age structure (Benton et al. 2006, Bullock et al. 2012) of the population. The former is complex and may depend not solely on the current conditions (Beckerman et al. 2002, Cormont et al. 2011) but also those experienced by individuals beforehand (Bonte et al. 2008, Gibbs et al. 2011) and even, through maternal effects, environments experienced in previous generations (Plaistow and Benton 2009). In addition to potentially quite complex influences of plasticity, there is increasing evidence that evolution may also affect the life history (and therefore the population dynamics) on timescales that are much shorter than would have previously been expected (Lambrinos 2004, Moloney et al. 2008, Hendry et al. 2010) and even that ecological and evolutionary dynamics are inseparable in timescale (Carroll et al. 2007). Importantly, life-history evolution and plasticity are likely to play joint roles in determining how species respond to environmental changes and indeed the plasticity can itself come under strong selection through the evolution of an organism's reaction norm (Lande et al. 2014).

Our motivation within this study is to extend previous theory on the spatial dynamics of species' range shifts to consider two potentially important aspects that remain under explored, namely the roles of age/stage structure and plasticity. We develop a novel model, that incorporates a greater degree of mechanism than previous theory, to address the issue of how a species' response to environmental change may be dependent on a set of potentially interacting biological details (such as age/stage structure, life-history plasticity in response to resource levels and the potential for life-history evolution). The model is stage-structured and individual-based, where each individual's life-history is determined by the resources available within a patch (which results from an interaction between the resources in the environment and depletion by competition). Individuals have two genes which govern their allocation of resources to maintenance and therefore survival; as a juvenile, resources not allocated to survival are allocated to dispersal and, as an adult, resources not allocated to survival are allocated to reproduction. The population dynamics are determined by the resources available and the individual's genetics, and, importantly, there is

no phenomenological density dependence imposed, rather the density dependence emerges solely as a consequence of resource levels decreasing as population density increases. Using this simple model, we ask the question 'how much does the choice of eco-evolutionary processes that we incorporate in the model matter to the speed with which a species is projected to invade a new landscape?' We ask this question under two scenarios, one where the landscape is constant in the amount of resources available and the other where the resources are changing (as a proxy for climate change). If the details incorporated in the model make little difference to the range-shifting dynamics, then it would suggest that simple statistical pattern-matching models could reasonably be used to predict responses to climate change, or at least that simple unstructured, fixed-parameter, non-evolutionary dynamic models of the type beginning to be used to predict species' future ranges (Engler and Guisan 2009, Willis et al. 2009, Midgley et al. 2010, Nathan et al. 2011) may suffice. However, if the greater mechanistic details incorporated in our modelling do matter, it is important to have some understanding as to how much.

Method

Description of the model

We use an individual-based, stage-structured, discrete time model with individuals located in continuous space and explicit allocation of resources to survival, reproduction and dispersal. Although individuals are located in continuous space, they compete for resources that are represented in square patches of unit size. There are two life stages (juveniles and adults) and only one 'gene' to describe the resource allocation at each stage (G1 and G2) which can take on any value between 0 and 1 describing the proportion of available resources allocated to survival. For juveniles remaining resource is allocated to dispersal, while for adults it is allocated to reproduction (Fig. 1). Time passes in 'years' and individuals acquire resources from the local area (resource patch). Individuals can live for several years and must spend at least one year as a juvenile.

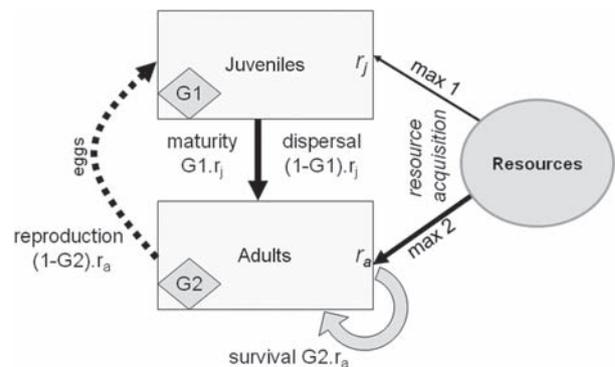


Figure 1. An outline of the method. G1 determines the proportion of resource acquired by juveniles that is assigned to survival, the remainder is assigned to dispersal. G2 determines the proportion of resource assigned by adults to survival, the remainder is assigned to reproduction.

Resources are added to the environment at the end of each year. For most scenarios a random amount of resource drawn from a Poisson distribution with a mean of 20 is added to each cell. Resources are depleted by individuals and, for simplicity, we assume both juvenile and adult stages use the same resource. We assume that adults are better at resource acquisition than juveniles. Each juvenile can remove up to 1 unit of resource and each adult up to 2. If the amount of resource that could be taken exceeds the amount of resource in the cell the resource is divided equally among all individuals in the patch with the caveat that adult shares are twice as large as juvenile shares. So, in a cell with 30 resource units and a population of 1 juvenile and 1 adult the individuals will take 1 and 2 resource units respectively, leaving 27 units. However, if there was only 1 resource unit in the cell the juvenile would acquire 1/3 and the adult 2/3 of a unit of resource leaving none.

An individual's survival is determined by the resources it has acquired and its genes. A juvenile with $G1 = 0.5$ (or an adult with $G2 = 0.5$) that has acquired exactly 1 unit of resource will have a 50% chance of survival. However, the juvenile from our previous example, which only acquired 0.33 units of resource has a 16.5% (0.5×0.33) chance of survival.

For surviving juveniles, resources not used in survival (i.e. $(1 - G1) \times$ resource acquired) are used in dispersal. A random number is drawn from a negative exponential distribution with a mean of $((1 - G1) \times$ resource acquired) and the result is multiplied by a dispersal scalar (D , a variable, usually 2, that converts resources allocated to dispersal to a dispersal distance) to give an achieved dispersal distance. A random direction (uniform between 0 and 2π radians) is chosen and this movement (distance and direction) is converted from polar to rectangular coordinates and the location of the individual is updated. There is no mortality during dispersal whatever the distance moved. The simulated area is a torus with periodic boundaries (except for the invasion scenario). Juveniles make the transition to adulthood immediately after dispersal.

For surviving adults, the remaining resources after investment in survival (i.e. $(1 - G2) \times$ resource acquired) are converted to offspring. The cost of offspring is variable, but unless specified otherwise, it is 0.65. Available resources are depleted until there is a fraction of the cost of an offspring remaining. This fraction becomes the probability of producing an additional offspring. So, an adult with a $G2$ of 0.5 that acquires 1.6 units of resource, has a 0.8 survival probability and 0.8 units of resource ($(1 - G2) \times 1.6$) available to invest in offspring. It will always have at least one offspring as $0.8 > 0.65$. However, the resources used in producing that offspring leave it with 0.15 units and it produces a second offspring with probability 0.15/0.65. No resources are stored.

Offspring appear at exactly the same location as their parent and disperse as described above. They inherit $G1$ and $G2$, although in all simulations described here, except where mutations have been excluded, there is a 1% chance of a mutation at each birth event (which is towards the top end of the range of possible values for mutations). Mutations affect $G1$ and $G2$ with equal probability and mutants inherit their parental strategy plus a uniform variate between -0.02 and $+0.02$, limited to the range 0–1.

Behaviour of the model and evolved strategies in a stationary range

We model a population in a 50×50 cell area, initiated with 50 000 individuals assigned a random location and random values of $G1$ and $G2$ (drawn from a uniform distribution, [0–1]). The simulation runs for 30 000 yr and then outputs the values of $G1$ and $G2$ for each juvenile during the last 200 yr of the simulation (adults will not be representative of the gene frequencies in the population due to mortality). We also determine the achieved dispersal distances and offspring abundances for this population. We used a range of costs of offspring and dispersal multipliers, D . We had previously established that 30 000 yr was more than sufficient for a quasi-evolutionary equilibrium to be obtained. Indeed, regardless of initialisation rules, evolution typically occurs rapidly over the first 2000 yr and the quasi-equilibrium is obtained then or soon afterwards (Supplementary material Appendix 1, Fig. A1 for typical examples).

Scenarios

Invasion

Our approach to modelling range expansions is similar to those previously used to explore evolutionary dynamics during range expansions (Travis et al. 2009, Burton et al. 2010, Barton et al. 2012). The resource grid is 50×300 cells, with the long edges being joined to avoid edge effects (so a partial torus rather than a full torus). The invasion scenario is initiated with a seed population derived from a simulation that had been run for 30 000 yr. The same seed population is used in all invasion scenarios with the population restricted to an area of 50×50 cells for 1000 yr. It is then released so it may expand unrestricted in one direction and we track the position of the range margin for 200 yr. We repeat this with different aspects of the model turned off (i.e. excluded from the model). In turn, we remove mutation, inter-individual variation in $G1$ and $G2$ (i.e. at the point of release all individuals have the same, set level of $G1$ or $G2$), the relationship between resource and dispersal (i.e. all individuals have the population's mean dispersal distance regardless of resources acquired) and combinations of these. For scenarios where the values of $G1$ and $G2$ are fixed, we arbitrarily take values of 0.838 and 0.498 respectively. A mean achieved dispersal distance of 0.186 was recorded with cost of offspring 0.65 and dispersal multiplier 2. Each scenario was repeated 20 times.

Climate change

Here we adopt a similar approach to previous theoretical work focussing on climate-driven range shifts (Travis 2003, Mustin et al. 2008). The resource grid is 50×300 cells with long edges joined to avoid edge effects. An area of suitable habitat which is 50×50 cells, centred on row 50, forms the core of the range and has a full amount of resource. Then moving away from the edges of that core is a margin of 25×50 cells with resources declining at 1 unit per cell from the edge of the core. This resource distribution remains static for 1000 yr, then moves at $0.6 \text{ cells yr}^{-1}$ for 200 yr, simulating a period of climate change. Climate change is assumed

to end at year = 1200 and the spatial resource distribution is stable in time beyond this point.

Results

Evolutionary stability in a stationary range

The evolved mean values of G1 and G2 (Fig. 2) are both sensitive to the cost of offspring, and this is particularly true for G2. As offspring become more expensive, G2 increases from values around 0.05 to values around 0.5. This indicates a shift from a semelparous life-history strategy (where adults reproduce using all their resources and therefore do not survive) to an iteroparous one (where adults invest resources in their survival, often live for more than one year, and so have the potential to breed more than once). The evolved mean G1 is constant across the range of offspring costs for which iteroparity evolves. However, semelparous individuals evolve lower mean G1 when the cost of an offspring is very low (e.g. 0.2) than they do at higher costs. Interestingly the shift from a semelparous to an iteroparous strategy (when cost of an offspring = 0.55) coincides with evolution of increased dispersal and lower juvenile survival as indicated by a reduction in the mean evolved G1.

Expansion scenarios

Invasion

During range expansion there is a clear shift in the mean life-history strategy (Fig. 3): mean G1 decreases at the front compared to the core (indicating a shift away from juvenile survival towards increased dispersiveness) and G2 decreases (indicating a shift from investing in survival towards investing in reproduction – i.e. a shift towards semelparity). Interestingly, during the shift from iteroparity to semelparity we often observe a period where the distribution of strategies

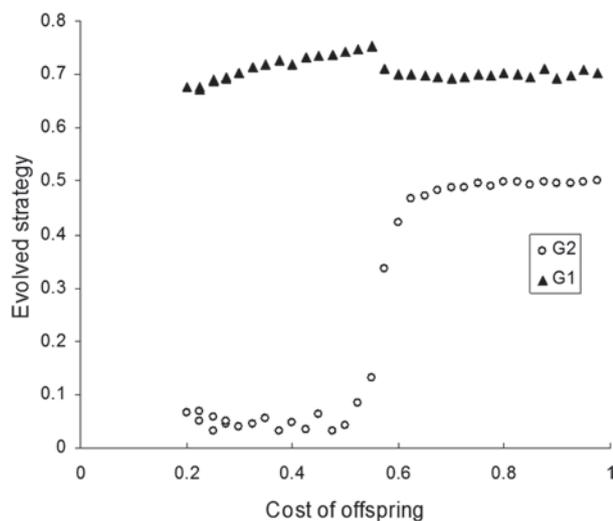


Figure 2. Evolved strategies for G1 (proportion of resources allocated to survival in juveniles) and G2 (proportion of resources allocated to survival in adults) after 1000 generations for a range of costs of offspring. Each pair of points shows the mean of 20 realisations of the model.

at the front is bimodal with a proportion of the population having G2 values around 0.5 and a proportion having much lower values, typically less than 0.1 (see Fig. 3b for a clear example).

Qualitatively, we observe similar range expansion dynamics for our sets of simulations where we in turn switch off different aspects, but the rate of expansion varies substantially between sets. In all cases, the range front expands approximately linearly (Fig. 4) during the 200 yr period with more variation in the position of the range front as time progresses. The position of the range front after 100 and 200 yr is not significantly affected by mutation (Fig. 4). However, the range moves more slowly when G1 and G2 are fixed values, more slowly still if dispersal distance is unaffected by resources acquired and slowest if dispersal distance, G1 and G2 are all fixed (Fig. 4).

Climate change

Recall that in running these simulations we first allow a population to establish (quasi) equilibrium across a resource gradient. Under a stable climate, we obtain clear variation in both local population density and evolved life-history and this is structured across the resource gradient (Fig. 5a). Population density (relative to unit space) is higher towards the core of the range where resources are more abundant and drops off towards the margins (triangles on Fig. 5a). Spatial variation across the range in G1 is also clearly apparent (black line on Fig. 5a) with a reduction in G1 at the margin (i.e. more investment in dispersal in marginal populations). In contrast, there is relatively little variation across the range in G2 (not shown in Fig. 5 – but see Supplementary material Appendix 2, Fig. A2 for illustration).

At the point when climate change ceases (year = 1200), the range is substantially narrower (Fig. 5b) and there is much reduced variability in G1; across the range, the mean G1 is close to that which evolved in the marginal populations in a static climate (i.e. relatively low G1 indicating higher investment in dispersal). After a further 200 yr, the range has expanded such that its extent is very similar to that prior to climate change (Fig. 5c), but the density of individuals in the high resource regions remains substantially depressed relative to that prior to climate change. Additionally, the mean value in G1 has remained almost invariant across the range and has not increased in the two hundred years post climate change (i.e. there is much less variation in dispersal investment across the range than there was before climate change).

Sets of simulations run with different aspects turned off clearly reveal the relative importance of the different factors (see Supplementary material Appendix 3, Fig. A3 for illustrations). Simulations with mutation switched off behave essentially the same with as those with everything switched on; total population abundance and the position of the front are very similar. However, when inter-individual variability in G1 and G2 is removed (by setting all individuals to have the mean values that evolved in a stationary range) there is a substantial effect: the population range does not move as quickly and therefore lags further behind the climate. In the particular example in Supplementary material Appendix 3, Fig. A3 the population is nearly expunged and takes a long time to recover after the period of climate change. When

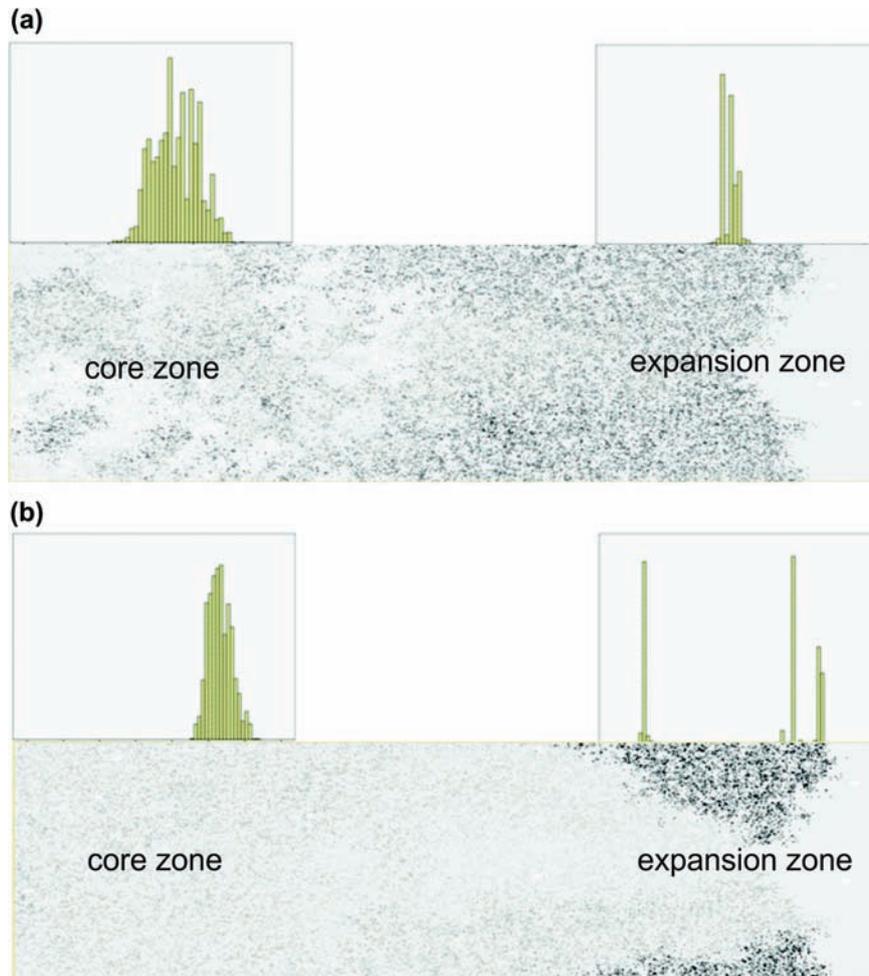


Figure 3. (a) Frequency distribution of G1 (proportion of effort to survival for juveniles, remainder is dispersal) from one realisation of the simulation in the core zone and expansion zone with a snapshot of the spatial distribution of individuals shaded by G1 (dark = low value of G1 indicating more investment in dispersal). (b) Frequency distribution of G2 in the same realisation (proportion of effort to survival for adults, remainder is fecundity) with a snapshot of individuals shaded according to their G2 (dark = low investment in survival which indicates a semelparous life history).

all individuals are given the mean dispersal propensity that evolved in a stationary range, population abundance is actually higher prior to the onset of climate change than it is when there is inter-individual variability in dispersal. However, once the climate begins to change, this simulation lags even further behind and the population is extinguished completely before the end of the climate moving phase.

Discussion

Projecting the likely future distribution of species has, until recently, relied almost exclusively on static, correlative models (Berry et al. 2002, Araujo et al. 2005, 2006, Beaumont et al. 2005, Pearson et al. 2006). There has, however, been considerable progress towards the incorporation of population dynamics and dispersal and this is apparent in recently published model frameworks, including BioMove (Midgley et al. 2010), MigClim (Engler and Guisan 2009) and RangeShifter (Bocedi et al. 2014). By incorporating species-level dispersal parameters in making projections of future

distributions these modelling frameworks have already made considerable progress. However, the results from our simulation experiments highlight that treating dispersal as a species-level characteristic may lead to biased projections of spread rates. Our results indicate that the considerable, and often observed empirically (Bowler and Benton 2005, Stevens et al. 2010), variation between individuals, driven by genetic variation, variation in per capita resources (itself driven by variation in the environment and population density) and therefore variation in the demography makes a marked difference to the rate of spread of organisms across a landscape in response to environmental change (up to 4-fold increase in the rate of expansion). Given the strength of this effect, models predicting species' distributional shifts should consider carefully whether a 'population mean approach' will be sufficiently realistic to make informative predictions at a decadal timescale. Extending current integration of modelling approaches further to link environmental niche modelling with individual-based models to explore the role of inter-individual variability in, and evolution of, life-history strategies would potentially improve our projections and, at the

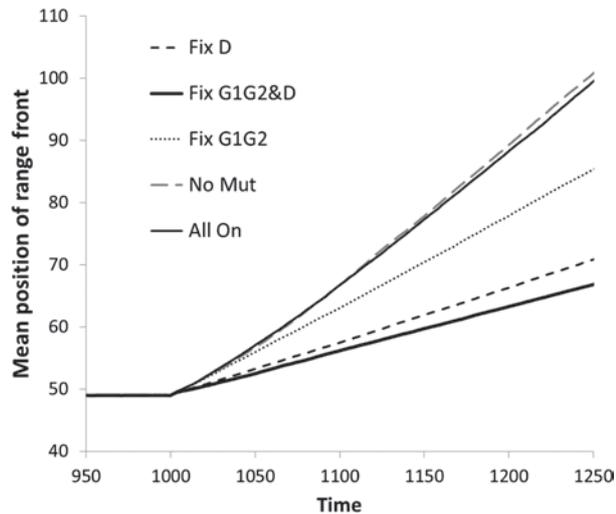


Figure 4. Mean position of the range front with elements of the model excluded (20 realisations for each scenario). Mutation on/off has no effect, fixing G1 and G2 at the population mean has some effect, but stopping dispersal being plastic (Fix D) has a huge effect. ANOVA $p < 0.001$ for time, treatment and interaction, SNK (Student–Neuman–Keuls) post hoc test for treatment shows all factor levels differ from all others at $p < 0.01$ except ‘All on’ vs ‘No mutation’ which is not significant.

very least, enable us to provide some measure of the degree to which real biological detail (Kim and Donohue 2012) is likely to generate uncertainty in our projections.

The model we have developed, and the results obtained, extend and integrate several recent developments. In population genetics there has been considerable progress in understanding the dynamics of mutations that arise at an expanding front (Excoffier et al. 2009) and of how alleles present in range margins prior to climate change have elevated probabilities of increasing in abundance during environmental change (McInerney et al. 2009). While much of this work has focussed on neutral mutations, it is now clear that during range expansions mutation surfing effects can also influence alleles that are under selection (Travis et al. 2007, Burton and Travis 2008). Figure 3 shows a clear example of surfing type dynamics with substantially lower G2 alleles surfing the wave of advance either from variability in G2 present prior to the expansion or following a mutation event close to the front that resulted in a lower G2 allele arising.

Both theoretical (Travis and Dytham 2002, Phillips et al. 2008, Travis et al. 2009) and empirical studies (Simmons and Thomas 2004, Léotard et al. 2009, Phillips et al. 2010b) have emphasised how important the evolution of dispersal can be during range expansions. In our model dispersal propensity is plastic, being dependent upon local resource availability, the density of conspecifics and the resource allocation strategy of the individual. We previously demonstrated that during range expansion selection should favour a strategy where dispersal occurs even at low local density (Travis et al. 2009), but the method was very different to that presented here as the density dependence was phenomenological rather than arising out of the resource competition mechanism. Interestingly, while our new results also demonstrate that selection for increased dispersal occurs during range expansion, we typically observe rapid selection for a frontal strategy

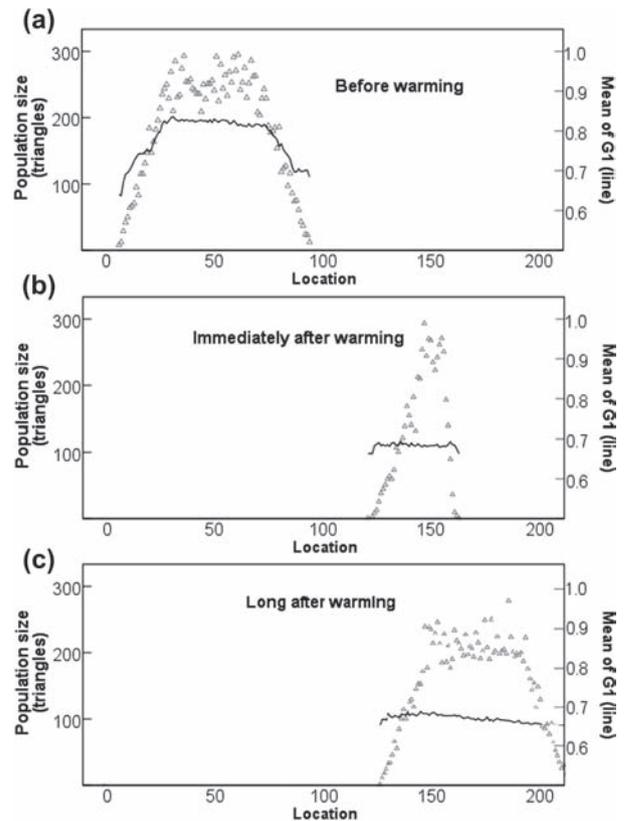


Figure 5. Results from a single realisation from climate change scenario where cost of offspring is 0.65, climate moves between years 1000 and 1200, rate of climate moving $0.6 \text{ cells yr}^{-1}$ and mutation rate is 0.01. The population size, depicted by triangles, and mean values of G1, depicted by a line, respectively is shown in (a) at the end of a period of stasis, (b) at the end of period of expansion and (c) after a further 200 yr of stasis.

from the variation that already exists in the stationary range, as has been suggested to have occurred during invasion of *Acer negundo* (Erfmeier et al. 2010). In contrast to (Travis and Dytham 2002, Travis et al. 2009), we do not see the gradual acceleration in dispersal occurring due to selection acting on successive novel mutations that occur during the period of range expansion. The difference between results is likely to be due to differences in the extent of inter-individual variability present in the range prior to range expansion, but may also, in part, be a consequence of the different modelling approaches (the one presented here incorporating much greater mechanistic realism). Assortment for dispersal strategies clearly plays a vital role in driving range expansions and future theoretical and empirical studies are required that consider density dependent effects, resource allocation and, especially, the extent of inter-individual variability in strategies.

Our results emphasise two other potentially important effects that to date have received rather little attention and are deserving of further work. First, there is clear potential for selection to operate very strongly on the fecundity schedule of a species expanding its range. Whilst previous work has explored conditions under which iteroparity and semelparity evolve (Ranta et al. 2000, 2002, Crespi and Teo 2002), this is the first to highlight a potential shift from iteroparity to semelparity during a range expansion. This shift in life

history is perhaps an extreme case, but in general we might expect to see selection favouring life-history strategies that have increased early life reproduction at the expense of later life reproduction. Second, evolution that occurs during relatively short periods of range shifting can have long-lasting impacts even after climate has stabilised and a species has obtained a new quasi-equilibrium. We find that both population abundance and the distribution of phenotypes within a species can be very different post climate change to those found prior to climate change and that this pattern persists long after the episode of climate change. This highlights the need for more theory and for applied modelling considering not only whether species will survive, but asking in what form they will survive and what will the consequences of this be both for conservation and for the sustainability of ecosystem services.

In conclusion, we suggest that predictions of rates of range expansion may be systematically wrong if they fail to account for inter-individual variability and, even if variation is incorporated, the wrong result is likely to be attained if the resource allocation strategy is specified incorrectly. Adding sufficient realism to obtain reliable estimates is clearly challenging (Evans et al. 2012). However, we believe that future empirical work directed at understanding the causes (both plastic and heritable) and extent of inter-individual variability in life-history strategies can lead to rapid progress. A combination of experimental work on a set of case study organisms together with sampling and monitoring across large scale environmental gradients of populations (and, importantly, the variation in life-histories found within and between them) is required for moving from strategic modelling of the type presented here towards the incorporation of greater biological realism in predictive, species-specific or scenario-specific modelling.

Acknowledgements – The authors would like to thank the participants of UKPopNet Working Group ‘Integrating spatially explicit statistical models and individual-based modelling using Bayesian statistics II’, especially Barbara J. Anderson.

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Supplementary material (Appendix ECOG-01194 at <www.ecography.org/readers/appendix>). Appendix 1–3.