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Local adaptation and the evolution of species' ranges under climate change

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ABSTRACT

The potential impact of climate change on biodiversity is well documented. A well developed range of statistical methods currently exists that projects the possible future habitat of a species directly from the current climate and a species distribution. However, studies incorporating ecological and evolutionary processes remain limited. Here, we focus on the potential role that local adaptation to climate may play in driving the range dynamics of sessile organisms. Incorporating environmental adaptation into a stochastic simulation yields several new insights. Counter-intuitively, our simulation results suggest that species with broader ranges are not necessarily 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 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 will not always be the cold-adapted phenotypes that drive polewards range expansion. Instead, range shifts may be driven by phenotypes conferring adaptation to conditions prevalent towards the centre of a species' equilibrium distribution. This may have important consequences for the conservation method termed predictive provenancing. These initial results highlight the potential importance of local adaptation in determining how species will respond to climate change and we argue that this is an area requiring urgent theoretical and empirical attention.

1. Introduction

The threat that climate change poses to biodiversity is well documented (Parmesan and Yohe, 2003; Pearson et al., 2002; Peterson et al., 2002; Thomas et al., 2004; 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 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 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 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 38–52%. Whilst this study represents a useful exercise, not least in terms of focussing minds on the problem at hand, it simultaneously highlights some important deficiencies 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 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 and evolutionary processes for range dynamics under climate change. Local adaptation is a good example of one of these processes: many species comprise collections of 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 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 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 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 model to explore the issue of how local adaptation influences a species ability to track changing climate.

A plethora of studies have used bioclimate envelope modelling to predict the future biogeographic ranges of species (Bakkenes

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et al., 2002; Broennimann et al., 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 (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 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 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' 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 correlational approach alone is ill-equipped to predict future species ranges (Davis et al., 2005; Hampe, 2004; Lawton, 2000; Woodward and Beerling, 1997).

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 processes. 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 (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. 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. (2002) take an important step in the right direction.

Theoretical studies, often focussing on invasion biology rather than range dynamics under climate change, have considered a range of evolutionary dynamics during expansions: Garcia-Ramos and Rodriguez (2002) demonstrate the interacting roles played by local adaptation and habitat heterogeneity in determining spread rate; several theoretical studies have now demonstrated that range expansion might be accelerated by the evolution of increased dispersal propensity at expanding fronts (e.g. Travis and Dytham, 2002; Burton et al., in press) and recent empirical evidence confirms that this is an important effect (Phillips et al., 2006); Klopfstein et al. (2006) demonstrate that neutral mutations arising on the edge of a range expansion sometimes '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. Klopfstein 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 demonstrated that this surfing dynamic can be important for non-neutral mutations. Even deleterious mutations can sometimes attain high abundance at an expanding front (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 (Burton and Travis, 2008b). In this paper we concentrate on local adaptation, an important evolutionary process that, to date, has rather surprisingly received little attention in terms of its potential role in range expansions and determining a species dynamics during an episode of climate change.

Considerable empirical evidence indicates that locally adapted phenotypes are commonplace within many species (Lambrechts et al., 1996; McNeilly and Antonovic, 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 flowering McNeilly and Antonovic (1968); this variation is frequently clinal with northern populations consistently different from southern counterparts (Riihimaki 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 have been described for a bird species: across Europe, blue tits exhibit adaptive differences in photoresponsiveness that results in laying dates coinciding with local caterpillar availability (Lambrechts et al., 1996). These two examples both involve the timing of key events being optimally aligned to seasonal environmental conditions, 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 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 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 Scriber, 1994).

There is now recognition that local adaptation is likely to be an important determinant of species' responses to climate change and an interdisciplinary treatment 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 ranges during and following a period of climate change. We utilise a spatially explicit individual based simulation to model the impact of climate change on a single species. This model uses both stochastic demographic parameters and allows inclusion of local density dependent rates for survival of individuals. In our discussion we emphasise the potential implications of our results for conservation biology and highlight where we believe future effort is required to develop improved theory related to the evolutionary ecology of range shifting.

2. The model

There has been considerable recent interest in modelling the ecological and evolutionary dynamics of spatially structured populations that live along environmental gradients (e.g. Alleaume-Benharira et al., 2006; Travis et al., 2006; Dytham, 2009) and some studies have extended this approach to consider the range shifting of populations structured in this way (e.g. Brooker et al., 2007; Burton 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.

2.1. The environment

Individuals of the single species inhabit a two-dimensional landscape that, unless specified otherwise, has dimensions 200 rows (x value) by 200 columns (y value), which are ordered from the bottom left hand corner (i.e. increasing an individual's x location would move the individual up the grid, whilst increasing its y location would move it to the right of the grid). A value of (x,y) determines an individual's location. We assume that environmental conditions vary latitudinally (i.e. 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, 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 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 the grid. In all our simulations, we allow populations to first establish under stable environmental conditions and in these periods the environmental conditions within each row remain constant through time.