



Spatial sorting and range shifts: Consequences for evolutionary potential and genetic signature of a dispersal trait



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HIGHLIGHTS

- We simulate a species' range shift under climate change.
- The allele for low dispersal rate is prone to extinction at the retracting margin.
- Recovery of the original genotype distribution after the shift takes a long time.
- The time to recovery depends on the total displacement of the climate optimum.

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ABSTRACT

Species are shifting their ranges under climate change, with genetic and evolutionary consequences. As a result, the spatial distribution of genetic diversity in a species' range can show a signature of range expansion. This genetic signature takes time to decay after the range stops expanding and it is important to take that lag time into account when interpreting contemporary spatial patterns of genetic diversity. In addition, the return to spatial equilibrium on an ecologically relevant timescale will depend on migration of genetic diversity across the species' range. However, during a range shift alleles may go extinct at the retracting range margin due to spatial sorting. Here we studied the spatial pattern of genotypes that differ in dispersal rate across the species range before, during and after a range shift, assessed the effect of range retraction on this pattern, and quantified the duration of the ephemeral genetic signature of range expansion for this trait. We performed simulation experiments with an individual-based metapopulation model under several contemporary climate change scenarios. The results show an increase of the number of individuals with high dispersal rate. If the temperature increased long enough the allele coding for low dispersal rate would go extinct. The duration of the genetic signature of range expansion after stabilisation of the species' distribution lasted up to 1200 generations after a temperature increase for 60 years at the contemporary rate. This depended on the total displacement of the climate optimum, as the product of the rate of temperature increase and its duration. So genetic data collected in the field do not necessarily reflect current selection pressures but can be affected by historic changes in species distribution, long after the establishment of the current species' range. Return to equilibrium patterns may be hampered by loss of evolutionary potential during range shift.

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1. Introduction

Species are shifting their ranges under climate change (Chen et al., 2011; Parmesan and Yohe, 2003), which has genetic and evolutionary consequences (Excoffier et al., 2009; Kubisch et al., 2014; Parmesan, 2006). The genetic diversity present at the expanding range margin is smeared across the landscape on the expansion wave (Excoffier and Ray, 2008). This is the case for neutral as well as adaptive genetic

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variation (Cobben et al., 2012a, 2011; Edmonds et al., 2004; Hewitt, 1996; Ibrahim et al., 1996; Klopstein et al., 2006; Travis et al., 2007, 2010). Under these conditions, the genetic configuration of the newly colonised populations is largely the result of the demographic process under range expansion, and not of selection (Travis et al., 2007), although some traits are selected for under range expansion, particularly the ability to disperse and traits related to population growth rate (Hill et al., 2011; Moreau et al., 2011; Phillips et al., 2010).

With regard to the ability to disperse, both theoretical and empirical studies report an increased dispersal capacity as a result of spatial sorting under range expansions (e.g. Burton et al., 2010; Phillips et al., 2006; Thomas et al., 2001; Travis and Dytham, 2002; Travis et al., 2013). Good dispersers gather at the range margin and from there they colonise new territory, while the poor dispersers lag behind. This eventually leads to a spatial gradient in dispersal capacity across the species' range, which can be regarded as a genetic signature of range expansion (Phillips et al., 2010). After the range stops expanding, it takes time for such a genetic signature of range expansion to decay, especially when the variation for these traits needs to migrate from the centre of the range or to develop through *de novo* mutations (Dytham et al., 2014; Phillips et al., 2010). During that time period populations are in spatial disequilibrium as a result of the past range expansion. In a time when many investigators are gathering genetic data from natural populations to study selection pressures and micro-evolution, accounting for different explanations of genetic make-up is crucial (Currat et al., 2006; Ray and Excoffier, 2009). Investigating the genetic signature of range expansion is therefore of importance for the interpretation of contemporary spatial patterns in genetic diversity.

Particularly for a dispersal trait, it can be expected that the decay of this genetic signature of range expansion may take a long time: after the range expansion stops the net effect of selection will be for lower dispersal capacity, yet low dispersal genotypes are by definition slow dispersers. Kubisch et al. (2010) showed that the establishment of genotypes with low dispersal rates after range expansion is the result of the migration of variation, and does not involve the establishment of new, beneficial mutations. In their study we see a slow return to equilibrium dispersal rate values at the expanding range margin after range expansion, but this result is not specifically quantified or discussed. In contrast, Henry et al. (2014) claimed a fast return to equilibrium values after range expansion, resulting from selection for beneficial mutations. In a mechanistically more realistic model, Dytham et al. (2014) showed that the state of spatial disequilibrium can last for a substantial time period after the range expansion. In addition, they observed that the speed of range expansion depends on selection for existing variation rather than for new variation due to mutations, even under a high mutation rate (Dytham et al., 2014). This is in line with theory and empirical data on micro-evolution, in which evolutionary changes that are relevant at ecological timescales depend on changes in allele frequencies rather than on new mutations. However, none of the above studies have explicitly discussed or tried to quantify the time period during which populations are in spatial disequilibrium.

Under a climate change scenario with continued temperature increase, many species' ranges are expected to retract at the margin with the deteriorating thermal conditions, resulting in a range shift rather than a range expansion (Gillings et al., 2015; Thomas et al., 2006). This means that slow dispersers might be lost as a result of spatial sorting and subsequent extinction of populations at the retracting margin (Cobben et al., 2012a; Cobben et al., 2011), while return to equilibrium values after range expansion likely depends on such existing genetic diversity as argued above (Dytham et al., 2014; Kubisch et al., 2010). Many studies have reported increased dispersal under range expansion (e.g. Burton et al., 2010; Phillips et al., 2006; Thomas et al., 2001; Travis and Dytham, 2002; Travis et al., 2013), but little attention has been given to the consequences of a retracting range margin for dispersal traits (but see Henry et al., 2014).

In this paper we investigated how range shifts affect the distribution of different genotypes coding for low, medium and high rates of dispersal across the species range. In addition, we studied the duration of the ephemeral genetic signature of range expansion. For both, we used a mechanistically realistic model of a range shifting species under climate change. We simulated a period of temperature increase in several scenarios, during and after which we registered the distribution of the different dispersal rate genotypes in the landscape up until 5000 years after model initialisation. To warrant sufficient variation in the existing genetic diversity under stationary conditions, we employed diploid inheritance, fragmented habitat and temperature variability. The genetic architecture was designed to get a clear signature of spatial sorting as well as distinct differences between phenotypes.

2. Methods

We used a spatially explicit, individual-based simulation model of a sexually reproducing species with overlapping generations. The model is called METAPHOR (Verboom et al., 2001; Vos et al., 2001) and has previously been extended to allow for stochastic temperature increase (Schippers et al., 2011) and with a genetic module for neutral (Cobben et al., 2011, 2012b) and adaptive traits (Cobben et al., 2012a). It was parameterised based on empirical data for the middle spotted woodpecker (*Dendrocopos medius*), a woodland bird (Hagemeijer and Blair, 1997; Kosenko and Kaigorodova, 2001; Kosinski and Ksit, 2006; Kosinski et al., 2004; Michalek and Winkler, 2001; Pasinelli, 2000; Pettersson, 1985). Table 1 gives an overview of the parameters used. For the current study we allowed the dispersal rate to be adaptive and investigated the spatial distribution of the allele frequencies at the dispersal gene during and after range shift.

2.1. Landscape

The landscape was 15 km wide (horizontal axis) by 2000 km long (vertical axis). In horizontal direction the borders were merged, creating a (vertical) tube. The landscape contained 3000 randomly distributed habitat patches, equalling a total of 5% habitat area. In vertical direction, a Gaussian temperature curve was shifting across the landscape at various speeds, and with a standard deviation of 140 km (see Appendix A). This temperature was used to determine the local habitat quality and each row in the landscape was as such characterised by a time-specific habitat quality q [0..1], being 1 at the peak of the distribution and 0 outside the curve area. We used three temperature increase scenarios, based on work by the IPCC (2013), of a respective temperature increase of 1 °C, 2 °C and 4 °C by the year 2100, resulting in equivalent isocline shift rates of 2, 4 and 8 km per year, respectively (see Appendix A).

2.2. Population demography

The patches in the landscape were inhabited by individuals that were characterised by their sex, and their dispersal alleles (see below under Genetics). The yearly life cycle consisted of recruitment, dispersal, and survival, in this order. Per patch, in each year, the number of offspring per unique pair of individuals of opposite sex was dependent on local habitat quality q and population density d , following:

$$R = R_{d0q1} \left(1 - \left(1 - \frac{R_{d0q0}}{R_{d0q1}} \right) (1 - q) \right) \left(1 - \left(1 - \frac{R_{d1q1}}{R_{d0q1}} \right) d \right)$$

with R_{d0q1} is the number of offspring at $d=0$ and $q=1$, and similar for R_{d0q0} and R_{d1q1} .

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