Increasing evolvability of local adaptation during range expansion.

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Abstract

Increasing dispersal under range expansion increases invasion speed, which implies that a species needs to adapt more rapidly to newly experienced local conditions. However, due to iterated founder effects, local genetic diversity under range expansion is low. Evolvability (the evolution of mutation rates) has been reported to possibly be an adaptive trait itself. Thus, we expect that increased dispersal during range expansion may raise the evolvability of local adaptation, and thus increase the survival of expanding populations. We have studied this phenomenon with a spatially explicit individual-based metapopulation model of a sexually reproducing species with discrete generations, expanding into an elevational gradient. Our results show that evolvability is likely to evolve as a result of spatial variation experienced under range expansion. In addition, we show that different spatial phenomena associated with range expansion, in this case spatial sorting / kin selection and priority effects, can enforce each other.

Introduction

Many species are currently expanding their ranges, both polewards and uphill, as a response to increasing global temperatures under climate change (Parmesan and Yohe 2003; Chen et al. 2011). Range expansions are known to have profound effects on the genetic composition of populations, regarding both neutral and adaptive genetic diversity (Hewitt 1996; Thomas et al. 2001; Travis and Dytham 2002; Edmonds et al. 2004; Klopfstein et al. 2006; Phillips et al. 2006; Travis et al. 2007; Excoffier et al. 2009; Cobben et al. 2011; Cobben et al. 2012b). Traits that are to increase species dispersal capabilities and population growth rates are selected for under range expansions (Parmesan 2006; Burton et al. 2010; Phillips et al. 2010b; Hill et al. 2011; Shine et al. 2011). This may lead to the evolutionary increase of dispersal rate (Thomas et al. 2001; Travis and Dytham 2002; Kubisch et al. 2010; Henry et al. 2014), dispersal distance (Phillips et al. 2006) and effective fertility (Moreau et al. 2011) during periods of range expansion. In contrast, traits that affect the local adaptation of individuals may be affected by gene surfing (Cobben et al. 2012b), which is a consequence of the demographic processes occurring during colonization (Edmonds et al. 2004; Klopfstein et al. 2006), but the selective pressure on such traits is resulting only from the location of the individual and not the expansion itself. An increasing dispersal rate under range expansion will increase the invasion speed (Travis and Dytham 2002; Phillips et al. 2006) and has the implication that a species needs to be able to adapt to newly experienced local conditions more rapidly than before. However, Kubisch et al. (2013a) showed that high dispersal rates prevent the evolution of local adaptation. Now there is both theoretical and empirical evidence that evolvability can be adaptive itself under conditions that require an increased rate of adaptation, e.g. under increasing environmental stochasticity and stress (Leigh Jr 1970; Ishii et al. 1989; Sniegowski et al. 1997; Kashtan et al. 2007; Lee and Gelembiuk 2008).

Evolvability generally refers to the ability of populations to evolve in an adaptive way

(Brookfield 2009) and is associated with varying environments (Kashtan et al. 2007). Many studies have speculated and shown the increase of evolvability under temporally varying environmental conditions (Leigh Jr 1970; Ishii et al. 1989; Sniegowski et al. 1997; Kashtan et al. 2007). Under such conditions, a high mutation rate serves to replenish the local genetic variation, which has beforehand been strongly reduced under differing selection regimes (Brookfield 2009). With a high frequency of local disturbances, the mutation rate is expected to be maintained at a constantly high level (Ishii et al. 1989; Earl and Deem 2004). In contrast, when we take a spatial perspective, spatial heterogeneity may lead to differing selection pressures between habitat patches. High levels of dispersal can thus result in individuals experiencing a varying environment in space rather than time (Lee and Gelembiuk 2008). In a scenario of range expansion, increasing relatedness between individuals reduces local genetic diversity (Kubisch et al. 2013b), while dispersal rates increase. Under such low local genetic diversity, this high dispersal rate should then be accompanied by high mutation rates, i.e. high evolvability, to increase local adaptation and survival.

In this study, we have sought to elaborate on these thoughts and used a simulation model to investigate the interplay between the evolution of dispersal rate and the evolution of evolvability under range expansion across a spatial gradient in altitude.

The Model

We are using a spatially explicit individual-based metapopulation model of a sexually reproducing species with discrete generations distributed along an elevational gradient. The basic model has already been successfully applied in theoretical studies, mainly focused on dispersal evolution (Travis et al. 1999; Kubisch et al. 2010; Fronhofer et al. 2011; Kubisch et al. 2013a; Kubisch et al. 2013b) and was parameterized using empirical data (Poethke et al. 1996; Amler et al. 1999). For the current study we allow evolvability of local adaptation to be adaptive, and investigate the interplay with the

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evolution of dispersal rate.

Landscape

The simulated landscape consists of 250 columns (x-dimension) of 20 patches each (y-dimension). We assume wrapped borders, building a torus. Hence, if an individual leaves the world in y-direction during dispersal, it will reenter the simulated world on the opposite side. However, if it leaves the world in the x-direction, it is lost from the simulation. While most studies investigating range expansions across an environmental gradient, for the sake of simplicity focus on a single parameter changing along space, a typical elevational gradient is known to involve both a decreasing temperature and increasing habitat fragmentation (Körner and Paulsen 2004). Thus, in our model firstly every column of patches (x-position) is characterized by its specific abiotic habitat conditions τ_x. Throughout this manuscript, τ_x will be interpreted as 'mean temperature'. This mean local temperature is used for the determination of local adaptation of individuals. To simulate a large-scale habitat gradient, x changes linearly from $\tau_{x=1} = 0$ to $\tau_{x=250} = 0$ along the x-dimension, i.e. by $\Delta_{\tau,x} = 0.04$ when moving one step in x-direction. Secondly, to account for habitat fragmentation in terms of patch isolation, each x-position is characterized by a certain degree of dispersal mortality. The probability to die upon emigration μ changes linearly from $\mu_{x=1} = 0$ to $\mu_{x=250} = 1$ along the x-dimension.

Population dynamics and survival of offspring

Local populations are composed of individuals that are characterized by several traits: 1) their sex, 2) two alleles at locus 1 coding for the individuals emigration propensity, 3) two alleles at locus 2 coding for the individual's 'habitat preference', i.e. the environmental conditions (temperature τ) under which the individual survives best (see below for details), and 4) another 2 alleles at locus 3 coding for the mutation

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probability of the alleles at locus 2, i.e. the evolvability of habitat preference (see below under Genetics).

Local population dynamics follow the time-discrete BevertonHolt model (Beverton and Holt 1957). Each individual female in patch x, y is therefore assigned a random male from the same habitat patch (males can potentially mate several times) and gives birth to a number of offspring drawn from a Poisson distribution with mean $\Lambda_{x,y,t}$. The offspring's sex is chosen at random. Density-dependent survival probability s_1 of offspring due to competition is calculated as:

$$s_1 = \frac{1}{1 + \frac{\lambda - 1}{K} \cdot Nx, y, t} \tag{1}$$

Finally, the surviving offspring experience a further density-independent mortality risk $(1 - s_2)$ that depends on the matching of their genetically determined optimal temperature (τ_{opt}) to the temperature conditions in patch x, y (τ_x) according to the following equation:

$$s_2 = exp\left[-\frac{1}{2} \cdot \left(\frac{\tau_{opt} - \tau x}{\eta}\right)^2\right] \tag{2}$$

Density-independent survival depends on adaptation to local conditions, i.e. on the difference between the genetically encoded optimal temperature τ_{opt} of an individual and local temperature conditions τ_x. η describes the niche width or 'tolerance' of the species. We performed simulations for the species with a niche width of $\eta = 0.5$, equivalent to a decrease of survival probability of about 0.02 when dispersing one patch away from the optimal habitat. By using this approach we assume that density-dependent mortality $(1 - s_1)$ acts before mortality due to maladaptation to local conditions $(1 - s_2)$.

Individual surviving offspring disperse with probability d that is determined by their dispersal locus (see below). If an individual emigrates it dies with probability μ, which

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is calculated as the arithmetic mean of the dispersal mortality values of its natal and its target patch, respectively. This mortality accounts for various costs that may be associated with dispersal in real populations, like fertility reduction or predation risk (Bonte et al. 2012). We assume nearest-neighbor dispersal, i.e. successful dispersers settle randomly in one of the eight surrounding habitat patches.

Genetics

As mentioned above, every individual carries three unlinked, diploid loci coding for its emigration probability, its habitat preference (optimum temperature), and the mutation rate of the optimum temperature alleles (evolvability of habitat preference), respectively. The phenotype of an individual is determined by calculating the arithmetic means of the two corresponding alleles. Hence, dispersal probability d is given by $d = \frac{l_{d,1}+l_{d,2}}{2}$ (with $l_{d,1}$ and $l_{d,2}$ giving the 2 'values' of the two dispersal alleles), optimal temperature τ_{opt} is calculated as $\tau_{opt} = \frac{l_{a,1}+l_{a,2}}{2}$ (with $l_{a,1}$ and $l_{a,2}$ giving the 'values' of the two adaptation alleles), and similarly the mutation rate of optimal temperature $m(\tau_{opt}) = 10^{-exp}$ (with $exp = \frac{l_{e,1}+l_{e,2}}{2}$, and $l_{e,1}$ and $l_{e,2}$ the 'values' of the two evolvability alleles). At each of the three loci, newborn individuals inherit alleles, randomly chosen, from the corresponding loci of each of their parents. During transition from one generation to the next an allele may mutate. Alleles at the dispersal locus and the evolvability locus mutate with a probability of $m = 10^{-4}$. Alleles at the adaptation locus however, mutate with the probability $m(\tau_{opt})$ given by the value based on its two alleles at the evolvability locus as elaborated above. Mutations are simulated by adding a random number drawn from a Gaussian distribution with mean 0 and standard deviation 0.2 (in case of the alleles coding for optimal temperature the standard deviation is 0.5) to the value calculated from the mean of the inherited alleles.

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Simulation Experiments

Simulations were initialized with a 'native area' (from $x = 1$ to $x = 50$) from where the species was able to colonize the world, while the rest of the world was initially kept free of individuals. Upon initialization, dispersal alleles ($l_{d,i}$) were randomly drawn from the interval $0 < l_{d,i} < 1$, and evolvability alleles $l_{e,i}$ were set to 4, added a Gaussian random number with mean zero and standard deviation one. Populations were initialized with K locally optimally adapted individuals, i.e. preference alleles were initialized according to the local temperature τ_x. However, to account for some standing genetic variation we also added to every respective optimal temperature allele a Gaussian random number with mean zero and standard deviation 0.5. We performed 100 replicate simulations, which all covered a time span of $60,000$ generations. To establish equilibrium conditions, individuals were confined to their native area during the first $1,000$ generations. After this burn-in period, the species was allowed to pass the $x = 50$ border. Table 1 summarizes all relevant model parameters, their meanings and the standard values used for the simulations.

Analysis

The individual phenotypes for the three traits were documented in time and space throughout the simulations. Genetic diversity was calculated as the variance in allelic values at the adaptation locus per x-position. The marginal values of dispersal propensity and evolvability were calculated as the arithmetic mean of all individual values at the range border, i.e., the mean of all patches in the y dimension of the last five x-positions of the gradient counted from the most-forward occupied patch (which is time dependent).

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Table 1: Used parameter values.

parameter/variable	value	meaning
individual variables:		
$l_{d,1}, l_{d,2}$	evolving	alleles coding for the dispersal propensity
$l_{a,1}, l_{a,2}$	evolving	alleles coding for the optimal temperature
$l_{e,1}, l_{e,2}$	evolving	alleles coding for the mutation rate of the optimal temperature
simulation parameters:		
K	100	carrying capacity
λ	2	per capita growth rate
ϵ	0.05	local extinction probability
m	10^{-4}	mutation rate for dispersal and evolvability alleles
μ_x	[0..1]	local dispersal mortality
τ_x	[0..10]	local temperature
η	0.5	niche width
x_{max}	250	extent of simulated landscape in x-direction
y_{max}		extent of simulated landscape in y-direction

Results

After the burn-in phase, the dispersal propensity d in the core area, so under low dispersal mortality, was on average approximately 0.35. Maximum population density was around 0.85 here, accompanied by a high level of local adaptation s_2 (i.e. adaptation-dependent offspring survival probability) close to one (not shown), the mutation rate of the optimum temperature $m(\tau_{opt})$ remained low, between 10^{-4} and 10^{-5}.

Under range expansion, the dispersal rate d increased in the populations at the expansion front, and in time decreased again as these populations got older and adapted locally (Figure 1B). During range expansion the maximum established dispersal rate d was approximately 0.25 (Figure 1B). As the species expanded its range further across the gradient of increasing dispersal mortality (and increasing temperature), the maximum established dispersal rates at the range front decreased (Figure 1B). The range border established at an average dispersal mortality of 0.8, and
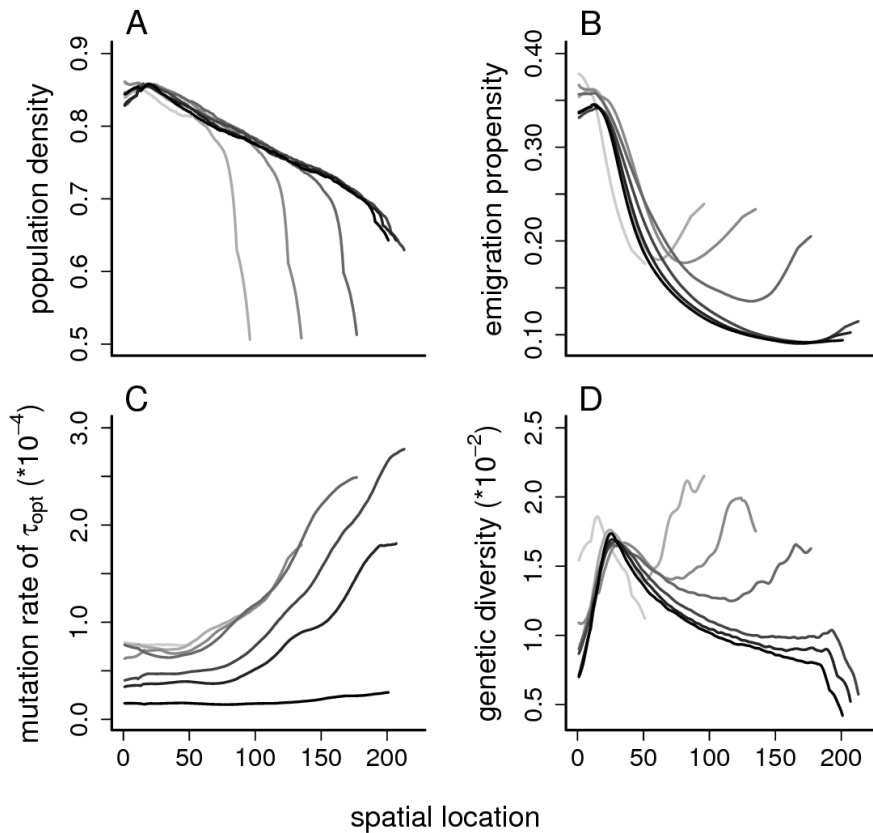
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Figure 1: The average values over 100 simulations during and after range expansion across the gradient (horizontal axis) in time (gray scaling from light to dark, as time proceeds, which is given in a sequence of generations 1000, 1250, 1500, 2000, 5000, 10000, 60000) of A. population density, B. emigration propensity, C. evolvability, i.e. mutation rate of the adaptation alleles, and D. genetic diversity measured as the variance in adaptation alleles. Shown are mean values. For reasons of clarity, a moving average with a window size of 20 has been applied (data were present in 10-generation intervals).

a temperature value of 8. After reaching spatial equilibrium, the spatial distribution of dispersal rates showed a decaying exponential trend. The mutation rate of the temperature optimum $m(\tau_{opt})$ showed no spatial pattern before range expansion, but rapidly increased once the populations invaded into the landscape. After $5,000$ generations of expansion, this mutation rate was on average almost seven times higher at the range margin than in the core (Figure 1C). As a result of this increased mutation rate, genetic diversity was also increased at the range front, compared to regions, which have been populated for longer time (Figure 1D). Diversity in the initial
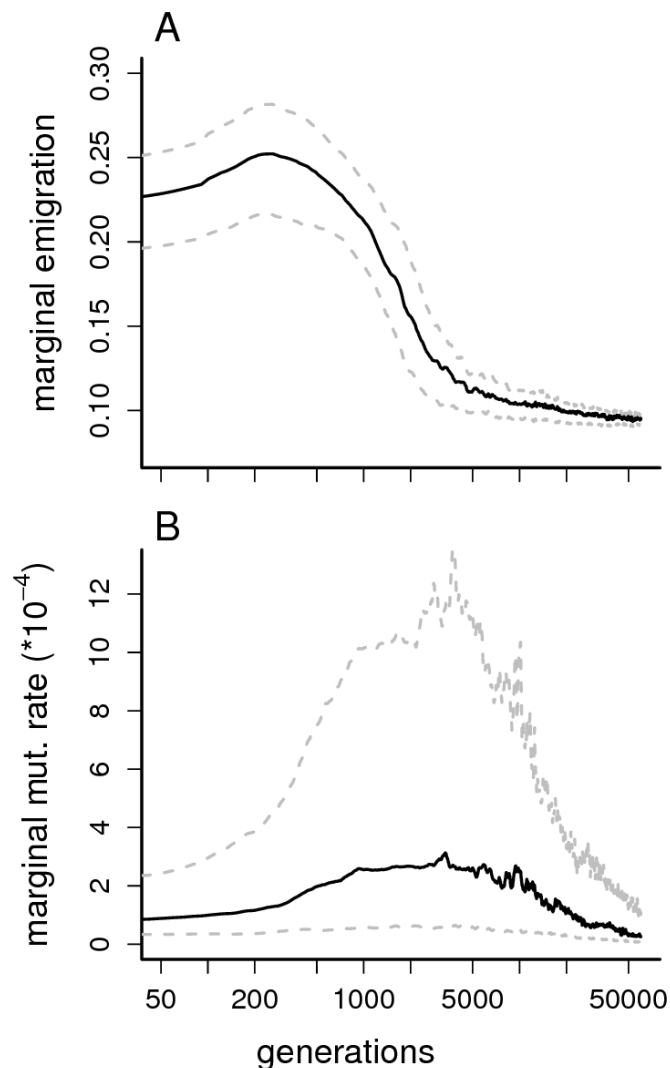
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Figure 2: The average values over 100 simulations at the range border of A. the emigration propensity and B. the mutation rate in time (note the logarithmic scale). Shown are mean values (solid black lines) and 25%- and 75%-quartiles (dashed grey lines). For reasons of clarity, a moving average with a window size of 20 has been applied. For details see main text.

core area, however, stayed at fairly high levels. Similar to mean dispersal propensity,

mutation rates decreased again when the populations were getting older (Figure 1C).

However, the time lag between the local decrease of the dispersal rate and the decrease

of the mutation rate $m(\tau_{opt})$ was steadily increasing across space. At the range border

it took $45,000$ generations for the mutation rate to decrease to equilibrium values

after the dispersal rate had decreased (Figure 2A,B). Note also that variability in

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mutation rates was very high. While the maximum average mutation rate was found to be around $2 \cdot 10^{-4}$, the third quartile was measured at about $1.3 \cdot 10^{-3}$. The local level of adaptation s_2 was close to one throughout the simulation time and across the complete species range.

Discussion

In this study we investigated, whether an increase in dispersal rate under range expansion can lead to the evolution of higher evolvability, enabling species to more rapidly adapt to local conditions with an increasing invasion speed. We found an increase of evolvability, which is dependent on the local level of genetic diversity, with high mutation rates evolving under high rates of dispersal. Evolved high mutation rates took an extensive period of time to return to lower mutation rates after the local dispersal rates decreased again, due to a priority effect (De Meester et al. 2002; Urban and De Meester 2009).

This modeling study shows for the first time that evolvability can evolve as a result of spatial variation, experienced under range expansion. This high evolvability increases genetic diversity and thus adaptive potential in newly colonized areas. In addition, we show that different spatial phenomena associated with range expansion, in this case spatial sorting / kin competition and priority effects, can enforce each other. The genetic signature of spatial sorting is then extended in longevity due to a priority effect, where high local adaptation further delays the establishment of lower dispersal rates. This may have implications for the interpretation of field data.

During range expansion the dispersal rate was showing a clear signal of spatial sorting (Shine et al. 2011) and kin competition (Kubisch et al. 2013b), with good dispersers gathering at the expanding wave front (Phillips et al. 2010a). The immigration of different individuals is expected to maintain a high local level of genetic variation (Holt and Barfield 2011), from which one would expect high levels of dispersal to

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be accompanied by a low local mutation rate and we indeed find this pattern in the range core throughout the simulation. At the margin, however, relatedness amongst individuals increases at an advancing range front (Kubisch et al. 2013b), reducing both local genetic diversity and the diversity of immigrants. Under these conditions an increase of the evolvability of local adaptation evolved, which compensated for the experienced spatial variation in local temperature. Both high rate signals of dispersal and mutation rate disappeared with time. At the range border, individuals with a high dispersal rate were locally well-adapted as a result of the high mutation rate. While a lower dispersal rate is beneficial under conditions of high dispersal mortality, slow dispersers took a long time to reach the area (genetic signature of range expansion, Phillips et al. 2010b). They were in addition hindered by the high dispersal mortality, and on top of that needed to compete with better locally adapted individuals (priority effect, De Meester et al. 2002). This has implications for field work, where the cause of an observed local high dispersal rate requires careful interpretation, as it can be the result of natural selection, spatial selection, spatial disequilibrium, or priority effects. The dispersal rate decreased first and was only after an extensive time lag of ten thousands of generations followed by a decrease in mutation rate. This again was caused by a priority effect (De Meester et al. 2002), where a high level of local adaptation prevents the establishment of individuals with a lower mutation rate. We speculate that this second time lag was larger than the first because selection on evolvability is weaker than on dispersal, with dispersal having more direct and drastic effects on population dynamics. However, this remains to be investigated.

Holt and Barfield (2011) investigated niche evolution at species range margins and found that local evolution was hampered when source populations of immigrating individuals were at low density, as a result of the stochastic processes in such populations (Pearson et al. 2009; Bridle et al. 2010; Turner and Wong 2010). The likelihood of observing niche evolution was further affected by the mutation rate, where dispersal limited local evolution in the sink population under a higher mutation rate,

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because of the increased numbers of maladapted individuals from the source (Holt and Barfield 2011). They did, however, not allow the joint evolution of mutation rate and dispersal rate, but instead used fixed rates. Our results can be affected by the used genetic architecture, where linkage between traits (Blows and Hoffmann 2005; Hellmann and Pineda-Krch 2007), polygeny, and the magnitude of mutations can be of importance in range dynamics (Kawecki 2000; Kawecki 2008; Walsh and Blows 2009; Gomulkiewicz et al. 2010; Kimbrell 2010). Increased evolvability can be modelled in different ways, e.g. an increased magnitude of the phenotypic effect of mutations (Griswold 2006), the evolution of modularity (Kashtan et al. 2009), or the evolution of generalism or plasticity (Lee and Gelembiuk 2008; Chevin and Lande 2011), where we have restricted evolvability to the mutation rate. Although empirical studies support the decision to focus on mutation rate (Sniegowski et al. 2000; Earl and Deem 2004), this can have an effect on our results.

There is an ever-expanding pool of literature discussing the ecological and evolutionary dynamics of dispersal in the formation of species ranges (reviewed in Kubisch et al. 2014). The evolution of dispersal has been shown to increase invasion speeds (Thomas et al. 2001; Travis and Dytham 2002; Phillips et al. 2010a), affect the fate of neutral mutations (Travis et al. 2010), as well as the level of local adaptation (Kubisch et al. 2013a; Bourne et al. 2014), and local population dynamics (Travis et al. 2007; Burton et al. 2010), and in addition cause strong patterns of spatial disequilibrium (Ibrahim et al. 1996; Phillips et al. 2010b). While individual-based models have recently largely extended our theoretical knowledge of interactions and evolution of traits during range expansion, empirical data have been restricted to a few well-known cases (Thomas et al. 2001; Phillips et al. 2006; Moreau et al. 2011). Increasing ecological realism in our models (Cobben et al. 2011; Cobben et al. 2012a; Cobben et al. 2012b; Bocedi et al. 2014) might improve the predictability of theoretical phenomena and support field studies. These are, however, always constrained by the required temporal and spatial scales, which are particularly restrictive in terrestrial systems.

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Acknowledgements

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