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Latitudinal-diversity gradients can be shaped by biotic processes: new insights from an eco-evolutionary model

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The processes involved in shaping latitudinal-diversity gradients (LDGs) have been a longstanding source of debate and research. Climatic, historical and evolutionary factors have all been shown to contribute to the formation of LDGs. However, meta-analyses have shown that different clades have LDG slopes that may vary in more than one order of magnitude. Such large variation cannot be explained solely by climatic or historical factors (e.g. difference in surface area between temperate and tropical zones) given that all clades within a geographic region are subject to the same conditions. Therefore, biotic processes intrinsic to each taxonomic group could be relevant in explaining rate differences in diversity decline across latitudinal gradients among groups. In this study, we developed a model simulating multiple competing species subjected (or not) to a demographic Allee effect. We simulated the range expansion of these species across an environmental gradient to show how these two overlooked factors (competition and Allee effects) are capable of modulating LDGs. Allee effects resulted in a steeper LDG given a higher probability of local extinction and lower colonization capacity compared to species without Allee effects. Likewise, stronger competition also led to a steeper decline in species diversity compared to scenarios with weaker species antagonistic interactions. This pattern occurred mostly due to the strength of priority effects, wherein scenarios with strong competition, species that dispersed earlier in the landscape were able to secure many patches whereas late-arriving species were progressively precluded from expanding their ranges. Overall, our results suggest that the effect of biotic processes in shaping macroecological patterns could be more important than it is currently appreciated.

Keywords: biogeography, incumbency, preemption

Introduction

For decades ecologists have sought to understand the mechanisms underlying the latitudinal-diversity gradient (LDG), a negative relationship between species richness and latitude (Hillebrand 2004, Valentine et al. 2008). Prominent theories concerning LDGs emphasize climate (Hawkins et al. 2003), historical events (Dynesius and Jansson

2000), tropical niche conservatism (i.e. the tendency of tropical clades to retain their ancestral niche; Wiens and Donoghue 2004), as well as differences in speciation and extinction rates across latitude (Mittelbach et al. 2007, Gillman and Wright 2014) as important mechanisms. Climate is often invoked as a driver of LDGs given that temperature, precipitation and productivity are generally correlated with diversity patterns (Hawkins et al. 2003). Historical hypotheses propose that past climate and/or geographical dispersal barriers may have shaped differential rates of speciation, extinction and range expansion across latitudinal gradients (Dynesius and Jansson 2000). While these processes may well underlie LDGs, they cannot explain the large variation found across different taxonomic groups (Hillebrand 2004) for which the slopes of their diversity gradients vary considerably under similar climatic conditions (Hillebrand 2004, Hawkins et al. 2006, Henriques-Silva et al. 2016). Processes intrinsic to the different clades must, therefore, underlie their differential rates of diversity decline across the latitudinal gradient. Competition through priority effects (i.e. numerical advantage of first colonist species over later colonizers; Fukami 2015) has recently been suggested to affect diversity gradients (i.e. incumbency hypothesis; Valentine et al. 2008, De Meester et al. 2016) and may also explain differences among clades in their LDGs. The geographic incumbency effect may explain variation in diversity gradients among groups that have similar biogeographic origins and expansion (e.g. tropical origin and temperate expansion or vice-versa; Jablonski et al. 2006, Pyron and Burbrink 2009) given that it does not rely on external factors (e.g. climate, history). However, the incumbency hypothesis has so far received little attention, likely because it opposes a longstanding hypothesis, the species interactions-abiotic stress hypothesis (SIASH; reviewed by Louthan et al. 2015). The SIASH posits that northern limits of species ranges are determined by climatic factors while southern limits (e.g. tropical) are set by biotic interactions (Gaston and Blackburn 2000, Swenson et al. 2006). Nevertheless, there is still great ongoing debate about the generality of the SIASH (Louthan et al. 2015) and whether biotic factors are stronger or not in the tropics (Schemske et al. 2009, Moles and Ollerton 2016).

Two important density-dependent biotic mechanisms, competition and Allee effect, are known to affect range expansion (Case et al. 2005, Kubisch et al. 2011, Svenning et al. 2014, Louthan et al. 2015). For instance, many species form stable northern range limits without dispersal barriers or steep environmental gradients due to competition with ecologically similar species (Bullock et al. 2000, Wethey 2002, Cunningham et al. 2016). Interspecific interactions may preclude range expansion through competitive priority effects if resources are monopolized by first colonizers (Urban and De Meester 2009) or by preventing local adaptation of late-arriving species (Case and Taper 2000). Furthermore, given that most invasions start at low densities, the establishment of range limits may occur due to the Allee effect (Kubisch et al. 2011). Allee effect, a decrease

in individuals' average fitness when populations are at low densities (Courchamp et al. 1999), lowers reproduction and/or survival rates. Allee effects may arise through difficulties in finding mates (in the case of a sexual species), inefficacy of predator avoidance strategies, or predator cooperation strategies at low densities, and demographic stochasticity (Courchamp et al. 1999, Thum 2007). While the effects of these density-dependent processes on range limits are well understood, their effects on multiple species ranges, and consequent influences in shaping spatial diversity gradients are poorly known.

In this study, we developed a simulation model to investigate how competition and Allee effects can shape spatial diversity gradients. Our aim is not to propose a new competing hypothesis to the existing body of theory underlying the LDG. Rather, we want to demonstrate how biotic processes can serve as an explanation for the large variation in LDG steepness found across different taxonomic groups (Hillebrand 2004) and, as a consequence, generate novel testable predictions of species diversity. We take a bottom-up approach by modeling the eco-evolutionary dynamics of multiple species undergoing range expansion (Kubisch et al. 2014). Our model also provides new insights on the factors underlying Rapoport's rule, another common latitudinal gradient characterized by an increase in species' average geographic range size (GRS) from low to high latitudes (Rapoport 1975). It has been repeatedly observed that in most taxonomic groups there are a few widespread and many narrowly-distributed, species (Gaston and Blackburn 2000). Indeed, it should be expected that only a few species evolve to become wide-range generalists given the evolutionary challenges related to the trade-offs among the multiple axes of their niches (e.g. resource-use, competitive ability, environmental tolerance; Stearns 1989, Kneitel and Chase 2004). As diversity and GRS gradients emerge from the overlap of multiple species ranges across space, the eco-evolutionary forces regulating range dynamics may underlie both LDGs and Rapoport's rule (Stevens 1989). Understanding how these mechanisms operate on the range dynamics of multiple interacting species has thus the potential to reveal common underlying processes between these two well-known latitudinal gradients.

We approach the problem with an individual-based model, which allows us to explicitly simulate adaptive interactions of individuals with one another and their environment, thus revealing how eco-evolutionary dynamics at the individual level promote emerging patterns at large spatial scales. We simulated the dispersal and expansion of multiple species across an environmental gradient and developed multiple scenarios in which we varied the strength of species' competitive interactions and tested the importance of a demographic Allee effect. Our model revealed a novel, potentially generalizable, mechanism that regulates the steepness of gradients in GRS and diversity, based on these density-dependent biotic processes.

Methods

The model

Our simulation aims at representing the invasion of a vacant landscape by multiple species and illustrates biogeographic events, such as the recent post-glacial recolonization of the northern hemisphere (Griffiths 2010) or the expansion of tropical clades towards temperate regions (Jablonski et al. 2006, Valentine et al. 2008). We extended a spatially-explicit individual-based model (IBM) frequently used in studies of single species range dynamics (Kubisch et al. 2014 and references therein) to multiple taxa expanding their ranges across a vacant environmental gradient. The different parameters of this IBM have been rigorously evaluated by previous studies (Travis and Dytham 1998, Poethke and Hovestadt 2002, Kubisch et al. 2011, 2013) and it is a well-established model for the study of dispersal evolution and range expansion. The landscape consisted of a rectangular grid containing 200 rows (y-dimension) × 30 columns (x-dimension), totaling 6000 patches that were connected to their eight closest neighbors (i.e. Moore neighborhood). Colonization occurred along the y-dimension (Fig. 1a) where its borders have reflecting boundaries whereas the borders from the x-dimension are wrapped to avoid edge effects. Each patch is characterized by an environmental value $e_{x,y}$ (e.g. temperature), representing the optimum phenotype for survival in that patch (Fig. 1b). Environmental values were simulated to be spatially autocorrelated using the diamond-square algorithm (Miller 1986). These values were arbitrarily bounded between 0 and 10 and define the steepness of a potentially adaptive environmental gradient (e.g. temperature). These values exhibit spatial variation and increase linearly across the y-axis (Fig. 1a). Note that the same environmental structure (i.e. same values) was used in all replicates.

Individuals, genetics and reproduction

Initially, species were ecologically and evolutionarily equivalent, but niche and dispersal traits were allowed to evolve. Each individual was characterized by its dispersal phenotype, environmental optima phenotype, species identity and location in the landscape. Each simulation time-step was generated by the following sequence of events: reproduction, adults perish (i.e. individuals are semelparous and generations do not overlap), density-dependent (i.e. competition) and density-independent (adaptation to local environment) survival of offspring and dispersal.

The dispersal phenotype (d) and environmental optimum (e_{opt}) of each individual were controlled by an explicit genetic structure. For simplicity, and to save computational time, we simulated asexually-reproducing organisms with a haploid unilocus system where phenotypic values were represented by the value of their unique allele (Kubisch et al. 2014). Following previous models (Hovestadt et al. 2010, Kubisch et al. 2014, Henriques-Silva et al. 2015), alleles from both traits (d and e_{opt}) inherited by the offspring had a small probability of mutation ($m = 1 \times 10^{-3}$), in which a normally-distributed random number N (0, 0.04) was added to the allele's value.

The fertility (λ) of individuals was drawn from a lognormal distribution with mean μ and standard deviation σ, which were set to 2 and 0.5 respectively. These values are representative of the population dynamics of a wide range of species such as arthropods (Hassell et al. 1976) and mammals (Ericsson et al. 2001), and have been previously used in IBMs simulating range dynamics (Kubisch et al. 2011). Individual's number of offspring was then drawn from a Poisson distribution with mean λ that was assumed to be independent of the individual's fit to the local environment.
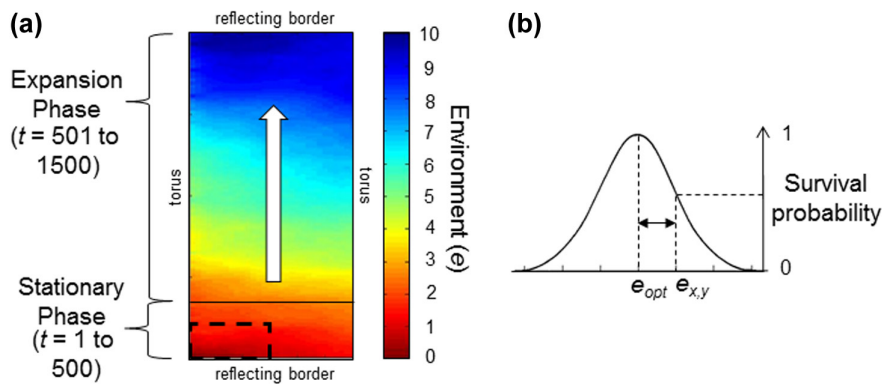

Figure 1. Overall framework of the landscape, environmental structure and the different tested scenarios. (a) Representation of the environmental structure in the landscape. Individuals are restricted to the area between $y=1$ and $y=10$ (i.e. where the black line crosses the landscape) for 500 generations (stationary phase) and then are allowed to expand for 1000 generation (expansion phase). The dashed square in the landscape represents a region, the scale in which diversity and average GRS were measured in the analysis (see Material and methods). (b) We assume a Gaussian shape between adaptation-dependent individual survival (i.e. their environmental optima phenotype (e_{opt})) and the local patch's environment ($e_{x,y}$).

Offspring survival

Offspring survival was regulated by two main processes. First, a density-independent survival probability s_1 related to how close their environmental optima phenotype (e_{opt}) matched the patch environment ($e_{x,y}$):

$$s_1 = \exp\left(-\frac{1}{2}\left(\frac{e_{x,y} - e_{opt}}{\eta}\right)^2\right)$$

where η denotes the niche breath of individuals (i.e. the width of the stabilizing selection) and similarly to other studies (Kubisch et al. 2013, Vanoverbeke al. 2016), was set to 0.5 in all simulations (Fig. 1b). We thus assumed a Gaussian relationship between adaptation-related survival and habitat phenotype mismatch. For a more detailed analysis of niche width on range dynamics refer to Kubisch et al. (2013). Second, a density-dependent survival probability s_2 related to competition with both conspecifics and allospecifics. For simplicity, all scenarios were characterized by symmetrical interspecific competition where the effect of species i on species j was similar to the effect of species j on species i. We varied the degree of interspecific competition strength by using a modified version of Hassel's (1975) density-dependent growth model:

$$s_2 = \frac{b}{1 + \left(\frac{\mu - 1}{K}\right)N_{x,y,t,i}}$$

where K refers to the equilibrium density, μ is the population intrinsic growth rate (i.e. used previously to determine individual's fertility) and $N_{x,y,t,i}$ to perceived density of patch x,y at generation t to an individual of species i and represent a combined effect of intraspecific and interspecific competition. $N_{x,y,t,i}$ is the only parameter that changes across the different scenarios regarding interspecific competition and is calculated as:

$$N_{x,y,t,i} = N_i + N_j\omega$$

where N_i is the number of individuals of species i, N_j is the number of individuals of all other species and ω is a weighting factor, for which we assumed the following values: 1.0, 0.8, 0.6, 0.5, 0.3 and 0.2. In the first scenario ($\omega = 1.0$), species exhibited 100% overlap in their resource, which implied equal strength for both inter and intra-specific competition. In all other scenarios, the importance of interspecific competition was lowered by ω, which decreased the degree of resource-use overlap among species (80, 60, 50, 30 and 20%). Classic competition theory predicts that co-existence is only possible if the strength of intra-specific is higher than inter-specific competition (MacArthur and Levins 1967), where stabilizing niche differences (e.g. resource partitioning, host-specific natural enemies; Chesson 2000) result in species limiting themselves more than they limit others species. Thus,

lowering ω decreases the strength of interspecific competition, increasing species coexistence. Finally, b is defined as:

$$b = \frac{\left(\frac{N_{x,y,t,i}}{K}\right)^2}{\left(\frac{N_{x,y,t,i}}{K}\right)^2 + \alpha^2}$$

The parameter α describes the strength of the demographic Allee effect and following Kubisch et al. (2011), was set to 0.05 and 0 in scenarios with and without Allee effects, respectively. It assumes a sigmoid increase in survival probability of individuals for species i as it becomes more abundant. Thus, individuals from a given species in a population at density $N_{i,t}/K = \alpha$ will have a 50% reduction in their survival probability. For all scenarios, the final survival probability was set as $s = s_1 s_2$.

Dispersal

After survival, offspring individuals may disperse to one of the 8 adjacent patches with a probability d given by their dispersal phenotype. Dispersers have a fixed 10% probability of dying before reaching another patch, thus accounting for the explicit risks of dispersal (e.g. predation) and/or implicit costs related to such energetic expense (Bonte et al. 2012). Dispersal was modelled using a density-dependent function developed by Poethke and Hovestadt (2002), which has been shown to be adequate for individual-based simulations with discrete generations (Hovestadt et al. 2010). It is characterized by the absence of dispersal below a certain density C_{TH}, and a non-linear increase in dispersal probability (d) for densities above this threshold.

$$d = \begin{cases} 0 & for \ \dfrac{N_{x,y}}{K} \leq C_{TH} \\ 1 - \dfrac{C_{TH}K}{N_{x,y}} & for \ \dfrac{N_{x,y}}{K} > C_{TH} \end{cases}$$

Thus, the lower the C_{TH} is, the higher the probability of the individual to disperse. The single allele value from the dispersal locus determines their critical threshold population density C_{TH} (i.e. the value in which the dispersal probability becomes greater than zero).

Model initialization and analysis

In all simulations, the landscape was initially populated with 20 species, which were distributed across all patches within the region between $y = 1$ and $y = 10$ (i.e. the 'southern' most region of the gradient; Fig. 1a). All patches within this region were populated to carrying capacity ($K = 160$) with 8 individuals per species, assuring that there was no specific advantage during the expansion phase. This K value was chosen as a compromise between computational time and populations having enough individuals of each species for

them to survive stochasticity in population dynamics during the stationary phase (Supplementary material Appendix 1 Fig. A1). Individual dispersal allele values were randomly drawn from a uniform distribution between 0.8 and 1, setting the initial emigration rate at approximately 20%. Environmental optima alleles' values (e_{opt}) were chosen to be equivalent to the individuals' starting patches' environmental values ($e_{x,y}$) plus a random normally-distributed number N (0,0.04). Given that all species were present across all initial patches, species started the simulation with similar environmental niches that then evolved through time. Each simulation was initialized with a 500 generation forerun period to allow local adaptation of populations (i.e. the stationary phase). After the 500th generation, the other patches become available for colonization and the model run for an additional 1000 generations during the expansion phase. We ran 20 replicates for each scenario (i.e. a combination of competition strength and presence/absence of demographic Allee effect). All simulations were performed in Matlab (MathWorks 2014).

At the end of each simulation, the GRS of each species was measured as the number of patches occupied across the entire landscape. The shape of the range-size distributions in each scenario was analyzed by computing their skewness. To assess the impact of Allee effects and competition on the evolution of niche and dispersal traits during range expansion, we recorded the average value of these traits across all patches in each generation for each species separately.

Given that we were interested in stable large-scale ecological patterns, both diversity and geographic range size gradients were analyzed at the regional scale (i.e. gamma diversity and gamma average GRS). It has been shown that evidence for latitudinal gradients are stronger when evaluated at the regional scale (Hillebrand 2004), probably due to a weaker importance of stochastic processes at this scale. We thus emulate studies that use latitudinal bands or large-scale

equal-area quadrats (geographic cells) to evaluate diversity gradients. A total of 100 regions were considered by dividing the landscape into equal-sized sub-regions (15 × 4) containing 60 local patches each (Fig. 1a). The diversity of each region was computed by pooling the number of different species found across their local patches, and the region's GRS was computed as the average GRS value from these species. To estimate the spatial gradient curves, we fitted a sigmoidal function:

$$\tau = \frac{\tau_0}{1 + \exp\left(-\beta * \left(latitude - c\right)\right)}$$

where τ represents either regional diversity or average GRS, τ_0 is the asymptote of the curve (i.e. maximum diversity or average range size), β represents the steepness of the curve at the inflection point and c is the inflection point (i.e. the y-position where τ reaches half of its maximum) while latitude is as the average y position of the region in the grid. The parameters τ_0, β, and c were estimated using the R package 'nls2'. Hereafter, the steepness of the slope is described by β. Finally, to explore the parameter space and the robustness of our results, we conducted a sensitivity analysis following Henriques-Silva et al. (2015). Details and results of this analysis are presented in Supplementary material Appendix 2 and 3.

Results

Allee effects and interspecific competition had a negative effect on species GRS (Fig. 2) and modulated the gradient steepness of both diversity and average GRS (Fig. 3). Species with Allee effects consistently exhibited smaller geographic ranges than the ones without, regardless of the interspecific competition strength (Table 1; Fig. 2). This resulted in a larger
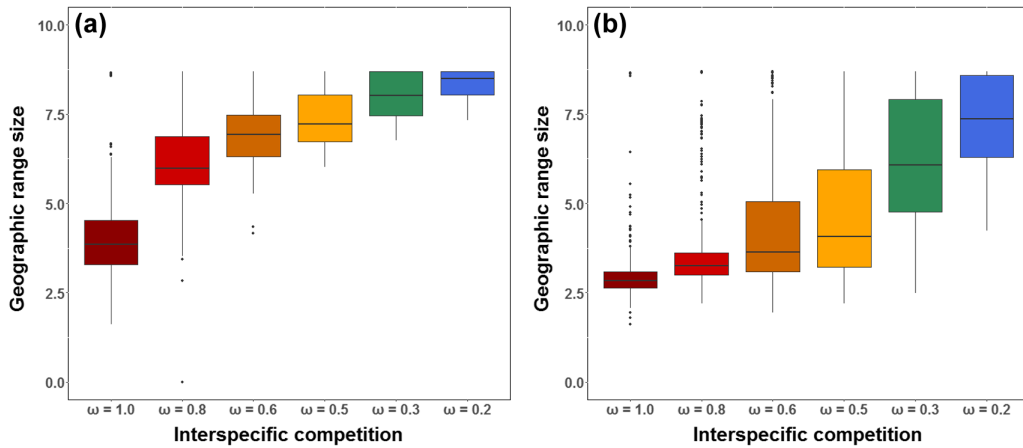

Figure 2. Boxplot depicting the log-transformed average geographic range size (GRS) of all species pooled from the 20 replicates for each competition strength scenario among species without (a) and with (b) demographic Allee effects (n = 20 × 20 = 400 species per boxplot). The GRS of each species was measured as the number of patches they occupied at the end of the simulation. The bottom and top boundary of the box plots represent the 25 and 75% percentiles, respectively, while the line within the box plots represents the median. Top and bottom whiskers outside the box plots represent ± 1.5 times the distance between the first and third quartiles.
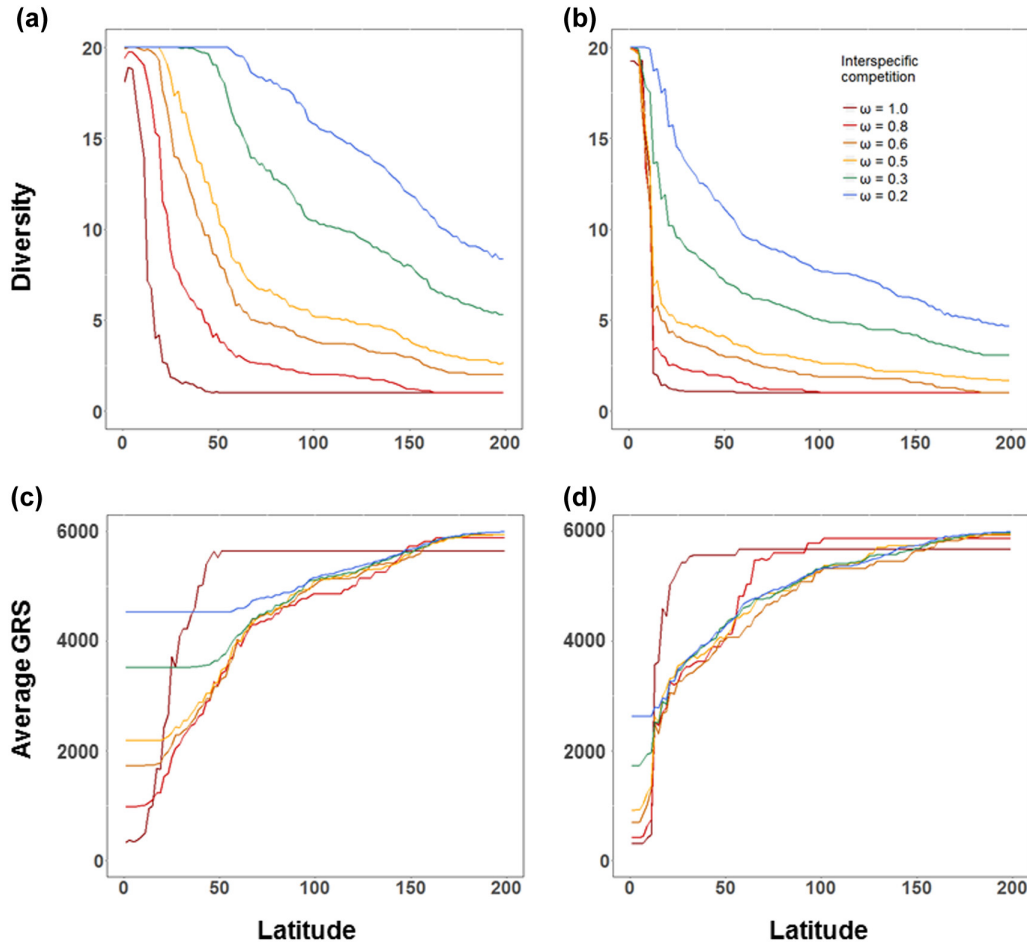
Figure 3. Plots depicting the spatial gradients in diversity and average geographic range size (GRS) for species without (a, c) and with (b, d) demographic Allee effects. Each colored line represents the average result of the 20 replicates for each competition scenario. Relationship between regional diversity (a, b) or regional average GRS (c, d) with latitude (*y*-position).

skewness in GRS distribution for species with Allee effects across most competition scenarios (Table 1; Supplementary material Appendix 4 Fig. A3, A4). The magnitude of the difference in average GRS between species affected or not by Allee effects varied across competition scenarios (Fig. 2). Species without Allee effects had an average GRS 2.35, 2.51, 2.40 and 2.04 larger than species with Allee effects in intermediary competition ($\omega = 0.8, 0.6, 0.5$ and 0.3, respectively), while the difference was smaller (1.17 and 1.73) for scenarios with very high or low competition (i.e. $\omega = 1.0, 0.2$, respectively) (Table 1). Moreover, demographic Allee effects increased the variance in average GRS (Fig. 2b), likely due to higher stochasticity in colonization–extinction dynamics.

Finally, interspecific interactions had a strong and predictable effect on species average GRS, i.e. when interspecific competition was higher, species average GRS was lower (Fig. 2).

Interspecific competition had the strongest effect on diversity gradients under equal intra and interspecific competition strength (i.e. $\omega = 1.0$): diversity decline was very steep because the portion of the landscape available for expansion after the stationary phase was mostly occupied by one or two species while the remaining ones were constrained to the initial southern regions. When the relative importance of interspecific competition decreased, more species were able to expand their ranges across the landscape, resulting in a smother diversity-gradient (Fig. 3a, b). This process was

Table 1. Mean ± standard deviation (STD) of geographic range size (GRS) pooled across the 20 replicates for scenarios without and with demographic Allee-effects across competition scenarios.

		$\omega = 1.0$	$\omega = 0.8$	$\omega = 0.6$	$\omega = 0.5$	$\omega = 0.3$	$\omega = 0.2$
Without Allee	mean ± STD	305.8 ± 1254.5	399.2 ± 1312.4	646.5 ± 1494.9	895.9 ± 1744.6	1704.1 ± 2119.2	2604.2 ± 2161.4
	skewness	4.11	3.78	2.69	2.17	1.18	0.59
With Allee	mean ± STD	303.9 ± 1244.1	337.3 ± 1299.1	456.8 ± 1378.6	601.0 ± 1530.4	1135.3 ± 1951.4	1819.3 ± 2207.1
	skewness	4.11	4.03	3.38	2.79	1.72	1.03

Table 2. Parameter estimation (τ_0, β and c) for the sigmoidal function used to characterize diversity gradients species without and with demographic Allee effects across the six competition scenarios ($\omega=0.2$, 0.3, 0.5, 0.6, 0.8 and 1.0). Comp.=competition scenario; τ_0= asymptote of the curve (i.e. maximum diversity); β=steepness of the curve at the inflection point; c=inflection point; ε=standard error; p=p-value.

	Comp.	τ_0 value	ε	p	β value	ε	p	c value	ε	p
Without Allee effects	$\omega=1.0$	20.00	1.44	< 0.0001	–0.278	0.052	< 0.0001	12.41	0.45	< 0.0001
	$\omega=0.8$	20.00	2.57	< 0.0001	–0.076	0.015	< 0.0001	29.24	3.64	< 0.0001
	$\omega=0.6$	20.00	2.16	< 0.0001	–0.051	0.01	< 0.0001	50.89	66.26	< 0.0001
	$\omega=0.5$	20.00	2.98	< 0.0001	–0.025	0.005	< 0.0001	70.13	53.36	< 0.0001
	$\omega=0.3$	20.00	0.96	< 0.0001	–0.025	0.003	< 0.0001	123.04	30.28	< 0.0001
	$\omega=0.2$	20.00	0.29	< 0.0001	–0.025	0.002	< 0.0001	168.73	16.18	< 0.0001
With Allee effects	$\omega=1.0$	20.00	0.79	< 0.0001	–0.835	0.198	0.0001	10.00	0.33	< 0.0001
	$\omega=0.8$	20.00	1.32	< 0.0001	–0.532	0.138	0.0004	10.00	0.59	< 0.0001
	$\omega=0.6$	20.00	4.21	< 0.0001	–0.203	0.078	0.0127	12.41	3.08	0.0002
	$\omega=0.5$	20.00	9.24	0.304	–0.025	0.011	0.0278	10.00	72.94	0.8915
	$\omega=0.3$	19.00	5.58	0.0014	–0.025	0.007	0.0005	48.48	26.94	0.0784
	$\omega=0.2$	16.00	1.56	< 0.0001	–0.025	0.005	< 0.0001	111.01	11.29	< 0.0001

substantiated by the fact that the β parameter (i.e. steepness of the curve at the inflection point in the sigmoidal fit) was the highest under strong competition (i.e. $\omega=1.0$; no Allee effect $\beta=-0.263$; with Allee effect $\beta=-0.83$; Table 2). Moreover, competition strongly affected the inflection point (c; i.e. the y-position where diversity was half of the maximum observed diversity), which was much greater under weak ($\omega=0.2$; no Allee effect, $c=178.89$; with Allee effect, $c=83.89$) than under strong competition ($\omega=1.0$; no Allee effect, $c=10.00$; with Allee effect, $c=10.00$; Table 2). Allee effects had an impact on diversity gradients given that across all competition scenarios, a relatively lower number of species reached the end of the landscape (i.e. northern regions) under demographic Allee effects (Fig. 3b). Except for the scenario with highest competition, the inflection point (c) for species under demographic Allee effects was always lower than for species not affected by them (Table 2), meaning that the diversity of the former group of species started to decline in y-positions that were closer to the southern border of the

landscape (i.e. the initial positions from the stationary phase; Fig. 1a).

The spatial gradient in average GRS was smooth under weak competition and became stronger as these interactions strengthen (Fig. 3c, d). The slope (β) decreased by 90 and 95% between the high ($\omega=1.0$) and the very low competition scenarios ($\omega=0.2$) for species without or with demographic Allee effects, respectively (Table 3). The difference in steepness across competition scenarios was mostly driven by a change in the average GRS of species found in the 'southern' regions, which increased with decreasing competition, rather than the ones found at the 'northern regions' of the landscape, which remained fairly similar across all competition scenarios (Fig. 3c, d).

In Fig. 4, we present the average expansion speed, dispersal rates and environmental phenotype (e_{opt}) over time across the 20 replicates for all species ranked by their abundances in the intermediary competition scenario ($\omega=0.5$). Similar results for other competition scenarios are reported in the

Table 3. Parameter estimation (τ_0, β and c) for the sigmoidal function used to characterize average geographic range size (GRS) gradients for asexual and sexual species across the six competition scenarios ($\omega=0.2$, 0.3, 0.5, 0.6, 0.8 and 1.0). Comp.=competition scenario; τ_0= asymptote of the curve (i.e. maximum diversity); β=steepness of the curve at the inflection point; c=inflection point; ε=standard error; p=p-value.

|	Comp.	τ_0 value	ε	p	β value	ε	p	c value	ε	p
Without Allee effects	$\omega=1.0$	5641.68	19.42	< 0.0001	0.141	0.005	< 0.0001	22.99	0.28	< 0.0001
	$\omega=0.8$	5737.43	61.69	< 0.0001	0.035	0.002	< 0.0001	45.13	1.31	< 0.0001
	$\omega=0.6$	5904.49	51.42	< 0.0001	0.029	0.001	< 0.0001	41.59	1.09	< 0.0001
	$\omega=0.5$	6016.58	70.26	< 0.0001	0.025	0.001	< 0.0001	37.40	1.47	< 0.0001
	$\omega=0.3$	6364.03	106.33	< 0.0001	0.017	0.001	< 0.0001	28.42	2.16	< 0.0001
	$\omega=0.2$	6617.80	119.42	< 0.0001	0.013	0.001	< 0.0001	12.82	2.48	< 0.0001
With Allee effects	$\omega=1.0$	5745.46	16.53	< 0.0001	0.729	0.045	< 0.0001	11.39	0.12	< 0.0001
	$\omega=0.8$	5936.06	33.13	< 0.0001	0.067	0.003	< 0.0001	23.39	0.64	< 0.0001
	$\omega=0.6$	5894.87	74.00	< 0.0001	0.031	0.002	< 0.0001	30.23	1.65	< 0.0001
	$\omega=0.5$	5858.73	33.86	< 0.0001	0.037	0.001	< 0.0001	27.37	0.77	< 0.0001
	$\omega=0.3$	5947.40	21.41	< 0.0001	0.030	0.001	< 0.0001	25.57	0.49	< 0.0001
	$\omega=0.2$	6115.38	36.28	< 0.0001	0.022	0.001	< 0.0001	20.86	0.78	< 0.0001
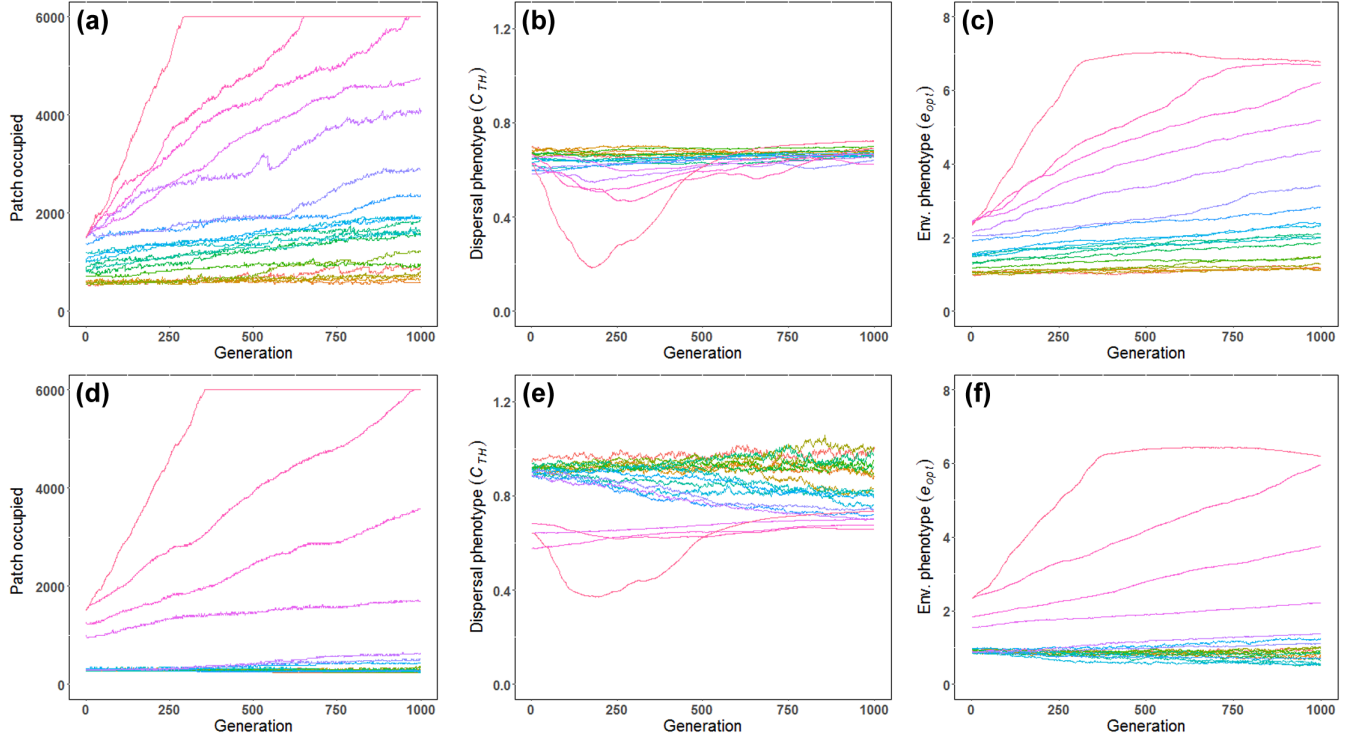
Figure 4. Results for range expansion speed (a, d), dispersal evolution (b, e) and niche evolution (c, f) for the competition scenario $\omega = 0.5$. Panels in the top and bottom rows refer to scenarios without and with demographic Allee effects, respectively. Species where ranked by their abundances in all replicates and each colored line represents the average values across replicates for each species. The light pink line represents the fastest species, which is the first to attain the patch no. 6000 in panel (a). Range expansion panels show the farthest occupied patch in which the species was found in generation t. Dispersal evolution panels show the average value of the dispersal phenotype (C_{TH}) for each species across time. Note that dispersal probability is higher when the dispersal phenotype (C_{TH}; threshold density) is lower. Finally, niche evolution panels show the average value of the environmental optima phenotype (e_{opt}) for each species across time.

Supplementary material Appendix 5 Fig. A5, A6, A7, A8 and A9. The species with the highest expansion speed (light pink line; Fig. 4a, d) underwent a strong positive selection for dispersal within the first 250 generations before decreasing towards initial values after expansion (light pink line; Fig. 4b, e). This effect was progressively weaker for subsequent species and practically disappeared for late-arriving species (Fig. 4b, e). Likewise, evolution of the environmental optima phenotype (e_{opt}) was much faster for the first species colonizing the landscape (i.e. light pink line) and became increasingly slower for other species (Fig. 4c, f).

The sensitivity analysis (Supplementary material Appendix 2) demonstrated that the quantitative results from our main simulations were, to a certain degree, sensitive to parameter change (Supplementary material Appendix 3 Table A1, A2, A3). In general, wider niche breadth (η) and higher mutation rates (m) allowed a greater number of species to expand given their higher survivability and capacity for local adaptation. Likewise, narrower niche breadth and lower mutation rates resulted in less species expanding across the environmental gradient. Higher population growth rates (μ) and lower carrying capacity (K) increased the intensity of competition within and among species, thus resulting in steeper diversity-declines. In contrast, lower μ and higher K dampened competitive interactions and promoted smoother diversity-declines. Nevertheless, our main result, i.e. stronger competition leads to steeper diversity gradients, remained unchanged. Although there were some changes in the steepness of the diversity-decline slopes, the order of these slopes in respect to the strength of competitive interactions remained the same (Supplementary material Appendix 3 Fig. A2) regardless of parameter variation (refer to Supplementary material Appendix 2 for a more detailed description of these results).

Discussion

The simulation experiment presented here was set to understand how density-dependent biotic processes shape large-scale ecological patterns through the differential evolution of species range dynamics across a heterogeneous landscape. The model showed that species under Allee effects established smaller geographical ranges than species without these effects, independently of interspecific competition (Table 1; Fig. 2). Likewise, competition intensity decreased species average GRS independently of demographic Allee effects (Fig. 2). The intensity of interspecific competition modulated both diversity and GRS gradients, promoting

steeper diversity decays and steeper average GRS increases under stronger competitive interactions (Fig. 3). The results from our model thus suggest that biotic density-dependent processes may modulate the steepness of diversity and GRS gradients by influencing differences in range expansion rates and capability.

Allee effects hindered species' colonization ability and consequently their geographic range size. Recent empirical studies corroborate our results; Grossenbacher et al. (2015) demonstrated that selfing plant species had an average GRS twice as large as their outcrossing sister species; while it was shown that, among freshwater microcrustaceans, cyclical parthenogenetic cladocerans exhibited GRS 70% larger than obligate sexual copepods (Henriques-Silva et al. 2016). Allee effects are known to slow down or even prevent species spread because populations at the range edge are generally at low densities (Taylor and Hastings 2005, Hargreaves et al. 2014). Although we modelled demographic Allee effects linked to survival probability (Kubisch et al. 2011), a common example of Allee effect is mate-finding difficulties in population at low densities. Thus, any trait that increases the likelihood of reproduction (e.g. sperm storage in females, mating timing, sex-biased dispersal, group dispersal) may improve species capacity for range expansion (Shaw and Kokko 2014). For instance, species that mate before or during dispersal should have larger range sizes compared to ones that mate after (Miller and Inouye 2013). Except in scenarios of very high interspecific competition ($\omega = 1.0$), Allee effects influenced the shape of diversity gradients because they promote more spatially restricted distributions that results in lower diversity at the end of the latitudinal gradient (Fig. 3b). Nevertheless, the generality of this process is still an open question given that, to the best of our knowledge, no study has contrasted large-scale ecological patterns among several clades with different susceptibilities to Allee effects (but see Henriques-Silva et al. 2016 for a comparison between two freshwater zooplankton groups).

The implicit degree of resource-use overlap among competing species implemented in our simulation had a strong effect on species' range expansions through priority effects. Fast dispersing individuals (i.e. those with high d) at the expanding front had higher fitness because they benefited from a low competition milieu (i.e. spatial selection; Phillips et al. 2010). This created a strong selection for highly dispersive individuals and increased the species' overall dispersal rates (Fig. 4b, e; see also Supplementary material Appendix 5). Spatial selection has been empirically demonstrated in the cane-toad invasion in Australia (Brown et al. 2013) as well as in experiments on protists' range expansion (Fronhofer and Altermatt 2015). Note that the spatial selection was more intense and affected fewer species under strong competition (Supplementary material Appendix 5 Fig. A9) compared to the scenario with lower interspecific competition (Supplementary material Appendix 5 Fig. A5), suggesting that dispersal evolution responds to both intra- and interspecific competition, a process demonstrated in experimental protist metacommunities (Fronhofer et al. 2015). Spatial selection allows early-arriving species to spread their ranges much faster than later colonizers (Fig. 4a, d) and, as a consequence, to build large populations (Fronhofer and Altermatt 2015). Moreover, these species might not only experience a demographic release from resource limitation but also an evolutionary release from biotic constraints (Yoder et al. 2010, Vanoverbeke et al. 2016), allowing them to adapt faster (Fig. 4c, f) to the environmental gradient than late-arriving species (Urban and De Meester 2009). Finally, given their large populations and longer time for local adaptation, early colonizers are more likely to resist posterior invasions through niche preemption (i.e. priority effects; Fukami 2015, De Meester et al. 2016). In sexually-reproducing species, however, this pre-emptive adaptation process should also depend on the steepness of the environmental gradient and the strength of the migration load on early colonizers (Holt and Gomulkiewicz 1997).

Further, our simulation also shows that the steepness of GRS gradients (i.e. Rapoport's rule) may also vary due to the strength of competitive interactions (Fig. 3c, d). The mechanisms discussed above (i.e. increase dispersal rates and priority effects) may also be an alternative explanation for the Rapoport's rule. Tropical species that dispersed earlier into temperate regions (or first species colonizing an elevation gradient) may have evolved higher dispersal rates and broader environmental niche breadths, becoming widespread generalist species. In contrast, species that dispersed later were affected by competition from adapted early-colonizers, thus prevented from undergoing the same evolutionary processes and unable to further expand their ranges across the latitudinal (or elevational) gradient (Stevens 1989, Valentine et al. 2008). Therefore, priority effects may have a role in structuring spatial ecological gradients (De Meester et al. 2016), especially for clades that mostly diversified in the tropics and consequently spread towards higher latitudes (Valentine et al. 2008).

How likely priority effects are to drive diversity patterns will depend on particular species' traits (e.g. generation time, dispersal ability, reproduction mode) of different clades (De Meester et al. 2016). In addition, the functional similarity among early and later colonizers should play an important role. For instance, experimental evidence has shown that prairie grassland species became less abundant when introduced into communities that were composed of functionally similar species, compared to situations in which the recipient community was composed of species from other guilds (Fargione et al. 2003). Thus, species' range dynamics can be regulated by the extent of the competitive pressure of other species at range limits (Alexander et al. 2015) and it should be easier for a species to adapt to novel environmental conditions when the biotic resistance is low at the expansion front (Case et al. 2005).

Historically, the effect of biotic interactions on ecological dynamics has been widely thought to be restricted to small scales. The idea that they may also influence range dynamics

and large-scale patterns of diversity have only recently gained attention (Araújo and Luoto 2007, Pigot and Tobias 2013, Svenning et al. 2014, Fukami 2015, Louthan et al. 2015, Morales-Castilla et al. 2015) and our simulation study allows understanding of how local biotic interactions can lead to large scale ecological patterns with related evolutionary consequences. That said, generating empirical evidence demonstrating that density-dependent biotic factors can lead to large scales patterns remains challenging. While there is still ongoing debate on the drivers of the LDG (Mittelbach et al. 2007), we argue that this research topic would benefit from better understanding the large variation in LDG slopes among different taxonomic groups (Hillebrand 2004). Future studies should thus contrast the LDG steepness of a broad number of clades that differ in the degree of resource-use overlap among species. We predict that clades with higher resource-use overlap would have a steeper decline in LDGs than clades with low overlap because they would be more prone to strong interspecific competition and priority effects (Vannette and Fukami 2014). For instance, it was shown that the latitudinal-diversity gradient is much steeper for cladocerans than copepods (Henriques-Silva et al. 2016). In addition to different susceptibility to Allee effects between these two groups, it follows that most cladoceran species are herbivorous and exhibit high resource overlap, whereas copepods comprise many specialized species with herbivorous, omnivorous or carnivorous diets (Guisande et al. 2003, Barnett et al. 2007). It is possible that differential diet overlap (i.e. differential resource-competition intensity) may have also influenced how the diversity gradients of these groups were structured.

Model constraints and assumptions

As in any simulation study, we are constrained by computational capacity and model assumptions that could influence our results. The limited number of generations for the expansion phase raises the question of whether observed patterns reached dynamic equilibrium. We performed an additional simulation in which we allowed the expansion phase to last for 4000 generations. Given the computational cost of our model, we limited this simulation to 10 replicates per competition scenario and conducted it only for the species not subjected to Allee effects. The results of this exercise show that the observed patterns are quite robust when competition intensity is intermediary or high ($\omega = 0.5$ and above) (Supplementary material Appendix 6 Fig. A10). In contrast, scenarios with weaker competitive interactions changed substantially (Supplementary material Appendix 6 Fig. A10) as more species were allowed to expand their ranges due to a weaker biotic barrier. These results have implications for the debate on whether large-scale diversity patterns have reached equilibrium (Rabosky and Hurlbert 2015) or not (Harmon and Harrison 2015). They suggest that whether observed diversity patterns have reached equilibrium may be clade-dependent as it would be contingent on how strong are the

interactions among the constituent species of the studied clade. This process is likely to be reinforced if species are subject to Allee effects given that it hinders species invasive potential because colonization generally starts at low densities (Fukami 2015).

It has been shown that long-distance dispersal (LDD) may also play an important role in species range expansion (Higgins and Richardson 1999, Figuerola and Green 2002). Whether LDD could impact or not the rate of diversity-decline through a faster head start in adaptation (i.e. monopolization priority effects) will depend on the niche breadth of individuals (i.e. their tolerance to a very different environment) as well as rates of local adaptation (De Meester et al. 2016). Nevertheless, LDDs are very rare and active dispersing organisms have a tendency to disperse to habitat patches that have similar environment conditions to their natal patch (Edelaar and Bolnick 2012). Accounting for LDDs would imply increasing the complexity of our model by making another assumption on the likelihood of this event without necessarily adding new conclusions or predictions. As such, we modelled the movement of organisms only using nearest-neighbor dispersal and emulated the range expansion of species under a spreading-dye model (Gotelli et al. 2009).

Although we modelled fixed mutation rates, it is known that they may evolve (Kimura 1967, Bedau and Packard 2003), resulting in higher genetic variability, consequently speeding up adaptation and range expansion. However, mutation rate is not a phenotype and thus cannot be affected by natural selection. Mutation rate evolves mainly through genetic hitchhiking when the locus of the mutation rate (e.g. one that influences DNA repair and replication) is linked to another allele that is under selection (Johnson 1999). This process has been shown to accelerate range expansion in single species model (Cobben et al. 2017) but its effects are unknown for multiple competing species. However, modelling a realistic evolving mutation rate with linkage disequilibrium, multiple alleles and deleterious mutations would complicate unnecessarily the model and would go outside the scope of our study. Furthermore, among the parameters analyzed in the sensitivity analysis, mutation rate was the one that least affected the diversity-decline slopes (Supplementary material Appendix 3). Thus we are confident that our results are robust if this assumption is relaxed.

Modelling interspecific competition through implicit resource-use prevented us to explore how evolution of interactions could influence diversity patterns. For instance, strong biotic interactions among sympatric species may drive ecological trait divergence (i.e. character displacement) and consequently foster local diversity (Pfennig and Pfennig 2010). This process should be contingent on the strength of selection on resource-use traits as well the colonization rates of the interacting species (Vanoverbeke et al. 2016). Future studies should investigate how the evolution of species interactions may change the strength of priority effects and whether these eco-evolutionary dynamics could influence patterns of species diversity.

We simulated asexually-reproducing species and, as such, our results do not account for processes that may potentially influence adaptive rates during range expansion. For instance, models using more complex genetic architectures have shown that genetic correlation between multiple quantitative traits may preclude species range shift under large spatiotemporal environmental variation (Duputié et al. 2012). Another process that may be important in sexual populations is migration load, i.e. the swamping of alleles of populations at the expansion front from maladapted individuals originated in the species range's core, which has been suggested to slow or prevent local adaptation (Lenormand 2002). Given that peripheral populations are generally at low densities, maladapted immigrants from the range core would likely have a relevant effect on its genetic structure, which in turn would hinder local adaptation. However, peripheral populations are also sinks (i.e. they have negative growth rate) and thus depending on immigration to persist, and eventually adapt (Holt and Gomulkiewicz 1997). Moreover, migration can increase genetic variation in peripheral populations and facilitate adaptation (Alleaume-Benharira et al. 2006). Hence, the adaptive potential of a sink population will be a function of the intensity of immigration, the fitness of the immigrant (i.e. how much maladapted individuals are to the local environment) as well as the steepness of the environmental gradient (Holt and Gomulkiewicz 1997). In the case of multiple competing species, migration load could decrease the advantage of initial colonizers because the evolution of high dispersal rates (i.e. through spatial selection) would encounter stronger migration load. This would in turn increase the odds of other species expanding, and resulting in relatively smoother diversity-decline gradients. Nonetheless, previous models have shown that biotic interactions can halt range expansion even without invoking the disruptive effect of migration load (Price and Kirkpatrick 2009). As such, we are confident that migration load should not really affect the generality of our results.

Conclusion

In conclusion, our simulation study provides a compelling context for biotic factors such as Allee effects and competitive interactions to explain the strong variation in diversity and GRS gradients observed across multiple taxonomic groups. We showed that the structure of these gradients can be generated through Allee effects as well as spatial selection and priority effects experienced by species dispersing early. However, the importance of these processes will depend on the strength of interspecific competition. In other words, fewer species are able to expand their ranges and reach the extreme of gradients as competition intensity increases. We expect that our results will foster new research to test the predictions derived from our model and advance our understanding regarding the mechanisms underlying large-scale ecological gradients.

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