PROCEEDINGS B

Research

Author for correspondence:
Sarah P. Otto
e-mail: otto@zoology.ubc.ca

†Co-first author

Asymmetric competition impacts evolutionary rescue in a changing environment

Courtney L. Van Den Elzen[1,2,†], Elizabeth J. Kleynhans[1,†] and Sarah P. Otto[1]

[1]Department of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4
[2]Department of Ecology and Evolutionary Biology, University of Colorado at Boulder, 1900 Pleasant Street, 334 UCB, Boulder, CO 80309-0334, USA

CLVDE, 0000-0001-9995-1954; SPO, 0000-0003-3042-0818

Interspecific competition can strongly influence the evolutionary response of a species to a changing environment, impacting the chance that the species survives or goes extinct. Previous work has shown that when two species compete for a temporally shifting resource distribution, the species lagging behind the resource peak is the first to go extinct due to competitive exclusion. However, this work assumed symmetrically distributed resources and competition. Asymmetries can generate differences between species in population sizes, genetic variation and trait means. We show that asymmetric resource availability or competition can facilitate coexistence and even occasionally cause the leading species to go extinct first. Surprisingly, we also find cases where traits evolve in the opposite direction to the changing environment because of a 'vacuum of competitive release' created when the lagging species declines in number. Thus, the species exhibiting the slowest rate of trait evolution is not always the most likely to go extinct in a changing environment. Our results demonstrate that the extent to which species appear to be tracking environmental change and the extent to which they are preadapted to that change may not necessarily determine which species will be the winners and which will be the losers in a rapidly changing world.

1. Introduction

For species with limited dispersal abilities, phenotypic plasticity may allow survival in a changing environment over the short term, but persistence ultimately depends on evolutionary adaptation. Most studies have investigated adaptation to abiotic change in isolation from other species [1–4]. Yet the evolutionary potential and trajectory that a species follows can be strongly shaped by other species within the community. For example, interspecific competition can drive changes in population size [5], and the strength and direction of selection [6–8]. Consequently, we expect interspecific competition to be an important determinant of whether and how species adapt to abiotic change. In this paper, we explore how competition for resources—particularly symmetric versus asymmetric competition for resources—determines the persistence and evolution of species competing in a changing environment.

Previous work on the subject has found that resource competition can increase or decrease adaptation to abiotic change [9–14]. On one hand, competition can prevent adaptation if it causes competitive exclusion [9–12]. Theoretical work has shown that higher species diversity increases the chance that one or more species may be preadapted to a new environment, reducing the ecological opportunity for an evolutionary response in the remainder of the community [9,13]. Furthermore, preadapted species are able to maintain larger population sizes for longer, facilitating their adaptation, while maladapted species may fail to track a temporally shifting resource distribution because of declining population sizes [10]. On the other hand, competition can exert an additional selective

2

pressure, facilitating adaptation when the abiotic and biotic selection pressures are concordant [11]. However, this will only assist adaptation when the increased selection pressure is enough to overcome the negative effect of a reduced population size due to competition [14]. Furthermore, the nature of competition may itself evolve, and the impact of a changing environment can be muted if species that become competitively inferior in a new environment evolve to be fiercer competitors [15]. More likely, however, declines in population size of the competitively inferior species may cause it to evolve to be a weaker competitor, exacerbating the impact of environmental change on this species [15].

In this paper, we explore a model of competition where two species use a common resource abundance distribution that shifts through time. Previous theoretical work on the effect of competition on adaptation to environmental change had assumed that resource availability [10,11,14] and strength of competition (i.e. competition coefficients) [10] follow symmetrical distributions. These symmetry assumptions cause the initial equilibrium population sizes to be equal, with two competing species possessing trait values equidistant but on opposite sides of the resource peak. As the resource distribution shifts (environment changes) in time, the species whose trait value lies in the direction of the changing resource (hereafter referred to as the *leading species*) is more likely to persist because its trait is preadapted to the changing environment and, consequently, its population size remains higher for longer. The species whose trait value lies behind the direction of the changing resource (hereafter referred to as the *lagging species*) must persist in the tail of the resource distribution and thus often declines in abundance. Ultimately, lagging species are more likely to go extinct, even with environments that are changing slowly enough to allow one species to persist [10].

Asymmetries are rife in nature. Resource distributions commonly exhibit skew [16–20]. Such asymmetries can reflect age or stage structure of prey or plant species, or can emerge from differential contributions from a variety of resource species (e.g. producing a variety of seed sizes from different plants). The competitive impact of individuals on one another is also often asymmetric in nature [21–25] and can arise as a result of size differences between species or due to 'prior-residence effects'. For example, in plant communities, taller individuals shade smaller individuals, gaining a disproportionate share of light [25–27], and in animals larger males often win more contests, gaining access to a larger proportion of females [28], or earlier arrivers have a competitive advantage over resources [29]. Asymmetries in either resources or competition coefficients generally alter the population sizes of species competing for resources so that the species with the trait value closest to the resource peak or the species that is more competitively dominant has a larger population size. With different population sizes, species will have different levels of standing genetic variation, will experience different rates of novel mutation and will be subject to different degrees of demographic stochasticity, all of which could alter the relative probability of extinction of each species when facing a changing environment [30,31]. Allowing for different initial population sizes is also more realistic, as species competing for resources typically do not have equivalent population sizes (e.g. mammalian carnivores [32], mammalian herbivores [20] or fish [33]). Thus, we explore whether asymmetric forms of competition fundamentally alter how communities of species respond to a changing environment. In theoretical studies, asymmetries in resources

and in competition coefficients have previously been incorporated into models of taxon cycles [34,35] and disruptive selection [36–38]. However, they have not, to our knowledge, been used in the context of adaptation to a changing environment. Building on the methods of Johansson [10], we investigate how asymmetries in resource availability or competition coefficients, by generating differences in population size and in traits related to resource consumption, impact the evolutionary dynamics of each species, and how they alter which species survive and which go extinct in a changing environment.

In brief, we develop an individual-based model with a single continuous trait that governs competitive interactions and is subject to selection. The strength of competition is assumed to depend only on the similarity of individuals' trait values, whether those individuals are from the same or different species. The trait may represent a resource preference (e.g. preferred prey size), a habitat preference (e.g. preferred temperature), a developmental trait (e.g. flowering time), etc. Following a burn-in period, we allow the environment to change in a manner that shifts the distribution of available resources. For example, ocean acidification may alter the developmental rate and/or degree of calcification for marine prey (e.g. [39]), rising global temperatures may shift the availability of sites at a given mean temperature [40], or delays in killing frosts at the end of the growing season may shift flowering time [41]. As a consequence of this shift in available resources, the trait values of each species experience selection to track the changing environment. We model the evolutionary response by tracking alleles at 10 unlinked, diploid genetic loci subject to mutation following the method of Johansson [10]. We assume that individuals move freely across their range, at least when seeking a mate, so that mating is random within a species but absent between species.

We find that asymmetrical resource distributions or competition coefficients can facilitate coexistence when species lagging behind the changing resource distribution have a larger population size and can even cause extinction of the preadapted leading species before the lagging species. Surprisingly, we also find cases where traits evolve in the opposite direction to the changing environment. This occurs because a shifting environment relaxes competition exerted by the lagging species on the leading species, particularly when the leading species has a smaller initial population size. This creates a 'vacuum of competitive release' that causes traits to evolve in the opposite direction of environmental change. Interestingly, this vacuum means that species that appear to be failing to adapt to a changing environment might actually be competitive leaders that are simply taking advantage of steeper declines in lagging competitors. As a consequence, the species exhibiting the slowest rate of trait evolution is not always the species most likely to go extinct in a changing environment.

2. Model

Our model is an extension of that of Johansson [10], which explored a Lotka-Volterra-based model of competition for resources in a changing environment. We follow the methods of Johansson [10] closely with the exception of adding asymmetry to the resource distribution and competition coefficients. We find that results are similar for both forms of asymmetry, and thus we present the findings for asymmetric resources in the body of the paper and results for asymmetric

Table 1. Model parameters. Default values are given, along with alternative values considered as described in the text (square brackets). Additional intermediate values ($V_m = 0.0001$ and 0.00015) were used in search of leading species extinction with an increased mutation rate.

parameter	value	definition
F	4	fecundity
r_k	1	intrinsic growth rate
ν	0.02 [0.2]	genome-wide mutation rate
σ_ν	0.0015 [0.015]	standard deviation of mutational effect size
K_m	variable	maximum resource abundance
σ_K	1	standard deviation of the resource abundance distribution
μ_K	0 [$+V_m t$]	mean of the resource abundance distribution
κ	0 [± 4]	degree of asymmetry in the resource abundance distribution
σ_α	0.85	breadth of the competition function
β	0 [± 0.6]	degree of asymmetry in competition function
V_m	0.00005 (slow); 0.0005 (fast)	speed of environmental change

competition coefficients in the supplementary information. Simulations were written in MATHEMATICA 9.0, and the key model parameters are summarized in table 1. The model tracked diploid hermaphroditic individuals, with non-overlapping generations. During reproduction, each individual was chosen as a mother, a mate of the same species was identified (including potentially the mother herself), and a constant number of offspring, F, was produced with that mate. The probability that an offspring of genotype i survives was set to $W(u_i)/F$, where

$$W(u_i) = 1 + r_k \left(1 - \frac{\sum_k \sum_j \alpha_{ij} n_{jk}}{K(u_i)} \right), \qquad (2.1)$$

which depends on the offspring phenotype (u_i), the intrinsic growth rate of species k (r_k), the resource abundance at u_i ($K(u_i)$), the competition exerted by each of the j types of the k species on individual i (α_{ij}, including itself), and the number of individuals of phenotype u_j of species k (n_{jk}). If a mother's offspring all had the same genotype i (temporarily ignoring recombination and mutation), $W(u_i)$ would represent the mother's expected number of surviving offspring, and the number of individuals of phenotype u_i in species k would be expected to change over time according to

$$n_{ik}(t + 1) = W(u_i) n_{ik}(t). \qquad (2.2)$$

The need to calculate $W(u_i)$ over the entire distribution of individuals of each generation greatly slows the simulations. For speed, Johansson [10] linearly interpolated $W(u_i)$ using 100 values of u_i in each generation. We instead round individual trait values to three significant figures and calculate $W(u_i)$ from these rounded values. Therefore, when there is more trait diversity, the fitness function is calculated based on more points. We believe this helps capture the nonlinearities in the fitness function when many phenotypes are present.

Assuming rare mutations and a population initially fixed for phenotype u_i, the expected rate of evolution of species k would be

$$\frac{\mathrm{d} u_i}{\mathrm{d} t} = \frac{1}{2} \nu \sigma_\nu^2 \hat{n}_k \left. \frac{\partial W(u')}{\partial u'} \right|_{u' = u_i} \qquad (2.3)$$

[42], where ν is the mutation rate, σ_ν^2 is the variance of mutation effect sizes, $\hat{n}_k$ is the equilibrium population size

of species k and $\partial W(u')/\partial u'|_{u' = u_i}$ is the fitness gradient evaluated at the phenotype u_i. Equations (2.2) and (2.3) were used to determine equilibrium configurations that were both ecologically and evolutionarily stable (see the electronic supplementary material, MATHEMATICA package).

Following Johansson [10], an individual's phenotype was based on the additive effects of twenty alleles at ten diploid loci. Offspring acquired a mutation with probability ν per diploid genome, with the mutational effect drawn from a normal distribution with a mean equal to the parental allelic value and variance σ_ν^2.

The resource distribution, $K(u_i)$, represents the resources available to individuals of phenotype u_i. We assumed that $K(u_i)$ has a single peak [43], and we introduced asymmetry into this resource distribution by using a skew-normal distribution [44]:

$$K(u_i) = K_m \frac{\mathrm{e}^{-(u_i - \xi)^2 / 2\omega^2}}{\sqrt{2\pi\omega^2}} \operatorname{erfc}\left(-\frac{\kappa(u_i - \xi)}{\sqrt{2\omega^2}} \right). \qquad (2.4)$$

Here, κ modifies the skew (asymmetry) of the distribution (figure 1a); with $\kappa = 0$, we regain the Gaussian distribution of Johansson [10] and others [34,45–47]. K_m scales the height of the resource abundance, ξ determines the position of the distribution along the resource axis (corresponding to u_M in [10]), ω controls the breadth of the distribution and erfc() represents the complimentary error function.

In order to hold the mean and variance of the resource distribution constant while varying the skew, we set the first and second moments of the skew-normal distribution equal to those for a Gaussian distribution with mean μ_K and variance σ_K^2, yielding

$$\xi = \mu_K - \frac{\kappa \sigma_K}{\sqrt{(1 + \kappa^2)(\pi/2 - 1) + 1}} \qquad (2.5)$$

for the location of the resource distribution and

$$\omega = \sigma_K \frac{1}{\sqrt{1 - 2\kappa^2/(\pi(1 + \kappa^2))}} \qquad (2.6)$$
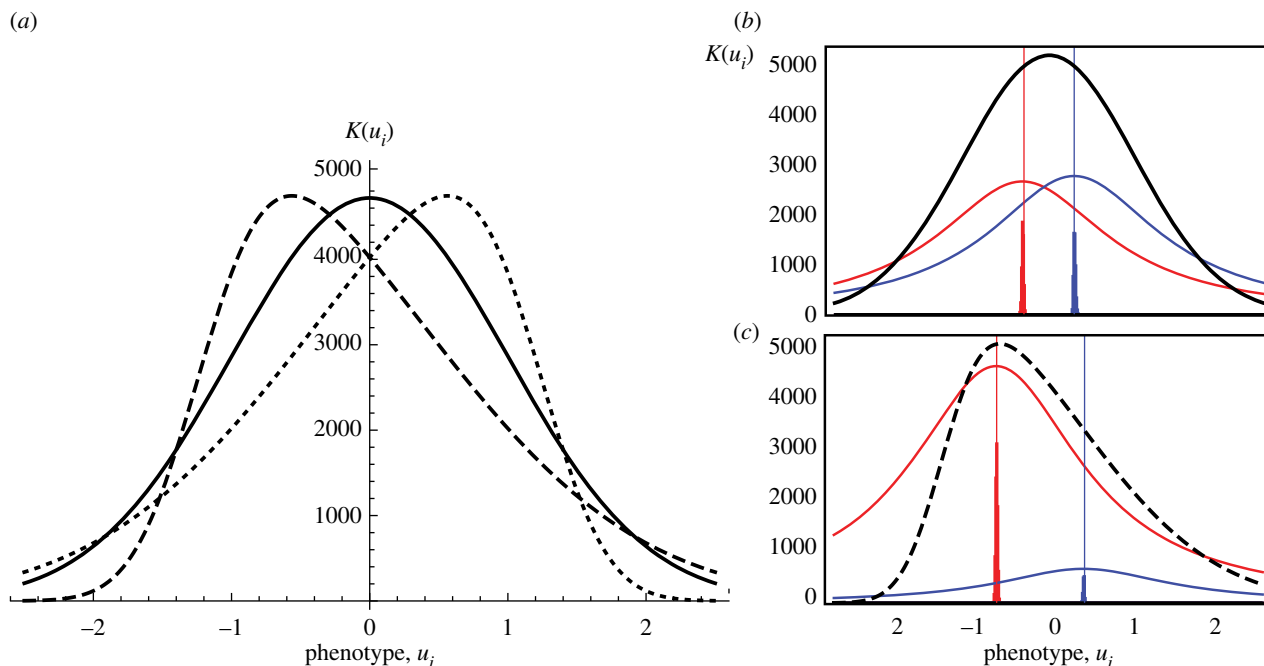
for the breadth of the distribution.

Figure 1. Symmetric and asymmetric resources and their impact on population size and trait value. (a) The resource distribution (equation (2.4)) available to individuals of phenotype u_i is shown for $\kappa = 0$ (solid line, symmetrical), $\kappa = 4$ (dashed line, right-skewed) and $\kappa = -4$ (dotted line, left-skewed). (b,c) The initial ESS for each species (thin red and blue vertical lines), the post-burn-in species distributions (in 0.01 bins, narrow red and blue histograms, doubled in height for clarity), and the competition exerted by those two populations on individuals of phenotype u_i (red and blue curves, respectively) for (b) the symmetrical resource distribution case ($\kappa = \beta = 0$) and (c) the right-skewed resource distribution case ($\kappa = 4$, $\beta = 0$). Note in (c) that the species with a negative phenotype has a larger population size (red histogram) than the species with a positive phenotype (blue histogram).

Alternatively, we introduced asymmetrical competition coefficients using the function

$$\alpha_{ij} = \left(\frac{1}{1 + (u_i - u_j + \beta)^2/(2\sigma_\alpha^2)} \right)\left(1 + \frac{\beta^2}{2\sigma_\alpha^2} \right). \quad (2.7)$$

The parameter β describes the asymmetry of competition coefficients, and the width of the competition kernel is controlled by σ_α. When $\beta = 0$, we regain the symmetrical case considered by Johansson [10], with $\alpha_{ij} = \alpha_{ji}$. When $\beta > 0$, the distribution is right-skewed, implying that individuals exert the strongest competitive effects on individuals of a slightly smaller phenotype (electronic supplementary material, figure S1a). The last parenthetical term in equation (2.7) scales competition so that the effect of individuals on others of the same phenotype is, by definition, one (i.e. $\alpha_{ii} = 1$).

The evolutionary stability of communities with one or more species depends on the ratio of the curvature at the modes of the competition and resource functions [43,47]. For symmetric distributions, there is only one evolutionarily stable species when $\sigma_\alpha/\sigma_K > 1$, but multi-species communities can persist for $\sigma_\alpha/\sigma_K < 1$ [10,37]. For this reason, Johansson [10] chose to use different values of σ_α/σ_K for his simulations with one species ($\sigma_\alpha/\sigma_K = 1.5$) versus two species (typically using 0.85). He also showed, however, that increasing σ_α/σ_K reduced the maximum velocity that could be sustained in the two-species case (see table B2 in [10]).

To avoid confounding the potential effects of σ_α/σ_K and the number of species, we chose to fix σ_α/σ_K at 0.85. Because neither assortative mating nor asexuality were allowed to evolve within species, branching was not possible [37,43], and consequently this choice allowed both one-species and two-species communities to persist at equilibrium. Interestingly, for the asymmetry parameters considered ($\kappa = \pm 4$ or $\beta = \pm 0.6$;

figure 1; electronic supplementary material, figure S1), both two- and one-species communities are not only stable equilibria, but they also represent evolutionarily stable strategies, at least locally. That is, branching by small mutational steps would not be expected from either equilibrium, even if the population were asexual (see the electronic supplementary material, MATHEMATICA package). The parameter values governing asymmetry were chosen to generate similar ESS trait values and population sizes, regardless of whether asymmetries were introduced into the resource distribution ($\kappa = \pm 4$; figure 1) or the competition coefficients ($\beta = \pm 0.6$; electronic supplementary material, figure S1). Specifically, these parameter choices led to trait values near 0.5 for the leading species and -0.5 for the lagging species, where the larger of the two populations was six to seven times the size of the smaller (see the electronic supplementary material, MATHEMATICA package).

Simulations were initiated from communities of one or two species, each of which was initially fixed phenotypically according to the evolutionarily stable strategy (ESS) obtained numerically (or in the symmetric case with one species at the singular point; electronic supplementary material, table S1). With one species, the ESS phenotype was centred at the peak—not the mean—of the resource distribution when the resource distribution was asymmetric ($\kappa \neq 0$). Asymmetrical competition coefficients ($\beta \neq 0$), however, caused a shift in the ESS away from the peak of the resource distribution and towards phenotypes experiencing weaker competition (i.e. towards the right with right-skewed competition, $\beta > 0$). When two species were present and the distributions were perfectly symmetrical, the ESS consisted of two species of equal population size, lying equidistant but on opposite sides of the resource peak. With asymmetrical distributions (either $\kappa \neq 0$ or $\beta \neq 0$), however, the phenotypes of the two distributions were different distances away from the mode, and the
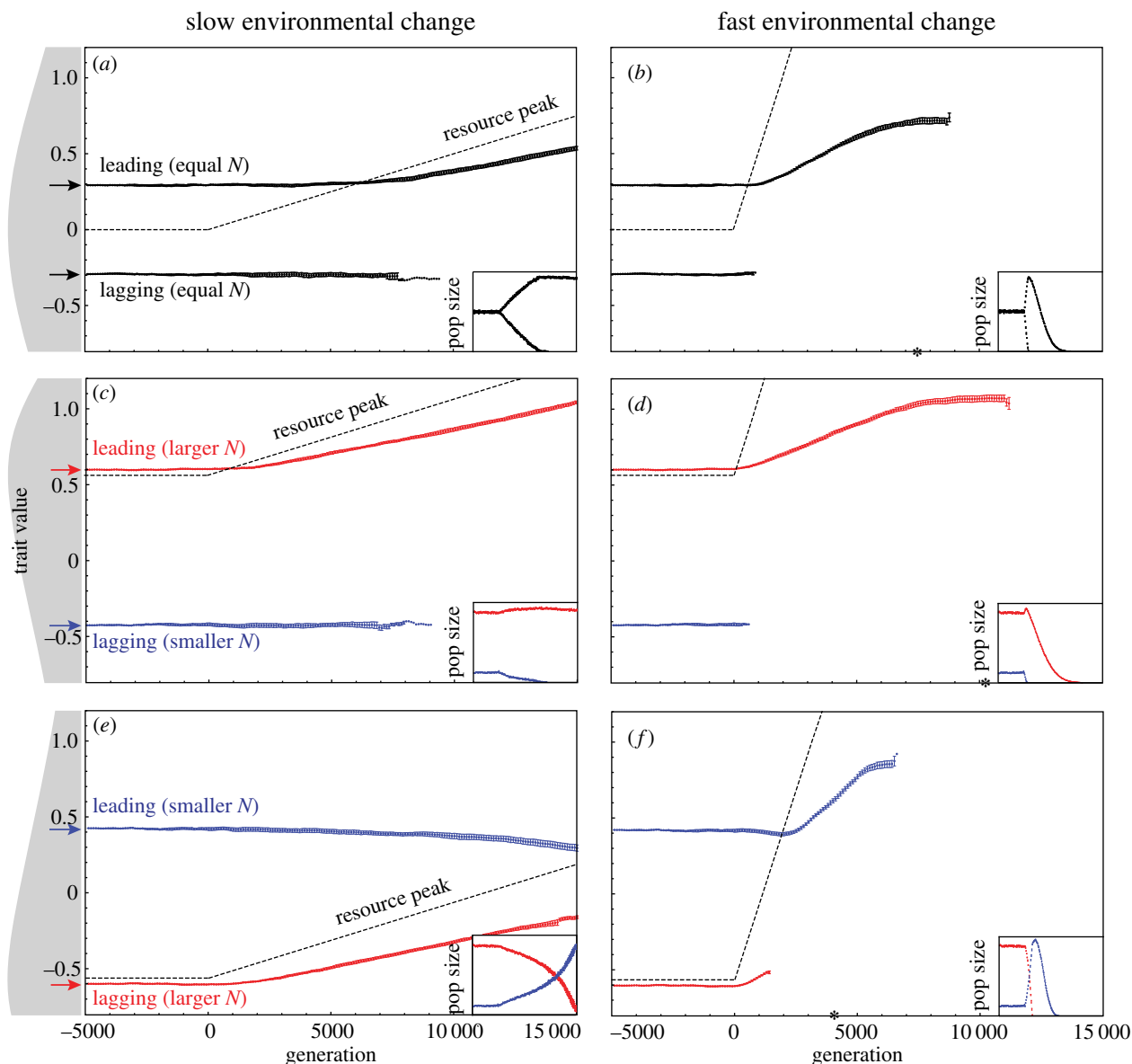
Figure 2. The evolution of two-species communities competing for asymmetrical resources in a changing environment. The resource distribution was (a,b) normally distributed, (c,d) left-skewed ($\kappa = -4$) or (e,f) right-skewed ($\kappa = 4$), as illustrated by the grey distribution along the y-axis. In all panels, the mean resource was initially zero for 5000 generations, after which the distribution shifted upwards (a,c,e) slowly ($V_m = 0.00005$) or (b,d,f) rapidly ($V_m = 0.0005$); the dashed line tracks the peak (mode) of this resource distribution and also corresponds to the trajectory of the mean in panels (a,d), where the distribution is symmetric. The initial ESS trait dynamics are given by the arrows on the left of panels (a,c,d) and the corresponding simulation trait dynamics are illustrated in the main plots (mean ± 1 s.e.m. shown while more than one replicate persisted). The asterisks show the average time that a single-species community went extinct (only observed in a rapidly changing environment). Inset plots show the population size dynamics for each species (inset plot x-axis: −5000 to 15 000 generations; y-axis: 0 – 5000 individuals), where red is the initially larger population and blue the initially smaller population. Remaining parameters were set to their default values (table 1).

equilibrium population sizes were unequal (see the electronic supplementary material, MATHEMATICA package and table S1).

In all cases, the height of the resource distribution, K_m, was chosen so that the average number of individuals per species was initially expected to equal 2500 at equilibrium, regardless of the parameter values (electronic supplementary material, table S1). While initial population sizes were equal in the symmetrical case, the two species varied substantially in population size with asymmetrical parameter choices (electronic supplementary material, table S1): 7.0-fold with asymmetrical resources ($\kappa \pm 4$) and 6.6-fold with asymmetrical competition coefficients ($\beta \pm 0.6$).

Starting from an initial resource mean of $\mu_K = 0$, we then allowed the communities to acquire genetic variation and stabilize for 5000 generations ('burn-in' from $t = -5000$ to 0).

At time $t = 0$, we simulated a changing environment by shifting the resource distribution linearly upwards at speed V_m over time, so that $\mu = V_m t$. The speed was chosen to be either slow enough that a single species could persist on its own for 15 000 generations ($V_m = 0.00005$) or fast enough that a single species went extinct by that time ($V_m = 0.0005$). We then examined the persistence of communities consisting of two species, relative to the one-species case.

3. Results

Figure 2 illustrates the effect of an asymmetric resource distribution on the persistence of a two-species community. When the environment changed slowly (figure 2a,c,e), the leading

Table 2. Extinction time in generations. Populations were censused every 100 generations for extinction or persistence. If no replicate went extinct by 15 000 generations, an asterisk is reported. In all other cases, the mean extinction time is recorded, with SEM in parentheses. One replicate went extinct at 14 200 generations and the remaining four persisted to 15 000 generations; these simulations were extended until all replicates went extinct, which occurred on average after 15 300 (329) generations.

		slow environmental change			fast environmental change		
		one species	two species		one species	two species	
κ	β		leading	lagging		leading	lagging
0	0	*	*	7880 (404)	7480 (97)	8720 (37)	820 (20)
4	0	*	*	14 840 (160)	4100 (55)	6480 (37)	1380 (20)
−4	0	*	*	7740 (385)	10 200 (95)	11 100 (45)	520 (20)
0	0.6	*	*	1640 (51)	9440 (68)	10 260 (81)	160 (24)
0	−0.6	*	*	13 640 (316)	6060 (75)	8660 (40)	1400 (0)

species (higher data points) persisted the full 15000 generations, as observed in the single-species communities (electronic supplementary material, figure S2; table 2). Persistence was observed whether the leading species was initially larger (red indicates species with the larger initial population size; figure 2c) or smaller (blue; figure 2e) than the lagging species. By contrast, the lagging species (lower data points) typically went extinct before 15 000 generations, unless resource asymmetries allowed the lagging species to have access to substantially more resources (figure 2e); in this case, with a larger initial population size, the lagging species better tracked the changing environment, and most replicates (4 out of 5) persisted throughout the 15 000 generations of environmental change.

When the environment changed rapidly (figure 2b,d,f), however, all species went extinct by generation 15 000. Nevertheless, species with initially larger population sizes persisted for longer than they would have had they had smaller population sizes. Furthermore, for these parameter values, the leading species always persisted longer than the lagging species, regardless of whether it was smaller or larger initially. The leading species also persisted longer than a single-species community (see asterisks on x-axis and electronic supplementary material, figure S2).

The leading species from the two-species communities had two separate advantages that allowed it to persist longer than single-species communities when the environment changed rapidly: a 'head start' in the trait mean and, eventually, a larger population size. The head start was due to the 'competitive push' by the lagging species (cf. [11]), causing the leading species to have a higher initial trait mean and hence to be better preadapted to the environmental change. The larger population size was due to our assumption that, initially, the average population size for the two-species communities was equal to that of the single-species community (2500 individuals). Consequently, once the lagging species went extinct, the leading species had access to more resources, causing its population size to rise above 2500 at least transiently (inset panels in figure 2). In the electronic supplementary material, Methods, we describe additional simulations to disentangle the head-start effect from the population size effect. These simulations indicate that both play a role; the head start was most important in figure 2f, where the leading species was small initially and the trait far ahead of the peak resource,

while the population size advantage was most important in figure 2d, where the leading species initially had a large population size but a trait value close to the resource peak.

Very similar patterns were also observed when competition coefficients, not resources, were asymmetric (electronic supplementary material, figure S3). In particular, asymmetries helped maintain both species in a community over longer periods of time when the lagging species had a larger population size (electronic supplementary material, figure S3e,f). The leading species in the two-species community also persisted longer than either the lagging-species or the single-species communities (electronic supplementary material, figure S4). The fact that the source of the asymmetry did not greatly impact the results is not unexpected, given that we chose the parameters κ and β so that the initial abundances and trait values for the lagging and leading species were similar in the two cases.

One of the more intriguing patterns seen with either form of asymmetry was evolutionary responses in the opposite direction to the changing environment. This was repeatedly observed when the leading species had the smaller initial population size (figure 2; electronic supplementary material, figure S3e,f). As the resource peak moved away from the lagging species, its population size began to decline, increasing the resources available at the lower end of the resource distribution for use by the leading species. The leading species then evolved to monopolize the resource left behind by the declining lagging species, rather than evolving in the direction of the environmental change. In other words, the decline of the lagging species caused a vacuum of decreased competition into which the leading species evolved. In all cases, we only observed this pattern while the peak of the resource distribution remained between the mean phenotypes of the two species. Once the peak crossed over both species' mean trait, the direction of evolution for the leading species shifted to track the change in the environment. Trait evolution in the opposite direction of the environmental change persisted for the entire 15 000 generations in the case of a slowly changing environment, but was transient with a rapidly changing environment, reversing soon after the lagging species went extinct. On the basis of these results, we emphasize that species appearing to fail in tracking a changing environment may, in fact, be gaining an ecological foothold, evolving into the niches of species declining within the community.
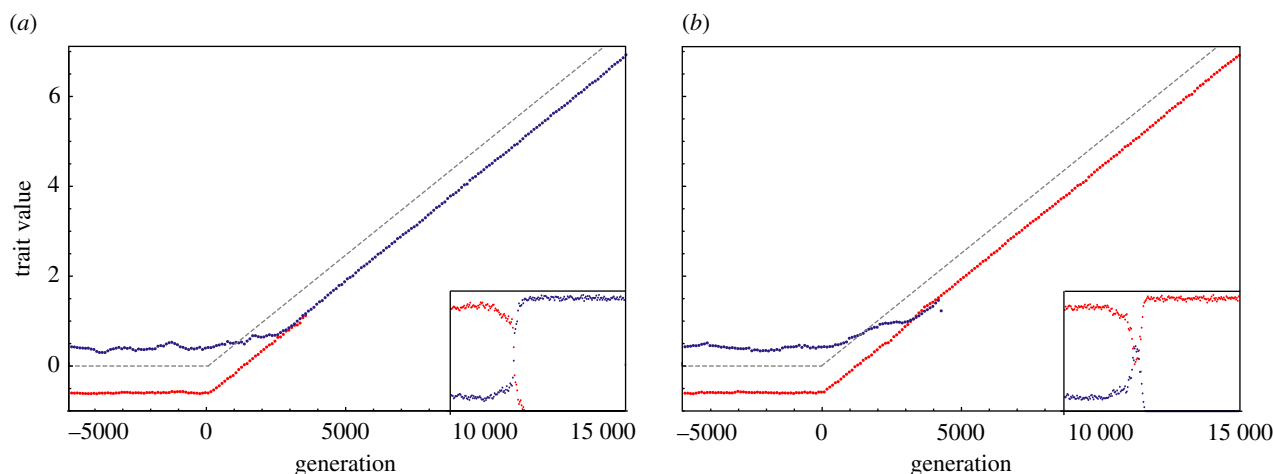
Figure 3. Higher adaptability can allow a lagging species to out-evolve a leading species in a rapidly changing environment when mutational effects are larger. The parameters for these simulations were identical to figure 2f except for $\sigma_\nu = 0.015$. Four out of five *original* replicates (see Results section for additional simulations) showed patterns similar to (a), but in one replicate, the lagging species survived, driving the leading population to extinction (b). Observe that the two species are very similar in mean trait (main plots) and population size (insets) at around 3000 generations, which is when the fate of the two species is determined stochastically by which species has the largest positive mutation. See figure 2 for further details and table 1 for parameter values.

In none of the cases explored above, however, did the lagging species ever advance ahead of the leading species. We speculated that this might have been due to the low amount of genetic variation for the trait under the default parameter set based on Johansson [10]. We thus ran simulations with either an increased mutation rate ($\nu = 0.2$ rather than 0.02) or mutational effect size ($\sigma_\nu = 0.015$ rather than 0.0015) and an asymmetric resource distribution ($\kappa = \pm 4$). In these cases, genetic variation was sufficient to ensure that one of the two species always survived, even in a rapidly changing environment (electronic supplementary material, table S2). The surviving species was always the leading species when it had the larger initial population size. When instead the lagging species had the larger population size, however, the lagging species had access to more genetic variation (both standing and de novo) and was capable of evolving faster than the leading species. Thus, evolutionary advantage allowed the lagging species to persist, in some cases, while the leading species went extinct. The competitive exclusion of the leading species was observed in one of five original replicates with a larger mutational effect size ($\sigma_\nu = 0.015$; see figure 3; electronic supplementary material, figure S6). To better estimate the frequency of leading species extinction, we ran 15 additional replicate simulations (three from each original burn-in) and observed two more cases where the leading species went extinct while the lagging species persisted (for a total of 3/20 replicates, unrelated to which of the five burn-in populations was used). For these parameters, the faster evolution of the lagging species brought its trait value towards that of the leading species; at that point, population sizes of the two species converged, and which species ultimately prevailed was stochastic (recall that there are no other ecological differences between these species). By contrast, competitive exclusion of the leading species by the lagging species was not initially observed when the mutation rates were higher ($\nu = 0.2$ rather than 0.02; electronic supplementary material, figure S5). To explore this case further, we ran 10 additional replicate simulations (two per burn-in), for each of two intermediate environmental change speeds ($V_m = 0.0001$ and $V_m = 0.00015$) that were chosen to allow for greater trait convergence before extinction. While the trait values did become

3closer, the leading species always stayed ahead of the lagging species, despite its smaller initial population size, and never went extinct before the lagging species. Finally, we extended the original five replicates and also ran ten additional simulations at the slow rate of environmental change ($V_m = 0.00005$) until one of the two species went extinct (after 42 986 generations, on average). With such slow environmental change, the traits converged even more closely, and the leading species went extinct first in three of fifteen total replicates (electronic supplementary material, table S2), unrelated to which burn-in population was used. We thus conclude that asymmetries in resource competition make it possible for lagging species with a larger population size to out-evolve a preadapted species along a resource gradient, as long as there is sufficient genetic variance to allow the trait values to converge given the rate of environmental change.

4. Discussion

Predicting how species will adapt to abiotic change when in competition with other species remains a challenge for biologists, given that competition can alter the population sizes of the component species, as well as the strength and direction of selection [6,8]. Our study contributes to understanding how competitive interactions between species might influence adaptation to abiotic change in several distinct ways.

First, by exploring skewed resource distributions, we were able to manipulate the population sizes of competing species. As expected, species with initially larger populations persisted for longer, probably because larger populations take longer to decline deterministically to zero (even when holding trait values constant), are better protected from demographic stochasticity, maintain more standing genetic variation and produce more beneficial mutations [48,49]. The advantage of a larger population size was most pronounced when the species with the larger population size was also the leading species (figure 2c,d). In comparison with previous models [10,11], our work adds additional support to the finding that population size is an important determinant of persistence and adaptation to abiotic change in communities of competitors.

An additional consequence of interspecific competition is that it drives character displacement. With symmetrically distributed resources in a constant environment, two symmetrically competing species evolve the same distance away from, but on opposite sides of, the resource peak. By contrast, resource skew alters trait values of coexisting species by displacing them from their symmetrical equilibrium position. For example, Slatkin [50] noted that, with an asymmetrical resource distribution, one species will occupy a position near the centre of the resource distribution and the other will be displaced to the tail of the distribution. The species in the tail is prevented from adapting to utilize more abundant resources by competition from the species occupying the centre of the distribution. We found very similar results and in addition found that the competitive push exerted by the abundant species on the less abundant species can influence adaptation to abiotic change. With a right-skewed resource distribution (figure 2e,f), the leading species (blue) is pushed far in front of the peak of the resource distribution. This 'head-start' allows it to persist for longer than it would have in the absence of competition (see asterisk), even though its population size was initially lower. By restarting single-species simulations with the same head start but the same population size as in a single-species community, we confirmed that this head start could greatly lengthen the persistence time of the leading species (electronic supplementary materials). This preadaptation is a second way in which competition can aid persistence to a changing environment, beyond the selective push that occurs while the environment is changing if competition selects in the same direction as the environmental change [14]. Mellard et al. [51] also highlighted the importance of a head start in facilitating adaptation in a plant–herbivore system, suggesting that similar mechanisms may be at play across trophic levels.

We also repeatedly observed adaptation in the opposite direction, relative to the environmental change, when the leading species initially had a lower population size. This phenomenon, which we call the 'vacuum of competitive release', occurred during the decline in population size of the lagging species in the face of environmental change, which released resources at the trailing end of the resource distribution. Consequently, the leading species evolved to use available resources (in the opposite direction to the shifting environment) and only later tracked the environment after the lagging species went extinct.

Another contribution of our study is that we found that it is not universally true that the lagging species will go extinct before the leading species, in contrast to previous results [10,11]. In particular, when the lagging species initially had the larger population size and had substantial genetic variation (figure 3), the trait value of the lagging species could evolve rapidly towards that of the leading species as the environment changed, occasionally allowing the leading species to go extinct and the lagging species to be rescued. The competitive exclusion of the leading species by the lagging species was observed both when mutational effects were larger (raising σ_ν from 0.0015 to 0.015; electronic supplementary material, figure S6d with $V_m = 0.0005$) and when the mutation rate was higher (raising ν from 0.02 to 0.2; electronic supplementary material, table S2 with $V_m = 0.00005$). Given that the two species initially differed by about one phenotypic unit in the trait, a mean mutational effect size (i.e. mean absolute deviation) of 0.0012 ($\sqrt{2\sigma^2/\pi}$) implies that the species differ in this trait by about 836 mutations of average effect, which is

orders of magnitude larger than the average number of QTL estimated from studies of recent species [52]. Thus, increasing the mutational effect size to 0.012 (with $\sigma_\nu = 0.015$), an expected difference of 84 genes, is not unreasonable. Importantly, even if a species has little standing genetic variation (assessed at marker sites), access to sufficiently large-effect mutations may still allow it to be rescued from extinction.

In general, we conclude that competition for resources makes it difficult for multi-species communities to persist in a changing environment. That said, competition also sets up the conditions whereby speciation (or spread of an invasive competitor) could recur [10,37], as seen in the branching–extinction cycles of Kisdi et al. [53]. Given that one of the two species always went extinct under rapid environmental change, we infer that it would be difficult for new or invading species to persist until the environment stabilizes.

Although a few empirical examples exist that show adaptation in the opposite direction to that predicted by the changing environment [54–56], finding clear empirical examples for the vacuum of competitive release is challenging, requiring that we track changes in population size and mean trait values as well as infer shifts in the trait optimum with environmental change. One promising approach is to examine phenological shifts due to climate change for evidence of a vacuum of competitive release (assuming that population sizes do differ, because of asymmetric resources and/or asymmetric competition coefficients). For example, common buzzards (Buteo buteo) breeding at the northern distribution limit in Finland have advanced their timing of breeding by 11 days over the past 30 years. This shift in breeding is correlated with a warming climate and is thought to benefit this species through facilitating range expansion. Nevertheless, populations of common buzzards in northern Finland are declining [54]. Goshawks (Accipiter gentilis), a possible competitor for nest sites, have instead been marginally increasing in abundance, even though they have not advanced their timing of breeding to the same extent [55]. Although not the conclusion of these studies, it would be interesting to investigate whether goshawks are under less selective pressure to alter their breeding date partly because of release from competition by buzzards. A second system in which this could be occurring is among tits. Great tits (Parus major), as well as other tit species such as blue tits (Cyanistes caeruleus) and willow tits (Poecile montanus), rely on insect larvae to feed their young during the breeding season [57–59]. With warming spring temperatures, the peak larval abundance has shifted earlier in the season. Great tits, which breed later in the season, are not, however, keeping up with this resource shift, creating an increasing lag between breeding and food supply [60]. Our work suggests that blue tits and willow tits, which initiate breeding earlier, may be selected to shift to later breeding dates because of the release of resources from declining great tit populations, despite the advance in peak food supply with advancing spring temperatures.

Laboratory experiments may be particularly suitable for demonstrating the vacuum of competitive release. The classic Asterionella–Cyclotella system of algae competing for phosphorus and silicate (studied by Tilman [61]) could be used, for example, starting with a stable community where Asterionella is initially rare. Environmental change could then be induced by decreasing the phosphorus to silicate ratio. Given that Asterionella is the better competitor under phosphate-limited

conditions, this species would be predicted to rise numerically over time. In terms of traits, however, its ability to use the limiting phosphorus resource may initially decline before improving, as the initially more common *Cyclotella* drop in numbers and release competitive pressure on phosphorus. Similarly, shifts in the distribution of food size availability (algal size) could be used to explore the evolution of artificial communities of competing *Daphnia* clones. By increasing the average size of supplied algae over time, the prey preference of larger clones (leading) could be tracked as smaller clones (lagging) decline in numbers, again looking for evidence of counter-selection between the environmental change and release of resources from competition.

Overall, we find that accounting for asymmetries in resource distributions and competition coefficients has substantial impacts on the fate of competing species in a changing environment, even leading to the persistence of species whose traits are initially maladapted over those that are preadapted to a changing environment. Counterintuitively, when the population size was smaller for the leading species, we typically observed a period of adaptation in the opposite direction to

the environmental change. In these cases, the species that appears to be failing to track a changing environment is not necessarily the one most at risk of extinction.

References

1. Huey RB, Kingsolver JG. 1993 Evolution of resistance to high temperature in ectotherms. *Am. Nat.* **142**, S21–S46. (doi:10.1086/285521)

2. Lenski RE, Bennett AF. 1993 Evolutionary response of *Escherichia coli* to thermal stress. *Am. Nat.* **142**, S47–S64. (doi:10.1086/285522)

3. Partridge L, Barrie B, Barton NH, Fowler K, French V. 1995 Rapid laboratory evolution of adult life-history traits in *Drosophila melanogaster* in response to temperature. *Evolution* **49**, 538–544. (doi:10.1111/j.1558-5646.1995.tb02285.x)

4. van Doorslaer W, Stoks R, Duvivier C, Bednarska A, de Meester L. 2009 Population dynamics determine genetic adaptation to temperature in *Daphnia*. *Evolution* **63**, 1867–1878. (doi:10.1111/j.1558-5646.2009.00679.x)

5. Gause G. 1934 *The struggle for existence*. Baltimore, MD: Williams and Wilkins Co.

6. Grant PR, Grant BR. 2006 Evolution of character displacement in Darwin's finches. *Science* **313**, 224–226. (doi:10.1126/science.1128374)

7. Kleynhans EJ, Otto S, Reich P, Vellend M. 2016 Adaptation to elevated CO_2 in different biodiversity contexts. *Nat. Commun.* **7**, 12 358. (doi:10.1038/ncomms12358)

8. Lawrence D, Fiegna F, Behrends V, Bundy JG, Phillimore AB, Bell T, Barraclough TG. 2012 Species interactions alter evolutionary responses to a novel environment. *PLoS Biol.* **10**, e1001330. (doi:10.1371/journal.pbio.1001330)

9. de Mazancourt C, Johnson E, Barraclough TG. 2008 Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11**, 380–388. (doi:10.1111/j.1461-0248.2008.01152.x)

10. Johansson J. 2008 Evolutionary responses to environmental changes: how does competition

affect adaptation? *Evolution* **62**, 421–435. (doi:10.1111/j.1558-5646.2007.00301.x)

11. Jones AG. 2008 A theoretical quantitative genetic study of negative ecological interactions and extinction times in changing environments. *BMC. Evol. Biol.* **8**, 119. (doi:10.1186/1471-2148-8-119)

12. Price TD, Kirkpatrick M. 2009 Evolutionarily stable range limits set by interspecific competition. *Proc. R. Soc. B* **276**, 1429–1434. (doi:10.1098/rspb.2008.1199)

13. Norberg J, Urban MC, Vellend M, Klausmeier CA, Loeuille N. 2012 Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Change* **2**, 747–751. (doi:10.1038/nclimate1588)

14. Osmond MM, de Mazancourt C. 2013 How competition affects evolutionary rescue. *Phil. Trans. R. Soc. B* **368**, 20120085. (doi:10.1098/rstb.2012.0085)

15. Northfield TD, Ives AR. 2013 Coevolution and the effects of climate change on interacting species. *PLoS Biol.* **11**, e1001685. (doi:10.1371/journal.pbio.1001685)

16. Ashmole NP. 1968 Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). *Syst. Zool.* **17**, 292–304. (doi:10.2307/2412008)

17. Boag PT, Grant PR. 1984 Darwin's finches (Geospiza) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. *Ecol. Monogr.* **54**, 463–489. (doi:10.2307/1942596)

18. Brown JH, Lieberman GA. 1973 Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* **54**, 788–797. (doi:10.2307/1935673)

19. Fenchel T, Kofoed L. 1976 Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos* **27**, 367–376. (doi:10.2307/3543455)

20. Kleynhans EJ, Jolles AE, Bos MRE, Olff H. 2011 Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos* **120**, 591–600. (doi:10.1111/j.1600-0706.2010.18712.x)

21. Bonin MC, Boström-Einarsson L, Munday PL, Jones GP. 2015 The prevalence and importance of competition among coral reef fishes. *Annu. Rev. Ecol. Evol. Syst.* **46**, 169–190. (doi:10.1146/annurev-ecolsys-112414-054413)

22. Connell J. 1983 On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**, 661–696. (doi:10.1086/284165)

23. Kaplan I, Denno RF. 2007 Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol. Lett.* **10**, 977–994. (doi:10.1111/j.1461-0248.2007.01093.x)

24. Lawton J, Hassell M. 1981 Asymmetrical competition in insects. *Nature* **289**, 793–795. (doi:10.1038/289793a0)

25. Weiner J. 1990 Asymmetric competition in plant populations. *Trends Ecol. Evol. (Amst.)* **5**, 360–364. (doi:10.1016/0169-5347(90)90095-U)

26. Falster DS, Westoby M. 2003 Plant height and evolutionary games. *Trends Ecol. Evol. (Amst.)* **18**, 337–343. (doi:10.1016/S0169-5347(03)00061-2)

27. Schwinning S, Weiner J. 1998 Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* **113**, 447–455. (doi:10.1007/s004420050397)

28. Clutton-Brock T, Albon S, Gibson R, Guinness F. 1979 The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus* l.). *Anim. Behav.* **27**, 211–225. (doi:10.1016/0003-3472(79)90141-6)

29. Kokko H, López-Sepulcre A, Morrell LJ. 2006 From hawks and doves to self-consistent games of

9

rspb.royalsocietypublishing.org *Proc. R. Soc. B* **284**: 20170374

territorial behavior. *Am. Nat.* **167**, 901–912. (doi:10.1086/504604)

30. Bell G, Gonzalez A. 2009 Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* **12**, 942–948. (doi:10.1111/j.1461-0248.2009.01350.x)

31. Gomulkiewicz R, Holt RD. 1995 When does evolution by natural selection prevent extinction? *Evolution* **49**, 201–207. (doi:10.2307/2410305)

32. Jones ME, Barmuta LA. 1998 Diet overlap and relative abundance of sympatric Dasyurid carnivores: a hypothesis of competition. *J. Anim. Ecol.* **67**, 410–421. (doi:10.1046/j.1365-2656.1998.00203.x)

33. Persson L. 1983 Effects of intra- and interspecific competition on dynamics and size structure of a perch *Perca fluviatilis* and roach *Rutilus rutilus* population. *Oikos* **41**, 126–132. (doi:10.2307/3544354)

34. Rummel JD, Roughgarden J. 1983 Some difference between invasion-structured and coevolution-structured competitive communities: a preliminary theoretical analysis. *Oikos* **41**, 477–486. (doi:10.2307/3544107)

35. Matsuda H, Abrams PA. 1994 Runaway evolution to self-extinction under asymmetrical competition. *Evolution* **48**, 1764–1772. (doi:10.1111/j.1558-5646.1994.tb02212.x)

36. Kisdi E. 1999 Evolutionary branching under asymmetric competition. *J. Theor. Biol.* **197**, 149–162. (doi:10.1006/jtbi.1998.0864)

37. Doebeli M, Dieckmann U. 2000 Evolutionary branching and sympatric speciation caused by different types of ecological interactions. *Am. Nat.* **156**, S77–S101. (doi:10.1086/303417)

38. Baptestini EM, de Aguiar MA, Bolnick DI, Araujo MS. 2009 The shape of the competition and carrying capacity kernels affects the likelihood of disruptive selection. *J. Theor. Biol.* **259**, 5–11. (doi:10.1016/j.jtbi.2009.02.023)

39. Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009 Ocean acidification: the other CO_2 problem. *Mar. Sci.* **1**, 169–192. (doi:10.1146/annurev.marine.010908.163834)

40. Burrows MT *et al.* 2014 Geographical limits to species-range shifts are suggested by climate

velocity. *Nature* **507**, 492–495. (doi:10.1038/nature12976)

41. Dunnell KL, Travers SE. 2011 Shifts in the flowering phenology of the northern great plains: patterns over 100 years. *Am. J. Bot.* **98**, 935–945. (doi:10.3732/ajb.1000363)

42. Dieckmann U, Law R. 1996 The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.* **34**, 579–612. (doi:10.1007/BF02409751)

43. Doebeli M. 2011 *Adaptive diversification*. Princeton, NJ: Princeton University Press.

44. Lovric M (ed.). 2011 Skew-normal distribution. In *International encyclopedia of statistical science* (ed. M Lovric), pp. 1342–1344. Berlin, Germany: Springer.

45. Roughgarden J. 1979 *Theory of population genetics and evolutionary ecology: an introduction*. New York, NY: Macmillan.

46. Drossel B, McKane A. 1999 Ecological character displacement in quantitative genetic models. *J. Theor. Biol.* **196**, 363–376. (doi:10.1006/jtbi.1998.0847)

47. Dieckmann U, Doebeli M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354–257. (doi:10.1038/22521)

48. Holt RD, Gomulkiewicz R. 1997 How does immigration influence local adaptation? A re-examination of a familiar paradigm. *Am. Nat.* **149**, 563–572. (doi:10.1086/286005)

49. Hufbauer RA, Szücs M, Kasyon E, Youngberg C, Koontz MJ, Richards C, Tuff T, Melbourne BA. 2015 Three types of rescue can avert extinction in a changing environment. *Proc. Natl Acad. Sci. USA* **112**, 10 557–10 562. (doi:10.1073/pnas.1504732112)

50. Slatkin M. 1980 Ecological character displacement. *Ecology* **61**, 163–177. (doi:10.2307/1937166)

51. Mellard JP, de Mazancourt C, Loreau M. 2015 Evolutionary responses to environmental change: trophic interactions affect adaptation and persistence. *Proc. R. Soc. B* **282**, 20141351. (doi:10.1098/rspb.2014.1351)

52. Orr HA. 2001 The genetics of species differences. *Trends. Ecol. Evol.* (*Amst.*) **16**, 343–350. (doi:10.1016/S0169-5347(01)02167-X)

53. Kisdi E, Jacobs F, Geritz S. 2002 Red queen evolution by cycles of evolutionary branching and extinction. *Selection* **2**, 161–176. (doi:10.1556/Select.2.2001.1-2.12)

54. Lehikoinen A, Byholm P, Ranta E, Saurola P, Valkama J, Korpimäki E, Pietiäinen H, Henttonen H. 2009 Reproduction of the common buzzard at its northern range margin under climatic change. *Oikos* **118**, 829–836. (doi:10.1111/j.1600-0706.2008.17440.x)

55. Lehikoinen A, Lindén A, Byholm P, Ranta E, Saurola P, Valkama J, Kaitala V, Lindén H. 2013 Impact of climate change and prey abundance on nesting success of a top predator, the goshawk. *Oecologia* **171**, 283–293. (doi:10.1007/s00442-012-2411-z)

56. Kimball S, Angert AL, Huxman TE, Lawrence Venable D. 2010 Contemporary climate change in the Sonoran desert favors cold-adapted species. *Glob. Change Biol.* **16**, 1555–1565. (doi:10.1111/j.1365-2486.2009.02106.x)

57. Dhondt AA. 1977 Interspecific competition between great and blue tit. *Nature* **268**, 521–523. (doi:10.1038/268521a0)

58. Dhondt AA, Adriaensen F. 1999 Experiments on competition between great and blue tit: effects on blue tit reproductive success and population processes. *Ostrich* **70**, 39–48. (doi:10.1080/00306525.1999.9639748)

59. Pakanen VM, Orell M, Vatka E, Rytkönen S, Broggi J. 2016 Different ultimate factors define timing of breeding in two related species. *PLoS ONE* **11**, e0162643. (doi:10.1371/journal.pone.0162643)

60. Visser M, van Noordwijk A, Tinbergen J, Lessells C. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **265**, 1867–1870. (doi:10.1098/rspb.1998.0514)

61. Tilman D. 1977 Resource competition between plankton algae: an experimental and theoretical approach. *Ecology* **58**, 338–348. (doi:10.2307/1935608)

62. Van Den Elzen CL, Kleynhans EJ, Otto SP. 2017 Data from: Asymmetric competition impacts evolutionary rescue in a changing environment. Dryad Digital Repository. (doi:10.5061/dryad.72k67)