Asymmetric competition impacts evolutionary rescue in a changing environment

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

<table>
<thead>
<tr>
<th>parameter</th>
<th>value</th>
<th>definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>$f$</td>
<td>4</td>
<td>fecundity</td>
</tr>
<tr>
<td>$r_k$</td>
<td>1</td>
<td>intrinsic growth rate</td>
</tr>
<tr>
<td>$v$</td>
<td>0.02 [0.2]</td>
<td>genome-wide mutation rate</td>
</tr>
<tr>
<td>$\sigma_v$</td>
<td>0.0015 [0.015]</td>
<td>standard deviation of mutational effect size</td>
</tr>
<tr>
<td>$K_m$</td>
<td>variable</td>
<td>maximum resource abundance</td>
</tr>
<tr>
<td>$\sigma_k$</td>
<td>1</td>
<td>standard deviation of the resource abundance distribution</td>
</tr>
<tr>
<td>$\mu_k$</td>
<td>0 [±4]</td>
<td>mean of the resource abundance distribution</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.85</td>
<td>breadth of the competition function</td>
</tr>
<tr>
<td>$\beta$</td>
<td>0 [±0.6]</td>
<td>degree of asymmetry in competition function</td>
</tr>
<tr>
<td>$V_m$</td>
<td>0.00005 (slow); 0.0005 (fast)</td>
<td>speed of environmental change</td>
</tr>
</tbody>
</table>

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

$$
\frac{du}{dt} = \frac{1}{2} v \sigma_v^2 \frac{\partial W(u_i)}{\partial u_i} |_{u_i = u_i}
$$

[42], where $v$ is the mutation rate, $\sigma_v^2$ is the variance of mutation effect sizes, $\bar{n}_k$ is the equilibrium population size of species $k$ and $\partial W(u)/\partial u_i |_{u_i = u_i}$ 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 $v$ per diploid genome, with the mutational effect drawn from a normal distribution with a mean equal to the parental allelic value and variance $\sigma_v^2$.

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]:

$$
K(u_i) = K_m e^{-\frac{(u_i - \bar{u})^2}{2\sigma^2}} \text{erfc} \left( -\frac{\kappa (u_i - \bar{u})}{\sqrt{2}\sigma} \right).
$$

Here, $\kappa$ 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, $\xi$ determines the position of the distribution along the resource axis (corresponding to $u_M$ in [10]), $\omega$ 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 $\mu_k$ and variance $\sigma_k^2$, yielding

$$
\xi = \mu_k - \frac{\kappa \sigma_k^2}{\sqrt{(1 + \kappa^2)(\pi/2 - 1) + 1}}
$$

for the location of the resource distribution and

$$
\omega = \sigma_k \sqrt{1 - 2\kappa^2/(\pi(1 + \kappa^2))}
$$

for the breadth of the distribution.
Alternatively, we introduced asymmetrical competition coefficients using the function
\[
\alpha_{ij} = \frac{1}{1 + (u_i - u_j + \beta y)/(2\sigma^2_i)} 
\]
\[\times \left(1 + \frac{\beta y}{2\sigma^2_i}\right). \tag{2.7}\]

The parameter $\beta$ describes the asymmetry of competition coefficients, and the width of the competition kernel is controlled by $\sigma_a$. 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. $\alpha_{ij} = 1$).

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 $\sigma_a/\sigma_k > 1$, but multi-species communities can persist for $\sigma_a/\sigma_k < 1$ [10,37]. For this reason, Johansson [10] chose to use different values of $\sigma_a/\sigma_k$ for his simulations with one species ($\sigma_a/\sigma_k = 1.5$) versus two species (typically using 0.85). He also showed, however, that increasing $\sigma_a/\sigma_k$ 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 $\sigma_a/\sigma_k$ and the number of species, we chose to fix $\sigma_a/\sigma_k$ 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 [37,43]. For symmetric distributions, there is only one evolutionarily stable species when $\sigma_a/\sigma_k > 1$, but multi-species communities can persist for $\sigma_a/\sigma_k < 1$ [10,37]. For this reason, Johansson [10] chose to use different values of $\sigma_a/\sigma_k$ for his simulations with one species ($\sigma_a/\sigma_k = 1.5$) versus two species (typically using 0.85). He also showed, however, that increasing $\sigma_a/\sigma_k$ reduced the maximum velocity that could be sustained in the two-species case (see table B2 in [10]).

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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 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).
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 ($K_m = 4$) and 6.6-fold with asymmetrical competition coefficients ($b = 0.6$).

Starting from an initial resource mean of $m_K = 0$, 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.

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

species (higher data points) persisted the full 15 000 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 2h,i), 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 2l, 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 (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.
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 ($\sigma_r = 0.015$ 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 ($\sigma_r = 0.015$; 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 closer, 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 2c,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 $\sigma_r$ from 0.0015 to 0.015, electronic supplementary material, figure S6d with $V_{\text{mut}} = 0.00005$) and when the mutation rate was higher (raising $\nu$ from 0.02 to 0.2, electronic supplementary material, table S2 with $V_{\text{mut}} = 0.00005$). 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 $\sigma_r = 0.015$), 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 phosphorous to silicate ratio. Given that Asterionella is the better competitor under phosphate-limited...
conditions, this species was 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.

Data accessibility. All data have been submitted to Dryad (http://dx.doi.org/10.5061/dryad.72K67) [62].

Author’s contributions. C.I.V.D.E. wrote the simulations and drafted the methods and results sections of the manuscript. E.J.K. conceived the original idea and drafted the abstract, introduction and discussion sections of the manuscript. S.P.O. helped draft all sections. All authors participated in the design of the study, ran the simulations and gave their final approval for publication.

Competing interests. We declare we have no competing interests.

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