Allee effects and species co-existence in an environment where resource abundance varies

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HIGHLIGHTS

- We model two species competing for a resource across a continuous landscape.
- Allee effects can promote their co-existence if resources are distributed unevenly.
- This happens despite a reduction in population density caused by the Allee effect.

ARTICLE INFO

ABSTRACT

Explaining patterns of diversity has long been a central focus in ecology. One of the most challenging problems has been to understand how species occupying similar ecological niches can co-exist because, with limited resources, demographic stochasticity is expected to lead to the eventual extinction of all but one of them. The Allee effect has been widely studied for its impact on the extinction risk of rare species. Its potential role in promoting co-existence has received less attention. Here, we present a model in which two species compete for a single resource across a continuous landscape. We show that Allee effects can promote their co-existence when a simple condition is met: resources are distributed unevenly across space. Furthermore, the Allee effect can stabilize co-existence despite the reduction in population density and consequent increase in demographic stochasticity that it causes. The Allee effect might, therefore, be an important force maintaining diverse communities.

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1. Introduction

It is becoming ever more apparent that positively density dependent interactions, or Allee effects, impact community dynamics in important ways (Courchamp et al., 2008; Kramer et al., 2009). In general, Allee effects occur when a species attains a higher growth rate at higher densities. Allee effects can be caused by numerous types of processes (see Table 2.1 in Courchamp et al., 2008). For example, populations may experience Allee effects if finding mates becomes difficult at low population densities (Gascoigne et al., 2009). The gypsy moth, Lymantria dispar is thought to exhibit strong Allee effects for this reason (Sharov et al., 1995; Johnson et al., 2006). Predation can also cause Allee effects in a prey species when the probability that a predation event occurs is regulated by factors other than prey density. For example, if predator density is independent of

the availability of a focal prey species, reductions in this prey species' density can occur without the corresponding reductions in predator density that would be predicted in a Lotka–Volterra framework. Because a reduction in the prey, but not predator density occurs, there is an increase in the per-capita rate of attack. On the Channel Islands in California, the island fox, Urocyon littoralis, is preyed upon by golden eagles, whose population density is regulated by the abundance of introduced pigs. Therefore, as fox population sizes decline, per-capita predation increases (Angulo et al., 2007). When larger group sizes result in greater social benefits, cooperative species can also exhibit Allee effects. In social spiders, which cooperate in both prey capture and brood care, individual survival is higher in larger social groups (Avilés and Tufiño, 1998).

For the most part, the literature on Allee effects has focused on their role in population decline and extinction (Berec et al., 2007). Zhou and Zhang (2006) showed that Allee effects, by accelerating extinction, make co-existence in neutral models more difficult. There is, however, theoretical work showing that Allee effects can also promote co-existence (Levin, 1974; Ferdy and Molofsky, 2002; Molofsky and Bever, 2002). In an early work, Levin (1974)

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showed that spatial structure in a meta-population can permit co-existence of species that would not be able to co-exist in a freely mixing population. This required that the presence of one species within a patch inhibits establishment of another species (i.e., "priority effects"; Slatkin, 1974). More recently, Ferdy and Molofsky (2002) extended this model to explicitly investigate how the Allee effect influences the formation of spatial patterns, again in a discrete patch framework. Molofsky and Bever (2002) then used a cellular automaton model to extend these ideas to a spatially structured two-dimensional lattice and showed that positive frequency dependence can enhance species co-existence, as long as enough cells in the landscape are uninhabitable. These dead zones essentially fragment the landscape into a spatial array of near-isolated islands which, once colonized, are difficult to perturb, because foreign migrants suffer locally reduced fitness.

While this work has demonstrated convincingly that the Allee effect can promote species co-existence in discrete space, it is not known whether the same mechanism can operate in continuous space. Unlike in discrete space, where there is a fixed spatial boundary separating patches, the region where species' ranges meet in continuous space is not constrained and can, instead, move freely. Thus, one species can gradually encroach into the other's range. This has the potential to make co-existence more difficult.

Here we develop a simple model to investigate whether Allee effects can promote species co-existence for a single population inhabiting a continuous landscape. We show that Allee effects can facilitate species co-existence when resources are distributed unevenly across space. Interestingly, this facilitation occurs despite the reduction in population densities and consequent increase in demographic stochasticity that results from the Allee effect. These results, along with those of earlier studies, suggest that Allee effects might be a general mechanism promoting the co-existence of ecologically equivalent species, and thus a factor helping to maintain diverse communities.

2. Model description

We consider a simple individual-based model in which two species occupy a continuous two-dimensional landscape. Individuals compete locally for resources, with those experiencing stronger competition having lower fecundity. Fecundity is further reduced for individuals occupying sparsely inhabited areas (Allee effects). After reproduction, parents die and offspring disperse from their natal locations to found the next generation. Below we describe each of these steps in more detail. The names and descriptions of all parameters and variables are listed in Table 1.

2.1. Competition for resources

We let $k(x, y)$ denote the surface of the resource landscape, for x in $[0, 1]$ and y in $[0, 0.5]$. Following M'Gonigle et al. (2012), we compare a landscape in which resources are distributed uniformly (Fig. 1a) to one in which they are distributed according to two symmetric Gaussian peaks, centered at $(x, y) = (0.25, 0.25)$ and $(x, y) = (0.75, 0.25)$ and with widths given by σ_k (Fig. 1b). The landscape is normalized, such that the total amount of resources, $\iint k(x, y) \, dx \, dy$, is equal to 1. Co-existence in our model only happens when a different species resides on each of the two peaks. We built wrap around boundaries such that a peak primarily inhabited by one species would be surrounded in all directions by peaks with the other species; this assumption makes co-existence more difficult. Specifically, when travelling horizontally, individuals that cross $x = 0$ or $x = 1$ appear on the other side of the landscape at $x = 1$ or $x = 0$, respectively, with the same vertical position. Vertically, individuals who cross $y = 0$ or $y = 0.5$ appear on the other side of the landscape at $y = 0.5$ or $y = 0$, respectively, but with a vertical position of $(1 - x)$, where x denotes their horizontal coordinate before they crossed the boundary. Such a transformation does not create any discontinuities and yields a landscape in which the two resource peaks are adjacent in every direction, as desired. We also investigate other simple bimodal landscapes (Fig. S1) as well as a more complex, multi-peaked landscapes (discussed below).

For the bimodal landscapes, we calculate the spatial variation in the distribution of resources, v, along the transect that spans both peaks, as

$$v = \frac{\max k(x, y) - \min k(x, y)}{\min k(x, y)}. \tag{1}$$

For example, a value of $v = 0.25$ means that the resource peaks are 25% higher than the valley between them.

Individuals compete for resources, with the competitive impact of individual j on individual i, denoted n_{ij}, decreasing with the distance between them, d_{ij}, according to a Gaussian function with

Table 1
Model parameters and model variables.

Symbol	Description	Range explored
Model parameters		
a	Strength of Allee effects	[0,4000]
f_{max}	Maximum fecundity	[100,300]
$k(x, y)$	Local resource abundance at location (x,y)	
c	Strength of competition for resources	[1/15,1/5]
v	Spatial variation in resource abundance	[0,1]
N	Initial population size	[50,1500]
σ_a	Width of Allee effect distribution	[0.04,0.06]
σ_k	Width of peaks in local resource abundance	0.05
σ_m	Width of movement distribution	[0.04,0.06]
σ_s	Width of competition distribution	[0.04,0.06]
Model variables		
d_{ij}	Spatial distance between individuals i and j	
f_i	Fecundity of individual i	
n_{ij}	Competitive effect of individual j on individual i	
γ_i	Allee fitness of individual i	
ρ_i	Resource share of individual i	
τ_i	Competitive fitness of individual i	
ω_i	Effective local density of conspecifics experienced by individual i	
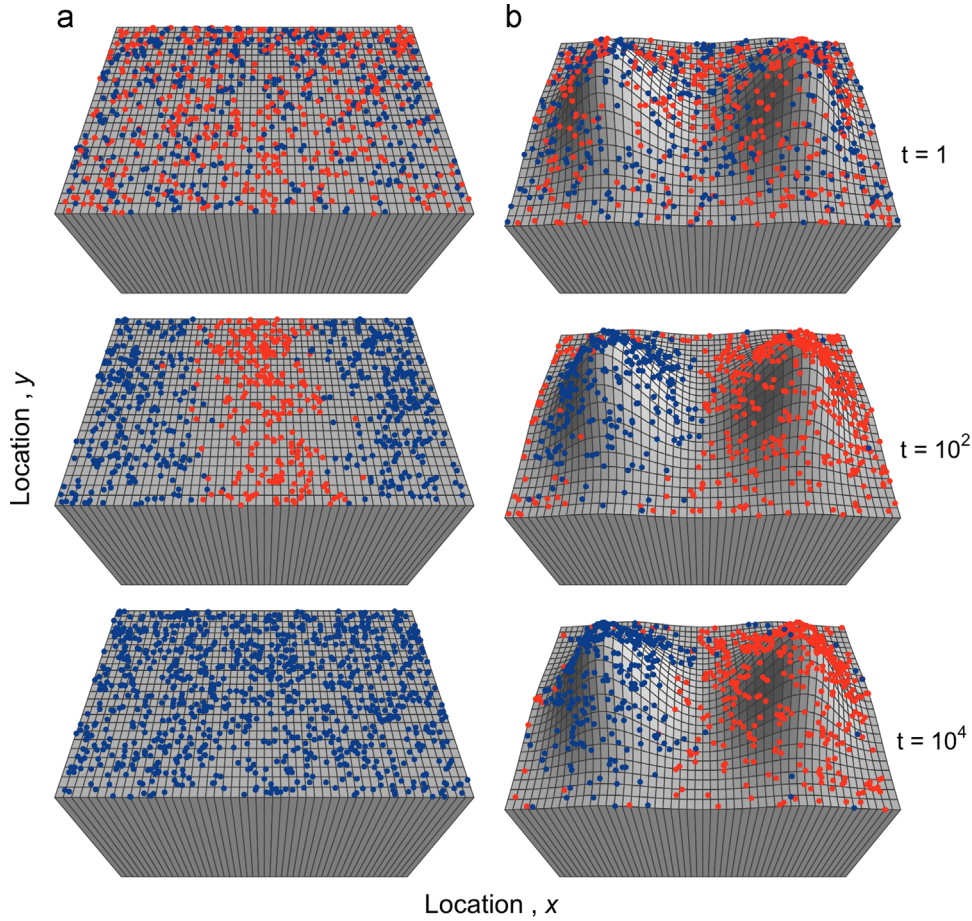
Fig. 1. Sample runs in a landscape where resources are (**a**) uniformly distributed and (**b**) distributed according to two symmetric Gaussian peaks, as described in Section 2.1. The height of the surface indicates the resource abundance at each location. The initial population was dispersed randomly across the landscape. Rows correspond to time points indicated by corresponding labels. $\sigma_k = 0.1$ and $\nu = 0.5$ for the landscape in panel (b). Other parameters were $\sigma_s = 0.05$, $\sigma_a = 0.05$, $\sigma_m = 0.05$, $a = 2000$, $c = 1/10$, and $f_{max} = 200$ and populations were initially seeded with 1500 individuals. For the model runs shown here, one species excluded the other after 745 generations in (a), while co-existence lasted at least 10^5 generations (at which point the simulation was terminated) in (b).

standard deviation σ_s. Specifically,

$$n_{ij} = \frac{\exp(-d_{ij}^2/2\sigma_s^2)}{2\pi\sigma_s^2}. \tag{2}$$

The ith individual's resource share, ρ_i, can then be computed as

$$\rho_i = \frac{k(x_i, y_i)}{\sum_j n_{ij}}, \tag{3}$$

where x_i and y_i denote the individual's x and y-coordinates. The sum is over all individuals in the population. Note that we make the conservative assumption that conspecifics and heterospecifics exert the same competitive forces on one another. If intra-specific competition were stronger than inter-specific competition, as might occur when the two species utilize the resource in different ways, co-existence would occur more easily (e.g., see Haigh and Maynard-Smith, 1972; Abrams, 1988).

2.2. Reproduction

An individual's reproductive success is affected by both its resource acquisition (i.e., competition) and positive interactions with nearby conspecifics (i.e., Allee effects). These component effects act multiplicatively to determine an individual's fecundity. For the ith individual, we let τ_i and γ_i denote its "competitive" and "Allee" fitness components, respectively. In the literature on the

Allee effect, there is often a distinction made between "component Allee effects", in which some component of fitness is positively affected by the density of conspecifics, and "demographic Allee effects", in which population growth rate increases with density when density is low (Courchamp et al., 2008). We consider the former here and, while component Allee effects may induce a demographic Allee effect, this is not necessarily the case. For a fuller discussion of this distinction, see the recent meta-analysis by Kramer et al. (2009) who found that definitive empirical demonstrations of demographic Allee effects were much less common than were examples of component Allee effects.

We calculate the competitive fitness of individual i as

$$\tau_i = \frac{\rho_i}{c + \rho_i}, \tag{4}$$

where ρ_i is that individual's resource share, as computed in Eq. (3) and c determines how fast τ_i increases with ρ_i. When $\rho_i = c$, for example, then $\tau_i = 1/2$, so the individual obtains half of the maximum possible competitive fitness. When c equals 0, all individuals experience the same competitive fitness, regardless of differences in resource shares. As c increases, differences in competitive fitness resulting from differences in resource shares become greater. While this is not necessarily always true for the functional form of Eq. (4) (i.e., if many ρ_i are sufficiently small this will not hold), we confirmed that it is true for the parameters we

consider by plotting the coefficient of variation in competitive fitness as a function of c (see Fig. S2a). We, therefore, refer to c as the "strength of competition for resources". We generally make the simplifying assumption that the growth rates of the two species are equally suppressed by the effects of competition (i.e., reduced share of resources, ρ_i), although we later consider the effect of relaxing this assumption by allowing the value of parameter c to differ between species.

To calculate the Allee fitness, γ_i, we first compute the effective local density of conspecifics experienced by individual i, which we denote ω_i. This quantity can be interpreted as the summed strength of interactions with conspecifics, where the strength of an interaction between two conspecifics is assumed to decline according to a Gaussian function with the distance between them, d_{ij}. Specifically,

$$\omega_i = \sum_j \frac{\exp(-d_{ij}^2/2\sigma_a^2)}{2\pi\sigma_a^2}, \tag{5}$$

where the sum is taken over all other individuals of the same species. Here σ_a determines how quickly interaction strength declines with distance (larger σ_a means individuals interact over larger spatial scales). Finally, we can calculate an individual's Allee fitness as

$$\gamma_i = \frac{\omega_i}{a+\omega_i}, \tag{6}$$

where a determines how fast γ_i increases with ω_i. When a equals 0, all individuals have equal Allee fitness, regardless of interactions with others. For larger values, fitness differences associated with differences in local conspecific density become greater. As we did for the strength of competition, we also verified that increases in a do lead to greater variation in Allee fitness (Fig. S2b). We, therefore, refer to a as the "strength of Allee effects". We also note that the functional form of Eq. (6) was chosen for consistency with past work on this topic (e.g., Stephens and Sutherland, 1999; Ferdy and Molofsky, 2002).

The functional form specifying the relationship between the effective local density of conspecifics experienced by an individual and that individual's Allee fitness (Eq. (6)) is the same as that specifying the relationship between an individual's resource share and that individual's competitive fitness (Eq. (4)). An individual's local density of conspecifics, ω_i, and resource share, ρ_i, can differ by several orders of magnitude, as the *numerator* in the former (Eq. (5)) contains the sum $\sum_j \exp(-d_{ij}^2/2\sigma_a^2)$, while the *denominator* in the latter (Eq. (3)) contains the sum $\sum_j \exp(-d_{ij}^2/2\sigma_s^2)$, and each of these sums is inversely related to the population density. Thus, the relevant scale for the parameter c is generally smaller than the relevant scale for the parameter a by a factor of the same magnitude as the ratio between these two quantities.

We compute the expected fecundity of individual i by multiplicatively combining the above fitness components to get

$$f_i = f_{max}\tau_i\gamma_i, \tag{7}$$

where f_{max} is the maximum possible expected fecundity of an individual. In general, increasing f_{max} has the effect of increasing the total number of individuals inhabiting the landscape. Individual i's realized fecundity is then drawn from a Poisson distribution with mean f_i. We have chosen to use a Poisson distribution here for simplicity, and for consistency with numerous other demographic models. However, other distributions might be more suitable when modelling specific systems. It is also worth pointing out that taking the mean of the quantity $f_i - 1$ across all individuals of either species gives that species' mean per capita rate of increase, typically denoted r. After reproduction parents die.

2.3. Movement

Offspring disperse from their parental locations, with movement distances drawn from a Gaussian function centered at zero and with standard deviation σ_m. Movements occur in all directions with equal probability.

3. Results

When fecundity is positively density dependent ($a > 0$), our model confirms previous findings that species segregate into relatively homogeneous clusters (Fig. 1) (Ferdy and Molofsky, 2002; Molofsky and Bever, 2002; Eppstein et al., 2006; M'Gonigle et al., 2012). In a landscape where resources are distributed uniformly, stochastic fluctuations in the relative size and location of these clusters leads to the eventual exclusion of one species by the other (Fig. 1a). However, when resources are distributed non-uniformly, maintenance of both species becomes possible (Fig. 1b). For the bimodal landscape investigated here, co-existence occurs when each peak is colonized by a different species. The contact region between the two species then occurs in the resource valley where low population density reduces Allee fitness of would-be colonists, thus preventing range expansion.

The two components of fitness ("competitive" and "Allee") are maximized in different regions of the landscape. Individuals occupying regions with abundant resources (i.e., resource peaks) typically experience high Allee fitness (Fig. 2a) but low competitive fitness (Fig. 2b), because the density of individuals is highest there. In contrast, individuals occupying regions with few resources (i.e., resource valleys) experience low Allee fitness but
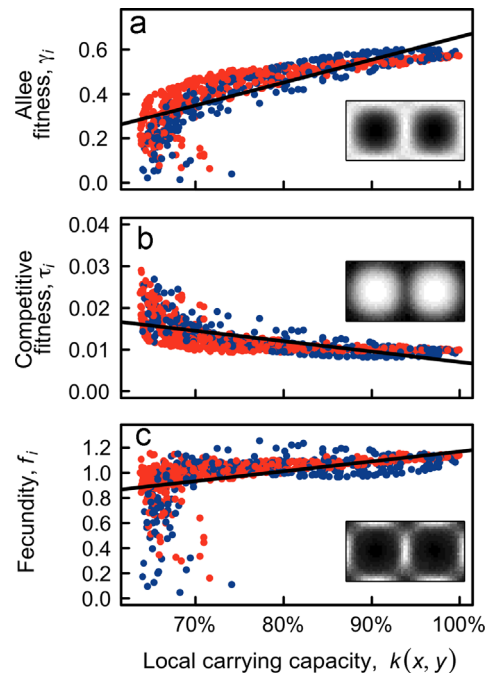
Fig. 2. Allee fitness (**a**), competitive fitness (**b**), and fecundity (**c**) for the individuals shown in the $t = 10^4$ generation in Fig. 1b, plotted against the local resource abundance experienced by those individuals. Lines show least-squares regressions. For clarity of presentation, the values of local resource abundance along the horizontal axis are expressed as percentages of the maximum resource abundance across the landscape. Inset panels show how these fitness components are distributed across the 2D landscape, with darker shading indicating higher relative values within each panel. Panels were created by averaging fitness across 1000 model runs with populations initialized in a configuration similar to that shown in the $t = 10^4$ generation of Fig. 1b.
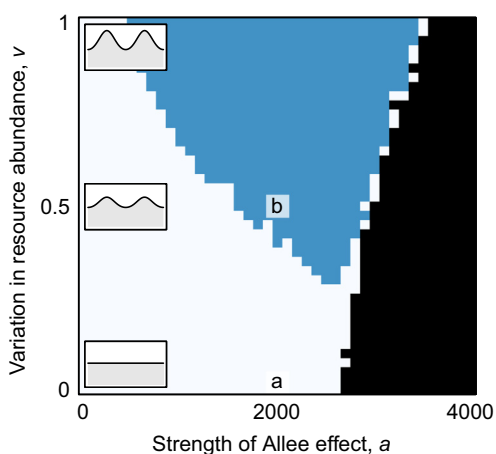
Fig. 3. Duration of co-existence with varying strengths of Allee effects and heterogeneity in resource abundance. Dark blue cells indicate cases where both species persisted for at least 10^4 generations in each of 10 replicate runs. Light blue and black cells indicate cases where extinction of one or both species occurred, respectively, in at least one of the replicates. Letters indicate parameter combinations used in Fig. 1. Inset panels show resource variation along transects spanning both peaks for landscapes with the corresponding value of v. For example, the panel at $v=0.5$ shows a cross-section through Fig. 1b along the transect $y=0.25$. While the total resources in each landscape is the same, a transect spanning both peaks has a greater average height for more heterogeneous environments. This is why, for the transects shown, the size of the grey area increases with greater v. Because we are not interested in the probability that different species colonize each peak, but instead in characterizing whether co-existence occurs once such colonization has happened, we begin runs with two equally sized and spatially segregated populations (i.e., individuals on the left side of the arena are initially one species and individuals on the right side the other, for a total of $N=1500$ individuals). All other parameters are as in Fig. 1b. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

high competitive fitness, because the density of individuals is lowest there. Combined, these effects roughly balance out, yielding variation in overall fecundity that is less extreme than variation in either component (Fig. 2c).

We find that Allee effects can only facilitate long-term co-existence when heterogeneity in the distribution of resources exceeds a critical value (Fig. 3). Interestingly, however, this critical value is lowest (i.e., co-existence is easiest) for intermediate strengths of Allee effects. With very strong Allee effects, population sizes decline to the point where demographic stochasticity dominates population dynamics, resulting in extinction of either or both species (right side of Fig. 3 and see also Fig. S3). Allee effects must, therefore, be strong enough that they create a local disadvantage to rarity, but not so strong that they lead a population to extinction. This result parallels previous analytical work that found that Allee effects of intermediate strength are most conducive to persistence of multiple species in a meta-population framework (Ferdy and Molofsky, 2002) and along ecological gradients (Hopf and Hopf, 1985).

The above illustrates an interesting consequence of Allee effects; they have both stabilizing and de-stabilizing effects on species co-existence. The stabilizing effect results from the positive density dependent interactions that reduce the amount of overlap between the species' ranges, whereas the de-stabilizing effect results from a higher risk of extinction when rare. For example, in Fig. 3 with $v=0.5$, there are approximately 2000 individuals when Allee effects are absent ($a=0$) and only approximately 700 individuals when Allee effects are strong enough to maintain co-existence ($a=2000$) (see also Fig. S3). We would expect then, that, all else being equal, species with large population sizes would co-exist more easily than sparsely populated species. Indeed, we find that co-existence becomes easier as competition for resources becomes weaker (smaller c; Fig. 4a) or
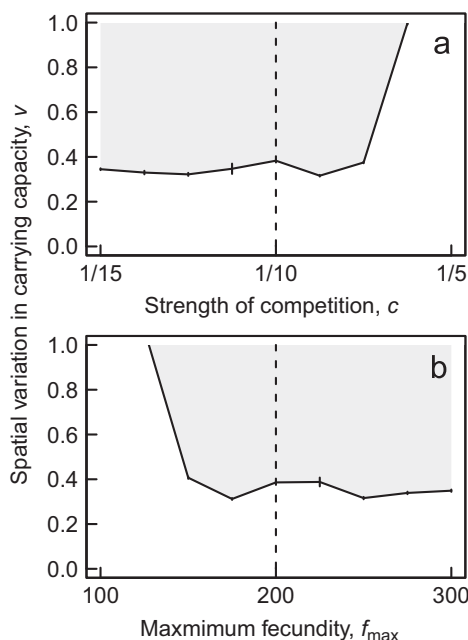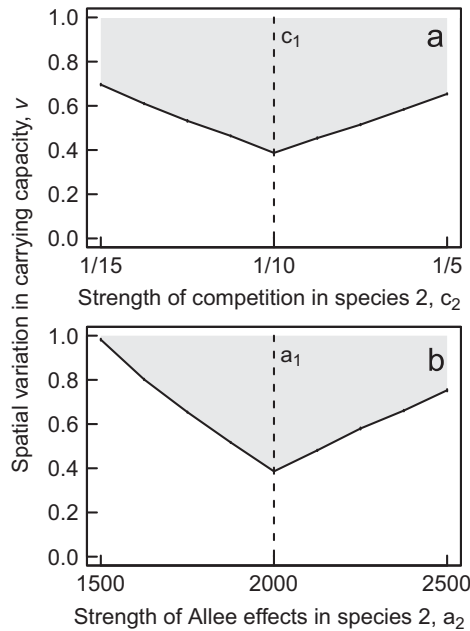

Fig. 4. The minimum level of spatial variation in resources, v, required to stabilize co-existence for at least 10^4 generations with (**a**) varying strengths of competition (c) and (**b**) varying maximum fecundities (f_{max}). To create the black curves, we increase the spatial variation v until the average co-existence time across 10 replicate runs exceeds 10^4 generations. Vertical bars denote standard errors across these replicates. Grey shading denotes regions where co-existence is expected. Dashed vertical lines indicate values used in Fig. 1. All other parameters are as in Fig. 1 and model runs were initialized as described in Fig. 3.
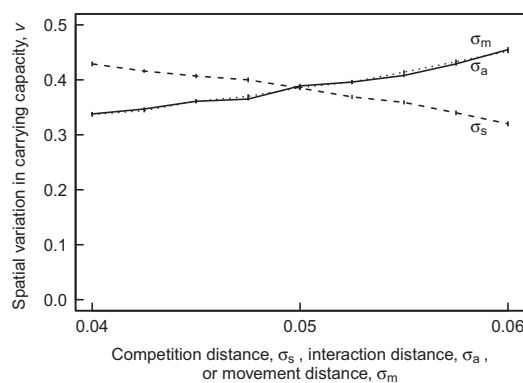
Fig. 5. The minimum level of spatial variation in resources, v, required to stabilize co-existence for at least 10^4 generations with varying competition distance, σ_s (dashed line), Allee effect distance, σ_a (solid line), and movement distance, σ_m (dotted line). To create the curves, we increase the spatial variation v until the average co-existence time across 10 replicate runs exceeds 10^4 generations. Vertical bars denote standard errors across these replicates. All other parameters are as in Fig. 1 and model runs were initialized as described in Fig. 3.

when the maximum fecundity is higher (larger f_{max}; Fig. 4b), as both of these conditions lead to greater overall population sizes. Initial population sizes matter much less in determining whether co-existence occurs (Fig. S4).

Our results are robust to changes in both the scale of movement and the scale of interactions between individuals (Fig. 5). Increasing the average movement distance, σ_m, makes co-existence more difficult. With greater movement distances, individuals of a given species will more often cross into the territory dominated by the other species and increase their probability of founding a viable satellite population that could potentially drive the other species to extinction. This is analogous to the finding that a single species that exhibits Allee effects must exceed some

Fig. 6. The minimum level of spatial variation in resources, v, required to stabilize co-existence for at least 10^4 generations when (**a**) the two species respond to competitive interactions differently or when (**b**) the species differ in their strengths of Allee effects. This figure was created using the same methods as described for Fig. 4. To vary how one species responds to competition or Allee effects relative to the other, we vary the parameter corresponding to species 2 (i.e., c_2 and a_2) while leaving that for species 1 fixed. The vertical dashed lines indicate the strengths of (a) competition effects, c_1, and (b) Allee effects, a_1, in species 1. All other parameters are as in Fig. 1 and model runs were initialized as described in Fig. 3.

minimum dispersal rate to undergo a range expansion (Keitt et al., 2001). By this same reasoning, we would expect that dispersal functions with a greater proportion of long-distance dispersal events (e.g., leptokurtic dispersal kernels) would also make co-existence more difficult. When beneficial interactions between conspecifics occur over a larger spatial scale (larger σ_a), co-existence is, again, more difficult. Larger neighbourhoods increase the density in the resource valley, because individuals in the valley can enjoy positive interactions with individuals on the peaks. The role of neighbourhood size was also investigated by Eppstein et al. (2006), who similarly found that larger neighbourhoods made co-existence more difficult (e.g., see their Fig. 5b). In contrast to the above effects, co-existence becomes easier when competitive interactions occur over a broader spatial scale (larger σ_s). When individuals at the peaks can compete more broadly for resources, they deplete the population densities in the valley and facilitate isolation between the populations occupying the resource peaks.

We also investigated the robustness of our results to differences between the two species in how they respond to competitive interactions (i.e., species-specific values of the parameter c) and Allee effects (i.e., species-specific values of the parameter a) (Fig. 6). Although co-existence becomes more difficult when the strength of either of these effects differs between species, higher levels of variation in resource abundance, v, can recover co-existence in both cases. When the strengths of the Allee effect differ between the two species, the species with a stronger Allee effect (i.e., higher a) experiences an overall greater fitness cost associated with rarity, and, thus, will tend to be displaced. Similarly, when one species is more vulnerable to competition, it is more likely to be displaced. Eppstein et al. (2006), also found that co-existence was sensitive to asymmetry in Allee effects (see
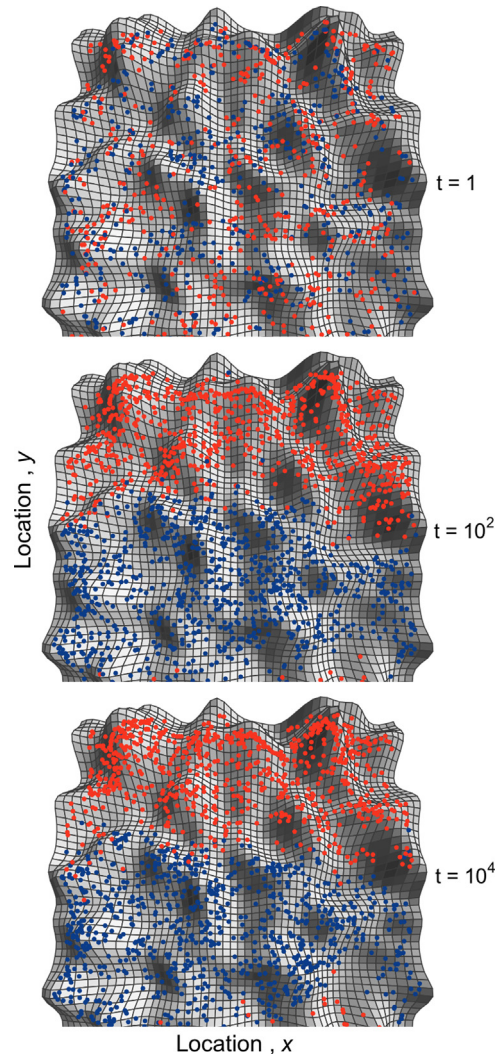
Fig. 7. A sample model run in a landscape with random variation in local resource abundance and standard wrap-around boundaries. All parameters are the same as in Fig. 1, except that there are twice as many total resources available across the landscape to account for the fact that it is twice the area (i.e., y ranges from 0 to 1 here, compared to 0 to 0.5 in Fig. 1). The base level of resources was chosen such that the maximum resource abundance across the landscape was twice that of the minimum.

their Fig. 2b), although they did not investigate the role of spatial resource heterogeneity, as we have done here.

Lastly, we extended our model to two other simple landscapes (Fig. S1), as well as to a more natural landscapes where variation in resource abundance was generated randomly with spatial autocorrelation (Fig. 7). In these bimodal landscapes and the stochastically generated landscape, we confirmed that co-existence is stabilized by variation in resource abundance. While the pattern that results from the colonization phase can vary across replicate model runs for the stochastic landscape (results not shown), we observed that species boundaries align with the valleys in resource abundance and remain relatively static through time.

4. Discussion

Understanding how consumer–resource interactions enable diverse communities to exist has been a long-standing topic of interest in community ecology. It had long been thought that a habitat could support no more species than the number of limiting

resources it contained (Haigh and Maynard-Smith, 1972). This perspective originated with Volterra (1928) who showed that when two consumers use the same resource, the more efficient of the two will eventually out-compete the other.

Numerous theoretical studies since Volterra's initial work have shown that multiple consumer species can in fact persist on a single resource, provided that not all of Volterra's assumptions are met (see Armstrong and McGehee, 1980). For example, when resource and/or consumer dynamics are density dependent (Koch, 1974; Armstrong and McGehee, 1976) more consumers can persist than there are types of resources. Persistence of more consumer types can also occur when those types use the resource in functionally different ways (Haigh and Maynard-Smith, 1972). Additionally, if species use the same resources, but use them at different rates and are differentially limited by them, more species can co-exist than the number of resources, provided that the abundance of those resources varies across the habitat (Tilman, 1982). Less is known, however, about how a single resource might be able to support multiple species when those species use that resource in the same way.

Levin (1974) presented one of the first analyses of this problem. In a discrete patch model with migration, he showed that multiple species utilizing a single resource in the same way can co-exist if each species inhibits the growth rate of rare heterospecific invaders. Effectively, these interspecific interactions create an Allee effect that helps maintain both species across the larger meta-population.

More recently, other authors have investigated how Allee effects influence co-existence in spatially explicit models (Molofsky et al., 2001; Ferdy and Molofsky, 2002; Molofsky and Bever, 2002). For example, Molofsky and Bever (2002) showed that, across a two dimensional lattice, Allee effects could lead to the maintenance of multiple species across the lattice, as long as some of the patches were uninhabitable by either type. These uninhabitable cells essentially fragment the two dimensional landscape into a meta-population of patches separated by walls. Here we have shown that Allee effects can, in a similar manner, stabilize co-existence of ecologically equivalent species in a *continuous* spatial landscape in which a single resource is distributed non-uniformly across space. Just as Molofsky and Bever (2002) found that uninhabitable cells can act as barriers that prevent species from expanding into one another's ranges, we find that regions of low resource abundance act to anchor species' ranges.

Continuous space differs from a meta-population or discrete patch model in an important way. Meta-population models do not allow for any within-patch spatial structure, without which it is not possible for one species to gradually encroach on the range of another species. This is because any expansion of a species' range would require successful invasion of entire patches by the expanding species. In contrast, in continuous space one species can completely surround and subsequently encroach on the range of the other species in arbitrarily small steps. For this reason, one might expect that co-existence would be more difficult in continuous space models. We have shown, however, that Allee effects can still promote co-existence even with this additional challenge.

Other relevant work, without considering species co-existence *per se* has examined how the Allee effect might affect a single species' range. Keitt et al. (2001) found that Allee effects can stabilize a lone species' range in a discrete-patch model, even when the landscape does not vary in resource abundance. When considering continuous space, however, these authors found that a species either expands or contracts its range indefinitely. In contrast, we observe stable species' boundaries in our model as long as there is (1) variation in resource availability across the landscape and (2) a competitor species inhabiting the other resource peak. Keitt et al. (2001) extended their model to consider

heterogeneity in resource abundance, and found that the outer limit of the single species' range tends to form near patches containing fewer resources; however, they did not extend this analysis to continuous space, nor to multiple species. Theoretical work on hybrid zones has similarly shown that the boundary between hybridizing species should move to and settle in areas of low population density (Barton and Hewitt, 1989, 1985) and, furthermore, that Allee effects (induced by assortative mating and/or selection against hybrids) can stabilize mosaic patterns (M'Gonigle and FitzJohn, 2010).

M'Gonigle et al. (2012) recently found that sexual selection could stabilize co-existence of ecologically equivalent species in a continuous landscape with a heterogeneous distribution of resources, as long as the mate choice mechanism created a rare-type disadvantage in both sexes. Fitness reductions due to sexual choosiness when selecting a mate can induce an Allee effect (Møller and Legendre, 2001) and thus the model of M'Gonigle et al. (2012) can be regarded as a special case of the model presented here. Unlike us, however, M'Gonigle et al. (2012) assumed global population sizes regulation, despite local species interactions, in order to keep population size constant. We, in contrast, let the population densities decrease naturally as the strength of Allee effects increases. Critically, we find that the stabilizing effect of Allee effects still occurs, despite the de-stabilizing effect of reduced population sizes.

Throughout our analyses, we have used co-existence time as a proxy for stability. With finite populations, however, demographic stochasticity will eventually lead to the domination of one species (Bolker et al., 2003). Nevertheless, the time required for such takeovers is so long that this theoretical inevitability is likely not relevant in real ecological communities (e.g., in Fig. 1b both species were still present when the simulation was terminated after 10^5 generations). Furthermore, the contrast between cases in which we observe co-existence and cases in which we do not is dramatic: when co-existence is not maintained according to our criteria, we often observe one species taking over rapidly (e.g., 745 generations in Fig. 1a; see also the sharp boundary demarcating the region of co-existence in Fig. 3).

In our model, individuals "compete" locally for resources that are present, with competition dissipating as the distance between them increases. We deliberately did not consider explicit resource dynamics here, nor did we specify the mechanistic cause of the Allee effect. This was done in an effort to keep our model general and free of mechanistic assumptions. However, a more complex model incorporating explicit consumer–resource dynamics could yield different outcomes. For example, if feedbacks exist between consumer densities and local resource abundance, such that locations of high and low consumer density are not permanent through time, we might expect co-existence to become less likely. Examining more explicit consumer–resource models would provide an interesting avenue for future work.

Although our analysis was performed in a simple landscape with two Gaussian resource peaks, we have shown that our findings extend to other types of bimodal landscapes (Fig. S1), and to more natural resource distributions (Fig. 7). Hence, we might expect that in nature many resources vary in abundance across space in such a way that they could facilitate co-existence of closely related species that exhibit Allee effects. Moreover, we found that stable co-existence occurred more easily when population sizes were larger and demographic stochasticity was lower, suggesting that even slight amounts of variation in nature might be sufficient to stabilize co-existence for large populations (Fig. 4).

Considering Allee effects as a process that can maintain species diversity may help us to better understand how ecological communities form and persist across diverse landscapes. Empirical tests examining the role of the Allee effect in maintaining co-

existence would be useful. Collins et al. (2010) showed that positive frequency-dependence occurred in plots containing genetic variants of a single grass species. Longer-term experiments like this would be necessary to test whether positive frequency dependence can facilitate co-existence. Combining such findings with the theoretical predictions presented here and in earlier studies will help inform whether Allee effects may contribute to maintaining species diversity.

5. Conclusions

There has been much effort devoted to understanding how diverse communities of species can persist on a limited number of resources. One general conclusion that has arisen from this previous work is that, in order for more species to persist than there are limiting resources, the species must use the resources in different ways. Less emphasis has been placed on understanding how species that use resources in the same way can co-exist. Several important studies have, however, shown that Allee effects can stabilize co-existence of species on a single resource when situated in a spatial context. Here we extend this past work from discrete space to continuous space and show that Allee effects, combined with spatial variation in the distribution of resources can also stabilize co-existence of ecologically equivalent species, despite the fact that they reduce population sizes and increase demographic stochasticity. This, combined with earlier findings, suggests that Allee effects might be a generally important force for maintaining co-existence of ecologically equivalent species.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.jtbi.2014.07.014.

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