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.

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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	