

# Relative ranges of mating and dispersal modulate Allee thresholds in sessile species

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## Abstract

Sessile organisms, including plants and benthic macrofauna, are often restricted in the ranges over which they are able to reproduce and disperse. This leads to spatial patterning within populations, causing the effective population density around each individual to depart from the average across its range. This has important implications for population dynamics, in particular the minimum density at which populations are able to maintain positive growth (the Allee threshold). Here we compare the population dynamics of species with three syndromes — spatially restricted mating, dispersal or both — against a null model of a species with no spatial limitations. First we demonstrate mathematically that the population density at which Allee effects occur systematically shifts in each case. Next we use individual-based models representing three exemplar species to simulate the implications for the Allee threshold of each within a fixed area. In the case where mating occurs over long ranges but dispersal is restricted (e.g. the wind-pollinated silver fir, *Abies alba* Mill.), there is a negligible impact on the Allee threshold. When mating is also spatially restricted (e.g. the dipterocarp tree *Shorea curtisii* Dyer ex King), the Allee threshold reduces, unless high death rates prevent the stabilisation of aggregations. This occurs because offspring remain within the range of potential mating partners.

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Finally we consider a case in which mating is short-ranged, and dispersal effectively unrestricted, but in which individuals choose to locate themselves in the vicinity of conspecifics (e.g. acorn barnacles, *Semibalanus balanoides*). This has the effect of maintaining clustering in the face of high dispersal, reducing the Allee threshold, and compensating for the apparent cost of short-range mating. Incorporating information on ranges of mating and dispersal can lead to more effective models for the management of populations at low density, in particular the identification of species with syndromes which make them vulnerable to Allee effects. Most notably, mechanisms which increase the degree of clustering in populations increase both their resilience and persistence when finding a mate is the greatest challenge faced by a sessile organism.

*Keywords:* , Allee effect, individual-based model, minimum viable population (MVP), pollen limitation, resilience, seed dispersal

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## 1. Introduction

The Allee effect describes positive density dependence in populations (Allee, 1931; Stephens et al., 1999; Courchamp et al., 2008). It is believed to be widespread in low-density populations of both animals (Gascoigne et al., 2009) and plants (Ghazoul, 2005), with ramifications for the management of natural systems, whether for the conservation of species at low abundances (Stephens and Sutherland, 1999), sustainable exploitation of resources (Hutchings, 2015) or the management and eradication of invasive species (Tobin et al., 2011). While basic models of population dynamics predict rapid growth at low density, Allee effects are often attributed to factors such as the inability of individuals to find mating partners or to form aggregations of sufficient size to resist predators or environmental fluctuations (Courchamp et al., 2008). These ‘component Allee effects’, where single fitness-determining parameters show positive density dependence, can lead to a ‘demographic Allee effect’, where the growth rate of the entire population is reduced (Stephens et al., 1999; Berec et al., 2007).

The density at which population growth rates switch from being positive

to negative is an interior critical point in their dynamics and is referred to as the ‘Allee threshold’ (Fig. 1; Courchamp et al., 2008). The Allee threshold has particular implications in conservation, where the Minimum Viable Population (MVP) of a species may be determined by such intrinsic effects (Shaffer, 1981),  
20 or for the efficient control of invasive species (Tobin et al., 2011). Understanding what determines the density at which population growth switches from positive to negative therefore has great importance in both fundamental and applied ecology.

25 The distribution of individual members of a population in space is seldom regular, and more often clustered, dispersed or random. This causes the local density experienced by individuals in a population to deviate from the density as measured at larger scales. As a consequence the effective rates of ecological processes differ from those which would be predicted based on population-level  
30 models (Harada and Iwasa, 1994; Law et al., 2003). One potential outcome of spatial structure might therefore be to alter the rate of population growth, and therefore also the threshold density at which the Allee effect begins to operate. Spatial patterns can be created by localised interactions such as competition, interference, mating and dispersal. Spatially-restricted processes might there-  
35 fore generate patterns which cause populations to become intrinsically unstable (Durrett and Levin, 1994), and thereby determine the effective parameter space for the functional traits of species. Sessile organisms, such as plants or benthic fauna, are likely to be especially sensitive to spatially-generated Allee effects, as individuals are unable to escape the neighbourhood within which they have es-  
40 tablished. In contrast, motile species often aggregate facultatively and thereby reduce the problem of mate-finding at low densities (Gascoigne et al., 2009).

Here we assess the impacts of the relative ranges of mating and dispersal on the ability of populations of sessile organisms to maintain themselves at low densities. First we develop a mathematical framework for the expected pop-  
45 ulation dynamics when mating and dispersal occur over limited distances. To explore the implications for persistence of populations with restricted ranges, such as in habitat fragments or islands, we create individual-based models for

three contrasting syndromes. Each represents an exemplar species: a coniferous tree (long-range mating, short-range dispersal), a dipterocarp tree (short-range mating and dispersal) and a barnacle (short-range mating, long-range dispersal). Using these species as starting points we explore the potential impacts of variation in the relative ranges of mating and dispersal for the Allee threshold. We find that when sessile organisms are restricted in the range over which they are able to mate, any mechanism that generates clustering in the spatial pattern lowers the density at which Allee effects occur and thereby increases the resilience of the population to external causes of mortality despite the consequent increase in intra-specific competition for space.

## 2. Materials and Methods

### 2.1. The mean-field model

The mean-field model provides the expected population dynamics if all individuals experience identical conditions. The number of individuals per unit area is given by  $\rho$ . Each individual attempts to reproduce at rate  $\beta$ , but successful mating is proportional to the density of individuals within the mating range  $\rho^{(m)}$ . Hence individuals mate successfully at a per-capita rate  $\beta\rho^{(m)}$ . Whether mating gives rise to a successful new offspring is dependent on the available space  $(1 - \rho^{(d)})$ , where  $\rho^{(d)}$  represents the average population density within the range of dispersal  $\sigma^{(d)}$ . Finally, individuals die with an intrinsic per-capita death rate  $\mu$ .

The dynamics of population density  $\rho$  in the mean-field approximation can therefore be described as:

$$\dot{\rho} = \beta\rho\rho^{(m)}(1 - \rho^{(d)}) - \mu\rho \quad (1)$$

Note that this model generates an Allee effect even in the absence of spatial heterogeneity in the population (solid line in Fig. 2). This can be demonstrated by setting all local densities in equation 1 to the mean population density ( $\rho^{(m)} = \rho^{(d)} = \rho$ ) and plotting the resultant per-capita growth rate for values of

75 population density  $\rho$  from 0 (extinct) to 1 (all sites occupied). At low population densities,  $\beta\rho(1 - \rho) < \mu$  and the per-capita growth rate falls below 0.

## 2.2. Incorporating spatial structure

In spatially-structured populations, the local density of conspecifics surrounding each individual differs from the average for the population as a whole. This effect is introduced to the model by a set of additional free parameters representing the deviation from the average density of conspecifics within either the mating range  $\kappa^{(m)}$  or the dispersal range  $\kappa^{(d)}$ . These quantities are equivalent to the widely-used Ripley's  $K(r)$  function (Ripley, 1977) divided by the area within range, hence  $\kappa^{(m)} = K(\sigma^{(m)})/\pi(\sigma^{(m)})^2$  and  $\kappa^{(d)} = K(\sigma^{(d)})/\pi(\sigma^{(d)})^2$ . Thus  $\rho^{(m)} = \kappa^{(m)}\rho$  and  $\rho^{(d)} = \kappa^{(d)}\rho$ .

As a first step in exploring the behaviour of these systems, we begin by creating a set of spatially-implicit models in which we assume that a clustered spatial pattern exists, such that short range mating and dispersal occur at greater effective densities than the mean-field average. In these models  $\kappa$  is a summary measure of the spatial structure relating the individual-based perspective of effective density. Hence for the purposes of mating  $\kappa^{(m)} > 1$ , and for dispersal  $\kappa^{(d)} > 1$ . These are compared against the null model in which both mating and dispersal are effectively unlimited, and therefore occur at a rate determined by the conditions  $\kappa^{(m)} = \kappa^{(d)} = 1$ . We thereby generate three models in addition to the null (equation 1):

$$\dot{\rho} = \beta\rho\rho(1 - \kappa^{(d)}\rho) - \mu\rho \quad \text{localised dispersal} \quad (2)$$

$$\dot{\rho} = \beta\rho\kappa^{(m)}\rho(1 - \kappa^{(d)}\rho) - \mu\rho \quad \text{localised mating and dispersal} \quad (3)$$

$$\dot{\rho} = \beta\rho\kappa^{(m)}\rho(1 - \rho) - \mu\rho \quad \text{localised mating} \quad (4)$$

First we explore the behaviour of this set of models, and their implications for the minimum density at which the population is able to maintain positive growth. We initially compare model behaviour when  $\kappa^{(m)} = \kappa^{(d)} = 1.1$ , then

investigate the impacts of changes in local spatial structure by plotting the  
100 density at which the Allee threshold occurs for  $\kappa^{(d)}$  values from 1–1.5.

### 2.3. Individual-based models

In order to investigate the implications of altering the relative ranges of mat-  
ing and dispersal, we model the population dynamics of three exemplar species  
with contrasting features matching the theoretical cases outlined above (Ta-  
105 ble 1). Although the absolute ranges of their interactions vary by two orders  
of magnitude, it is the relative ranges within each species which influence the  
emergent patterns. All species are sessile, hermaphroditic and predominantly  
out-crossing. These features ensure that (a) spatial patterns are the direct  
consequence of spatially-constrained processes rather than individual decision-  
110 making; (b) all individuals are capable of mating with all other individuals,  
and of generating offspring; and (c) individuals need to mate in order to repro-  
duce. Our models are not intended to be comprehensive representations of each  
species; more detailed natural history information would be required to generate  
models which fully captured or predicted their spatial dynamics. Rather we use  
115 them to illustrate particular syndromes based on their general traits.

The null model against which we compare our species is one in which mating  
and dispersal within patches are effectively unconstrained. There are many  
such examples in nature; grasses and corals provide appropriate benchmarks in  
terrestrial and marine environments respectively.

120 We model the dynamics of each population within a field represented as a  
square grid of size  $50 \times 50$  with toroidal boundaries. Each site of the grid can be  
occupied, representing a single individual, or empty. The maximum potential  
size of the population is therefore fixed, corresponding to a habitat fragment  
or island system. The initial population density was  $\rho = 0.4$  with a completely  
125 spatially random pattern, with a birth rate  $\beta = 1.0$ . Ranges of processes were  
measured in units of individual cell sizes, where  $\sigma^{(m)} = \sigma^{(d)} = 2$  for short-range  
effects, and  $\sigma^{(m)} = \sigma^{(d)} = 50$  for long-range effects; the latter ensured that  
any individual could potentially mate with any other individual or disperse its

offspring to any vacant site.

130 Three processes govern the behaviour of individuals: mating (reproduction),  
dispersal (generation of new individuals), and death. The model runs in con-  
tinuous time, with asynchronous updating of model cells, and order driven by  
a Poisson process. Individuals seek local mating opportunities with a rate  $\beta$   
and die with rate  $\mu$ , giving a mean lifespan of  $1/\mu$ . In each step an individual  
135 is chosen randomly, and attempts to mate with probability  $\beta/(\beta + \mu)$  or dies  
with probability  $\mu/(\beta + \mu)$ . In order to mate, the individuals select at random  
a site within a radius  $\sigma^{(m)}$ . If the chosen site is occupied then the mating is  
successful. Each time a successful mating occurs, a new offspring is generated;  
this does not however mean that the offspring will establish successfully. Its  
140 ability to survive is determined by its ability to find an empty site to occupy.  
A site is chosen randomly within a distance  $\sigma^{(d)}$  from its original parent. If the  
site is already occupied then the new offspring is not successful. In this way  
we introduce both dispersal limitation and competition for space. Although we  
use a flat isotropic kernel for both mating and dispersal, it is likely that natural  
145 systems contain a range of more complex patterns. Nevertheless, introducing  
a generalised kernel function into the model would have a limited impact on  
the fundamental dynamics (Durrett and Levin, 1994). Model time advances by  
 $1/N(\beta + \mu)$  where  $N$  is the number of individuals. Each combination of model  
parameters was run with 20 replicates and mean values are presented.

150 For a species with long-range mating and short-range dispersal, we use the  
European silver fir, *Abies alba*. Seed dispersal distances estimated by genetic  
techniques suggest a median range of 31 m, and although the maximum distance  
is likely to be considerably greater, few individuals will achieve this (Cremer  
et al., 2012). In contrast, as a wind-pollinated conifer, the range over which it  
155 is able to mate is effectively unlimited, at least from the perspective of local  
population processes.

We contrast the silver fir with a species which combines both short-range  
dispersal and mating. Tropical trees in the Dipterocarpaceae produce large seeds  
with limited dispersal. In our chosen example, *Shorea curtisii*, the majority of

160 seeds fall within 40 m of the parent tree, with a maximum range of 80 m (Tamari  
and Jacalne, 1984; Tani et al., 2012). The mating distance is dependent on the  
movement of the main pollinators of dipterocarps, which are believed to be  
thrips (Appanah and Chan, 1981) and small beetles (Momose et al., 1998) with  
limited flight capabilities. As a result, genetic analyses detect effective mating  
165 ranges for this species of around 71 m (mean of estimates in each of three years;  
Tani et al., 2012).

Our third example is a species with short-range mating but for which dis-  
persal is effectively unlimited: the acorn barnacle *Semibalanus balanoides*. It  
requires direct contact to reproduce, with a range physically constrained by a  
170 penis length of 2.5 cm (Kent et al., 2003). Barnacle larvae are planktonic, and  
disperse freely through the water column. Nevertheless, the dispersal process  
is not entirely random. Cyprid larvae, once they reach a suitable rock, actively  
move to select an appropriate site for establishment (Southward, 1987), after  
which they remain entirely sessile. This position is chosen to be within a pre-  
175 ferred distance from conspecifics, generating clusters which reach a radius of up  
to 5 cm in size (Hooper and Eichhorn, 2016). We therefore add an additional  
process to the model in which once an offspring is successful in finding a vacant  
site, maintaining population-level competition for space, it changes its location  
to a random empty cell with an adjacent occupied cell. Given that dispersal is  
180 long-ranged, excluding this additional mechanism would lead to the breakdown  
of any spatial structure and the population dynamics would be identical to the  
null model even with short range mating.

To investigate the impacts of the death rate  $\mu$  on Allee thresholds, it was  
systematically varied from 0.01 to 0.2, reflecting an increase in external stress  
185 or harvesting. We first ran 20 simulations with a starting density  $\rho_0 = 0.01$   
and  $\mu = 0.01$ . If all simulations resulted in population extinction then a further  
200 runs were conducted. If in all of these the final population remained zero  
then  $\rho_0$  was raised in steps of 0.01 until a non-zero population was obtained; the  
previous iteration was then counted as the lower-bound estimate of the Allee  
190 threshold. To obtain an upper-bound estimate, starting density was then raised



further until a non-zero population density was obtained at least five times. The Allee threshold was calculated as the average between the two estimates. This process was then repeated with increases in  $\mu$  of 0.01 up to  $\mu = 0.20$ . All simulations ran for an arbitrarily long time to ensure that a stationary state  
195 had been reached. We thereby show how variable mating and dispersal ranges influence the resilience of populations to increasing mortality rates.

### 3. Results

#### 3.1. Mathematical results

The basic population model generates an Allee effect with negative popula-  
200 tion growth at low densities. Adding terms for localised mating and dispersal alters the dynamics of populations, with particular implications for the Allee threshold, that is the minimum density at which they are able to maintain positive growth (Fig. 2). In the case of localised dispersal ( $\kappa^{(d)} > 1$ ) but long range mating ( $\kappa^{(m)} = 1$ ), the Allee threshold is given by  $1/2\kappa^{(d)}(1 - \sqrt{1 - 4\kappa^{(d)}\mu/\beta})$ ,  
205 indicating a small increase relative to the null model. This is because short-range dispersal generates clusters that increase competition for space. Because mating is long-ranged, the spatial structure has no impact on the rate of mating, i.e.  $\rho^{(m)} = \rho$ . Overall, however, the change in the Allee threshold is minor (Fig. 3) relative to the marked reduction in both maximum per-capita growth rate and population carrying capacity (Fig. 2).  
210

When localised mating is combined with restricted dispersal the Allee thresh-  
old is given by  $1/2\kappa^{(d)}(1 - \sqrt{1 - 4\kappa^{(d)}\mu/\beta\kappa^{(m)}})$ , indicating a decrease in the Allee threshold with greater clustering (Fig. 3). In this case the cost of reduced reproductive range is compensated for by the increased clustering generated by  
215 short-range dispersal, which ensures that mating partners are available. Attempts at mating are more likely to be successful as the effective density within the mating range is greater than the average density. Once again this is accompanied by a reduction in population carrying capacity, though not of maximal per-capita growth rates (Fig. 2).

220 When dispersal is long-ranged the spatial structure breaks down unless an  
additional mechanism is introduced to maintain the presence of clusters, ensur-  
ing that localised mating takes place with  $\kappa^{(m)} > 1$ . If this is the case, the  
Allee threshold is  $1/2(1 - \sqrt{1 - 4\mu/\beta\kappa^{(m)}})$  which indicates a reduction rela-  
225 tive to the null model (Fig. 3). The Allee threshold is reduced even further  
than is the case with short range dispersal, because even though a clustered  
spatial structure exists, there is no localised competition for space. Individuals  
are effectively choosing to aggregate by selecting available locations. Maximum  
per-capita growth rates exceed those for the null model, and carrying capacity  
also increases marginally (Fig. 2).

### 230 3.2. Individual-based models

The results from the individual-based models concur with the mathematical  
predictions and allow for a more detailed assessment of the effects of variable  
scales of mating and dispersal on population dynamics. In Fig. 4 we show  
how the Allee threshold changes as the intrinsic death rate of the population  $\mu$   
235 increases; this can be interpreted as an increase in harvesting rate or environ-  
mental stress.

When dispersal occurs over short scales but mating remains at large scales,  
as with the conifer *Abies alba*, the Allee threshold is identical to the null model  
for low values of  $\mu$  but then increases relative to the null model at higher  
240 values. Even at high rates of mortality, short-range dispersal generates a degree  
of clustering and thereby inherent space competition during the dispersal phase.  
This reduces the per-capita birth rate and the species becomes more sensitive  
to extrinsic causes of death.

If both mating and dispersal take place over short distances, as for the rain  
245 forest tree *Shorea curtisii*, the Allee threshold is reduced for almost all values  
of  $\mu$  which do not lead to extinction (Fig. 4). The reduced range of mating is  
offset by the increased clustering caused by localised dispersal, which means that  
the effective density of conspecifics in the mating area around each individual  
increases relative to the spatial average, and to a greater extent than in the

250 other models (Appendix A1). This has the effect of making mating easier and  
thereby diminishing the impact of the Allee effect on population dynamics.  
The effect disappears for large values of  $\mu$  because when death rates become  
too high the clusters are broken down, which means that the mating advantage  
within clusters is no longer sufficient to exceed the disadvantage of intra-specific  
255 competition.

Finally, in the case of the barnacle *Semibalanus balanoides*, mating is lo-  
calised but dispersal is long-ranged. An additional mechanism is introduced  
to represent the active decision by barnacle larvae to select sites adjacent to  
neighbours, thereby generating clusters. The Allee threshold is then reduced by  
260 a greater degree than in all other examples (Fig. 4). This occurs because of the  
combined benefit of a higher effective density of mating partners within range,  
and a reduction in intra-specific competition for space due to long-range disper-  
sal. Removing the mechanism for site selection by barnacles would cause any  
spatial structure to break down and the population would behave according to  
265 null model expectations, i.e. with a markedly higher Allee threshold. Thus the  
movement of barnacle larvae increases the overall resilience of the population.

#### 4. Discussion

The relative distances over which mating and dispersal occur have important  
consequences for the spatial patterns formed by sessile species and therefore  
270 also the minimum density at which their population is able to persist. This  
creates the potential for trade-offs and constraints in the parameter space within  
which species might evolve. Traits leading to short-ranged mating necessitate  
a further mechanism for maintaining clustered populations, whether through  
a similar reduction in dispersal (as in the dipterocarp *Shorea curtisii*) or an  
275 active movement phase in the life-cycle, as with cyprid larvae of the barnacle  
*Semibalanus balanoides*. A species whose capacity for dispersal outstrips its  
reproductive range is likely to be susceptible to Allee effects in limited areas  
such as islands or in the face of stochastic environmental variation.

The potential for aggregation to mitigate component Allee effects has been  
280 recognised previously in motile animals (Gascoigne et al., 2009; Kanarek et al.,  
2013). Our individual-based model is similar in form to that used in an inves-  
tigation of the implications of dispersal and mating ranges for rates of range  
spread in territorial birds and mammals (South and Kenward, 2001). In the  
context of species invasions, founder populations that begin in a more clustered  
285 state have a higher probability of establishing, and those with long-range dis-  
persal trade a increased rate of spread for reduced persistence (Kanarek et al.,  
2013). We build on this previous work by demonstrating that clustering can  
be generated endogenously by processes occurring within populations, and that  
the increase in clustering reduces the Allee threshold when reproductive ranges  
290 are limited, despite the concurrent increase in competition for space.

Considering each of our exemplar species in turn reveals the nature of the  
trade-off implicit in the relative ranges of mating and dispersal. Long-range  
wind-pollination in the conifer *Abies alba* diminishes the impact of short-range  
dispersal on population dynamics as individuals are able to mate with con-  
295 specifics beyond their own cluster. This can be contrasted with *Shorea curtisii*,  
in which mating occurs over relatively short distances, limited by the flight dis-  
tances of its pollinators (Appanah and Chan, 1981; Momose et al., 1998). In  
terms of overall population dynamics, however, the apparent costs are offset  
by a limited dispersal distance, which allows members of the population to re-  
300 main within reproductive contact. The spatial patterning of populations might  
therefore be an important consideration in their management.

Pollen limitation is common among plant species, imposing fitness costs  
and leading to Allee effects (Ghazoul, 2005; Gascoigne et al., 2009). Tropical  
trees may be particularly vulnerable to pollination failure as a result of typically  
305 being widely dispersed in space, self-incompatible, dependent on a small range of  
pollinators and unable to propagate vegetatively (Wilcock and Neiland, 2002).  
A broad spectrum of reproductive ranges occurs in trees, determined by the  
effective range of movement of pollen and pollinators (Ghazoul, 2005), as well  
as the landscape context (e.g. Dick et al., 2003). Even within congeneric species

310 of *Shorea*, pollen movement estimates extend to 314 m for *S. leprosula* and  
852 m for *S. parviflora* (Tani et al., 2009).

The probability of a successful mating in our model depends upon the local  
density of potential partners within range. This assumption is reasonable for  
trees whose pollinators are relatively unspecialised, and where probability of  
315 pollen reaching a conspecific is likely to be determined by their density within  
flight range. In plants with more specialised interactions, directed movement  
by pollinators will compensate to some extent for reduced local densities. Iso-  
lated individuals remain likely to suffer from reproductive costs through pollen  
limitation, and may compensate through self-fertilisation (e.g. Rodger et al.,  
320 2013). Plants which are unable to do so are likely to be particularly vulner-  
able to Allee effects, which may drive evolutionary responses at low densities  
(Gascoigne et al., 2009).

Our model in its present form does not discriminate between individuals as  
potential mating partners. Small populations of related individuals can suffer  
325 inbreeding depression and consequently a loss of fitness of offspring (Berec et al.,  
2007). The same may apply to highly clustered populations, which will select  
for tolerance of inbreeding (e.g. Ward et al., 2005). Previous studies have noted  
a propensity for trees pollinated by insects with short flight ranges to increase  
their rate of self-fertilisation at low densities (Tani et al., 2009). Incorporat-  
330 ing a cost to mating with close relatives would modulate the dynamics of our  
model and provide additional dimensions through which organisms may trade  
off adaptations for increasing their ranges of dispersal or mating.

Spatial patterns formed by trees are contingent on their mechanism of seed  
dispersal (Seidler and Plotkin, 2006); similar impacts may arise through pol-  
335 lination and drive both the spatial patterns of populations and the density at  
which they are able to maintain themselves. The mechanism used for seed  
dispersal shapes both its absolute range and distribution, although relatively  
few estimates exist for tropical trees (Kettle, 2012). Among dipterocarps, seed  
dispersal estimates vary among species from 17–77 m under normal conditions  
340 (Smith et al., 2016), but gusts of wind preceding storms extend the maximum

achieved (Smith et al., 2015, and pers. obs. MPE). Nevertheless, 90% of seeds are thought to disperse less than 10 m (see Smith et al., 2015, and references therein). *S. curtisii* has a relatively long dispersal ability relative to other dipterocarps, yet is still recorded as only recruiting successfully within 30 m of  
345 a mother tree (Tamari and Jacalne, 1984). Short-range propagule dispersal by rain forest trees is usually attributed to the necessity of producing large seeds for establishment in deeply shaded understorey conditions; our model suggests that this trait may carry benefits for the resilience of populations when mating also occurs over short distances.

350 In the case of acorn barnacles, which require direct physical contact to reproduce, an additional mechanism is required to maintain clusters despite long-range dispersal of propagules. Indeed, establishing barnacles choose to locate themselves so close to conspecifics as to incur fitness costs, implying that the aggregative drive is strong (Hooper and Eichhorn, 2016). Our simulations suggest  
355 that this enables barnacles to persist at lower densities than would be stable given entirely random settlement patterns. Intertidal habitats are characterised by high rates of disturbance and predation; we propose that clustering offers population-scale resilience to these extrinsic causes of mortality.

The pelagic larval phase of barnacles is likely to result in well-mixed popula-  
360 tions with a low risk of inbreeding within clusters. Individuals can also choose to mate with whichever conspecific is in range. Nevertheless, receptivity to mating (or fertility) might decline at high local densities, adding a cost to clustering in addition to an increased individual-level risk of mortality due to crowding (Hooper and Eichhorn, 2016).

365 While we chose the acorn barnacle as our starting point, other barnacle species exhibit a wide range of reproductive strategies. Those which sperm-cast are able to increase the range over which they reproduce (Barazandeh et al., 2013), though the lifespan of sperm in water is less than that of larvae, and therefore the relative range of mating remains much shorter than dispersal. We  
370 would therefore predict that the net costs of clustering would be greater for sperm-casting species. In other benthic fauna such as corals which exhibit mass

fertilisation and spawning we would not expect mating or dispersal to play a dominant role in determining local spatial patterning, though Allee effects might still occur due to the reduced probability of successful mating at low densities  
375 (Berec et al., 2007; Gascoigne et al., 2009).

The reduction in the Allee threshold which occurs when mechanisms exist to promote clustering provides an interesting parallel to the syndrome of reduced dispersal in island species (Whittaker and Fernández-Palacios, 2007). While the evolution of limited dispersal is usually explained on an individual basis  
380 as reducing the proportion of propagules that land in unsuitable areas (Cody and Overton, 1996), it may offer an additional population-level benefit promoting the persistence of endemic island species. Species which already possess such adaptations may be better adapted to persist in fragmented landscapes. This contradicts the conventional intuition that well-dispersed species should  
385 be favoured under such conditions (but see (Liao et al., 2013)).

While our model implies reproductive benefits to aggregation, it omits localised resource competition, which is likely to increase the costs. In plants this is typically both strong and occurs within spatial neighbourhoods, altering population dynamics (Law et al., 2003). In benthic macrofauna it is generally  
390 believed that competition for space exceeds that for resources, though presumably the latter still occurs. Models incorporating resource competition will offer additional dimensions for trade-offs in the traits of species.

Applications of models simulating the behaviour of populations at low density include in conservation, management of exploited resources, and the control  
395 of invasive species, where the cost of reducing a population to below the Allee threshold is likely to be much lower than for complete eradication (Stephens and Sutherland, 1999; Tobin et al., 2011; Hutchings, 2015). Our basic model can, with appropriate parametrisation, be applied to a wide range of sessile species and spatial contexts. While for mathematical efficiency it is most straightforward  
400 to model population density, in field applications it is likely that absolute population size will be a more useful metric, as with the widely-recognised conservation paradigm of a Minimum Viable Population (*sensu* Shaffer, 1981).

Alternatively, there is evidence from some systems that minimum patch size can be the crucial factor in population persistence (Vercken et al., 2011). Note that  
405 we have focussed on strong Allee effects, i.e. those which lead to negative population growth. Weak Allee effects, which cause positive density dependence but which do not themselves lead to population decline, should not be ignored, and indeed can interact with other pressures on species (Berec et al., 2007). From an applied perspective it is often more useful to identify the density at which  
410 growth rates decline, which indicates the point at which Allee effects first start to influence population dynamics (Hutchings, 2015). Incorporating key species traits such as the ranges of dispersal and mating, and their implications for the spatial structuring of populations, will improve our ability to predict and manage the dynamics of populations at low densities.

## 415 **Conclusions**

The implication of our model is that sessile species with localised mating, but which lack a compensatory mechanism to generate aggregations, are likely to be particularly susceptible to Allee effects when reductions occur in their population density. This will have repercussions for the conservation of species  
420 in fragmented or shrunken habitats, in which their Allee threshold will be increased relative to other species. Simulations which incorporate the effective ranges of mating and dispersal can play a valuable role in identifying species with syndromes that might reduce their resilience to extrinsic causes of mortality. Furthermore, our framework provides a means of exploring the evolutionary  
425 constraints acting on the traits of species with restricted reproductive ranges.

## **Acknowledgments**

Preparation of this work was supported by a DGRIIA-BUAP researcher exchange grant awarded to JVC.



## Appendices

430 *Figure A1.* Pair correlation function  $g(r)$  describing local spatial density of individuals with increasing distance  $r$  (measured in grid squares) in the individual based models.

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## Tables

Table 1: Traits of exemplar species used for illustration of individual-based models simulating dynamics of populations with variable syndromes.

Species	Reproductive range	Dispersal range	Source
<i>Abies alba</i>	—	31 m	Cremer et al. (2012)
<i>Shorea curtisii</i>	71 m	80 m	Tamari and Jacalne (1984); Tani et al. (2012)
<i>Semibalanus balanoides</i>	2.5 cm	—	Kent et al. (2003)

## Figure legends

*Figure 1.* Conceptual diagram showing relationship between per-capita growth rate  $\dot{\rho}$  and the population density  $\rho$ . The Allee threshold is an unstable equilibrium point (empty circle); below this density the population will decline to extinction. The upper equilibrium point, known as the carrying capacity of the population, is stable (closed circle).

*Figure 2.* Mathematical results for per-capita growth rate variation with population density  $\rho$  based on equations 1–4 in the text; for illustration purposes  $\beta = 1$ ,  $\mu = 0.1$ . Solid line: homogeneous, unrestricted dispersal and mating ( $\kappa^{(m)} = \kappa^{(d)} = 1$ ). Dashed line: short-range dispersal, long-range mating ( $\kappa^{(m)} = 1$ ,  $\kappa^{(d)} = 1.1$ ). Dotted line: short-range dispersal and short-range mating ( $\kappa^{(m)} = \kappa^{(d)} = 1.1$ ). Dot-dashed line: clustered spatial pattern with short-range mating ( $\kappa^{(m)} = 1.1$ ,  $\kappa^{(d)} = 1$ ).

*Figure 3.* Mathematical results for Allee threshold (the lower-bound population density at which per-capita growth rates fall below 0) variation with increasing local density within the dispersal range of individuals  $\kappa^{(d)}$ ; vertical line shows the level used in Fig. 2. Dashed line: short-range dispersal, long-range mating ( $\kappa^{(m)} = 1$ ). Dotted line: short-range dispersal and short-range mating ( $\kappa^{(m)} = 1.1$ ). Dot-dashed line: clustered spatial pattern with short-range mating ( $\kappa^{(m)} = 1.1$ ). See equations 2–4 for full details.

*Figure 4.* Allee threshold variation with increasing per-capita death rates  $\mu$  in the individual-based models (see Methods for details). Symbols indicate empirical values obtained from simulations; lines as Fig. 2. Circles: mean-field approximation (long-range dispersal and mating). Diamonds: short-range dispersal, long-range mating (e.g. *Abies alba*). Squares: short-range dispersal and short-range mating (e.g. *Shorea curtisii*). Stars: clustered spatial pattern with short-range mating (e.g. *Semibalanus balanoides*). Each curve represents the combined results of 1820 component simulations.

Figure 1: Conceptual diagram showing relationship between per-capita growth rate  $\dot{\rho}$  and the population density  $\rho$ . The Allee threshold is an unstable equilibrium point (empty circle); below this density the population will decline to extinction. The upper equilibrium point, known as the carrying capacity of the population, is stable (closed circle).

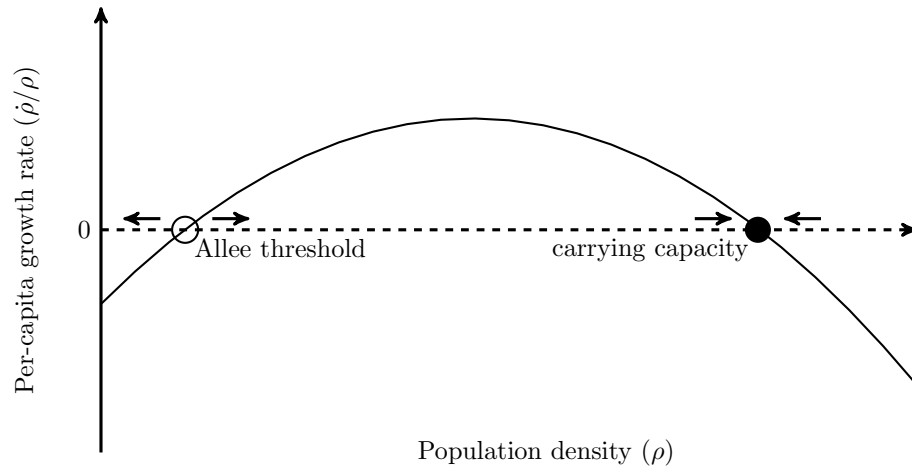




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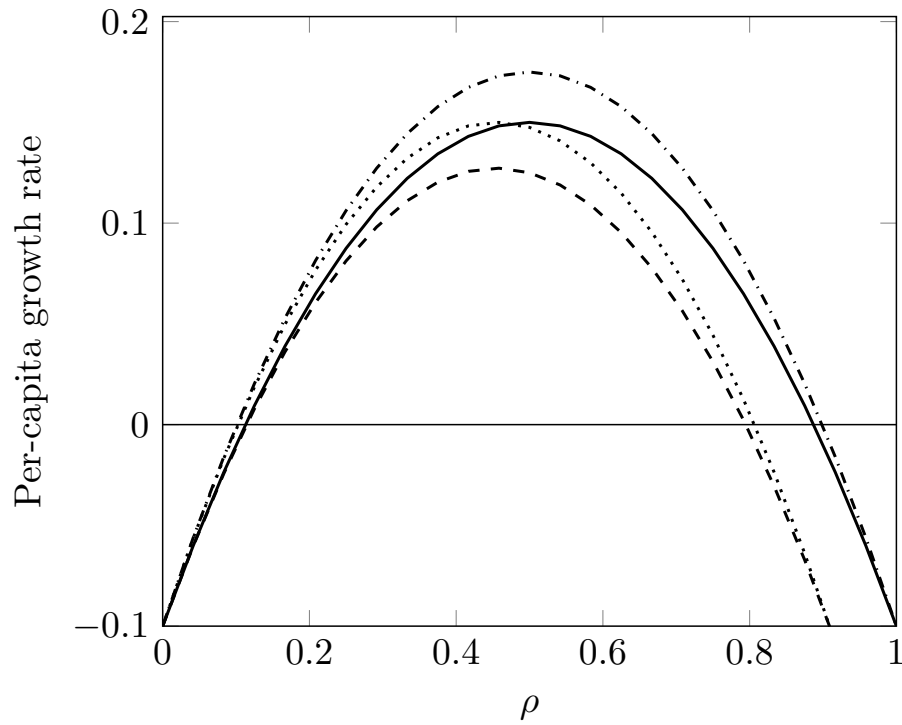


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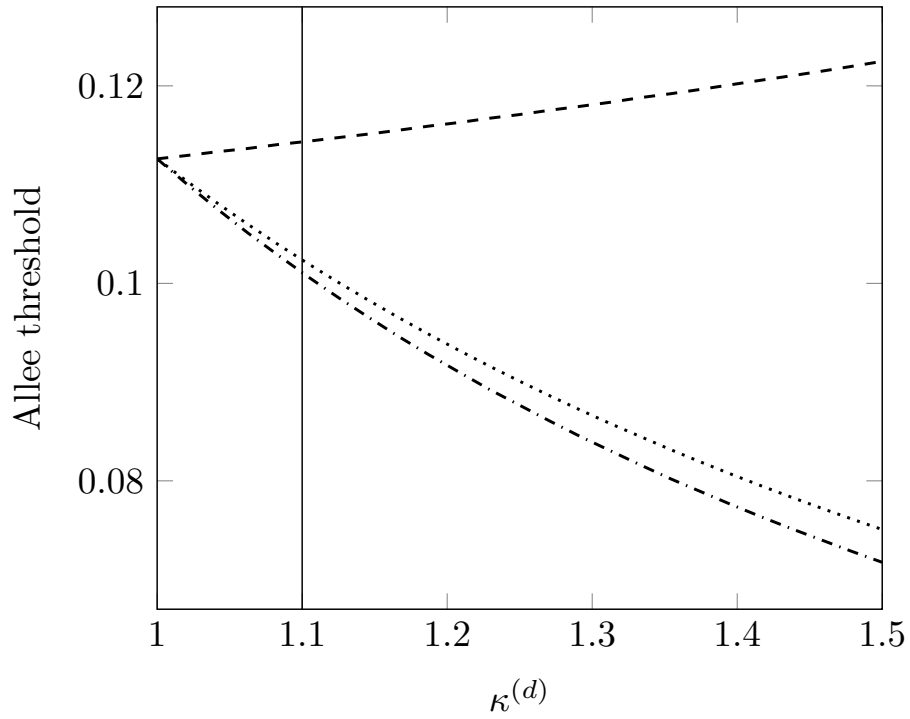


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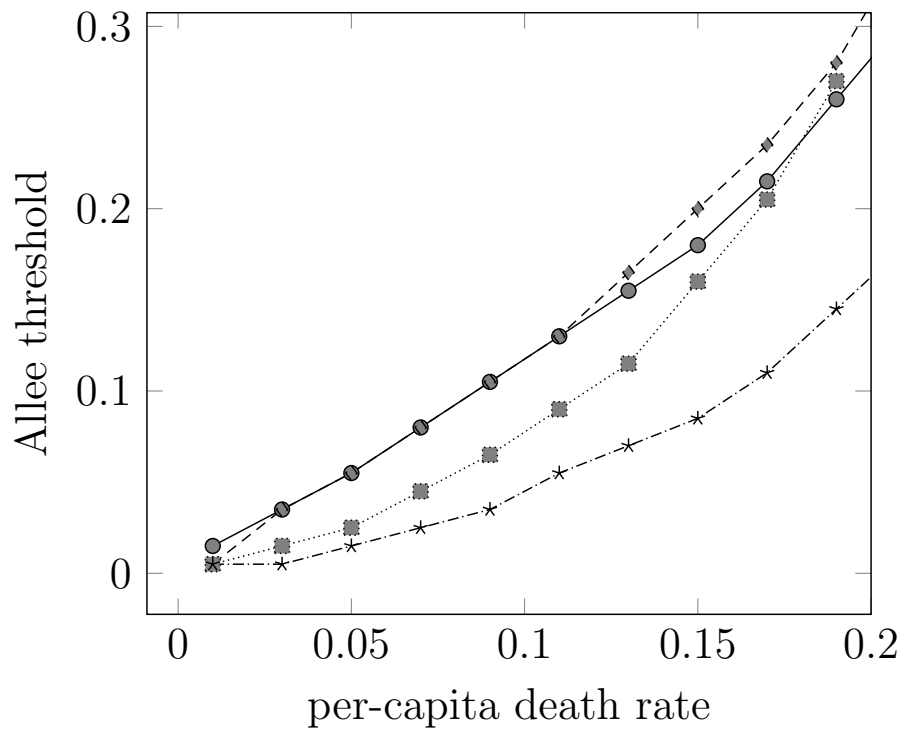


Figure A1: Pair correlation function  $g(r)$  describing local spatial density of individuals relative to mean-field density with increasing distance  $r$  (measured in grid squares) in the individual based models; it is defined as  $g(r) = \frac{\lambda}{2\pi r} \frac{dK(r)}{dr}$  based on Ripley's  $K(r)$  function (Ripley, 1977). Symbols indicate empirical values obtained from simulations; lines as Fig. 2. Circles with solid lines: mean-field approximation (long-range dispersal and mating). Diamonds with dashed lines: short-range dispersal, long-range mating (e.g. *Abies alba*). Squares with dotted lines: short-range dispersal and short-range mating (e.g. *Shorea curtisii*). Stars with dot-dashed line: clustered spatial pattern with short-range mating (e.g. *Semibalanus balanoides*).

