Research

Spatial variation in Allee effects influences patterns of range expansion

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Allee effects are thought to slow range expansion and contribute to stable range boundaries. Recent studies have shown Allee effects to vary spatiotemporally due to influences of environmental heterogeneity on population processes. Gradients in Allee effects might occur as a species' range approaches suboptimal conditions while expanding into new territory. Allee effects could exhibit patchiness if drivers of positive density dependence (e.g. mate finding rates) are influenced by habitat patchiness. However, theoretical studies have largely assumed Allee effects to be spatially constant. The goal of this study was to evaluate how spatiotemporal patterns of range expansion respond to spatial variations in Allee effects. We simulated spread in landscapes that differed in the spatial configuration and range of Allee thresholds. We compared spread with a constant Allee effect to spread in landscapes where the Allee threshold varied along a gradient or in a patchy fashion. Landscape configuration affected patterns of range expansion when Allee thresholds were near or exceeded the number of colonizing immigrants. In gradient landscapes, spread decelerated as the range edge approached higher Allee thresholds. In patchy landscapes, spread advanced quickly through areas with lower Allee thresholds and stalled in areas with higher Allee thresholds. Both focal and neighboring locations influenced spread. Spatial variation in Allee effects may be an underappreciated source of heterogeneity in patterns of range expansion. When Allee effects vary, spread estimates based on a spatially averaged Allee threshold may not accurately predict realized rates of spread. Our findings suggest that spread can occur despite generally high Allee thresholds if Allee thresholds are low in a subset of patches. This result has negative implications for controlling the spread of invasive species, but it also suggests range shifts by native species in response to climate change may be possible with even sparsely distributed refugia from Allee effects.

A rich body of theory indicates that demographic Allee effects, defined by positive correlations between population size and the per-capita population growth rate, slow rates of geographic range expansion and contribute to the formation of stable range boundaries (Lewis and Kareiva 1993, Keitt et al. 2001, Wang et al. 2002, Johnson et al. 2006). Impacts of Allee effects can be particularly dramatic when the Allee affect is strong, i.e. there is a critical population density, the Allee threshold, beneath which the population is deterministically unable to replace itself (Lewis and Kareiva 1993, Wang et al. 2002). Despite difficulties of detecting demographic Allee effects (Gregory et al. 2010), these theoretical predictions are supported by a number of empirical studies (Davis et al. 2004, Taylor et al. 2004, Tobin et al. 2007, Lynch et al. 2014). There is also growing evidence that Allee effects may vary in time and space (Angulo et al. 2007, Tobin et al. 2007, Kramer and Drake 2010, Kramer et al. 2011, Walter et al. 2015), yet theoretical studies have largely considered Allee effects to be constant. The present study investigates how spatial variability in Allee effects influences patterns of range expansion using a theoretical model simulated on different Allee effect landscapes.

Spatial variation in Allee effects may often be attributable to spatial heterogeneity in environmental conditions that influence the biotic processes producing Allee effects. For example, Kramer et al. (2009) experimentally demonstrated that the presence of a type-II predator can produce a demographic Allee effect, and used a model to predict how the presence of refugia could alter the Allee threshold of the prey population. In addition, Walter et al. (2015) found that effects of topography on temperature produced spatial variability in reproductive asynchrony in the gypsy moth, leading to variation in an Allee effect driven by reduced mating success in low-density populations. These studies highlight two mechanisms of Allee effects – failure to satiate predators and mating failure, respectively – but known causes of Allee effects also include inbreeding depression and breakdown of cooperative behaviors such as for defense or feeding (Kramer et al. 2009).

Because environmental and biotic conditions vary across real-world landscapes, it is simplistic to treat Allee effects as constant through space when investigating range boundary dynamics. This should apply to both exotic invaders and species that are shifting their range in response to climate

change or other environmental perturbations. Given evidence of strong influences of Allee effects on spread (Keitt et al. 2001, Taylor and Hastings 2005, Johnson et al. 2006), it is likely that spatial variation in Allee effects shapes fine-scale patterns of range dynamics. However, it is not known how Allee effects in neighboring sites affect spread into or out of a focal site. Additionally, at coarser spatial scales, a constant Allee effect could be viewed as the average of a spatially-varying Allee effect, but it is unclear whether knowing the average Allee effect is sufficient to understand larger-scale patterns of invasion, or whether the presence of spatial variation alters large-scale range boundary dynamics.

We assumed that Allee effects in nature will vary gradually through space along certain environmental gradients (e.g. climate), and also vary in response to habitat patchiness. Gradients in Allee effects could result if, for example, there are elevational or latitudinal gradients in mating success (Rhainds and Fagan 2010, Lynch et al. 2014, Walter et al. 2015), predation pressure (McKinnon et al. 2010), or other biotic interactions (Schemske et al. 2009). Other types of landscape heterogeneity, such as variation in habitat type, often display patchiness, and the spatial scale of habitat patchiness – relative to the scale of dispersal – may impact habitat occupancy (Hanski et al. 1994) and rates of movement (With and Crist 1995) of a focal species as well as its natural enemies (Yahner and Smith 1991, Cronin and Reeve 2014). Hence, habitat patchiness plays an important role in mediating ecological interactions, such as predation (Bernstein et al. 1988), that impact Allee effects.

To explore how spatial variability in Allee effects impacts spatiotemporal patterns of range expansion, we applied a theoretical model to simulate population spread in landscapes that differed in their spatial configuration and the range of Allee thresholds present on the landscape. Within a range of Allee thresholds, we distributed the Allee thresholds in different ways reflecting gradients and patchiness in Allee effects. We assessed the results of changing the spatial configuration of Allee thresholds, and whether effects of landscape configuration on spread are mediated by the range of Allee thresholds present. We show that, when Allee effects vary spatially, an average Allee threshold may over-predict or under-predict actual rates of spread, depending on the magnitude of the Allee threshold relative to the flux of immigrants to uncolonized sites. In addition, our results suggest that a small number of sites with low Allee thresholds in a landscape with generally high Allee thresholds can facilitate spread.

Methods

The population model

We examined effects of spatial variability in Allee effects on range expansion using a discrete-time logistic growth population model (Gregory et al. 2010), extended in two dimensions of discrete space:

$$N(t)_{x,y} = N(t-1)_{x,y} \exp\left[r\left(1 - \frac{N(t-1)_{x,y}}{K} \right)\left(\frac{N(t-1)_{x,y} - A_{x,y}}{N(t-1)_{x,y}} \right) \right]$$

$$+ S(t)_{x,y} + L(t)_{x,y} \qquad (1)$$

Here, the population size N at location x, y on a two-dimensional coordinate plane, at time t, depends on the population size $N_{x,y}$ at time $t - 1$, the intrinsic rate of population growth (r), the carrying capacity K, the Allee effect parameter $A_{x,y}$, and the net contributions of short-distance $[S(t)_{x,y}]$ and long-distance $[L(t)_{x,y}]$ dispersal. The Allee parameter $A_{x,y}$ sets the Allee threshold, but also affects the rate at which increases in the population density translate to increases in the rate of population growth (i.e. the slope of the population density-growth rate relationship). As increasing A raises the Allee threshold, increasing A also lowers the maximum per-capita population growth rate realized by the population and reduces the slope of the density-growth rate relationship.

Short-distance dispersal occurred stochastically with probability p_s by distributing $f_s N(t)_{x,y}$ immigrants evenly among the 8 adjacent grid cells (i.e. queen adjacency), where f_s is a proportion of the source population. Long-distance dispersal occurred stochastically with probability p_l by transporting $f_l N(t)_{x,y}$ immigrants from source cell x, y to a new grid cell. However, in this case the displacements of dispersers in the x and y directions were determined by independently drawing values from a Gaussian distribution having zero mean and variance d_l, controlling the scale of long-distance dispersal. That is, for every patch x, y, a long-distance dispersal event of $f_l N(t)_{x,y}$ individuals occurred with probability p_l to patch $x + m, y + n$ where $m \sim$ Gaussian$(0, d_l)$ and $n \sim$ Gaussian$(0, d_l)$.

We included both short and long-distance dispersal processes to simulate stratified diffusion, which is likely to be a feature of range expansion for many species and can strongly influence patterns of spread (Shigesada et al. 1995, Shigesada and Kawasaki 1997). We assume that the likelihood of a long-distance dispersal event occurring does not change with population density, but that the number of dispersers increases with the density of the source populations. We further assume that all long-distance emigrants from a source population in a given time step move to only one location. This design approximates accidental transport by humans, a common component of biological invasions (Suarez et al. 2001, Johnson et al. 2006, Muirhead et al. 2006). We model short-distance dispersal by transporting a fraction of the source population to a neighboring cell, which assumes an abrupt distance-decay in dispersal rather than a gradual decay. Similar representations of dispersal are not uncommon among other models representing space on a discrete grid (Allstadt et al. 2009, Ferreira et al. 2014). We also assume that short-distance dispersal is probabilistic (rather than occurring deterministically at every time step for every source population) to minimize computational requirements.

Landscapes and simulation design

To investigate how spatial variation in Allee effects influences spread patterns, we applied the population model in simulated landscapes where the Allee threshold, A, took on 5 spatial patterns: increasing linear gradient, fine patches, coarse patches, random, and constant (no variation). We also explored how the range of Allee thresholds on the landscape affect spread patterns by considering landscapes

with 'low' ($0 \leq A \leq 5$), 'medium' ($2.5 \leq A \leq 7.5$), and 'high' ($5 \leq A \leq 10$) Allee thresholds, and 'high variability' in the Allee threshold ($0 \leq A \leq 10$). A fully factorial design was employed, in which we tested all 5 spatial configurations at each Allee parameter level. We demonstrate the impact of spatial patterns in A on spread patterns by comparing invasion development through space and time using a combination of visualizations and quantitative tools. Additionally, we assessed how population establishment in a focal cell was affected by Allee effects in nearby locations.

All landscapes were 40×100 arrays of grid cells, with spread occurring from left to right along the longer (100 cell) axis. In gradient landscapes, A increased linearly from the beginning to the end of the landscape. In random landscapes, the values of A for individual grid cells were independently drawn from a uniform distribution. Although random, uncorrelated variation in Allee effects is unlikely to occur in nature, randomly generated landscapes without autocorrelation in habitat type provide null models for investigating the effects of landscape patchiness on ecological processes (With and Crist 1995). Patchy landscapes were constructed by assigning random A values from a uniform distribution to n × n square blocks of grid cells. We used n = 2 to create fine patches and n = 4 to create coarse patches. While simple, this method simulated two important features of real landscapes: sharp discontinuities in A, which might occur at edges between suitable and unsuitable habitats, and contiguous zones having similar values of A. Local variability in A was created in our patchy landscapes by adding Gaussian noise ($\mu = 0$, $\sigma = 1$) to individual grid cells. This allowed us to analyze the effects of local vs neighborhood-level variations in A. After adding random noise, any values of A beyond the specified range (e.g. $0 \leq A \leq 5$ for low A landscapes) were constrained to the minimum or maximum for that scenario, as appropriate.

Spread in landscapes with spatially varying Allee effects was compared to spread with constant Allee effects, where levels of A match the median of the ranges over which A was specified to vary in different scenarios. Spatially constant Allee landscapes took the values $A = 2.5$, 5.0, and 7.5 which, respectively, correspond to the low, medium and high-variability, and high Allee threshold scenarios for spatially varying landscapes. The medium ($2.5 \leq A \leq 7.5$) and high variability ($0 \leq A \leq 10$) scenarios each have a median of 5.0 to assess whether varying A over a wider range effects spread independent of the median strength of the Allee effect.

To isolate the effect of varying A, the values of all other model parameters remained constant throughout each simulation. We began with simulations where the intrinsic rate of population growth $r = 1$, the carrying capacity $K = 100$, the probability of short-distance dispersal $p_s = 0.2$, the fraction of the source population moving via short-distance dispersal $f_s = 0.1$, the probability of long-distance dispersal $p_l = 0.05$, the fraction of the source population transported by long-distance dispersal $f_l = 0.1$, and the scale of long-distance dispersal $d_l = 10$. This parameter set was selected to be within a range of reasonable values for a variety of organisms. We investigated the sensitivity of our model results to variability in each parameter by running simulations in which one parameter at a time was assigned a value higher or lower than the main value (Table 1). We also considered the effects of

Table 1. Parameter values used in the main simulations and sensitivity analyses.

Parameter		Low	Main	High
r	Intrinsic rate of population growth	0.5	1	2
K	Carrying capacity	50	100	200
p_s	Short distance dispersal probability	0.1	0.2	0.4
f_s	Fraction dispersing short distance	0.05	0.1	0.2
p_l	Long distance dispersal probability	0	0.05	0.1
f_l	Fraction dispersing long distance	0.05	0.1	0.2
d_l	Scale of long distance dispersal	5	10	20

demographic stochasticity on spread patterns, but this did not qualitatively affect our findings and so we focus on results from the model with deterministic population growth (Supplementary material Appendix 1).

Simulations were initialized with all grid cells in the column $x = 1$ having 15 individuals. Initial population sizes were larger than any Allee threshold because we were not interested in situations in which the population would go extinct in the arena. Simulations were run for up to 200 time steps, with spread in the x direction measured by fitting a cubic spline to the mean population density in each column x; the range boundary was determined as the right-most column x where the average density was ≥ 5 individuals. We ran 50 replicate simulations for each combination of landscape configuration, range of the Allee parameter, and population/dispersal parameter. For the random, fine, and coarse landscapes, a new landscape was randomly generated for each replicate.

A combination of tools were used to visualize and quantitatively describe how spatial variation in Allee effects influenced spread. We mapped 'snapshots' of the population distribution throughout a simulation replicate, and we plotted mean spread trajectories to show how landscape configuration affects range expansion on average. We also examined two kinds of variations from mean spread patterns: temporal fluctuations (within-replicate) in the range boundary, and between-replicate variations in the overall rate of spread. The former indicates the magnitude of within-simulation deviations from the mean spread rate (i.e. pulses of advance or retreat of the range boundary). The latter indicates how strongly specific landscape configurations within a model scenario affects rates of spread. Temporal fluctuations were quantified by taking the standard deviation (SD) of spread deviations, after removing the trend for the range to expand over time. Variations in the overall rate of spread were quantified using the coefficient of variation (CV) of spread rates within a group of replicate simulations. See Supplementary material Appendix 1 for additional details on quantifying spread variations.

We assessed the sensitivity of spread rates to model parameters with the goal of evaluating how altering demographic and dispersal parameters influences the spread rate, and to investigate whether landscape spatial configuration or Allee threshold range affect how changing these parameters influence the spread rate. Sensitivity of spread rates to model parameters was assessed in two ways. In scenarios with the constant, random, fine, and coarse landscapes, we measured the percent difference in the mean spread rate, relative to the mean spread rate obtained from simulations using the

main parameter set. In gradient landscapes, spread tended to decelerate as the range boundary advanced, making differences in the mean spread rate less well suited to representing how altering demographic and dispersal parameters affects spread. For the gradient landscapes, we instead plot the mean position of the invasion front over time because this does not obscure the non-linear spread pattern.

We assessed the influence of local and neighborhood average Allee thresholds on spread patterns using the random, fine, and coarse landscapes. We ask 1) whether local and neighborhood measures of Allee effects predict establishment time, and 2) does this change with landscape configuration or the range of Allee parameters. We defined the time at which the population in cell x, y became established as when the density exceeded one half of the carrying capacity (i.e. $N_{x,y} \geq K/2$). We then used generalized linear models to quantify effects on establishment time of the local Allee threshold, $A_{x,y}$, the neighborhood mean Allee threshold within the nearest 8 grid cells, A_{nb8}, and the neighborhood mean Allee threshold within the nearest 24 grid cells, A_{nb24}. Cell column (x) was included as a covariate to account for spread from left to right; thus, our analyses effectively quantify how $A_{x,y}$, A_{nb8}, and A_{nb24} affect deviations from the mean spread rate. Considering in particular spatial non-independence of our predictor variables, we tested for colinearity among predictor variables and for residual spatial autocorrelation. Based on preliminary analyses indicating high colinearity, we did not consider models containing interaction terms, or both neighborhood scales. Thus, we compared six models: 1) $t_{est} = \beta_0 + \beta_1(x)$; 2) $t_{est} = \beta_0 + \beta_1(x) + \beta_2(A_{x,y})$; 3) $t_{est} = \beta_0 + \beta_1(x) + \beta_2(A_{nb8})$; 4) $t_{est} = \beta_0 + \beta_1(x) + \beta_2(A_{nb24})$; 5) $t_{est} = \beta_0 + \beta_1(x) + \beta_2(A_{x,y}) + \beta_3(A_{nb8})$; and 6) $t_{est} = \beta_0 + \beta_1(x) + \beta_2(A_{x,y}) + \beta_3(A_{nb24})$. Here, t_{est} indicates establishment time, β_n indicate regression coefficients, and x indicates cell column. The mean variance inflation factors for all terms in the candidate models were < 0.4. The mean Moran's I of model residuals was ≤ 0.05 across landscape configurations and Allee threshold ranges.

Model performance was assessed using bias-corrected Akaike's information criterion (AICc) and Akaike weights, which signify the probability that a model is the best in a group of candidate models. Raw AICc values are not suitable for comparing statistical models that explain different observations, but Akaike weights can be used to ask which model(s) – relative to the other candidate models in the set – best explain spatiotemporal establishment patterns, and how the relative information content of a candidate model changes with the spatial configuration and range of Allee thresholds on a landscape. Mean ($\pm$ SD) regression coefficients were used to determine the direction and strength of individual effects. All simulations and analyses were conducted in R (R Core Team).

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.32q7v > (Walter et al. 2016).

Results

Periodic 'snapshots' from individual simulations, showing the population distribution in both spatial dimensions at a given time, indicated a response of spatiotemporal patterns of range expansion to variations in the Allee threshold. In landscapes with variability in the Allee threshold A, earlier colonization and higher population densities corresponded to areas with lower Allee thresholds. For example, the population distribution in the coarse landscape is itself patchy, especially near the invasion front, which contrasts the relatively even population distribution when the landscape had a constant Allee effect (Fig. 1). Spread 'snapshots' for other landscape configurations can be found in Supplementary material Appendix 3.

Taking replicate simulations as a group, increasing the Allee parameter slowed mean rates of spread (Table 2, Fig. 2). In low Allee threshold landscapes, spread was up to 58% faster when the Allee effect varied versus when it was constant ($A = 2.5$). In medium Allee threshold landscapes ($2.5 \leq A \leq 7.5$), the mean rate of spread was up to 7% faster when the Allee effect varied (Table 2). In high Allee threshold landscapes ($5 \leq A \leq 10$), the mean rate of spread was minimally ($< 3\%$) faster in the gradient than the constant landscape, but was up to 11% slower in patchy landscapes. Spread was up to 65% faster in the high variability landscapes ($0 \leq A \leq 10$) than when the Allee threshold was constant. In the low and high variability landscapes, the rate of spread increased as the scale of patchiness increased, but this effect was not consistent in the medium and high Allee threshold landscapes (Table 2). In gradient landscapes, spread decelerated as the range boundary advanced through the landscape; this effect was strongest in the low Allee threshold and high variability landscapes (Fig. 2). Variability in the overall rate of spread did not appear to be affected by landscape configuration, but increasing the Allee parameter tended to reduce variations in the overall rate of spread (Table 2).

Temporal fluctuations in spread (pulses of advance and retreat of the range boundary within replicate simulations) were influenced by landscape configuration and the level of Allee thresholds on the landscape. The gradient landscapes followed a different pattern from the random, fine, and coarse landscapes (Table 3). In the gradient landscapes, temporal fluctuations in spread were less than in a constant Allee landscape, and temporal fluctuations increased from the low to medium to high Allee scenarios, although the high variability gradient landscape exhibited the least degree of temporal variation in spread (Table 3). In random, fine, and coarse landscapes, range boundary fluctuations tended to be larger than in comparable constant Allee effect landscapes when the Allee threshold was low. In the low Allee and high variability scenarios, range boundary fluctuations tended to increase with the scale of patchiness (Table 3). By contrast, in patchy landscapes with medium and high Allee thresholds, spread fluctuations were similar to those with a constant Allee threshold, and tended to decrease with increases in the scale of patchiness (Table 3).

Sensitivity analyses suggest that patterns of spread were most strongly affected by the parameters determining the carrying capacity (K), and long-distance dispersal (p_l, f_l, and d_l). Spread patterns were affected to a lesser degree by the intrinsic rate of population growth (r) and parameters controlling short-distance dispersal (p_s, f_s). The effect of population parameters on spread patterns was affected by landscape spatial configuration (Fig. 3–4). For example, in
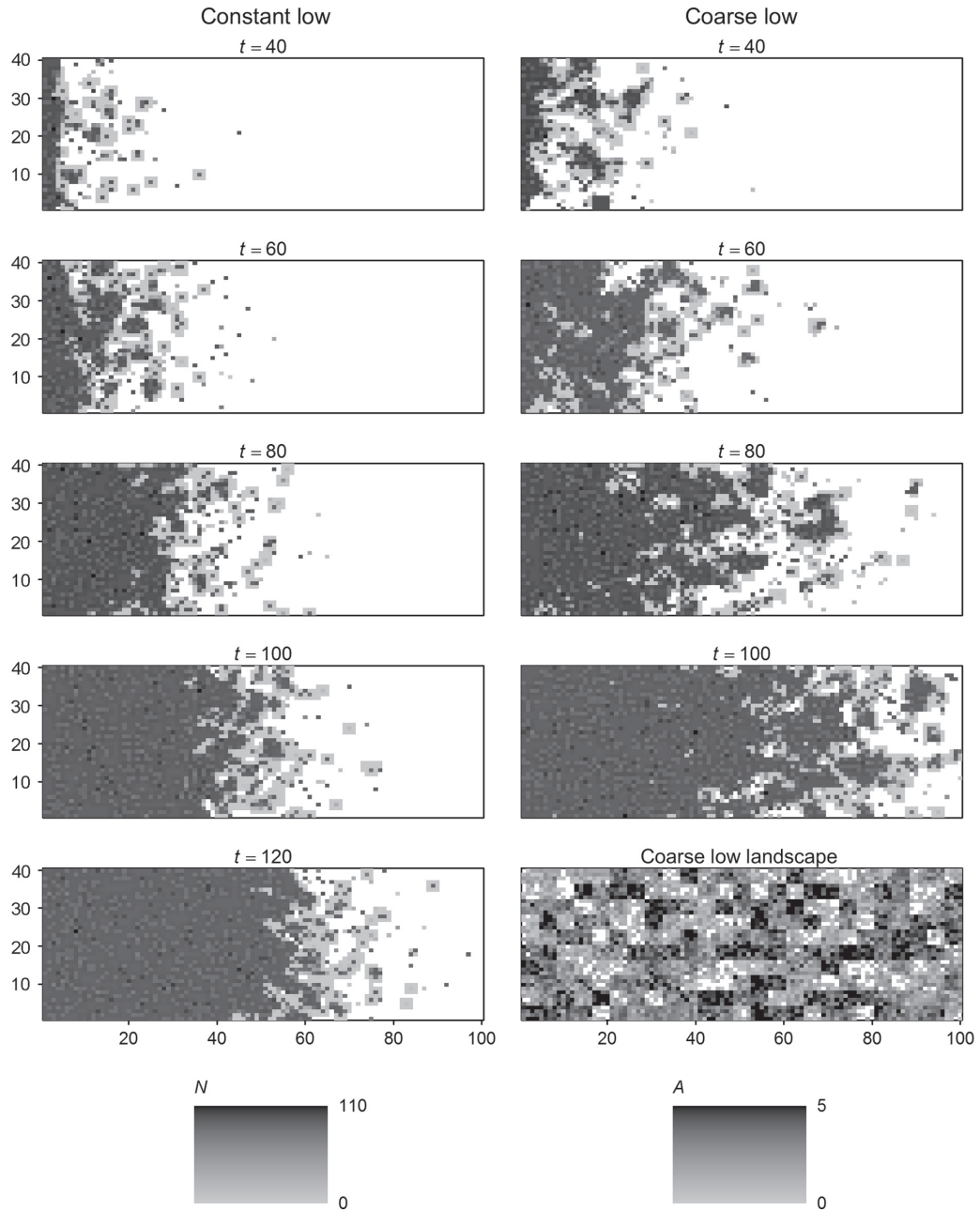
Figure 1. Spread 'snapshots' for landscapes with (left) constant $A = 2.5$ and (right) coarse patches with low Allee thresholds ($0 \leq A \leq 5$). Darker grey indicates higher population density. The configuration of the patchy coarse landscape is shown in the bottom right; here, darker grey indicates higher Allee thresholds. Spread snapshots for other landscape types can be found in Supplementary material Appendix 3.

the highly variable ($0 \leq A \leq 10$) gradient landscapes, spread decelerated dramatically when K and f_l are low (Fig. 4). The range of Allee thresholds also affected the sensitivity of spread

patterns to changing demographic and dispersal parameters. For example, in all landscape configurations, when $0 \leq A \leq 5$ (low Allee thresholds), spread was slowest when $p_l = 0$ (no

Table 2. Mean $\pm$ CV (n = 50) spread rates for landscapes varying in spatial configuration and Allee parameter range.

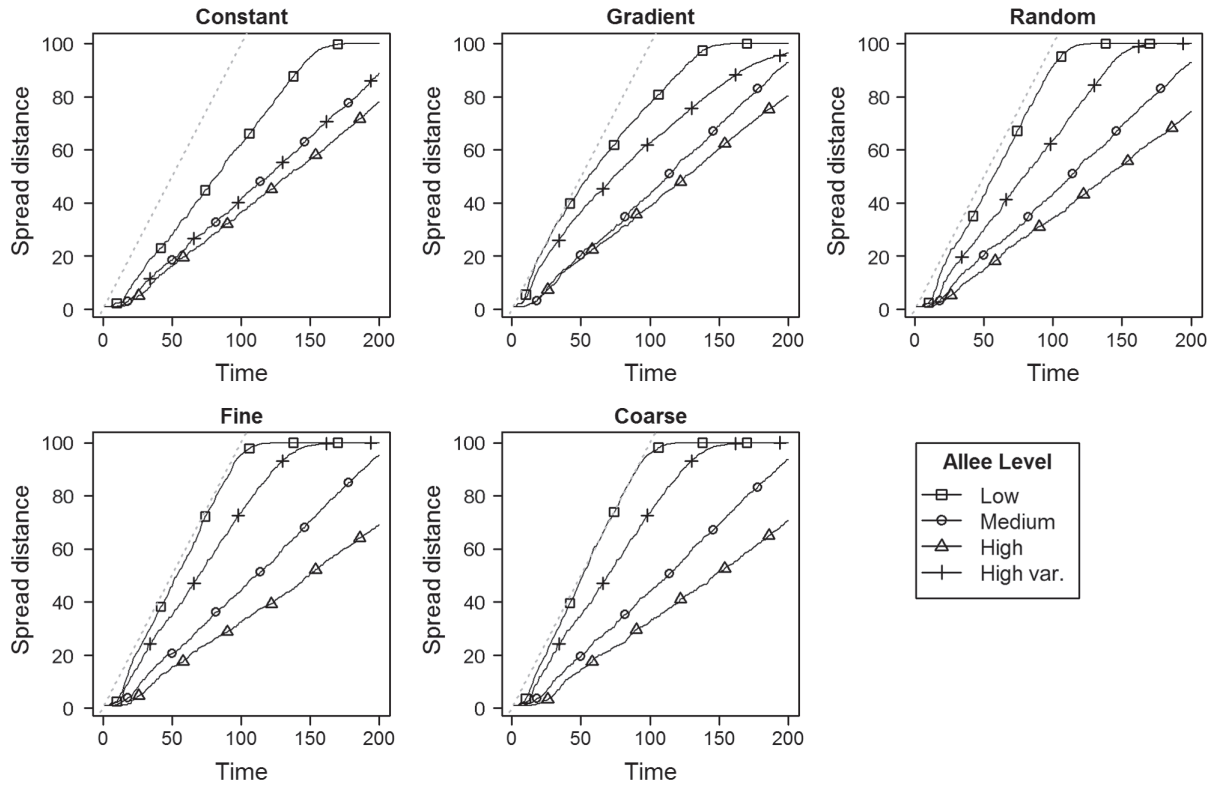| Configuration	Allee parameter range			
	Low	Medium	High	High var.
Constant	0.635 ± 0.076	0.447 ± 0.082	0.391 ± 0.097	–
Gradient	0.699 ± 0.067	0.479 ± 0.067	0.402 ± 0.057	0.482 ± 0.011
Random	0.903 ± 0.094	0.471 ± 0.077	0.373 ± 0.083	0.649 ± 0.088
Fine	0.964 ± 0.112	0.480 ± 0.049	0.347 ± 0.072	0.715 ± 0.105
Coarse	1.005 ± 0.144	0.472 ± 0.064	0.354 ± 0.093	0.739 ± 0.132

Figure 2. Mean trajectories for spread into landscapes with different spatial configurations and levels of Allee effects. The apparent slowing in the rate of spread as the invasion approached the end of the landscape ($y = 100$) is an artifact resulting from replicates that already reached the end of the landscape having nowhere further to spread. For reference, the dashed grey lines represent a spread rate of 1 grid cell per time step.

long-distance dispersal), but when $2.5 \leq A \leq 7.5$ (medium Allee thresholds), spread was slowest when $K = 50$ (low carrying capacity). In the sensitivity analyses, there were few differences between the medium and high variability scenarios; a notable exception is that sensitivity to K was greater in medium that high variability landscapes with fine and coarse spatial configurations.

Regression analyses indicated that both local and neighborhood Allee effects influence spread, and that the strength of these effects depends on spatial configuration and Allee thresholds. In nearly all scenarios, adding effects of neighborhood Allee parameters to those of local Allee effects improved the mean AICc value and Akaike weight, but the top model differed by landscape spatial structure and Allee threshold level (Table 4). As evidenced by the R^2 values and

Table 3. Temporal range boundary fluctuations were quantified by taking the standard deviation (SD) of deviations from the mean spread pattern; reported are SD of spread deviations, averaged over $n = 50$ replicates. See Supplementary material Appendix 1 for details.

	Allee parameter range			
Configuration	Low	Medium	High	High var.
Constant	3.422	3.155	3.303	–
Gradient	2.484	2.718	2.810	2.131
Random	4.145	3.295	3.254	3.815
Fine	4.359	3.228	3.193	4.585
Coarse	4.375	3.063	3.178	4.505

Akaike weights of the top models, spatiotemporal patterns of establishment were more difficult to predict in the medium and high Allee threshold landscapes. Increasing local Allee parameters ($A_{x, y}$) caused establishment time to increase, and increasing neighborhood Allee parameters (A_{nb8}, A_{nb24}) also tended to cause increases in establishment time, but regression coefficients on A_{nb8} and A_{nb24} were highly variable (Table 4).

Discussion

This study demonstrates the potential for spatial variations in Allee effects to influence spatiotemporal patterns of range expansion. Consistent with many studies (Keitt et al. 2001, Wang and Kot 2001, Wang et al. 2002), increasing the Allee parameter slowed the mean rate of spread. These and other studies, however, represented Allee effects using a constant value and our findings, motivated by growing recognition of spatiotemporal variability in Allee effects (Tobin et al. 2007, Kramer and Drake 2010, Kramer et al. 2011, Walter et al. 2015), add nuance to predictions of range expansion in heterogeneous landscapes. We found that spatial variations in Allee effects, and the structure of the variation, can drive deviations from predictions generated assuming a spatially constant Allee effect (Table 2, Fig. 2), induce fluctuations in the location of the range boundary (Table 3), and lead to deceleration of range expansion when there are increasing gradients in the Allee threshold (Fig. 2, 4). We also found
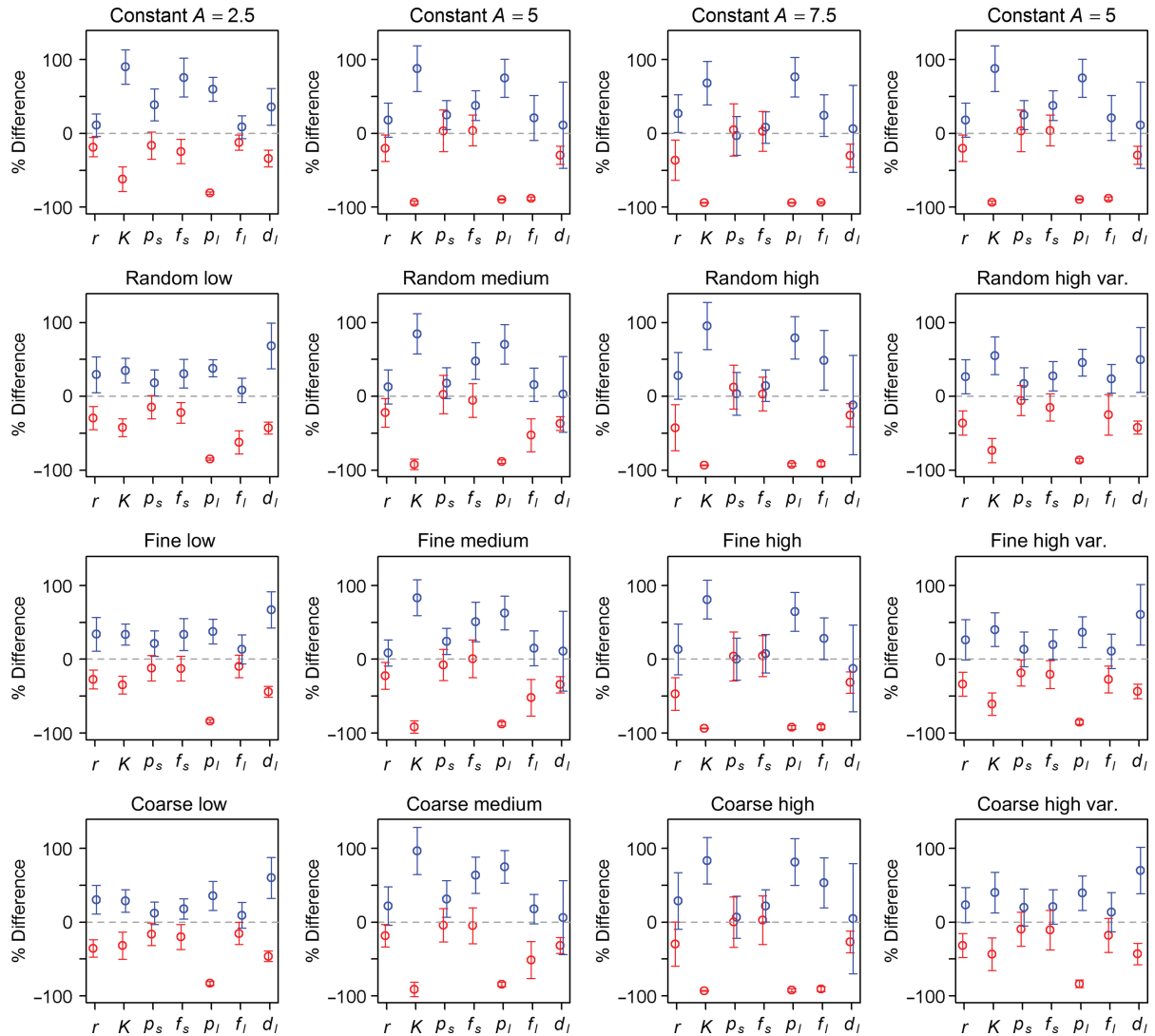
Figure 3. In the constant, random, fine, and coarse landscape configurations, sensitivity to model parameters was assessed by plotting the % difference in the spread rate relative to the main parameter set. Each model parameter took a value higher (blue symbols) and lower (red symbols) than the main value. Parameter values are listed in Table 1.

that the neighborhood of Allee effects influences population establishment in a focal patch (Table 4). Hence, variations in Allee effects may be an underappreciated source of variability in patterns of range expansion.

Whether or not spatial patterns of Allee effects influence spread appeared to depend on the magnitude of Allee thresholds relative to the number of dispersers. Variability in A had the greatest influence on spread in low ($0 \leq A \leq 5$) and high variability ($0 \leq A \leq 10$) landscapes (Table 2), in which the Allee threshold varied such that some locations had Allee thresholds that were less than the typical number of immigrants, and some locations had higher Allee thresholds. For the main parameter set, a population at carrying capacity yielded 1.25 short-distance immigrants and 10 long-distance immigrants to each recipient location. In medium and high Allee landscapes, the Allee threshold provided a consistent barrier to population establishment via short-distance dispersal; as a result, spread was driven mainly by stochastic long-distance dispersal events and

responded little to landscape spatial configuration. Graphical depictions of range expansion through time showing little apparent effect of spatial configuration in Allee effects on spatiotemporal patterns of spread in the medium and high Allee landscapes (Fig. 2, Supplementary material Appendix 3) are corroborated by the reduced information content and predictive power of statistical models explaining establishment time using local and neighborhood Allee thresholds.

We find perhaps the most dramatic evidence of this interaction between Allee threshold and dispersal in landscapes where A followed an increasing gradient (Fig. 2, 4). This configuration interested us because of evidence of elevational and latitudinal trends in factors that could give rise to Allee effects (Schemske et al. 2009, McKinnon et al. 2010, Rhainds and Fagan 2010, Walter et al. 2015). When the Allee parameter took values both less than and greater than the number of dispersers (low and high variability scenarios), spread decelerated along increasing linear gradients in A (Fig. 2, 4). When K or f_b, which jointly determine the number
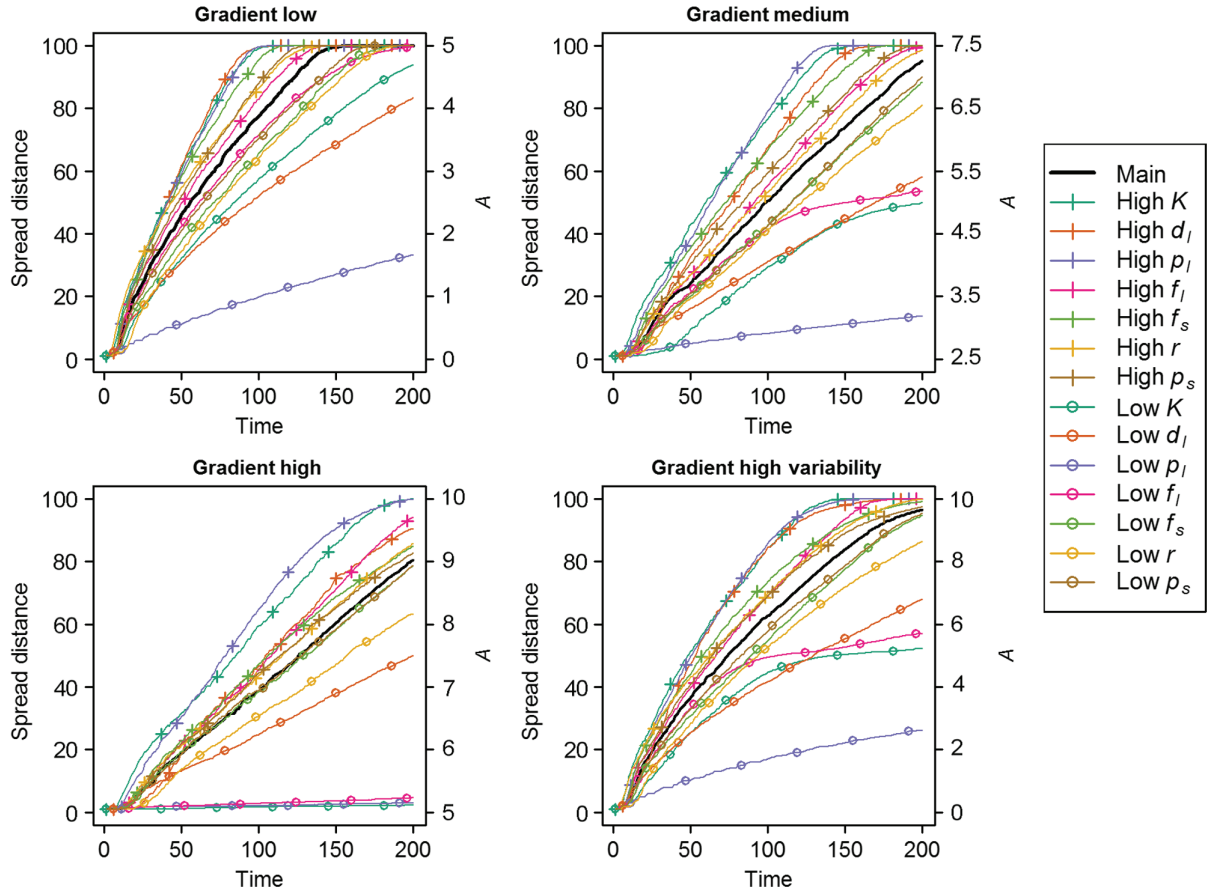
Figure 4. Mean spread trajectories showing sensitivity to model parameters for gradient landscapes. For reference, the right-hand y-axis indicates values of the Allee threshold.

of long-distance emigrants from a source population, were reduced, the rate of spread was particularly slow when $A \geq 5$ (Fig. 4), causing rapid deceleration in the medium and high variability landscapes. The Allee threshold of 5 was significant because this was also the number of long-distance emigrants from a source population at its carrying capacity when K or f_l are reduced. Hence, groups of immigrants colonizing an empty site failed to become established increasingly often, leading to substantially slowed spread.

Patchiness in Allee effects, given relatively high Allee thresholds, was also shown to induce spatiotemporal variability in spread patterns. Here, our random, fine, and coarse landscapes are all characterized by patchiness, but differ in the scale of patchiness. 'Snapshots' of spread in patchy landscapes show invasion patterns responding to the configuration of the Allee landscape (Fig. 1, Supplementary material Appendix 2), and range boundary fluctuations were greatest in these landscapes (Table 3). Similar to effects

Table 4. Summary of best-performing models predicting establishment time based on local ($A_{x, y}$) and neighborhood (A_{nb8} or A_{nb24}) Allee parameters, while controlling for distance from the left edge of the landscape (x). Missing values indicate that parameter was not included in the best-performing model. We report mean ± SD parameter values (n = 50) and the mean Akaike model weight for the top model, signifying the probability that the selected model is the best in the group.

Landscape	x	$A_{x, y}$	A_{nb8}	A_{nb24}	$\overline{W_{AIC}}$	$\overline{R^2_{adj}}$
Random low	0.927 ± 0.101	3.227 ± 0.153	2.876 ± 0.735	–	0.783	0.780
Random medium	1.517 ± 0.148	3.345 ± 0.335	–	1.640 ± 3.805	0.367	0.574
Random high	1.194 ± 0.153	1.091 ± 0.736	–	0.791 ± 5.526	0.265	0.222
Random high var.	1.125 ± 0.123	3.461 ± 0.256	1.933 ± 0.641	–	0.655	0.613
Fine low	0.864 ± 0.107	2.973 ± 0.219	3.142 ± 0.790	–	0.648	0.757
Fine medium	1.507 ± 0.113	3.584 ± 0.403	–	2.324 ± 1.883	0.423	0.600
Fine high	1.307 ± 0.147	1.642 ± 0.639	–	1.227 ± 3.858	0.270	0.227
Fine high var.	0.989 ± 0.146	3.564 ± 0.639	–	1.681 ± 0.829	0.544	0.583
Coarse low	0.826 ± 0.124	2.924 ± 0.233	2.933 ± 0.578	–	0.569	0.743
Coarse medium	1.534 ± 0.117	3.396 ± 0.489	–	2.128 ± 1.750	0.530	0.607
Coarse high	1.281 ± 0.159	2.003 ± 0.924	–	–	0.300	0.224
Coarse high. var.	0.995 ± 0.147	3.237 ± 0.452	–	1.791 ± 0.762	0.583	0.595

of habitat fragmentation (Dewhirst and Lutscher 2009, Kinezaki et al. 2010), spread may be stalled by encountering areas where local environmental conditions lead to high Allee thresholds or enhanced where local environmental conditions support rapid growth of nascent populations, and the effect is likely to be particularly dramatic when the scale of patchiness is large relative to the dispersal capabilities of the organism. For example, a rare long-distance dispersal event may be necessary to cross a region with uniformly high Allee thresholds.

The establishment of nascent, low-density populations may be affected by demographic stochasticity in addition to Allee effects (Lande 1998, Potapov and Rajakaruna 2013, Roth and Schreiber 2014). Our finding that demographic stochasticity tended to increase rates of spread (Supplementary material Appendix 1) suggests that demographic stochasticity sometimes allowed nascent populations formed by immigration to exceed the Allee threshold and become established that would not otherwise (Potapov and Rajakaruna 2013). This raises the question of whether stochastic temporal variability in the strength of Allee effects might favor spread into areas where the Allee effect typically prevents population establishment.

Spatial variability in Allee effects combined with dispersal raises the possibility that range expansion may be affected not only by local Allee effects, but also by Allee effects in the surrounding landscape. We found support for this hypothesis in our regression analyses, in which local establishment times were influenced by both local Allee effects and those in neighboring patches, but local Allee thresholds were more important than those at regional scales (Table 4). Neighboring patches likely affect establishment in a focal patch because, for example, weaker Allee effects in the surrounding landscape would facilitate the establishment of populations that would act as sources of immigrants into a focal patch. However, neighborhood effects may be strongly context-dependent given their high degree of variability (Table 4). Additionally, the importance of local Allee effects suggests that, even if a low-*A* site is surrounded by high-*A* sites, the low-*A* site can become established and facilitate further spread, provided immigrants can reach it.

We observed interactive effects of variability in *A* and median *A* on the mean rate of spread, (Table 2, Fig. 2), which we attribute to non-linear population growth around an Allee threshold, and its effects on establishment (Lewis and Kareiva 1993, Keitt et al. 2001). When the median Allee parameter was low, spread was faster when the Allee parameter varied than when it remained constant, probably because patches with very low Allee thresholds allowed populations to establish and grow rapidly (Table 2). In contrast, in high Allee threshold landscapes, spread was mainly slower when the Allee threshold varied than when it remained constant, likely because Allee thresholds in most patches were high relative to the number of immigrants. These findings imply that spread rates predicted using an average Allee threshold may under-predict or over-predict actual rates of spread, depending on the mean and degree of spatial variability in Allee thresholds.

In summary, our results indicate that spatial variability in Allee effects can influence patterns of range expansion. Impacts of spatial patterns in Allee effects on spread may be driven largely by an interaction between the Allee threshold and the number of immigrants arriving by long-distance dispersal. One important implication is that isolated patches favoring the growth of low-density populations (low Allee thresholds), provided they are large enough in area (Vercken et al. 2011), could act as stepping stones facilitating range expansion through regions otherwise dominated by stronger Allee effects. In an applied context, this could pose a challenge to efforts to restrict the spread of invasive species, but could also be a boon to those seeking to assist northward or upslope migrations of species (e.g. in light of climate change) through maintenance of a small number of very good habitat patches. Although geographical variations in Allee effects have currently been detected in only a few taxa, the commonness of spatial environmental heterogeneity makes it rather likely that spatially varying Allee effects are ubiquitous. A more thorough understanding of Allee effects has been hampered by difficulties of studying the low-density populations in which they occur. We suggest that observing patterns of range dynamics such as we have highlighted here could provide indirect evidence for Allee effects in spreading populations and lead to testable hypotheses regarding their underlying mechanisms.

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Supplementary material (Appendix ECOG-01951 at <www.ecography.org/appendix/ecog-01951>). Appendix 1–3.