

Allee Effects, Invasion Pinning, and Species' Borders

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Submitted August 18, 1999; Accepted September 21, 2000

ABSTRACT: All species' ranges are the result of successful past invasions. Thus, models of species' invasions and their failure can provide insight into the formation of a species' geographic range. Here, we study the properties of invasion models when a species cannot persist below a critical population density known as an "Allee threshold." In both spatially continuous reaction-diffusion models and spatially discrete coupled ordinary-differential-equation models, the Allee effect can cause an invasion to fail. In patchy landscapes (with dynamics described by the spatially discrete model), range limits caused by propagation failure (pinning) are stable over a wide range of parameters, whereas, in an uninterrupted habitat (with dynamics described by a spatially continuous model), the zero velocity solution is structurally unstable and thus unlikely to persist in nature. We derive conditions under which invasion waves are pinned in the discrete space model and discuss their implications for spatially complex dynamics, including critical phenomena, in ecological landscapes. Our results suggest caution when interpreting abrupt range limits as stemming either from competition between species or a hard environmental limit that cannot be crossed: under a wide range of plausible ecological conditions, species' ranges may be limited by an Allee effect. Several example systems appear to fit our general model.

Keywords: Allee effects, critical phenomena, invasions, range limits, species' borders.

Understanding the factors that lead to the current distributional limits of species is a fundamental goal of eco-

logical biogeography. Most discussions concerning species' borders focus on the role of broadscale gradients or interspecific interactions. A largely unaddressed question is, Can stable range limits arise in the absence of clear environmental gradients in abiotic or biotic conditions? In this article, we will show that, for species with strong Allee effects, a range may be both stable against contraction and prevented from expansion, even in the absence of any broadscale environmental gradient, as long as there exists some form of fine-scale heterogeneity or patchiness in the environment. Propagation failure owing to bistable Allee-like dynamics is generally referred to, outside ecology, as "pinning" (e.g., Fath 1998). We will argue that Allee effects can readily "pin" range limits, even without gradients, and that this phenomenon magnifies the importance of historical accidents in defining range limits.

It is useful to contrast this suggestion with more traditional approaches to range limits. Distributional limits can, of course, arise because of environmental gradients or broadscale heterogeneity that influence demographic processes (Caughley et al. 1988; Root 1988), including dispersal (Gaylord and Gaines 2000). Along a gradient, local habitat conditions may become unsuitable, such that individual populations are no longer sustained by local recruitment, either because local deaths exceed local births or because local extinction rates exceed colonization rates (Holt and Keitt 1999). When there is significant long-range dispersal, the edge of the range may extend some distance beyond the point along the gradient where birth and death rates match, forming a ring of sink populations sustained by recurrent immigration from source habitats (Holt 1983; Pulliam 1988). A primary mechanism generating a range boundary can thus be a deterioration of the environment along a gradient (from the species' perspective) as one moves from the center to the edge of the range.

Biotic interactions may also lead to a range boundary. For example, the interface between two strongly competing species can form a stable boundary (Heller and Gates 1971; Bull and Possingham 1995; Case and Taper 2000). Competition may be indirect, such as when two species limit each other's distribution by hosting pathogens or parasites that are highly virulent to the other species (Holt and Lawton 1994; Schmitz and Nudds 1994). Similarly, the

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distribution limit of a prey species will set the boundary of its predator in the absence of an alternative prey species (Hochberg and van Baalen 1998). In all three cases, the factor that limits a species' range is itself spatially delimited, and so again the realized range limit reflects real spatial heterogeneity in the circumstances facing a species.

Species' Borders as Pinned Invasions

On historical timescales, species' ranges can expand by invasion into unoccupied habitats. One way to view species' distributional limits is that they may represent points in space where invasions have halted. An invasion may halt because of broadscale environmental gradients, as noted above, or may halt, we suggest, for purely demographic reasons having nothing to do with changes in local conditions across a species range.

From a demographic standpoint, the success or failure of invasions depends crucially on the rate of population growth at small population size. Invasions succeed because individuals that disperse beyond the current range limit establish viable populations. The local density of individuals in newly colonized areas is typically low at early stages of invasion. For the species to persist locally and thereby contribute propagules to yet a further round of invasion, individuals in these local populations must reproduce at a rate that exceeds its mortality. An ability to reproduce sufficiently from very small numbers leads to a growth curve that is strictly positive for any population number greater than zero, up until the point where the local habitat is saturated and the population reaches carrying capacity. The classic example is the logistic growth curve (May 1973; Berryman 1981; Royama 1992). If the growth function is positive for all values of population size greater than zero and less than the carrying capacity, a viable population will establish in any local region receiving any propagules at all, as long as the dynamics can be assumed to be deterministic to a reasonable approximation. As a result, a species will expand its range to fill all available habitats, unless barriers to dispersal are absolute. The rate of expansion may be slowed by demographic stochasticity, disturbance events, and zones of lower dispersal rate, but eventually, in a constant environment, the range will expand to occupy all suitable habitats.

It is increasingly recognized that many species have depressed growth rates at low density (Allee 1938; Dennis 1989; Wilson and Agnew 1992; Veit and Lewis 1996) and that such "Allee" effects may have important consequences for population and community ecology and for conservation (Courchamp et al. 1999; Stephens and Sutherland 1999). If reproduction does not match mortality when local density is below a threshold size, the population will decline in abundance despite living in a basically favorable

environment. Allee effects may occur for many reasons. For instance, at very low population density, finding a mate can be difficult for sexually reproducing organisms (but see Kindvall et al. 1998 for a counterexample; Lande 1987; McCarthy 1997). Similarly, in small patches, sex ratios can become unbalanced, leading to reduced reproduction and enhanced extinction risk (Legendre et al. 1999). Plant species that depend on animal vectors for dispersal often experience an Allee effect in small, isolated patches because of decreased visitation rates by pollinators (Rathcke 1983; Jennersten 1988; Aizen and Feinsinger 1994; Groom 1998). For example, Lamont et al. (1993) report zero reproductive success in small, isolated patches of the endangered Australian plant *Banksia goodii*. Another general mechanism that can result in an Allee effect is saturation by prey of a generalist predator's functional response (de Roos et al. 1998); at low densities, individual prey experience elevated predation risk. Finally, many species have specific cooperative behaviors (e.g., defensive herding in musk oxen), which can be disrupted at low population density (see also Robinson 1988; Wilson and Nisbet 1997; Avilés and Tufiño 1998; Avilés 1999).

A negative growth rate below a threshold density leads to a stable equilibrium at zero population size. In this case, introductions at low density may fail, opening the possibility of propagation failure or pinning for a species moving into a habitable landscape and generating a stable range limit. In this article, we argue that this scenario is particularly likely for species occupying patchy environments. First, we briefly summarize salient prior results for continuous, homogeneous environments. We then examine invasion dynamics in spatially discrete environments, where all suitable habitat patches are identical in quality and uniformly spaced. In both cases, some of the technical results we present are present in the literature but have not been explicitly applied to the issue of species' range limits. In "Discussion," we relate these results to a core concern of landscape ecology—critical thresholds in habitat connectedness—and touch on plausible empirical examples.

Invasion into a Continuous Environment with Uniform Habitat Quality

There is a rich theoretical literature on invasions, based on partial differential equations, known as "reaction-diffusion models" (Okubo 1980; Hastings 1996; Shigesada 1997). The simplest such model is

$$\frac{\partial N}{\partial t} = D\nabla^2 N + f(N), \quad (1)$$

where ∇ is the gradient operator (defined as $\partial/\partial x$ for a one-dimensional gradient and $[\partial/\partial x], [\partial/\partial y]$ for a two-

dimensional gradient), D is the diffusion coefficient, t is time, and $f(N)$ is the net population change at population density N as a result of local birth and death (for simplicity, N denotes $N(x, t)$ in a one-dimensional environment or $N(x, y, t)$ in a two-dimensional environment).

Diffusion models such as (1) are idealizations, since they ignore stochastic events and assume that reproduction and mortality are continuous in time. Model (1), as written, also assumes that the environment is spatially homogeneous. Nonetheless, diffusion models are useful because they provide testable predictions about invasion rates (see, e.g., Andow et al. 1990). For example, with logistic growth (fig. 1, *top*), the minimum speed of the advancing front (for a single dimension) is $2(rD)^{1/2}$, where r is the intrinsic growth rate of the invading species (Fisher 1937; Mollison 1991).

An Allee effect can be added to the reaction-diffusion model, such that growth is negative at low population densities (fig. 1, *bottom*). For instance, $f(N)$ may be characterized by a “cubic-shaped” curve, which is negative for $0 < N < C$, positive for $C < N < K$, and negative for $N > K$. Here, K is carrying capacity, and C is a critical threshold, above which the population grows and below which it declines to extinction. Such an $f(N)$ leads to what is referred to as a “bistable” equation (Fife 1979) because the extinction and carrying-capacity steady states are both locally stable. Over a wide range of initial conditions, in a homogeneous, continuous environment, the solution to the diffusion model with a bistable growth term converges to a moving wave joining the carrying capacity and extinction steady states and traveling at a constant speed (Aronson and Weinberger 1975). Whether the velocity is positive (i.e., range expansion) or negative (i.e., a range contraction and ultimately extinction) is governed by the area of $f(N)$ that falls above and below zero growth (Murray 1989). If the positive area $A_2 = \int_C^K f(N)dN$ exceeds the negative area $A_1 = \int_0^C f(N)dN$ (as in fig. 1, *bottom*), then the velocity is positive and the population invades. If instead A_2 is smaller in size than A_1 , the population recedes. In a homogeneous continuous environment, the fate of an invasion can thus be predicted simply by inspecting the qualitative form of the species growth curve.

A special, well-understood case of bistability is given by

$$f(N) = rN \left(\frac{K-N}{K} \right) \left(\frac{N-C}{K} \right). \quad (2)$$

The two stable equilibria, at $N = K$ and $N = 0$, are separated by an unstable equilibrium at $N = C$. A qualitatively similar growth term $f(N)$ can be defined from a mechanistic model describing interactions between males and females in a population (A. Ashih and W. Wilson,

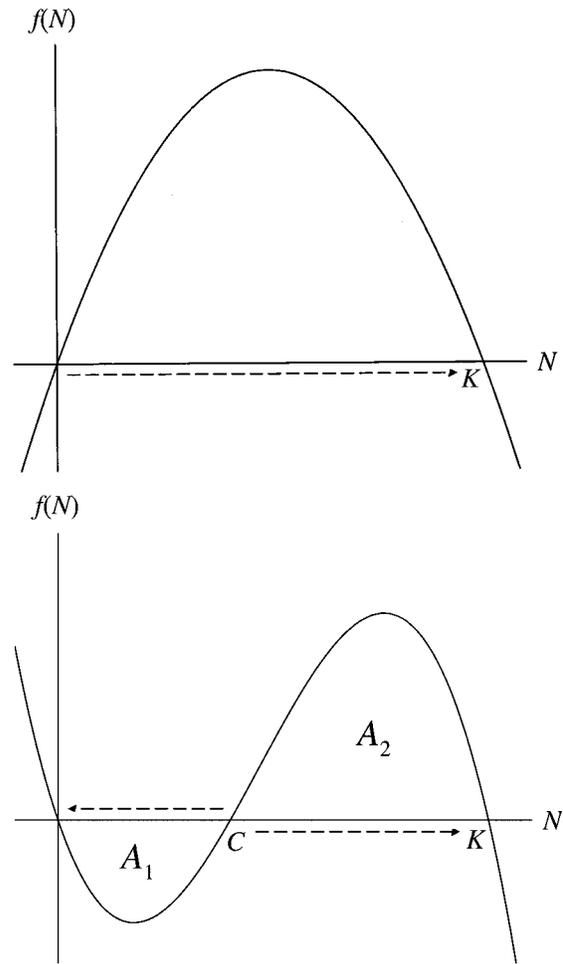


Figure 1: Standard and bistable growth functions. *Top*, logistic growth with a single stable fixed point (K). *Bottom*, cubic (Nagumo-type) growth function with two stable fixed points ($0, K$) separated by an unstable fixed point (C). The shaded regions labeled A_1 and A_2 correspond to the negative and positive contributions of f to $\int_0^K f(N)dN$. The dotted arrows indicate the direction of population change for a given N .

unpublished manuscript). Over a wide range of initial conditions, the solution of (1) and (2) asymptotically converges to a traveling wave with constant velocity,

$$v = \sqrt{2rKD}(1/2 - C/K), \quad (3)$$

where $0 < C < K$ (see Lewis and Kareiva 1993 for an ecological discussion; Haderler and Rothe 1975; Fife 1979). The species invades with positive velocity if $C < K/2$ and retreats if $C > K/2$. These conditions correspond to $A_1 < A_2$ and $A_1 > A_2$, respectively. When $C = K/2$, the invasion front stalls, neither advancing nor retreating. A stationary species’ border thus requires a delicate balancing of pa-

rameters, which in general seem unlikely to be realized in nature. Hence, Allee effects alone are insufficient to produce stable species' borders in homogeneous, continuous environments.

Invasion into a Discrete Environment with Uniform Habitat Quality

Diffusion models such as (1) generally treat space as a homogeneous continuum. However, few if any natural environments are homogeneous in properties relevant to organisms at local scales (Levin 1992). Habitat fragmentation, reticulate road and stream networks, and fine-scale topographic variation can lead to patchy environments, even in the absence of any broadscale environmental gradient. In this section, we demonstrate that these local spatial inhomogeneities can lead to propagation failure or invasion pinning, defining a species' border, and we characterize what is required for this phenomenon to occur.

Given a patchy landscape in modeling population dynamics, it is often appropriate to replace continuous space with a sequence of habitat patches coupled by dispersal (Levin 1976). We assume there exists a series of equivalent but discrete patches whose dynamics can be studied with a series of ordinary differential equations. For instance, for a chain of m linearly coupled, equally spaced patches, we might have

$$\frac{dN_i}{dt} = d(N_{i-1} - 2N_i + N_{i+1}) + f(N_i), \quad (4)$$

($2 < i < m - 1$), where d , a per capita density-independent movement rate, is a discrete analog of the diffusion coefficient and N_i is population density in patch i . As long as m is large, the dynamics at either end of the array of patches ($i = 1, m$) are inconsequential to our analysis and are omitted from (4). As in model (1), local dynamics are described by $f(N)$, which we assume to be identical for all patches. The migration term $d(N_{i-1} - 2N_i + N_{i+1})$ shuffles individuals between adjacent patches with no directional bias. Our model does not allow for spatial variation in movement rates (or equivalently, spatial variation in interpatch distances). We also assume no mortality during dispersal.

An interesting property of the discrete-space model with local Allee dynamics is that it results in an overall reduction in the invasion velocity compared to an analogous continuous-space diffusion model (fig. 2 shows an example). Furthermore, at sufficiently small d , velocity of the invasion front reaches 0, even though individuals continue to disperse beyond the invaded territory. Moreover, for any given array of patches, this condition of stasis can be realized for a many different combinations

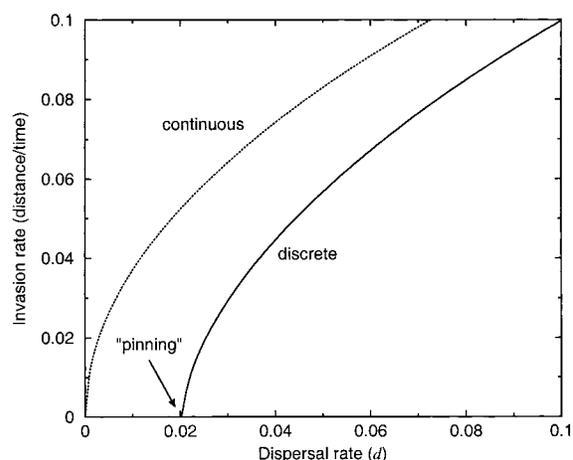


Figure 2: Invasion rate in continuous and discrete habitats. The dotted line is the theoretical prediction for diffusion with Allee growth given in (3). The solid line shows the result for Allee invasion in a discrete environment and was obtained by numerical integration of (4). After 100 initial time steps, the following 900 time steps were used to determine the rate of invasion. (Since the invasion rate is asymptotically constant, the invasion rate can be determined by a simple linear regression of the position where $N = C$ versus time.) Parameters were $r = 1.1$, $K = 1$, and $C/K = 0.25$.

of occupied patches (a fact that magnifies the importance of historical accidents). This is in contrast to diffusion in continuous, homogeneous landscapes where, as noted above, Allee effects do not generate stable distributional limits.

The importance of bistable dynamics in preventing the propagation of waves in discrete media has been recognized in disciplines such as physiology (Keener 1987), statistical physics (Bressloff and Rowlands 1997; Fáth 1998), and applied mathematics (Cahn et al. 1998), and the term "pinning" has been coined to denote this cause of propagation failure. Stable, spatially inhomogeneous solutions to reaction-diffusion equations can also arise in continuous but inhomogeneous domains. For instance, if two large regions are connected by a narrow dispersal corridor, limited dispersal along the corridor in combination with an Allee effect can lead to a stable, noninvading solution (Levin 1979; Matano 1979). To our knowledge, however, the concept of pinning has not been directly applied to understanding species' geographic range limits.

Bounds on Model Parameters That Allow Invasion Pinning

We can explain propagation failure of the discrete bistable case using a simple geometric argument (see also Nekorkin et al. 1997). Recall that in each patch $f(N)$ is assumed to

have an extinction equilibrium $N = 0$, a carrying capacity $N = K$, and a threshold $N = C$, above which the population grows and below which it decreases. Consider a focal patch i in a one-dimensional array of patches whose local population sizes are bounded between 0 and N_{\max} . Possibly after a transient period, a reasonable value for the population maximum is $N_{\max} \approx K$. The maximum value of the dispersal term $d(N_{i-1} - 2N_i + N_{i+1})$ is then bounded by two scenarios. In the first scenario, the focal patch is empty, but the two neighboring patches each have N_{\max} individuals. This configuration implies an upper bound to dispersal flux of $\Phi_{\max} = 2dN_{\max}$. In the second scenario, the focal patch has N_{\max} individuals, but the neighboring patches are empty. This configuration leads to a lower bound to dispersal flux, $\Phi_{\min} = -2dN_{\max}$. We refer to this scenario as a “two-sided” invasion because both right and left neighbors are involved.

We now ask whether net dispersal flux in an uninhabited patch is sufficient to overcome the Allee effect that new immigrants face. Our equation (4) is now

$$\frac{dN_i}{dt} = f(N_i) + \Phi_i. \quad (5)$$

Graphically, the net flux term Φ , simply serves to raise or lower the local “cubic-shaped” population growth term (fig. 3). A necessary and sufficient condition for overcoming the Allee effect is that Φ raises the local minimum population growth rate (f_{\min}) above 0 (fig. 3, *middle*). This, in turn, requires that Φ_{\max} exceed $|f_{\min}|$. In other words, if $2dN_{\max} < |f_{\min}|$, then the population cannot spread spatially. Similar arguments using Φ_{\min} can be used to show that, if $2dN_{\max} < f_{\max}$, the population cannot contract spatially (fig. 3, *middle*). Using $N_{\max} = K$, we see the population distribution is stationary for a given set of patches occupied and at K if

$$d < \min \left\{ \frac{|f_{\min}|, f_{\max}}{2K} \right\}. \quad (6)$$

The condition for propagation failure can be made less restrictive if we consider a second scenario in which the distribution of individuals in a species range is described by a monotonically changing density profile, that is, a density profile without “peaks” and “troughs.” Here, we have $N_{-\infty} = K$ and $N_{\infty} = 0$ and a single patch in the chain at which $N_i > C$ and $N_{i+1} < C$. We refer to this as a “one-sided” invasion. In this case, the minimum dispersal flux Φ_{\min} can be changed from $2dN_{\max}$ to dN_{\max} to reflect the fact that an “occupied” patch ($N > C$) can only have at most one unoccupied neighbor ($N < C$). Similarly, the maximum dispersal flux Φ_{\max} can be changed to $-dN_{\max}$

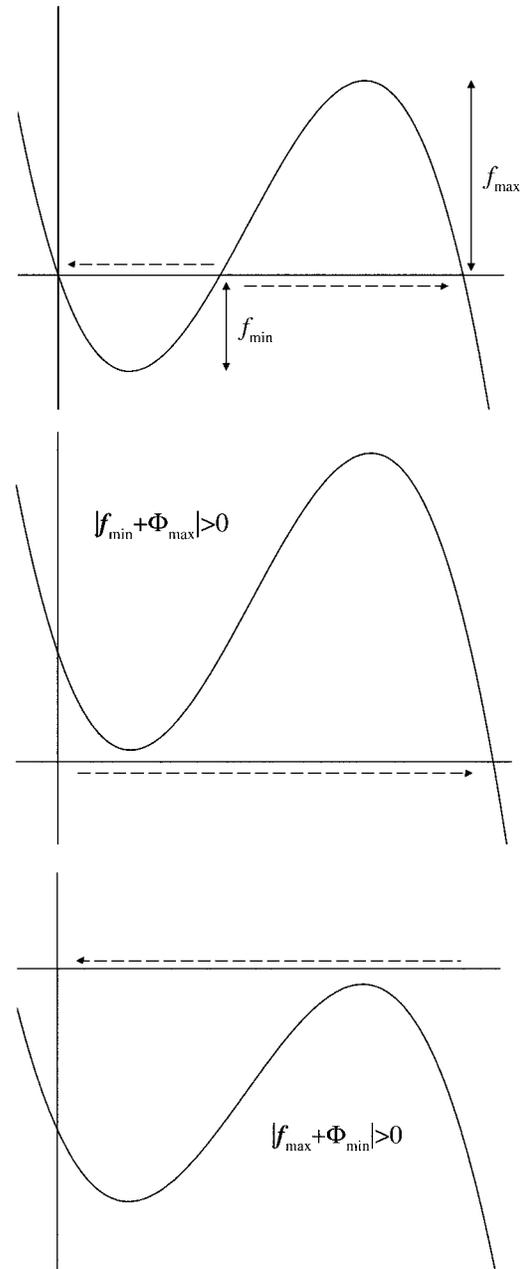


Figure 3: “Depinning” transition in the bistable Allee growth function. *Top*, cubic growth function with graphical depiction of f_{\min} and f_{\max} . *Middle*, immigration Φ_{\max} is sufficient to overcome the Allee effect. The unstable fixed point disappears, and the population increases locally to K moving the range boundary forward. *Bottom*, emigration Φ_{\min} is sufficient to overcome the Allee effect. Again, the unstable fixed point disappears. In this case, the population becomes locally extinct and the range boundary retreats.

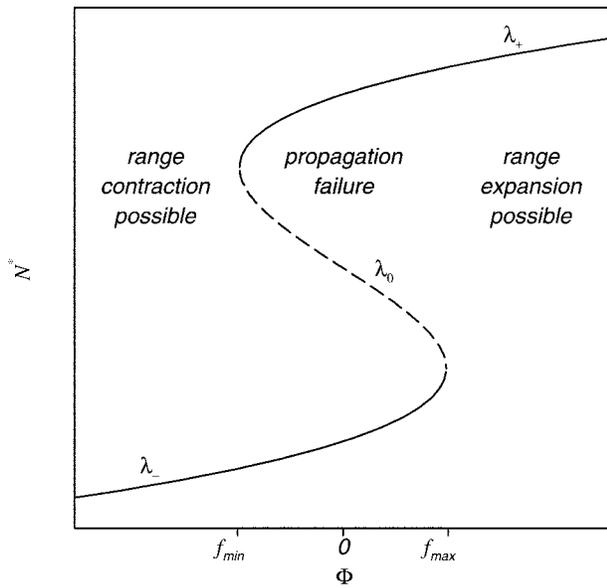


Figure 4: Bifurcation plot of Allee growth with dispersal flux Φ . Solid lines show stable equilibria, and the dashed line, the unstable separatrix; λ_+ corresponds to the carrying capacity K ; λ_- is the lower stable equilibrium that may or may not be equal 0, depending on the details of the growth function; and λ_0 indicates the unstable equilibrium. Propagation failure occurs in the shaded region.

to reflect the fact that an unoccupied patch can only have at most one occupied neighbor. This gives a wider range of d values that result in a stationary solution

$$d < \min \left\{ \frac{|f_{\min}|, f_{\max}}{K} \right\}. \tag{7}$$

Note that conditions (6) and (7) are sufficient to guarantee propagation failure. However, propagation failure can occur for values of d greater than these, if N_{\max} is significantly less than K near the transition from high local-density patches to low local-density patches. This will typically be the case when $\int_0^K f(N)dN$ is close to 0 or if the upper and lower equilibria are only weakly stable.

The relationship between propagation failure and bistability is clear in the bifurcation plot of the system (fig. 4). Both forward and backward invasions correspond to a critical transition across a limit point (Seydel 1988; Erneux and Nicolis 1993) where one of the stable solutions joins the unstable solution and disappears, leaving behind a single stable equilibrium. Once bistability is broken, there is either a positive or negative net growth rate, depending on whether immigration into the local patch exceeds emigration.

The conditions for propagation failure given in in-

equalities (6) and (7) are general in the sense that they apply to any bistable function $f(N)$. However, in the cubic case, we can solve explicitly for f_{\max} and f_{\min} :

$$f_{\max} = \frac{r(C + K + q)(C - 2K + q)(-2C + K + q)}{27K^2}, \tag{8}$$

$$f_{\min} = \frac{r(-C - K + q)(-C + 2K + q)(2C - K + q)}{27K^2}, \tag{9}$$

where $q = (C^2 - KC + K^2)^{1/2}$.

Using the information in (8) and (9), along with equation (7), we can paint a more general picture of the region of propagation failure for the cubic growth function (fig. 5). Pinning occurs for all values of C/K when $d = 0$, but the region over which pinning is guaranteed shrinks as d increases. As shown by the dashed lines delineating the numerically calculated transitions between pinned and moving fronts, pinning is still possible outside of the shaded region in figure 5. This occurs because equation (7) is a sufficient condition to guarantee pinning but is not a necessary condition. As d grows large, K is no longer a tight upper bound for N in the occupied region, particularly near the boundary and when the population threshold is close to $C/K = 0.5$. Population sizes in patches on the leading edge of the invaded region will generally be smaller than K when d is large because of loss of individuals into neighboring patches where growth rates are negative. It is this loss of individuals because of dispersal that partly accounts for the observed difference between the analytic and numeric results.

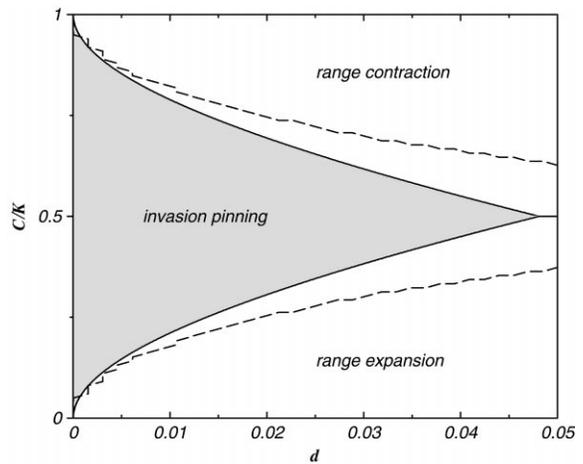


Figure 5: Invariant domains of the discrete Allee invasion dynamics in one dimension. These results are for $K = 1$ and $r = 1$. Solid lines are analytic results based on the approximate inequality (7). The dashed lines are numerical results obtained by directly integrating the coupled ordinary differential equations.

Nonlinear Spatial Effects

The combination of discrete space and multiple stable equilibria in the Allee model gives rise to a number of interesting nonlinear effects. One effect is related to the frequency of occupied patches adjacent to an unoccupied patch. Greater occupancy of neighboring patches results in greater immigration and hence an increased likelihood of receiving enough propagules to grow locally above C and eventually reach carrying capacity. This implies a high degree of history dependence in the model dynamics. Different spatial configurations of initially occupied patches can lead to quite different steady states even though the model parameters are the same (fig. 6). If the dispersal rate is slightly below the critical value for a one-sided invasion but is above the critical value for a two-sided invasion, then there will be a tendency for small holes or defects in the distribution to fill in whereas large holes (those with much greater width than typical dispersal distances) in the distribution will remain unoccupied. From an empirical perspective, these strongly nonlinear responses to spatial pattern could lead to considerable confusion when attempting to validate linear source-sink (Pulliam 1988) and metapopulation models (Levins 1969; Hanski and Gilpin 1991) because the realized location of source and sink populations or occupied and unoccupied patches depends only on the vicissitudes of history and is not due to variation in intrinsic habitat quality or repeated extinction and colonization events.

Another nonlinear effect induced by the bistability of the underlying dynamics is the presence of extended quasi-stable epochs followed by rapid shift from one steady state to another. This is apparent in figure 6, *middle*. The center patches, initially empty, remain below C for a considerable period before bursting up to K . This phenomenon is easily explained by examining figure 3, *middle*. Notice that, near the depinning transition, when immigration is barely sufficient to overcome the Allee effect, f_{\min} is close to 0. The long period of slow growth occurs as the local population squeezes through this bottleneck in the growth curve. Once the population grows above the constriction, the growth rate increases rapidly, and the population bursts upward toward its carrying capacity. An invasion into a patchy landscape consists of a series of these local burst events. Initially, there is a long delay while the patch just beyond the leading edge of the invasion front slowly increases past the Allee bottleneck. Then the front shifts forward one patch after a rapid burst above the Allee threshold. The process is then repeated in the next patch. Thus, we can interpret the fine-scale invasion dynamics of the discrete Allee model as a periodic repetition of local transitions between quasi-stable states, with the cycle time (in space) determined by the mean patch size and the dispersal rate

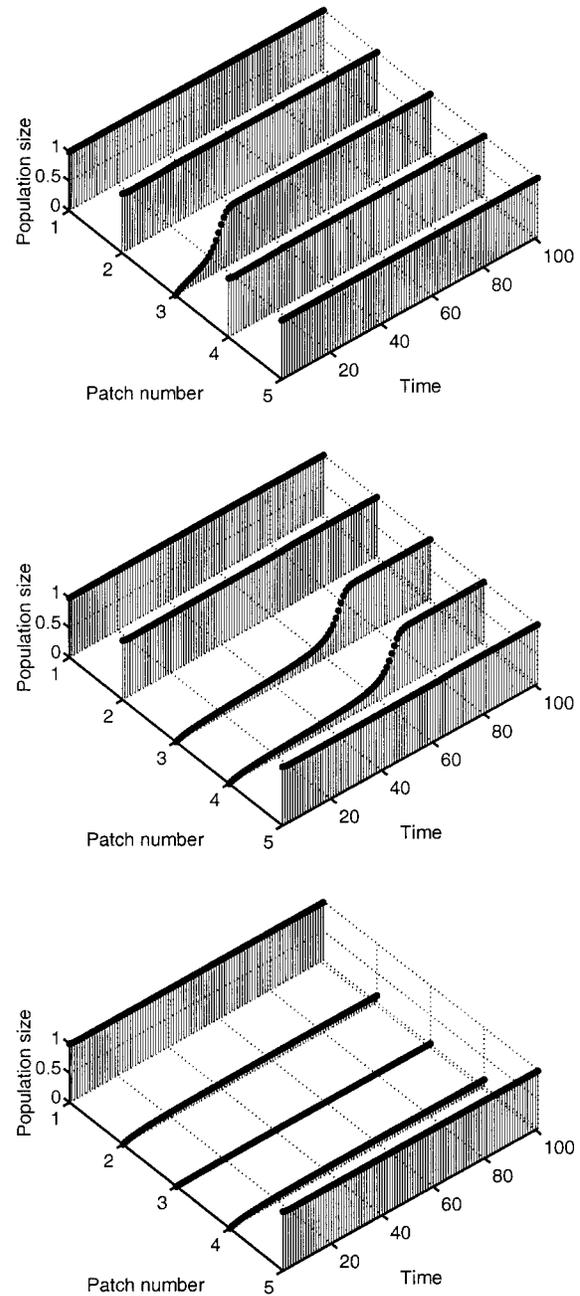


Figure 6: Example of nonlinear spatial effects in the pinned domain of the spatially discrete Allee model. *Top*, single empty patch receives sufficient immigration from its two neighbors to overcome the Allee effect for the parameters used. *Middle*, two unoccupied patches are also able to reach carrying capacity but required significantly longer time. *Bottom*, three unoccupied patches remain a permanent history-dependent sink. Parameters were as in figure 2, except that $d = 0.02$.

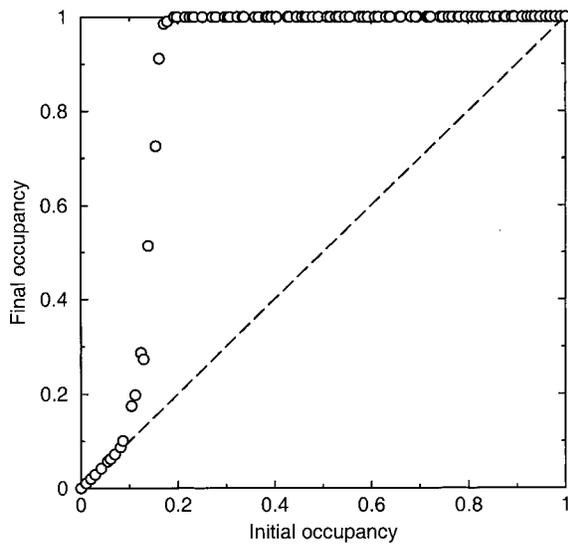


Figure 7: Invasion on a two-dimensional lattice with spatially random initial conditions. Below a critical initial occupancy, here $p_{crit} \approx 0.1$, no invasion occurs and the initial condition persists indefinitely. When more than p_{crit} of the lattice is randomly seeded, the population invades to occupy the entire lattice.

(see Mitkov et al. 1998 for an example in continuous space; Fáth 1998).

The effects of local bistability may also propagate up to the scale of the entire landscape. An interesting scenario unfolds when the landscape is initially occupied in random locations with a density p and when the dispersal coefficient d is just small enough for propagation failure to occur. Again, we can numerically determine a critical value of a parameter, initial density p , at which the dynamics shift rapidly between steady states (fig. 7). Below the critical initial density, unoccupied patches do not have enough occupied neighbors to overcome the Allee effect, and the entire landscape remains frozen in its initial condition. Above $p = p_{crit}$ (~ 0.11 in fig. 7), the cooperative effect of multiple neighbors contributing propagules into patches allows patches below the Allee threshold to grow above C and reach carrying capacity. If the species in question were an introduced pest, one might conclude that the species was not invasive because small random introductions do not lead to invasion. Iterated over time, however, these small local introductions may become sufficiently widespread to cross the critical landscape-scale density, and the pest species will suddenly become pandemic.

Sharpening of Range Boundaries along Environmental Gradients

As noted in the introductory paragraphs, one standard explanation for species' borders involves environmental

gradients. Allee effects can magnify the impact of gradients on species' distributions. One potential effect of a decrease in productivity and population carrying capacity K near a species' border is a reduction in the number of individuals that disperse into unoccupied patches beyond the current range limit. If the Allee effect is weak or non-existent such that $dN/dt > 0$ for all values where $0 < N < K$, then the decrease in K would not stop the population from spreading to occupy all habitats where $K > 0$. The ultimate distribution in the absence of an Allee effect will closely mirror the gradual decline in K (fig. 8, top), and

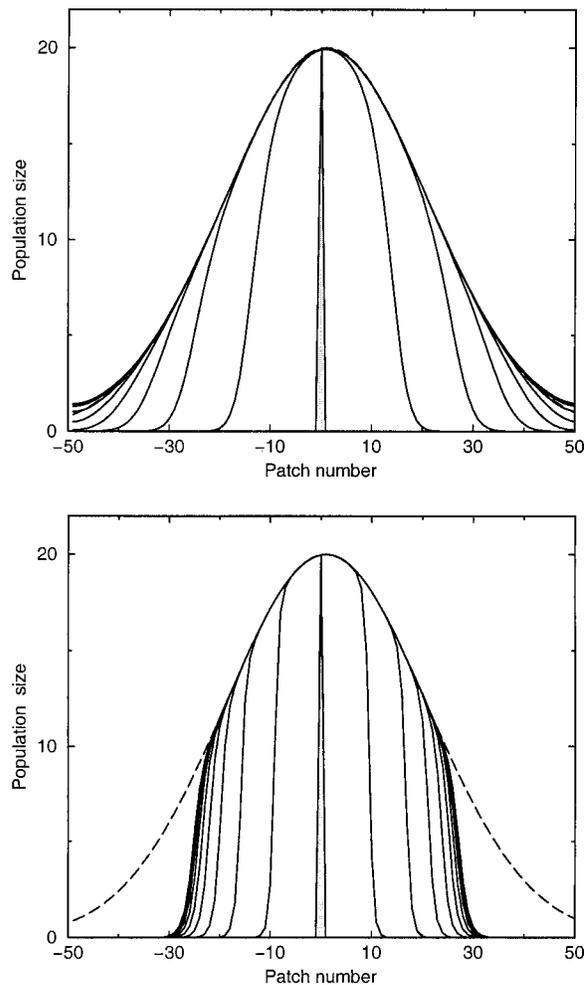


Figure 8: Comparison of invasions along a gradient in carrying capacity K (dashed line), with and without an Allee effect. Here, K varies from the center of the figure to the edge as $20 \times \exp[-x^2/(2\sigma^2)]$, where x is the patch number and $\sigma = 20$. Solid lines are 100 time steps apart. The initial condition is shaded grey. Top, logistic growth $f(N) = rN(1 - N/K)$ with $r = 0.1$ and $d = 0.1$. Bottom, Allee growth (see eq. [2]) with $r = 1.1$, $C = 0.25$, and $d = 0.1$. The invasion is pinned at roughly patch number ± 30 .

the species border will occur only when K is 0. However, in the presence of a strong Allee effect, a gradual decrease in K (for fixed values of d and f) will eventually lead to propagation failure, at which point the invasion will stall and leave behind an abrupt boundary between occupied and unoccupied patches (fig. 8). Further invasion of suitable habitats would require sufficient immigration into unoccupied patches to overcome the local Allee effect.

The overall result of Allee growth in a patchy environment is an increased sensitivity to local gradients and a significant reduction in range area compared to the area that could be occupied in the absence of an Allee effect. It is tempting to interpret an abrupt boundary as a response to an environmental gradient, such as decreasing temperature, that has reached a threshold, below which the species cannot persist. This conclusion is tantamount to saying that the carrying capacity has reached 0. As figure 8 illustrates, an abrupt transition in density can occur even when K is still positive (see also Wilson et al. 1996).

Discussion

We have demonstrated a potential mechanism that can limit a species' range. We have not however considered how ranges come into being in the first place. Because the dynamics of the discrete Allee invasion model are either moving or pinned, we must consider a scenario that would allow a species to expand (or equivalently collapse) its range and then stop moving, thereby leaving a fixed range limit. The transition from a moving boundary to a pinned boundary could occur in several ways. For example, our discrete space model predicts that if there is a transient increase in local productivity leading to an increase in abundance within occupied patches, then this may "spill-over" to unoccupied patches, leading to an expansion in range size that persists after the temporary flush in production or abundance has subsided.

As a simple example, consider a grid of identical, uniformly spaced cells, in one of which there has been colonization at sufficient density to permit local persistence. Our model defines conditions that lead to the pinning of the species in this initially occupied patch. A spatially uniform increase of carrying capacity of all patches could lead to a wave of invasion across the landscape. If this in turn is followed by a spatially uniform decline in local carrying capacities, the species could again become trapped in a new larger area of occupied patches defining its new range. Similarly, transient and spatially uniform changes in dispersal rates can lead to episodic expansions of species' ranges. To explore theoretically the long-term dynamics of range limits in the face of environmental variation, it would be useful to extend model (1) to include the in-

roduction of stochastic variation in local recruitment rates, the Allee threshold, and dispersal rates.

A comparable effect may explain an interesting pattern observed by Duncan et al. (1999). These authors observed that the ultimate range size of bird species introduced into New Zealand was strongly correlated with the size of the initial introduction (controlling for other variables such as life history). Duncan et al. (1999) were unsure how to interpret this pattern but tentatively suggested that it could reflect the importance of priority effects in interspecific competition. Our model predicts exactly this pattern if species inhabit patchy environments and experience Allee effects, even in the absence of interspecific competition; species introduced at very high local densities are likely to successfully colonize a larger number of patches before the pinning effect comes into play.

Critical Landscape Connectivity

Our results concerning propagation failure bear on an ongoing discussion of critical connectivity in landscapes (Taylor et al. 1993). A number of authors have noted that, in patchy environments, there exists a threshold at which habitat connectivity, and the potential for successful invasion, suddenly increases, either at a critical density of randomly placed patches (Gardner et al. 1989; Milne et al. 1996) or at a critical distance required to disperse between habitat patches (Keitt et al. 1997). Generally, these studies have not made a connection between local bistability and critical phenomena nor between these issues and species' range limits. Here, we have shown that an Allee effect can lead to a sudden and nonlinear change in the ability of an organism to invade into a landscape as the rate of movement between patches is gradually increased. An increase in the frequency of movement among patches could occur either because of a reduction in a species' resistance to crossing the intervening, nonhabitat matrix or because patches are closer together or a combination of these. In addition, we have shown that there is a fundamental relationship between critical phenomena in spatial population processes and the presence of multiple stable equilibria in the underlying dynamics, a point that has largely been overlooked in previous work on critical connectivity in landscapes.

Our results have several advantages over previous efforts concerning critical connectivity. One advantage is that our results are not limited to the assumption that habitat fragmentation is either a uniform random or even a contagious spatial process but can easily be generalized to include arbitrary landscape structure. Propagation failure in the Allee model is not tied to a particular kind of habitat heterogeneity. Instead, it depends on a quite general mechanism: an inability of isolated populations to persist below

a threshold density. Furthermore, by focusing on simple, process-based population models, we can potentially estimate model parameters and make testable predictions concerning invasions and their failure.

One interesting prediction that derives from the theory of critical phenomena is the appearance of invariant scaling behavior in regions of parameter space where the dynamics shift between different qualitative domains (Stanley 1971; Stanley et al. 1996). In the Allee invasion model, these transitions correspond to moving across the pinning threshold as d is decreased, or switching from positive to negative invasion velocity as C is increased. Near these transitions, we expect to observe large classes of invasion models that share identical, power-law scaling behavior in the rate at which the invasion velocity approaches 0 as the dispersal rate d is driven toward the critical point (Erneux and Nicolis 1993). The reason that widely different models, and their corresponding empirical systems, may possess identical behavior is that the dynamics near a critical point are dominated by long-range spatial correlations that depend only on the presence of bistable local dynamics and simple geometric properties of the patch network, for example, one versus two spatial dimensions (Goldenfeld 1992). An interesting test of the theory would be to measure scaling exponents of the depinning transition among a wide range of species with different life-history traits and determine whether or not there are large classes of species that, despite their individual differences, share identical scaling exponents near the transition from invasive dynamics to propagation failure.

Sources, Sinks, and Spatial Variation in Abundance

It is interesting to consider how multiple stable equilibria in population size and pinned invasions relate to spatial variation in species' abundances. Brown et al. (1995) have noted that many species have relatively clustered distributions with many low-abundance sites and a few, relatively long-lived hot spots of high local abundances. Although a similar distribution of abundances can be generated by simultaneously sampling many local populations whose local dynamics are strongly influenced by multiplicative random noise (Ives and Klopfer 1997), there are some features of the pattern reported by Brown et al. (1995) that are not consistent with the temporal variation hypothesis. In particular, hot spots in abundance appear to remain in the same location for long periods (Brown et al. 1995). Whereas it is likely that both fixed spatial variation in environmental conditions and temporal population variability play a role in determining abundance, our model provides an additional scenario complementing these two potential causes of the Brown et al. (1995) phenomenon. Multiple stable equilibria in abundance can lead to patterns of spatial var-

iation in abundance comparable to those observed by Brown et al. (1995). Multiple equilibria often result in population outbreaks (Ludwig et al. 1978; McCann et al. 2000). If there are strong Allee effects present and dispersal rates are relatively low, then local outbreaks may remain for long periods at the high abundance equilibrium because the spatial boundaries separating regions in different stable equilibria are themselves stable. Thus, spatial pinning of population outbreaks could lead to long-lived hot spots, with relatively stable abundance.

Multispecies Interactions and Alternative Landscape States

In some cases, an Allee effect might be caused by the presence of another species, for example, priority effects in interspecific competition. Another scenario involves a generalist predator that might only be able to contain a prey species when the prey is rare. A classic example is the periodic emergence of cicadas throughout deciduous forests in eastern North America (Lloyd and Dybas 1966). When rare, the cicadas are decimated by avian predators (Karban 1982). An apparently clever evolutionary response by the cicadas is to synchronize their emergence into the adult stage, during which they are susceptible to predation, and to overwhelm the predatory response by sheer numbers (Williams et al. 1993). However, the cicadas are believed to be highly vulnerable to predators at low density where there is no escape in numbers (Lloyd and Dybas 1966; Williams et al. 1993). This fact has been used to explain tight synchronization of local cicada emergences in time (Lloyd and Dybas 1966). According to our theory, the same mechanism should lead to sharp distribution boundaries for cicada "broods," boundaries that reflect idiosyncratic historical events (see fig. 8). Preliminary evidence (S. Liebhold, personal communication) suggests that cicada broods indeed have sharp spatial edges. Future studies should examine the potential role of Allee effects and patchiness in producing this distributional pattern.

A system similar to cicada broods has been described by Harrison (1994). This system involves the western tussock moth (*Orgyia vetusta*), a parasitoid of the moth, and a number of generalist predators. Local outbreaks of tussock moths have remained spatially restricted despite the presence of suitable host plants (a shrub) beyond the current limit of the invasion (Maron and Harrison 1997). The mechanism that apparently limits the spread of the moth is essentially a multispecies Allee effect. The moths have a low dispersal rate, but the parasitoid is relatively vagile. Beyond the edge of the epidemic, the moth is rare and therefore easily controlled by the mobile parasitoid and other, predatory species (Brodmann et al. 1997).

Theoretical models of the tussock moth invasion have tended to emphasize the role of antagonistic interactions

in a spatially continuous environment to explain the formation of stable patterns (Hastings et al. 1997; Wilson et al. 1999). It is difficult, however, to imagine that the distribution of host plants is entirely continuous in space (see also McCann et al. 2000). For example, Maron and Harrison (1997) report differences in tussock moth invasion dynamics between a grassland environment, where we imagine that host plants may be close together, and a dune environment, where we imagine that host plants may not form a continuous canopy. It would be fascinating to study the effect of fine-scale landscape heterogeneity on propagation failure in tussock moths and to add various forms of patchiness to current theoretical models of tussock moth invasion (see also M. Owen and M. A. Lewis, unpublished manuscript). Our results also suggest an interesting and easily constructed experiment: small gaps in the moth's distribution should be invaded, but larger holes in the initial distribution, beyond a critical radius, should remain empty. The critical gap size might a priori be estimated from moth and parasitoid dispersal data.

Interpreting Invasion Failure

In conclusion, our results suggest a cautionary note when interpreting the failure of species' invasions either as reflecting an incompatibility between the invading species and the environmental conditions beyond the invaded territory or as the result of strong interspecific interactions. In the presence of an Allee effect, a species that attempts to invade a patchy landscape may become trapped by an inability to generate a net positive growth rate beyond a break in the distribution of suitable habitats, despite the fact that some individuals successfully disperse into suitable habitats beyond the interruption. Population processes can lead to Allee effects, even in the absence of obvious mechanisms of positive density dependence. Lande (1998) has noted that, in addition to cooperative breeding and other biotic interactions, stochastic effects inherent in small populations can create an Allee effect under quite general circumstances. If anything, density-independent disturbances should increase, not decrease, an Allee effect by differentially affecting small populations (Shaffer 1987; Amarasekare 1998), particularly if the disturbances are themselves manifest at small scales. It is in general premature to conclude, in the absence of experimental or other evidence, that the failure of a species to invade some region is due either to interspecific interactions, such as predation or competition, or to a decline in habitat quality as one approaches the edge of the range. An alternative mechanism that must be considered is a locally patchy, but otherwise suitable and homogeneous, landscape combined with a local Allee effect in local population dynamics. Moreover, our results suggest that historical accidents should be important in defining current

range limits, given Allee effects in a patchy environment. Gauging the relative importance of this cause of range limits from more traditional explanations based on responses to environmental gradients or interspecific interactions is a challenging task for future research.

Acknowledgments

This work was conducted as part of the Species' Borders Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation (NSF; grant DEB-94-21535), the University of California, Santa Barbara, the California Resources Agency, and the California Environmental Protection Agency. Additional support was also provided for T.H.K., a postdoctoral associate. R.D.H. received additional support from NSF. Work by M.A.L. was also supported in part by the NSF (grants DMS-9457816 and DMS-9973212) and by the Institute for Mathematics and Its Applications with funds provided by the NSF.

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Associate Editor: Lenore Fahrig