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Theoretical models of species' borders: single species approaches

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The range of potential mechanisms limiting species' distributions in space is nearly as varied and complex as the diversity of life itself. Yet viewed abstractly, a species' border is a geographic manifestation of a species' demographic responses to a spatially and temporally varying world. Population dynamic models provide insight into the different routes by which range limits can arise owing to gradients in demographic rates. In a metapopulation context, for example, range limits may be caused by gradients in extinction rates, colonization rates or habitat availability. We have consider invasion models in uniform and heterogeneous environments as a framework for understanding non-equilibrium range limits, and explore conditions under which invasions may cease to spread leaving behind a stationary range limit. We conclude that non-equilibrial range dynamics need further theoretical and empirical attention.

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Empirical studies have revealed a rich panoply of proximal causes for species' range limits, such as dispersal barriers, unfavorable abiotic conditions, hybridization, interspecific competition, impacts of generalist enemies, and shortages of essential resources or mutualists (Caughley et al. 1988, Lawton and Woodroffe 1991, Krebs 1994, Gaston 2003). Yet viewed abstractly, a species' border is a geographical manifestation of a species' demographic responses to a spatially and temporally varying world. Lawton (1995) has suggested that underlying the manifest diversity of organisms is a limited repertoire of distinct population dynamic behaviors. Putting Lawton's suggestion into a spatial context, we propose that there may be a modest number of distinct explanations for species' borders, when cast abstractly in terms of spatial demography – how birth, death, and dispersal rates vary across space and time – rather than of detailed mechanisms.

Theoretical models of population dynamics in spatially heterogeneous environments (e.g. along gradients) provide useful tools for characterizing the demographic underpinning of species' borders. Our aim here is to provide a conceptual framework that captures the major population dynamical causes of range limits. We emphasize single species dynamics and ecological processes; a complementary paper by Case et al. (this issue) examines range limits in the context of interspecific interactions and evolutionary dynamics. We begin by considering range limits for species with local dynamics not strongly perturbed by dispersal, then examine the consequences of dispersal and in particular the interplay of colonization and extinction in setting range limits. We believe the framework we propose will facilitate comparative analyses of range limits (Parmesan et al. this issue) and helps highlight critical gaps in our current understanding. Major challenges remain, both theoretically and empiri-

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cally, in our understanding of non-equilibrial range dynamics, and in elucidating the implications of landscape structure and Allee effects for range limits.

Gradient models for stable range boundaries

For simplicity, we begin with a species whose local dynamics are described by a differential equation with negative density dependence (e.g. logistic growth). N(x) denotes population size at site x. A general model for population dynamics at site x is

$$\frac{dN(x)}{dt} = B(x) - D(x) + I(x) - E(x) \qquad (1)$$

where B, D, I and E are respectively total birth, death, immigration, and emigration rates (any of which can vary with density, with space, and over time, Williamson 1972, Holt 1979, Maurer 1990).

As a useful limiting case, imagine that within a biogeographical region dispersal has historically sufficed to expose sites to occasional colonization, so that suitable sites can be occupied, but that dispersal is too low to perturb local dynamics after establishment. Hence, I(x) and $E(x) \approx 0$. In this low (but non-zero) dispersal limit, the species' range is that sub-set of local sites where populations do not go extinct, based solely upon local population processes.

A key determinant of a species' range is thus spatial variation in factors driving local extinction (Maurer and Taper 2002, Brewer and Gaston 2003). We identify three broad classes of such factors: i) deterministic extinction in constant environments, ii) extinction from demographic stochasticity, and, iii) extinction arising from temporal variability.

i. Ranges caused by niche limits

Let r(x) be the intrinsic rate of increase [i.e. (dN/dt)/N at low N] at site x. If $r(x) < 0$, without immigration N approaches zero, and site x is outside the range. This implies the existence of deterministic processes (e.g. high predation, insufficient resources) pushing populations to extinction. Spatial variation in density-independent components of local birth or death rates can lead to negative r(x). In Fig. 1, along a gradient the intrinsic birth rate remains constant, as does density-dependence in births. However, death rates rise so that deaths exceed the maximal birth rate at one end of the gradient, causing a range limit. Range limits can thus reflect spatial variation in r, sufficiently great that some sites have negative r. Such variation has even been estimated in the field (Lele et al. 1998). There is a close link between the niche concept and the deterministic role of r in setting range limits (Holt and Gaines 1992, Pulliam 2000). To a first approximation, a species' range is a spatial expression of its niche (Brown 1984). However, numerous additional factors alter realized ranges beyond what is expected from niche requirements alone (Brown and Lomolino 1998, and below).

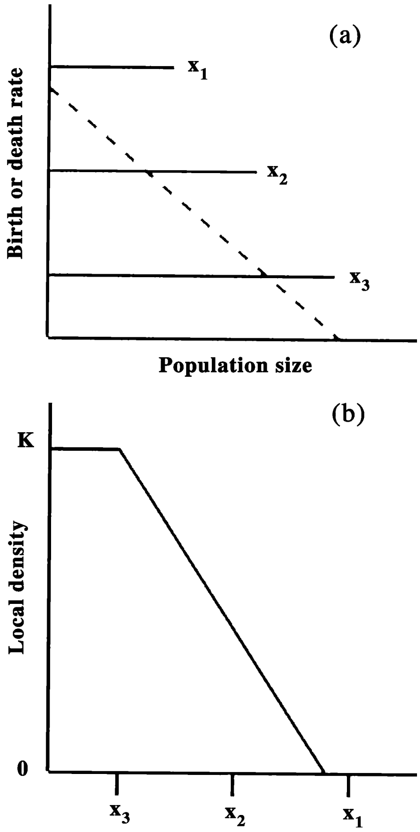

Fig. 1. A species border arising from a gradient in density-independent mortality. (a) Vital rates: density dependent birth rate (dotted line) is spatially uniform, but density independent mortality rate (solid line) increases from site 3 to site 1. This implies (b) declining carrying capacity K(x) along the gradient.

ii. Ranges caused by demographic stochasticity

Births and deaths are inherently stochastic. Theoretical studies of demographic stochasticity (Renshaw 1991, Lande 1998) show that extinction will eventually occur even in favorable environments with positive r and is likely to occur rapidly if N is chronically low. There are several distinct reasons a site with positive r may have low absolute N and experience rapid extinction: 1) strong density-dependence, 2) low (but positive) r, or 3) small habitable area. Figure 2 depicts a hypothetical example in which r is constant but density-dependence strengthens along a gradient, lowering carrying capacity, K(x). With strong density-dependence, a local population stops growing at low absolute N and is vulnerable to extinction. If (as we for the moment assume) coloniza-

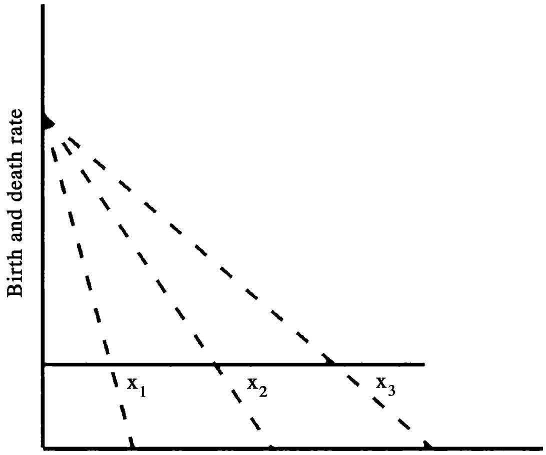

Fig. 2. A species border arising from a gradient of increasing density dependence. Mortality (solid line) is constant across sites. Density dependence in births increases from site 3 to site 1, resulting in a lower K and increased chance of stochastic extinction (see text).

tion is rare, sites with very low K are unlikely to retain the species because of demographic fluctuations and will tend to be outside the species' realized range.

iii. Ranges caused by temporal variability

Many environments are highly unstable (Easterling et al. 2000), with short-term fluctuations or disturbance driving populations to very low N. Even if average r and K at a site are consistent with species persistence, temporal variation enhances extinction risk. Range limits may well be determined more frequently by extreme events, than by mean conditions (Klok et al. 2003).

This limiting case suggests three classes of demographic reasons for range limits:

1) A range limit may arise because a species' niche requirements are not met (i.e. $r(x) < 0$).
2) A range limit may reflect low absolute population sizes (e.g. due to strong density-dependence at one end of a gradient) leading to high extinction risk.
3) In unstable environments, there could be high temporal variance in demographic parameters, or catastrophes, leading to elevated extinction risk.

We suggest that these three causes formally span the demographic reasons underpinning species' borders, when dispersal is very rare (but not totally absent). The relative importance of each in setting actual range limits is unknown, though we suspect that mapping species' niches onto the spectrum of available environments is often the most important factor sculpting species' ranges. Moreover, these three causes may interact. If environmental conditions are near the edge of a species' niche, density-dependence may also be strong (e.g. if resources are scarce, competition may be intense; Maurer and Taper 2002), and species may be more sensitive to variation in the environment. We now relax the crucial assumption that dispersal is of only historical importance in setting range limits.

The diverse roles of dispersal in defining range limits

With dispersal, range limits become fuzzier (Fortin et al. this issue). If immigration into site x occurs continually, the species will (in effect by definition) always be present. Pragmatically, one can prescribe a density, N_{crit}, below which a species is deemed absent (as in range maps in field guides). It is useful to distinguish several distinct mechanisms by which dispersal can influence range limits.

Source–sink dynamics

Recurrent immigration from 'source' populations can maintain a species at sites ('sink' habitats) where $r(x) < 0$. The range of a species can expand beyond just those sites with favorable niche conditions (Keddy 1982, Holt 1985, 1993, Pulliam 1988, 2000, Lawton 1993, Dias 1996). To illustrate this effect (Holt 1993), let I(x) be the rate of immigration into the sink. Assuming that direct density-dependence is negligible, as would be expected if population density is low, and a constant but negative growth rate, leads to a simple model: $dN(x)/dt = I(x) + r(x)\,N(x)$. At equilibrium, $N(x) = I(x)/|r(x)|$. Even low immigration ensures that $N(x) > N_{crit}$, if r is not too negative. Source–sink dynamics can inflate the size of the realized range.

Effects of immigration on extinction

Recurrent immigration can elevate local abundance (Brown and Kodric-Brown 1977) and reduce extinction risk from demographic stochasticity or catastrophes (Stacey and Taper 1992, Stacey et al. 1997). This effect is large if density-dependence is weak (Renshaw 1991). When a population declines drastically due to disturbance, after conditions recover it grows exponentially. But it may spend a considerable period at low abundance with continued risk of extinction from demographic stochasticity (particularly at low r). Immigration boosts abundance and reduces the time a rebounding population is at dangerously low densities.

Immigration can dramatically affect population size in temporally variable sinks. As described more fully elsewhere (Holt et al. 2003), if growth rates fluctuate and are serially autocorrelated, in a sink population maintained by immigration time-averaged abundance can be inflated greatly above that expected in a constant environment. Basically, immigration provides a 'floor' that permits a population to rebound and quickly exploit occasional runs of good years. Using a N_{crit} measure to define range limits, this effect could greatly inflate the realized size of species' ranges.

Dispersal may also at times reduce population size, and hence magnify extinction risk. For instance, immigrants may bring with them pathogens, or genes maladapted to the local environment (Harding and McNamara 2002). Moreover, with strong time-lagged density-dependence, immigration may reduce local fitness and generate population cycles (Gomulkiewicz et al. 1999), potentially hampering local persistence (particularly if immigration is pulsed). Finally, in patchy landscapes with long distances between habitable patches, dispersal at short distances can drain individuals from inhabited patches, increasing extinction risk (Okubo 1980, Holt 1985).

Colonization–extinction dynamics

Finally, and crucially, dispersal permits sites to be colonized in the first place, and to be recolonized after extinction. Range limits will then be molded by large-scale constraints on dispersal, and metapopulation dynamics. In the next section, we examine these effects more closely. Overall, linking detailed analyses of how dispersal modifies local population dynamics to the study of range limits is crucial, and deserves much more detailed attention in the literature (Guo et al. this issue).

Interference with local adaptation

Gene flow caused by dispersal can introduce genetic material not adapted to local conditions (Haldane 1956, Kirkpatrick and Barton 1997). This genetic load can by itself lead to range limits or can act in concert with other mechanisms of range limitations (Case and Taper 2000, Case et al. this issue). This mechanism may not be a strong factor leading to permanent range limits, however, because gene flow can also provide novel variation upon which selection can then operate (Gomulkiewicz et al. 1999, Barton 2001, Holt et al. 2003).

Three routes to range limits in metapopulations

Metapopulation dynamics (Hanski 1999) provide a powerful perspective for interpreting distributional limits. Carter and Prince (1981, 1987) in a pioneering paper observed that range limits could arise given metapopulation dynamics, even with no overall decline in quality of habitable sites along a gradient. Lennon et al. (1997) reported detailed simulation studies amplifying the metapopulation perspective on species' range limits. Here, we use a simple metapopulation model parallel to (1) that highlights three distinct ways in which range limits can arise, given recurrent colonization and extinctions along a gradient (Holt and Keitt 2000).

Consider a species occupying discrete patches in a landscape of otherwise inhospitable habitats. Within a given landscape there are colonizations and extinctions. We assume there is a gradient at a broader spatial scale than defined by local landscapes, and use x to indicate the location of a landscape along the gradient. In effect, we make the parameters of the classical Levins metapopulation model (Hanski 1999) functions of x. This is a reasonable approximation if the distance over which the gradient changes is large relative to the distance over which there is recurrent colonization among patches within a landscape, and very occasional colonization events 'seed' local landscapes at the larger spatial scale of the gradient.

Let k(x) be the maximal fraction of patches suitable for occupancy in the landscape at gradient position x, n(x) the fraction actually occupied, e(x) the extinction rate (per occupied patch), and c(x) the colonization rate (of empty patches, per occupied patch). The model is

$$\frac{dn(x)}{dt} = n(x)c(x)[k(x) - n(x)] - e(x)n(x)$$

At equilibrium, $n \times (x) = k(x) - e(x)/c(x)$, thus $n \times (x) > 0$ if $k(x) > e(x)/c(x)$. There are three distinct dynamical routes to range limits (Holt and Keitt 2000).

i. Gradients in habitat availability

Extinction (e) and colonization (c) may be constant over space, whereas k varies. Where $k(x) < e/c$, the species disappears. Hence, a species limit may arise simply because insufficient habitat is available at the periphery (Gonzalez-Guzman and Mehlman 2001). As Carter and Prince (1981, 1987) noted, at range limits individuals within suitable patches may experience environments no different at all from those experienced by individuals in the range center.

ii. Gradients in local extinction rates

Habitat availability and colonization rates (k, c) may be spatially invariant, but extinction rates rise along a gradient. A range limit exists if $e(x) > ck$. Extinction rates may increase at the margin because of lower population sizes or because of higher environmental instability.

iii. Gradients in colonization rates

Finally, extinction and habitat availability may be fixed but per-patch colonization rates decline along a gradient. A range limit occurs if $c(x) < e/k$. This can reflect increased hostility or reduced penetrability of the matrix to dispersal. Consider a plant dependent upon animals for dispersal. Any factor reducing abundance or activity of dispersal agents along a gradient could limit the colonizing potential of plants from occupied patches into empty patches, indirectly causing a range limit. Likewise, decreased carrying capacity along a gradient might not inflate local extinction rates but instead reduce the output of dispersers and thereby cause a border.

In short, given metapopulation dynamics, range limits may arise because: 1) there is less habitat available at the periphery, 2) there is lower-quality habitat at the periphery (expressed in higher extinction rates), 3) the matrix habitat is more hostile to dispersal, or occupied patches produce fewer dispersal propagules. Maurer and Taper (2002) indicate that the second of these may be common. Recent empirical studies suggest that metapopulation dynamics may be common at range boundaries (Wilson et al. 2002).

Equilibrial vs non-equilibrial perspectives on range limits

Up to now, we have simply assumed that range limits are stationary, making it sensible to search for proximal explanations for range limits in terms of demographic responses to worsening conditions along a gradient. Yet the earth's surface is highly dynamic, and over long time-scales species' ranges must also be dynamic, with limits wandering across space (Graham et al. 1996). Observed borders could be transients, snapshots of the slowly shifting wavefronts of sluggishly invasive or contractive species, responding to past climatological events. An important, largely unanswered empirical question is the spatial and temporal scales over which species' ranges are stationary, or at least near enough stability to be analyzed using equilibrial assumptions about population and evolutionary dynamics.

Theoretical studies of range dynamics help highlight when to expect non-equilibrial ranges. In the above metapopulation model, space enters at two hierarchical spatial scales: the local scale (within-landscape colonization), and a regional or biogeographical scale (how colonization and extinction rates vary along a gradient). There is no explicit provision for communication via dispersal among different landscapes. To address non-equilibrial range dynamics requires more complex model structures, such as reaction-diffusion models (Okubo 1980) and related discrete patch models (Keitt et al. 2001). Here we do not delve into the mathematical formalism of such models, but instead highlight insights regarding non-equilibrial range dynamics which emerge from their study.

An invasive species, by definition, has an expanding range. A stationary range limit arises as an invasion halts. Theoretical studies of invasions in homogeneous environments (Skellam 1973, Okubo 1980, Andow et al. 1990) for species with intrinsic growth rate r and random Brownian motion (with a diffusion coefficient of D) predict an asymptotic invasion speed of $v = \sqrt{rD}$. This formula matches some, but not all, invasion data. Using well-documented invasions of muskrat (*Ondatra zibethica*) in Europe and the cereal leaf beetle (*Oulema melanopus*) and cabbage white butterfly (*Pieris (=Arogeia) rapae*) in North America and parameters taken from data on individual behavior, Andow et al. (1990) found the theory matched the data well in all cases, except for the cereal leaf beetle, which spread much faster than predicted. Andow and coworkers suggested this discrepancy is expected if the beetle disperses in a non-Brownian manner, perhaps by macro-scale 'jumps' on air currents. Other potential causes of discrepancies include seasonality, spatial variability, behavioral variation among individuals, stochastic events, interspecific competition or predation, and Allee effects. Of 28 bird species introduced into North America, only 9 have spread more than 20 miles from their point of introduction (Veit and Lewis 1996). The reasons for failures of introduced species to spread as predicted are myriad and not fully understood but are likely to include these factors. It is conceivable that the borders are not stable but simply shifting very slowly.

Recent theoretical studies have examined the influence of these realistic complications on invasion speed (Shigesada and Kawasaki 1997). Here we consider how three factors influence non-equilibrial range dynamics: (i) rare, long-distance dispersal events, (ii) Allee effects, and (iii) spatial variability.

i. Long-distance dispersal

Brownian motion implies the distribution of total movement distances over a fixed time interval fits a Gaussian curve. This often is not the case. For example, blue jays transport acorns up to several kilometers from the parent tree, whereas other dispersal agents such as squirrels transport acorns hundreds of meters. This mix of dispersal agents implies a leptokurtic distribution of dispersal, with more very short and very long distance events than predicted by Brownian motion (Clark et al. 1998). Kot et al. (1996) showed that invasion rate depends critically upon very long-distance dispersal events; leptokurtic distributions greatly inflate the rate of spread. This may explain rapid recolonization of North America by trees after the last ice age (Clark et al.

1998) and the rapid spread of the cereal leaf beetle. Turning these results around, non-equilibrial ranges are much more likely to persist for species without access to means of long-distance dispersal.

ii. Allee effects and invasion

The term 'Allee effect' (Allee 1938) describes a depression of per capita growth rates at low population densities (Courchamp et al. 1999, Stephens and Sutherland 1999). Lewis and Kareiva (1993) showed that Allee effects substantially reduce invasion speeds, and can even reverse invasions, generating a wave of extinction. Allee effects make disequilibrial range limits more likely in continuous environments. Below we show that an Allee effect in a patchy environment can even produce stationary range limits without gradients.

iii. Environmental heterogeneity

Shigesada et al. (1986, 1987) studied a reaction-diffusion model in which invasion occurs into a patchwork of two intermingled, distinct habitats. They studied both periodic and random variation in space of both intrinsic growth and dispersal rates. In a limiting case of small patches, the propagation speed of the invasion is proportional to $\sqrt{<\mathrm{r}><\mathrm{D}>}$, where $<\mathrm{r}>$ is the arithmetic mean r, and $<\mathrm{D}>$ is the harmonic mean of D (weighted by relative proportions of good and bad habitat). This interesting result can be used to assess the likelihood of non-equilibrial range dynamics.

Geographical ranges usually greatly exceed individual dispersal distances. Along a shallow environmental gradient (e.g. in the relative abundance of good and bad habitats), in the neighborhood of each point it may be reasonable to consider reaction–diffusion models to adequately characterize invasion. Consider a system where r and/or D vary smoothly along a gradient, x. With sufficiently smooth, gradual spatial variation, one might surmise that $\sqrt{(\mathrm{r(x)D(x)})}$ defines the local rate of invasion of a species. One might conjecture that a species' range would be quasi-stable in zones where either r or D were near 0.

Now assume that superimposed on this broad-scale gradient is local heterogeneity in growth or dispersal rates. The work of Shigesada et al. (1986, 1987) suggests a low rate of range movement may arise either because the arithmetic average intrinsic growth rate is zero or negative or the harmonic average dispersal rate is near zero. Because of the large sensitivity of the harmonic mean to small values, even rare habitats over which dispersal is difficult can lead to non-equilibrial range limits, with range limits shifting very slowly past dispersal barriers. These theoretical results suggest that non-equilibrial ranges are much more likely to be observed if there is local heterogeneity in dispersal, rather than growth rates.

Now, consider an entire community experiencing an abrupt environmental change. The time-scale of advance into newly favorable terrain could be very long for those species with low $<\mathrm{r}>$'s or $<\mathrm{D}>$'s. Species vary enormously in intrinsic rates of increase, dispersal rates, and sensitivity (in either growth or dispersal) to environmental heterogeneity (Holt 1993). In any community, there are likely to be some species with low r and/or D. These will require considerable time to reach new limits following abrupt environmental change. In particular, species with substantial spatial variation in dispersal rates are expected to have retarded broad-scale responses to environmental change. An open question in biogeography is the fraction of species' range limits within contemporaneous multispecies assemblages which are not in equilibrium and still responding to (e.g.) past climate change. The answer to this question will depend on another open question: how fast does a species approach a range equilibrium, and how does the answer to this question depend upon the spatial structure of the environment?

Landscape structure and species' borders: critical thresholds in connectivity

For species whose movement is restricted to a single habitat type, a range limit may exist simply because of a large gap in that habitat (e.g. a forest interior bird species that behaviorally avoids open habitats). Obviously, a species' range could abut a large expanse of habitat that is behaviorally avoided. However, range limits may also arise because of synergistic effects of numerous small gaps in the habitat distribution. From general studies of non-linear transitions in the connectivity of random landscapes (Stauffer and Aharony 1985, Gardner et al. 1987), we know that if habitats are made unsuitable for occupancy or dispersal in a spatially uncorrelated fashion, when around 60% of an originally contiguous habitat is degraded, the functional connectedness of the landscape begins to decrease dramatically. At this threshold level, even a few percent added habitat loss results in the effective isolation of remaining habitat islands.

Interestingly, near this 60% critical threshold in habitat connectedness, the results cited above concerning the rate of a species' invasion do not hold. At the threshold, the landscape pattern is strongly fractal; as a result, diffusion rates through the landscape will be altered, compared to homogeneous landscapes. In a fractal landscape, the dimension of the habitat pattern must be considered when computing the expected diffusion rate. In a uniform environment, the mean squared displacement of a diffusing particle grows linearly with time. However, in a fractal environment mean squared displacement increases as a power-law function of time (Havlin 1989). The exponent of the power-law depends on the fractal dimension of the environment through which dispersers move, constrained by the assumption that movements occur only through suitable habitat (Johnson et al. 1992). These results suggest that along a gradient of decreasing habitat availability, for species which can behaviorally avoid movements across unsuitable terrain one might observe relatively abrupt range limits, with ragged, fractal-like distributional patterns at the range edge (Milne et al. 1996, Holt and Keitt 2000, Travis and Dytham 2004).

Can stable range limits exist without large-scale spatial gradients?

We have thus far focused on species range limits along environmental gradients. An interesting question largely neglected in the literature is whether a stable species border can exist in the absence of environmental gradients (or interspecific interactions, Case et al. this issue). Recent theoretical studies demonstrate that an interaction between spatial movement and non-linear local population dynamics can result in stable distributional limits in environments without broad-scale gradients. For example, Lewis and Kareiva (1993) show that spatially-continuous diffusion models, when coupled with strong Allee effects, have solutions in which a species will settle into a constant range, despite the fact that the environment is perfectly homogeneous (Fig. 3). But in their model, the stationary solution requires parameters to have particular values; any perturbation to the parameters leads to either permanent range expansion or retraction.

Keitt et al. (2001) expand on these previous results and show that stable range limits emerge over a much broader range of parameters if suitable habitats are patchy. In effect, the range limit occurs when there is insufficient dispersal to overcome the Allee effect in patches beyond the species' current distribution. The result is a stable range of occupied habitat patches surrounded by a zone of patches with populations below the Allee threshold (Fig. 4).

Similar models have been analyzed by Wilson and Nisbet (1997) and Gaylord and Gaines (2000). The model of Gaylord and Gaines (2000) is specifically tailored to marine environments. In this model, the principal mechanism generating an Allee effect arises from the effect of strong advective flows on larval transport and subsequent recruitment. Larval recruitment can be dramatically reduced by along-shore and off-shore flows that carry larvae away from potential settlement sites, leading to extinction because larval recruitment cannot compensate for adult mortality. Recirculating eddy currents (a common occurrence where coastal points jut into along-shore flows) can result in localized containment of dispersing larvae and increased local recruitment. Under these conditions, the

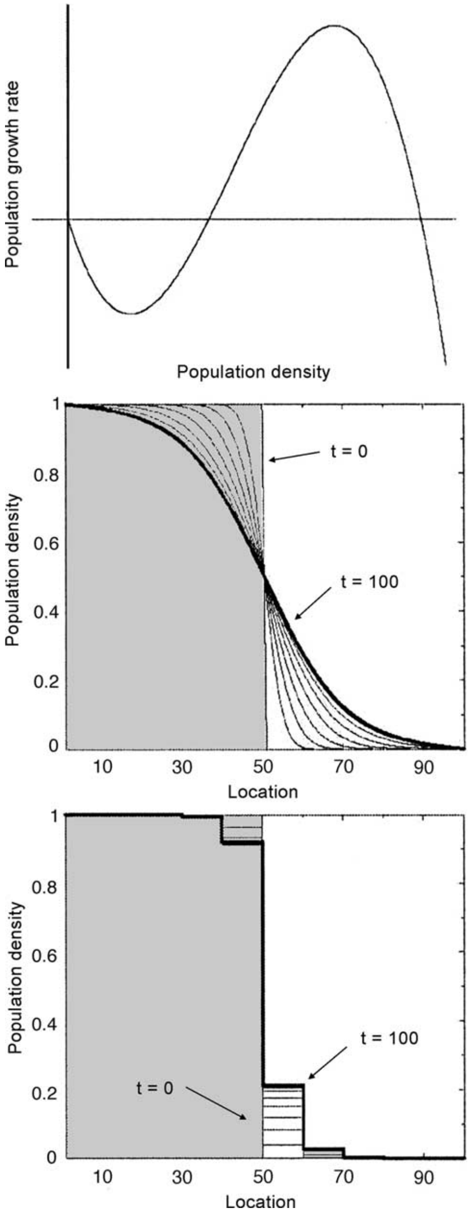

Fig. 3. Influence of Allee dynamics on species' borders. (a) Allee-type growth function. (b) Numerical solution to a reaction-diffusion model with Allee dynamics. Local growth is $dn/dt = rn(1-n)(n-a)$ (n = scaled population density, r = intrinsic growth parameter, and a sets the strength of the Allee effect). Initially occupied region is shaded. In continuous space, for this example a stationary range limit results only when $a = 1/2$ (Lewis and Kareiva 1993). (c) Numerical solution to a spatially discrete, coupled ODE model with Allee dynamics. Local growth function as in (b), except that the Allee parameter $a = 0.4$. The long-term solution is stable. The stair-step pattern reflects discrete habitat patches (within which density is assumed spatially uniform).

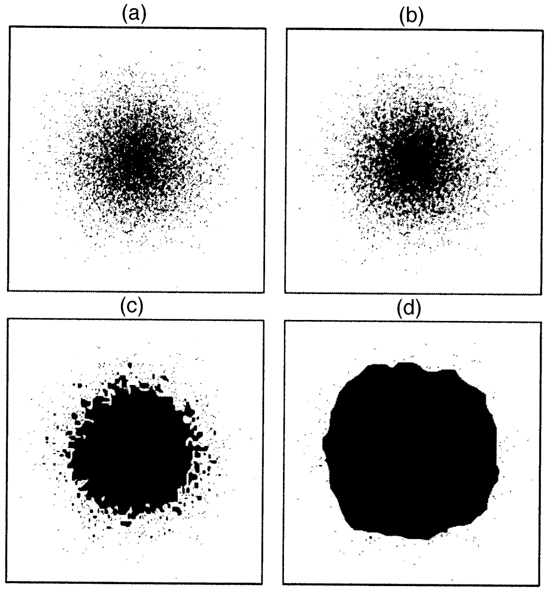

Fig. 4. Numerical simulation of the spatially discrete, coupled ODE model in two dimensions. The panels show successive snap-shots of the model output (at t = 0, 10, 100, 1000). Growth function and parameters are as in Fig. 3c. The initial state is a centered Gaussian distribution of occupied states. In this example, no broad-scale invasion occurs. A stable range limit forms when there are too few occupied cells within a neighborhood to overcome the Allee effect in initially empty cells (as in (d)).

model permits a stable, flow-induced range limit, with population extinction outside the area influenced by the recirculation, and population persistence in areas where the eddy carries larvae on-shore.

We suggest that stationary range limits may be common in relatively homogeneous environments for taxa with strong Allee effects (e.g. insect species subject to generalist predators with strongly saturating functional responses). Such species may successfully invade during periods with favorable conditions when the Allee effect is weak (e.g. due to high local recruitment rates), but later become trapped in particular spatial configurations as conditions gradually deteriorate throughout the species' range, say because of regional climate change (Keitt et al. 2001). Given this historical process, the specific locations of range limits would have no obvious, contemporaneous causal explanation, since the locations of the edges would depend only on historical accidents of initial occupancy, spatially frozen by the Allee effect, and not to responses to a gradually deteriorating environment along any particular environmental gradient.

Future directions and conclusions

As outlined in this section, there now exists a rich body of theory for understanding species' borders. Our understanding of species' range limits is however substantially limited by a lack of suitable data and experiments to validate current theory. In the absence of detailed, long-term studies at the range limit (Parmesan et al. this issue), a promising approach is spatial analysis of broad-scale survey data (Fortin, et al. this issue). Many theoretical models discussed here lead to distinctive spatial signatures (e.g. Fig. 4), and therefore might be tested by matching expected patterns to those observed in nature. Synoptic studies could provide an important guide for matching models to different ecological scenarios and species life-histories. For example, the three routes to metapopulation species' borders discussed above produce different spatiotemporal patterns of habitat occupancy (Holt and Keitt 2000). Allee effects can generate puzzling range limits in seemingly homogeneous environments (Keitt et al. 2001), and different dispersal modalities have distinct implications for borders (Guo et al., this issue). Future studies could attempt to distinguish among these scenarios using survey data, but such synoptic data analyses should be supported, when possible, by detailed, long-term experimental research on population dynamics near species borders and the development of explicit population models (Parmesan et al. this issue).

We also emphasize the need for more explicit studies of non-equilibrial dynamics (e.g. invasions and retractions) along strong environmental gradients (Zacherl et al. 2003). Why so many range limits remain stationary over perceptible time scales, while some species suddenly expand their distributions, sometimes over entire continents, remains a fascinating and largely unanswered question. There are many possible explanations for this phenomenon. Subtle changes in climate might open corridors for species movement that were previously blocked, operating in much the same way as land bridges that come and go with changes in sea levels. Sudden range expansions could reflect local Allee effects, circumvented when conditions improve sufficiently across the entire range to increase local production. A sudden increase in range may thus not reflect a change in conditions at the range margin, but instead shifts at sites internal to the already occupied range.

Species could also switch from an equilibrial to non-equilibrial range limit as a consequence of evolutionary processes (e.g. adaptive evolution in sink habitats at range margins; Holt and Gaines 1992, Kawecki 1995, Gomulkiewicz et al. 1999, Wiens 2004). There are an increasing number of examples of range shifts that appear to involve evolutionary responses (Davis and Shaw 2001, Helberg et al. 2001, Thomas et al. 2001). If a key innovation is discovered (in the evolutionary sense) that allows a species to persist and reproduce in previously inhospitable environments abutting the current limit, one might observe range expansion. If range expansion is due to evolutionary adaptation, one might expect a period with increasing rate of spread as the adaptation is refined by selection. Alternatively, demographic asymmetries could lead to the loss of peripheral habitats (Holt 1985, Kirkpatrick and Barton 1997, Holt 2003). The Haldane effect can influence the collapse of species ranges as well as limit their expansion. As a species' range decreases, for whatever reason, the population carries a smaller dispersal-generated genetic load and can thus better adapt to its remaining habitat (Case and Taper 2000). Species interactions and coevolution can also lead to sudden range shifts (Case et al. this issue). A species may not be able to expand its range because of competition or predation at the range margin. Subtle changes in community structure, due to shifts in the physical environment or species invasion or extinction, may render the community suddenly invadable by a formerly restricted species and allow it to expand its range; these ecological shifts could be amplified by concurrent evolutionary processes.

As noted by Parmesan et al. (this issue), vastly more studies have analyzed the dynamics of local populations, than the dynamics of geographical ranges. It strikes us that there are entire classes of questions which have barely been broached in the literature of geographical ecology, questions broadly parallel to familiar issues in population dynamics. Understanding the dynamics of local populations involves answering a series of questions: Will the population persist? If so, does it settle into a tight point equilibrium, or instead into a cyclic or chaotic attractor? How long does it take to recover from large perturbations? In like manner, when analyzing species' ranges, the most basic question is how to understand global persistence as a function of the interplay of local and regional processes. Given persistence, what determines the shape of the range? Given that a range has an asymptotic spatial equilibrium, what factors are most critical in determining the approach to this equilibrium following environmental change? Are there circumstances when one might see periodic cycles, quasi-periodic behaviors, or even chaotic wanderings in range limits? The theoretical studies we have explored above provide preliminary answers to some of these questions. But much remains to be done.

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