Ecology Letters, (2000) 3 : 41–47

REPORT

Alternative causes for range limits: a metapopulation perspective

Robert D. Holt[1] **and Timothy H. Keitt**[2]
[1]*Department of Ecology and Evolutionary Biology, Natural History Museum and Center for Biodiversity Research, University of Kansas, Lawrence, Kansas 66045, USA.*
E-mail: predator@ukans.edu
[2]*National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101, USA.*

Abstract

All species have limited distributions at broad geographical scales. At local scales, the distribution of many species is influenced by the interplay of the three factors of habitat availability, local extinctions and colonization dynamics. We use the standard Levins metapopulation model to illustrate how gradients in these three factors can generate species' range limits. We suggest that the three routes to range limits have radically different evolutionary implications. Because the Levins model makes simplifying assumptions about the spatial coupling of local populations, we present numerical studies of spatially explicit metapopulation models that complement the analytical model. The three routes to range limits give rise to distinct spatiotemporal patterns. Range limits in one species can also arise because of environmental gradients impinging upon other species. We briefly discuss a predator–prey example, which illustrates indirect routes to range limits in a metacommunity context.

Keywords

Ecological constraints on evolutionary dynamics, gradients, metapopulation dynamics, species borders.

Ecology Letters (2000) 3 : 41–47

INTRODUCTION

It is a truism of biogeography that species have limited distributions in space (Brown & Lomolino 1998). It is also a truism of population biology that local populations are often quite dynamic, fluctuating greatly in abundance, even to the point of experiencing local extinctions. A powerful mechanism for the persistence of species experiencing the vicissitudes of local extinctions is the coupling of populations via dispersal (MacArthur & Wilson 1967). Ecologists are becoming increasingly aware of how local populations and communities bear the imprint of spatial processes operating over large spatial scales (Ricklefs & Schluter 1993). For instance, the likelihood that a given species is found in a parcel of habitat does not depend just upon the local qualities of that habitat, but also upon the overall level of occupancy of habitats at broader spatial scales, which defines a regional pool of source populations available for colonizing suitable, empty sites. Understanding such metapopulation dynamics – the influence of coupling via dispersal among populations in heterogeneous landscapes – has become an increasingly pervasive theme in population and community ecology (Hanski & Gilpin 1997).

Traditional explanations for range limits emphasize variation in local demographic processes along gradients (for a recent example, see Wilson *et al.* 1996). Carter & Prince (1981) apparently were the first authors to elaborate the hypothesis that species' distributional limits may arise from metapopulation dynamics. (Levins 1970, p. 82, briefly mentions range limits as a consequence of metapopulation dynamics.) Lennon *et al.* (1997) have recently presented a detailed simulation model of a landscape metapopulation model exploring this suggestion, and showed how relatively sharp edges to a species distribution may arise even along smooth environmental gradients. In this paper, we show how a simple interpretation of the classical Levins metapopulation model (Levins 1969) can be used to discriminate three distinct causal routes to range limits.

The basic Levins model (as extended by Nee & May 1992) assumes that out of all patches available in a landscape, a fraction k are potentially suitable for a focal organism. Each occupied patch goes extinct at a constant per patch rate, e. Each empty patch is colonized at a per patch rate that increases with the fraction of the suitable patches that are already occupied. Given a large number of patches, one treats the fraction of patches occupied, n, as a continuous variable, which changes with time as follows:

$$\frac{dn}{dt} = cn(k - n) - en \qquad (1)$$

The species persists in the landscape with an equilibrial occupancy of $n^* = k - e/c$.

METAPOPULATIONS ALONG GRADIENTS

The Levins model (Hanski 1997) assumes that each empty patch is equally accessible for colonization from each occupied patch. This may at times be a reasonable assumption for some landscapes, but it clearly is a stretch to assume that all patches are equally accessible across the entire geographical range of a species, at least if range sizes are large relative to individual mobility. Lennon *et al.* (1997) deal with this problem by simulating localized dispersal in a spatially explicit patch model. We suggest that qualitative insight into range limits can come from a simple extension of model (1) to a smooth environmental gradient.

Assume that in a given landscape, defined by a particular spatial scale, equation 1 provides a good description of a species' dynamics. There will be a larger scale, much greater than that defining colonization among patches, where it is reasonable to assume that different landscapes provide different and largely uncoupled spatial arenas for local dynamics. Now imagine that these landscapes in turn are organized along a smooth environmental gradient, characterized by a single spatial dimension x. In effect, the distance over which conditions on the environmental gradient change is assumed to be quite large, compared with the distances over which it is sensible to imagine colonization among patches over ecological time-scales. One can mimic this large spatial scale with the Levins model quite simply by making its parameters functions of landscape position along the gradient, as follows:

$$\frac{dn(x)}{dt} = n(x)[k(x) - n(x)]c(x) - e(x)n(x) \qquad (2)$$

The quantity $k(x)$ describes the maximal fraction of suitable patches at point x along the gradient, $n(x)$ is the actual fraction of patches occupied at x, $e(x)$ is the extinction rate (per occupied patch) at point x on the gradient, and $c(x)$ scales the colonization rate of suitable, empty patches, per occupied patch. At equilibrium, at position x along the gradient, $n^*(x) = k(x) - e(x)/c(x)$. The species is thus expected to be absent at all points along the gradient x where $k(x) < e(x)/c(x)$. These points, by definition, fall outside the range occupied by a species.

Model (2) is obviously an idealization, because it does not incorporate dispersal linkages among metapopulations along the gradient (we discuss an approach to modelling coupled metapopulations below). Our main reason to ignore, for the moment, colonization across metapopulation boundaries, is that the addition of dispersal across metapopulation boundaries would have only a minor impact on our results, as long as typical dispersal distances are small relative to the width of a given metapopulation. Instead of arbitrarily making the model more complex, we focus on developing a general picture of causes for metapopulation range limits.

Because the metapopulation model has three parameters that define the condition for persistence in a landscape, a range limit can in principle arise because of variation along the gradient in any of these. In effect, given metapopulation dynamics, there are three distinct routes to range limits. We discuss each of these in turn below.

Route I. Gradients in habitat availability, $k(x)$

Imagine that extinction rates $e(x)$ are independent of position along the gradient x [$e(x) = e$, a constant], as is the colonization rate $c(x)$[$c(x) = c$, a constant] of empty, suitable patches from occupied patches. A range limit may nonetheless arise because the fraction of suitable patches k declines along the gradient. The range edge is defined by those landscapes where $k(x) < e/c$. Figure 1(a) shows a schematic example.

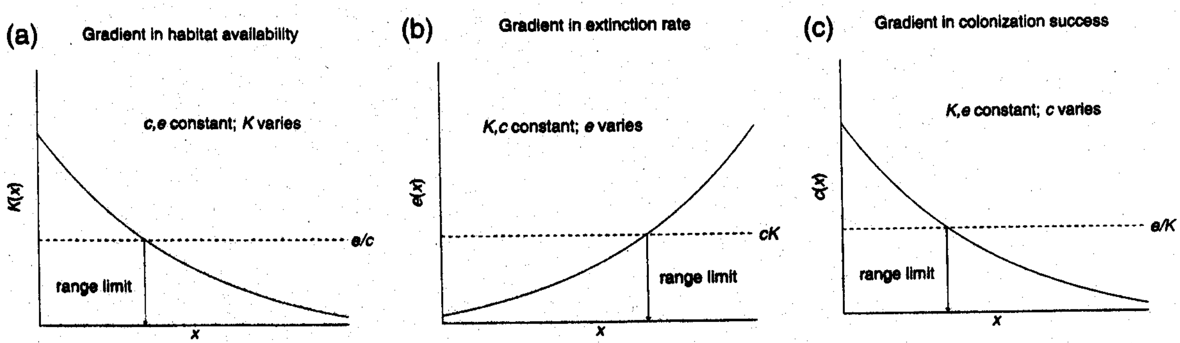

Figure 1 Graphical depiction of three routes to range limits in metapopulations along gradients. (a) Colonization and extinction rates are constant along the gradient, but habitat availability varies. (b) Habitats are uniformly available along gradient, as are colonization rates, but extinction rates increase. (c) Habitats are uniformly available, and extinction rates are constant, but the rate of colonization per habitable, empty patches, per occupied patch, declines. The specific shape of the parameter gradients is arbitrary.

Thus, a species' range limit may arise simply because insufficient habitat is available at the periphery for overall colonization rates to match local extinction rates. Changes in landscape structure along smooth environmental gradients can lead to range limits, even if local conditions remain uniform across the range. Deliberate species introductions into habitable patches outside the normal range of a species should be able to succeed for a time (which might give a misleading impression as to the permanence of the range boundary). As Carter & Prince (1981) observed, individuals actually occupying patches might experience no difference within their local environments (i.e. in patch interiors, as one goes from the centre to the edge of the range).

Route II. Gradients in local extinction rates

Now, imagine that the structure of the landscape (defined by k) and the colonization parameter c are invariant along the gradient, but the extinction rate e rises (Fig. 1b). In this case, the range limit is defined by those positions on the gradient where $e(x) > ck$.

There are many distinct biological reasons why local extinction rates might vary along an environmental gradient. For instance, population sizes may on average be lower toward the end of a gradient, because of lower intrinsic growth rates or very strong density-dependence (Holt *et al.* 1997), or an increasing impact of natural enemies or competitors, leading to higher rates of extinction because populations are constrained to low abundances. Or, there may be more frequent disturbances wiping out populations at one end of a gradient. Or, a species may be physiologically less well buffered against temporal variation in the environment, leading to an enhanced risk of extinction due to the combined effects of demographic and environmental stochasticity.

In contrast to causal mechanism I, higher extinction rates will often reflect environmental factors that can be directly perceived by individuals within patches, e.g. more intense predation near the edge. In this case, selection could act differently at the margin of the species' range, than in the range interior. Over evolutionary time-scales, variation in environmental conditions from the centre to the edge of the range could promote the evolution of spatially varying local adaptation.

Route III. Gradients in local colonization rates

Finally, we imagine that the landscape structure (k) is unchanged along the gradient, as is the local extinction rate (e). Instead, per-patch colonization rates decline along the gradient. In this case, a range limit will arise where $c(x) < e/k$ (Fig. 1c).

There are a number of reasons why the per-patch colonization rate might vary along an environmental gradient. First, any environmental factor that influences local population size can potentially influence the number of dispersing propagules emanating from occupied patches. This can be the case even if population sizes are always too large for such variation to influence markedly extinction risk. Second, successful colonization requires that the dispersers leaving an occupied patch move across unsuitable habitats to arrive at suitable, empty patches. Any physical or biotic factor influencing rates of dispersal or survival of dispersers across the interstitial landscape separating suitable habitat patches could vary along a gradient. As a hypothetical example, a species border in an oak species might arise as an indirect consequence of the diminished abundance of squirrels and other vertebrate dispersal agents along a major environmental gradient, or increased mortality risks for dispersing propagules, even in the absence of systematic variation in the number of suitable patches or their biotic or abiotic properties.

Dynamic similarities and differences among the three scenarios: Responses to local disturbances, and population lifetimes

In model (1), perturbations in population occupancy are damped at a rate described by $\lambda = \partial/\partial n(\mathrm{d}n/\mathrm{d}t)$, evaluated at n^*. The rate of return to equilibrium is $\lambda = -cn^* = e - ck$. The maximal value of λ is $-c$. Near the border, $n^* \sim 0$, so $\lambda \sim 0$ for all three scenarios. Qualitatively, species should be less resilient to perturbations near range margins, than in range interiors.

The Levins model assumes a constant per patch extinction rate, hence an exponential distribution of waiting times to extinctions. The mean time to extinction for a newly founded population (i.e. expected population lifetime) is $1/e$. If a range limit arises because of gradients in habitat availability or colonization rates, all populations in the range will on average have the same expected lifetime. By contrast, along extinction gradients populations tend to be younger near the range edge. This could have important evolutionary implications. If advantageous alleles that influence adaptation arise rarely (e.g. major genes), the opportunity for such mutational input should scale with population longevity. If central populations in a species' range persist longer than do peripheral populations, they may be more likely to develop adaptive responses honed to their local environments. This suggests that peripheral populations should be less well adapted to their local environments, compared with central populations, whenever enhanced extinction rates cause the range limit.

Communicating landscapes

The above approach assumes a gradient that is shallow enough that dispersal along the gradient can be ignored. Moreover, the Levins model assumes an effectively infinite number of equally accessible patches. In real-world landscapes, there will often be dispersal among patches at different points along a gradient, and a limited number of patches. There are two basic approaches to modelling such dispersal along a gradient: continuum models and spatially explicit models. A continuum model can be generated from model (1), if one replaces the colonization term with an expression such as $c(x, y)n(y)\mathrm{d}y$, which describes the contribution to colonization at each site by colonists emanating from all other sites. The quantity $c(x, y)$ is a "dispersal kernel" that typically declines with increasing magnitude of distance ($|x-y|$) between sites. This approach leads to an integrodifferential equation, which can be approximated by a reaction-diffusion equation (M.A. Lewis, T.H. Keitt & R.D. Holt, unpublished results). We do not pursue this approach here, but instead present some examples from spatially explicit models that portray the spatial implications of the three metapopulation routes to species' borders (see also Lennon *et al.* 1997 for a comparable example of simulations describing an extinction-driven metapopulation border).

The spatially explicit model consisted of a square lattice with reflecting boundary conditions and gradients superimposed across the lattice. We assumed discrete time, i.e. simultaneous cell updates across the entire lattice. Colonization and extinction occurred in two separate phases, and populations were surveyed after colonization. Extinction was modelled as a probability e that an occupied cell would become extinct during the extinction phase. The probability of colonization was proportional to the number of occupied cells in a four cell neighbourhood. If n_i is the number of occupied cells neighbouring cell i, then the probability of colonization is assumed to be $cn_i/4$, where c is a colonization parameter that can range from 0.0 to 1.0. Habitat suitability was modelled by assigning a probability $0 < k(x) < 1$ of a patch being suitable for occupancy, or not, to each cell along a gradient x. For purposes of illustration, we feel a two-dimensional spatially explicit model is more useful than a one-dimensional linear array. The metapopulation model (1) assumes a large number of patches, all of which are interacting via colonization. In a one-dimensional array along a smooth gradient, just one cell is found for any given combination of parameters, whereas there are a large number of comparable cells in the two-dimensional lattice with a gradient.

One of the interesting results of these simulations was the similarity among static "snap shot" patterns near the range limit (modulo shifts in position across the gradient owing to the particular parameters chosen). Despite the similarity in the static patterns, the underlying dynamics were quite different. The extinction-gradient driven case (i.e. colonization was held constant and extinction was increased across the lattice) produced a relatively sharp boundary between a largely occupied region and a largely unoccupied region (Fig. 2a). The sharpness of the boundary derives from the cooperative effect of local neighbourhood interactions (Wilson *et al.* 1996). However, we were able to generate a more diffuse edge by imposing a more gradual increase in the extinction parameter across the lattice.

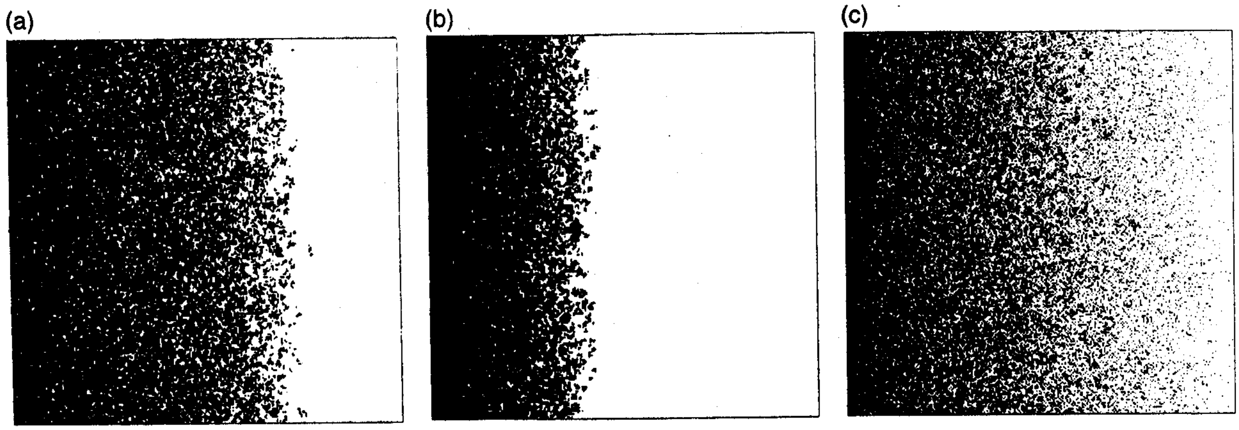

Figure 2 Simulation of three routes to borders for the spatially explicit model (see text). Spatial grids were 256 × 256 in size, with a linear gradient imposed from left to right. (a) Colonization was uniform ($c = 1$) at all locations and extinction e varied from 0 on the left side to 1 on the right. Cells occupied after 1000 iterations are in black. (b) Extinction was uniform ($e = 0.15$) but the colonization parameter varied from 1 on the left to 0 on the right. (c) Habitat availability varied along gradient. Grey coloured patches can never be occupied. Both colonization and extinction parameters were uniform ($c = 1$, $e = 0.15$) but the amount of suitable habitat varied from 100% on the left to 0% on the right. The figure depicts in a spatially explicit landscape the three scenarios generating range boundaries described in the text: gradients in extinction, or colonization from occupied into suitable, empty patches, or in the fraction of habitat suitable for occupancy.

When extinction rate was held constant, but colonization rate varied along the gradient, a much broader and more fragmented range edge appeared (Fig. 2b). Both the position along the gradient of the range limit, and the degree of fragmentation of the range edge depend in part on the particular parameters chosen in these simulations. However, the dynamics of the range edge under the different scenarios were strikingly different. In the extinction driven case, patches near the range limit turnover at high rates, whereas in the colonization driven case (with a relatively low rate of local extinction) the rate of patch turnover near the range limit is slow. Thus, to empirically distinguish between these two routes to a metapopulation species' border may require information on local rates of population turnover, and may be difficult in cases where only a spatial snap-shot is available. As a general comparison, over much of the parameter space the extinction driven case does tend to generate a more abrupt boundary, but this result should only be applied with some caution.

In the final scenario, we held extinction and colonization parameters constant and varied the amount of habitat available across the gradient (Fig. 2c). Of all three scenarios, the gradient in habitat availability produced the most fragmented edge, largely mirroring the increasing fragmentation of the underlying habitat. Patch turnover near the edge, as with the gradient in colonization, was considerably slower than in the extinction case. Because habitat patches were placed randomly along the gradient, reduced habitat area also leads to loss of habitat connectivity. The result therefore likely reflects both the effect of reduced area and the increased isolation. (We could have chosen to reduce area in a manner orthogonal to fragmentation by using a habitat "wedge" that tapered to a single patch across the lattice. However, we feel that the random habitat fragmentation scenario is more relevant to observed patterns of habitat fragmentation.)

Across all three scenarios, as one approaches the range boundary, occupancy of sites decreases until no patches remain occupied (Fig. 3). In both the colonization and the extinction gradients, the decrease in occupancy is strongly nonlinear and exhibits a convex shape. This convex shape reflects the recursive effect of colonization-extinction dynamics – decreased occupancy leads to decreased colonization, which in turn leads to decreased occupancy, and so on. (In the examples shown, the more rapid decline of occupancy in the extinction gradient as compared with the colonization gradient is simply a result of the parameters chosen. If the uniform extinction rate applied across the entire colonization gradient were increased, it would shift the border further left and produce a spatial pattern broadly similar to that produced by the extinction gradient; however, the noted differences among patch turnover rates would remain.)

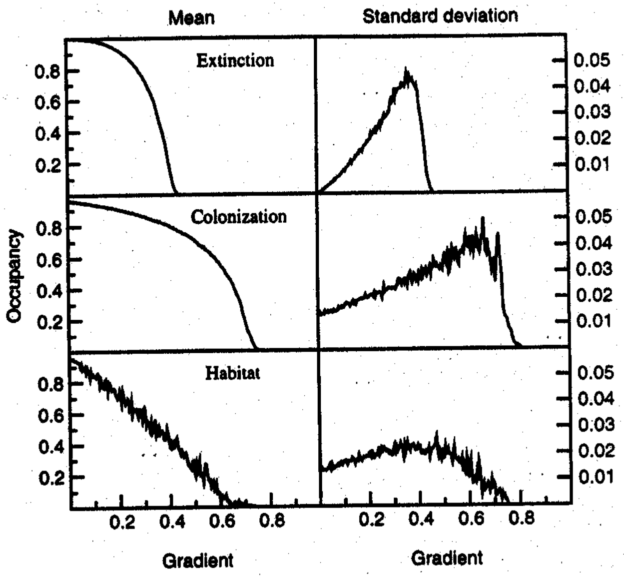

Figure 3 Patterns of patch occupancy for the species' borders depicted in Fig. 2. The left panels show mean occupancy, computed over 800 iterations following 200 initial iterations to remove transient behaviour. The gradients along the *x*-axis match those of the previous figure. The three routes result in quite different patterns of occupancy across the gradient. The right panels show standard deviations of occupancy. The distinct peak indicates a phase transition in the behaviour (Goldenfeld 1992; Milne *et al.* 1996).

Occupancy along the habitat gradient decays linearly in accord with the linear gradient in habitat availability. However, occupancy reaches zero while there is still some suitable habitat remaining near the species' border, a result also reported in previous studies (e.g. Lande 1987). For the parameters chosen here, colonization failed to balance extinction beyond about 70% habitat loss. The habitat availability gradient also resulted in increased variability when comparing occupancy between adjacent sites. The increased variability was largely a result of the stochastic nature of the underlying habitat distribution; at point x along the gradient, a particular cell is either habitable, or not, with probability $k(x)$. There is thus an inherent randomness in the landscape structure that stems from this parameter and provides a source of stochastic variation not present in the other two parameters.

Concurrent with the decrease in occupancy was a large increase in the standard deviation of occupancy near the range boundary (Fig. 3). These fluctuations are caused by repeated extinction and colonization events along the border. Particularly in the extinction-driven case, small clusters of occupied cells would break off from the main species distribution and form a transient "island" of occupied habitat. In some cases, the island may rejoin the main distribution. In other cases, the cluster dies out without ever rejoining the main distribution; this happens particularly frequently near the species' range limit. Population clusters that never rejoin the main distribution form a kind of evolutionary "dead end", since unique alleles that arise in these isolated clusters will never propagate back to the main population.

DISCUSSION

If a species has metapopulation dynamics within local landscapes, and if at large spatial scales the species range in effect is comprised of numerous such landscapes arranged along major environmental gradients, range limits may arise because:

1 there is less suitable habitat available at the periphery (as measured by *k*),

2 there is lower-quality habitat available at the periphery (as expressed in *e*), or

3 the matrix habitat separating patches is more hostile to dispersal, and/or occupied patches produce fewer dispersing individuals at the periphery (measured by *c*).

Of course, any of these mechanisms may act in combination to produce a range limit. In particular, the rescue effect may interlink colonization and extinction rates; a reduction in *c* may be correlated with enhanced *e*. This should tend to sharpen the range boundary.

This general approach to understanding range limits can be extended in a number of different directions.

For instance, many ecologists (e.g. MacArthur 1972) have argued that species' range limits arise as frequently from interspecific interactions as from the direct effects of habitat availability or the abiotic environment. In principle, for any multispecies metapopulation model, if one were to make its parameters functions of position along a gradient, one could generate a suite of potential causal routes to a species' distributional limit. For example, in the metapopulation models for specialist predator–prey interaction considered by Holt (1997), patches can be in one of three states: empty, prey present alone, prey present but with predator too. In this model, a species border for a predator might arise because of direct responses of the predator to the gradient (e.g. increasing predator extinction rates, or decreasing predator colonization rates), or indirectly because of the gradient influencing prey colonization or extinction rates.

In this model, a species' border for a specialist predator species can also arise directly because of the predator's own colonization and extinction dynamics, or indirectly because of a gradient in habitat suitable for its prey, or in the colonization rate of its prey, or in the extinction rate of its prey. A full explanation of the predator species' border needs to consider both direct and indirect changes along environmental gradients. In more general models with substantial dispersal along the gradient by the predator, spillover effects (Holt 1995) can lead to a limited range for the prey, maintained by the specialist predator. This effect has been explored by Hochberg & Ives (1999) for a standard predator-prey (non-metapopulation) interaction along an environmental gradient.

In conclusion, for species whose persistence depends upon a balance between colonization and local extinctions, there are three distinct routes to species' range limits: gradients in habitat availability, gradients in local extinction rates, and gradients in interpatch colonization rates. Any given species range limit could in principle arise because of any one (or combinations) of these factors. Discriminating among these routes to range limits is necessary to predict the pattern of long-term species evolution across its geographical range. Moreover, in a community of interacting species a range limit could arise as an indirect reflection in one species of environmental gradients directly affecting the dynamics of other species. A fundamental question for empirical studies of species range limits is to assess the importance of the basic metapopulation processes of ongoing colonization and local extinctions in defining the realized spatial patterns of habitat occupancy at distributional boundaries.

ACKNOWLEDGEMENTS

The work reported here was supported under the aegis of "The Ecological and Evolutionary Dynamics of Species Borders" working group at the National Center for Ecological Analysis and Synthesis, funded by the National Science Foundation. RDH also acknowledges National Science Foundation support.

REFERENCES

Brown, J.H. & Lomolino, M.V. (1998). *Biogeography*, 2nd edn. Sinauer, Massachusetts.

Carter, R.N. & Prince, S.D. (1981). Epidemic models used to explain biogeographical distribution limits. *Nature*, 293, 644–645.

Goldenfeld, N. (1992). *Lectures on Phase Transitions and the Renormalization Group*. Addison Wesley, New York.

Hanski, I. (1997). Metapopulation dynamics: from concepts and observations to predictive models. In: *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds Hanski, I. & Gilpin, M.E.), pp. 69–92. Academic Press, San Diego.

Hanski, I. & Gilpin, M.E. (1997). *Metapopulation Biology: Ecology, Genetics, and Evolution*. Academic Press, San Diego.

Hochberg, M.E. & Ives, A.R. (1999). Can natural enemies enforce geographical range Limits? *Ecography*, 22, 268–276.

Holt, R.D. (1995). Food webs in space: an island biogeographic perspective. In: *Food Webs: Integration of Patterns and Dynamics* (eds Polis, G.A. & Winemiller, K.O.), pp. 313–323. Chapman & Hall, London.

Holt, R.D. (1997). From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. In: *Metapopulation Biology: Ecology, Genetics, and Evolution* (eds Hanski, I. & Gilpin, M.E.), pp. 149–165. Academic Press, San Diego.

Holt, R.D., Lawton, J.H., Gaston, K.J. & Blackburn, T.M. (1997). On the relationship between range size and local abundance: back to basics. *Oikos*, 78, 183–190.

Lande, R. (1987). Extinction thresholds in demographic models of territorial populations. *Am. Naturalist*, 130, 624–635.

Lennon, J.J., Turner, J.R.G. & Connell, D. (1997). A metapopulation model of species boundaries. *Oikos*, 78, 486–502.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol Soc. Am.*, 15, 237–240.

Levins, R. (1970). Extinction. In: *Some Mathematical Problems in Biology* (eds Gesternhaber, M.), pp. 77–107. American Mathematical Society, Providence, RI.

MacArthur, R.H. (1972). *Geographical Ecology*. Harper & Row, New York.

MacArthur, R.H. & Wilson, E.O. (1967). *The Equilibrium Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Milne, B.T., Johnson, A.R., Keitt, T.H., Hatfield, C.A., David, J. & Hraber, P.T. (1996). Detection of critical densities associated with piñon-juniper woodland ecotones. *Ecology*, 77, 805821.

Nee, S. & May, R.M. (1992). Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecology*, 61, 37–40.

Ricklefs, R.E. & Schluter, D. (1993). Species diversity: regional and historical Influences. In: *Species Diversity in Ecological Communities: Historical and Geographic Perspectives* (eds Ricklefs, R.E. & Schluter, D.), pp. 350–363. University of Chicago Press, Chicago.

Wilson, W.G., Nisbet, R.M., Ross, A.H., Robles, C. & Desharnais, R.A. (1996). Abrupt population change along smooth environmental gradients. *Bull. Mathemat. Biology*, 5, 907–922.

BIOSKETCH

Robert D. Holt has broad interests in ecology and evolutionary theory, and has focused in particular on the dynamics of multispecies interactions, and ecological constraints on evolutionary processes.

Editor, P. Marquet
Manuscript received 25 October 1999
Manuscript accepted 25 October 1999