REVIEW

On the relationship between niche and distribution

H. Ronald Pulliam
Institute of Ecology, University of Georgia, Athens, Georgia, 30602, U.S.A.
E-mail:
pulliam@ecology.uga.edu

Abstract

Applications of Hutchinson's *n*-dimensional niche concept are often focused on the role of interspecific competition in shaping species distribution patterns. In this paper, I discuss a variety of factors, in addition to competition, that influence the observed relationship between species distribution and the availability of suitable habitat. In particular, I show that Hutchinson's niche concept can be modified to incorporate the influences of niche width, habitat availability and dispersal, as well as interspecific competition *per se*. I introduce a simulation model called NICHE that embodies many of Hutchinson's original niche concepts and use this model to predict patterns of species distribution. The model may help to clarify how dispersal, niche size and competition interact, and under what conditions species might be common in unsuitable habitat or absent from suitable habitat. A brief review of the pertinent literature suggests that species are often absent from suitable habitat and present in unsuitable habitat, in ways predicted by theory. However, most tests of niche theory are hampered by inadequate consideration of what does and does not constitute suitable habitat. More conclusive evidence for these predictions will require rigorous determination of habitat suitability under field conditions. I suggest that to do this, ecologists must measure habitat specific demography and quantify how demographic parameters vary in response to temporal and spatial variation in measurable niche dimensions.

Keywords

Dispersal, habitat specific demography, Hutchinsonian *n*-dimensional niche, species distributions.

"It is not necessary in any empirical science to keep an elaborate logicomathematical system always apparent, any more than it is necessary to keep a vacuum cleaner conspicuously in the middle of a room at all times. When a lot of irrelevant litter has accumulated, the machine must be brought out, used, and then put away."
G.E. Hutchinson, 1957, Concluding Remarks, p. 415.

INTRODUCTION

In his famous "Concluding remarks", G. Evelyn Hutchinson (1957) provided a new formalization of the niche concept that has since become central to much ecological reasoning and theory. Hutchinson defined the fundamental niche of a species as an "*n*-dimensional hypervolume", every point in which corresponds to a state of the environment which would permit a species to exist indefinitely. Over the 40 plus years since Hutchinson's remarks, a lot of irrelevant litter has accumulated regarding the niche concept, and it is perhaps now a good time to bring Hutchinson's niche machine out and use it to clean up the mess we have made.

Hutchinson's hypervolume concept provides a simple, although rigorous, approach to quantifying the niche. As stated by Hutchinson (1957, p. 416) "consider two independent environmental variables e_1 and e_2 which can be measured along ordinary rectangular coordinates . . . an area is defined, each point of which corresponds to a possible environmental state permitting the species to exist indefinitely." The simplest interpretation of this view of the niche is shown in Fig. 1(A): a species occurs everywhere that conditions are suitable (pluses) and never occurs where conditions are unsuitable (open circles). This is what James *et al.* (1984) have referred to as the "Grinnellian niche", stating that "under normal conditions of reproduction and dispersal, the species is expected to occupy a geographical region that is directly congruent with the distribution of its niche".

Unfortunately, Hutchinson no sooner introduced his concept of the fundamental niche than he told the reader that a species will not utilize its entire fundamental niche, but rather the "realized niche" actually occupied by the species will be smaller, only consisting of those portions

of the fundamental niche where the species is competitively dominant. Hutchinson argued that Volterra and Gause had already "demonstrated by elementary analytic methods that under constant conditions two species utilizing, and limited by, a common resource cannot coexist in a limited system". As a result of competitive exclusion, according to Hutchinson, the realized niche is smaller than the fundamental niche, and a species may frequently be absent from portions of its fundamental niche because of competition with other species.

Figure 1(B) illustrates Hutchinson's concept of realized niche. The species is shown to be absent from a portion of its fundamental niche due to competition with another species that is presumably a superior competitor for that portion of the niche space. Figures 1(A) and 1(B) might be combined into a single graph by adding a third dimension, representing the abundance of a "hidden" competitor species. In such a combined graph, Fig. 1(A) might represent a cross-section of the three dimensional graph for zero abundance of the competitor, and Fig. 1(B) might represent another cross-section when the hidden competitor is at its equilibrium abundance. However, such a depiction of the niche confuses the concepts of environmental requirements and environmental impacts (*sensu* Liebold 1995). The axes in Figs 1(A) and 1(B), environmental variables e_1 and e_2, indicate the requirements of the species in as much as they show the range of values of e_1 and e_2 for which the species can survive and reproduce. These requirements for e_1 and e_2 do not change in the presence and/or absence of the competitor species, and the abundance of a competitor is not a requirement for existence of the species. The abundance of the competitor is important only to the extent that the competitor impacts an environmental requirement, such as food or light. Leibold (1995) stated the problem clearly by saying that although "Hutchinson used a definition of the niche explicitly focusing on requirements, his use of the niche in discussing competition was much more related to impacts and roles of species".

Hutchinson may have contributed to the confusion surrounding the niche concept by ignoring previous usage of the term. As pointed out by Colwell (1992), Griesemer
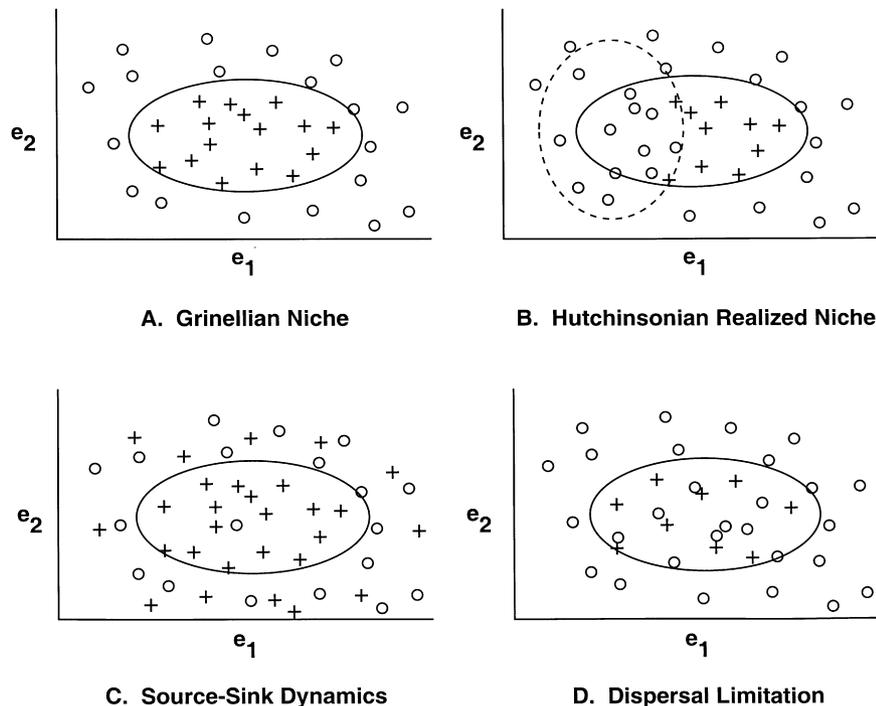
Figure 1 Four views of the relationship between niche and species distribution. In each diagram, the solid oval refers to the fundamental niche or the combination of environmental factors (e_1 and e_2) for which the species has a finite rate of increase (λ) greater than or equal to 1.0. The "pluses" indicate the presence of the species in a patch of habitat characterized by particular values of e_1 and e_2, and the "zeroes" similarly indicate the absence of the species in a patch of habitat. According to the Grinnellian niche concept (A), a species occurs everywhere that conditions are suitable and nowhere else. Hutchinson's realized niche concept (B) postulates that a species will be absent for those portions of the niche space that are utilized by a dominant competitor. According to source–sink theory (C), a species may commonly occur in sink habitat where λ is less than 1.0. Metapopulation dynamics and dispersal limitation (D) posit that species are frequently absent from suitable habitat because of frequent local extinctions and the time required to recolonize suitable patches.

(1992) and Schoener (1989), Hutchinson (1957) used the word niche to refer to the environmental requirements of a species, whereas earlier authors, especially Elton (1927) and Grinnell (1917), had used the term niche to refer to a place or "recess" in the environment that has the potential to support a species. Hutchinson, in a sense, turned the niche concept on its head, emphasizing attributes of species or populations rather than attributes of the environment. According to Hutchinson, species, not environments, have niches.

Some of the confusion over the niche concept can be clarified by keeping in mind that all species not only respond to variation in the environment, but they also all change the environments in which they occur. Thus when two or more species occur together they change both their own and one another's environment. In some cases, species directly interact with one another, as in predator–prey and interspecific territorial interactions. More often, species interact indirectly, by jointly influencing the environments in which they occur. Most cases of interspecific competition are indirect interactions between species mediated by the influence of one species on the limiting resources of another species.

The presumed relationship between niche and distribution can become even more complicated when one considers the recent concepts of metapopulations, source–sink dynamics and dispersal limitation. Pulliam (1988) differentiated between source habitats, where local reproduction exceeds local mortality, and sink habitats, where the opposite holds. Sink habitats, by definition, do not have "conditions necessary and sufficient for a species to carry out its life history" (James *et al.* 1984); nonetheless, large numbers of individuals may occur in sinks because of immigration from source areas (Pulliam 1988). Since a species may frequently be found in unsuitable sites where environmental conditions do not permit it to persist indefinitely in the absence of continued immigration, it has been said (Pulliam 1988) that the realized niche is often larger than the fundamental niche. Perhaps a clearer way of stating this is that the range of conditions actually experienced by the species is greater than the range of conditions for which birth rates equal or exceed death rate.

There is growing evidence that some organisms are "dispersal limited" (Cain *et al.* 1998; Clark *et al.* 1998), meaning that they often do not reach, and are therefore often absent from, suitable habitat. Furthermore, the modern theory of metapopulations posits that populations frequently go locally extinct and that, even at equilibrium, only a fraction of suitable habitat will be occupied. Figures 1(C) and 1(D) illustrate the relationship between niche and distribution under source–sink dynamics and

dispersal limitation, respectively. In a source–sink situation, a species can be expected to frequently occur outside the bounds of its fundamental niche, in as much as frequent immigration to sinks may maintain large numbers of individuals in places where the environmental state does not permit the species to exist in the absence of immigration (Pulliam 1988). Finally, in the case of dispersal limitation, a species may frequently be absent from suitable (source) habitat because of the difficulty of reaching such areas.

At the time of Huthinson's "Concluding remarks" paper, ecologists were very much concerned about the role of competition in structuring natural communities, but they paid very little attention to dispersal, habitat heterogeneity and habitat-specific demography. The primary purposes of the current paper are to incorporate dispersal into the Hutchinsonian niche concept and to present the case that dispersal may be at least as important as competition in determining the relationship between niche and distribution.

EXPANDING THE NICHE CONCEPT

Niche width, dispersal and habitat availability and stability all contribute to the relationship between niche and distribution. To explore the complex relationships among these variables, I introduce a landscape population model called NICHE that simulates niche and population dynamics of one or more species on a complex landscape. NICHE begins with a quantitative description of the niche of each species of interest and a description of the landscape where these species occur. The landscape consists of a grid of cells, and each cell in the grid is characterized by particular values of environmental variables, e_1, e_2, etc. Each species in NICHE is characterized by its own species-specific demographic response function to each environmental variable. The demographic response functions may take on many shapes, such as normal, parabolic, logistic, etc. For example, in the examples presented here, juvenile survival (P_j) for each species is given by the parabolic equation

$$P_j = P_j^{\max}\{1 - a_1(e_1 - \mathrm{opt\_}e_1)^2\} \qquad (1)$$

where $P_j^{\max}$ is the maximum juvenile survival, opt_e_1, or optimal e_1, is the value of variable e_1 for which the species has its highest juvenile survival, and a_1 is a parameter that specifies how rapidly P_j declines as e_1 deviates from its optimal value, opt_e_1.

By specifying demographic response functions for all environmental variables that influence the demography of a species, the niche of a species may be quantitatively specified. For example, consider an annual plant species

that responds to environmental variable 1 according to equation (1), and to environmental variable 2 (perhaps soil moisture) according to

$$\beta = \beta^{max}\{1 - a_2(e_2 - \text{opt}\_e_2)^2\} \qquad (2)$$

where β is the mean number of seeds produced and β^{max} is maximum number of seeds. (In the simulation examples presented later, β is taken as the mean of a Poisson distribution that specifies the complete probability distribution for the number of seeds produced.) In this example, one environmental factor (e_1) only influences juvenile survival, and the other environmental factor (e_2) only influences reproductive success. Though these specific assumptions are made to illustrate how the model works, the basic model is completely general and allows for different factors to influence different or the same demographic variables. In a real application, how the environmental factors influence demographic variables should be determined by empirical evidence.

The fundamental niche of a species may be depicted by plotting the finite rate of increase (λ) as a function of the environmental variables influencing λ. For the annual plant example discussed above, λ is given by the product βP_j, and by specifying particular values for the parameters in equations (1) and (2), we can depict the niche of our annual plant in environmental dimensions e_1 and e_2 as shown in Fig. 2. Consider the simple case where the environmental state of each grid cell is specified by two variables e_1 and e_2, which can be thought of as soil pH and soil moisture (in bars of pressure). Assume that the optimal soil pH for the single plant species under consideration is 7.0, but that the various grid cells may have pH ranging from very acid to very basic. Similarly, assume that the plant species under consideration does best when soil moisture is 3.0 bars and less well when soil is very wet or very dry. Using equations (1) and (2), the finite rate of increase in this case is given by

$$\lambda = P_j^{max}\{1 - a_1(e_1 - \text{opt}\_e_1)^2\}\beta^{max}\{1 - a_2(e_2 - \text{opt}\_e_2)^2\}. \quad (3)$$

Figure 2(A) shows contours of $\lambda = 0.5$, $\lambda = 1.0$ and $\lambda = 2.0$, for the case where $\beta^{max} = 20$, $P_j^{max} = 0.2$, $a_1 = 0.2$ and $a_2 = 0.5$. In this case, grid cells with pH 7 and moisture of 3 bars have the greatest potential for population increase with $\lambda = 4.0$. All of the points within the contour of $\lambda = 1$ can be ascribed to the fundamental niche of the species, since for these particular combinations of e_1 and e_2 the species can increase in population. The contour $\lambda = 2$ can be interpreted as the combination of environmental conditions for which the population doubles each year and the contour $\lambda = 0.5$ is the combination of conditions for which the population declines by 50% each year (in the absence of immigration).

The landscape in the NICHE model consists of a two-dimensional array of grid cells. The landscape represents the environmental conditions in "ordinary physical space" and corresponds to what Huthchinson called the "biotope". As stated by Hutchinson (1957, p. 416), "the fundamental niche may be regarded as a set of points in an abstract *n*-dimensional **N** space. If the ordinary physical space **B** of a given biotope be considered, it will be apparent that any point p(N) in N can correspond to a number of points $p_i(B)$ in B, at each one of which the conditions specified by p(N) are realized in B." Perhaps, had Hutchinson been a terrestrial ecologist he would have referred to the biotope as a landscape. However, being an aquatic ecologist, Hutchinson used the more general term biotope, which includes the three dimensional possibilities of an aquatic world, or of the soil environment for that matter.

The environmental conditions at any point in space and time are specified for each grid cell, and all individual organisms in a grid cell at that time are assumed to experience the same environmental conditions. Figure 2(B) shows a discrete approximation of how λ changes with e_1 and e_2 for the same conditions shown in Fig. 2(A), and this approximation can be used to classify and map environmental conditions on a real landscape or biotope. By dividing the landscape into grid cells small enough that environmental conditions are approximately uniform within a cell, each cell can be classified according to the discrete values of environmental factors, as shown in Fig. 2(C). Classifying the grid cells in this way not only specifies the values of the environmental variables, e_1 and e_2, but also, indirectly, specifies the demographic parameters β, P_j and λ for each cell.

So far we have treated λ as a density-independent parameter whose value is determined solely by the physical environmental conditions on a given grid cell. One way to introduce density-dependent population growth into the NICHE model is by making environmental conditions depend on the density of individuals. For example, at high population densities, the activities of the organisms may alter pH, moisture, nutrient availability or some other environmental factor, making conditions less favourable for population growth. The problem with this approach is that for sessile organisms, these changes are likely to be very localized and may not occur at the scale of an entire grid cell (Huston & DeAngelis 1994), especially if that grid cell is large enough to support many individuals. NICHE can be modified to account for localized interactions within a grid cell by keeping track of the exact location of all individuals so that the impact of each individual on the environmental conditions experienced by its neighbours can be calculated. For example, moisture availability may be influenced at the level of the grid cell by topography
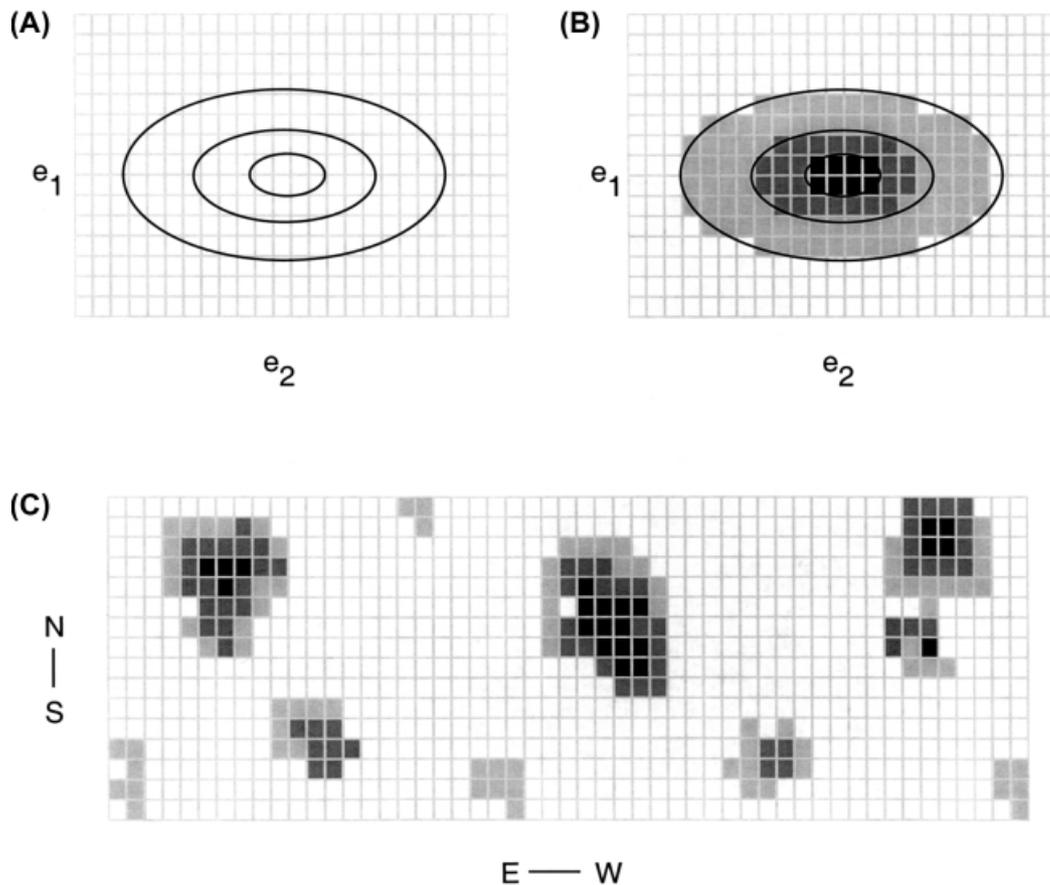
Figure 2 The relationship between species distribution in niche space and suitable habitat in real (geographical) space. (A) Contours of λ in two niche dimensions (e_1 and e_2); (B) a discrete approximation of the same information. The discrete categories shown in (B) can be used to map habitat quality in real space. Notice that part (C) has geographical axes (north–south and east–west) and thus refers to environmental conditions on an actual landscape. The shades of grey on the landscape depicted in (C) refer to degrees of habitat suitability as categorized in the (B) (black, $\lambda > 1.5$; dark grey, $2.0 < \lambda < 1.0$; light grey, $0.5 < \lambda < 1.0$).

and aspect, but the actual moisture level experienced by an individual at a particular location within a grid cell may be further influenced by how far that individual is from its nearest neighbours. Incorporating this local effect, however, requires detailed information about how individuals influence their immediate surroundings and, in turn, how this impact influences the growth of their neighbours.

For the results presented below, an alternative, and much simpler, way of modelling density dependence is employed. In the model presented below, it is assumed that individuals influence each other directly by "occupying" available space rather than indirectly by changing the environmental conditions experienced by their neighbours. When a seed reaches an unoccupied grid cell, it is assumed to germinate and survive with probability P_j, specified, as before, by the environmental conditions on the grid cell. However, when a seed reaches a grid cell already occupied by n individuals, it is assumed that n of k possible microsites are already occupied, so that the seed

survives and germinates with probability $(1 - n/k)P_j$. Because density dependence is experienced locally, each grid cell, c, can be said to have its own finite rate of increase given by:

$$
\lambda_c(n_c) = (1 - n_c/k)P_j^{max}\{1 - a_1(e_{c1} - \text{opt\_}e_1)^2\}\ \beta^{max}\{1 - a_2(e_{c2} - \text{opt\_}e_2)^2\}
\tag{4}
$$

In other words, local growth rate depends on local environmental conditions, including local population size (n_c), local pH (e_{c1}) and local soil moisture (e_{c2}). Although the model could easily be adapted to allow k, the number of available microsites per grid cell, to vary between grid cells, for the examples presented below k is constant and arbitrarily set at 100.

To complete a model of population growth, even for this relatively simple situation, we must specify both landscape structure, which is to say the environmental conditions (e_1 and e_2) on all cells, and the dispersal rules,

which govern the probability that seeds produced on any one cell migrate to any other cell in the landscape. For all simulation results considered in this paper, migration is equally likely to occur in all directions and distances travelled are assumed to follow an exponential distribution (corresponding to $c = 1$ in the dispersal models of Clark *et al.* 1998, also see Ribbens *et al.* 1994). In the exponential distribution, the probability that a seed travels distance x is given by $\sigma \exp(-\sigma x)$, and the mean distance travelled is $1/\sigma$. All of the simulations are conducted on a grid of cells with each cell having unit width. Thus, if the dispersal parameter σ equals 1, the mean seed dispersal distance is the width of one cell, and if $\sigma = 0.5$ the mean dispersal distance is the width of two cells.

Migration, for the purposes of this paper, occurs each time a seed moves out of the grid cell in which it is produced. Movement is calculated from the centre of the grid cell, thus seeds travelling more than half of the width of a grid cell contribute to migration, and those travelling less than this distance do not. For the simulations discussed below, σ ranged from 0.5 to 32, and for the exponential distribution, the fraction of individuals travelling more than 0.5 unit distance is given by $1 - \exp(-\sigma/2)$. Thus when $\sigma = 1.0$, approximately 61% of the seeds migrate, when $\sigma = 4.0$, ~14% of the seeds migrate, and when $\sigma = 16$, only about 0.3% migrate from their natal site. Furthermore, when $\sigma = 1.0$, about 22% of seeds travel at least two grid cells from the natal site and ~8% travel three or more cells away, but for σ of 8.0 or more, less than 1% of seeds travel more than one grid cell way from their natal site. Because low values of σ result in high dispersal values, low values of σ (<0.5) also frequently result in population extinction on landscapes where the majority of cells represent sink habitat, because most seeds migrate into unfavourable habitat. Finally, seeds that migrate beyond the boundaries of the landscape are considered lost, increasing the probability of local extinction on very small landscapes.

The simulation results reported here are for landscapes composed of 400 grid cells (20×20). For each simulation, each grid cell was randomly assigned an integer value of environmental variable e_1 (pH) between 1 and 9 and an integer value of environmental variable e_2 (soil moisture) between 1 and 10. Thus, there are 90 different types of grid cells, which can be thought of as 90 habitat types, each with a different environmental state, and on average there are four or five cells of each type randomly distributed across the landscape. Individuals on cells with $e_1 = 7$ and $e_2 = 3$ have the highest survival and reproductive success. Using the parameters $a_1 = 0.2$ and $a_2 = 0.5$, grid cells with e_1 (pH) between 6 and 8 and e_2 (moisture) between 2 and 4 have $\lambda > 1.0$ and are called sources or source habitats, and all other cells are called sinks or sink habitats. However, not all sinks are equal. For example, those with pH of 5 or 9 and moisture of 3 have $\lambda = 0.8$, and those with pH 5 or 9 and moisture of 2 or 4 have $\lambda = 0.4$. All other sinks have $\lambda = 0$ (if equation (3) yields a negative value, λ is set to 0). Overall, the landscape used in the simulations can be described as a few patches of source habitat (usually 20–25) randomly scattered in a sea of sink habitat (375–380).

At the beginning of each simulation run, each source cell is initialized with five adult individuals. Each of these adults reproduces and produces an average of β seeds (a randomly chosen number from a Poisson distribution with mean given by equation (2)). Each seed individually moves in a random direction according to an exponential distribution with parameter σ (between 0.5 and 32) and, upon migrating, becomes a juvenile (seedling) located in the grid cell containing its landing point. At this point all adults die and seedlings survive to become new adults with probability given by equation (4), depending on local conditions. Those seedlings that survive become the adults of the next year. Since survival and reproduction are stochastic (depending on independent random draws from a Poisson distribution), there is a finite chance of extinction each time step, and all populations will eventually go extinct unless there is immigration (rescue, *sensu* Brown & Kodric Brown 1977) from the outside. All simulations are run for 500 years and in most cases there is relatively little extinction during this time period.

IMPLICATIONS OF THE NICHE MODEL

Hutchinson, of course, was correct in assuming that the presence of a competitor reduces the realized niche relative to the fundamental niche. This can be seen by examining Fig. 3, which compares the abundance of a focal species in the presence and absence of a competitor. Both species have the same niche breadth (set by $a_1 = 0.2$ and $a_2 = 0.5$), the same low dispersal rate ($\sigma = 16.0$) and the same optimum e_2 (3.0). The competitor species is similar in all ways except that it has an optimum e_1 of 6.0 as compared with an optimum e_1 of 7.0 for the focal species. The presence of a competitor results in a 26.8% decrease in the overall abundance of the focal species (737.0 ± 60.1 (SE) when alone *versus* 541.6 ± 51.7 when competitor is present). As can be seen in Fig. 3, most of the reduction in abundance of the focal species in the presence of the competitor occurs, as expected, in the habitat types more suitable for the competitor than for the focal species. At pH 6.0, which is optimal for the competitor species but below the optimum for the focal species, the mean density of the focal species is 5.12 ± 0.38 (SE) individuals per grid cell in the absence of the competitor species, *versus* only 2.93 ± 0.74 in its presence.
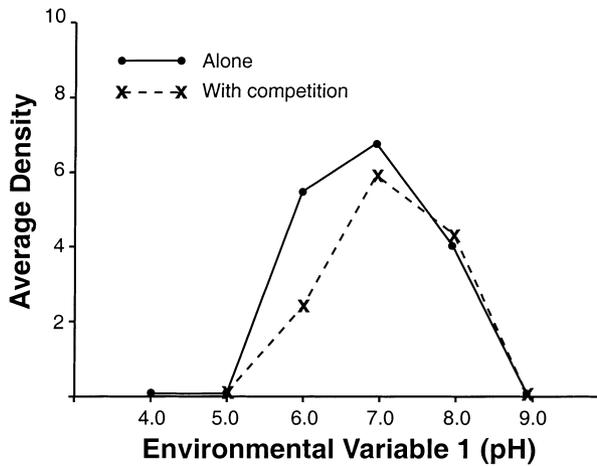
Figure 3 Population density in the presence and absence of a competitor. The solid line shows the mean density of a species with optimum pH of 7.0 along a pH gradient in the absence of a competitor species. The dotted line shows the abundance of the same species along the pH gradient in the presence of a competitor that has an optimal pH of 6.0. The presence of a competitor results in a statistically significant reduction in density of the focal species in habitat patches characterized by pH 6.0. Each value of "average density" in this figure is the number of individuals per grid cell, averaged over five separate simulations after 500 years.

Although the results in Fig. 3 are supportive of the idea of niche reduction in the presence of a competitor, they do not fully support Hutchinson's assertion that the "realized niche is smaller than the fundamental niche". Both in the presence and in the absence of the competitor, a large fraction of the population of the focal species occurs outside the fundamental niche in the sense that individuals are present in grid cells where λ is less than 1.0. The fraction of the population outside the bounds of the fundamental niche increases with increasing dispersal rate. When a similar set of simulations were performed with higher dispersal rates ($\sigma = 1.0$ *versus* $\sigma = 16$), the reduction in niche size in the presence of the competitor was barely discernible, and there was no significant reduction in total population size when the competitor was present. These results suggest that, whereas interspecific competition may have a discernible influence on distribution, other factors such as dispersal may, in some circumstances, be more influential and have an overriding influence on the effects of competition *per se.*

To explore the effect of dispersal *per se* on the relationship between fundamental and realized niche, a series of simulations were run with only one species at a time, but with separate simulations conducted for a variety of species with different values of the dispersal parameter (s). Figure 4 compares the cumulative fraction of the total population in various portions of niche space after 500 time steps (years) for a range of species with dispersal rates varying from very high dispersal ($\sigma = 1$, Fig. 4A) to very low dispersal ($\sigma = 16$, Fig. 4 *C*). As expected, a greater proportion of the population is contained within the portion of niche space for which λ exceeds 1.0 (shaded area) for the species with low dispersal than for the species with higher dispersal. This trend can also be seen in Fig. 5(A), which shows the proportion of the entire population in source habitat for a wide range of dispersal parameters (σ). When dispersal rate is high ($\sigma < 2$), on average about 60% of the entire population is in source habitat, and about 40% is in sink habitat. At the other extreme, when dispersal is low, the great majority of individuals ($>95\%$) are in source habitat when $\sigma = 16$ and 100% of the individuals are in source habitat for $\sigma = 32$. This increase in the percentage of the population in source habitat occurs despite a decrease in the fraction of source patches occupied, from about 80% occupied when $\sigma = 1$ to an average of less than 20% when $\sigma = 32$ (Fig. 5 *B*). These two trends taken together correspond nicely to the situation depicted in Fig. 1(C, D), with a high fraction of the population occurring outside the bounds of the niche when dispersal is high and a large fraction of empty suitable sites when dispersal is low.

OPEN QUESTIONS AND RESEARCH NEEDS

Clearly, competition, dispersal, niche size and the distribution of environmental conditions in space and time all play some role in determining species distributions in relationship to the distribution of suitable habitat. Theory suggests that species might be absent from suitable habitat and present in unsuitable habitat, but how common is this in nature? Part of the answer depends, of course, on the scale of resolution. For very fine-scale resolution, say on the order of individual forbs in the forest understory, an unoccupied spot may be just as suitable as the occupied one a few centimetres away, and, at this scale, there may be little or no relationship between distribution and suitability. At the other extreme, that of entire biogeographic regions, a species may be present in the only region which provides suitable conditions, resulting in a perfect, although trivial, match between distribution and suitable conditions. The question of the relationship between the distribution of a species and the distribution of its habitat may be most interesting at the landscape scale where the mean width of habitat patches is roughly an order of magnitude or two greater than dispersal distances. It is at this scale that dispersing propagules frequently reach unsuitable habitat while, at the same time, some suitable patches go uncolonized.
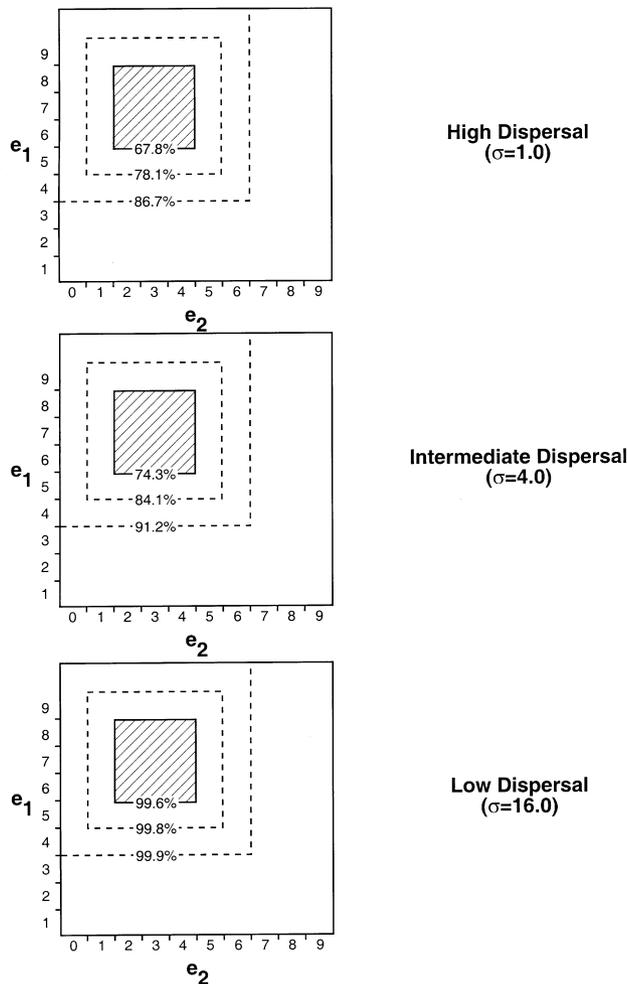
Figure 4 Fraction of the total population in various portions of niche space for species with different dispersal parameters. The crosshatched area in each panel indicates the fundamental niche ($\lambda > 1.0$), and the contours indicate the fraction of the total population that occurs in grid cells (habitat patches) within the indicated environmental range. The fraction of the population occurring outside the bounds of the fundamental niche increases with increasing dispersal rate. Lower values of σ refer to higher dispersal rates. Species with low dispersal rates tend to occur only, or almost only, in suitable habitat patches, while species with high dispersal may frequently occur in unsuitable habitat patches.

How often are species absent from suitable habitat?

Natural historians have often noted the absence of species from what appears to be suitable habitat, but it is theory, not natural history observations, that has focused attention on the absence of species from suitable habitat. Metapopulation theory and landscape ecology have added substantially to our understanding of the distribution of

organisms in heterogeneous landscapes (Schmida & Ellner 1984; Turner *et al.* 1989; Venable & Brown 1993; Beshkarev *et al.* 1994; Dias 1996; Eriksson 1996; Hanski 1996). We now understand that, for many species, local extinctions and recolonizations are common in nature (Hanski *et al.* 1994), and that organisms may frequently be absent from suitable habitat because of local extinctions and/or dispersal limitation (Kadmon & Pulliam 1993, 1995; Hanski 1994; Pulliam & Dunning 1994).

In discussing classical (or "Levins-type") metapopulations, Hanski (1998) stated "population extinction is a recurrent rather than a unique event". The extinction events may be due to small population size and the random stochastic nature of birth and death, leading to a finite probability of extinction despite an expectation of $\lambda > 1.0$. In addition to demographic stochasticity, environmental variability may lead to local population extinctions. In this case, habitats become temporarily unsuitable, leading to the extinction event, and this may be followed by a period of habitat being empty after it has once again become suitable. Local extinction in a suitable habitat may also be due to genetic stochasticity or drift, leading to genotypes maladapted to local conditions. This too may be viewed as a case of empty suitable habitat if, in the population at large, there are genotypes for which the local habitat patch is suitable. One of the best known cases of metapopulation dynamics and a species being absent from suitable habitat is that of the threatened Bay checkerspot butterfly, *Euphydryas editha bayensis* (Murphy *et al.* 1990; Ehrlich & Murphy 1987). Local extinctions are common in this species due to a combination of unpredictable rainfall, the dynamics of its host plants and demographic stochasticity. The Glanville fritillary butterfly (*Melitaea cinxia*) is another species that shows metapopulation dynamics on a fragmented landscape (Hanski 1998; Saccheri *et al.* 1998). In this case, low genetic heterozygosity as well as habitat quality and demographic stochasticity contribute to its high extinction rate on small and isolated patches.

Metapopulation models are equilibrium models and they assume a balance has been reached between extinction and colonization rates. For example, Valverde & Silvertown (1997, 1998) studied the woodland herb *Primula vulgaris*, which forms small tree gap populations. As tree gaps form and conditions become suitable for this species, some of these gaps are colonized, but eventually the gaps close and local extinction follows. The persistence of the metapopulation requires a high production of dispersing seeds and a large number of gaps being available for potential colonization. Valverde and Silvertown develop a metapopulation model that results in an equilibrium with only a small fraction of all suitable forest patches being occupied by this species.
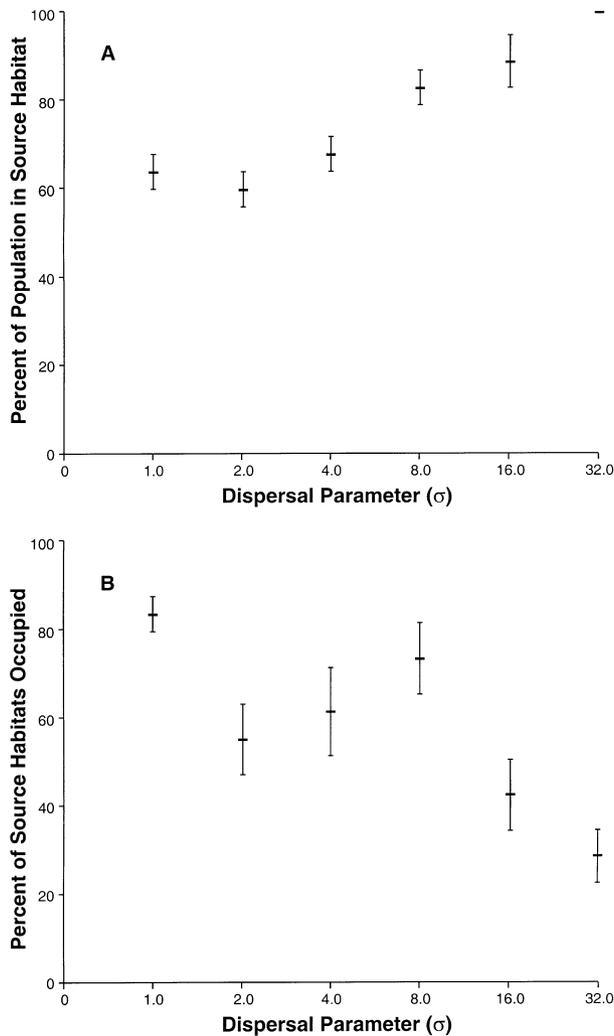
Figure 5 The proportion of the population in source habitat and the fraction of source habitat patches occupied for a wide range of dispersal parameters (σ). As shown in (A), when dispersal rate is high ($\sigma < 2$), only about 60% of the population is in source habitat, but when dispersal rate is low, most individuals are in source habitat (>95%). At the highest dispersal rate ($\sigma = 32$), 100% of the individuals occur in source habitat for all replications. This increase in the percentage of the population in source habitat occurs despite a decrease in the fraction of source patches occupied, from about 80% occupied when $\sigma = 1$ to an average of less than 30% when $\sigma = 32$ (B).

Limited reproduction combined with low migration rates can limit recruitment into suitable habitat (Pulliam & Danielson 1991; Eriksson & Ehrlen 1992; Honnay *et al.* 1999) and can result in a species being absent from a large fraction of its suitable habitat. Such recruitment limitation can occur across a vast range of spatial scales, from microsites within a relatively uniform area, to tree gaps within a forest patch, to successional stages across a large landscape, to geographical regions across a species range. Primack & Miao (1992) demonstrated dispersal limitation experimentally by introducing seeds of a variety of annual plant species into "unoccupied but apparently suitable" habitat in Massachusetts. They found that several species established populations that thrived for at least several years and concluded "that dispersal limitation can limit the distribution of annual plant species on a local scale". Several studies have demonstrated that patches of ancient or old growth forest can be sources of recolonization for younger successional forests surrounding them, but that reestablishment is often a very slow process limited by dispersal. Brunet & von Oheimb (1998), for example, studied the migration of understory plants from ancient Swedish woodlands into surrounding deciduous woods varying in age from 30 to 75 years old. Typical migration rates were on the order of 0.3–0.5 m year, and young forests nearer to the ancient reserves were colonized first. Matlack (1994) reached similar conclusions in the Piedmont forests of the north-eastern United States, but he also found that plants with seeds that were ingested by, or otherwise adhered to, birds and mammals migrated into the regenerating forest more quickly than those dispersed by wind or ants.

Species distributions may be limited at the scale of their geographical ranges if suitable habitat changes rapidly, as might be expected during times of climate change. As early as 1899, in what has now been called Reid's Paradox (reviewed in Clark 1998), Clement Reid puzzled over how oaks reestablished themselves in Europe after the Pliestocene glaciations, given the relatively short distances that acorns were known to move. Similarly, Cain *et al.* (1998) argued that many woodland herbs in eastern North America have current distributions that extend hundreds or thousands of kilometres north of the southern limit of the Pliestocene glaciation, despite the fact that many of the same species have observed mean annual dispersal distances of only a few metres per year or less. At this rate, a plant species could migrate only tens of kilometres in the entire 16 000 years or so since the end of the last glaciation. In reviewing Reid's paradox, Clark concluded that there must be a "fat tail" to dispersal curves that accounts for rare long distance movements that establish populations far beyond their primary distribution. Petit *et al.* (1997) have now found strong genetic evidence supporting this point of view in the distribution of chloroplast DNA variants in European oaks. This accumulating evidence suggests that there is a considerable time lag between changes in climate and changes in distribution and that during much of this time, species may be absent from large portions of their potential geographical ranges.

How often are species found in unsuitable habitat?

Much of the theory of community ecology has been built around the notion that the presence of a species in a given area indicates that that species is somehow adapted to local conditions and that it has evolved a mechanism, such as niche specialization, to coexist with the other species in the area. Contrary to this view, source–sink theory predicts that organisms regularly occur, and sometimes may even be common, in unsuitable (sink) habitat, if immigration from productive source areas is sufficiently large (Holt 1985; Kadmon & Schmida 1990; Pulliam & Danielson 1991; Pulliam 1996). At the community level, this prediction suggests the possibility that the majority of species co-occurring in an area may be in sink habitat and that the elimination of immigration would result in substantial simplification of communities.

Due to the difficulty of defining and measuring habitat suitability, there are substantial methodological problems to demonstrating that species regularly occur in unsuitable habitat. Several methods, however, have been used to bolster the case for the presence of a species in unsuitable habitat. At the level of natural history observations, the absence of reproduction coupled with the observation of frequent immigration into an area has been used as indirect evidence for the presence of a species in unsuitable habitat. A good example comes from Mark Bush (personal communication) who made extensive floral surveys of the Krakatau Islands and found that the fig *Ficus pubinervis* is a common tree on the islands despite the absence of fig wasps which are essential for the successful sexual reproduction of the species. Bush argues that fig seeds are frequently brought to the islands in the digestive tracts of pigeons, thus maintaining the species in the absence of local reproduction.

Stronger evidence for the regular presence of species in unsuitable habitat comes from demographic studies that establish that local reproduction is more than sufficient to account for recruitment in some habitats (sources) but less than sufficient in other habitats (sinks). For example, recruitment of caribou (*Rangifer tarandus*) substantially exceeds mortality in tundra habitat, but in woodland habitat where predation by wolves is much more prevalent, annual mortality exceeds local reproduction by a factor of two (Bergerud 1988). Many other demographic studies have established wide variation in local population growth rates, suggesting source sink dynamics. For example, Werner & Caswell (1977) found that local population growth rates (λ) of teasel (*Dipsacus sylvestris*) ranged from 0.63 to 2.60 in different habitats in Michigan (a λ of 1.0 is necessary to maintain a local population in the absence of immigration).

In a few studies, it is relatively apparent what environmental conditions are associated with good and poor habitats. For example, Robinson *et al.* (1995) have found that large portions of the midwestern United States are sink habitat for several species of migratory passerine birds, due to forest fragmentation. Menges (1990) found that Furbish's lousewort (*Pedicularis furbishae*) had population growth rates greater than 1.0 in moist habitats with low plant cover but had negative growth rates in areas with dry soils or dense plant cover. Kadmon & Schmida (1990) measured survival and reproductive rates of the desert annual *Stipa capensis* in three habitats (slopes, depressions and wadis). The wadis were moist year round and the depressions held moisture longer after rainfall events than did the slopes. Kadmon demonstrated that, although only 10% of the plants occurred in wadi and depression habitats, 75%–99% of the seeds were produced in these habitats, and that net reproduction (natality minus mortality) in the slope habitat was negative while net gain from dispersal (immigration minus emigration) was positive.

Although there are other good demographic studies providing some evidence that local sink populations are maintained by immigration from productive source areas (see Keddy 1981, 1982; Hubbell *et al.* 1990; Eriksson & Bremer 1993; Watkinson & Sutherland 1995; Dias *et al.* 1996), there are very few cases of experimental confirmation of the role of immigration in maintaining sink populations. The absence of such experimental evidence leaves open alternative explanations such as rare good years that produce seed banks or otherwise buffer populations from decline in poor years when λ is less than 1.0. In one of the few attempts to demonstrate the importance of immigration, Kadmon & Tielborger (1999) experimentally prevented immigration of seeds from 34 plant species in putative source habitat and found a reduction of only one of the species in the putative sink habitat. Although Kadmon and Tielborger interpreted this result as contradicting the predictions of source–sink dynamics, they had no independent confirmation that most of the species in question had negative population growth rates in the putative sink.

I began this paper with a brief review of Hutchinson's *n*-dimensional niche concept and an argument that Hutchinson's "niche machinery" could, after 40 years, still help us understand the relationship between the distribution of species and the distribution of suitable habitat. Hutchinson's niche concept, metapopulation theory, and source–sink theory together provide a solid theoretical foundation for understanding the distribution of species. Unfortunately, the empirical verification of this large body of theory is less impressive than the theory itself. This may be due in part to 40 years of having a theory of the niche without any real attempt to actually measure niches directly. Virtually all of the examples cited

above attempt to test predictions about the distribution of species without actually establishing what does and what does not constitute suitable habitat. Numerous studies, many referenced above, have attempted to measure site-specific demography. Age- and stage-specific birth, death, immigration and emigration rates have been measured at multiple study sites for many species, but details of the physical and biological dimensions of the environment that directly influence population growth rates have rarely been measured on the sites where these demographic studies have been conducted.

Of course ecologists do routinely measure the responses of organisms, especially plants and microbes, to variations in environmental factors; however, this is usually done by physiological ecologists interested in individual level responses like rate of photosynthesis or carbon allocation (e.g. Bazzaz & Wayne 1994; Caldwell & Pearcy 1994), or by community ecologists interested in competition between species and community structure (e.g. Tilman 1997), or by ecosystem ecologists interested in ecosystem responses such as NPP or carbon storage (e.g. Hobbie & Chapin 1996; Jonasson *et al.* 1999). With few exceptions, even simple measurements like temperature, pH, nutrient levels and light intensities are not reported by population ecologists doing demographic studies. In several examples presented above (Menges 1990; Kadmon 1993), soil moisture was implicated as an important environmental determinant of population growth rate, but in no case was soil moisture actually measured.

Hutchinson's niche concept is a powerful tool greatly underutilized by ecologists (Holyoak & Ray 1999; Austin 1999). By measuring environmental conditions on the same sites where population growth rates are measured, ecologists can begin to determine what constitutes suitable and unsuitable habitat for the species they study. Furthermore, by coupling niche models with models of the physical environment, ecologists working with physical scientists may develop portable models of habitat suitability that allow them to predict the dynamics of species in places and times where they have not yet measured population dynamics. For example, a strong relationship between soil moisture and l, coupled with a model of how soil moisture changes with topographic position, soil type and precipitation, may allow ecologists to extend their predictions to other places or to climatic conditions anticipated for the future.

ACKNOWLEDGEMENTS

REFERENCES

Austin, M.P. (1999). A silent clash of paradigms: some inconsistencies in community ecology. *Oikos*, 86, 170–178.

Bazzaz, F.A. & Wayne, P.M. (1994). Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. In: *Exploitation of Environmental Heterogeneity by Plants* (eds Caldwell, M.M. & Pearcy, R.W.) . Academic Press, San Diego, pp. 349–389.

Bergerud, A.T. (1988). Caribou, wolves, and man. *Trends Ecol. Evolution*, 3, 68–72.

Beshkarev, J.E., Swenson, J.E., Anglestram, P., Andren, H. & Blagovidov, A.B. (1994). Long-term dynamics of hazel grouse populations in source-and sink-dominated pristine taiga landscapes. *Oikos*, 71, 375–380.

Brown, J.H. & Kodrick Brown, A. (1977). Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology*, 58, 445–449.

Brunet, J. & von Oheimb, G. (1998). Migration of vascular plants to secondary woodlands in southern Sweden. *J. Ecol.*, 86, 429–438.

Cain, M.L., Damman, H. & Muir, A. (1998). Seed dispersal and the Holocene migration of woodland herbs. *Ecol. Monographs*, 68, 325–347.

Caldwell, M.M. & Pearcy, R.W. (1994). *Exploitation of Environmental Heterogeneity by Plants.* Academic Press, San Diego.

Clark, J.S. (1998). Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Naturalist*, 152, 204–224.

Clark, J.S., Macklin E. & Wood, L. (1998). Stages and spatial scale of recruitment limitation in southern Appalachian forests. *Ecology*, 79, 195–217.

Colwell, R.K. (1992). Niche: a bifurcation in the conceptual lineage of the term. In: *Keywords in Evolutionary Biology* (eds Fox-Keller, E. & Lloyd, E.A.). Harvard University Press, Cambridge, MA, pp. 241–248.

Dias, P.C. (1996). Sources and sinks in population biology. *Trends Ecol. Evolution*, 11, 326–330.

Dias, P.C., Verheyen, G.R. & Raymond, M. (1996). Source-sink populations in Mediterranean Blue tits: evidence using single-locus minisatellite probes. *J. Evol. Biol.*, 9, 965–978.

Ehrlich, P.R. & Murphy, D.D. (1987). Conservation lessons from long-term studies of checkerspot butterflies. *Conservation Biol.*, 1, 122–131.

Elton, C. (1927). *Animal Ecology.* Sidgwick & Jackson, London.

Eriksson, O. (1996). Regional dynamics of plants: a review for remnant, source-sink and metapopulations. *Oikos*, 77, 248–258.

Eriksson, O. & Bremer, B. (1993). Genet dynamics of the clonal plant *Rubus saxatilis*. *J. Ecol.*, 81, 533–542.

Eriksson, O. & Ehrlen, J. (1992). Seed and microsite limitation of recruitment in plant populations. *Oecologia*, 91, 360–364.

Griesemer, J.R. (1992). Niche: historical perspectives. In: *Keywords in Evolutionary Biology* (eds Fox-Keller, E. & Lloyd,

E.A.). Harvard University Press, Cambridge, MA, pp. 231–240.

Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk*, 34, 427–433.

Hanski, I. (1994). Patch occupancy dynamics in fragmented landscapes. *Trends Ecol. Evolution*, 9, 131–135.

Hanski, I. (1996). Metapopulation ecology. In: *Population Dynamics in Ecological Space and Time* (edsRhodes, O.E. Jr,Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396, 41–49.

Hanski, I., Kuussari, M. & Nieminen, M. (1994). Metapopulation structure and migration in the butterfly (*Melitea cinxia*). *Ecology*, 75, 747–762.

Hobbie, S.E. & Chapin, F.S., III (1996). Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry*, 35, 327–338.

Holyoak, M. & Ray, C. (1999). A roadmap for metapopulation research. *Ecol. Lett.*, 2, 273–275.

Honnay, O., Hermy, M. & Coppin, P. (1999). Impact of habitat quality on plant species colonization. *For. Ecol. Management*, 115, 157–170.

Holt, R.D. (1985). Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.*, 28, 181–208.

Hubbell, S.P., Condit, R. & Foster, R.B. (1990). Presence and absence of density dependence in a neotropical tree community. *Phil. Trans. R. Soc. London Ser. B*, 330, 269–281.

Huston, M. & DeAngelis, D. (1994). Competition and coexistence: the effects of resource transport and supply rates. *Am. Naturalist*, 144, 954–977.

Hutchinson, G.E. (1957). Concluding remarks. *Cold Spring Harbor Symp Quantitative Biol.*, 22, 415–427.

James, F.C., Johnston, R.F., Wamer, N.O., Niemi, G.J. & Boecklen, W.J. (1984). The Grinnellian niche of the Wood Thrush. *Am. Naturalist*, 124, 17–47.

Jonasson, S., Michelsen, A., Schmidt, I.K. & Nielsen, E.V. (1999). Responses in microbes and plants to changed temperatures, nutrient, and light regimes in the Artic. *Ecology*, 80, 1828–1843.

Kadmon, R. & Pulliam, H.R. (1993). Island biogeography: Effect of geographical isolation on species composition. *Ecology*, 74, 977–981.

Kadmon, R. & Pulliam, H.R. (1995). Effects of isolation, logging, and dispersal on woody-species richness of islands. *Vegetatio*, 4, 1–7.

Kadmon, R. & Schmida, A. (1990). Spatiotemporal demographic processes in plant populations: an approach and case study. *Am. Naturalist*, 135, 382–397.

Kadmon, R. & Tielborger, K. (1999). Testing for source-sink population dynamics: an experimental approach exemplified with desert annuals. *Oikos*, 86(3), 417–429.

Keddy, P.A. (1981). Experimental demography of the sanddune annual, *Cakile edentula*, growing along an elevational gradient in Nova Scotia. *J. Ecol.*, 69, 615–630.

Keddy, P.A. (1982). Population ecology on an environmental gradient: Cakile edentula on a sand dune. *Oecologia*, 52, 348–355.

Leibold, M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology*, 76, 1371–1382.

Matlack, G.R. (1994). Plant species migration in a mixed-history forest landscape in Eastern North America. *Ecology*, 75, 1491–1502.

Menges, E.S. (1990). Population viability analysis for an endangered plant. *Conservation Biol.*, 4, 52–62.

Murphy, D.D., Freas, K.S. & Weiss, S.B. (1990). An environment-metapopulation approach to the conservation of an endangered invertebrate. *Conservation Biol.*, 4, 41–51.

Petit, R.J., Pineu, E., Demesure, B., Bacilieri, Alexis Ducousso, R. & Kremer, A. (1997). Chloroplast DNA footprints of postglacial recolonization by oaks. *Proc. Natl. Acad. Sci.*, 94, 9996–10001.

Primack, R.B. & Miao, S.L. (1992). Dispersal can limit local plant distribution. *Conservation Biol.*, 6, 513–519.

Pulliam, H.R. (1988). Sources, sinks and population regulation. *Am. Naturalist*, 132, 652–661.

Pulliam, H.R. (1996). Sources and sinks: empirical evidence and population consequences. In: *Population Dynamics in Ecological Space and Time* (edsRhodes, O.E. Jr,Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago.

Pulliam, H.R. & Danielson, B.J. (1991). Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Naturalist*, 137, S51–S66.

Pulliam, H.R. & Dunning, J.B. (1994). Demographic processes: Population dynamics on heterogeneous landscapes. In: *Principles of Conservation Biology* (eds Meffe, G.K. & Carroll, C.R.). Sinauer Associates, Inc, Sunderland, MA, Chapter 7

Ribbens, E., Silander, J.A. & Pacala, S.W. (1994). Seedling recruitment in forests: Calibrating models to predict patterns of true seedling dispersal. *Ecology*, 75, 1794–1806.

Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995). Regional forest fragmentation and the nesting success of migratory birds. *Science*, 267, 1987–1990.

Saccheri, I.J., Kuussaari, M. & Kankare, M. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature*, 392, 491–494.

Schmida, A. & Ellner, S. (1984). Coexistence of plant species with similar niches. *Vegetatio*, 58, 29–55.

Schoener, T.W. (1989). The ecological niche. In: *Ecological Concepts: the Contribution of Ecology to an Understanding of the Natural World* (ed. Cherrett, J.M.). Blackwell Scientific, Oxford, pp. 79–114.

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.

Turner, M.G., Dale, V.H. & Gardner, R.H. (1989). Predicting across scales: theory development and testing. *Landscape Ecology*, 3, 245–252.

Valverde, T. & Silvertown, J. (1997). A metapopulation model for *Primula vulgaris*, a temperate forest understorey herb. *J. Ecol.*, 85, 193–210.

Valverde, T. & Silvertown, J. (1998). Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. *J. Ecol.*, 86, 545–562.

Venable, D.L. & Brown, J.S. (1993). The population dynamic functions of seed dispersal. *Vegetatio*, 107/108, 31–55.

Watkinson, A.R. & Sutherland, W.J. (1995). Sources, sinks, and pseudosinks. *J. Anim. Ecology*, 64, 126–130.

Werner, P. & Caswell, H. (1977). Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology*, 58, 1103–1111.

BIOSKETCH

H. Ronald Pulliam is Regents Professor of Ecology at the University of Georgia. His major research contributions have been in biological diversity, community ecology, behavioural ecology, source-sink theory, and population dynamics in heterogeneous landscapes. He has also served as President of the Ecological Society of America, Science Advisor to the US Secretary of Interior, and Director of the National Biological Service.