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Distributional consequences of spatial variation in local demographic processes

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The population density of a species in space usually is highest near the center of its geographic range and declines with increasing distance away from the center. Since a large number of biotic and abiotic factors may act simultaneously to limit local densities of species populations, rather than trying to identify these, we focus o the general processes by which environmental factors affect population density. Four processes determine the rate of population change: birth, death, immigration, and emigration. These are functions of both space (density independent factors) and population size (density dependent factors). Death and emigration should be increasing functions of population density. Birth rate should increase with population density up to a point, then begin to decrease. Immigration should decrease with increases in density. Birth and immigration sum to a net rate of population gain and death emigration sum to a net rate of population loss. These two functions intersect to give a stable equilibrium point. The set of equilibrium points of populations in space determines the general pattern of population abundance in space. In order for population density to be a nonincreasing function of the distance from the geographic center, either population gain rate must be a nonincreasing function of distance from the geographic center and population density, or population loss rate must be a nondecreasing function of distance from the geographic center and population size, or both must occur.

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1. Introduction

A major activity in ecology has been to attempt to identify the factors that limit local population densities and geographic distributions of species. This has proven to be extremely difficult, because even for a single species many variables are probably important, and often these are not independent either in their effects on organisms, or in their pattern of spatial variation. Recently, multivariate statistical methods have been used to identify complex combinations of variables that appear to account for some spatial variation in population density (e.g. for plants: Kercher & Goldstein 1977, Strahler 1978; for invertebrates: Green 1971, 1974; for birds: Whitmore 1975, 1977; Rotenberry & Wiens 1980; Noon 1981; Collins et al. 1982; for mammals: Crowell & Pimm 1976; M'Closkey 1976; Dueser & Shugart 1978, 1979). These analyses assume linear responses of organisms to environmental variables, or at least that population responses can be approximated adequately by linear statistics (see review papers in Capen 1981). Westman (1980) has been able to test for curvilinear relationships by fitting Guassian curves to species population densities along environmental gradients. Regardless of the statistical approach, one problem common to all of these studies is that they seemingly fail to yield satisfying general principles. By definition each species and higher taxon is unique and its abundance and distribution are limited by different combinations of abiotic factors and biotic interactions. Consequently, the greater the precision with which these factors are enumerated and their complex interacting effects are elucidated, the less the ability to extrapolate the results to other taxa or even to additional populations of the same species.

An alternative approach to examining in detail the relationships between individual species and their environments (biotic and abiotic) is to search for and attempt to explain general statistical patterns that characterize the variation of local population density of many species over transects or gradients in geographic space (Hengeveld & Haeck 1981, Brown 1984). This procedure has the advantage of elucidating large scale patterns that cannot be described by studying small collections of local sites.

Species are not equally abundant throughout their ranges; rather, there is a general tendency for population density to be highest near the center of the geographic range and to decline relatively gradually and often symmetrically toward the boundaries (Whittaker 1961, Westman 1980, Hengeveld & Haeck 1982). Brown (1984) has proposed the following explanation for this pattern. The local population densities of species are affected by many biotic and abiotic variables that comprise the multiple dimensions of the Hutchinsonian (1957) niche. For any widespread species, the relative importance of these different factors varies from site to site over the geographic range. When all factors are considered, the pattern of spatial variation in environmental conditions tends to be autocorrelated so that nearby sites tend to have more similar combinations of variables than distant ones. Those places that offer the most favorable conditions support the highest population densities, and these will tend to be clustered together. With increasing distance away from the most favorable sites in any direction, one or more variables will become less favorable and lead to decreasing population densities. If the number of effectively independent limiting factors is reasonably large, and if environmental variation in those factors is reasonably gradual, the spatial distribution of population density along any transect which runs through the center of the species' range will tend to resemble a normal, or bell-shaped, curve (Brown 1984; see also Ramensky 1924, Whittaker 1967, Westman 1980). Brown's (1984) model applies only to species with a unimodal pattern of abundance in space. Obviously, species abundance patterns which are not unimodal violate one or more of these conditions. We do not consider such patterns here.

The present paper provides a mechanistic model that develops the relationship between the demographic processes (birth, death, immigration, and emigration) that determine local population density and spatial variation in the environment which results in geographic variation of abundance. We begin by considering the processes limiting the density of a single, local population, and then in later sections investigate how these processes vary among collections of spatially distinct populations.

2. Regulation of local population density

The dynamics of a single local population may be viewed as a change in density over time, dN/dt. There are four processes that together determine this rate. Positive increments, or gains, result from births and immigration, while decreases, or losses, whill be due to death and emigration. A simple representation of this is

$$\frac{dN}{dt} = (b + i) - (d + e),$$
$$= g - l,$$

where b, i, d, and e are the rates of birth, immigration, death, and emigration, g is the rate of gain and l is the rate of loss. In real populations, the gain and loss rates will have both density dependent and density independent components. Density dependent factors may be viewed as making the functions, b, i, d, and e functions of N. Density independent factors result from environmental variation in space and time, although only spatial variation is considered here. Consequently, b, i, d, and e also be functions of space. Let X represent space, then

$$\frac{dN}{dt} = b(N, X) + i(N, X) - d(N, X) - e(N, X),$$
$$= g(N, X) - l(N, X). \qquad (1)$$

The demographic significance of Eq. 1 is that the functions b, i, d, and e integrate information from a multivariate vector of environmental factors (where population density is also considered a factor) into a single population response.

In the rest of this section we will assume that X is fixed, and hence that dN/dt is a function only of

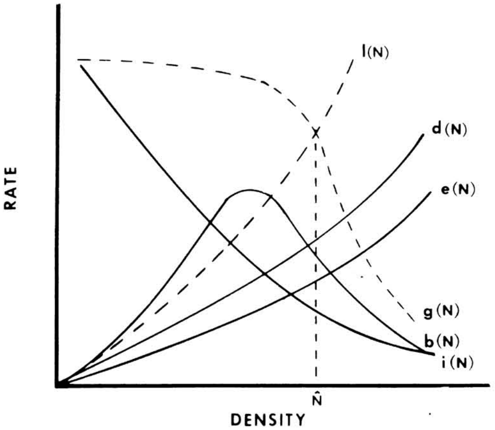

Fig. 1. General forms of functions relating birth rate (*b*), immigration rate (*i*), death rate (*d*), and emigration rate (*e*) to population density (*N*). The dashed lines indicate sums of birth and immigration rates (*g*) and death and emigration rates (*l*). The intersection of the population gain function (*g*) and the population loss function (*l*) determines the equilibrial density ($\hat{N}$).

population density. In a later section we will examine the situation where *X* is allowed to vary. We may infer something about the general shape of *b, i, d,* and *e* from the general properties of these processes. Given a fixed number of potential immigrants, the rate of immigration should decrease with increasing population density. We have shown *i* as a convex downward function in Fig. 1, but it may be concave without affecting the argument below. The important feature of this assumption is that population increases lead to decreases in the rates of immigration into the population (MacArthur & Wilson 1967). Reproduction or birth rate in a population should increase as the population density increases up to a point, at which, in most populations, birth rate should begin to decrease due to density dependent factors (e.g., increased competition for limited resources, aggressive encounters, and susceptibility to predators and pathogens). In Figure 1, we have represented *b* as a unimodal, symmetrical function, but neither the precise shape nor the symetricity need be assumed. These two rates *b* and *i,* will sum to a rate of gain, *g,* which is the simplest case we assume to be a noincreasing function of population density. This assumption may be relaxed by letting *g* be an increasing function of population density when densities are low, and becoming nonincreasing for high population densities, as would occur, for example, if immigration were negligible. Both death and emigration rates should be nondecreasing functions of population size. In fact, it is reasonable to suspect that both of these functions will be convex downward, since the change in death rate (and perhaps also emigration rate) should increase rapidly with population density as crowding and intraspecific competition become severe. The sum of these two functions should give a nondecreasing loss function, which is zero when $N=0$.

The point at which the functions *g* and *l* intersect is an attractor point at which recruitment into the population equals losses from the population and towards which population density moves. That is, if we let *N* be the population density at which $g = l$, then population densities larger than *N* will have negative growth rates while those smaller will have positive growth rates. We now investigate some implications of these ideas.

2.1. Logistic growth

Pielou (1977) has shown that if the per capita gain rate decreases linearly, while the per capita loss rate increases linearly with *N,* then the logistic form of population growth is obtained. That is, let

$$(1/N)\ g = a_1 - b_1 N$$
$$(1/N)\ l = a_2 + b_2 N$$

then Eq. (1) becomes

$$\frac{dN}{dt} = N\ [(a_1 - a_2) - (b_1 + b_2)N\ ]. \quad (2)$$

Figure 2a shows the form of *g* and *l* under logistic growth. There are two equilibrium points: $N=0$ and $N = (a_1 - a_2)/\ (b_1 + b_2)$. Reparameterizing Eq. (2) into the form commonly seen in textbooks, we have $r = (a_1 - a_2)$ and $K = (a_1 - a_2)/\ (b_1 + b_2)$.

We point out two features of the logistic here. First, notice that an underlying assumption of the logistic is that when $N=0$ the net rate of population gain is zero (i.e., *g* is forced through the origin). Hence, the logistic assumes no immigration is occurring. Second, there are only two equilibrium points, $N=\hat{N}$ and $N=0$. $N=0$ is unstable, hence any perturbations away from zero will always result in population growth towards $\hat{N}$.

Now consider the more realistic situation of a minimum population size below which reproduction cannot occur. This may be represented by letting

$$g = a_1 N - b_1 N^2 - c, \qquad (3)$$

where a_1, b_1, and c are all positive. Then the threshold population is

$$N_0 = \frac{a_1 - \sqrt{a_1^2 - 4b_1 c}}{2b_1},$$

which gives c as

$$c = \frac{a_1^2 - (2b_1 N_0 - a_1)^2}{4b_1}.$$

using Eq. (3), and setting $g = l$ we can solve for the equilibrium density:

$$\hat{N} = \frac{(a_1 - a_2) \pm \sqrt{(a_1 - a_2)^2 - 4(b_1 + b_2)c}}{2(b_1 + b_2)}, \qquad (4)$$

Since $a_1 > a_2$ (this condition assures positive per capita population growth), in order to have two positive $\hat{N}$, c must be greater than zero, which it is if $0 < N_0 < a_1/b_1$. That is, if a threshold population level for reproduction (N_0) exists, then there will be two positive equilibrium densities. The lower equilibrium point given by Equation (4) is unstable since for values of N lower than the smaller equilibrium point, dN/dt will be negative, and hence lead to extinction, while values of N greater than the lower point will cause N to grow towards the upper stable equilibrium point (Fig. 2b). Notice also that the lower equilibrium point will always be greater than N_0. Hence, a population may be able to reproduce, yet fail to persists because its gain rate is not high enough to overcome the loss rate from the combined effects of mortality and emigration.

2.2. Populations with low dispersal rates

In the preceding section it was pointed out that the logistic equation assumes that immigration is zero. For some populations this condition may be approximated. We explore this idea in a more general way here. For a population with very low dispersal rates, changes in population densities will be affected mainly through reproduction and death; i.e., as i and e approach zero, g and l approach b and d respectively. It is then possible for two equilibrium points to occur, since the recruitment function will be bowed upward and intersect the loss function twice. This is likely to occur, for example, whenever a cost rarity (Hopf & Hopf 1985) imposes a minimum population size for successful reproduction.

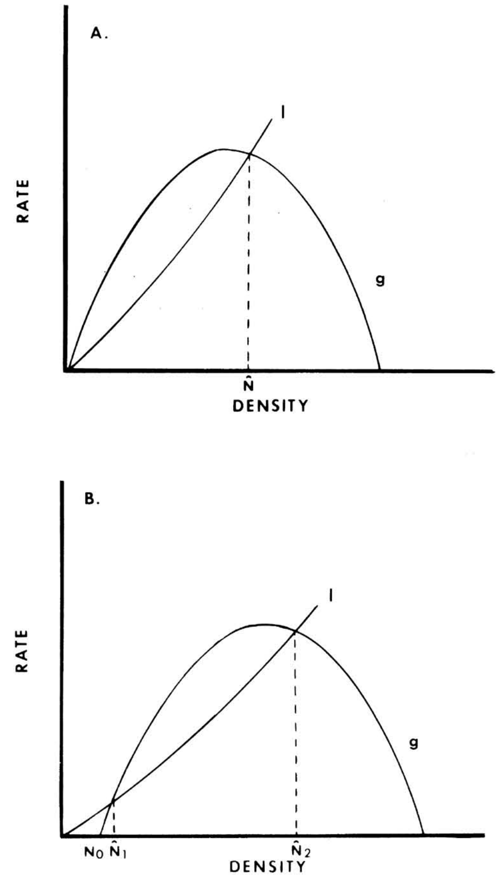

Fig. 2. A. Gain and loss functions of the logistic equation of population growth. Note that both g and l are parabolas. B. Logistic gain and loss functions when a threshold density for reproduction (N_0) exists. The gain and loss functions intersect 2 times. The lower equilibrium density ($\hat{N}_1$) is unstable and the higher ($\hat{N}_2$) is stable. Populations that have densities between N_0 and $\hat{N}_1$ will have reproduction but maintain negative growth rates and eventually go extinct.

Populations inhabiting islands and insular habitats are often special cases of populations with low dispersal rates. Hence, insular species may have populations existing at or near unstable densities. Stochastic fluctuations in the size of such populations may cause them to drop below the critical density necessary to maintain population growth.

Consider two populations of a species, one inhabiting an island and the other inhabiting the mainland. The loss functions of the island and mainland both pass through the origin, and from there they will tend to diverge in proportion to the extent that the island population has a reduced emigration rate. Thus, l_m, the loss function of the mainland population will be greater than l_i, the loss function of the island population for all values of N, and $l_m - l_i$ will be an increasing function of population density. Similarly, immigration will also be lower for island populations than mainland populations, so $g_m > g_i$, and $g_m - g_i$ will be a decreasing function of population size (Figure 3). We can compare the equilibrium densities of the island and mainland populations as follows. If $l_m - l_i > g_m - g_i$ in the neighborhood of $\hat{N}_m$, then at $\hat{N}_m$ we have $l_m = g_m$, so $l_i < g_i$. Hence population growth of the island population at the island density equivalent to $\hat{N}_m$ will be positive, implying that $\hat{N}_i > \hat{N}_m$ (Fig. 3A). On the other hand, if in the neighborhood of $\hat{N}_m$, $l_m - l_i < g_m - g_i$, then at $\hat{N}_m$ we have $l_m - g_m$ and $l_i > g_i$. Thus, the island population density equivalent to N_m will experience negative growth and $\hat{N}_i < \hat{N}_m$ (Fig. 3B). If $l_m - l_i = g_m - g_i$ at $\hat{N}_m$ then $\hat{N}_i = \hat{N}_m$.

Many observers have noted that island populations are often significantly denser than populations in comparable habitats on nearby mainlands (e.g. Crowell 1962, Grant 1966, Diamond 1970, Emlen 1978, 1979). Since islands usually have substantially fewer species than mainlands, these differences in population size often have been attributed to decreased interspecific competition on islands. The phenomenon has been referred to as insular density compensation (e.g. Crowell 1962, Diamond 1970, 1975). Other investigators have suggested that reduced predation pressure might explain high insular population densities (R. Holt, pers. comm.). Emlen (1979), however, argued that neither of these factors, nor any general pattern in resource abundances could account for higher densities of some land bird species on islands in Baja California. He suggested that on mainland sites there were "sink" habitats into which individuals produced in favorable habitats were forced by intraspecific interactions. Reproduction in these sink habitats was less than recruitment. On islands, such dispersal out of favorable habitats was prevented, which lead to higher insular population densities. Our model formalizes this idea and extends it. Any mechanism that causes a large reduction in the population loss rate relative to the reduction in gain rate on an island will result in higher island densities. Picture, for example, island and mainland habitats that are similar and highly productive. Immigration

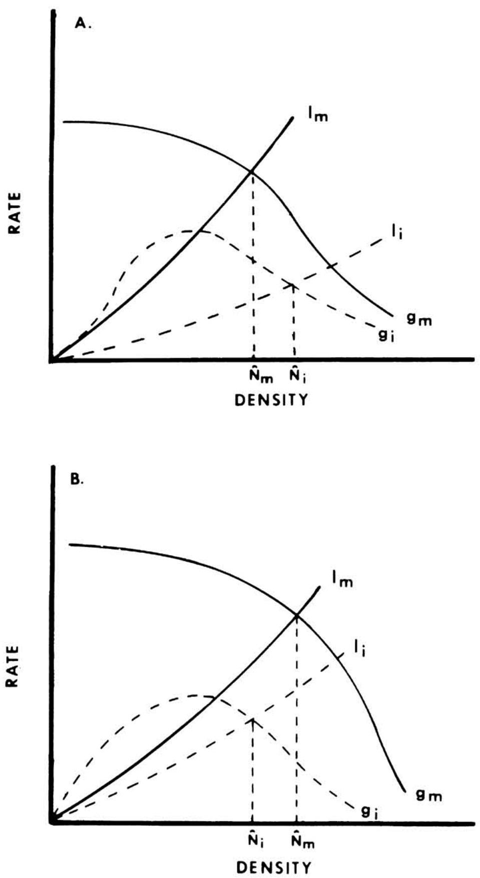

Fig. 3. Comparison of population gain and loss functions of island and mainland populations. Because rates of immigration and emigration are lower on islands, gain and loss functions in island populations must be lower than in mainland populations in habitats of equivalent productivity. A. When the difference between loss rates on islands and mainlands is greater than the differences between gain rates, then island population density at equilibrium ($\hat{N}_i$) will be greater than the corresponding mainland equilibrium density ($\hat{N}_m$). B. When the difference between loss rates on islands and mainlands is less than the difference between gain rates, then population density at equilibrium for the island population ($\hat{N}_i$) will be less than the corresponding mainland equilibrium density ($\hat{N}_m$).

rates might be suspected to be much higher for the mainland population, however, intraspecific competition and crowding should work to discourage immigrations. Mainland habitats which are highly productive should be constantly producing emigrants that disperse to other areas. Thus, the major difference between the island and mainland populations in this situation would be the low emigration rate on the island since the surrounding barrier would prevent individuals from leaving. This interpretation is supported by the results of experiments with small mammals. Krebs and his coworkers (Krebs et al. 1973) constructed fences around populations, preventing dispersal into and out of population enclosed in favorable habitat. Substantially higher population densities were maintained inside the enclosures than on unfenced, control plots. Our model provides a single parsimonious explanation for the high densities of insular and enclosed populations that does not require invoking particular biotic or abiotic mechanisms other than straightforward effects of barriers to dispersal.

3. Variation in density among spatially separated populations

In the previous section we argued that the gain and loss function of a single population will intersect to produce one or more equilibrium points. The population of an entire species can be viewed as a collection of many spatially distinct local populations, each characterized by its own gain and loss functions and equilibrium points. Differences in gain (or loss) functions among local populations will be environmentally determined, though gain and loss functions of adjacent populations might be expected to be similar since environmental variation is autocorrelated. We noted in Eq. (1) that the functions *b, l, d,* and *e* may be functions both of population density (*N*) and of spatially varying environmental variables (symbolized collectively by *X*). In this section we develop this idea further and ask what are reasonable shapes for *g* and *l* as functions of space and how do they interact with local population densities to produce variations in population densities in space? In particular, we are interested in how *g* and *l* may vary among local populations to produce the unimodal, Gaussian-like curve of species abundance in space which is so often observed in nature.

Changes in the *g* and *l* functions in space can be attributed to spatial variation in environmental factors

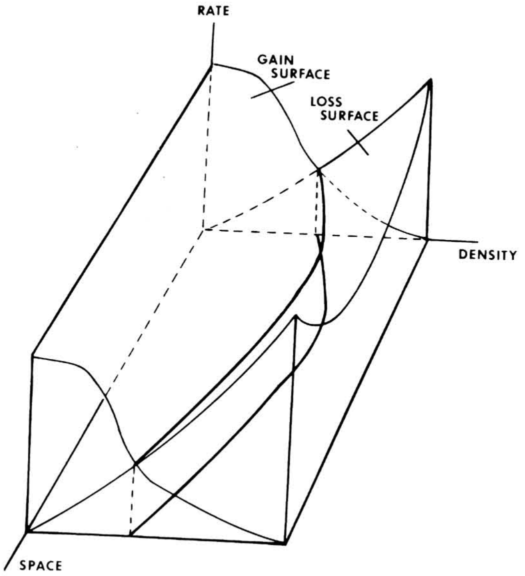

Fig. 4. Spatial pattern of population gains and losses can be represented as surfaces in a three-dimensional coordinate system composed of rate (the rates of population processes), space (the spatial location of each individual population), and population density. Each population existing at a given point in space has a characteristic gain and loss function that intersects to give an equilibrium density. Over space, the collection of equilibrium points defined by the intersection of gain and loss functions determines the relationship between space and population density (projected on the density-space plane). In order for population density to be unimodal in space when there is no spatial variation in population gain functions, population loss functions must be lowest for populations at the center of the spatial gradient and increase in populations nearer to the periphery of the gradient.

that are independent of population size. Over their geographic ranges, most species not only experience significant variation in abiotic factors, such as temperature and moisture, but also encounter varying biotic conditions, such as different combinations of competitors, mutualist, predator, and prey species in different parts of the species range (Brown &Kurzius 1987). Species may respond to this variation in several ways. Highly vagile species may maintain sufficiently high immigration rates to balance lower reproductive rates in poor habitats and thus maintain a relatively constant gain rate in space. On the other hand, poorly dispersing species may have reproductive rates that are relatively constant in space, and

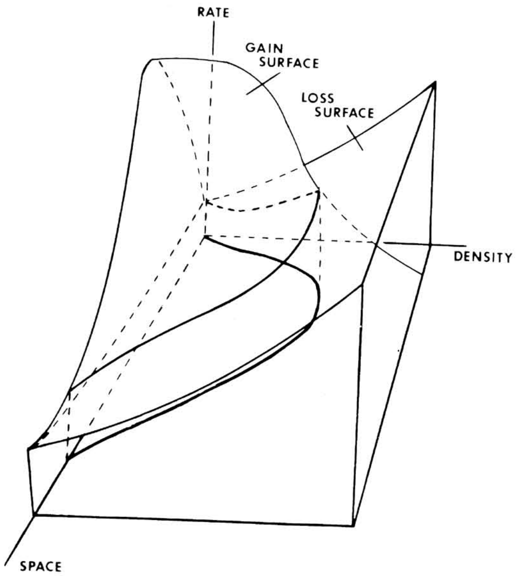

Fig. 5. In order for population density to be unimodal in space when there is no spatial variation in population loss functions, population gain function must be highest for populations at the center of the spatial gradient. See the legend of Fig. 4 for a description of gain and loss surfaces.

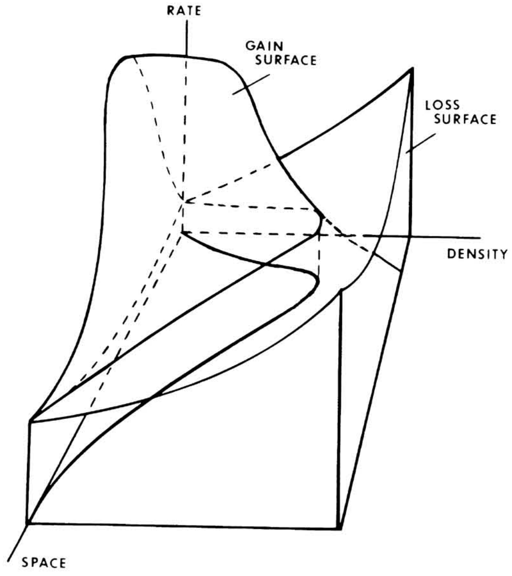

Fig. 6. If populations at the center of a spatial gradient have both the highest rates of gain and lowest rates of loss, then equilibrium population densities will be highest at the center of the gradient and decrease peripherally. See legend of Fig. 4 for a description of gain and loss surfaces.

hence maintain relatively uniform recruitment rates in space. For such species to achieve a bell-shaped distribution in space their loss rate must increase away from the central area of the species range (Fig. 4).

On the other hand species may have relatively constant loss rates in space. For such species to maintain a bell-shaped distribution in space, it is necessary for their gain rate to decline from the center toward the edge of the range (Fig. 5). This may be achieved in a number of ways. Species which have high dispersal rates and hence high immigration rates must have lower population birth rates in populations occupying peripheral sites. On the other hand, poorly dispersing species may have relatively constant birth rates, but be unable to colonize or immigrate to peripheral sites, thus leading to decreased immigration rates in peripheral populations.

In many species, populations in peripheral sites may have both higher loss rates and lower recruitment rates than central populations, which would again lead to a bell-shaped distribution (Fig. 6). It is likely that most species fall into this category since factors which affect reproduction (e.g. energy availability and physiological stress) are also likely to influence immigration, death and emigration rates. As environmental favorability decreases, reproduction and immigration are likely to decrease while death and emigration should generally increase.

In the above discussion it can be seen that there is no need to require symmetricity in the changes in recruitment and loss functions over space. From the simplest considerations, we might expect that most species will have asymmetrical spatial abundance curves because the set of environmental factors which operate to modify g and l are likely to be different in different directions away from the center of the geographic range. On the other hand, species may tend to evolve to mitigate the effects of the most severe limiting factors, so that over evolutionary time there may be a tendency for distribution to become more symmetrical. Certainly many empirical data sets appear to exhibit symmetrical distributions (Brown 1984).

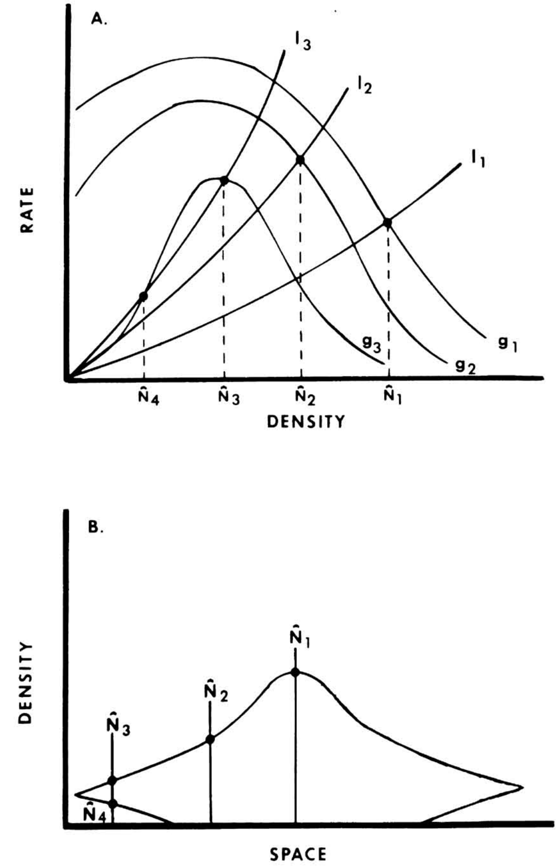

Fig. 7. A. Central populations (population 1) have lower rates of loss (l_1) and higher rates of gain (g_1) than peripheral populations, and consequently have higher equilibrial population densities ($\hat{N}_1$). Populations on the edge of the spatial gradient (population 3) may have sufficiently low rates of population gain (g_3) that there are two equilibrium densities, one stable ($\hat{N}_3$) and one unstable ($\hat{N}_4$). B. Spatial pattern of equilibrium population densities when peripheral populations have two equilibria. Fluctuations in population density that drop peripheral populations below unstable equilibrial densities ($\hat{N}_4$) will go extinct.

The generality of these conclusions are not affected by the particular functional form of g and l with space and population density. While the particular shape of the functions will influence the specific shape of the population distribution over space, only very general conditions on g and l need be met for the spatial distribution function to be a nonincreasing function of distance away from the geographic center of a species. These conditions are: (i) Recruitment (gain) must be a nonincreasing function of both distance from the geographic center and population density; or (ii) loss must be a nondecreasing function of both distance from the geographic center and population density; or (iii) both (i) and (ii).

3.1. Peripheral populations

We previously noted that in some populations where immigration was very low, two equilibrium points can be achieved, one stable and the second unstable, leading to a minimum population density necessary to prevent local extinction. In some species, peripheral populations may have sufficiently low immigration rates that when they are subject to acute reductions in population density due to action of stochastic factors, they are unable to recover (Fig. 7). This suggests that the proportion of suitable sites with populations will be both lower and more variable in peripheral habitats than in habitats near the center of a species range.

4. Dynamics of spatial variation in density

The equilibrium density of a local population determines the direction of change (i.e. increases or decreases) that the population will experience at a given density. Each local population will experience a specific set of conditions which regulates its dynamic behavior. Thus a local population might smoothly approach its equilibrium density, it might oscillate about its equilibrium in a periodic or chaotic fashion, or it might suffer continual stochastic perturbations which constantly prevent it from approaching equilibrium. The dynamics of local populations will also be tied to one another by the processes of immigration and emigration. Since local densities might fluctuate from generation to generation due to stochastic and dynamic processes, small samples of populations taken over short periods of time might exhibit highly variable densities and possibly obscure general patterns attributable to geographic trends in equilibrium densities. However, when local population trends are averaged over a sufficient period of time, the mean patterns of population densities in space might better reflect the underlying equilibrial structure.

Certain species may continually undergo stochastic perturbations so that they are continually in a nonequilibrial state. This might be particularly true of expanding populations. Several authors have suggested that for expanding populations simple diffusion processes might lead to Gaussian distributions in space (Hengeveld and Haeck 1981, Rapoport 1982). According to this view, the leading edge of the invasion will consist of populations with low densities while populations near the initial site of establishment should maintain high densities (Skellan 1951). It is conceivable that some populations might regularly undergo population crashes across their ranges, and thus be in a continual state of expansion as they reinvade portions of their range from refugia. However, this is not likely to be the case if a species maintains a relatively stable geographic boundary over time.

5. Discussion

Recently Brown (1984) has proposed an empirically motivated theory to explain the spatial distribution of abundance within and among species. Our concern here is not to evaluate that theory but to place it in the context of the underlying demographic processes which may act to produce the spatial patterns.

Brown's theory rests on the empirical generalization that on a large scale species nearly always are most dense near the center of their geographic range and on a smaller scale that species also tend to be most abundant near the center of local gradients of rapid environmental change, such as on mountainsides or within the intertidal zone. Brown's theory requires two premises. First, it is assumed that the abundance and distribution of a species is the result of the interplay of many different biotic and abiotic factors that collectively define Hutchingson's (1957) niche hypervolume. Spatial variation in population density of the species is assumed to reflect the probability density function of the required combination of niche factors along a spatial dimension. The second premise is that each niche variable is spatially autocorrelated, so that sites in closest proximity tend to offer the most similar combinations of environmental variables. The environmental variables that characterize the niche of each species are actually comprised of groups of covarying factors, so that the original multidimensional niche can be viewed as a lower dimensional set of independently varying factors.

From these two assumptions, Brown (1984) reasons that there is some area where the combination of independently varying environmental factors allows the species to obtain its maximum population density, and that as one moves away from this area in any direction, one or more environmental factors attain values that limit the density of the populations to progressively lower levels until a point is reached beyond which local populations can no longer be sustained. This statistical pattern seems to characterize the spatial distributions of many kinds of plants and animals. Brown's (1984) evaluation of distributional patterns suggests that normal (or Gaussian) distributions can often be used to fit these distributions, but there is no need to invoke the specific features of this distributions.

The ideas presented in this paper extend Brown's (1984) theory by showing how spatially varying combinations of independent environmental factors can result in spatial variation in population size through differential rates of birth, death, immigration and emigration in local populations. An important feature of these ideas is that they do not depend on the particular kinds of variables that limit individual species.

One major advantage of the general approach we have taken here is that attention is diverted away from microscopic (local scale) phenomena that may often have limited generality to macroscopic (large-scale) statistical patterns and processes that may have much wider applicability. Much of the ecological research during the last several decades has been devoted to investigating the environmental factors that determine the abundance and distribution of populations and the organization of communities. Much time has been spent debating the relative importance of biotic and abiotic factors, such as physical disturbance, competition, and predation. Our own assessment is that all of these factors are important for almost all species and communities, and that because they interact in complex ways it is often impossible and misleading to try to assess their relative importance. Niches are truly multidimensional, and though groups of factors may covary independent of other groups, many of the dimensions, including abiotic and biotic ones, are not independent.

The evolution of multidimensional niches may proceed in a number of ways. If one single factor were of overwhelming importance in limiting the abundance and distribution of a species, strong selection would produce adaptations which would tend to mitigate the effects of that factor. Such selection should continue to modify the species until a second limiting factor assumed equal or greater importance. Further phenotypic change in response to the first factor would be constrained by selection operating on the second factor, and selection would operate to ameliorate the simultaneous effects of both factors. A more dynamic process, however, might be envisioned. If the biological and physical environments in which a species existed were constantly changing, at any given instant in evolutionary time only a few of the many factors in the environment might be responsible for selection of the traits characterizing the niche. In the next instant another small set of factors might be responsible for the selection operating on the species, and would likely have different consequences. This constantly changing array of selective forces might result in simultaneous phenotypic change resulting in limitations occurring in many niche dimensions, and preventing any one niche dimension from being the major factor limiting the species geographically.

We suggest that attention needs to be focussed on classes of patterns and processes that are general in the sense that their expression is not highly dependent on the nature of the underlying microscopic interactions. While an improved understanding of local patterns and processes may help elucidate some of the underlying complexity which is responsible for macroscopic patterns, these macroscopic phenomena may result from any number of microscopic processes. Both the general patterns described by Brown (1984) and the more specific models presented here do not depend on whether a local population is limited primarily by temperature or moisture, competition or predation, physical disturbance or biotic resources, or some complex combination of all these and still other factors. The present models assume only that there is some most favorable site for each species and the suitability of the site declines with increasing distance from this site. Additional restrictions on the number of niche variables, the extent to which they are independent in their effects on the organism, and their pattern of variation in space seem necessary to account for the symmetrical, approximately normal-shaped distributions that appear to be observed frequently in nature, but none of these are inconsistent with our models. From the discussion above, it appears that several combinations of demographic processes can result in superficially similar patterns of spatial variation in density. All that is necessary to produce bell-shaped distributions is that overall gain and loss functions assume certain reasonable forms, but the component rates of immigration and birth and emigration and death can make very different contributions and still satisfy these conditions. Thus, as ecological conditions change from the center of the species range to its periphery, our models predict a decrease in average local density regardless of the specific environmental factors involved.

Much of the emphasis of the models we have discussed is on spatial patterns, and we feel that this focus is timely. Despite the fact that spatial variation in populations and communities is one of the most obvious features of the natural world, most ecological models are concerned with variation as a function of time, and variation in space is left largely to the poorly developed science of biogeography. Nevertheless, statistical phenomena that are revealed in space clearly must be viewed as manifestations of underlying dynamic processes. The present paper has explored some of the relationships between these spatial and temporal patterns and processes. We hope it will be possible to test and extend these ideas, both by acquiring data on the comparative demography of local populations in different parts of a species' range and by constructing and evaluating more sophisticated models. For example, Peakall (1970) collected data on clutch size variation in Eastern Bluebirds (*Sialia sialias*) throughout its range in North America. He found that clutch size was highest in the center of this species range. He further found that there was a positive correlation between clutch size and local population density. This suggests that reproductive rates (and hence gain rates) of local populations of Eastern Bluebirds decrease with increasing distance from its geographic center. The generality of this phenomenon needs to be evaluated, and would provide data which would help evaluate the biogeographic significance of the models we have presented here.

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