

Temporal variation, habitat selection and community structure

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Isodar theory, a model of density-dependent habitat selection, is used to examine how temporal variation affects community organization. An isodar is a plot of the density of a species in one habitat versus its corresponding density in a second habitat such that an individual's expected fitness in the two habitats is the same. Isodars can also be plotted by using the density in one habitat at different times. Ecological succession modifies habitat, the expected reproductive success of individuals living in the habitat, and thus, population density. These effects can be detected in the slopes and intercepts of isodars. It is possible, therefore, to use density estimates alone to predict the time-course of community structure with ecological succession. The proper protocol for this analysis requires replicated population estimates for each temporal stage as well as simultaneous estimates from adjacent undisturbed controls. Previous empirical studies on mice demonstrate the ability of such analyses to reveal the joint effects of temporal and spatial variation on community structure. Extension of the theory to evaluate the relative use of different habitats shows that niche width can increase, decrease, or remain constant with changes in population density. Niche metrics based on habitat are thus likely to give biased interpretations about density-dependent competitive interaction.

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Introduction

It is clear from many recent empirical studies that a complete understanding of the structure of any community is possible only in the context of temporal and spatial variation. Community composition of shrub-steppe birds is dynamic in time and space (Wiens 1986), and patterns of habitat use vary between biogeographical, regional and local scales of analysis. The structure of *Anolis* lizard communities depends upon habitat selection and species interactions at a local scale, but the nature of these interactions varies regionally (Roughgarden et al. 1987). Low frequency invasions from other islands modify *Anolis* community composition whereas the initial structure is derived geologically by the fragmentation and movement of islands and island systems (Roughgarden et al. 1987).

Biogeographical comparisons of desert rodents sug-

gest that distributional patterns are related to each species' ecological requirements except for instances where glacial events during the Pleistocene resulted in restricted distribution (Brown 1987). The number of desert rodent species at any one site is positively correlated with primary productivity, but species interactions and habitat selection are also important (Brown 1987). Local communities are non-random assemblies of those available (e.g. Bowers and Brown 1982) and patterns of local assembly are predictable in the context of micro-habitat variation (M'Closkey 1978).

Evolutionary, geological, palaeoclimatic, and historical events determine the pool of species and phenotypes available to colonize local habitats and exploit their resources. Geological and meteorological processes operating across a spectrum of temporal scales determine regional landscapes and local geography. Habitats and their associated communities are further

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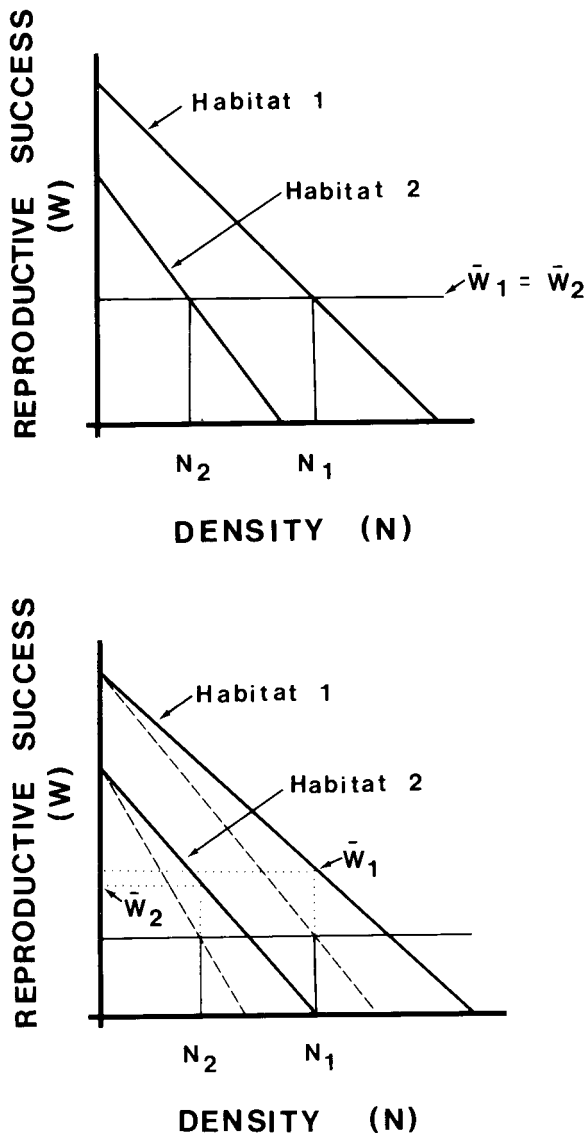


Fig. 1. Upper: An example of an ideal free distribution. The density in each habitat (N_i) is adjusted such that average reproductive success is equal (horizontal line). Lower: Despotic and pre-emptive distributions (dashed lines) reduce the slope of fitness density curves. Dotted lines demonstrate that mean fitness actually differs between habitats, but 'colonizing' individuals are unable to occupy the superior habitat. For despotic distributions, dominant individuals interfere with colonists and reduce the perception of fitness at any given population size. For pre-emptive distributions, sites vary in fitness and high quality sites are occupied to the exclusion of other individuals.

modified by history and ecological succession as well as by annual and seasonal variation. Thus the patterns we observe in the spatial dimension reflect the processes that have created them in time.

The necessary linkage between spatial pattern and temporal process greatly simplifies the difficulty ecologists face at disentangling their relative effects. The dependence of habitat on temporal process suggests,

perhaps, that we shouldn't even try. Temporal variation determines habitat kind and patchiness, and thus its effects on ecological communities are likely to be mediated by habitat selection.

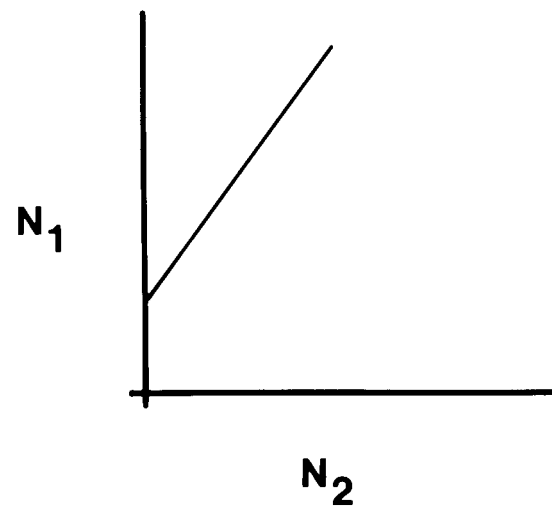
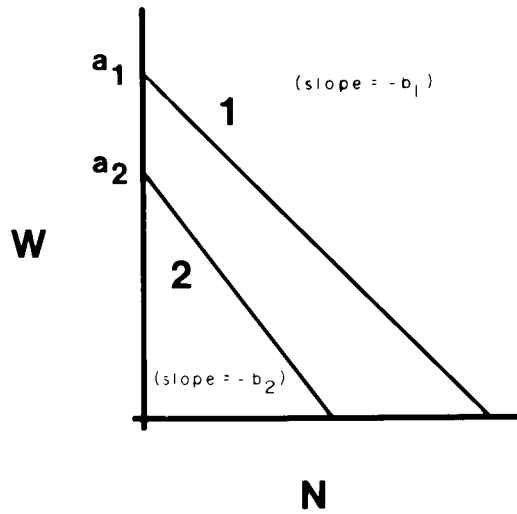
In this paper I explore the relationships between two fundamental differences in habitat with successional, annual, and seasonal variation. Qualitative differences occur when individuals are more efficient at extracting and consuming resources, and converting them into descendants, in one habitat than in another (Morris 1988). A pair of habitats are qualitatively different, for example, if they vary in structure or resource type such that the cost of foraging over a given area (or volume) is different between them. Quantitative differences occur when habitats contain similar resources but vary in net productivity. A pair of habitats would be quantitatively different if the maximum gain due to foraging on a particular resource over a given area (or volume) is greater in one than in the other.

I first review density-dependent habitat selection from the perspective of isodar theory to show how qualitative and quantitative differences in habitat determine patterns of community structure. I then evaluate the likely influences of temporal variation on these habitat components, and how their variation in time will affect ecological communities. I show how we can predict changes in community structure through time and discuss the effectiveness of different sampling protocols at detecting temporal and spatial variation in ecological communities. Isodar theory is then extended to infer relationships between population density and niche breadth, and to test between equilibrium and non-equilibrium population dynamics.

Isodar theory

Individuals should select habitat in such a way as to maximize their lifetime reproductive success. If reproductive success declines with increased population density, habitat selection theory predicts that the density in different habitats be adjusted such that an additional individual could expect to have similar fitness regardless of which habitat it selected (Fretwell and Lucas 1970, Rosenzweig 1974, 1981, Pulliam and Danielson, in press).

Current theory suggests that individuals might select habitat in one of three distinct ways. According to the ideal free distribution, all individuals have equal access to resources and average reproductive success in different habitats should be the same (Fretwell and Lucas 1970). In many species territorial or dominant individuals may inhibit colonization by subordinates. Under these conditions habitat selection may follow an ideal despotic distribution where average reproductive success is greater in some habitats than in others (Fretwell and Lucas 1970). Average fitness will also differ be-



slope of the fitness density function, and the expected density in each habitat determined similarly (Fig. 1).

Consider a two habitat system and assume for simplicity that fitness curves are negative linear functions of density. Then the fitness density functions are described by

$$W_i = a_i - b_i N_i \quad (1)$$

where W_i is the expected fitness of an individual in habitat i , a_i is the maximum fitness in habitat i , b_i is the per-capita reduction of fitness and N_i is population density. According to theory the densities in each will be adjusted such that average fitness (ideal free) or perceived fitness (ideal despotic, ideal pre-emptive) is the same. Thus

$$a_1 - b_1 N_1 = a_2 - b_2 N_2 \quad (2)$$

which can be rearranged as

$$N_1 = ((a_1 - a_2)/b_1) + (b_2/b_1)N_2 \quad (3)$$

Equation (3) is also a linear function which defines the set of densities in habitats 1 and 2 predicted by ideal density-dependent habitat selection. I call these lines of 'equal fitness' isodars (Fig. 2). The isodar slope is the ratio of the slopes of the fitness density functions, it corresponds to the qualitative difference between habitats. Individuals living in qualitatively identical habitats are likely to be equally efficient at converting resources to descendants in both, and the fitness density curves will be parallel (isodar slope = 1.0). Qualitatively different habitats will produce non-parallel fitness density curves. If these curves diverge ($b_1 < b_2$) the isodar slope will be greater than 1.0. If the fitness-density curves converge ($b_1 > b_2$) the isodar slope will be less than 1.0.

The isodar intercept corresponds to the difference in maximum fitness between the two habitats corrected by the density-dependent decline in fitness in habitat 1. The intercept represents the quantitative difference between habitats. Individuals living in quantitatively identical habitats should be able to achieve similar maximum fitness at low density (isodar intercept = 0). Habitats which differ quantitatively will often have different intercepts on fitness density graphs ($a_1 \neq a_2$) and non-zero intercepts on isodars.

Few natural communities are composed of single species and the population dynamics of any one species is often influenced by those of others. If species A coexploits resources with a second species (B), species A's isodar becomes

$$N_{A1} + \alpha_1 N_{B1} = ((a_1 - a_2)/b_1) + (b_2/b_1)(N_{A2} + \alpha_2 N_{B2}) \quad (4)$$

where α_1 is the average competitive effect of one individual of species B on A in habitat 1 and α_2 is the same effect in habitat 2 (Morris 1988, 1989a). The slope and

Fig. 2. Upper: Hypothetical fitness density functions for two habitats. Habitat 1 is quantitatively (higher intercept) and qualitatively (shallower slope) superior to habitat 2. Lower: An isodar plot of the diverging fitness density functions. The density in habitat 1 is plotted versus the corresponding density in habitat 2 such that fitness is equal in each.

tween habitats if individual sites are selected in order of their fitness value (ideal pre-emptive distribution, Pulliam and Danielson, in press).

The expected density of individuals in different habitats can be determined for all three distributions by plotting fitness as a function of population density (Fig. 1). In the case of an ideal free distribution, population densities equilibrate at those values where average reproductive success is the same in each. The density in each habitat is given by the intercepts of the fitness density functions with a family of horizontal lines representing equal fitness. The effects of territoriality and pre-emption can both be modeled by a reduction in

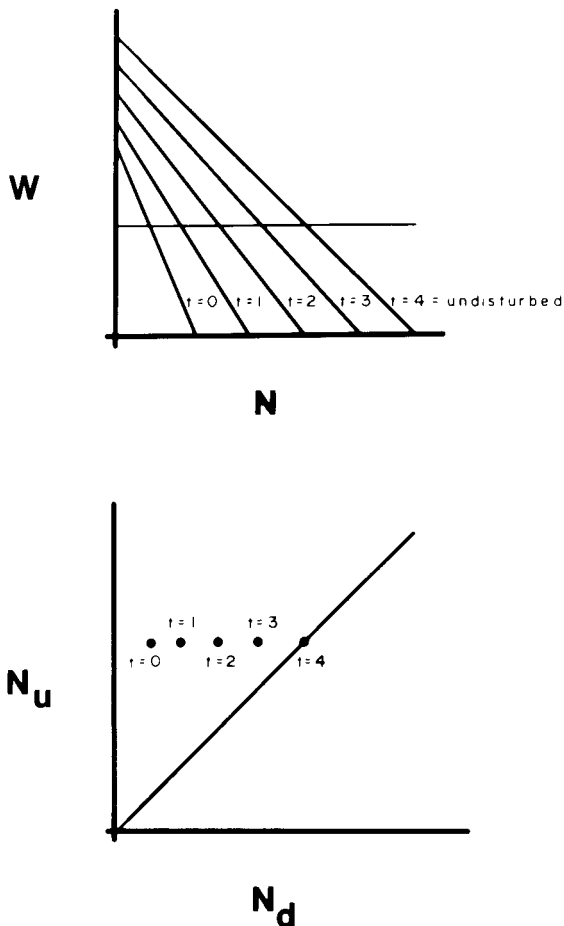


Fig. 3. Upper: Time course of recovery of a disturbed plot ($t = 0$); both quantitative and qualitative differences) until it converges on the undisturbed control ($t = 4$ in this example). Lower: Isodar plots of density estimates following a temporally stratified sampling regime (horizontal sampling, upper). Only the isodar of the undisturbed site can be drawn as it must pass through the origin with slope = 1.0. The sampling design provides insufficient detail to calculate either slopes or intercepts of the successional isodars.

intercept of the isodar is unchanged because the joint density of the two species is evaluated in terms of the number of species A equivalents. Multiple species isodars can also incorporate interference competition and can be analyzed by multiple regression to describe the competitive relations among co-occurring species (Morris 1989a).

Qualitative and quantitative differences in habitat give rise to different modes of community organization (Pimm and Rosenzweig 1981, Rosenzweig 1985, 1987, 1989, Rosenzweig and Abramsky 1986, Morris 1988). Qualitative differences between habitats allow competing species to specialize on the habitat in which they are most efficient (*distinct preferences*). Quantitatively different habitats can be exploited by different species with equal efficiency, and such *shared preferences* favor the

evolution of dominance where subordinate species (or phenotypes) are excluded from the most productive habitats (the idea to classify communities by distinct and shared preference organization was conceived by S. Pimm [Rosenzweig and Abramsky 1986]). If the habitats are also similar qualitatively, competing species have *equal preference* (Morris 1988) with the dominant still in control.

Various combinations of quantitative and qualitative differences in habitat lead to a variety of other kinds of community organization. These range from *centrifugal organization* (Rosenzweig and Abramsky 1986) where each species achieves maximum fitness in the same core habitat at low density, but also lives in distinctly different habitats at high density, to *differential preferences* (Morris 1988) where some species perceive habitats as being similar while others perceive them as being different. Isodars, by queuing in on qualitative and quantitative differences in habitat, can distinguish among many different kinds of community organization (Morris 1988).

Effect of disturbance on isodars

Most forms of disturbance modify habitat structure and will result in qualitative changes in habitat. Many will cause quantitative differences as well. Ecological succession tends to equalize both components of habitat between the disturbed and undisturbed sites. Successional habitats can thus be defined as those where directional changes in quantitative and qualitative components result in repeatable temporal trends in population density.

Consider two adjacent homogeneous patches of, say, temperate North American forest. Before disturbance community organization in the two identical patches would be dictated by equal preference. Imagine that one of the two equal patches is catastrophically disturbed by fire or clearcutting. Through time, the disturbed plot will usually converge on the undisturbed plot (both change in time, but the rate of change of the successional plot is likely to be more rapid) (Fig. 3). Noting these changes, what is the proper design to adequately depict habitat differences and associated community structure at a given moment during succession?

Let us evaluate the common protocol of sampling one or more controls and several disturbed sites of different ages. If we make the simplifying assumption that density in the undisturbed controls is constant, this design is equivalent to a horizontal census across the different successional classes (Fig. 3, upper). When we plot these data on an isodar graph, what can we conclude? We know that the slope of the isodar for replicated control plots must pass through the origin with slope 1.0 (no quantitative or qualitative difference), but we have in-

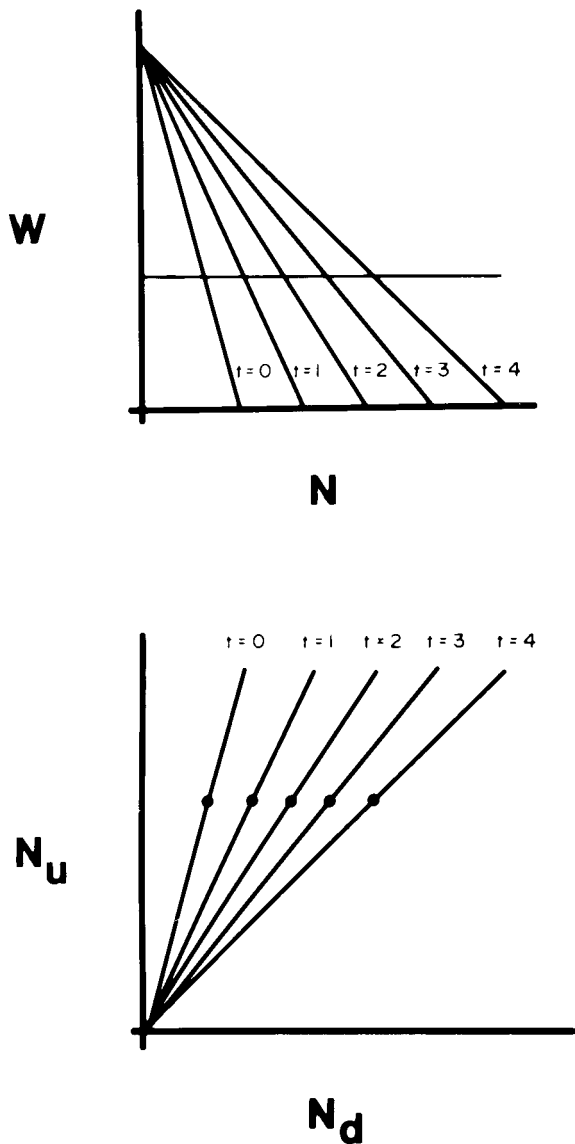


Fig. 4. Upper: Structural recovery of a disturbed habitat patch (no quantitative effect by disturbance). After four time-intervals the patch has converged on the structure of an undisturbed control. Lower: Results of horizontal sampling for successional habitats that differ only qualitatively. We can plot the isodars because qualitative differences imply that all isodars pass through the origin.

sufficient data to infer the slopes and intercepts for the other habitat comparisons. Thus our knowledge of factors influencing community organization with successional history is limited.

If our inferences about community organization and composition are to be correct, we require information on the density in the undisturbed control. If that density is low, early successional habitats may be unoccupied. If the density in the control is high, all sites should be occupied, but the relative abundances may change (see later). Is it any wonder why studies of successional

change so frequently give different results (e.g. compare Martell and Radvanyi (1977) and Clough (1987) who found relatively low small mammal abundance in clearcuts to Kirkland (1977) who reported high abundance). If both quantitative and qualitative components of habitat are altered by disturbance there appears to be no alternative but to obtain simultaneous replicated estimates of population density in both undisturbed and disturbed sites of similar age. These estimates should contain samples across a range of population densities in the undisturbed controls in order to reveal the density-dependent pattern of habitat occupancy. Population densities in control plots in any one area at any particular time are likely to be similar. It may be necessary, therefore, to obtain the desired variation in density by replicating on a regional scale or by collecting estimates of population density over several years.

If, on the other hand, disturbance affects only quantitative or qualitative components of habitat, the 'horizontal' protocol is adequate to evaluate community structure. Assume that the available productivity, to say a group of small mammal consumers, is unchanged by disturbance. Plot the time course of structural recovery of the disturbed patch as a series of fitness density functions (Fig. 4, upper).

According to the Pimm and Rosenzweig (1981) theory, qualitative differences early in the successional sequence should shift community organization in the two patches toward distinct preference. Each habitat would have its own specialist. If we assume that the undisturbed patch maintains its structure between time $t = 0$ and $t = 4$, equal preference will be restored after recovery. Furthermore, our horizontal sampling protocol allows us to estimate the isodar slopes since they should all pass through the origin. It turns out that we can actually do much more.

When, for example, will convergence occur? From Eq. (3), let the isodar for a given forest-dwelling species at time 0 be

$$N_{u(0)} = C_{(0)} + B_{(0)}N_{d(0)} \quad (5)$$

where $C_{(0)} = (a_{u(0)} - a_{d(0)})/b_{u(0)}$, $B_{(0)} = b_{d(0)}/b_{u(0)}$, and where subscripts u and d denote undisturbed and disturbed plots respectively. The isodar at some future time t will be given by

$$N_{u(t)} = [C_{(0)} - (\Delta C)t] + [B_{(0)} - (\Delta B)t]N_{d(t)} \quad (6)$$

where ΔC and ΔB represent the reduction in the isodar intercept and slope per unit time, and

$$N_{u(t)}/N_{d(t)} = [C_{(0)} - (\Delta C)t]/N_{d(t)} + B_{(0)} - (\Delta B)t. \quad (7)$$

If the habitats are quantitatively identical, then $C_{(0)} - (\Delta C)t = 0$ and Eq. (7) simplifies to

$$N_{u(t)}/N_{d(t)} = B_{(0)} - (\Delta B)t. \quad (8)$$

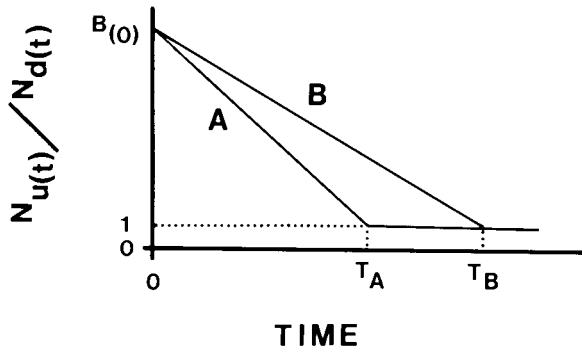


Fig. 5. Time-course of a disturbed site's qualitative convergence on an undisturbed control for species A and B (assumes that the initial qualitative difference is equal for both species). Community structure to the left of T_A is characterized by distinct preference, between T_A and T_B there is differential preference, and to the right there is equal preference.

Note that the ratio of densities at any time t is equal to the isodar slope at that time. Thus the ratio of densities at the time of convergence, T , is

$$N_{u(T)}/N_{d(T)} = B_{(0)} - (\Delta B)T \quad (9)$$

but

$$N_{u(T)}/N_{d(T)} = 1 \quad (10)$$

and

$$T = B_{(0)} - 1/\Delta B. \quad (11)$$

T will vary for different species and allows the ecologist to calculate the time course of community change after qualitative disturbance to habitat (Fig. 5).

Unfortunately, we may not be certain whether or not disturbance has created only qualitative differences. We can, however, be certain that there are quantitative differences among successional habitats whenever we find species restricted in distribution. Qualitative differences imply that all habitats should be occupied, even at low density (Fig. 4, upper).

Now consider a manipulation that affects only quantitative components of habitat. Under these conditions $B_{(0)} = 1$, $\Delta B = 0$, so Eq. (6) becomes

$$N_{u(t)} = [C_{(0)}] - (\Delta C)t + N_{d(t)} \quad (12)$$

and

$$N_{u(t)} - N_{d(t)} = C_{(0)} - (\Delta C)t. \quad (13)$$

Convergence occurs when $N_{u(t)} - N_{d(t)} = 0$, thus

$$0 = C_{(0)} - (\Delta C)T \quad (14)$$

and

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$$T = C_{(0)}/\Delta C \quad (15)$$

(Fig. 6).

My 'tests' of qualitative or quantitative changes with ecological succession may appear to apply only to those species which characteristically attain their highest densities in undisturbed patches. Successional specialists, on the other hand, will attain maximum density at some intermediate seral stage. Such an effect will be easily detected by the graphical tests for successional change. In the case of qualitative differences, the ratio N_u/N_d will fall below 1.0 for those seral stages where density is greatest in the disturbed habitat. In the case of quantitative differences, the value of $N_u - N_d$ will be negative when density is greatest in the disturbed habitat.

Population density and niche breadth

A favorite axiom in community ecology is that increasing intraspecific density leads to increased niche breadth. With the exception of centrifugal organization (Rosenzweig and Abramsky 1986) most habitat selection models are interpreted to predict that the diversity of habitats used should increase with increased density (e.g. Rosenzweig and Abramsky 1985). Isodars can be used to test this idea because they give a graphical presentation of changes in niche breadth.

Consider a pair of habitats that differ only qualitatively and calculate the resulting isodar. Since there are no quantitative differences, this isodar is a straight line passing through the origin (Eq. (3)) and the relative density in the two habitats (the isodar slope) is constant. Qualitative differences, alone, have no effect on the relative use of different habitats. If niche metrics are estimated from the diversity of habitat use, those metrics, contrary to most theory, will often be invariant with changes in population density.

Patterns of relative density in a set of habitats are likely to vary as those habitats recover from disturb-

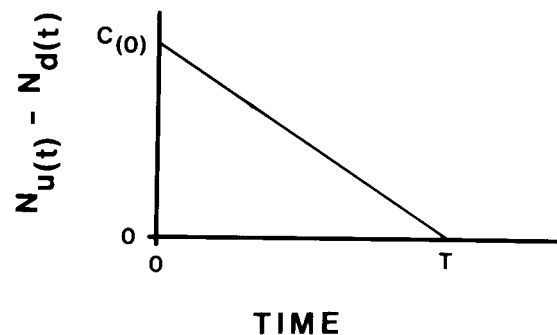


Fig. 6. Time-course of a disturbed site's quantitative convergence on an undisturbed control. To the left of T community organization is based on shared preference, to the right there is equal preference. In both cases dominant species or individuals should win in competition.

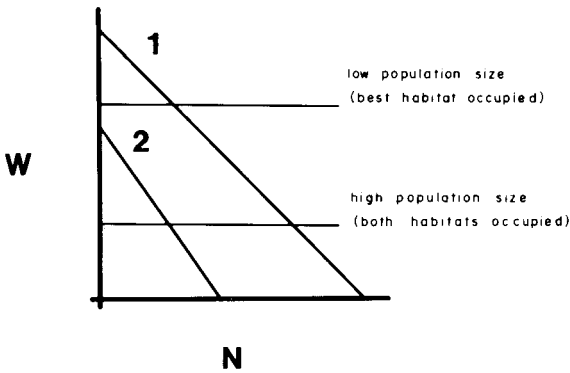


Fig. 7. If habitats differ quantitatively the range of habitats used increases with increased density.

ance. Changes in qualitative components through time alter expected abundances in different habitat patches. Other things being equal, niche breadth should increase with successional stage (Fig. 5).

Now consider a pair of habitats that differ both qualitatively and quantitatively. Only the 'best' habitat will be occupied at low density, and the range of habitats used will necessarily increase with increased density (Fig. 7). Once both habitats are occupied, however, their diversity of use depends upon qualitative differences. The initial density in the quantitatively superior habitat exceeds that in the other. If the isodar slope is greater than or equal to unity (diverging fitness density functions), increases in density in the two habitats reduce the initial density advantage of the quantitatively superior habitat. The ratio of densities in the two habitats will consistently converge (for linear functions) and niche breadth increases with population size.

If the isodar slope is less than one (converging fitness density functions) the initial density advantage in the quantitatively superior habitat is again progressively reduced, and niche breadth will increase with increased population size. If, however, the converging functions cross, the isodar slope is less than one and passes through the point $N_1 = N_2$ (Morris 1988). As population size increases, niche breadth will thus increase to a maximum and decline thereafter.

Groups of coexisting competitors are likely to be composed of species that use habitats that differ in the magnitude of qualitative and quantitative variation. Niche breadth may increase with density for some species and remain constant for others. Such effects greatly complicate the usefulness of any niche metric at interpreting community structure.

Short-term dynamics

Competition theory's limited success at resolving issues in community ecology is largely due to its assumptions

that populations of coexisting species are at equilibrium with resource abundance, and with each other (Chesson and Case 1986). Annual and even seasonal fluctuations in abundance are often interpreted as demonstrating that populations are not in equilibrium (Wiens 1977, 1986), yet these fluctuations may simply represent overall changes in carrying capacity. Can we use our models of density-dependent habitat selection to differentiate between 'non-equilibrium' density variation versus that due to changes in carrying capacity?

In scenario 1, assume that density is determined by variation in carrying capacity. In scenario 2, assume that carrying capacity is constant, and that population density varies independently. Now imagine that we have censused population density at different times. Can we differentiate between equilibrium and non-equilibrium dynamics?

Consider a sampling protocol where replicated estimates of population density are taken in permanent plots of a habitat at different times during which overall population size has changed. Graph the density estimates per replicate at high population size against their corresponding estimates at low population size, and evaluate for statistical significance by model II regression. A significant regression equation implies a density-dependent habitat selector.

Now allow the habitat to change both quantitatively and qualitatively through time. Its fitness density curves at time t and $t+1$ can be described as

$$W_t = a_t - b_t N_t \quad (16)$$

and

$$W_{t+1} = a_{t+1} - b_{t+1} N_{t+1} \quad (17)$$

respectively.

Assume that $N_t > N_{t+1}$. Estimate average fitness by λ . According to equilibrium scenario 1, $\lambda_t = \lambda_{t+1} = 1.0$, thus

$$a_t - b_t N_t = a_{t+1} - b_{t+1} N_{t+1} \quad (18)$$

and

$$N_t = ((a_t - a_{t+1})/b_t) + (b_{t+1}/b_t) N_{t+1}. \quad (19)$$

According to scenario 1, $a_t > a_{t+1}$ (quantitative change) and an 'isodar' of N_t versus N_{t+1} will have a significant positive intercept. If there has been no qualitative change between the two sampling periods, $b_t = b_{t+1}$, and the isodar slope = 1.0.

Now consider the non-equilibrium scenario 2. Assume again that $N_t > N_{t+1}$, and as above, plot N_t versus N_{t+1} . Two possibilities can account for apparent patterns of non-equilibrium density variation.

First, the dynamics within and among patches may be independent of density. Under these conditions there

will not be any consistent relationship between our estimates of density at N_t and N_{t+1} . The species is not selecting patches in a density-dependent manner.

Second, population size may be modified by density-independent processes, yet individuals may still select habitat according to the density-dependent theory. The outcome in terms of habitat use may be similar to that of scenario 1. A reduction in population size will result in a re-distribution of surviving individuals in the habitat such that their reproductive success, relative to that of other individuals, is similar to its value before population decline. Equation (19) is still a valid representation of habitat selection and the change in density will appear to reflect quantitative and qualitative differences in habitat. It may thus be necessary to obtain estimates of population growth rates to unambiguously distinguish between equilibrium and non-equilibrium dynamics.

Discussion

I have tried to demonstrate some of the ways that temporal processes effect spatial patterns in natural communities through qualitative and quantitative differences in habitat. These differences are directly linked to alternative forms of community organization, and should be easy to detect by isodar analysis on census data.

Morris (1988) used isodar analysis on the density of white-footed mice (*Peromyscus leucopus*) to evaluate qualitative and quantitative differences between old field, sumac, and forest habitats in Point Pelee National Park in southern Canada. *P. leucopus* is primarily a woodland resident in this part of its geographical range. Consistent with the theory, forest and sumac contrasts with the old field yielded isodars with slopes tending to be greater than 1.0 and with intercepts significantly greater than zero. The forest and sumac appeared qualitatively and quantitatively superior to the old field.

Sumac represents a successional stage at Point Pelee that is intermediate between old field and hardwood forest. Slopes of isodar regressions comparing forest and sumac plots were very close to 1.0 and their intercepts were not significantly different from zero (Morris 1988). In the perception of white-footed mice, as revealed by their population density, the 3 m tall sumac habitat had converged on the 20 m tall forest. Isodar analysis was thus able to reveal crucial details of how white-footed mice perceive ecological succession toward hardwood forest.

Successional differences expected to modify either quantitative or qualitative components of habitat can be evaluated by current field protocols, such as that used above, where several different successional patches are compared with an unmanipulated control. Such studies implicitly assume that population density in nearby con-

trol habitat is constant for all successional stages. This was not a problem in my work at Point Pelee which examined habitat use in adjacent plots on a small (11.5 ha) scale. A more effective protocol for larger-scale studies would be to simultaneously census different successional seres and adjacent controls.

Most successional sequences are likely to alter both qualitative and quantitative components of habitat. Under these conditions there appears to be no alternative to replicated simultaneous sampling of equivalent seres and their respective controls. Any other form of sampling will confuse the two components of habitat, and may be incapable of resolving consistent trends in population dynamics and community organization.

Similar caution in experimental design should be used in studies which use habitat to estimate relative degrees of specialization among coexisting species (e.g. Krebs and Wingate 1976, Millar et al. 1985, Llewellyn and Jenkins 1987). Qualitative habitat designations made on the basis of structural characters, for example, may be inappropriate to testing ideas on density-dependent niche specialization. Niche widths calculated from such data should be insensitive to changes in population density. In this regard it is interesting that Morris (1984a) observed a significant positive correlation between microhabitat use and small mammal density at Point Pelee in only one of four comparisons.

Niche estimates made across successional sequences may confuse the effect of changes in population density with quantitative and qualitative differences in habitat. At a given population size, niche breadth necessarily increases as habitats become more similar. If population density also varies from site to site, the successional effect may be either accentuated or reduced. This difficulty can only be overcome with adequate temporal and spatial controls in 'undisturbed' plots.

Spatial scale may also have a significant influence on the choice of field design. Small-scale disturbances (e.g. death of single trees in forest) can easily be incorporated into a replicated design evaluating intensity of use of different microhabitats through time. This is the scale appropriate to many theories of habitat selection. Most successional studies, however, investigate a much larger scale of disturbance resulting from activities like fire or clearcutting. Replication in such large-scale designs is often on a geographical scale where the selection and placement of 'replicates' can have a major effect on the effectiveness of the design at capturing population dynamics and species interaction appropriate to that scale. The 'best' but logistically demanding design would appear to be one that had replication at both scales. Microhabitat and macrohabitat selection processes could then be evaluated by scale analysis (Morris 1984b, 1987b,c, 1989c).

Communities need not be structured on the basis of density-dependent habitat selection. Yet most small mammal studies which have looked for density-dependent processes of habitat selection have found them (Ro-

senzweig and Abramsky 1986, Morris 1987a). Perhaps the most convincing evidence supporting density-dependent habitat selection in small mammals comes from studies which have contrasted reproductive success between habitats. Litter success (success at recruiting at least one offspring to the adult population), the best estimate of reproductive success in white-footed mice (*Peromyscus leucopus*) (Morris 1986), was greater in forest than in edge habitats (Morris 1989a), supporting despotic or pre-emptive models of habitat selection. Litter success also varied between seasons, but the habitat X season interaction was comparatively small (Morris 1989b) suggesting that seasonal differences, at least, do not significantly modify habitats used by these small mammals.

To briefly summarize:

- 1) Density-dependent successional changes in qualitative and quantitative components of habitat lead to predictable temporal changes in community organization.
- 2) The time course of succession can be estimated from census data as long as succession modifies only qualitative or only quantitative components of habitat.
- 3) The diversity of habitat use is invariant with population density when habitats differ only qualitatively. The use of qualitative characteristics of habitat to estimate niche metrics may lead to erroneous conclusions about density-dependent competitive interactions.
- 4) The most effective field protocol to evaluate successional changes in natural communities is to simultaneously census population density in paired replicates of successional seres and adjacent control habitats.

Many questions remain to be answered. What influence do different proximate mechanisms of foraging and predator avoidance have on shapes and slopes of fitness density functions? What effects do curvilinear fitness density functions have on predictions of habitat selection and community organization? How do asynchronous population dynamics of co-existing species influence density-dependent habitat selection strategies? What effects do characteristics of habitat other than qualitative and quantitative differences have on population regulation and community structure? What ecological conditions lead to the evolution of density-dependent versus density-independent habitat selectors? What is the influence of spatial scale on temporal patterns in communities? How do different rates of temporal change influence the identity and abundance of animal species specializing on different habitats?

There are equally pressing questions in need of empirical solutions. How does habitat selection vary in response to quantitative and qualitative manipulations of habitat? How does habitat selection change with habitat-dependent manipulations of population den-

sity? Do isodar estimates of species interaction correspond to those of experimental removal or addition studies? Do linear isodars give a reasonable fit to census data of coexisting species? Are apparent random patterns of density in ecological communities predictable when the influence of habitat is included in the analyses? How do quantitative and qualitative components of natural habitats vary along temporal and spatial gradients? How long does it take for density-dependent habitat selectors to respond to quantitative and qualitative differences in habitat? How does the rate of 'numerical response' to habitat vary with different magnitudes of quantitative and qualitative change? Do species with different life histories show different degrees of density-dependent habitat selection? How do the mechanisms of habitat selection change with population density, with the spatial scale of habitat patches, with the magnitude of habitat differences and with the rate of change of habitats through time? Do these 'functional responses' vary among coexisting species?

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