

Ecology at the Mesoscale: The Influence of Regional Processes on Local Communities

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A local community—to a first approximation, and viewed over a sufficiently long time span—is an ephemeral ensemble of species that originated somewhere else (Davis 1986). The species composition of local communities should thus reflect historical processes, such as speciation, vicariance, and dispersal, operating at very large spatial and temporal scales. Much of this volume is concerned with how community structure expresses the imprint of these biogeographical and evolutionary processes. I will instead examine a more strictly ecological problem: How do spatial processes acting over time scales shorter than that needed for speciation (i.e., $< 1 - 100$ generations) influence the structure of local communities? Because different species experience the spatial dimension of the environment in radically different ways (Wiens 1989b; Robinson et al. 1992), a community will reflect the compound action of many distinct spatial processes. I present a classificatory scheme for regional effects on local communities, in effect using local communities as a lens to examine regional processes. The issues I discuss below lie in a gray zone between the local mechanisms that are the traditional concern of community ecologists and the large-scale processes that are the province of biogeographers and systematists—hence, this chapter is an exercise

in ecology at the mesoscale (Roughgarden, Gaines, and Possingham 1988).

It is useful to begin by returning to a familiar theme from island biogeography: the weaker relationship between sample area and species richness within continents, as compared with the species-area relation among islands. This observation (Preston 1962) was a key stimulus in the development of the equilibrium theory of island biogeography (MacArthur and Wilson 1967), which took as its basic variable the total number of species on entire islands, and as its core processes long-distance colonization, extinction, and in situ speciation.

If one is concerned with the dynamics of local communities, one needs to know the number of species present within a defined area, rather than the total species list for an entire island or continent. Because the drawing of community boundaries is often a bit arbitrary (Underwood 1986), it is even more useful to ascertain how species richness scales with sample area for each island or continent being compared (Hart and Horwitz 1991; Holt 1992). Unfortunately, few island studies have constructed within-island, species-sample area curves across a range of island sizes such as that shown schematically in figure 7.1 (although investigators are converging on this topic

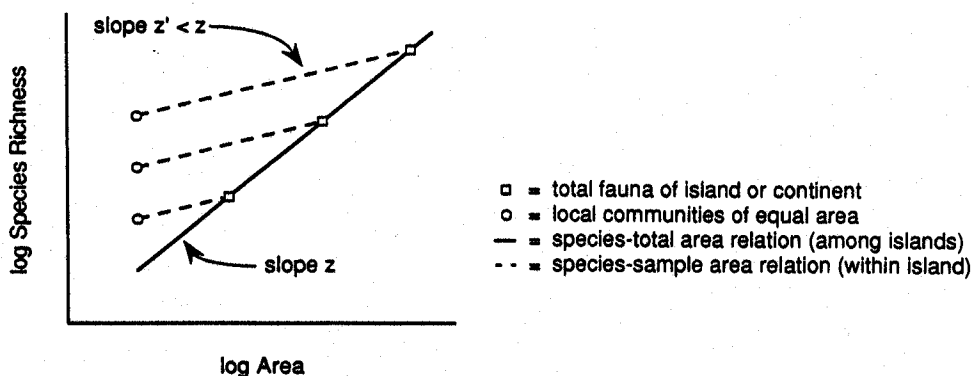


Figure 7.1 Two kinds of species-area curves. The total species pool $S(A)$ of an island/continent is assumed to depend upon its total area A as described by the power law, which can be transformed to a straight line on a log-log plot: $\log(S) = \log(c) + z\log(A)$. The number of species $S(a,A)$ found within a sample area of size a on an island/continent of size A is also described by a power law: $\log(s) = \log(c')$

+ $z'\log(a)$. The species-sample area curve, for simplicity, is assumed to have the same slope z' across all islands. Given that $z' < z$, local communities increase in species richness with increasing A . For the purpose of illustration, the values of z and z' shown are at the upper limit of values reported in the literature (Connor and McCoy 1979).

with their increasing focus on the relation between local and regional species richness in continental samples: see, e.g., Compton, Lawton, and Rashbrook 1989; Lewinsohn 1991; Cornell and Lawton 1992; Lawton, Lewinsohn, and Compton, chap. 16).

For illustrative purposes (as in fig. 7.1), assume that the species-area relation within as well as among islands fits a power law (Sugihara 1981), extrapolated down to the spatial scale defining local communities. If $S(A)$ is the total number of species on an island/continent of size A , then $S(A) = cA^z$. If $s(a,A)$ is the number of species found in a sample of size a on an island/continent of size A , then $s(a,A) = c'(A)a^{z'}$. In general, the coefficients c' and z' could themselves vary with total area (e.g., larger islands might harbor more habitat specialists). If we assume that these coefficients are independent of island size, Preston's observation implies $z > z'$.

If small islands were passive samples of larger islands or continents (Haila 1983), one would expect that $z = z'$; the two kinds of species-area curves would coincide, and the average number of species in a local community would be independent of regional species richness. If, by contrast, local communities were saturated (*sensu* Terborgh and Faaborg 1980; Cornell and Lawton 1992), the power law would break down for sample areas corresponding to the spatial scale of direct interactions such as exploitative competition; $s(a,A)$ would converge on a common value s' with decreasing a , independent of A . In the remainder of this chapter I assume, in accord with a growing body of evidence (Ricklefs 1987, 1989b; Cornell and Lawton 1992; Lawton, Lewinsohn, and Compton, chap. 16), that neither local saturation nor passive sampling adequately describe the relationship of within- and between-island (or region) species-area relations.

On each island, we can pick a focal community, defined as those organisms within a prescribed sample of area a , and then ask how local species richness varies with total island size. Noting that $s(A,A) = S(A)$ and manipulating the two species-area relationships leads to $\partial \ln(s)/\partial \ln(A)|_a = z - z' > 0$. The difference in z -values quantifies how increasing the size of the total species pool (correlated with island area) is reflected in an enhancement of local species richness.

A CLASSIFICATION OF REGIONAL EFFECTS ON LOCAL SPECIES RICHNESS

Different species in the same community differ greatly in the spatial scale required for the successful completion of their life cycles and in their ecological and evolutionary responses to spatial heterogeneity (Wiens 1989b). This implies that a number of distinct spatial mechanisms may jointly influence the species composition of a local community embedded in a larger landscape. These include: (1) source pool effects, (2) the spatial dimension of species-specific, autecological requirements, (3) source-sink population structures in heterogeneous environments, (4) habitat selection in heterogeneous environments, and (5) metapopulation dynamics. An important and as yet poorly documented aspect of community ecology is to de-

fine the role of such spatial mechanisms in determining local community structure. Rather than attempting a comprehensive review of the burgeoning literature pertinent to these topics, I will emphasize issues deserving more attention by ecologists.

Source Pool Effects

Brown and Gibson (1983, 444) propose the following thought experiment to study the short-term consequences of regional dynamics for a local community: construct a dispersal-proof fence (or the invisible "force field" of science fiction yarns) around that community, and wait. The null model, of course, is that nothing happens: a local community with a high species richness (e.g., on a large continent, relative to a small island, as in fig. 7.1) sustains its high species richness when cut off from the surrounding landscape matrix.

This null model seems rather implausible as a general rule. Most naturalists would expect some species to disappear rapidly from small patches, and a few to vanish from nearly all isolated patches. In the case of land-bridge islands, nature has constructed the fences in the Brown-Gibson thought experiment for us, and as habitat fragmentation accelerates globally due to anthropogenic habitat destruction, an inadvertent, massive fencing experiment is in effect under way. The data to date suggest that contemporaneous regional processes have substantial effects on local communities. For instance, on landbridge islands in the Gulf of California, the estimated extinction rates of mammals and reptiles are inversely correlated with island size (Case and Cody 1987; Richman, Case, and Schwaner, 1988), and many species seem to disappear rapidly from small habitat fragments (Terborgh 1990; Soulé, Alberts, and Bolger 1992).

Although I am mainly concerned with elucidating the spatial mechanisms underlying such effects, one should always consider the possibility that for some community members, spatial dynamics (coupling the community to the external landscape) is unimportant in explaining persistence, average abundance, and so forth. "Source pool effects" encompass all spatially explicit explanations for the presence of species in a local community *not* dependent on dispersal subsequent to the initial colonization event that "seeded" the local community with those species. As noted above, over sufficiently long time-scales, most current community members will have colonized from elsewhere, and so spatial processes must always be invoked in community assembly (Drake 1990b). Compared with a small isolated region or island, a large contiguous region or continent can generate more species via speciation, accumulate more species from other regions, and provide more avenues for long-distance dispersal. A rate of dispersal that is insignificant for local population dynamics may suffice to supply a local community amply with colonizing propagules. Enhanced local species richness on large islands or continents, as compared with small islands, might reflect in part the effect of total area on total species richness and the biogeographical importance of ecologically trivial dispersal rates. Although source pool effects are unlikely to be

the sole explanation for local enhancement, it is entirely possible that for a core subset of the community, dispersal is of historical but not contemporaneous importance in accounting for species' presence and persistence (Williamson 1981).

Spatial Implications of Autecological Requirements

Together with species for which dispersal is dynamically irrelevant, most local communities also contain a few (and sometimes many) species that could not complete a single generation confined to the spatial bounds of those communities. For instance, top vertebrate predators often have enormous home ranges, and it is not surprising that they seem particularly prone to extinction on landbridge islands (Diamond 1984; Belovsky 1987). Yet terrestrial community studies often do not span even a single home range of top predators! Other examples include species with specialized resource requirements. A species may exploit seasonality by shuttling among distinct habitats or by utilizing different habitats at different stages in its life cycle. Such species cannot persist in an isolated local community for even a single generation.

The existence of species with large spatial requirements has multiple consequences for community structure and dynamics. Species that by virtue of their autecological requirements cannot persist in an isolated community will often be a biased subset of the nonisolated community (e.g., species with larger body sizes). A bias in short-term species losses following isolation may have predictable consequences for the residual community. For instance, the disappearance of a top predator that limited the abundance of its prey can produce ramifying shifts in abundance in the remaining community, including local extinctions or outbreaks (Soulé, Alberts, and Bolger 1992; Pimm 1991). Moreover, in a local community embedded in a large region, species with large spatial requirements can couple the dynamics of otherwise spatially separated communities. Thus, if the intensity of predation by mobile avian predators on a local rodent assemblage reflects local predator abundance, understanding the role of predation in structuring the rodent assemblage may require an analysis of broad, regional patterns of prey availability and productivity.

There can be predictable "bottom-up" as well as "top-down" effects: the disappearance of one species may make inevitable the extinction of other, dependent species. Consider, for instance, the phenomenon of sequential dependencies in food webs—schematic descriptions of the feeding relations among all organisms in a well-defined habitat. An enormous amount of work has been devoted to food webs (e.g., Cohen, Briand, and Newman 1990; Pimm 1991), yet surprisingly little attention has been given to the influence of spatial dynamics on local food web structure (Pimm, Lawton, and Cohen 1991; Drake 1990b; Yodzis, chap. 3).

A food web at the very least embodies one-way dependencies among organisms: species at high trophic levels depend on lower species for their continued existence (whether or not there exist strong reciprocal interactions). Extinctions at low trophic levels can drag down species

at higher levels; colonization at high levels must follow successful colonizations at lower levels.

Consider a food chain of "stacked specialists" in which species *i* occupies level *i* in the chain. Food chain length should be positively correlated with island area for two distinct reasons. First, trophic rank may predict population attributes that directly influence local persistence. For instance, if high trophic rank is correlated with small population size or large minimum home ranges (as in the "productive space" hypothesis of Schoener [1989]), high-ranking species may be unlikely to persist on small isolates. A second, subtler reason reflects the sequential dependencies per se of food webs: area (and other spatial) effects should be compounded up a food chain.

Diamond (1975) invented *incidence functions* to describe species' distributions on islands. An incidence function *p(i)* for species *i* describes how the fraction of islands occupied varies with island area, species richness, or other island attributes. The concept of an incidence function can be broadened to express interdependencies of species in food webs. For a chain of stacked trophic specialists, let *p(1)* be the incidence function for the basal species. For *i* > 1, the incidence of species *i* is constrained by the incidence of all lower-ranked species; if any of these are absent, so will be species *i*. Define the *conditional incidence function*, denoted *p(i|i - 1)*, as the probability that species *i* is present, given that its requisite foodstuff, species *i - 1*, is present. The incidence function for species *i* is a multiple of conditional incidence functions, one for each intermediate link:

$$p(i) = p(i|i - 1)p(i - 1) = p(1) \prod_{j=2}^i p(j|j - 1)$$

In general, incidence functions will depend on both trophic rank and autecological factors that influence population persistence. One community-level attribute we might like to predict is the expected food chain length on an island, *E_n(L)*, given that a chain of *n* species exists in the source pool. The fraction of islands with just *i* species is *p(i) [1 - p(i + 1|i)]*, so

$$E_n(L) = \sum_{i=0}^n ip(i) [1 - p(i + 1|i)] = \sum_{i=1}^n p(i).$$

As a "null model" of food chain assembly, let each species have the same conditional incidence function, *p(i + 1|i) = p*. Substituting into the above expression leads to

$$E_n(L) = p \frac{(1 - p^n)}{(1 - p)},$$

which in the limit of large *n* (a long food chain) converges on *p/(1 - p)*. Gilpin and Diamond (1981) found that the simple form *p = A/(A + q)* (where *A* is island area, and *q* is a fitted constant) described incidence functions for New Guinea birds. Using this for *p(i + 1|i)* leads to *E_n(L) ~ A/q* at large *n*. Larger areas should thus sustain longer food chains of stacked specialists. Analogous results emerge from patch dynamic models that explicitly track colonization and extinctions (Holt, unpublished results). The static incidence and dynamic colonization-extinction

models both predict that the slope of the species-area relationship should increase with trophic rank.

Little direct evidence is available to test this prediction. Glasser (1982) reanalyzed the classic data of Simberloff and Wilson (1969a) on arthropod colonization on mangrove islets and found some evidence for a temporal succession in trophic structure, with herbivores tending to colonize before their natural enemies. Although he does not remark on the fact, Glasser's figure 7 suggests that natural enemies are disproportionately underrepresented on small islands. Briand and Cohen (1987) compiled data on mean food chain lengths for a large set of food web data. In figure 7.2 the aquatic subset of this compilation is divided into three classes in accord with the size (volume) of the habitat providing the data (pond/stream < lake/river < bay/ocean). There appears to be a trend toward longer food chains in habitats of greater volume. Of course, many factors other than habitat volume that could influence food web structure vary along the pond-ocean axis (e.g., geological age, environmental variability), but the data at face value are consistent with the hypothesis that food chain length reflects the size of the region in which a local community is contained. A reanalysis by Schoener (1989) of this same data set buttresses this conclusion. However, a firmer affirmation of the potential influence of spatial dynamics on food chain length (and more generally on food web structure) must await better food web data (Cohen et al., 1993b).

The above model illustrates how one can start with a given species that, by virtue of its autecological requirements, persists in a local community only because that community is connected to a regional ensemble of communities, and then map out the community consequences entailed by the loss of that species without such spatial coupling. If a species' requirements extend beyond the spatial confines of the local community, then the scale used to define the local community does not adequately characterize even a single population of that species. I

now turn to other modes of spatial coupling, in which it is sensible to consider that the local community does contain a species' population.

"Source-Sink" Population Structures in Heterogeneous Environments

Extinction in closed populations may occur in two ways. First, if in a given habitat the death rate always exceeds the birth rate, the population deterministically goes extinct; this is assumed in the source-sink models discussed in this section. Second, with temporal fluctuations in birth and death rates, extinction may result from runs of bad luck (due to demographic or environmental stochasticity), even though the expected birth rate exceeds the expected death rate; this is assumed in many metapopulation models.

A population can persist in a focal community despite a negative expected growth rate if there is regular immigration from other communities. This is the "mass effect" of Shmida and Wilson (1985): a "flow of individuals from areas of high success (core areas) to unfavorable areas" such that "some individuals of a species will become established in sites in which they cannot maintain viable populations." A mass effect is an important limiting case of the "source-sink" population structure considered by Holt (1985) and Pulliam (1988). The characteristic signature of a source-sink population structure is that local population growth rates (birth rate - death rate) are not spatially uniform, but instead are positive in the source and negative in the sink; the demographic equation is balanced in each habitat and in the whole population by dispersal, with net emigration from the source, and net immigration into the sink. In general, the existence of a source-sink population need not imply a mass effect. If a species persists locally because of a mass effect, then (by definition) its population inexorably disappears following isolation. But given negative density dependence in growth rates, the lower density produced by reduced immigration may lead to a compensatory increase of in situ growth rates, so that the sink population equilibrates at a lower density rather than going extinct. In the following remarks, I concentrate on the important special case in which immigration in fact maintains the sink population.

Single-Species Source-Sink Systems. Two general mechanisms that can generate source-sink structures in heterogeneous environments are interference competition and passive (viz., density-independent) dispersal. Pulliam (1988) has argued that intraspecific social interactions can force subordinate individuals to reside in suboptimal habitats, as in the "despotic distribution" of Fretwell (1972), that otherwise would not sustain a permanent population. A model illustrating this source-sink effect assumes that the source is saturated at a population size K ; that these individuals continue to reproduce at a per capita rate r_{source} ; and that new recruits are forced into a suboptimal sink habitat, with no mortality during dispersal. The rate of emigration from the source and immigration into the sink is $I = Kr_{\text{source}}$. In the sink, in the absence of immigration, the population declines at a per capita rate

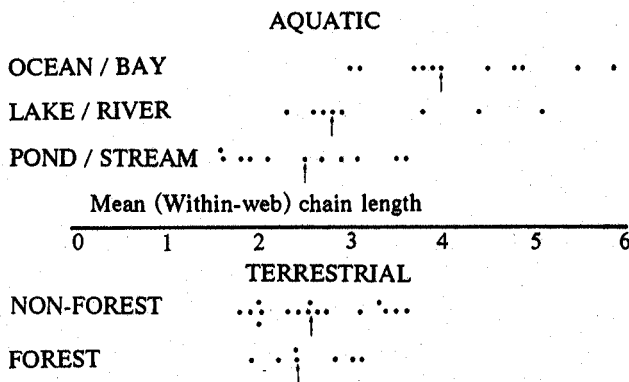


Figure 7.2 Mean food chain length for communities in different habitat types. The data is taken from the compilation of Briand and Cohen (1987). Means rather than maxima are used to give a more conservative assay of area effects. I have grouped the data from aquatic communities in accord with my estimate of the volume of the body of water from which the data is drawn. For completeness, the terrestrial data subset of Briand and Cohen is also shown; it is difficult to determine the area pertinent to these studies.

$r_{\text{sink}} < 0$, with no direct density dependence. The dynamics of the sink population, including both immigration and local growth, is described by $dN_{\text{sink}}/dt = Kr_{\text{source}} + r_{\text{sink}}N_{\text{sink}}$. The stable equilibrium density of the sink is $N_{\text{sink}}^* = Kr_{\text{source}}/|r_{\text{sink}}|$.

This simple model illustrates several general features also found in more complex source-sink systems. First, there are two distinct kinds of density dependence operating: (1) the direct density dependence in the source that determines carrying capacity (K) there, and (2) induced density dependence in the sink. The per capita growth rate in the sink is $I/N + r_{\text{sink}}$; the strength of density dependence (defined as the absolute value of d/dN [per capita growth rate]) is I/N^2 , which is large at low N . A constant immigration rate in effect induces stabilizing density dependence in local population dynamics, particularly at low densities. Second, the size of the sink population maintained by immigration is directly proportional to source productivity, and to the characteristic time scale of the sink population's exponential decay toward extinction without immigration. A productive source can maintain a substantial sink population if there is a gentle rate of population decline in the sink.

In this model, emigration does not affect the size of the source population. Often, however, emigration lowers recruitment and can potentially depress local population size. Moreover, for many organisms, dispersal is governed by physical transport processes rather than by density-dependent interactions. This generates source-sink population structures if there is spatial heterogeneity in carrying capacity and if dispersal influences local population size (Holt 1985). Passive dispersal generates a net flux of individuals from high- to low-density areas. Emigration, which can lower local density, should characterize high- K habitats, whereas immigration, which raises local density, should predominate in low- K habitats, particularly in sink habitats where species persistence requires immigration.

Consider the following source-sink model with passive dispersal (Holt 1985). Assume that a population grows logistically in a source with intrinsic growth rate $r_{\text{source}} > 0$ and carrying capacity K_{source} ; that it disperses at rate e between the source and a sink; and that in the sink it experiences a growth rate $r_{\text{sink}} > 0$ (and no direct density dependence). These assumptions imply the following equilibrium abundances:

$$N_{\text{sink}} = N_{\text{source}} \left(\frac{e}{e - r_{\text{sink}}} \right),$$

$$N_{\text{source}} = K_{\text{source}} \left[1 + \frac{r_{\text{sink}}}{r_{\text{source}}} \left(\frac{e}{e - r_{\text{sink}}} \right) \right]$$

With passive dispersal, a large sink population is maintained if the source population has high r and K , particularly if $|r_{\text{sink}}|$ is small. Without immigration, the sink population disappears, declining by a factor e^{-1} during a time period $1/|r_{\text{sink}}|$. Dispersal depresses N_{source} ; low dispersal rates increase N_{sink} , but at high dispersal densities in the two habitats converge, and total as well as local densities

may be depressed. The entire population risks extinction at high dispersal rates if $r_{\text{sink}} + r_{\text{source}} < 0$.

As with interference competition, passive dispersal may permit a species to occupy habitats it otherwise would not. But dispersal is not a universal enhancer of local species richness, for the simple reason that when emigration depresses local recruitment, passive dispersal may endanger the persistence of the source population. Source populations of small areal extent are particularly at risk because the magnitude of loss due to passive dispersal into unfavorable habitat, relative to the capacity of the source population to replace those losses, scales as the perimeter:area ratio of the source habitat. This deterministic cause of extinction is the basic extinction process assumed in models to predict the minimum critical patch size permitting population persistence (e.g., for planktonic organisms [Okubo 1980] and territorial birds [Lande 1987]).

The best examples to date of source-sink population structures come from plant ecology (e.g., Kadmon and Shmida 1990). A convincing example of a population maintained by flows from a source into a sink has been provided by Keddy (1981), who studied a summer annual, *Cakile edentula*, along a gradient across sand dunes in Nova Scotia. Population density was greatest in the middle of the gradient, but analyses of fecundity and mortality revealed that only at the end of the gradient nearest to the sea were in situ birth rates sufficient to replace deaths; directional seed dispersal (due to both wind and waves) sustained a large population in parts of the gradient where, in the absence of dispersal, local extinction would be predicted. Moreover, emigration seemed to depress density in the source.

Source-Sink Effects and Interspecific Competition. A local community might be a sink for a species because of interspecific competition; immigration from a source can sustain a sink population in the face of competitive exclusion. The resident's competitive edge could reflect either its intrinsic individual superiority in that habitat or local abundance (including priority effects). Abiotic and biotic differences between habitats provide axes for niche differentiation; each of a set of species could be the superior competitor in a particular habitat, which could then be a source sustaining sink populations elsewhere. Theoretical analyses of competition in patchy environments demonstrate that local habitat specialization and priority effects can promote both local and regional diversity (Levin 1974; Yodzis 1978).

This mechanism for enhancing local species richness may break down with large spatial differences in productivity and/or high dispersal rates (Levin 1974). In the source-sink models sketched above, the number of individuals maintained in the sink at equilibrium is directly proportional to the source carrying capacity. Now consider a second competing species, specialized for the sink habitat of species 1, with a carrying capacity there of K_2 . Using the usual Lotka-Volterra competition model, this species cannot increase when it is rare and species 1 is at equilibrium if $K_2 < \alpha_{21}N_{\text{sink}} = q\alpha_{21}K_{\text{source}}$, where α_{21} is the

competition coefficient and q is a complicated function of the rate of dispersal and intrinsic growth rates of species 1. Species 2 may be excluded, despite its inherent local superiority, if species 1 has a sufficiently high carrying capacity in its own source habitat to sustain a high abundance in the sink habitat. Moreover, alternative stable states (with and without the resident competitor) may occur (Christensen and Fenchel 1977). The mass effect most effectively enhances local species richness if the habitat heterogeneity that permits each species to be superior in a particular habitat occurs without substantial spatial variance in productivity, and if dispersal rates are low.

Source-Sink Effects and Predator-Prey Stability. Predator-prey systems tend to be dynamically unstable when predators limit prey well below carrying capacity. Elsewhere (Holt 1985), I have analyzed a general model in which a food-limited predator occurs in two habitats between which it passively disperses. The prey population in the source habitat is dynamically responsive to predation, but the prey population in the sink is not; in the sink habitat, the predator is "donor-controlled." In order for the latter habitat to be a predator sink, the resident prey must be sufficiently low in availability or poor in quality that the predator has a negative growth rate. The predator can nonetheless persist in the sink because of coupling to the source, and back-migration to the source can stabilize an otherwise unstable predator-prey interaction.

A similar stabilizing effect of predator dispersal occurs if the prey populations in both habitats are dynamically responsive to predation. Elsewhere (Holt 1984) I have examined a two-habitat model in which the predator-prey interaction in each patch is described by the classic, neutrally stable Lotka-Volterra model. If the two habitats are equivalent (i.e., uniform parameter values), predator dispersal has no effect on stability. However, if the two habitats vary in any way—say in the predator's density-independent mortality or the prey's intrinsic growth rate—predator dispersal is *always* stabilizing. My interpretation of this result is that passive dispersal in a heterogeneous environment generates a source-sink population structure, and that back-migration from the sink dampens predator-prey cycles in the source (Holt 1984; see also St. Amant, cited in Murdoch and Oaten 1975; McLaughlin and Roughgarden, chap. 8). Comparable effects occur in more realistic models that allow limit cycle behavior in the absence of dispersal (Holt, unpublished results).

Prey sinks can also be stabilizing. To illustrate this, assume that a predator is restricted to habitat 1, where the dynamics are described by the classic Lotka-Volterra model, and that prey passively disperse between habitat 1 and a refuge, habitat 2. The habitat-specific growth rates for the prey in the two habitats are r_1 and r_2 respectively; the per capita dispersal rates are e in the predator habitat and e' in the refuge. There are three possible outcomes for this predator-prey interaction (fig. 7.3): (1) If prey growth rates are too low (the region bounded by the hyperbolic line through the origin) the prey alone cannot persist, and so neither can the predator. (2) If prey growth in the refuge is too great (i.e., $r_2 > e'$), the predator cannot regulate the prey population at all. (3) Finally, the system may per-

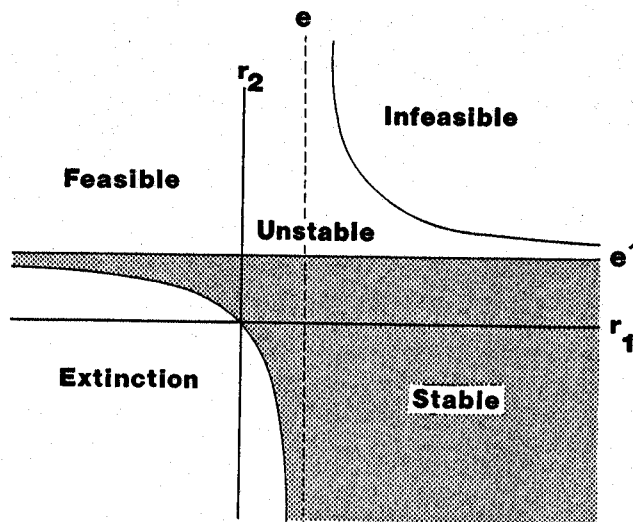


Figure 7.3 Conditions for stability in a predator-prey source-sink model. There are two habitats. The predator (density P) is restricted to habitat 1; prey occupy both this and a refuge (habitat 2). The prey have respective densities of R_1 and R_2 in the two habitats, and diffuse between them at constant per capita rates. The interaction in habitat 1 is described by the classic Lotka-Volterra model, and the prey grows or declines exponentially in habitat 2: $dP/dt = P(aR_1 - C)$; $dR_1/dt = R_1(r_1 - aP) - eR_1 + e'R_2$; $dR_2/dt = R_2r_2 - e'R_2 + eR_1$. The parameters are: a , attack rate; C , predator mortality; r_i , prey intrinsic rate of growth in habitat i ; e , rate of dispersal from habitat 1 to 2; e' , rate of dispersal from habitat 2 to 1. The three possible outcomes are: (1) extinction of both prey and predator; (2) unstable growth of prey, unregulated by the predator; (3) a locally stable equilibrium (the hatched region), determined by evaluating the eigenvalues of the 3×3 Jacobian matrix of the model at equilibrium. (A technical detail indicated in the figure is that for case (2), an unstable point equilibrium may [denoted "feasible"] or may not [denoted "infeasible"] exist.)

sist at a stable equilibrium. This is likely if the habitat with the predator is intrinsically a source habitat for the prey (i.e., $r_1 > 0$), and the refuge is a sink (i.e., $r_2 < 0$). By contrast, if the refuge is intrinsically a prey source, and the habitat with the predator intrinsically a prey sink, a much more delicate balancing of parameters is required for stability. Similarly, in host-parasitoid systems (which tend to be violently unstable), the stabilizing potential of refuges from parasitism is greatly enhanced if hosts in refuges have low intrinsic growth rates, so that refuge populations are intrinsically sink populations (Holt and Hassell, 1993).

There is thus a broad tendency for predator and prey dispersal that couples sources and sinks in heterogeneous environments to stabilize otherwise unstable predator-prey dynamics. I should stress that the mechanism involved here is quite different from that envisaged in metapopulation models for predator-prey persistence in patchy environments (e.g., Caswell 1978), in which global persistence depends upon a balance between local colonizations and extinctions.

If there are a limited number of refuges available, if prey compete for them, and if excess individuals are forced into the habitat containing the predator, then the prey population has a source-sink structure with strong density dependence in the source, and the predator-prey

interaction tends to be stable (Holt 1987b, Sih 1987). Likewise, if a predator population has a source-sink population structure because of intraspecific interference competition in the source (along the lines of Pulliam's (1988) model), this can be strongly stabilizing. In both cases, the predator-prey interaction in the sink habitat is stabilized because of induced density dependence, and the system as a whole is stabilized due to direct density dependence in the source.

As a cautionary note, it should be pointed out that in special circumstances, dispersal in source-sink situations is destabilizing. Consider a predator-prey interaction in a source habitat that without dispersal would stabilize at low prey densities because the predator has a type III functional response (Murdoch and Oaten 1975). Predator emigration tends to increase prey density in the source; density dependence in prey mortality can thereby be weakened or even reversed in sign, reducing the stabilizing influence of the predator's functional response. This indirect destabilizing effect of dispersal can outweigh the stabilizing effect of back-migration from the sink (Holt 1985). In general, dispersal can be destabilizing if either population exhibits local, positive density dependence in growth rates ("diffusive instability," Okubo 1980).

Source-Sink Effects on Prey Communities. Considering only specialist predator-prey pairs, source-sink structures arising from passive dispersal in heterogeneous environments should often enhance local species richness by stabilizing strong interactions. But if predators are generalists, passive dispersal by either predator or prey may in some situations reduce local species richness. Different prey species that do not compete for resources can nonetheless indirectly compete via a numerical response by the predator—an interaction I call "apparent competition" (Holt 1984). In apparent competition, the winning prey species is usually the one that can withstand the highest predator density—and that is usually the prey species with the highest value for r/a (intrinsic growth rate/per capita rate of mortality due to predation) (Holt 1984; Holt, Grover, and Tilman, in press). At low rates of dispersal, habitat heterogeneity permits a multiplicity of prey species to coexist regionally if each is superior at withstanding predation in its own habitat (Holt 1984).

But if predators passively disperse among habitats (or if some predators are forced out of high-quality habitats by intraspecific interference), prey in low-productivity habitats can suffer an increase in predation and even be driven extinct. In contrast, prey in high-productivity habitats may enjoy a relaxation in predation if predators emigrate. At sufficiently high rates of predator dispersal, the single prey species with the highest regional value for r/a tends to displace other prey (Holt 1984; for an example see Settle and Wilson 1990). A mass effect at one trophic level thus tends to reduce local species richness at the trophic level below it. (Oksanen [1990] has recently extended the models of Holt [1985] to three trophic levels and reached broadly similar conclusions.)

If each prey species in a region has an exclusive refuge from predation, or if prey productivities and attack rates

are homogeneous across space, low rates of prey dispersal tend to increase local prey species richness via a mass effect (Smith 1972; Holt 1987b). But if prey do not have exclusive refuges, prey dispersal indirectly increases predator densities in unproductive habitats, where the prey may be overexploited (even to the point of local extirpation) without the predator endangering its own persistence.

A good example of the indirect effect of the dispersal of one prey species on the limitation of another by predation has been described by Flaherty (1969). In the vineyards of the San Joaquin Valley, the abundance of the Willamette mite, *Eotetranychus willamettei*, was more effectively limited by a predatory mite, *Metaseiulus occidentalis*, on grapevines interspersed with Johnson grass than on grass-free vines. The Johnson grass supported a second prey species, the two-spotted mite, *Tetranychus urticae*, (but not the predatory mite). The two-spotted mite dispersed into the vines in response to a deterioration in grass quality (often associated with overutilization by the mites themselves). The influx of this alternative prey species sustained the predatory mite on the vines at a higher level when the Willamette mite was low in numbers; this in turn permitted the predatory mite to depress the Willamette mite to lower levels than otherwise possible. This example demonstrates how indirect interactions between prey species due to shared predation can be influenced by refuges (e.g., Johnson grass for the two-spotted mite) and spatial flows of prey individuals.

Optimal Habitat Selection in Heterogeneous Environments

Habitat selection has important implications for both population persistence and community structure. Natural selection favors organisms that select habitats so as to maximize their relative fitness (Fretwell 1972). In a spatially variable but temporally constant environment, if individuals move freely among habitats, choose where to settle without interference from conspecifics, and are sensitive to density-dependent effects on fitness (as in the ideal free distribution model of Fretwell 1972), habitat selection tends to equilibrate fitnesses across space (Fretwell 1972; for an example, see Valladares and Lawton 1991). If the total population is in demographic equilibrium, then total births must match total deaths; given an ideal free distribution as well, local births must also match local deaths. This implies that each local population settles to its local carrying capacity. More broadly, each local community should be at an equilibrium structured solely by local processes (Holt 1984, 1987a). Hence, in the absence of temporal variability, optimal habitat selection seems to dilute the effect of regional processes on local communities.

Habitat Selection and Population Persistence. The above conclusion ignores the interplay of temporal and spatial variability. Diamond (1975) has argued that organisms that exhibit habitat selection can track local "hot spots" in resource availability and productivity, buffering populations against extinction. Following a disturbance that

greatly reduces population size, intraspecific density dependence should be weak. In this case, habitat selection behavior maximizing individual fitness also maximizes the expected rate of population growth. When densities are higher and local density dependence occurs, optimal habitat selection does not necessarily maximize overall population growth rates (Holt 1987a). Because populations are most vulnerable to extinction at low densities, habitat selection can promote population persistence in variable environments by increasing population growth rates at low densities.

The Effects of Habitat Selection on Predator-Prey Stability. Habitat selection can be an important factor stabilizing predator-prey dynamics. There has been considerable interest for many years in the stabilizing influence of predator aggregation and prey refuges in predator-prey systems. For instance, Comins and Hassell (1979) analyzed a discrete-generation host-parasitoid model in which parasitoids sought out prey patches of high profitability, and showed that this behavior could be strongly stabilizing if the host has a moderate growth rate and exhibits sufficient spatial variance in local density. At the community level, if different prey species occupy different habitats, predator aggregation leads to prey "switching," so that relatively abundant prey are disproportionately represented in the predator's diet; theoretical models suggest that switching can stabilize otherwise unstable prey dynamics (Murdoch and Oaten 1975).

Spatial heterogeneity, alas, is not a universal stabilizer (Hochberg and Lawton 1990). Murdoch and his associates (Murdoch and Stewart-Oaten 1989; Murdoch et al. 1992; but see Godfray and Pacala 1992 for a contrary interpretation) have argued that in some circumstances, predator aggregation in continuous-time models of Lotka-Volterra form, contrary to the conventional wisdom, may be destabilizing. These recent results suggest that habitat selection by predators may not always be stabilizing. Having said this, I think it is nonetheless fair to conclude that in the majority of circumstances, dispersal and habitat selection in heterogeneous environments will prove to have a stabilizing effect on predator-prey interactions.

Fennoscandian ecologists have documented a striking geographical pattern in the cyclic fluctuations of microtine rodents in northern Europe. These multiannual cycles decrease in regularity, amplitude, and interspecific synchrony along a geographical gradient from north to south (Hansson and Henttonen 1988). Hanski, Hansson, and Henttonen (1991) argue that the southern microtine populations are more stable because of aggregation by mobile predators in heterogeneous landscapes. Along the gradient, the landscape shifts from mostly boreal forest in the north to a mosaic of several distinct habitats in the south. In the north, the predators are mainly specialists that are ineffective long-distance dispersers (e.g., least weasels); these predators appear to drive microtine cycles. Further south, the predator community comprises nomadic, specialist bird predators (which tend to concentrate in regions with higher than average prey density) and general-

ist mammalian predators (whose numbers are supported by a number of prey populations distributed across a number of distinct habitats). Korpimäki and Norrdahl (1991a, 1991b) have shown that nomadic avian predators do have pronounced aggregative responses to microtine populations, and that this leads to sufficiently strong density-dependent mortality to dampen population fluctuations. If the suggestion of Hanski, Hansson, and Henttonen (1991) is borne out by further work, it would provide a dramatic example of the effect of a regional process—the maintenance of a pool of mobile predator species expressing habitat selection in a mosaic landscape—on local population dynamics.

If both prey and predator are mobile habitat selectors, the spatial manifestation of their interaction could become quite complicated, and in general must be analyzed as a dynamical game. Because predators should concentrate on patches of high relative prey density, and prey should flee patches of high relative predator density, it is clear that a potential for sustained oscillations exists unless there are other stabilizing forces acting. Schwinnig and Rosenzweig (1990) have studied a simulation model for the within-generation spatial dynamics of a top predator feeding on two prey species, one of which also consumes the other, when all three species can move between two habitats (one being a relative refuge). They found that in some circumstances it was impossible for the system to settle into a stable distribution where each species' fitness was equilibrated across space; instead the system displayed sustained oscillations as predators chased prey between the two habitats. Stability was achieved by providing an absolute refuge or by allowing individuals to make "mistakes" in dispersal; these manipulations in effect introduced a modicum of source-sink stabilization into the system.

The Effect of Habitat Selection on Species Coexistence. Habitat selection promotes the regional coexistence of competing species by allowing them to sort out along stable environmental gradients, but it also reduces the number of species found within particular local habitats. Michael Rosenzweig and his associates (e.g., Rosenzweig 1987a; Abramsky et al. 1990; J. S. Brown 1990) have developed a systematic research program aimed at determining the effect of habitat selection on species coexistence. An interesting implication of this work is that if there are distinct habitat types, if potential competitors have distinct habitat preferences, and if there is no cost of habitat selection, then habitat selection at equilibrium can lead to complete species segregation. Two species may coexist regionally, but because each avoids the habitat containing the other, habitat selection reduces local, within-habitat species richness. Moreover, small perturbations in the density of one species do not affect the abundance of the other, so (at least by this measure) there appears to be no competition at equilibrium.

Optimal habitat selection by predators has two distinct effects on prey communities. First, if different prey species occupy different habitats, and if the system is demographically stable, then at equilibrium, optimal habitat selection

by predators decouples the predation pressure experienced by different prey (Holt 1984); predator abundance in a given habitat matches the productivity of the prey resident there and is independent of prey productivity in other habitats. If the predator population is regulated by prey availability, and if different prey species are superior at withstanding predation in different habitats, an ensemble of prey species can sort out among habitats and coexist regionally. This result parallels the effect of habitat selection on direct competitors. Second, different prey species in the same habitat may experience apparent competition if predators show an aggregative numerical response to local increases in total prey abundance (Holt and Kotler 1987).

In short, optimal habitat selection by mobile predators promotes the regional coexistence of prey species, but tends to reduce the number of prey species coexisting within particular habitats. These effects are enhanced if the prey directly compete (Comins and Hassell 1987). An elegant, experimentally based example of predator-mediated habitat segregation, in which segregation between gastropods and bivalves in a subtidal community is driven by the aggregative responses of predators (lobsters, octopi, and whelks), has been provided by Schmitt (1987).

Metapopulation Dynamics

To recapitulate, habitat selection enhances population persistence because individuals, by virtue of their own behavior, avoid environments in which they have relatively low fitness. In source-sink population structures, a species persists by a mass effect at one place because elsewhere there exist sites that sustain a persistent population providing a source of immigrants. The final possibility I consider is a species that persists regionally in a metapopulation although it occupies no site permanently. Because other chapters in this volume deal with metapopulations (e.g., Caswell and Cohen, chap. 9) and a number of excellent reviews and books on this subject have recently appeared (e.g., Shorrocks and Swingland 1990; Turner 1989; Taylor 1990; Hassell, Comins, and May 1991; Gilpin and Hanski 1991; Schoener 1991), I give this topic less attention than it deserves.

A "metapopulation" in its most general sense is defined as a system of local populations linked by dispersal (Gilpin and Hanski 1991). Usually the term is used to describe systems in which populations go extinct and are recolonized. In contrast to source-sink systems, in which extinction in the sink occurs deterministically if immigration is prevented, in the empirical systems that motivated much of the work on metapopulation dynamics (e.g., landscapes with shifting mosaics of patches at different stages of succession) there is a strong stochastic component to local extinction and/or colonization.

In recent years there has been a great deal of interest in characterizing species persistence in metapopulations (e.g., Fahrig and Merriam 1985). The essential idea is that transient differences among sites may arise from localized environmental fluctuations or by chance ("phase differences," *sensu* Levin 1976b), and that species may exploit

these differences by dispersal, forestalling extinction over the entire metapopulation even though every local population potentially goes extinct. Expanding on a scheme proposed by Taylor (1990), we can distinguish several roles dispersal plays in promoting the local and regional persistence of a metapopulation. First, following the extinction of a local population in a given community, dispersal permits recolonization so long as there are other communities with that species elsewhere in the regional ensemble of communities. This is most likely if there are local communities in the region where that species permanently resides (as in the source-sink scenarios sketched above; see Harrison 1991), but it can also occur if there are simply a large number of replicate patches experiencing uncorrelated extinctions (a kind of "spatial storage effect"; Holt 1992). Second, dispersal may mask or prevent local extinction. This has been called the "rescue effect" by Brown and Kodric-Brown (1977) in the context of classic island biogeography, and an "internal rescue effect" when applied to local sites in a metapopulation (Hanski 1982; Gotelli 1992; Holt 1992).

Dispersal may influence the frequency distribution of local abundances over time (Vance 1980) and thereby alter the probability of local extinction. To examine this effect, K. Parker and I have carried out numerical studies of populations distributed over an archipelago of patches, in each of which there is logistic-like density dependence and random variation in density-independent growth rates. We shall report this work elsewhere (Parker and Holt, unpublished results) and here simply summarize some pertinent findings (fig. 7.4). In our model, following local population growth, a fraction of each population either enters a dispersal pool, which is redistributed among all patches, or disperses to neighboring patches in a cellular lattice. Even low dispersal rates can substantially reduce the overall magnitude of fluctuations in abundance and the frequency of excursions to critically low population levels (fig. 7.4).

Intuitively, migration in a metapopulation tends to moderate local population fluctuations for two distinct reasons. When a local population at high density has an unusually high growth rate (compared with the average over the metapopulation), realized population growth is reduced because more individuals leave the patch than enter it. Conversely (and more importantly), when a local population is perturbed to low densities, more individuals immigrate than leave, thus increasing the rate at which the population rebounds. In the pool model, the stabilizing effect of immigration at low densities becomes more pronounced with an increase in the number of patches (though it exists even for coupled pairs), and for a given single patch coupling to a large metapopulation, is similar to that in a single-patch model with a constant rate of immigration. The reason is that with many patches, the effect of any single patch on the dispersal pool becomes negligible; because one is averaging over numerous patches, the rate of immigration into a single patch for all practical purposes becomes a constant decoupled from local dynamics.

A number of the authors who have investigated meta-

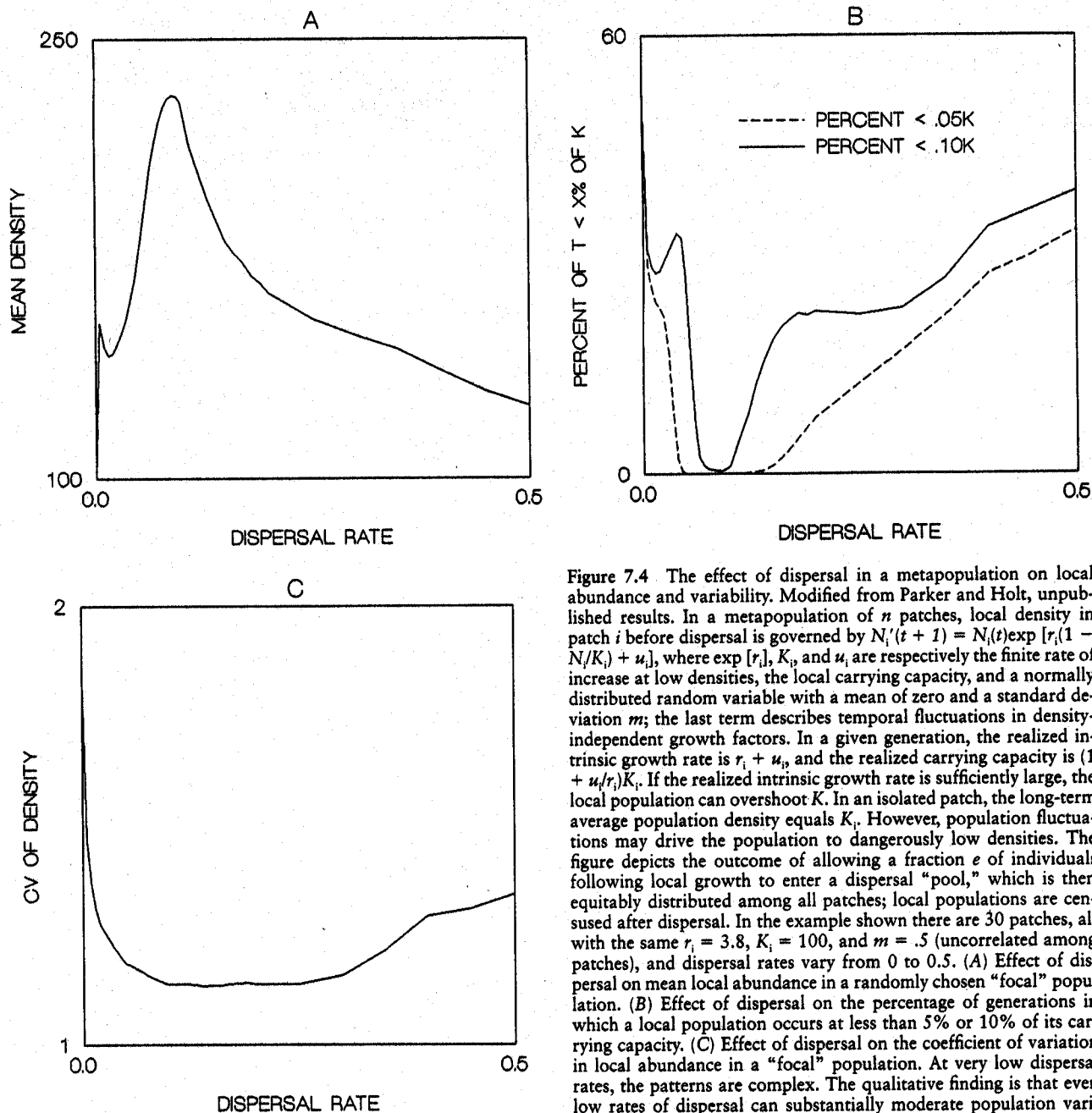


Figure 7.4 The effect of dispersal in a metapopulation on local abundance and variability. Modified from Parker and Holt, unpublished results. In a metapopulation of n patches, local density in patch i before dispersal is governed by $N_i'(t+1) = N_i(t)\exp[r_i(1 - N_i(t)/K_i) + u_i]$, where $\exp[r_i]$, K_i , and u_i are respectively the finite rate of increase at low densities, the local carrying capacity, and a normally distributed random variable with a mean of zero and a standard deviation m ; the last term describes temporal fluctuations in density-independent growth factors. In a given generation, the realized intrinsic growth rate is $r_i + u_i$, and the realized carrying capacity is $(1 + u_i/r_i)K_i$. If the realized intrinsic growth rate is sufficiently large, the local population can overshoot K . In an isolated patch, the long-term average population density equals K_i . However, population fluctuations may drive the population to dangerously low densities. The figure depicts the outcome of allowing a fraction e of individuals following local growth to enter a dispersal "pool," which is then equitably distributed among all patches; local populations are censused after dispersal. In the example shown there are 30 patches, all with the same $r_i = 3.8$, $K_i = 100$, and $m = .5$ (uncorrelated among patches), and dispersal rates vary from 0 to 0.5. (A) Effect of dispersal on mean local abundance in a randomly chosen "focal" population. (B) Effect of dispersal on the percentage of generations in which a local population occurs at less than 5% or 10% of its carrying capacity. (C) Effect of dispersal on the coefficient of variation in local abundance in a "focal" population. At very low dispersal rates, the patterns are complex. The qualitative finding is that even low rates of dispersal can substantially moderate population variability and the frequency of excursions to low levels; higher rates of dispersal weaken these effects by synchronizing patches.

population dynamics (cited above) have explored its implications for interspecific interactions. Analyses of single predator–single prey interactions (e.g., Caswell 1978; Crowley 1981; Sabelis and Diekmann 1988; Reeve 1988) suggest that colonization-extinction dynamics can permit the regional persistence of strong predator-prey interactions that are locally unstable. Competing species may coexist regionally, both because colonization-extinction dynamics open up additional axes for niche diversification (Pickett 1976), and because patchiness tends to augment intraspecific density dependence, making competitive co-

existence easier (e.g., Hanski 1983; Nee and May 1992). Caswell (1978), Hanski (1981), and Hastings (1978) have analyzed patch dynamic systems in which a predator attacks two competing prey species, and argue that all three interacting species could coexist for a long time regionally, even if local extinction is inevitable.

The overall impression one might draw from these studies is that metapopulation dynamics could be a significant factor enhancing local diversity on large islands or continents. Although I suspect this is true, it is worth emphasizing that metapopulation dynamics also opens up

additional mechanisms for species exclusion. For instance, one species may outcompete another because it has a dispersal strategy that gives it a head start in seizing newly available patches, rather than because of any advantage in head-to-head confrontations. In like manner, two prey species that could never directly interact because they occupy distinct patch types may nonetheless be locked in long-distance apparent competition if they support a regional pool of predators that can invade either patch type.

This raises a more general point. Because local species richness in practice tends to increase with island area, or more generally, the size of the regional species pool (see fig. 7.1), it is a natural temptation to concentrate on the enriching effect regional processes have on local communities. A consideration of the mechanistic bases for regional effects leads to a more complex view of the world. For instance, source-sink dynamics may permit a species to occur in a wider range of communities, but may also make that species more vulnerable to regional extinction, or alternatively, more able to exclude competitors from local habitats where it is an inferior competitor. Indeed, any mechanism involving dispersal which sometimes increases local species richness can, in other circumstances, have just the opposite effect. The search for regional mechanisms of persistence and coexistence should be balanced with a search for regional mechanisms of extinction and exclusion.

CODA

Let us return to our thought experiment, in which a local community has been freshly isolated from its surrounding landscape, and now try to characterize the net community response. The simplest description of a local community is a list of its members, so a useful profile of the community's response to isolation is given by the distribution among community members of expected time to extinction and of the variance in time to extinction. The regional mechanisms sketched above describe a range of first-order responses to the breakup of spatial coupling. For some species—those that are in the community because of source pool effects but are otherwise dynamically decoupled from the external landscape—there may be very long expected times to extinction. For others—which due to their autecological requirements straddle this and other local communities each generation—extinction will be swift and inevitable. For yet others—present in the nonisolated community as sink populations maintained by immigration—there will be a predictable time to extinction with low variance. Habitat selectors in a temporally varying environment will be present only when environmental conditions are appropriate, and so will go extinct on time scales driven by temporal variability. Species present because of metapopulation dynamics coupling the local community to many like communities may go extinct, but with high variance in time to extinction. On top of these first-order extinctions, second-order extinctions may occur due to shifts in the patterns and strength of interspecific interactions. The overall profile

of times to extinction in the newly isolated community is an assay of the importance of regional processes in determining the structure of the original nonisolated community.

A deep understanding of the local consequences of regional processes will require a melding of experimental, theoretical, and comparative techniques. I believe that an important item on the agenda for community ecology will be to grapple with the messy reality that local communities contain species that experience the world at vastly different spatial scales. The structure of a community will surely reflect the interplay of disparate regional processes. For instance, Schoener and Spiller (1987) suggest that in spider communities on small Bahamian islands, some species are highly persistent without immigration, whereas others persist only because of immigration. One could easily imagine that each group of species has a substantial impact upon the other; the abundance of the persistent species, whose presence is explained via source pool effects, might be strongly influenced (via competition or predation) by the collective flux of nonpersistent species.

Regional processes have an important methodological implication for community ecology: they make the detection of interspecific interactions in local communities by manipulative experiments more difficult, and indeed, cast doubt on the utility of detailed analyses of population dynamics in single local patches. Cooper, Walde, and Peckarsky (1990) reviewed the literature on predation effects in freshwater habitats and concluded that "the magnitude of prey exchange (=immigration/emigration) among substrate patches has an overwhelming influence on the perceived effects of predators on prey populations." I suspect that this conclusion applies quite generally to any interaction if the dynamics of any of the interactants is not circumscribed by the bounds of one's study. Moreover, regional processes can modify the qualitative character of interspecific interactions. For instance, Danielson (1991) has shown that two species may compete in each of an array of habitats, yet the overall interaction may be mutualistic when the interactions are averaged over space. Given the recent interest in indirect interactions in communities, it is also important to recognize that indirect interactions are often propagated by dispersal through space (e.g., prey species segregated into different habitats may experience strong apparent competition due to mobile predators; Holt 1984).

And finally, to the extent that regional ecological processes enhance local species richness, we might expect some species to show rather coarse, imprecise adaptation to many of the local environments they occupy (Futuyma 1986). If dispersal is important in facilitating the persistence of a species over ecological time in a local community, then that same dispersal iterated over evolutionary time scales could lead to a kind of adaptive averaging over space and communities, which in turn implies a degree of seeming maladaptation in some local communities (relative to highly persistent resident species). This is particularly likely in species with persistent source and sink populations; adaptive evolution is biased toward further adapta-

tion to the source environment, and relatively impotent at improving adaptation to the sink (Holt and Gaines 1992). These observations suggest that evolutionary ecologists should begin to place adaptive analyses of traits into the context of the classic gene flow–selection problem of evolutionary genetics (Antonovics 1968; Slatkin 1987; Pease,

Lande, and Bull 1989). Given that we need to develop an understanding of ecology at the mesoscale to understand population dynamics and community structure in local communities, our quest for an evolutionary understanding of phenotypic evolution and adaptation will ultimately need to be cast at the mesoscale, too.

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