METAPOPULATIONS

Peter Chesson
University of California, Davis

GLOSSARY

local population That part of the population of a species found in a particular habitat patch.

metapopulation The collection of local populations in a region.

patch An area of suitable habitat for a particular species or particular collection of species, ideally bounded by unsuitable habitat or habitat with different physical properties. Normally, it is one of many such areas in a region.

spatially structured population A population whose reproductive and survival rates vary over the region that it inhabits, and whose members stay long enough in a locality to experience the local reproductive and survival rates.

strict metapopulation (Also called a classical metapopulation.) A metapopulation satisfying the following conditions: (i) Local populations are partially isolated from one another and are frequently capable of sustaining themselves for several to many generations in the absence of immigration from other local populations, (ii) local population extinction occurs on a timescale of several to many generations, and (iii) migration between local populations leads to reestablishment of local populations following local extinction.

THE CONCEPT OF A METAPOPULATION has its beginnings in the suggestion of Andrewartha and Birch and others that some, if not most, local populations of organisms in nature frequently go extinct and are reestablished later by immigration from surrounding areas (Hanski, 1999). The metapopulation—the collection of all local populations—only persists if local extinction is balanced by recolonization. How this balance is achieved is an important focus of metapopulation theory.

I. INTRODUCTION

Because many human activities fragment natural habitats, humans may artificially create metapopulations or may decrease the density of local populations within existing metapopulations and may put the continued survival of natural populations at risk. Hence, metapopulations are a major topic in conservation biology. Regardless of whether or not a natural population is distributed over easily defined patches of habitat, on which distinct local populations may be recognized, essentially all natural populations are patchily distributed in space. Most ecologists believe that patchiness in space and time has functional roles in population dynamics, i.e., in the manner in which population densities change over time. Most important, population

dynamics at the regional or metapopulation scale are affected by the patchiness of the populations and their physical environment at lower spatial scales.

One very obvious way that patchiness is important is through mate finding. A sparse population evenly distributed over an area may have a low reproductive rate because males and females encounter each other too infrequently for many eggs to be fertilized. Patchiness can be a solution to this problem. High local concentrations or aggregations of a species solve the problem of low encounter rates of males and females consistent with a low average density. Similar effects occur from predation. Individuals may find safety from predators in a group but be vulnerable when isolated. Such effects of sparse populations are called Allee effects and are potentially one reason why patchiness in space is important. However, disadvantages from clumped distributions in space might also occur, for example, due to competition. Clumps of individuals in space deplete resources locally and reduce population growth rates compared to what would be experienced if the population were distributed more evenly. A similar effect results if predators are attracted to clumps of prey. Rather than prey finding safety in numbers, it is possible that they may be more vulnerable in clumps if predators increase their numbers at these locations.

These explanations for the importance of patchy distributions involve interactions between organisms in the same species and therefore involve density dependence—dependence of the probability that an individual survives, or dependence of its reproductive rate, on population density. The most striking theoretical predictions for the effects of patchiness, however, are for interactions between species for which one or more is patchily distributed. Major effects of patchiness on population dynamics also occur from spatial and temporal variation in the physical environment. Naturally, if species are concentrated in better localities, they will have higher growth rates in comparison with random distributions, but such environmental variation has its most striking effects by altering the interactions between organisms, locally in space, and hence by altering the collective outcome of those interactions at the level of regional populations. These ideas are all studied within the context of metapopulations but extend to spatially structured populations generally.

II. STRICT METAPOPULATIONS

The idea of a metapopulation is most commonly invoked when patchiness in space is so extreme that the regional population splits into local populations, each of which is too small to persist indefinitely (Hanski and Gilpin, 1997; Hanski, 1999). Local populations go extinct but may be recolonized by migration from other local populations. In the strict sense of a metapopulation, local populations are sustained primarily by reproduction of resident individuals but may be subsidized by infrequent immigration from other local populations. The role of immigration, however, is seen mainly as allowing recolonization of a local population after it has become extinct. Local extinction may occur for any of a variety of reasons, as discussed later, but is normally assumed to occur asynchronously in different local populations, or the metapopulation as a whole would be lost. Although nearly all organisms are patchy in space, there is some question regarding how frequently all the previously mentioned characteristics of a strict metapopulation are satisfied (Harrison and Taylor, 1997). Thus, in considering the results of metapopulation theory it is important to distinguish those features applicable only to strict metapopulations and those that apply more generally to spatially patchy populations.

A. Single Species Considerations

The main interest in metapopulations, strictly defined, is with colonization and extinction dynamics. The variable of prime concern is the proportion, p, of patches (places where a local population potentially could exist) that are occupied by the species. Two parameters are involved with the dynamics of this occupancy fraction: the extinction rate of local populations (ε) and the rate c at which empty patches are recolonized per fraction occupied. In essence, the fraction of local populations going extinct in one unit of time is ε. The probability of an extinct population being recolonized in one unit of time is cp because c is measured proportional to the fraction of occupied patches and incorporates the idea that the probability of recolonization should depend on the fraction of other patches that are occupied. Thus, the change in the fraction occupied with time may be expressed as the following differential equation, called the Levins equation:

$$\frac{dp}{dt} = cp(1 - p) - \varepsilon p.$$

If the rates ε and c remain constant with time, it follows that in a metapopulation with a large number of local populations, the fraction occupied will reach an approximate equilibrium at the value $1 - \varepsilon/c$, provided $c > \varepsilon$, because at this value extinction is balanced with

recolonization. If ε is greater than c, local extinction exceeds local colonization and the metapopulation as a whole goes extinct. Conversely, c must exceed ε for the metapopulation to persist. This result is often called the threshold condition, and it is of major concern for applications of metapopulation theory in conservation. Because actual metapopulations in nature never have infinitely many local populations, the system is never exactly at the equilibrium $1 - \varepsilon/c$ but rather fluctuates about this value. In metapopulations with only a few local populations there is a danger that all local populations will simultaneously go extinct, causing the extinction of the metapopulation even though $c > \varepsilon$.

On what biological features do these colonization and extinction rates depend? Consider extinction. Local extinction can occur in many ways, some of which stem directly from the activities of humans in habitat destruction or modification and hunting; however, metapopulation models are concerned with the case in which local extinction is a natural and repeated phenomenon, whose rate may be influenced by human activities but whose presence is not. Thus, local populations may become extinct by chance because of small population size. The phenomenon of demographic stochasticity refers to independent chance events in the lives of individual organisms. It is impossible to predict how long any individual will live and how many offspring it will have, and these effects summed over individuals in a population cause it to fluctuate. In a small local population, there is always a definite probability of below replacement reproduction in any year; and in a small population a chance run of such years can lead to extinction. These probabilities decrease dramatically as population size increases, but there are other factors that can also lead to local population crashes, including unstable population dynamics and disturbance.

Two different forms of disturbance are commonly considered. An environmental disturbance is caused by an environmental event such as a storm or fire, and a biological disturbance is caused by the invasion of predators or disease. In the strict metapopulation scenario, the interest is in disturbance events that lead to extinction of the local population either coincident with the disturbance or shortly after, following weakening of the population by disturbance. At any time, disturbances must strike patchily in space to cause extinction of only a proportion of local populations, or the metapopulation as a whole would be lost. It is very common for environmental disturbance agents, such as fires and storms, to distribute mortality very patchily in space even though they may affect a large area in a short period of time.

In a strict metapopulation, to which Levins equation applies, recolonization of a patch is from immigration from occupied patches. Many organisms may have means of recovering from disturbance by regrowth from seeds, roots, resting eggs, or spores within a recently disturbed patch, but with a strict metapopulation such populations have not gone extinct. They have merely died back and have been regenerated from dormant stages in the life cycle or belowground parts. The strict metapopulation idea that colonization occurs from external sources is the reason for the formula cp for the recolonization probability. Indeed, the rate of regeneration from sources within a patch should not depend on p. Confusion of regeneration with recolonization could potentially lead to serious errors in calculations and inferences.

Recolonization can be from mobile individuals, seeds, spores, or other propagules that arrive from external sources in sufficient quantity to reestablish a local population. The value of c will be affected by a variety of factors, such as the spacing of local populations. With large distances between local populations, many propagules may perish after leaving their source population before arrival in suitable habitat. The sizes of local populations will also influence c because larger local populations should be expected to send out more propagules. The size of the metapopulation, in terms of the number of local populations, is also important. Because the number of habitat patches is always finite, the fraction of patches occupied is not at the equilibrium value $1 - \varepsilon/c$ but rather fluctuates about this value; the smaller the number of habitat patches, the larger these fluctuations. If the number of habitat patches is too small, there is a danger of simultaneous extinction of all local populations eliminating the metapopulation even if $c > \varepsilon$.

Habitat fragmentation by human activities may lead to a metapopulation structure of local populations even if this was not the preexisting situation for the natural population of these organisms. With continuing habitat destruction, c will decline due to increased spacing and smaller size of suitable patches, and there is the danger that c will decrease below ε, especially because ε may increase as suitable patches decrease in size and support smaller local populations. Thus, even though there is habitat capable of sustaining local populations, the danger exists that local populations may be either small or so vulnerable because of other habitat alterations that the rate of local extinction exceeds local recolonization, which would lead to loss of the metapopulation altogether. Alternatively, if the organisms are not able to disperse between habitat patches, habitat fragmentation

is accompanied by zero colonization rates, and the metapopulation decreases to extinction at the rate ε the moment it is created.

The simple destruction of habitat reduces natural population sizes, putting species at risk independently of these metapopulation considerations. However, metapopulation theory emphasizes that the viability of populations in the remaining habitat may be seriously affected by its connectedness. A final feature of habitat destruction is that by reducing the areal extent of a population, the probability that extinction events occur simultaneously in different parts of the metapopulation increases. For example, fire might sweep through the whole area occupied by the metapopulation, or climate fluctuations might have severe effects in all parts of the metapopulation, endangering the metapopulation as a whole.

So far, the rates c and ε have been treated as though they are independent of p, the fraction occupied. This need not be the case. It has been suggested, for example, that extinction rates may decrease as the fraction occupied increases because extant local populations may tend to be larger and less vulnerable to extinction when they are subsidized by immigration. This could be especially important in the recovery of local populations after chance population declines, thus staving off extinction. As such, this phenomenon is called the rescue effect. If the rescue effect is required for c to exceed ε, the metapopulation as a whole may be especially vulnerable to extinction due to chance fluctuations in the fraction occupied; if this fraction becomes too low, ε will exceed c, promoting further decline and total extinction of the metapopulation. There are many other characteristics and complications that one can consider in single-species metapopulations, such as variation in the sizes of local populations, their distances from each other, and variation in habitat quality—features that are discussed by Hanski and Gilpin (1997) and Hanski (1999).

B. Multispecies Considerations: Predators and Parasitoids

Extinction and colonization rates may depend on other organisms. Indeed, as mentioned previously, as biological disturbance, local extinction may be a consequence of invasion of the local population by predators or disease. In this case, extinction rates vary with the abundance of predators within the metapopulation, which in turn depend on the abundance of prey. It is possible that only the prey has a metapopulation structure be-

cause predators may be more mobile, occupying all of the landscape (Harrison and Taylor, 1997). Their density must be taken into account in determining the extinction rate of the prey, but otherwise their inclusion does not result in major differences in the understanding of metapopulation dynamics, except possibly in terms of the effects of habitat destruction, as discussed later.

If both predator and prey have the same metapopulation structure, a metacommunity results. Simple predator–prey models of isolated local communities are often unstable, causing large fluctuations in their abundances and potentially leading to extinction of the prey or the predator (see Fig. 7). A metacommunity structure has long been suggested as one means by which predator–prey interactions may be stabilized in nature. The interaction between the two locally in space remains unstable: The prey is driven extinct by the predator, but provided the colonization rate c for the prey exceeds its extinction rate due to predation and other causes, it is able to persist in a metapopulation. Similarly, although the predator depends on the prey, whose local extinction leads to local predator extinction, provided the predator can find patches sufficiently well it can also persist in the system. In this way, it is possible for predator and prey to have a stable equilibrium at the metapopulation level despite unstable dynamics on the local scale (Nee et al., 1997). This metacommunity structure may have important conservation implications. Habitat destruction may more strongly affect the predator than the prey because prey numbers in a region may be buffered at first by reduction in predator numbers, with the effects of habitat destruction on prey being stronger after the predator has been eliminated (Nee et al., 1997).

The potential for metacommunity structure for predator and prey is also of great interest in the study of biological control of insect pests and introduced weeds. Commonly, in biological control, one seeks as a control agent a predator or parasitoid (a parasite that invariably kills parasitized hosts) that is specialized on the pest organism and causes sufficient damage to the pest to reduce its numbers greatly. Such a control agent, however, may have an unstable interaction with its host, leading to large oscillations in agent and pest densities, which is an undesirable outcome. However, there are many successful examples of biological control in which the pest is maintained at relatively low and stable numbers. One possible explanation for such control is that local population dynamics are indeed unstable, but regional dynamics are stable because they are metapopulation dynamics (Briggs et al., 1999).

C. Multispecies Considerations: Competition

One organism may cause another to go locally extinct not because it is a predator of that organism but because it is a competitor. Many years ago, G. E. Hutchinson and J. G. Skellam suggested that inferior competitors may persist regionally by being good colonizers of newly vacant habitat, where they persist only until their competitors find that habitat and drive them extinct. They termed such good colonizing inferior competitors "fugitive species" (Hanski, 1999). An essential component is a trade-off between dispersal ability and competitive ability: If the better competitors were not poorer colonizers, they would arrive too quickly in vacant habitat, giving insufficient opportunity for exploitation of that habitat by fugitives.

The fugitive species idea has been extended in recent years to consider the possibility that a suite of competitors in a system might have a competitive hierarchy, i.e., be strictly ranked in competitive ability with better competitors eliminating poor competitors whenever they occur in the same patch (Hastings, 1980). Such a competitive hierarchy prevents long-term coexistence in any patch, but if all local communities are ephemeral because disturbance takes place locally in space and removes whatever species happen to be there, then every so often any given local community becomes available for colonization by even inferior competitors. Colonization events in the presence of a competitive hierarchy drive succession (a change in species composition in a particular direction) within a local community toward domination by the best competitor. Assuming that inferior competitors have higher dispersal rates, then they have a higher probability, per unit occupancy (per unit p), of arriving in vacant habitat. Any species could actually arrive first, but inferior competitors have an arrival advantage. Any species arriving at a site that is a superior competitor to the current occupant takes that site. The local community shifts progressively in the direction of the best competitor in the system until disturbance occurs, interrupting the process and starting it over again.

Because both extinction and colonization occur patchily in space and time, the metacommunity consists of a mosaic of local communities in different stages of succession (Fig. 1). Each local community may have low species diversity because only the best competitor in the local community persists there for long. However, when considered over space, the metacommunity has high species diversity due to the fact that different local communities are in different successional states and have different species. It is possible for the metacommunity to be in equilibrium and maintain this high species diversity regionally. This equilibrium is dependent on the inverse ranking of competitive ability and colonizing ability, but it is not sufficient for an inferior competitor simply to be a better colonizer: It has to be better by more than a critical amount that depends on the colonizing abilities of superior competitors and the disturbance frequency (Hastings, 1980).

The disturbance frequency has a particularly important role in the maintenance of regional diversity. A higher disturbance frequency means that fewer patches have the best competitor and there are more patches available for other species. At too low a disturbance frequency, lower ranked species do not have sufficient opportunity for colonization and therefore may not persist regionally: Their ε values may exceed their c values. However, at higher disturbance frequencies, lower ranked species may persist and coexist regionally with higher ranked species. If the disturbance frequency is too high, the best competitors, which are by assumption poorer colonizers, have too high an extinction rate, ε, relative to their colonization rate, c, and disappear from the system. At extreme levels, only the very best colonizers can persist. It follows that with such competitive hierarchies, both high and low disturbance frequencies lead to low regional diversity. Diversity is maximized at some intermediate value of the disturbance frequency—an idea that is often referred to as the intermediate disturbance hypothesis (Connell, 1978). Disturbances here can be of the physical sort or of the biological sort provided the predators or other agents causing disturbance are generalists and therefore are dependent for their own persistence on all species in the system, not just particular species which they may control separately from other species. Specialist mortality agents may be important in the maintenance of diversity (Chesson and Huntly, 1997), but this idea is not included in the intermediate disturbance hypothesis.

The critical feature of the previously discussed mechanism of diversity maintenance is a metacommunity that exists as a successional mosaic, i.e., the system is diverse because local communities range over a variety of successional stages having different species that provide colonists of other local communities. Colonization moves succession along or reestablishes local communities following local disturbance (Chesson and Huntly, 1997). This successional mosaic model has been suggested to work with local populations consisting simply of single individuals, for example, single herbaceous plants in a meadow (Lehman and Tilman,
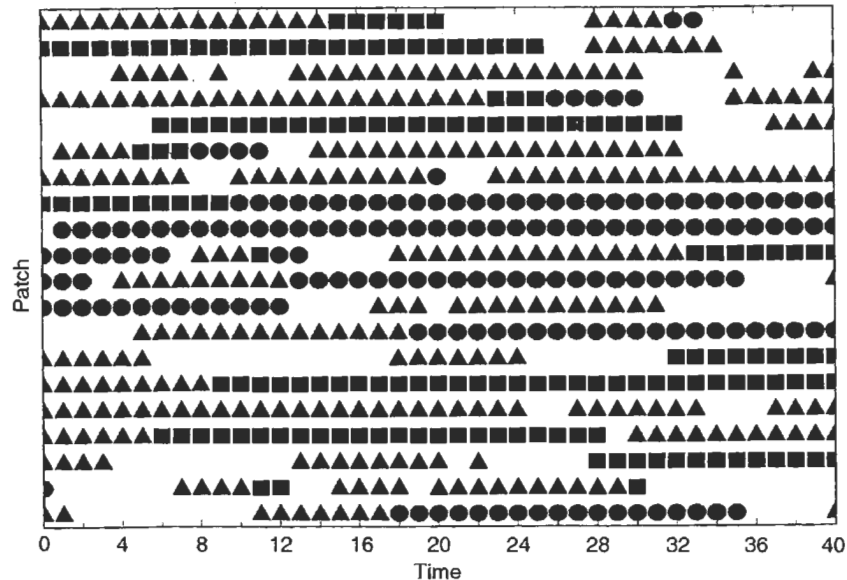
FIGURE 1 Turnover of species in a subset of the patches of a metacommunity with successional mosaic dynamics. Three different species are indicated by the symbols ●, ■, and ▲ in order of decreasing competitive ability and increasing colonizing ability. Blanks mean empty patches.

1997). Although this is not exactly what one might think of as a local population, none of the previous discussion depends on the size of a local population. Death of an individual is then equivalent to local population extinction. Death of an individual may be brought on by the arrival of a superior competitor at the site, disturbance, or simply senescence. Disturbance or senescence open the site to invasion by any species. Otherwise, the site can only be invaded by a superior competitor. The idea that many species may coexist in an area by this mechanism operating on a small spatial scale is referred to in the literature as coexistence by competition–colonization trade-off. This idea is particularly useful in the case of plants or sessile aquatic animals that hold space (Lehman and Tilman, 1997).

These ideas on diversity maintenance in metapopulations have important implications for conservation. If habitat destruction lowers colonization rates, as discussed previously, competitively superior species may be most at risk (Tilman and Lehman, 1997) because their already poor colonizing abilities make them less tolerant of decreases in colonization rates. These models predict that habitat destruction eventually negatively affects all species, however. When the per unit colonization rate, c, of the best colonizer is reduced below the extinction rate of local populations, all species are doomed to regional extinction even though patches of suitable habitat remain.

III. QUANTITATIVE EFFECTS OF SPATIAL VARIATION

The discussion so far has made the assumption that the only thing we need to know about a local population is its presence or absence: Is it extinct or not? This is a rather crude accounting because surely the number of colonists or propagules sent out by a local population depends on the size of that local population. Patches may be of different sizes and qualities and therefore support local populations of different sizes and densities, issues that are active areas of research in metapopulation theory (Hanski and Gilpin, 1997). Moreover, local populations vary in size over time in any one patch and in space from patch to patch even when patches of identical size and quality are compared. Ignoring changes in local abundance over time (i.e., ignoring the dynamics of local abundance) would be justified if local population buildup after colonization occurs quickly to some local population equilibrium (a population size at which, on average, reproduction and immigration balance deaths and emigration), around which population fluctuations occur until extinction. A broader variety of behaviors of metapopulations can be examined by taking actual local population sizes into account. At the same time, we can depart from the strict metapopulation assumption that recolonization occurs from ex-

ternal inputs. We shall now assume that there are two spatial scales in the system. The smaller scale is the spatial scale on which interactions between individual organisms occurs (i.e., it is the spatial scale of positive and negative density-dependent effects within species), the scale of competition between species, or the scale of predation, depending on which of these are important in the system of concern. This scale corresponds to the local population scale in the strict metapopulation sense and shall still be referred to in terms of the patch and the local population. The larger scale is the scale of the whole population, which corresponds to the metapopulation or regional scale in the previous discussion.

A. Single-Species Dynamics

To introduce the fundamental concepts, consider first density-dependent population dynamics applicable to organisms with annual life cycles. The dynamics of a local population in the absence of migration can be defined by plotting local population density (numbers per unit area), N_{t+1}, at time $t + 1$ as a function of its density, N_t, the previous year, as represented in Fig. 2. These curves are dynamical relationships, i.e., by applying them repeatedly, one can plot density as a function of time (Fig. 3). The straight line (relationship I) represents the density-independent case in which individual organisms do not interact with one another, and so an individual's contribution to future genera-

tions is independent of the number of other individuals. Thus, N_{t+1} is simply proportional to N_t. Relationships II and III are two cases of density-dependence and this density dependence means that they are nonlinear, i.e., they are curved or humped relationships (certainly not straight lines). For relationship II, the resources sustaining a local population are strictly limited, fixing an upper bound on the local population density, which is achieved if the resources are efficiently utilized. The larger the population at time t, the closer the population comes to using all resources and the closer the upper bound on population density is approached. Annual plant populations commonly accord at least approximately with this relationship, which is sometimes referred to as contest competition. Some insect populations may have dynamical relationships more like curve III. Above a certain density, the number of insects in year $t + 1$ is a decreasing function of the number of insects in year t. One explanation for a relationship such as this is scramble competition: At high densities, a high proportion of the population may starve to death, which leads to loss of the resources that these individuals consumed before death. Thus, a large fraction of the resources that could have been turned into new individuals at time $t + 1$ is lost, and the population crashes.

The three different dynamical relationships of Fig. 2 give very different local population dynamics (Fig. 3). The linear case (relationship I) gives simply a geometric increase. Relationship II (contest competition) gives highly stable dynamics: The population quickly converges on an equilibrium population size, which is determined by the point at which the diagonal line in Fig. 2 intersects the dynamical relationship. Relationship III (scramble competition), however, gives irregular fluctuations referred to as deterministic chaos which result here from the tendency of scramble competition to cause population crashes following population buildup. What happens when local populations with these various dynamics are connected regionally? If there is no variation in population density in space, then regional population dynamics are the same as local population dynamics. However, if there is a large amount of spatial variation in population densities (a common occurrence in nature), regional population dynamics can be very different from local dynamics (Fig. 4). The density-independent case (relationship I), however, does not show different local and regional dynamics because individuals are not affected by density, and therefore population dynamics cannot be affected by spatial variation in density. On the other hand, the strong density dependence arising from scramble competition leads to corre-
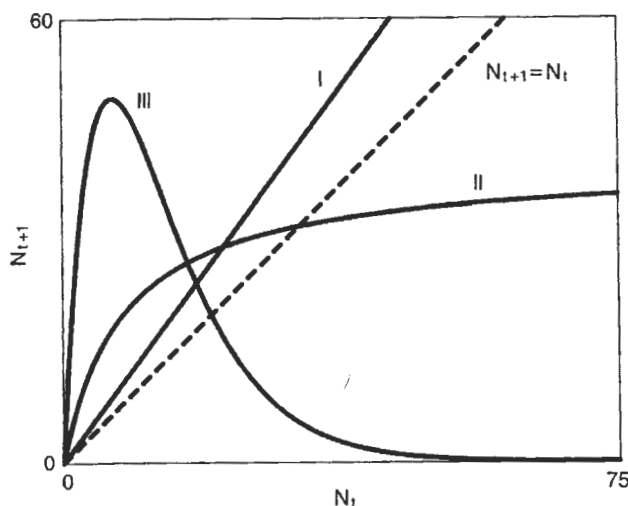

FIGURE 2 Solid curves, dynamical relationships of single-species local populations; I, density-independent dynamics; II, contest competition; and III, scramble competition. The equilibria are the intersections of these curves with the dashed line defining no change in local population size ($N_{t+1} = N_t$).
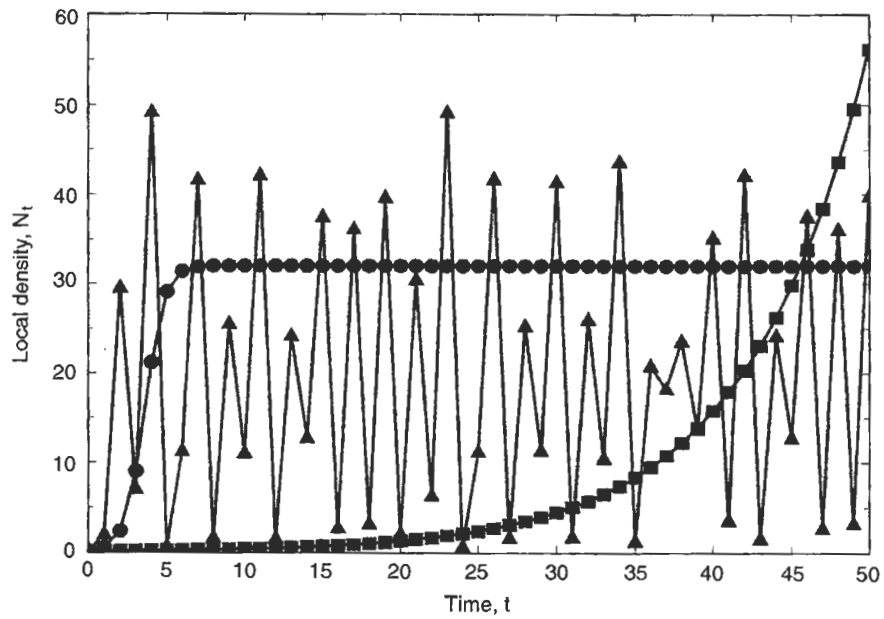
FIGURE 3 Local population dynamics generated by the dynamical relationships of Fig. 2. Relationship I (density independent), ■; relationship II (contest competition), ●; relationship III (scramble competition), ▲.
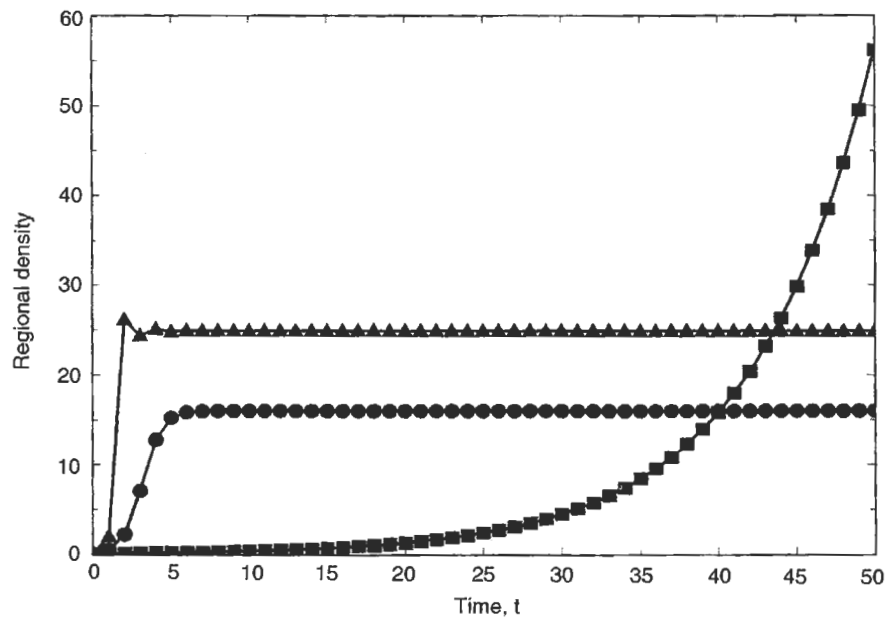

FIGURE 4 Regional dynamics generated by the interaction of the dynamical relationships of Fig. 2 with spatial variation in population densities. Relationship I, ■; relationship II, ●; relationship III, ▲.

spondingly striking differences between regional and local dynamics. For the situation depicted, which is defined in detail later, chaotic fluctuations have been replaced by a stable equilibrium. For contest competition (relationship II), the effect of spatial variation on regional population dynamics is quantitative and not qualitative: The equilibrium density is decreased.

What is the explanation for these changes in dynamics at the regional level in density-dependent situations? To answer this question, we need to work out the dynamical relationship between $\overline{N}_{t+1}$ and $\overline{N}_t$ defining the dynamics of population density at the regional level. These regional densities can be defined as the averages of the population densities in local populations, weighted if necessary by patch area. Dynamical relationships such as those in Fig. 2 continue to define dynamical change within patches, but disturbance and fluctuations due to small population size lead to random deviations in these relationships. Thus, these local dynamical relationships are mean relationships converting inputs of population density into outputs, and some of the output population in any patch may then disperse to other patches.

The essence of the difference between local and regional dynamics can be understood by imagining that dispersal occurs early each year and for the rest of the year patches are isolated with mean change governed by dynamical relationships in each patch. Further imagining that after dispersal local populations exist at just two densities (high and low) in equal abundance, then the regional dynamical relationship is easy to derive. This is done in Fig. 5, in which it is assumed that low-density patches have inputs 1/3 the regional density, $\overline{N}_t$, and high-density patches have inputs 5/3 of $\overline{N}_t$. The solid curve defines the relationship of local outputs to local inputs (scramble competition) and the dashed curve defines the relationship between $\overline{N}_{t+1}$ and $\overline{N}_t$, i.e., the regional dynamical relationship. This regional relationship is found by connecting pairs of points on the local relationship corresponding to low- and high-density inputs and finding the midpoints of the lines joining these pairs of points. For example, the points A and B in Fig. 5 are one such pair of points, and M is their midpoint. The x coordinate of M is thus the regional input, $\overline{N}_t$, which is the average of the x coordinates (local inputs) of A and B. The y coordinate of M is the regional output, $\overline{N}_{t+1}$, which is the average of the y coordinates (local outputs) of the points A and B. The complete regional relationship is found by repeating this procedure for every possible value of the input density $\overline{N}_t$.

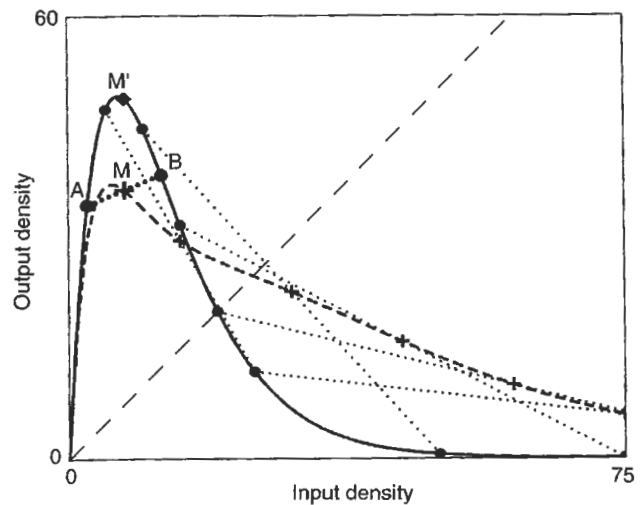Comparison of the point M on the regional relation-

FIGURE 5 Construction of the regional dynamical relationship from the local dynamical relationship III of Fig. 2 and spatial variation between two densities. Solid curve, local dynamical relationship; thick dashed curve, regional relationship.

ship with the point M' on the local relationship reveals the reason for the difference between local and regional relationships. These points both have the same input density, but M' is the output of the local dynamical relationship, whereas M is derived from averaging the outputs of the local dynamical relationship at two different input densities, which both give outputs less than M' due to nonlinearity (curvature) of the local relationship. Thus, nonlinearity in the local dynamical relationship combines with variation in local inputs reducing the hump on the regional dynamical relationship. A similar effect acting on the nonlinearity in the local dynamical relationship after the hump reduces the severity of the decline in the regional dynamical relationship, and it is the combination of these two effects that is responsible for the strong stability of the regional dynamics shown in Fig. 4. Nonlinearity and spatial variation also affect regional dynamics in the case of contest competition, but the effects are quantitative and not qualitative. The regional relationship for contest competition is shown in Fig. 6, in which it is assumed that 50% of local populations are extinct and the others have a density twice the regional density. Not surprisingly, the regional equilibrium is 50% of the local equilibrium, but this reduction, and the regional relationship in total, can be understood using the same averaging approach discussed for scramble competition.

Having local populations take on just two densities for any given average density is clearly unrealistic. However, the qualitative features of the previous results
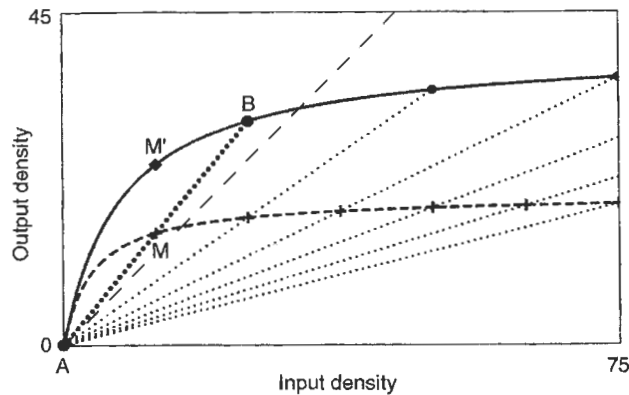
FIGURE 6   Construction of the regional dynamical relationship from the local dynamical relationship II of Fig. 2 in the presence of spatial variation between two densities. Solid curve, local relationship; thick dashed curve, regional relationship.

occur with general sorts of variation commonly observed in natural populations. The most common situation in nature is a negative binomial distribution of possible local population densities, which means that densities are somewhat more clumped than random in space. The striking change in dynamics from local to regional found for scramble competition is enhanced in this case (Chesson, 1998). In the density-independent case (relationship I) the dynamics at the regional level are unaffected by variation from patch to patch: M always equals M′, regardless of the pattern of variation. The nonlinearities, i.e., the deviations from a straight line relationship, present in relationships II and III, are necessary for variation in space to have an effect on the dynamics of regional density, and these nonlinearities occur from density dependence.

There are many causes for spatial variation in local densities, of which disturbance and fluctuations due to small population size were mentioned previously. Simple random dispersal processes also lead to some variation in density, but spatially varying environmental factors may have large effects on dispersal and on the ultimate distribution of organisms among patches. For example, in marine organisms such as reef fishes, local currents may transport larvae away from some places and toward others, and these currents may vary with time of year, storms, and other atmospheric conditions, potentially delivering dispersing larvae to reefs in a very patchy fashion. Moreover, organisms commonly actively seek particular places, and the relative attractiveness of different places may vary greatly. Organisms may also seek out their own species, and therefore any existing spatial variation in density may be magnified by

later dispersal. Unstable population dynamics occurring locally in space can be a cause of local variation in density, at least in models. In the illustrations here, spatial variation in density was assumed to have a fixed relationship to regional density [e.g., low-density patches ($\overline{N}_{t+1}/3$) and high-density patches ($5\overline{N}_{t+1}/3$)]. More realistically, local densities will not have fixed relationships to the mean, and therefore the regional relationship will in fact change over time as the relationship between spatial variation and regional density changes (Chesson, 1998). Nevertheless, the way in which nonlinearity and spatial variation change the regional relationship, illustrated in Figs. 5 and 6, remains the same despite all these complications. In particular, the stabilizing effect of spatial variation in densities on scramble competition continues to be seen in much more complex circumstances than illustrated here.

These quantitative considerations are very different from the colonization and extinction issues discussed previously for strict metapopulations, but the two approaches can be related. Colonization and extinction dynamics involve implicit density dependence: To count all occupied patches as equivalent, recently colonized patches must quickly increase in density to some sort of steady state, such as a local equilibrium density or fluctuation about a local equilibrium. Local dynamical relationship II would serve in this circumstance, with the mean output taking into account the probability of local disturbance. The example given previously with half the patches extinct corresponds to a c to ε ratio of 0.5.

These quantitative considerations also apply to spatially structured populations that are not strict metapopulations, for example, when recovery after disturbance depends to a large extent on regeneration rather than recolonization and also when only part of the life cycle is spatially confined. For example, it is very common for marine organisms that live on a reef, intertidally, or on the ocean floor to have widely dispersing larvae so that only the adult stage has clear spatial structure. The adult may be physically attached to the bottom, as in corals, barnacles, and mussels, or if it remains mobile it may have a territory or at least a home range that is much restricted in extent relative to the distance traveled by dispersing larvae, as in many reef fishes. Such spatial restrictions mean that interactions between individuals are localized because the individuals are localized and are likely most strongly affected by individuals living nearby, for example, on the same coral head or part of the reef. Similarly, in terrestrial plants a spatial unit of major importance is the immediate neighborhood of other plants close enough

to compete with it. Insect populations often have spatially confined larvae and dispersive adults. Although it is the adults that disperse in this case, the fundamental principles are the same in all of these cases, and the effects of variation in density in space are similar, even though in no case does spatial structure of one part of the life cycle qualify these populations as metapopulations in the strict sense. The effects of nonlinear dynamical relationships that we have explored depend on the smaller scale, which corresponds to the local population in a strict metapopulation, being the scale on which these nonlinear relationships apply. Because these nonlinear relationships derive from density dependence, the smaller scale is also the scale of density dependence.

How the scale of density dependence is determined depends on how the individuals in a population affect each other. For example, for territorial coral reef fishes, one source of density dependence may simply be competition for space to set up feeding territories. Other fishes may compete for hiding places from predators. The scale on which fishes may move to secure territories or hiding places defines the scale of density dependence. Predators may cause density dependence in their prey populations by responding to the density of the prey, for example, aggregating in areas of high prey density.

The scale of density dependence is the spatial scale on which predators respond to variation in prey density. Predators may also increase in numbers where prey are dense simply because they have more to eat and therefore reproduce faster. The scale on which this effect occurs is bound to be much larger than the scale of aggregation of predators to variation in prey density. The changes in dynamics with a change in scale demonstrated in Figs. 3–6 should occur in all these instances when one compares the dynamics defined on the scale of density dependence with the dynamics that emerge at the regional or metapopulation scale (Chesson, 1998).

B. Predators and Parasitoids

Like the dynamics of colonization and extinction, a rich array of phenomena is uncovered when the quantitative effects of spatial structure are examined in terms of interactions between species. In particular, predator–prey and host–parasitoid dynamics (Fig. 7) are often stabilized by local interactions and spatial variation (Hassell, 1997). This phenomenon is best understood in host–parasitoid systems in which a critical issue is spatial variation in the risk of parasitism experienced by a host, which may result from variation in parasitoid
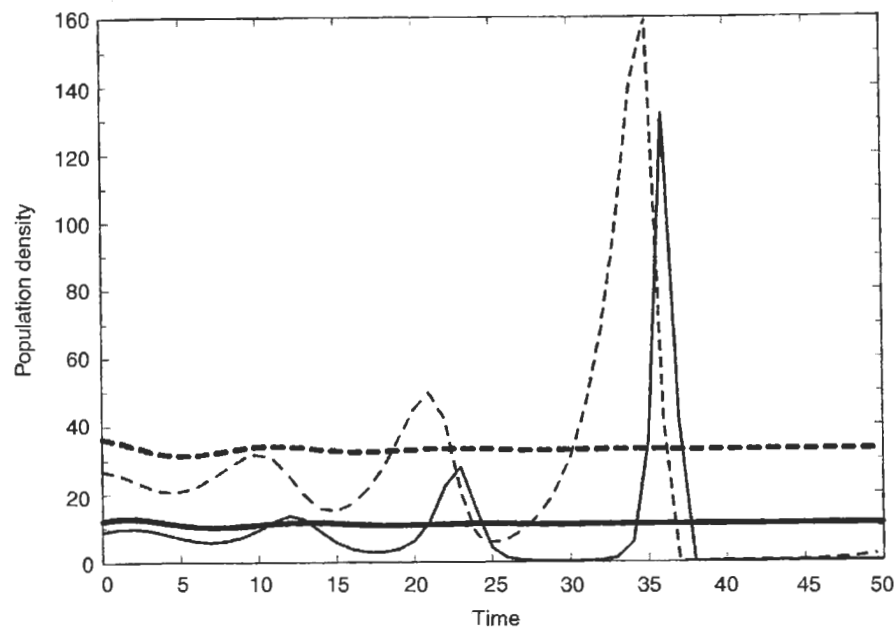

FIGURE 7 Host–parasitoid dynamics. Thin lines, local dynamics of an isolated host–parasitoid community in the absence of migration; thick lines, regional dynamics with parasitoids concentrated in half the patches. Hosts, dashed lines; parasitoids, solid lines.
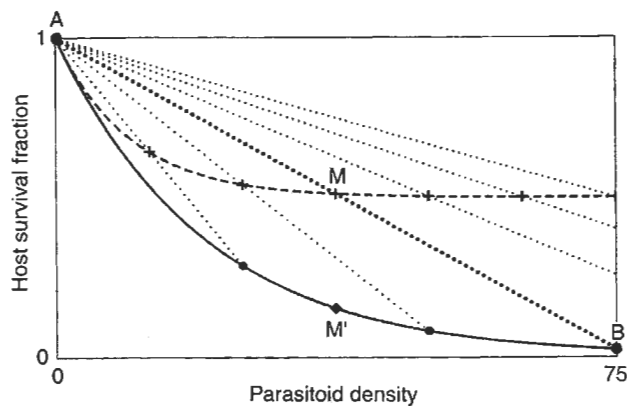
FIGURE 8   Local host survival rates and regional host survival rates as a function of parasitoid density with half the patches having no parasitoids.

density. Figure 8 illustrates how this works. The risk of surviving is thought to be an exponentially decreasing function of parasitoid density, as shown by the solid line.

Very simple two-level variation in parasitoids is assumed for ease of illustration: no parasitoids in half the patches and twice the mean parasitoid density in the other half. The effect of averaging different risk levels, exemplified by Fig. 8, is to moderate the decline in host survival with increasing parasitoid density, which means that host crashes following increases in parasitoid numbers are diminished, tending to stabilize the host–parasitoid interaction regionally (Fig. 7). Although the reasons for spatial variation in parasitoid density are poorly understood in general, an important feature of predator–prey and host–parasitoid interactions is the potential for the unstable nature of the interactions to generate variation in risk, which may then stabilize population dynamics on the larger spatial scale (Hassell, 1997).

C. Competitive Interactions

Competition–colonization trade-offs are one mechanism allowing coexistence of competing species in a patchy environment. Quantitative approaches allow the consideration of other mechanisms and more general spatial variation. Species fail to coexist (i.e., competitive exclusion occurs) when the species best adapted to the environment depletes resources to levels that are too low for other species to persist. Because the environment varies in space, different species may be the best

adapted under different environmental conditions. Then, many species that depend on the same resources may coexist regionally because each has patches in which it is the best competitor, i.e., each has its own spatial niche. If each of these patches were a closed community (i.e., not connected to other places by migration), then only a single species would dominate in each locality. However, in the presence of migration, each patch may have many species because a species that is not the best competitor in that local community has its reproduction supplemented by immigration from places where it is the best competitor.

If environmental characteristics vary over time also, favoring some species some times and others at other times, local diversity is even more likely to be maintained at high levels because trends in local species abundances will be reversed with reverses in the ranking of competitive superiority in a particular locality: Species tending toward low relative abundance will be partially restored to higher values. A phenomenon with the opposite effect has been discussed by Rosenzweig (1995) and may be particularly important in animals, especially those with complex behavior. Animals detecting a competitively superior species may leave or keep away from a patch, an effect that tends to divide a landscape into exclusive areas containing only the best species for those areas (Rosenzweig, 1995).

The various effects of spatial environmental variation do not require strict metapopulations but simply spatial structure. This more general theory can be applied, for example, to the coexistence of insects, especially various communities of flies such as *Drosophila* and carrion flies, which lay eggs in ephemeral patches of food such as fruit, mushrooms, or dead animals. In general, although the larvae of several species are commonly found developing in the same patch of food, it is also a common finding that there is segregation between species in choice of food patches. Although the underlying cause of the choice is not well understood, the effect is that it promotes stability very strongly (Ives, 1988). A second example of the potential importance of spatial environmental variation is marine communities, especially coral reef fishes but also various sedentary invertebrates that compete for space, with similar effects applicable to plant species. In marine communities, as discussed previously, dispersing larvae characteristically arrive at potential settling sites in a highly patchy manner. Such systems are said to be strongly affected by recruitment variation, where recruitment refers to the process of a larva settling at a particular in patch. Differences in the spatiotemporal patterns of recruitment have the potential to contribute to species coexis-

tence. In this case, the environmental advantage that a species has in a particular patch is proportional to its arrival rate in that patch.

There is a very simple graphical technique for understanding the effects of variation in recruitment rates in space, which serves to illustrate how spatial environmental variation and its interaction with population density may have important effects. Figure 9 assumes a community with two competing species and plots the proportion of new inputs to a local community as a function of the local environment and the regional abundance of the species. The solid curves correspond to two environment types. The x-axis is the proportion, p_t, of species 1 in the system as a whole. The y-axis is the proportion, s_{t+1}, of the available space at the site taken by new settlers of species 1 during the time interval from t to $t + 1$. The top curve refers to patches favoring settlement of species 1, whereas the bottom curve refers to patches favoring settlement of species 2. The difference between the different sorts of patches is in the relative arrival rates of larvae of the two species: More members of species 1 arrive at the top curve sites, and more members of species 2 arrive at the bottom curve sites. The species compete for available space at

a site, which is assumed to be limiting and thus filled by the larvae arriving each year. Note that if there were only one sort of patch in the system, eventually one species would eliminate the other because it would have higher settlement success everywhere and would increase in abundance relative to the other species. For example, if all sites favored species 1 (Fig. 9, top curve), then the fraction of species 1 settling would always be higher than p_t. It follows that species 1 would steadily increase until it had taken over altogether, assuming that settled individuals of both species have the same mortality rates (a simple adjustment, however, extends this diagram to different mortality rates; Chesson, 1985).

In Fig. 9, it is assumed that two-thirds of patches favor species 1 and one-third favor species 2. This means that the average proportion of settlers, s_{t+1}, that belong to species 1 regionally is (2/3) the top solid curve + (1/3) the bottom solid curve, which is given by the points dividing the vertical lines between the two solid curves in the ratio 1 : 2. The dynamics of regional settlement are then given by the wavy line between the two curves. Depending on the actual adult mortality rates of settled organisms, the regional proportion, p_{t+1}, of species 1 at time $t +1$ will lie somewhere between p_t and the regional s_{t+1}. Thus, the point where the wavy line crosses the diagonal is the equilibrium point for the system, i.e., the point where p_t does not change over time. It is a stable equilibrium point: If the value of p_t is less than the equilibrium, then the regional s_{t+1} is always greater than p_t, and therefore species 1 increases in relative abundance ($p_{t+1} > p_t$). However, if p_t is above the equilibrium, the regional s_{t+1} is less than p_t, and therefore species 1 decreases in the system. Hence, whenever away from equilibrium, the system moves back toward it over time.

These results apply no matter whether a patch continues to favor the same species forever or favors different species at different times, for example, if environmental conditions responsible for larval transport change over time. These results have to be modified, however, if instead all patches favor a particular species at a particular time but the favored species changes over time, for example, if the environmental conditions applicable to a particular year favor one species over the other everywhere. In this case, the environment is varying purely temporally. The way temporal variation affects the dynamics of an organism is greatly influenced by life history parameters such as the adult death rate because this determines how long past effects of fluctuations in settlement are reflected by the age structure of the population. A low adult death rate means that a
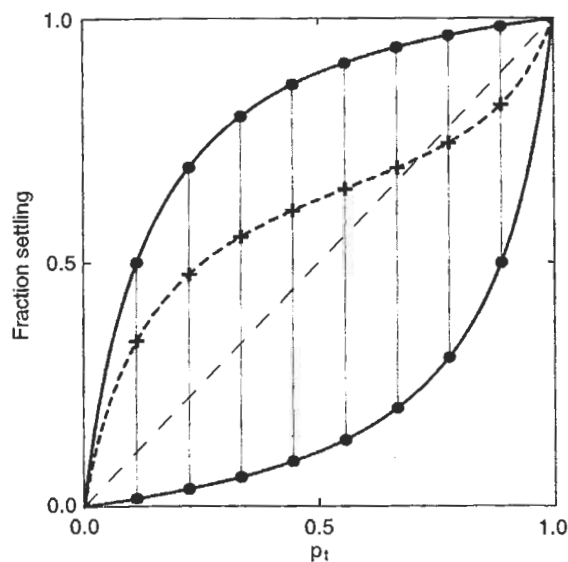

FIGURE 9 Local and regional settling fractions (proportion species 1) as a function of regional fractional abundance for a marine space-holding community with two species. Top solid curve, local environment favoring species 1; bottom solid curve, local environment favoring species 2; wavy dashed curve, regional settling fraction with two-thirds of patches favoring species 1. The regional equilibrium is the intersection of the wavy dashed curve with the diagonal dashed line.
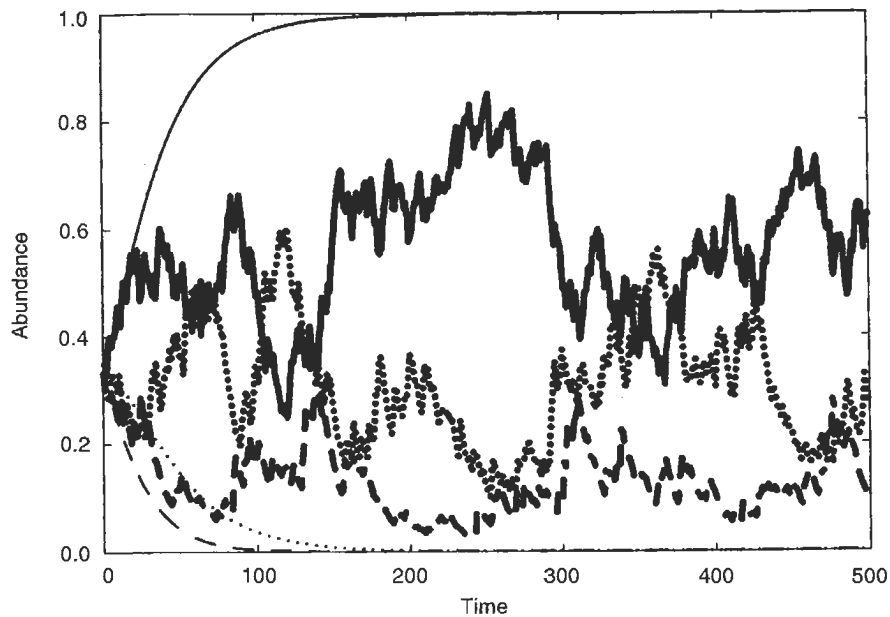
FIGURE 10 Fluctuations in abundance (proportion of sites held) for three competing space-holding species experiencing independent temporal fluctuations in recruitment rates (thick wiggly curves) and constant recruitment rates (thin smooth curves).

species can persist over periods when it is at a competitive disadvantage without its population density declining too greatly. If follows that the ability of species to coexist as a result of temporal variation varies inversely with the adult death rates (Chesson and Huntly, 1997). With irregular temporal fluctuations, the system does not have a traditional equilibrium but nevertheless can still exhibit stable fluctuations about a mean value as depicted in Fig. 10.

Temporal variation is an important feature of many systems, and a mechanism such as that described here has been suggested for coexistence in tropical trees in which highly variable fruit production occurs, in annual plants in which seed germination may vary greatly between years but seeds survive during unfavorable times in the soil seed bank, and also in annual zooplanton in lakes in which a resting egg bank takes the place of the seed bank.

IV. LESSONS FROM METAPOPULATION THEORY

A. Conservation

Few populations in nature exist without important spatial structure. Although there is debate regarding how often this structure conforms to a strict metapopulation, metapopulations are an important tool in conservation biology theory because habitat fragmentation creates distinct local populations even if they could not be defined before human interference. There is no question that the inhabitants of small isolated habitat fragments are at risk of local extinction. Although a collection of such habitat fragments may genuinely be thought of as a metapopulation, recolonization rates may be so low that each local population will go extinct before any are recolonized. Metapopulation theory emphasizes the need, at a very minimum, for the recolonization rates c to exceed the extinction rates ε. Habitat destruction not only puts populations at risk by reducing their total size and spatial extent but also, by altering the connectedness of the remaining habitat, it reduces the value of the remaining habitat.

Metapopulation theory also implies that even uniform reduction in recolonization rates with habitat destruction may have different impacts on different species in the system. Therefore, the system may change in character with habitat destruction even under conditions that may not appear to be biased in favor of one species or another. Such effects have the potential to disrupt the functioning of ecosystems. This is not specific to strict metapopulations. The metapopulation perspective also indicates that not just inhabited habitat is

suitable habitat. A species may be only temporally absent or in low abundance in an area, and this habitat may in fact be playing an important role in the system. Empty habitat must be judged in terms of its potential role as part of a larger connected system. Short-term environmental fluctuations may play a role in changing the suitability of habitat patches. Patches that are currently unsuitable may have the potential to become suitable in the future. With the prospect of global climate change, the maintenance of a diversity of patch types and a landscape structure suitable for migration of organisms between patches are of major importance in reducing the loss of biodiversity.

B. Nonequilibrium Dynamics

The metapopulation perspective highlights the role of nonequilibrium conditions in space, i.e., situations in which local populations do not remain near an equilibrium population size. Simple predator–prey and host–parasitoid models commonly do not have both species coexisting stably in isolated patches. Nonequilibrium locally in space that occurs asynchronously in different patches has an essential role in stabilizing the spatial extensions of these models. Similarly, in successional mosaic systems, perturbation from equilibrium (domination by one species), locally in space, is critical to the maintenance of the system. Such essential roles for nonequilibrium conditions have sometimes been considered as meaning that the system is particularly robust to perturbations, including habitat degradation, by human activities. There is no reason to expect this to be true. Indeed, the message here is that equilibrium occurs on the larger spatial or temporal scales. Interfering with the system through habitat destruction, alteration in the disturbance frequency, alteration in mean environmental states, and alteration of the variance in environmental states all have major consequences and are therefore of serious concern even though on small scales the system may not be at an equilibrium.

C. Population Regulation

These metapopulation and structured population perspectives also have the potential to resolve the long-standing debate regarding the relative importance of environmental fluctuations versus density-dependent interactions within and between species. Andrewartha and Birch were the first to clearly articulate metapopulation structure as an important feature of nature (Hanski, 1999), but because of the prominent role of stochastic factors (factors with random elements), such as extinc-

tion and colonization, they believed that density dependence was of minor importance. The quantitative analysis here shows that, far from being of minor importance, density dependence within local populations has a major role in shaping the nature of population dynamics at the metapopulation or regional scale. Density-dependent processes lead to nonlinear dynamical relationships, and it has been shown how such relationships interact with fluctuations in time and space to give outcomes at larger temporal and spatial scales that are not predictable on the basis of the separate effects of these factors.

See Also the Following Articles

COMPETITION, INTERSPECIFIC • DISTURBANCE, MECHANISMS OF • LOSS OF BIODIVERSITY, OVERVIEW • PARASITOIDS • POPULATION DYNAMICS • PREDATORS, ECOLOGICAL ROLE OF • SPECIES-AREA RELATIONSHIPS • SPECIES INTERACTIONS

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