COMMUNITIES IN A LANDSCAPE: THE INFLUENCE OF HABITAT HETEROGENEITY ON THE INTERACTIONS BETWEEN SPECIES

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Abstract.—A model similar to the single-species source-sink models developed by Pulliam and by Pulliam and Danielson is described for species that have "distinct" habitat preferences and preemptive occupation of sites within habitats. The model shows that the interactions between two species do not result solely from the intrinsic properties of the species involved. They are also functions of the landscape in which the species occur. One species may cause an increase (facilitation) in the equilibrium population size of another species if the high-quality source habitat for the second species is rare relative to the abundance of low-quality sink habitat. A species may inhibit another if the second species' source habitat is abundant. Combinations of facilitation and inhibition effects describe the interactions between two species. There are two sets of possible interactions for any landscape of two habitat types. These are \{(-, +), (-, -), (+, -)\} and \{(-, +), (+, +), (+, -)\}. Species for which individuals can sample a large number of sites are likely to exhibit one of the interactions in the first set. Species for which individuals sample only a few sites are likely to exhibit interactions from the second. Within each set of interactions, the relative abundances of each habitat will determine which interaction will occur in the landscape.

In general, if the resources that are shared by two species limit the species' population sizes, it is expected that any increase in resource availability will act to alleviate the intensity of the species' interaction. If the species respond to the increased availability of resources by increasing to a new carrying capacity, then the relaxation of interspecific competition may be only temporary. An alternative consequence is that the two species, being freed from these limiting resources, now become limited by some other factor. Perhaps predation, competition with other species, or abiotic factors will become the major regulating force when the populations reach new equilibria. In any event, the competitive interaction (-, -) that originally occurred between the two species will, at most, change to no interaction (0,0).

While competition is a common interaction between two species that share resources, it is not the only interaction that can occur (see, e.g., Baker 1978; Barnard 1984; Barnard and Thompson 1985; Waite and Grubb 1988). One particularly interesting and dynamic example is that of two *Drosophila* species. In a laboratory study of interspecific competition, Arthur (1986) found only one of the two possible (+, -) interactions. Because the (+, -) interaction is not a trophic

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interaction, it has been labeled "contramensalism" (Arthur 1986; Arthur and Mitchell 1989). Thus, it is of some interest to determine the range of interactions that can be brought about by changes in the environment and to show how the participating species may induce the environmental change that in turn induces the change in the interspecific interaction. It is the purpose of this article to demonstrate how an interspecific interaction that affects the process of habitat selection is as much a function of the environment being considered as it is a result of the intrinsic properties of the species involved.

HABITATS AS RESOURCES

For the purposes of this article, a set of definitions is useful. Three of these terms, landscape, patch, and site, refer to spatial units. The actual size of any one of these units will be determined by the ecologies of the organisms of interest. I leave the identification of the appropriate scale for any set of species to the intuitive judgment of those ecologists most familiar with the group. The definitions are as follows:

1. Habitat: a combination of biotic and/or abiotic features that provides a useful means of broadly classifying existing conditions into distinct types.
2. Landscape: a large area that comprises more than one type of habitat distributed in numerous patches.
3. Patch: an area, smaller than a landscape, that contains only one type of habitat. A single patch can have one or more individual sites.
4. Site: a patch or portion of a patch required by an individual to survive and produce offspring (e.g., territory or home range).

Pulliam (1988) and Pulliam and Danielson (1991) modeled the effects of resource abundances for a single species, where the resources are habitats of different qualities. In their models, the average high-quality habitat produced a surplus of offspring—they defined this type of habitat as source habitat. Low-quality habitat, on average, did not produce enough offspring to make up for mortality. This type of habitat was defined as sink habitat. They showed that, in a landscape where source habitat is greatly diluted with large amounts of sink habitat, species that can sample only a few sites will not discover and use all of the source habitat. Species that can sample a greater number of sites will discover a greater proportion of the source habitat sites. If the surplus individuals produced in source habitat can contribute even a small number of offspring by reproducing in sink habitat, larger populations will result.

Pulliam and Danielson showed that, for a given amount of source habitat, there exists a quantity of sink habitat, $r^*$, that maximizes the species' total population size (fig. 1A). Thus, for a landscape where sink habitat is scarce and the amount of sink habitat, $r$, is less than $r^*$, the factor limiting population size is breeding space. In landscapes where sink habitat is abundant and $r$ is greater than $r^*$, a species' population size is limited by the abilities of individuals to find the best sites because the source sites are diluted by sink sites. This dilution effect can be so extreme that the species is not able to persist in the landscape (Pulliam and Danielson 1991).
The source-sink model is similar to the ideal-despotic model of Fretwell and Lucas (1970) in that an individual’s reproduction and mortality are not density dependent (see Pulliam 1988 and Pulliam and Danielson 1991). The source-sink model also produces an evolutionarily stable strategy (ESS) at equilibrium, even though some individuals may occupy sink habitat sites that are not productive enough to balance mortality. However, D. Morris (1991) has shown that the use of sink habitat as part of an ESS requires an opportunity for a portion of the few individuals produced in sink habitat to eventually colonize in source habitat.

The amount of each habitat and each species’ ability to use them should play a critical role in determining the structure of the community and the strength of the interactions between the constituent species. If the Pulliam and Danielson source-sink model is a reasonable representation of single species, then what
might happen if a second species (species B) also occurs in the landscape? If species B can productively use habitat that is sink habitat for the first species (species A) and make this type of habitat unavailable for species A, then, from A’s perspective, the dilution of source habitat with sink habitat in the landscape may be effectively less in the presence of species B than in its absence.

The quality (positive or negative) of the effect of species B on species A may, however, depend on the actual ratio of each habitat in the landscape. Figure 1 suggests that, if \( r \) is less than \( r^* \), species B may make a portion of the sink habitat unavailable. This, in turn, would cause the equilibrium population size of species A to be reduced. Thus, the effect of B on A would be negative. If, however, \( r \) is greater than \( r^* \), the population size of A may be enhanced (fig. 1B). In this scenario, species B has a positive effect on species A. Hence, it appears that the effect of one species on another could be a function of the landscape in which they coexist.

The two scenarios just described make several implicit assumptions about species A and B. First of all, the arguments assume that species B prefers habitat that species A considers sink habitat. Obviously, this implies that habitat that is a sink for species A must be better for B than species A’s source habitat. Thus, source habitat for species B must be species A’s sink habitat (habitat 2 for the remainder of this article), and sink habitat for B must be species A’s source habitat (habitat 1). This arrangement of habitat preferences has been called “distinct preferences” (Pimm and Rosenzweig 1981).

The second assumption is that, when species B occupies a particular site, it makes that site unavailable to species A in such a way that the population of A behaves as if the ratio of sink to source habitat is lower than the actual ratio. This implies that individuals of species A do not invest much time or energy in sampling an occupied site and instead use the resources saved to sample another site that is unoccupied. Such an effect would be especially significant if the cost of dispersal to another site is low relative to sampling a site that has been found and if the cost of dispersal is density-independent.

The biological reality of this second assumption is largely unknown. However, sampling a particular site may be quite expensive as a large amount of time and energy may be necessary to estimate site quality with regard to potential nest locations, food, and other resources. Travel time and/or energy required to travel between sites could easily be very small relative to the expenditures of site sampling. A radio telemetry study of prairie voles (\textit{Microtus ochrogaster}) showed that individuals can thoroughly traverse an unfamiliar 2-ha enclosure in much less than 2 d (Danielson and Swihart 1987). However, it may take as long as 14 d for an individual to either disperse from the same enclosure or establish itself as a resident (Danielson and Gaines 1987). Thus, if time is valuable to a vole, traveling between sites within the enclosure appears to be much less expensive than sampling sites. If energy is a limiting resource, travel between sites may also be less expensive than sampling sites. Garland (1983) has shown that for small mammals the energetic cost of transport will be small relative to total energy expenditures.
The fact that another individual occupies a particular site is likely to be very easy for a dispersing animal to determine, perhaps much easier than determining the quality of the site. Many species, especially territorial species, advertise their presence with a combination of visual displays, auditory signals, and olfactory marking. Individuals may be capable of learning that the presence of the other species at a site is an indication that the site is of poor quality. Also, the first individual to colonize a site usually has a substantial advantage in winning any contest with subsequent dispersers for that site by virtue of priority, even if the current resident is usually subordinate in neutral circumstances (Hammerstein 1981). Examples of priority effects occurring within and between species are found in mammals (see, e.g., R. Morris 1969; Grant 1972; Gleason et al. 1980; Wolff et al. 1983; Danielson and Gaines 1987), birds (see, e.g., Beletsky and Orians 1987; Eden 1987), reptiles (Cooper and Vitt 1987), and reef fishes (Shulman et al. 1983). Whether a dispersing individual recognizes that the presence of the other species indicates sink habitat or that it cannot successfully contest for the site, time and energy are saved that can be used to sample another site that would not otherwise be experienced.

The proposed effect of species B on species A, as argued above, ignores the dynamics of species B. A low ratio of habitat 2 to habitat 1 represents a poor-quality landscape for species B and a rich landscape for species A (i.e., the landscape is to the left of \( r^* \) in fig. 1). Under such circumstances, species A may produce enough surplus animals to inundate all the habitat 2 sites, driving species B to extinction. The reverse outcome may result if the ratio of habitat 2 to habitat 1 is very high (i.e., the landscape is to the right of \( r^* \) in fig. 1). Thus, any positive effect of one species on the other in reducing the dilution of source habitat may be negated by an overwhelming numerical dominance.

To ascertain whether landscape heterogeneity affects the type (positive or negative) of interspecific interactions, I constructed a simulation model to mimic the processes of dispersal, sampling of potential breeding sites, and population dynamics for two species in a landscape with two habitat types. There are two specific goals to be accomplished: (1) determine whether the quality of an interspecific interaction is a function of the landscape, and (2) if the above is true, identify the sets of interactions that are possible for two species (i.e., determine whether all possible interspecific interactions can occur without changing the intrinsic characteristics of the species involved).

THE MODEL

To understand each species' effect on the other, the equilibrium population size for each species is found for a set of landscapes when they occupy those landscapes in the absence of the other species. Then, the equilibrium for each species is determined for the same set of landscapes when the two species co-occur. If species A has a lower equilibrium population size when species B is present in the landscape than when B is absent, the effect of B on A is negative for that particular landscape. The interactions between species can be defined by
a pair of signs. For example, \((-, +\)) indicates that, in the particular landscape being considered, the effect of species B on species A is negative while the effect of species A on species B is positive. A landscape is defined by the amounts of each of the two habitats, where habitat 1 is source habitat for species A and sink habitat for species B. Habitat 2 is sink habitat for species A and source habitat for B. Species A and B are identical except for their source and sink habitats. Thus, the interactions between species are due solely to the differences in habitat preferences and the effects of the landscape.

A general description of the simulation model is shown in figure 2. A single simulation represents a unique landscape made up of a fixed number of sites of each habitat. The landscape is seeded with the adults (described below), and these adults are allowed to sample and select from the available sites. After selection, the landscape is censused. As in Pulliam and Danielson (1991), reproduction is governed by site quality, whereas mortality is constant across the landscape. Mortality is higher for juveniles (young of the year) than for adults. In the examples discussed below, overwinter mortality is 40% for adults and 90% for juveniles. (Since the productivity of a habitat must ultimately incorporate both reproduction and mortality, interhabitat differences in productivity can arise through habitat-specific mortality, reproduction, or both. Thus, equivalent mortality in each habitat is not important to the model’s results.)

At the beginning of each reproductive cycle, all individuals are defined to be adults and must again select sites. Thus, there is no philopatry. By not allowing individuals to remain at the same site from one breeding season to the next, the site-selection process will occur more frequently. The lack of philopatry causes the full effect of the interspecific interaction to be realized from the initial conditions more quickly. If each individual selected a site only once in a lifetime, the simulations would have to run much longer before the equilibrium is achieved.

The rules of searching for, sampling, and selecting sites are as follows. Dispersion occurs sequentially such that only one animal goes through the site-selection process at a time. Sites are distributed at random (there is only one site per patch), and each site is equally likely to be found by the dispersing animal. Individuals of each species are chosen at random from the combined pool of dispersing adults of each species. Each individual is allowed to sample a fixed number of unoccupied sites. The animal selects the best site from the set of sampled sites and remains there for the rest of the breeding season. The cost of searching for a site is very low (zero in this extreme instance) relative to the cost of sampling a site to determine the site’s quality. In the Discussion, I will consider the ramifications of relaxing the assumption by assuming a cost to the search process. Searching and sampling costs are not density dependent or habitat specific.

If there are more individuals than sites, the excess animals exist as “floaters” (sensu Smith 1978; Arcese 1987) and do not reproduce. Floaters experience the same mortality as all other adults.

As in Pulliam’s (1988) and Pulliam and Danielson’s (1991) models, each site’s quality is defined in terms of the number of young, \(\beta\), that can be produced there. Each site has two associated qualities, one for how species A perceives the site
and another for how species B perceives it. Hence, if an individual of species A occupies a given site in habitat \(i\), it will produce \(\beta_{iA}\) offspring. If an individual of species B occupies that same site, it will produce \(\beta_{iB}\) offspring. The values of \(\beta\) are assigned at random from normal distributions with means of \(\hat{\beta}_{ij}\) and variances of 1.0. In the example simulations discussed in this article, the distributions of \(\beta_{ij}\) are \(\beta_{1A} = N(5,1); \beta_{2A} = N(2,1); \beta_{1B} = N(2,1); \) and \(\beta_{2B} = N(5,1)\).

The correlation between \(\beta_{iA}\) and \(\beta_{iB}\) for a given site could be positive, negative, or zero. A positive relationship seems unlikely for two species with distinct habitat preferences. A negative relationship seems intuitively more likely so that a particularly good site for species A in habitat \(i\) is likely to be a particularly bad site for species B. As a hypothetical example, a site’s quality for species A could be a function of the coverage of herbaceous plants that occurs on the site. A site’s quality for species B could be a function of the coverage of woody shrubs. Thus, any site that is particularly good for A (e.g., 80% herbaceous cover) is likely to be particularly bad for B. For the results shown here, the model assumes...
that there is a $-1.0$ correlation between $\beta_{IA}$ and $\beta_{IB}$ for each site. Assuming that $\beta_{IA}$ and $\beta_{IB}$ are independent, however, does not change the results of the model qualitatively.

To find equilibrium population sizes for each species alone and in the presence of the other species, simulations were initialized with 15 adults of species A, 15 adults of B, or 15 A adults and 15 B adults. The species reached equilibrium population sizes before 50 reproductive cycles (there being no significant difference in population sizes between test runs of 50 and 100 reproductive cycles). The number of adults after 50 cycles was averaged over 50 replicates of each landscape and species combination to produce an estimate of the expected equilibrium population sizes.

RESULTS

In figure 3A, the equilibrium population size for species A, when it occurs alone, is maximized at about 40 habitat 2 sites (sink habitat) for landscapes with 50 habitat 1 sites (source habitat). As discussed by Pulliam and Danielson (1991), in landscapes with few sink habitat sites, surplus individuals produced in source habitat sites do not have an opportunity to reproduce. When this happens, floaters can contribute only themselves to the total population, and the population is limited by breeding sites. Even marginal sink habitat sites would help increase the species’ population.

In landscapes with more than 40 habitat 2 sites, there are more sink habitat sites than required for the surplus individuals of species A. The effect of poor-quality sites is to make it more difficult for dispersing animals to find the best sites available. Under these conditions, some animals settle in sink habitat sites while better sites in source habitat remain undiscovered. This dilution effect is analogous to searching for a few needles in a large haystack and becomes progressively more severe with higher ratios of sink to source habitat. In this case, the ability to find source habitat sites limits the population. In extreme instances, the species simply will not be able to maintain itself, even though there is source habitat available.

When species A occurs with species B, the number of sink habitat sites that maximizes species A’s population is less than when it occurs alone (fig. 3A). More important, however, for landscapes with less than about 80 habitat 2 sites, species A has a lower equilibrium population size when species B is present. The effect of species B is to make the shortage of breeding space more acute than it would be otherwise.

When the amount of habitat 2 exceeds 80 sites there is a surprising result. The equilibrium number of species A is higher if B is present than if B is absent because species B makes it easier for A to find the better sites. In landscapes with high habitat-2-to-habitat-1 ratios, species A is strongly limited by its ability to find the best available sites. Note that the intersection of the curves for species A alone and in the presence of species B does not occur at either curve’s peak in figure 3A.

The equilibrium population sizes of species B for the same set of landscapes are shown in figure 3B with the curves for species A carried over from figure 3A.
In contrast to species A, species B does poorly when it occurs in landscapes with small amounts of habitat 2. Species A will, however, facilitate species B by making a large proportion of habitat 1 unavailable, thereby preventing B from wasting time and energy in sampling poor-quality sites when better ones are available. Relatively richer landscapes (from species B’s perspective) cause a reversal of the interaction in landscapes with more than 25 habitat 2 sites. In these landscapes, the negative consequence of species A’s occupying sites that species B could potentially use outweighs the benefit of species A’s saving species B from needlessly settling for an inferior site when a better site is available.

Figure 3 illustrates that the relative positions of the intersections for each species’ curves will determine the type of community that occurs in a given landscape. If the two species can coexist to the left of the intersection for species B, then the interaction can be described as exploitation (−, +) (Rosenzweig 1973).
Here species A’s efforts to find habitat 1 sites aid species B while B merely gets in the way of A and denies some individuals of species A the opportunity to reproduce. To the far right, the community is also an exploitation system, but the roles of exploiter and exploited are reversed. It is only for landscapes with intermediate mixtures of the two habitat types that interspecific competition (−, −) for space occurs.

Because the effect of each species on the other reflects the species’ sampling abilities, it is actually the ratio of the two habitat types that determines the location of the intersections, which, in turn, governs the type of interaction. Thus, if the amount of habitat 1 is doubled and the simulations repeated, the intersections of the pairs of curves for each species in figure 3 should occur with about twice as many sites of habitat 2. Additional simulations confirm this, making it possible to plot the different types of interactions as functions of the amounts of each habitat type.

In figure 4, the types of community interactions that are possible are mapped relative to the amounts of each habitat. The slopes of each line in figure 4 reflect the ratios of habitat 2 to habitat 1 that occur at the intersection of each species’ equilibrium population size. For this combination of species’ characteristics and relative habitat qualities, figure 4 reveals that mutualism (+, +) is not possible in this particular example. Mutualism will only be a possibility when the relative magnitudes of the slopes of the two lines in figure 4 are reversed. Then, and only then, would landscapes that fall between the lines produce mutualism. Hence, it can be clearly seen that not all interactions are necessarily possible for two species with just two habitat types.

The question then becomes, Under what circumstances would mutualism be more likely than interspecific competition? The answer lies in the combination of
characteristics that describe the species. Relative to poor habitat selectors, species that are good at finding source habitat sites will produce greater numbers of surplus animals by virtue of the fact that they find a greater percentage of the source habitat sites. Therefore, these species will need greater amounts of sink sites for the surplus animals and in that manner will interfere with each other to a greater extent. This should increase the likelihood of interspecific competition rather than mutualism. Poor habitat selectors should interact in a more mutualistic fashion. However, poor habitat selectors more frequently occupy sites that are not very good from their perspective but that may be excellent for the other species. Hence, mutualism may not be possible, but species with poor habitat-selecting abilities seem to be the most likely candidates to produce this interaction.

The results of a set of simulations using species with relatively poor habitat-selecting abilities are shown in figure 5. These simulations are exactly the same as those that produced figure 3, except that individuals of each species are allowed to sample only two unoccupied sites rather than three. The key difference between figures 3 and 5 is that the relative locations of the intersections of each species’ curves have changed. This results in a set of landscapes that produces mutualistic interactions between the two species. Note, however, that the interactions at the right and left extremes of figures 3 and 5 are the same. The critical ratios that identify the intersections in figure 5 are used to plot the possible interactions in relation to the amounts of each habitat type (fig. 6). Again, it can be seen that there are only three possible interactions when the two species coexist and that, in this case, interspecific competition is not one of them.
**DISCUSSION**

This model demonstrates "landscape" effects at both the population and community levels. The population size of a species is not a simple function of the average habitat quality. If this were so, population sizes would change monotonically for landscapes with larger amounts of sink habitat. Clearly, this is not the case shown for species A in figures 3 and 4. Thus, there must be some other factor involved. Indeed, Pulliam and Danielson (1991) describe how the need to search for the best suitable sites in a large matrix of habitats results in just the sorts of results seen for species A and B alone. The spatial property of a landscape, combined with a species' need to sample potential home sites, provides this first landscape effect at the level of the population.

The landscape's effect on a community is evidenced by the way that a second species influences the population of the first. If there is no landscape effect at the interspecific level, species A's equilibrium population size in the presence of species B might be some constant proportion of its population size in the absence of B for the various landscapes depicted in figures 3 and 4. Again, this is clearly not an adequate description for species A in the presence of species B. Thus, there is another landscape effect such that the habitat-selection process of species A is also a function of the population of species B and vice versa.

*The Habitat-Selection Process*

Both of these landscape effects are dependent on the details of the habitat-selection process. While we know that habitat selection is nearly ubiquitous, we unfortunately know little about the actual mechanics of habitat selection. For this model—and perhaps most organisms—the habitat-selection process can be broken down into two distinctly different and sequential parts. First, an individual must find a site that potentially could be colonized. How difficult and costly is
this? Vagile mammals and birds may find this part of the process relatively inexpensive in terms of metabolic costs or time. For some species, it has been shown that the habitat-selection process is somehow quite dangerous; only a small percentage of animals that disappear from their natal sites reappear elsewhere (see, e.g., Goundie and Vessey 1986; Jones 1986, 1988), but even in instances in which it is known that the danger is from predators (Metzgar 1967), it is not known whether predation more often occurs while searching for a site or while sampling a site that has already been found.

The second part of the habitat-selection process is the sampling of a potential site. How much time, energy, and risk of predation does sampling entail? Voles (*Microtus ochrogaster*) and lemmings (*Synaptomys cooperi*) can take up to 14 d to reject the potential home sites in a 0.8-ha enclosure (Danielson and Gaines 1987), even though radio telemetry data show that individuals can cover the entire 0.8 ha in much less than 2 d (Danielson and Swihart 1987). This suggests that sampling sites is much more costly in terms of time (and probably energy) than travel between sites. The results of the model described in this article rest on the assumption that the first part of the habitat-selection process is much less costly than the second part. The difference in the costs of these two components of habitat selection allows animals to spend their resources sampling another site if they should find one that is occupied. Should the relative magnitudes of the costs of searching and sampling be reversed, there would be little saved by not sampling already-occupied sites. Thus, species A would not be likely to gain a benefit from species B unless the landscape has an extremely high ratio of habitat 2 to habitat 1. Whether or not sampling has a high cost simply cannot be assessed with the currently available data. The model, however, demonstrates how essential the details of the habitat-selection process might be to the dynamics and structure of communities.

The Effects of Search Costs

The simulated landscape has only two types of habitats. Most natural landscapes, it may be argued, contain many distinct habitat types. Some of these may never be used, but they may make it more difficult for a disperser to find a usable site. All of these unused habitats can be lumped into a single type, labeled “unusable” habitat. Because this simulation assumes no cost to travel, even where the majority of the landscape is composed of totally unsuitable habitat, an individual would have no difficulty in sorting through the landscape, looking for sites worthy of investing sampling effort.

Suppose, however, that there is a small cost to travel between sites. In this scenario, the expected cost of traveling to the next usable site is proportional to the relative abundance of the unusable habitat sites. Individuals with a fixed amount of resources or time to invest in dispersal may find that, in landscapes with large amounts of this unusable habitat, they cannot sample as many sites as they would in landscapes with fewer unusable sites. Effectively, this is identical to taking the (−, −) system described by figure 3, reducing the individual’s ability to select sites, and producing the (+, +) mutualistic interaction described by figure 5. Hence, any pair of interactions may be possible for two particular spe-
cies. A landscape with relatively little unusable habitat, and occupied by good habitat selectors, could produce a \((-,-\)) interaction. A landscape with the same ratio of usable habitat types, but relatively more unusable habitat, could produce a \((+,+)\) interaction.

The Effects of Scale

The results of this model depend on the imperfect ability of an individual to find and colonize the best available site. Therefore, scale effects are likely to be important. At relatively small scales, individuals may have perfect knowledge of site quality and, thus, their habitat selection at this scale should be ideal, or very close to it. Other models will be more appropriate for answering ecological questions on this level (e.g., Fretwell and Lucas 1970; Pimm and Rosenzweig 1981; Rosenzweig 1981, 1985). For instance, if we consider the distribution of two species of rodents at a very small scale (say, 1 ha or less), we may find that the species are frequently found in different types of habitats and do not seem to interact. Brown and Rosenzweig (1986) have shown that distinct preferences can lead to complete habitat partitioning, so long as the individuals have complete knowledge of available habitat sites. Hence, at this small scale, \((0,0)\) may seem the appropriate type of interaction.

There must exist a larger scale, however, at which no species or individual is an ideal habitat selector. At this scale (perhaps 100 ha for small rodents), the distribution and abundance of habitats become much more important, and the source-sink model will have a much greater utility in describing interspecific interactions and community structure. If several landscapes with different amounts of each habitat type are compared, a whole set of interactions may be observed (e.g., \([-,+];[+,-];[+,-]) or \([-,+];[+,-];[+,-]). This spatial scale, I believe, represents the "real" landscape. Obviously, the size of that landscape, if it can be identified, will vary between species.

If we consider only the largest scale, which lumps together unknown combinations of landscapes, we might conclude that some "average interaction" is the only interaction that occurs between these two species. An understanding of coexistence relies on identifying the proper scale and collecting data appropriate to that scale. I feel that the appropriate scale for understanding community structure is the landscape, but determining the size of a landscape for real communities will be difficult, and this model does not produce an estimate of landscape size. Especially for vertebrates, few studies have examined a series of spatial scales in a way that allows the identification of the size of a species-specific "real" landscape. Nonetheless, this model indicates that such efforts should be very worthwhile.

A knowledge of landscape-level effects is also of substantial importance to the long-term maintenance of communities. Where habitats are put aside for the preservation of biological diversity, large-scale successional changes in the relative abundances of habitat types could have tremendous impacts on diversity. Even if the relative abundances of habitats do not change, the changing spatial distributions of habitat types may effectively change species’ abilities to select the best available sites, and this also has the potential of changing the interactions
between species. Hence, maintaining biological diversity through the maintenance of habitat diversity is a complex problem that requires knowing not only each species’ preferred habitat, but also how efficiently they use habitats when dispersed throughout large regions and how interactions with other species are affected by that dispersion. For a given set of target species, there may be optimal mixtures and distributions of habitat types that can maximize the probability of maintaining those species indefinitely.

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LITERATURE CITED


