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Biodiversity in Drylands

TOWARD A UNIFIED FRAMEWORK

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In Memory of Gary Allan Polis (28 August 1946–27 March 2000)

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Gary Polis loved deserts. Whenever he dealt with the topics of his major contributions to community ecology—the prevalence of intraguild predation and omnivory; the ubiquity of reticulate food web structures, with many weak and donor-controlled links; and the importance of allochthonous subsidies, detrital pathways, and temporal variability in food web dynamics—he would invariably lace the discussion with concrete examples from desert ecosystems. Among his many books is *The Ecology of Desert Communities* (1991), which in many ways can be viewed as a natural predecessor to the current volume.

Gary's boyhood fascination with deserts and scorpions broadened into a detailed understanding of food web interactions, providing an entrée to the ecological community, where he became a leader in food web ecology. It is in this arena that he made the greatest contributions to ecology, and this is one clear instance where an understanding of desert ecology has led to conceptual advances in ecology as a whole.

Gary was a superior naturalist. He could develop a sense about a place because he spent huge amounts of time in the deserts he studied. He was accomplished at making acute observations about patterns, and relating them to broader ecological concepts. For example, while collecting data to describe patterns of scorpion diversity and distribution on desert islands in the Gulf of California, he noticed that patterns of spider and lizard abundances and distributions seemed to covary with scorpion distribution patterns. He began to understand the web of interactions that could exist among these three higher-level consumers. Furthermore, he became aware that all of these patterns were intricately tied to the influences of the

surrounding ocean on the food webs of the desert islands, via the subsidy of their ecosystems by materials drawn from the marine environments. Gary's emphasis on the ubiquity and importance of such subsidies was a major contribution made in his last few years. Again, Gary tapped his passion for desert ecology to inform at a deeper level for the discipline as a whole.

The consummate educator, Gary taught everybody: undergraduate and graduate students, colleagues, his own children, dozens of volunteers who assisted him in the field, virtually anyone who would listen. Three generations of academic offspring have benefited from Gary's wonderful insights and worldview directly or indirectly, and his ideas and perspectives continue to resonate through ecology today.

Finally, Gary had an amazing talent for bringing together people who might not otherwise interact to create novel syntheses among previously disparate disciplines. His appreciation of people from diverse backgrounds (scientific and cultural) drew people to him and hence to each other. He ran his own research laboratory in an intellectually inclusive style—inviting students and post-docs with interests in plants, invertebrates, vertebrates, or soils, and ranging from taxonomy to physiology to landscape ecology—aiming toward a synthetic understanding of the desert systems he so loved. In particular, Gary believed that the interplay of temporal variability and spatial heterogeneity was fundamental to understanding desert communities.

Valuing biological diversity, scientific diversity, and the diversity of human perspectives alike. Gary recognized that any healthy assembly of species—or people—must include numerous functional groups to thrive. In this volume, we acknowledge that we are poorer for his loss, but richer for his having been among us.

Reference

- Polis, G.A. (ed.). 1991. *The Ecology of Desert Communities*. University of Arizona Press, Tucson, Arizona.

SHALOM

A Landscape Simulation Model for Understanding Animal Biodiversity

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The ecological complexity of landscape components of biodiversity may be understood by examining relatively simple landscapes such as those of arid and semiarid lands. It is believed that such lands provide easy recognition of their components and a relatively simple interaction between their different diversities (Safriel et al. 1989).

In general, ecological complexity emerges from the existence of environmental heterogeneity and scaling effects. The effects of scaling include the differential changes in observed patterns produced by processes that operate and interact at different tempospatial scales. For example, interspecific competition may have a strong influence on species coexistence and, therefore, diversity, at a local scale, may be insignificant for determining species diversity compared with a regional scale, where colonization-extinction dynamics may be the major determinant for species diversity.

Environmental heterogeneity mainly results from three components: habitat diversity (the number of different habitats), habitat size (the size of each habitat's patch), and habitat patchiness (the distribution of the different habitats' patches in the landscape). Each component may affect species diversity by providing specific processes for coexistence, colonization, extinction, and population-size dependent effects. Additionally, as emphasized by Kotliar and Wiens (1990), different scales (Wiens 1989) should introduce different levels of heterogeneity that may influence the way organisms respond to their environment. Morris (1987) suggested that an organism that does not respond to a particular heterogeneity presented at one scale may respond to the heterogeneity presented at another scale. This concept has led ecologists to accept the idea that ecological processes and patterns are not

fixed, but rather depend on the scale under study (e.g., Addicott et al. 1987, Kotliar and Wiens 1990, Dunning et al. 1992, Wiens et al. 1993).

In this chapter we describe a spatially explicit, multispecies, process-based landscape simulation model, SHALOM (Species-Habitat Arrangement-Landscape-Oriented-Model) that has been designed to explore ecological complexity of large scales. After describing the model, we will present several simulation results to demonstrate the strengths of using such models for understanding biodiversity processes and patterns. We believe that this model can serve an important tool for exploring biodiversity in arid and semiarid lands.

Model Design

The model is coded in C++ (Stroustrup 1995) using object-oriented programming (Booch 1991, Martin 1995) for designing the different components of ecological structure (e.g., species, habitats) as classes of objects. A class is a general template of a particular component of a model, treated as an autonomic unit obtaining its own characteristics and functions (i.e., encapsulation). Object-oriented programming allows us to model natural systems realistically because different components of a model can be designed and coded as classes of objects.

The model is based on ecological realism. First, it explicitly defines the processes affecting species, populations, and communities (hence, process-based model); in most cases it goes beyond the simple description of a process to characterize it by its mechanics. Second, it avoids arbitrary functions and arbitrary value assignments by relying on empirical ecological findings. Finally, many of the processes' coefficients depend on body size via allometric equations where parameters for these equations come from the empirical literature (see Peters 1983, Schmidt-Nielsen 1984, Calder 1996). This, in turn, ensures that values for many processes of the model are realistic.

Figure 5.1 describes the relationship between the different classes and the position of the processes between the classes according to the way they are modeled. Note the hierarchical structure of the model: the landscape-scale processes (described below) are invoked by the class landscape directly, while the local-scale processes are invoked at the patch-population level (described below). A detailed description of the model is found in Ziv (1998).

Model's Classes and Their Characteristics

The model defines seven biological (population, species, community) and physical (cell, patch, habitat, landscape) components that produce an ecological structure as the model's classes. It uses the current terminology of landscape ecology (e.g., Forman and Godron 1986, Turner 1989) for the terms used here.

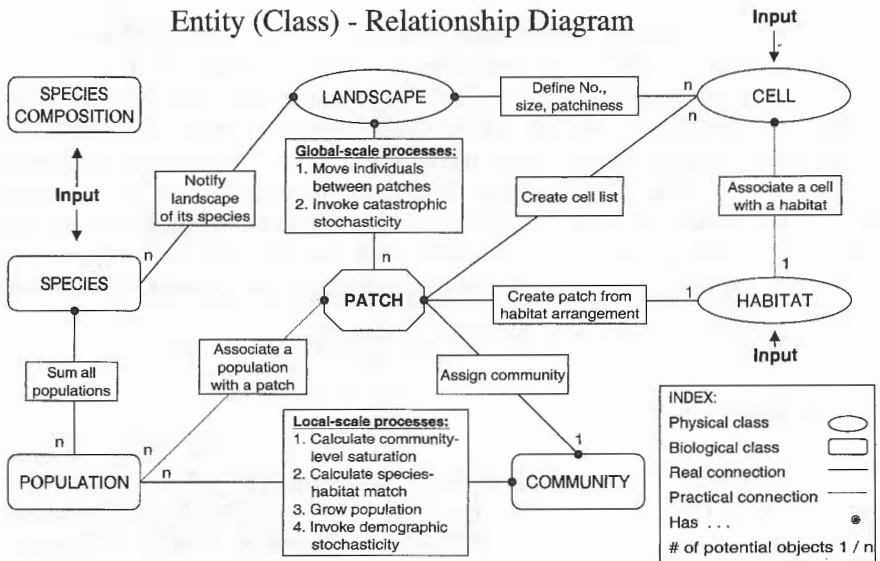


Figure 5.1 The class-relationship diagram of the model. Notice that, consistent with the multiscale design of the model, the landscape-scale processes are positioned between the landscape and the patch classes, while the local-scale processes are positioned at the population-community level.

- A *landscape* (the coarse grain of the model) is the entire area under study composed by a row-by-column matrix of cells. The size of the landscape is determined by its number of cells and the area of each cell in the matrix. Two processes are directly controlled by the landscape: “catastrophic stochasticity” and “dispersal” (detailed description of these processes is given in the “Model’s Processes” section below).
- A *cell* is a square in the landscape matrix that serves technically to produce patches. Each cell has an “area” and contains a single habitat type. It is the fine grain of the model.
- A *habitat* has relatively homogeneous physical and biological attributes. The physical characteristics are temperature and precipitation, because at large scales the combination of temperature and precipitation distinguishes particular ecosystems and biomes (Holdridge 1947, Lieth and Whittaker 1975). Temperature and precipitation are characterized by their long-term annual mean and standard deviation. These statistics may be linked in a probabilistic manner (the higher the standard deviation, the less likely that the mean is met in a given year).

The biological characteristics of a habitat are the list of “resources” it offers as well as the “resource-proportion distribution” of each of these resources. Resources are assumed to be discrete. “Resource-proportion distribution” represents the proportion of each resource

in the habitat (e.g., for two resources that occur equally in a habitat, each has a resource-proportion of 0.5).

- A *patch* is the area composed of all adjacent cells sharing a habitat type where the local-scale processes take place. Individuals of a species in one patch (population) interact among themselves independently of individuals in adjacent patches. Dispersal may connect patches. Variation in cells and habitat result in patch-specific characteristics, such as "energy supply" and "resource-proportion productivity." "Energy supply" is given by multiplying productivity (energy per unit of time per unit of area) by the patch's area, while productivity is calculated as a linear function of the product temperature times precipitation (Rosenzweig 1968, Lieth and Whittaker 1975). "Resource-proportion energy supply" is the amount of energy per unit time offered by each resource represented in the patch. The resources and their distribution are determined by the patch's habitat.
- A *species* is the sum of all populations in the landscape, that is, a species is a metapopulation. Each species has "body size," "niche position" (defined by habitat and resource utilization axes described below), and "dispersal coefficient." Body size plays an important role in the model. "Birth rate," "death rate," and "metabolic rate" can be body-size dependent ($Y = aM^b$, where Y is a rate, M is body size, and a and b are coefficients; Calder 1996).

Habitat utilization and resource utilization usually play important roles in a species' niche position. These utilizations reflect the physical and biological characteristics of a habitat. Thus the model can compare what is offered by a patch with what is required by a species in it. (This comparison takes place in the class "population" and is called "species-habitat match.")

Habitat utilization is defined by the "temperature" and "precipitation" requirements which, for simplicity, determine the species' niche. The temperature and precipitation requirements of a species are set by each characteristic's "mean" and "standard deviation." We assume that the mean represents the value at which a species reproduces best, while the standard deviation represents the species' tolerance to values that are different from the mean. We also assume a tradeoff between maximum performance and tolerance: the higher the standard deviation, the worse the species does at each point in its niche. This tradeoff allows for tolerance-intolerance community organization (see Colwell and Fuentes 1975, Rosenzweig 1991). Temperature and precipitation can be represented by a binormal distribution according to the "central limit theorem" (see Durrett 1991). Hence, a species' niche is characterized by a binormal space, shaped by the temperature and precipitation's mean and standard deviation. The lists of "resources" and "resource-proportion use" set the resource utilization of a species. As in class "habitat," resources are distributed discretely.

Each species also has a “dispersal coefficient,” which determines the intensity of dispersal when and if it is invoked. The dispersal coefficient is a species-specific dimensionless value that allows the model to speed up or slow down the movement of populations relative to other populations or relative to the same populations in other simulations.

- A *population* is the group of individuals belonging to a given species in a particular patch. Many of the population’s characteristics are determined by the “species” it belongs to. Some of these characteristics do not change during a simulation (“body size,” “birth rate,” “death rate,” “metabolic rate,” “habitat utilization,” and “dispersal coefficient”). Other characteristics do change according to the requirements and pressures a particular population faces in each “patch.” The information from the patch sets such changes.

The population’s “intrinsic rate of increase” (i.e., the maximal growth rate with no intra- and interspecific competitors) is calculated by subtracting the species’ death rate from its habitat-specific birth rate. The latter is obtained by multiplying the species–habitat match value (see “Model’s Processes” below) by the species birth rate. “Initial population size” is the number of individuals at the beginning of a run. The model allows initial population sizes to differ. Thus, one can explore how initial conditions may affect the community and landscape (e.g., priority effect; Quinn and Robinson 1987, Lawler and Morin 1993). The “carrying capacity” of a population is its population size at equilibrium in the absence of stochasticity.

The list of “resources” used by a population results from the resources used by its species and the resources available in the patch. The population’s resource-proportion use is then rescaled accordingly (considering only the resources that are actually used), maintaining the ratios of all resources used in the patch. For example, if only two resources can be used by the population and they have fundamental proportions (according to the species’ “resource-proportion use”) of 0.1 and 0.3 (i.e., 1:3 ratio), then they will be rescaled to have proportions of 0.25 and 0.75 in the population’s diet.

- A *community* is the set of nonzero populations in a patch.

Model’s Processes

Ecological processes are simulated on two scales—local and landscape—similar to the general separation made by Whittaker and Levin (1977). Local-scale processes occur within each patch, while the landscape-scale processes are those that occur across or between patches. This multiscale hierarchy allows most processes to work inside patches and to have a direct impact on population growth. Meanwhile, processes occurring between patches can affect population growth indirectly and at different temporal scales.

Local-Scale Processes

Community-level saturation effect, $f_{(s)}$ The community-level saturation effect builds on the ratio between the energy offered by a patch (i.e., energy supply) and the overall energy consumed by all populations in a patch. The energy consumed by all populations in the patch is the sum of each population's species-specific energy consumption, which is calculated by multiplying the metabolic rate of the species to which the population belongs by the number of individuals in that population. Because a patch's energy supply and a species' metabolic rate share units (energy/time), the division of these two gives a dimensionless variable (e.g., Vogel 1994) that ranges from zero (i.e., no individuals at all) to any positive value.

A patch may offer more than one resource. A population may consume all of the patch's resources or only a subset of them, depending on the population's list of resources. Each resource's energy in a patch is determined by its proportion (resource-proportion energy supply) out of the energy supply in that patch. An algorithm sets the relative use of each resource by those species that share it. The community-level saturation effect equation treats each resource one at a time and then sums all resources.

The following equation describes the community-level saturation effect on population j , $f_{(s)j}$, given its species i , for K resources:

$$f_{(s)j} = \sum_{k=1}^K \sum_{l=1}^S \frac{RPU_{kl} N_l E_{Mi}}{RPP_k} \quad (1)$$

where l is a population selected from all S existing populations in a patch, RPU_{kl} is the resource-proportion use of resource k by population l , N_l is the size of population l , E_{Mi} is the body-size dependent metabolic rate of species i , which population l belongs to, and RPP_k is the resource-proportion energy supply of resource k in a patch.

The community-level saturation effect is analogous to the carrying-capacity feedback function of the logistic equation (May 1981). However, the model does not assume an arbitrary value for carrying capacity. Instead, the value for carrying capacity comes from calculating the equilibrium of a population when saturation exists. It represents the density-dependent pressure a population experiences from all of a patch's populations, including its own. Hence, it includes both intra- and interspecific density dependence.

Species-habitat Match, $f_{(m)}$ The species-habitat match quantifies how well individuals of a particular population are suited to a particular patch, given the population's species and the patch's habitat. The function builds on the overlap between the temperature-precipitation binormal curve of the species and the temperature-precipitation biuniform curve of the habitat. Specifically, the population's niche space is given by the following binormal distribution equation:

$$D_1 = \frac{\exp \left\{ -0.5 \left[\frac{1}{1-p^2} \left(\left(\frac{x - X_{iT}}{SD_{iT}} \right)^2 - 2p \left(\frac{x - X_{iT}}{SD_{iT}} \right) \left(\frac{y - X_{iP}}{SD_{iP}} \right) + \left(\frac{y - X_{iP}}{SD_{iP}} \right)^2 \right) \right] \right\}}{2\pi SD_{iP} SD_{iT} \sqrt{(1-p^2)}} \quad (2)$$

where x and y are values of temperature and precipitation at the patch, X_{iT} is the species' temperature requirement's mean, SD_{iT} is the species' temperature requirement's standard deviation, X_{iP} is the species' precipitation requirement's mean, SD_{iP} is the species' precipitation requirement's standard deviation, and p is a covariance between the species temperature and precipitation.

The patch's habitat space is given by the following biuniform distribution equation:

$$D_2 = 4SD_{hT}4SD_{hP}D_1^\diamond \quad (3)$$

where D_1^\diamond is the highest distribution value of the population's species niche space, SD_{hT} is the habitat temperature characteristic's standard deviation, and SD_{hP} is the habitat precipitation characteristic's standard deviation.

The final species-habitat match value for a given population in a particular patch ($f_{(m)j}$) is given by dividing the population's niche space nested within the patch's habitat space by the patch's entire habitat space. The species-habitat match value represents the fraction of the population's species ability expressed in the particular patch given its habitat. A value of 1 represents a perfect match, while a value of 0 represents no match at all.

The above form of calculating species-habitat match provides two major outcomes that we should expect to see in nature. First, the more tolerant a species, the more likely it will match a habitat far away from the species population's temperature and precipitation mean values. Second, the lower the standard deviation of the habitat's precipitation and temperature characteristics, the higher the species-habitat match. This should be true because a habitat's standard deviations are negatively correlated with the probability of getting a particular value at a given time. Higher standard deviations represent a lower probability of any species finding a given value in a habitat. Ecologically, this should represent a measure of predictability: the lower the standard deviations of the habitat, the better it is for the populations occurring in that habitat.

The population dynamics equation (eq. (5)) uses a single value for the species-habitat match. Other functions can be used to get the desired value. When possible, the species-habitat match should be generated with empirically derived functions that use the natural history of the species and more accurate measurements of how well the species thrives in the available habitats.

Demographic stochasticity This refers to any change in population size caused by a chance event (resulting from sampling errors), independent of a

biological process. It tends to have critical effects when populations sizes are low.

We used a simple descriptive equation to model stochastic deviations from the deterministic, body-size-dependent birth and death rates. The deviations are negatively correlated with population size: the larger the population, the lower the deviations are likely to be. Although the equation does not relate to any specific process (e.g., sex ratio or encounter rate), its behavior does follow the typical expectations of such stochasticity. The equation affects demographic parameters randomly and it is density-dependent (e.g., Diamond 1984, Shaffer and Samson 1985, Pimm et al. 1988, Lande 1993).

The following equation defines the population's stochasticity in birth or death rates, Z_j , from a species' deterministic birth or death rates, z_j :

$$Z_j = z_j \pm \left(\frac{\varepsilon(0.5z_j)}{\gamma\sqrt{N_j}} \right) \quad (4)$$

where ε is a random number sampled from a Gaussian probability distribution (with a mean of zero and a symmetrical truncation of two standard deviations, of one unit each), $0.5z_j$ is a scaling term to make each distribution range between zero and twice the highest birth or death rate, γ is a demographic stochasticity coefficient that allows for changing the "intensity" of the effect, and N_j is population size.

We used a logistic-like continuous-time population growth for the local-scale population dynamics. Birth rate and death rate are handled independently. This separation is realistic (Begon et al. 1986) because birth rate and death rate may be limited by different processes, such as a need for protein-rich resources for lactating females that are not required by the rest of the population. Overall, the equation by which a given population grows in a patch given the above processes is

$$\frac{dN_j}{dt} = N_j b_i \{f_{(mj)}(1 - f_{(sj)})_+\} - N_j d_i \{1 + f_{(sj)}\} \quad (5)$$

where $f_{(mj)}$ and $f_{(sj)}$ are the species-habitat match effect and the saturation effect, respectively, and $(1 - f_{(sj)})_+$ indicates that the latter term cannot take a value lower than zero (see Wiegert 1979).

The community-level saturation effect ($f_{(sj)}$) enters the equation twice. First, we subtract the community-level saturation effect from one as in the carrying-capacity feedback function of the logistic equation (i.e., $1 - N/K$). This new term models the effect of the community saturation on birth. It is assumed (as in the logistic equation) that birth decreases linearly with an increase in community density. Oversaturation (i.e., $1 - f_{(sj)} < 0$) results in no birth. Second, we add one to the community-level saturation effect to model the effect of the community saturation on death. Here also, it is assumed that death rates decrease linearly with an increase in community density.

The local-scale population dynamics equation with its analytical solution and outcomes for body-size dependent habitat specificity are found in Ziv (2000).

Landscape-Scale Processes

Dispersal, $f(d)$ This is the movement of individuals from one patch to another (e.g., Levin 1974, Andow et al. 1990, Johnson et al. 1992, Gustafson and Gardner 1996). In the model, individuals of a particular population in a given patch migrate to adjacent patches if they can gain a higher potential fitness there. The dispersal function builds on the optimization principles used for intraspecific density-dependent habitat selection suggested by Fretwell and Lucas (1969) and Fretwell (1972) (ideal free distribution). In the model, the dispersal process assumes that a population's individuals can instantly assess the adjacent population's per-capita growth rate.

At each time step, the model calculates the per-capita growth rate of each population. Then it compares that rate with all adjacent populations' per-capita growth rate. Individuals move from patches with relative low per-capita growth rate (i.e., low fitness potential) to patches with high per-capita growth rate (i.e., higher fitness potential). This results in equalizing the per-capita growth rates of populations of the same species across patches (Fretwell 1972).

Dispersal occurs on a continuous-time scale. Hence, dispersal from a given patch to patches that are unadjacent can happen fast in appropriate conditions (e.g., some patches of low potential fitness and a patch of a very high potential fitness). However, there is an implicit distance effect because individuals need to cross the adjacent patches first, and because each population in the different patches experiences population change due to other processes. This effect can be controlled by changing the species dispersal coefficient such that the rate at which individuals of populations of a given species move agrees with the user's needs.

Catastrophic stochasticity Also known as disturbance-induced extinction (Levin and Paine 1974, Pickett and White 1985, Turner et al. 1989), this is a density-independent loss of individuals due to some event (e.g., extreme cold weather or a drought) that has a random probability of occurrence. Some environments may have a higher probability of being affected by catastrophes than others. Catastrophes may cause the disappearance of entire populations of a given community or only partial disappearance. The same catastrophe may eliminate some species from a patch but only reduce others. A catastrophic event may be very local, such as within a single habitat (e.g., a falling tree in a forest), or may cover an extensive area and include many different types of habitats (see Turner et al. 1989).

The catastrophic stochasticity of the model SHALOM relies on random-number-generating procedures (Press et al. 1995). These allow one to change the probability, intensity, and range of the density-independent loss of individuals and populations. The user sets the following options: the probability

function (either uniform or Gaussian) of the catastrophic stochasticity distribution, the threshold (a fraction between 0 and 1) below which catastrophic stochasticity is not invoked, the lower and the upper limits (a fraction between 0 and 1) for population loss once a catastrophic stochasticity is invoked, the probability function (either uniform or Gaussian) of the population loss, and the spatial distribution (either a random or a fixed distribution on a cell, or patch, or the entire landscape) of the catastrophic stochasticity.

The two landscape-scale processes affect population growth on two different time scales. As mentioned above, dispersal is assumed to occur on a continuous-time scale similar to the continuous-time scale of the local population dynamics. In fact, dispersal at any time step of the model depends on the local-scale per-capita growth rate of each population. Defining the local growth of population j in equation (5) as $F_{(l)j}$, the overall population growth, including dispersal, becomes

$$\frac{dN_j}{dt} = F_{(l)j} + \sum_{l=1}^{AP} (f_{(d)l} N_{j(-)/l(+)} \quad (6)$$

where AP is the number of adjacent patches and $N_{j(-)/l(+)}$ indicates that the per-capita migration is multiplied by the patch's population size or by the adjacent patch's population size, depending on the sign of the per-capita movement. A positive per-capita movement means that the particular patch's per-capita growth rate is higher than the one adjacent. Hence, individuals from the adjacent patch disperse into it. In contrast, a negative per-capita movement means that individuals should disperse into the adjacent patch.

Catastrophic stochasticity is simulated on a discrete time scale. Once a year (or on an interval that amounts to a year), the model invokes catastrophic stochasticity.

Model Mechanics

Before each run of the model, the user assigns the following: the species and their attributes, the habitats and their attributes, and the habitat arrangement in the landscape. Given this information, the model creates the patches as they would appear to organisms in the real world. Having modeled patches and species in the landscape, populations are then created. The species-habitat match of a population is then calculated. The option of invoking demographic stochasticity is set for each population. All populations of a particular patch create the patch's community. The community monitors the overall saturation effect in a patch as well as the different species' composition and diversity.

Once the landscape is completely defined, the model asks for information about the large-scale processes. Dispersal may or may not be invoked by the user. Similarly, catastrophic stochasticity may or may not be invoked. If catastrophic stochasticity is invoked, the model asks for information about its different options.

Following the specification of the initial population size for each population and the run time (in years), the model runs a population-growth simulation of the different populations in the different patches. The Runge-Kutta method (Press et al. 1995) is used to integrate the small steps ($dt = 0.001$ yr) on a continuous time axis.

The model returns the value of population size for each population in the different patches every 100 time steps (i.e., 0.1 yr). The information is saved to an output file for further analysis. At the end of the run, the model calculates the ratio of each population's size to its carrying capacity and returns values of the number of species and two species-diversity indices: Simpson's diversity index (Simpson 1949) and Fisher's alpha (Fisher et al. 1943).

Using the Model: An Example of the Effects of Ecological Processes on Community Structure in a Heterogeneous Landscape

How do different processes—interspecific competition, demographic stochasticity, and dispersal—known to affect communities at a local scale, affect species composition and species-diversity patterns in a spatially heterogeneous landscape scale? Many studies have explored various processes that affect communities in heterogeneous landscapes. However, these studies treat each process discretely (e.g., Andow et al. 1990, Dunning et al. 1992, Holt 1992). How the interaction of multiple processes affects community structure is rarely explored, except in the context of metapopulation dynamics. In the following sections, we will describe a simulation design that allows the modeling of several species of different body sizes in a very simple heterogeneous landscape without losing track of the species diversity in each patch or in the entire landscape. As will be shown later, this simple simulation will provide enough information to make some sophisticated predictions.

Simulation Design

We simulated a landscape with 2×2 cells, each 100 m^2 , having its own unique habitat (total of four habitats). We chose this simple landscape design because the existence of the different processes in the current simulation added a tremendous amount of complexity to the model. Thus, the simple landscape design provides focus on the processes' outcomes.

We assigned realistic productivity values for the different habitats without a specific process in mind in order to keep the model as general as possible. Note that also in this simulation, patch and habitat are synonymous. We also assigned different species-habitat matches to the different habitats, such that habitat 1 was the best habitat and habitat 4 was the worst (species-habitat match = 0.997, 0.987, 0.971, and 0.949 for habitats 1, 2, 3, and 4, respectively). To allow for competitive coexistence between the modeled species,

each habitat offered 28 different resources. To avoid a specific resource-productivity distribution, we assigned an equal productivity for each resource out of the total productivity of the habitat.

We simulated a total of 26 species. Species differed in only one characteristic—body size. Body size ranged between 5 g and 1585 g, corresponding to log values of body size ranging between 0.7 and 3.2. We assigned a unique preferred resource to each species and gave it a resource-proportion use of 0.5. Each species could consume two other resources, one on each side of the preferred resource; each of these had a resource-proportion use of 0.25 (e.g., species 1 is able to consume resources 1, 2, and 3 with a resource-proportion use of 0.25:0.5:0.25, species 2 is able to consume resources 2, 3, and 4 with a resource-proportion use of 0.25:0.5:0.25, and so on). Preliminary simulations have shown that this resource allocation was sufficient to produce a competitive relationship with resource partitioning without assuming any complex resource-use function.

Throughout the simulations, we used the allometric power coefficients known for eutherian mammals for birth rate (-0.33), death rate (-0.56), and metabolic rate (0.75) (Calder 1996).

When catastrophic stochasticity was invoked, we gave the system a 10% chance of suffering catastrophic stochasticity in a year (an average of one catastrophe every 10 years). In catastrophic years, stochasticity can affect up to 50% of the landscape with up to 50% loss of population size in those patches affected. These values were chosen after experimenting with many simulation designs. They are high enough to affect population and species distribution (Turner 1987), yet, low enough that no populations are driven to extinction.

Other than these first-level assignments of values for cells, habitats, and species, no other assignments were made for second-level procedures such as habitat-specific population abundance, etc. Therefore, any body-size-dependent patterns that emerge will result only from the basic rules described here.

To understand the effects of the different ecological processes, we initially explored the patterns emerging from communities not affected by any of the above processes (i.e., in which competition is strictly intraspecific). We then introduced interspecific competition, and added, thereafter, demographic stochasticity to interspecific competition to explore how it changes the predicted patterns. Finally, we allowed dispersal to connect all patches.

Results

Carrying capacities All habitats were suitable for all species. That is, without any population-reducing processes—interspecific competition and demographic and catastrophic stochasticities—all populations in all habitats could maintain a persistent population size. Figure 5.2 shows the carrying capacities of the different populations in the different habitats as well as the species abundance in the entire landscape. Because all populations can persist in

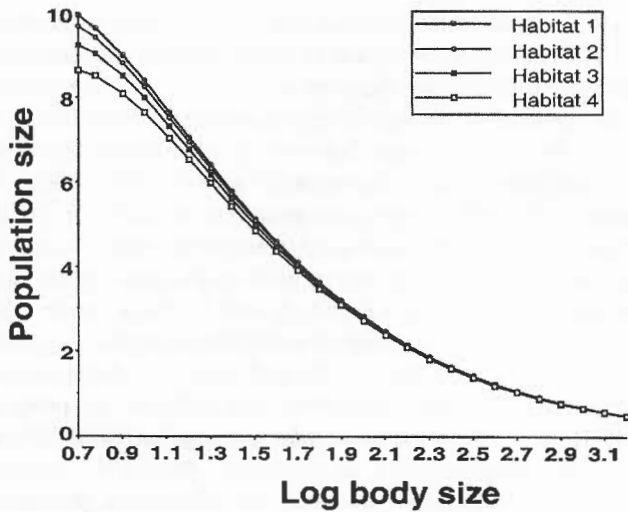


Figure 5.2 Carrying capacities of species as a function of their body size in the different patches (habitats) and in the entire landscape.

all habitats, and because no process other than intraspecific competition affects population growth, the same population size pattern in all the habitats and the same species diversity pattern across the entire landscape (i.e., the sum of all population sizes of each species) emerge. The only difference between habitats is that carrying capacities of populations of the same species are lower in habitats with fewer species-habitat matches.

The effect of interspecific competition Here we assumed that resource partitioning occurs such that the most preferred resource is different for each species. Because of the overlap in resource use, each resource is consumed by three species. This shared consumption can lead to competitive exclusion. When resources are equally shared by species of different body sizes, the larger species outcompetes the smaller species that use the same resources. This outcome results from the lower death rates of larger species. Regardless of the specific mechanism, this larger-species competitive advantage is consistent with competitive outcomes observed in many real systems (see Kotler and Brown 1988), confirming the effectiveness of the model SHALOM.

Due to the modeling of resource partitioning as a deterministic process that does not change between habitats, the same species composition exists in all four habitats of the model as well as for the entire landscape (fig. 5.3). With interspecific competition, some populations are outcompeted, leaving a discontinuous distribution of body sizes. The absence of a particular species depends on an intratrophic level cascading effect: the largest species depresses the second largest species population size due to the largest species' competitive advantage. Although the second largest species has the competitive

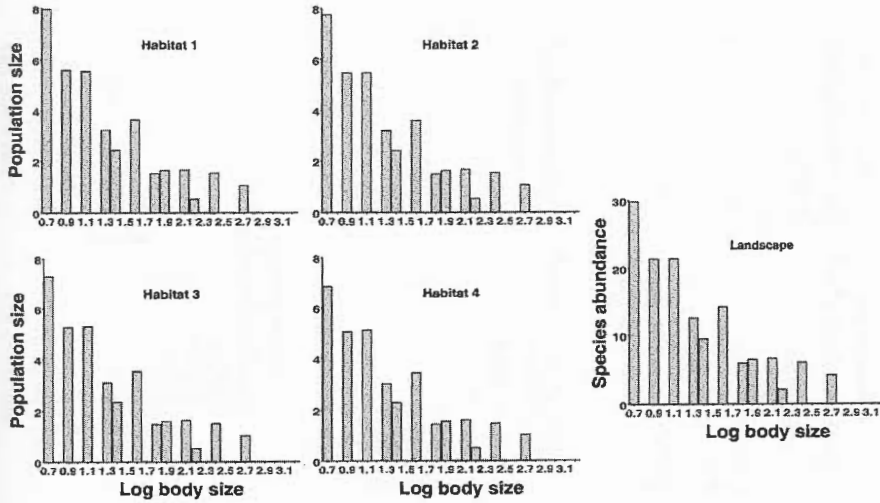


Figure 5.3 Sizes of all populations in the different patches (habitats) and in the entire landscape with interspecific competition. Interspecific competition deterministically affects all populations the same way. Identical pattern emerge for each patch and for the entire landscape.

advantage over the third largest species, the present but minimal effect of the third largest species on the second largest species is enough to depress the former further to local extinction. Because, in the present model, species share resources only with the species closest in body size, the third largest species, which does not share resources with the largest one, is saved from the potentially dominating effect by the extinction of the second largest species. The process repeats with the fourth, fifth, and sixth largest species, and so on. Because all interactions between all species are taking place simultaneously, the overall effect on the different species sometimes results in an absence of a species particular body size in between two coexisting species, each having close body sizes. The two species coexist because the larger species can consume its most preferred resource better, and has a competitive advantage, while the smaller species benefits from the other resource that is no longer used by the now extinct, smaller species. In the end, 12 species coexist in the landscape.

Adding demographic stochasticity to interspecific competition Demographic stochasticity, or the sampling effects regarding sex ratio, litter size, etc., that may promote local extinctions of small populations, exists no matter what other processes affect population growth (Pimm et al. 1988, Lande 1993). With demographic stochasticity, different patterns appear in the different habitats (fig. 5.4). Populations of larger species are more likely to become extinct because they exist in fewer numbers. However, the particular population that ends up extinct is determined randomly. Once a particular population becomes extinct, its closest competitor in body size

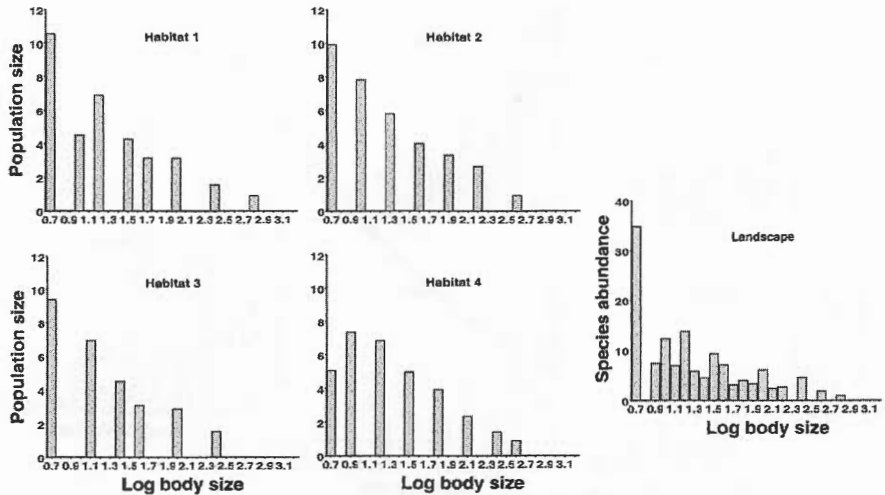


Figure 5.4 Typical sizes of all populations in the different patches (habitats) and in the entire landscape with interspecific competition and demographic stochasticity. The community structure in each patch is determined by those large populations that escaped extinction. Once a random extinction of a large-body population takes place, the community is well structured according to competitive interactions. Demographic stochasticity increases species diversity at the landscape scale.

benefits from a competitive release and enjoys a higher population size, hence, showing a negative autocorrelation in population size. The rest of the community is now competitively determined by the particular large body-sized species that escaped extinction. Because demographic stochasticity reduces species diversity in each habitat, population size of the survivors, on average, is higher than with interspecific competition alone; that is, the same resources are now divided among fewer species comprising more individuals. At the landscape scale, more species exist because of the randomness of some extinction in the different habitats. Hence, demographic stochasticity increases species diversity at the landscape scale (see also Chesson and Case 1986). Overall, on average, 17.59 ± 1.72 species exist in the landscape.

The effect of dispersal with stochastic effects and interspecific competition Dispersal (e.g., Levin 1974, Johnson et al. 1992) has consistently been shown to have major effects on single-species distributions as well as on multispecies community structures. With dispersal (fig. 5.5), colonists can restore local populations of their species. When the species is competitively subordinate, a permanent recovery is unlikely. However, the recovery of a competitively dominant population has a significant effect on community composition. If dispersal is frequent enough, dominant species can establish in all patches and, on average, overcome the stochastic effects that tend to produce locally different patterns.

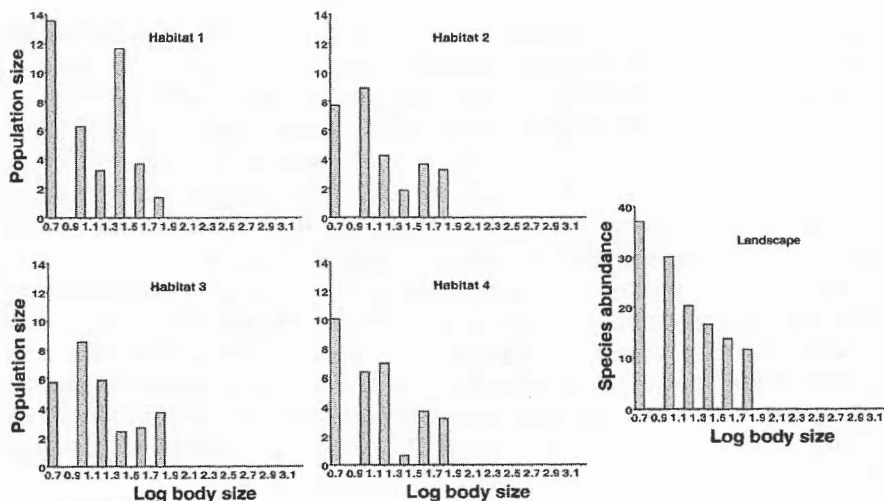


Figure 5.5 Typical sizes of all populations in the different patches (habitats) and in the entire landscape with interspecific competition, demographic stochasticity, and dispersal. Dispersal allows dominant populations that became extinct from a particular patch due to a chance event (stochasticity) to recolonize that patch and increase in numbers. As a result, the dominant species in the landscape reestablish their populations in all patches and, on average, overcome the stochastic effects that might locally produce different patterns.

Knowing the outcomes (or fingerprints) of the different processes (i.e., competition and demographic stochasticity), we can now detect the fingerprints of the different processes. As before, demographic stochasticities are responsible for larger discontinuities of body sizes and for the disappearance of the largest species from the landscape (the local extinction of the largest species from all the patches deprives them of colonists that could otherwise restore extinct populations). Dispersal allows dominant species to recolonize habitats in which they have previously become extinct, resulting in homogeneity among habitats in a landscape. At the landscape scale, the existence of dispersal together with demographic stochasticity and interspecific competition produces the lowest species diversity (5.08 ± 0.598). The main reason for this low species diversity is the ongoing disappearance of small populations that usually belong to species of large body size.

Discussion

This model presents a new approach to the study of complex ecological systems. This new approach contributes to our understanding of large-scale ecological processes and patterns by providing us with nontrivial predictions on the combination of spatial heterogeneity and multiple-process interac-

tions. The example given in this chapter demonstrates this contribution by providing specific outcomes that could have not been predicted otherwise.

Stochasticity depresses mean population sizes and allows different habitats to support different communities. These different communities are determined by which large species becomes locally extinct at random. The local extinction of a large species shifts the maximum body size of the competitively organized community. With both demographic and catastrophic stochasticities, species diversity is higher than with interspecific competition alone.

The effect of demographic stochasticity on species composition differs from that of catastrophic stochasticity. With demographic stochasticity, discontinuities of body sizes are larger, and no species of very similar body size coexist. With catastrophic stochasticity, all of the largest species disappear. Combined, each of the two stochasticities affects species composition in the different habitats and in the landscape. Hence, such communities have large discontinuities of body size and none of the largest species.

Dispersing individuals move between habitats and reestablish the local populations of their species. Thus, dispersal neutralizes the randomness of the assemblages produced by stochasticity. As a result, each habitat tends toward the same set of species. However, even with dispersal, stochasticity eliminates the largest species and produces large discontinuities in the body size distribution. Loss of randomness in the assemblages means that, at the landscape scale, dispersal reduces species diversity.

The predictions presented here about species composition and species diversity demonstrate the usefulness of the current model. The ability to characterize specific fingerprints of different processes and then analyze the joint effect of multiple processes by tracking these fingerprints should help us to understand natural systems better. We recommend that ecologists adopt such an approach for understanding ecological complexity. Ecologists need also to set up studies that will allow them to test whether the predicted patterns produced by particular processes in the model are indeed observed in the field.

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