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PREDICTING PATTERNS OF MAMMALIAN SPECIES DIVERSITY FROM A PROCESS-BASED SIMULATION MODEL

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Large-scale ecological patterns emerge from multiple biological processes that interact on several scales and are affected by the heterogeneity of the environment. I use a landscape simulation model to explore and analyze how interactions among various ecological processes affect patterns of mammalian species diversity according to body size. The model incorporates ecological realism by using mammalian allometric relationships with realistic values taken from field data. It uses energy as a common currency to model and compare how species of different sizes use their environment. Components of the model include landscape, habitat, patch, community, species, and population. Processes include continuous-time population growth, saturation effect, species–habitat matching, demographic stochasticity (local-scale), dispersal, and catastrophic stochasticity (landscape-scale). I simulated a 16-patch landscape, with each patch having a unique habitat, and a 10-species pool in which species differ only in body size. Summed over the landscape, a log-normal relationship between body size and species abundance emerges. Additionally, geographic range increases nonlinearly with the log of body size. These patterns are qualitatively consistent with patterns of mammalian species diversity observed in natural systems, suggesting that they can emerge from scaling of habitat use with body size. I also simulated a simple 4-patch landscape, with each patch having a unique habitat, and a 26-species pool to draw from in which species differ only in body size. The results show that interspecific competition by itself reduces species diversity in each habitat and in the entire landscape. Stochasticity depresses mean population sizes but opens opportunities for species to avoid competitive exclusion. It also allows different habitats to have different communities that are characterized by the consequences of which large species become locally extinct at random. Demographic and catastrophic stochasticities differ, however, in their characteristic effects on species diversity. These characteristic effects can be used as fingerprints to identify processes acting in nature. Dispersing individuals move between habitats and reestablish the local populations of their species. Overall, the model provides us with predictions of how process-interactions in heterogeneous landscape may affect species composition and community structure.

Key words: community structure, dispersal, geographic range, interspecific competition, mammals, SHALOM, species abundance, species diversity, stochasticity

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Large-scale ecological patterns have received a great deal of attention in recent years (Brown 1995; Ricklefs and Schluter 1993; Rosenzweig 1995). Many of these patterns deal with body size of animals, especially mammals (Blackburn et al. 1993; Holling 1992; Hutchinson and MacArthur 1959; May 1988). For example, many studies investigate the relationship between body size and abundance (Brown and Maurer 1989; Damuth 1991; Nee and Lawton 1996; Nee et al. 1991; Siemann et al. 1996). Other studies explore the relationship between geographic range and body size (Brown and Maurer 1987, 1989; Damuth 1987; Lawton and Brown 1986). The

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rationale behind focusing on body size lies in the fact that body size affects, both directly and indirectly, major biological parameters, leading to statistically significant allometric relationships (Calder 1996; Peters 1983; Schmidt-Nielsen 1984). Mammals, as homeotherms, should not be exceptions. In addition, it has been suggested that allometric relationships emerge from basic principles of biology (West et al. 1997).

The study of body-size patterns often suffers from 3 major weaknesses. First, patterns of body size usually are based on masses of data collected without a hypothetical framework. Second, although body size may affect different ecological patterns simultaneously, studies of body size focus on a single pattern at a time in isolation from the others. Finally, in spite of increased evidence for the contribution of landscape heterogeneity and discontinuity of environmental physical structure to observed ecological patterns, studies on body size patterns rarely incorporate an explicit consideration of habitat heterogeneity.

In this paper I describe a different approach to the study of body size–related species-diversity patterns that overcomes the above weaknesses. This approach relies on simulation modeling that uses basic mammalian allometric relationships in conjunction with fundamental ecological processes to model communities comprising mammals of various body sizes. I use the model to predict body size–related species-diversity patterns that emerge from considering complex ecological structures. Some of these patterns have already been studied in nature, and hence they can serve to test how well the model performs. Other patterns are new.

Here, I study 2 general patterns of body size: the relationship between body size and abundance and the relationship between body size and geographic range. The relationship between body size and species abundance has received a great deal of attention recently (Brown and Maurer 1989; Damuth 1991; Nee and Lawton 1996; Nee et al. 1991; Siemann et al. 1996). Body size and species abundance show a log-normal relationship (Brown and Maurer 1989; Siemann et al. 1996); small and large species have lower abundances, while intermediate-sized species have higher abundances.

The relationship between species of different body size and their geographic ranges has been studied by several ecologists (Brown and Maurer 1987, 1989; Damuth 1987; Lawton 1991; Lawton and Brown 1986). The most influential study on mammalian diversity is by Brown and Maurer (1986), who predicted through energetic considerations that larger species should have wider geographic ranges (but see Lawton and Brown 1986). Are the results of the new model simulation approach consistent with these patterns? Additionally, if the results are consistent with it, does the model suggest an explanation?

With respect to body size–dependent community structure, one could ask, how do different processes known to affect mammalian communities at a local scale, such as interspecific competition, habitat suitability, and demographic stochasticity, affect species composition and species-diversity patterns in a spatially heterogeneous landscape scale? Many studies explore different processes affecting communities in heterogeneous landscapes. However, these studies treat each process separately from others (Andow et al. 1990; Danielson 1991; Dunning et al. 1992; Holt 1992; Lindenmayer and Possingham 1996). How the interaction of multiple processes affects mammalian community structure is rarely explored, except in the context of metapopulation dynamics. The interaction of multiple processes is a realistic representation of the manner in which ecological communities are shaped. For example, competition may structure a particular community, but the presence of a dominant species may depend on the absence of certain other species due to other processes, such as demographic stochasticity or dispersal. Using the

new model-simulation approach described here, I can model several species of different body size in a very simple heterogeneous landscape without losing track of the species diversity in each locality (patch) or in the entire landscape. As will be shown later, this simple simulation is enough to make some sophisticated predictions. The predictions presented involve species composition (the particular species existing in each habitat or in the entire landscape) and species diversity (the number and the relative abundance of the existing species).

In this paper, I first describe aspects of the model that are relevant for the present simulation study. For more information on an extensive landscape simulation model, SHALOM, which provides a large range of opportunities, see Ziv (1998b). Then, I use a relatively simple simulation design to see whether we can generate empirical patterns between body size and species abundance and between body size and geographic range with the model. I explain these patterns from the manner in which habitat-specificity scales with body size (Ziv 1998a, 2000). Good fit of the model's patterns to field data provides the confidence to ask more sophisticated questions on process interactions and community structure. Finally, I use a simple simulation design to explore how different ecological processes such as interspecific competition, demographic and catastrophic stochasticities, and dispersal may affect species composition and diversity. I do this by introducing different processes separately and then investigating their emergent effects.

Materials and Methods

Model Design and Components

The simulation model of this study strives for ecological realism in several ways. First, it is process-based. It explicitly defines the processes found to affect mammalian species, populations, and communities and in most cases goes beyond the simple description of a process to characterize it by its mechanics. Second, it incorporates and combines various aspects of empirical ecological knowledge. The model thus avoids arbitrary functions and arbitrary value assignments. For example, the carrying capacity of a population emerges from equalizing the energy consumption rate of all the population's individuals with the energy flow rate supplied by the patch. Third, the coefficients of various processes depend on body size through allometric equations. Parameters for these equations come from the empirical literature (Calder 1996; Peters 1983; Schmidt-Nielsen 1984).

I adopted the current terminology of landscape ecology (Forman and Godron 1986; Turner 1989) for terms used here for components of the model. Two kinds of components that produce an ecological structure exist: biological components (population, species, community) and physical components (patch, habitat, landscape). In the following paragraphs I define these components and describe their characteristics as used in this paper. The landscape is the entire area under study (the extent), composed of a matrix of cells (a 2-dimensional array). In addition to tracking changes in each cell, the landscape controls 2 processes directly: catastrophic stochasticity and dispersal. The size of the landscape is determined by its number of rows and columns and the area of each cell in the row–column matrix.

A habitat is defined as a place with relatively homogeneous physical and biological characteristics. The biological characteristics of a habitat are productivity and the list of resources it offers. Productivity is the amount of energy made available per unit time per unit area.

A patch is the area covered by all adjacent cells of the same habitat. The model defines 2 cells of the same habitat that touch only at their corners to be different patches. The patch represents a local area in which a population of a species lives; therefore, a population is a collection of individuals from the same species that occur in a particular habitat. The model assumes that individuals of a population in 1 patch interact among themselves independent of individuals in adjacent patches. Dispersal of individuals across patches, however, does connect them. Hence, the local-scale processes that affect each of the existing populations of the patch's community operate within a patch.

Area of the patch is the sum of areas of its cells. The amount of energy per unit time available for organisms in a patch (hereafter, energy

supply) is the productivity of the patch's habitat multiplied by the area of the patch.

A species is the set of individuals in the landscape that share biological and physical characteristics. Each species has a body size (assumed to be the average size of adult), habitat match, resource utilization (the fraction of use of each resource relative to its total resource use), and dispersal coefficient. Body size is an important characteristic of mammalian species that affects their anatomical, physiological, and ecological function (Calder 1996; Peters 1983; Schmidt-Nielsen 1984). Here, birth rate and death rate are body size–dependent (for eutherian mammals, birth rate correlates with body size with the power coefficient −0.33, and death rate correlates with body size with the power coefficient −0.56—Calder 1996). Metabolic rate is also body size–dependent (for mammals, field metabolic rate correlates with body size with the power coefficient 0.81—Nagy 1987).

The habitat match of a species represents how well a given species does in a particular patch's habitat. For simplicity, I assume that all species consider the habitats in a similar manner, sharing the same habitat match for a particular habitat. From the species perspective, habitats differ in quality from one another because they provide different habitat matches for the species. Elsewhere (Ziv 1998b), I explicitly define the species–habitat match as the relationship between the physical space of the habitat and the niche of the species. To do this, however, I had to define additional parameters, which in turn limited the general conclusions of the model.

A population is the group of individuals of a species occurring in a particular patch. As mentioned above, the local-scale processes, including breeding, occur within the borders of a patch. Hence, a species is a metapopulation. The body size, birth rate, death rate, metabolic rate, and habitat match of a population are those of the species. The carrying capacity of a population is its size when growth rate equals 0. Hence, it locally depends on the species–habitat match in the particular patch. Finally, a community is the set of nonzero populations in a patch.

Model Processes

I simulated ecological processes on 2 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 have a direct impact on population growth inside patches. Meanwhile, processes occurring between patches can affect population growth indirectly through dispersal and disturbance.

Local-scale processes.—I used a modified version of the continuous-time logistic population growth to simulate the population dynamics of a population in a particular patch (equation 3). I separated birth rate from death rate in the equation to avoid an artifact of apparent population increase in a declining population occurring in an oversaturated patch. This separation is realistic (Begon et al. 1990) because birth rate and death rate may be limited by different processes. For example, birth rate may be limited by a need for protein-rich resources for lactating females that are not required by the rest of the population. In addition, this separation allows one to use allometric birth and death rates that are already available in the literature.

Two processes may affect a population in a patch: community-level saturation effect is a feedback function that represents the density-dependent pressure a population experiences from all populations of a patch, including its own (both intra- and interspecific density dependence). Its mechanics build on the ratio between the energy supplied by a patch and the overall energy consumed by all populations in a patch. Energy consumed by all populations in the patch is the sum of the species-specific energy consumption of each population. A population's species-specific energy consumption is calculated by multiplying metabolic rate of the species by number of individuals of that population. Because energy supply of a patch and metabolic rate of a species have the same units (energy/time), the division of these two gives a dimensionless variable (Vogel 1994) that ranges between 0 (no individuals at all) and any positive value.

The community-level saturation effect permits use of multiple resources. A population may consume all of the patch's resources or only a subset, depending on the list of resources of a population. Energy of each resource in a patch is determined by its proportion of the energy supply of that patch. An algorithm sets the relative use of each resource by those species that share it. The equation for community-level sat-

uration effect treats resources 1 at a time and then sums all resources.

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

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

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

A 2nd process that may affect a population in a patch is demographic stochasticity. Demographic stochasticity refers to any change in population size caused by a chance event independent of a biologically enhanced process. It has a stronger effect when population sizes are low. For example, the chance of a 2-female population leaving no females in the next generation due to the birth of only males is higher than in a 10-female population.

I used a simple descriptive equation to model stochastic deviations from deterministic, body size–dependent birth and death rates. If demographic stochasticity is invoked at every time step, a rate (either birth or death rate) is determined by adding a stochastic error to the deterministic rate. The stochastic error is a random number sampled from a Gaussian probability distribution with a mean of 0 and a symmetrical truncation of 2 *SD*, with a value of 1 each. An adjustment is made such that the final rate of population change never falls below 0. This adjustment also allows smaller species with higher birth rates to escape extinction faster (Pimm and Gilpin 1989). Additional adjustment is made such that deviations are negatively correlated with population size (density dependence—Lande 1993; Pimm et al. 1988; Shaffer 1981).

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

$$Z_j = z_i \pm \left(\frac{\varepsilon 0.5 z_i}{\gamma \sqrt{N_j}} \right) \quad (2)$$

where ε is a random number sampled from a Gaussian probability distribution, $0.5z_i$ is a scaling term to make each distribution range between 0 and twice the highest birth or death rate, and g is a demographic stochasticity coefficient allowing for changes in the intensity of the effect.

The equation by which a given population grows in a patch without the effects of dispersal and catastrophic stochasticity (global-scale processes) is

$$\frac{dN_j}{dt} = N_j b_i m_j (1 - f_{(s)j}) - N_j d_i (1 + f_{(s)j}) \quad (3)$$

where b_i and d_i are the birth rate and death rate of species i, to which population j belongs, and m_j is the species–habitat match.

The species–habitat match quantifies how well individuals of a particular population are suited to a particular patch, given the species and the habitat type. A value of 0 indicates no match, while a value of 1 indicates a perfect match.

The community-level saturation effect enters the equation twice. First, I subtract the community-level saturation effect from 1 as in the carrying capacity–feedback function of the logistic equation $(1 - N/K)$. I assume (as in the logistic equation) that birth decreases linearly with increase in community density (total number of individuals of all species). Oversaturation $(1 - f_{(s)j} < 0)$ results in no birth.

Second, I add 1 to the community-level saturation effect to model the effect of the community saturation on death. Here also, I assume that death increases linearly with an increase in community density.

A major advantage of the present equation for local-scale population growth is that it does not assume any arbitrary value for carrying capacity. Instead, carrying capacity is the single population size (with no competitors) resulting from the population's metabolic requirement (maintenance) and the available resources in the patch.

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

Global-scale processes.—Two major processes may affect populations and communities on a landscape scale (Hanski and Gilpin 1997). One is dispersal (Andow et al. 1990; Gustafson and

Gardner 1996; Johnson et al. 1992; Levin 1974). In the current model, individuals of a particular population in a given patch are assumed to migrate to adjacent patches if they can gain a higher potential fitness there. The dispersal function builds on optimization principles used for intraspecific density-dependent habitat selection suggested by Fretwell and Lucas (1969) and Fretwell (1972). At each time step, the model calculates the per capita growth rate of each population. Then, it compares it with all adjacent population per capita growth rates of the same species, assuming that individuals can instantly assess the adjacent population per capita growth rates. Individuals move from patches with relatively low per capita growth rates (low fitness potential) to patches with higher per capita growth rates (higher fitness potential). This results in equalizing the per capita growth rates of populations of the species across patches (Fretwell 1972). Dispersal is a population-level variable, represented by the movement of a fraction of the population.

The 2nd process operating at the landscape scale is catastrophic stochasticity (Levin and Paine 1974; Pickett and White 1985; Turner 1987). Catastrophic stochasticity, or disturbance-induced extinction, is a density-independent loss of individuals due to some event, such as extreme cold weather or a drought, that has a random probability of occurrence. For instance, if a catastrophic event causes a 20% loss of individuals in a particular habitat, all populations are reduced by this percentage regardless of their initial population size. Although this linear correlation may not apply equally to all species and populations in natural situations, I chose to use it for matters of simplicity. Future work is needed to incorporate a more realistic function to catastrophic stochasticity.

Catastrophes may cause the disappearance of entire populations of a given community or only their partial disappearance. A catastrophic event may be very local, such as within a single habitat, like a falling tree in a forest, or may cover an extensive area and include many different types of habitats (Turner 1987).

Catastrophic stochasticity in the present study relies on random number–generating procedures (Press et al. 1995) allowing one to change the probability, intensity, and range of the density-independent loss in populations.

Defining the local growth of population j in equation 3 as $F_{(L)j}$, the overall population growth, including dispersal, becomes

$$\frac{dN_j}{dt} = F_{(L)j} + \sum_{i=1}^{AP} \left\{ D_i \left[\left(\frac{dN_j}{dtN_j} \right) - \left(\frac{dN_i}{dtN_i} \right) \right] N_{j(-)/i(+)} \right\} \quad (4)$$

where AP is the number of adjacent patches, D_i is the dispersal coefficient (Hastings 1990), and Nj(−)/I(+) indicates that the per capita dispersal 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 individuals from the adjacent patch disperse into it. In contrast, a negative per capita movement means that individuals should disperse into the adjacent one.

Model Mechanics and Simulation Design

I used object-oriented programming (C++—Martin 1995) for my model, designing the different components of ecological structure, such as species and habitats, as classes of objects (Martin 1995). Hence, the model benefits from the ability of object-oriented programming to model natural systems in a relatively realistic way (Ferreira 1995) through built-in definitions of classes and objects and use of containment and inheritance to connect different class objects. The landscape is designed as an abstract class that serves as the system controller (Martin 1995). It controls the lists of other classes and ensures that the model functions and variables behave according to the system's defined needs.

For each simulation run, I used the same parameter values as mentioned in the simulation design and changed only the procedures that reflected ecological processes. I selected those parameter values because they have already been shown to produce realistic outcomes in previous simulations, such as carrying capacity and intrinsic rate of increase (Ziv 1998b). Additionally, a sensitivity analysis has been conducted on each parameter in previous studies. The sensitivity analyses showed that none of the parameter values and the procedures used in the model altered the results due to purely mathematical properties of the model.

The simulation model uses the Runge–Kutta

method (Press et al. 1995) to integrate the small steps (dt = 0.001 years) on a continuous-time axis. Without dispersal, at each time step each population grows according to the local-scale processes (equation 3). If populations disperse among patches, however, each population grows according to the local-scale processes and the migration-related movement of individuals (equation 4).

The model returns the value of population size for each population in the different patches every 100 time steps (every 0.1 year). The information is saved to an output file for further analysis. In cases where stochasticity (either demographic or catastrophic) has been invoked, I ran 100 simulations of the same design to avoid basing conclusions on a chance event obtained from a specific run.

I conducted 2 different sets of simulations. One aimed to study the 2 patterns mentioned above regarding body size–dependent species diversity, while the other aimed to study aspects of community structure with respect to body size.

First simulation design.—For the patterns of body size–dependent species diversity, I used only carrying capacities to avoid any influence of other processes of the model (interspecific competition, demographic and catastrophic stochasticities, and dispersal). The rationale of doing so was that if a pattern can be generated by simple, basic rules, we may not need to seek more complicated explanations. Additionally, due to the very large scale at which the 2 patterns—body size versus species abundance and body size versus geographic range—are observed, I simulated landscapes that allow incorporating a higher diversity of habitats with different habitat qualities.

I simulated a landscape with 4 by 4 cells, each having a unique habitat (total of 16 habitats). I assigned an area of 10,000 m^2 to each of the 16 patches. (Note that in this simulation, patch, habitat, and cell are synonymous.) The patches were distributed randomly in the landscape. I ran each set of simulations 10 times with different random distributions of habitats.

I assigned realistic productivity values for the different habitats without a specific process in mind in order to keep the model as general as possible. Elsewhere (Ziv 1998b), I provide an alternative assignment by calculating productivity as a linear function of the product of temperature and precipitation (Leigh 1965; Lieth 1975; Wright et al. 1993). All habitats had the same productivity (6,250 kcal m^{-2} $year^{-1}$), which represents semiarid environments, such as the ecotone between Mediterranean and desert regions. Having the same productivity for all patches prevents the possibility that productivity affects the results. However, I arbitrarily assigned different species–habitat matches to the different habitats, such that habitat 1 was the best habitat and habitat 16 was the worst (species–habitat match = 0.88, 0.82, 0.76, 0.69, 0.61, 0.55, 0.49, 0.43, 0.38, 0.33, 0.28, 0.25, 0.22, 0.19, 0.17, and 0.15 for habitats 1 through 16, respectively).

I simulated 10 species that differed only in body size. Body size ranged between 2 and 3,981 g, corresponding to log values of body size ranging between 0.36 and 3.6 (with a difference of log value of 0.36 between body sizes to ensure the pattern was revealed along the entire desired range).

I used allometric coefficients for birth rate (b), death rate (d), and metabolic rate (E_M) of eutherian mammals ($b \propto M^{-0.33}$, $d \propto M^{0.56}$, $E_M \propto M^{0.85}$, where M is body size—Calder 1996). The combination of 10 species and 16 patches created 160 populations.

Second simulation design.—I simulated a landscape with 2 by 2 cells, each having a unique habitat (total of 4 habitats). I chose this, the simplest, landscape design rather than the one I used in the previous simulation because the existence of different processes in the current simulation added a tremendous amount of complexity to the model. Thus, the simple landscape design allowed me to focus on the outcomes of the processes. I assigned an area of 100 m^2 to each cell. (Note that also in this simulation, patch and habitat are synonymous.)

As in the previous simulation, I assigned realistic productivity values for the different habitats without a specific process in mind, in order to keep the model as general as possible. I assigned different species–habitat matches to 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, I assigned an equal productiv-

ity for each resource out of the total productivity of the habitat.

I simulated a total of 26 species. Species differed in only 1 characteristic, body size. Body size ranged between 5 and 1,585 g, corresponding to log values of body size ranging between 0.7 and 3.2. I assigned a unique preferred resource to each species and gave it a resource-proportion use of 0.5. Each species could consume 2 other resources, 1 on each side of the preferred one; each of these had a resource-proportion use of 0.25 (for example, 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). From preliminary simulations, I found that this resource allocation was sufficient to produce a competitive relationship with resource partitioning without assuming any complex resource-use function. I used the allometric coefficients for birth rate, death rate, and metabolic rate of eutherian mammals, as described above.

The combination of 26 species and 4 patches created 104 populations. As mentioned above, each set of populations in a given patch, or community, is treated separately by the local-scale processes. The global-scale processes influenced extinction (catastrophic stochasticity) and movement (dispersal) of populations across patches.

When catastrophic stochasticity was invoked, I gave the system a 10% chance of suffering catastrophic stochasticity in a year (an average of 1 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 enough to affect population and species distribution (Turner 1987), yet the values were not high enough to drive all populations to extinction.

Other than these 1st-level assignments of values for cells, habitats, and species, no assignments were made for 2nd-level procedures such as habitat-specific population abundance. Therefore, any large-scale body size–dependent patterns that emerge were the result only of basic rules described here.

To understand the effects of the different ecological processes, I initially explored the patterns emerging from communities not affected by any of the above processes in which competition was strictly intraspecific. Then, I introduced interspecific competition. Thereafter, I separately added demographic and catastrophic stochasticities to interspecific competition to explore how each of these changes the predicted patterns. The single-process effects were used to identify specific "fingerprints" that distinguish between the 2. Finally, I allowed dispersal to connect all patches.

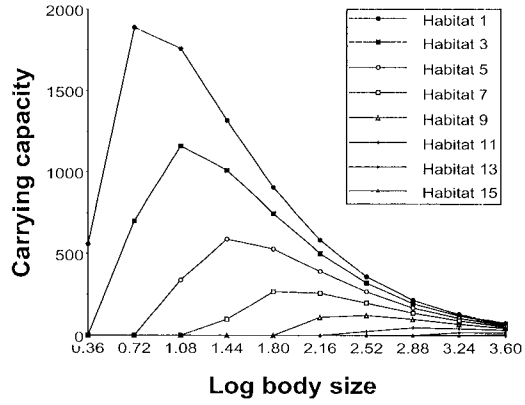

FIG. 1.—The larger the species the more habitats it can occupy (see also Ziv 1998a, 2000). The distribution of carrying capacities changes among habitats, changing from a right-skewed unimodal curve to a monotonically increasing one, depending on the quality (species–habitat match) of the habitat.

RESULTS

Two Body Size–Dependent Patterns of Species Diversity

Carrying capacities of the different populations of the 10 species in 8 habitats are shown in Fig. 1. (I included only 8 of the 16 habitats to present the patterns more clearly.) In a previous paper (Ziv 2000) I showed that, with equation 1 and the allometric relationships used for this paper, larger species occupy more habitats. This scaling relationship is also obtained here (Fig. 1). Distribution of carrying capacities changes between habitats, from a right-skewed unimodal curve to a monotonically increasing one. In other words, no single pattern characterizes all species' population distributions.

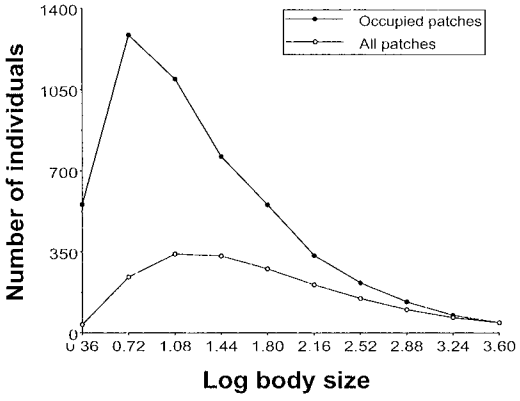

FIG. 2.—Average number of individuals for occupied patches only (closed circles) and average number of individuals for all patches (open circles). The curves were calculated by dividing total species abundance given for sum of a given species' populations in the different patches by number of patches it occupies and all patches in the landscape, respectively. The 2 curves are consistent with the observed pattern in natural systems.

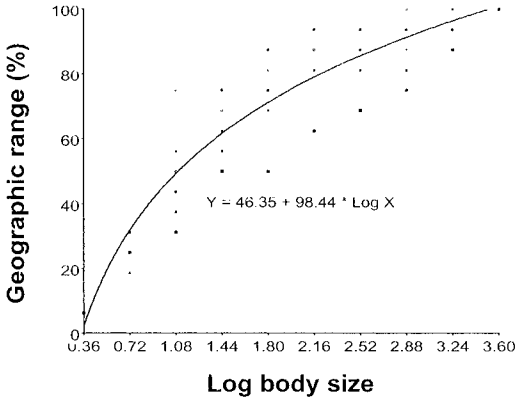

FIG. 3.—The larger the species, the wider its geographic range, represented by percentage of its occupancy relative to entire landscape (R^2 = 0.987).

Distribution of the patch-specific population abundance can be used to calculate the average species abundance in the landscape by dividing total species abundance by number of habitats it occupies (Fig. 2). The pattern agrees with the known pattern of the log, right-skewed, hump-shaped relationship between body size and abundance (see Brown 1995). But here, this relationship is the outcome of a process-based model; it is not merely an observed phenomenon. Larger species have lower abundances because their populations are smaller everywhere. Smaller species have a lower abundance because they occupy only a fraction of the available habitats in the landscape. In turn, the log, right-skewed, hump-shaped relationship of body size and abundance results from the existence of different qualities of habitats in a heterogeneous landscape; it is merely an averaging pattern expressed at large scales.

The larger the species, the wider its geographic range (Fig. 3). I fitted a semilogarithmic curve to the data, arriving at an explained variance of about 99%. This curve is partially consistent with the patterns observed by Brown and Maurer (1989). It does not show the left-hand truncation given by the triangular relationship presented in Brown and Maurer (1989); however, as in this study, intermediate-sized species show higher variability in the size of the geographic range they occupy. Future exploration is needed to explore the mechanism whereby small body sized species do not have small geographic ranges.

Having gained confidence in the model due to the similarity between the model's patterns and the patterns known from field data, we can now explore how different processes and combinations of processes may affect species composition and community structure.

Process-Based Community Structure

In the following section I present results for the simulation runs according to the process in focus.

Carrying capacities.—All habitats were suitable for all species. That is, without any population-reducing processes, i.e., interspecific competition and demographic and catastrophic stochasticities, all populations in all habitats could maintain a persistent

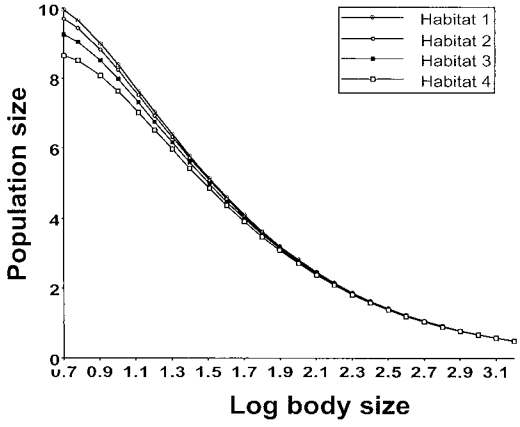

FIG. 4.—Carrying capacities of species as a function of body size in the different patches (habitats).

population size. A similar population-size pattern for all habitats emerges (Fig. 4) because all populations can persist in all habitats and because no process other than intraspecific competition affects population growth. The only difference between habitats is that carrying capacities of populations of the same species are lower in habitats with lower species–habitat match.

In the previous simulation, I demonstrated that, in a heterogeneous landscape composed of a mixture of different habitat qualities (some suitable and some unsuitable habitats for all species), body size and abundance form a log, right-skewed, hump-shaped relationship. This conclusion is also supported by the current simulation. If all populations in all patches could persist (all habitats are suitable for all species), the log, right-skewed, hump-shaped relationship would disappear (as in Fig. 4). The decreasing line of the log-normal curve for the small species does not exist because smaller species no longer use only a small fraction of the landscape, but rather use the entire landscape, as do larger species.

Effect of interspecific competition.—In the present simulation design, it is 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 3 species (except the smallest and largest species, which do not have to compete with a smaller species or a larger species, respectively). This shared consumption can lead to competitive exclusion. Imagine species 1, 2, and 3 consuming different preferred resources b, c, and d, respectively. However, species 1 and 3 also consume some of resource c. If species 1 and 3 maintain their abundances, say by being the only consumers of resources a and e, they can depress the abundance of species 2 to local extinction. 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 mammalian communities (Kotler and Brown 1988).

The same species composition exists in all habitats as well as for the entire landscape (Fig. 5) because of the modeling of resource partitioning as a deterministic process that does not change between habitats. With interspecific competition, some populations are outcompeted, leaving a discontinuous distribution of body sizes. The absence of particular species depends on an intratrophic cascading effect; the largest species depresses the population size of the 2nd largest species due to the competitive advantage of the largest species. Although the 2nd largest species has the competitive advantage over the 3rd largest species, the 3rd largest species also depresses the 2nd largest species, and though a small effect, this is enough to depress the former further to local extinction. The 3rd largest species, which does not share resources with the largest one, is saved from the potentially dominating effect by the extinction of the 2nd largest species because, in the present model, species share resources only with the species closest in body size. The process repeats with the 4th, 5th, and 6th largest

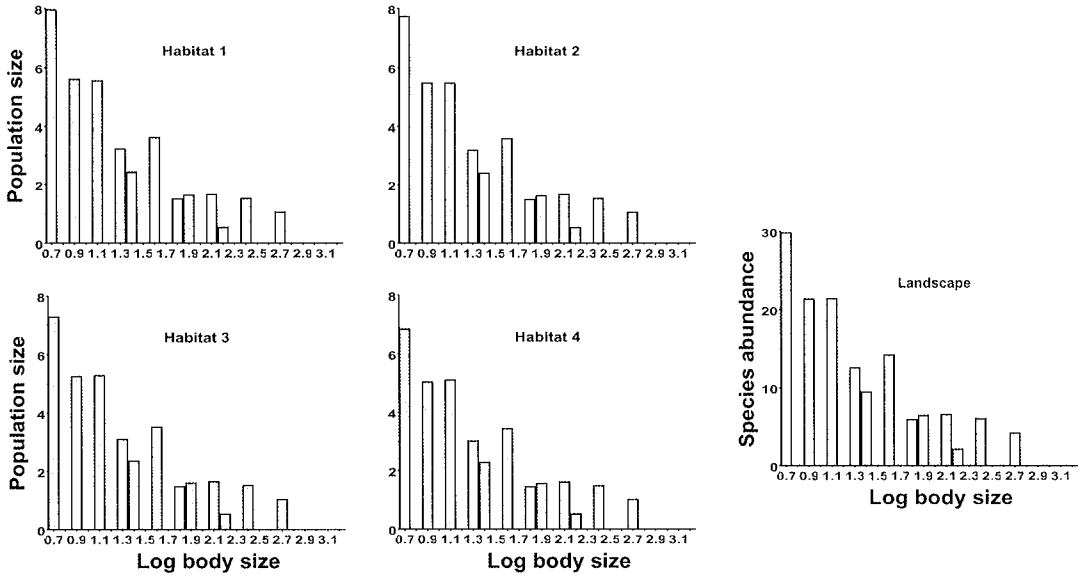

FIG. 5.—Sizes of all populations in the different patches (habitats) and in the entire landscape with interspecific competition. Interspecific competition deterministically affects all populations the same way. Identical patterns emerge for the patches and for the entire landscape.

species and so on. As all interactions between all species are taking place simultaneously, the overall effect on the different species sometimes results in an absence of a species of a particular body size between 2 coexisting species having close body sizes. The 2 species coexist because the larger can consume its most preferred resource better, apart from having a competitive advantage, while the smaller benefits from the other resource that is no longer used by the species smaller than it that went extinct. In the end, 12 species coexist in the landscape.

Adding demographic stochasticity to interspecific competition.—Demographic stochasticity (the sampling effects regarding sex ratio, litter size, and other factors), which may promote local extinctions of small populations, exists regardless of which other processes affect population growth (Lande 1993; Pimm et al. 1988; Shaffer 1981). With demographic stochasticity, different patterns appear in the different habitats (Fig. 6). Populations of larger species are more likely to become extinct because they have smaller populations. The particular population that ends up extinct, however, is determined randomly. Once a particular population becomes extinct, its closest competitor in body size benefits from a competitive release and enjoys a higher population size (hence, they show a negative autocorrelation in population size). The rest of the community is now competitively determined by the particular species of large body size that escaped extinction (a domino effect). Because demographic stochasticity reduces species diversity in each habitat, population size of the survivors, on average, is higher than with interspecific competition alone; 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 extinctions in the different habitats. Hence, demographic stochasticity increases species diversity at the landscape scale (Chesson and Case 1986). Overall, on average, 17.59 ± 1.72 (mean ± *SE*) species exist in the landscape.

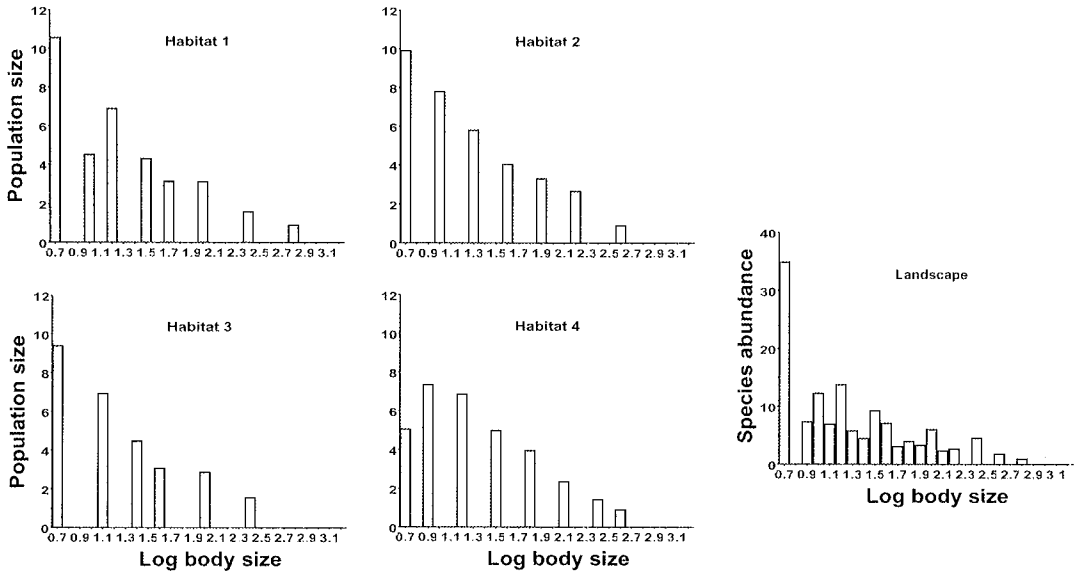

FIG. 6.—Typical sizes of all populations in different patches (habitats) and in entire landscape with interspecific competition and demographic stochasticity. Community structure in each patch is determined by those large populations that escaped extinction. Once a random extinction of a large body sized population takes place, the community is well structured according to competitive interactions. Demographic stochasticity increases species diversity at the landscape scale.

Adding catastrophic stochasticity to interspecific competition.—Catastrophic stochasticities, or disturbances, are common in natural systems (see Pickett and White 1985; Turner 1987). Furthermore, catastrophes may enhance coexistence between species of the same trophic level by reducing population sizes below the community carrying capacity so that resources are no longer limiting (Chesson and Case 1986; Levin and Paine 1974). As with demographic stochasticity, catastrophic stochasticity decreases diversity in each habitat but increases diversity for the entire landscape (Fig. 7).

The outcome of catastrophic stochasticity differs from that of demographic stochasticity in 2 major ways. First, in each habitat, with catastrophic stochasticity, the discontinuities of body sizes are smaller and some very similar-sized species coexist. Second, with catastrophic stochasticity all the largest species disappear. These differences are explicable. The local extinction of a particular large species due to demographic stochasticity promotes a higher chance for survival for other large species because when 1 population, independent of others, becomes extinct, other populations enjoy more available resources. Hence, with demographic stochasticity, strong competitors show a negative autocorrelation in their response. Catastrophic stochasticity, however, affects all species simultaneously. Therefore, a catastrophic event is likely to exterminate all larger species because they all have relatively small population sizes. Compared with the result for demographic stochasticity alone, on average, catastrophic stochasticity results in 5 fewer species (12.76 ± 1.71) in the landscape.

Combining catastrophic and demographic stochasticity.—Several studies dealing with stochastic effects (Lande 1993; Pimm et al. 1988; Shaffer 1981) have suggested that demographic and catastrophic stochasticities may work together in natural systems to drive species to extinction. Cata-

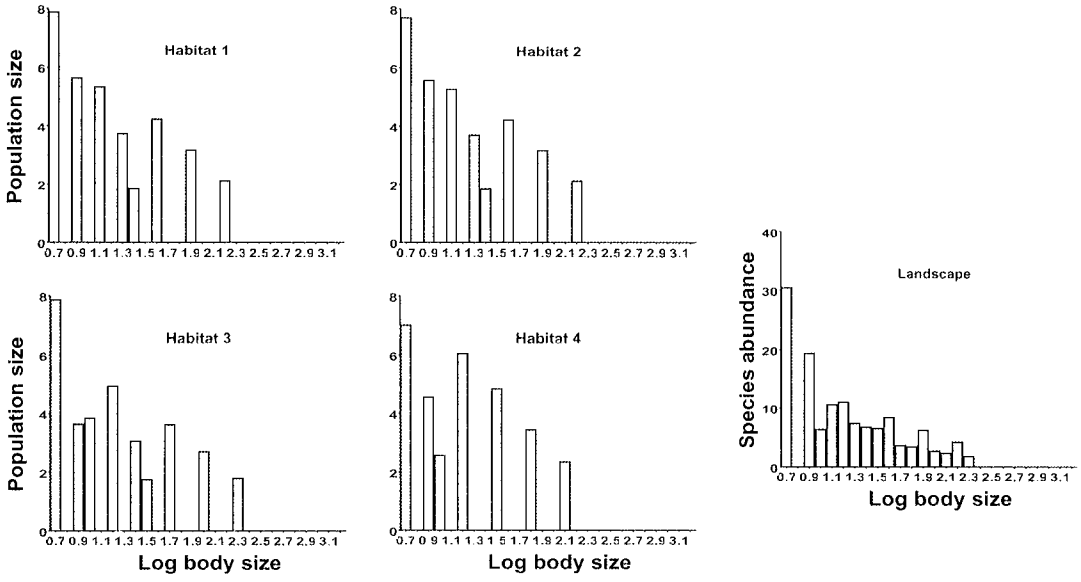

FIG. 7.—Typical sizes of all populations in different patches (habitats) and in entire landscape with interspecific competition and catastrophic stochasticity. In each patch, discontinuities of body sizes are smaller than those observed for demographic stochasticity (Fig. 6) due to coexistence of some populations with close body sizes. Catastrophic stochasticity causes disappearance of the largest populations and increases species diversity at the landscape scale.

strophic stochasticity reduces population sizes to low values, and demographic stochasticity further decreases them to the vanishing point.

Patterns emerging from combining the 2 stochasticities (Fig. 8) reflect their joint effect. First, owing to demographic stochasticity, discontinuities of body sizes are large, with no similar-sized species coexisting. Second, the largest species still disappear owing to catastrophic stochasticity. Knowing the specific outcome of either effect alone allows us to pick up the fingerprints of each one when both are invoked.

At the landscape scale, the joint effect of stochasticities reduces species diversity to a lower value than that expected for each alone. Interestingly, with both demographic stochasticity and catastrophic stochasticity, species diversity at the landscape scale is similar to that observed with competition alone (11.09 ± 1.54).

Effect of dispersal with stochastic effects and interspecific competition.—Dispersal of individuals in the landscape is probably the most studied process in landscape ecology (Johnson et al. 1992; Kareiva 1983; Levin 1974; Wiens 1992). Dispersal has consistently been shown to have major effects on single-species distributions as well as on multispecies community structures. In the current simulation study, dispersal from habitat to habitat depends on the ideal free distribution (Fretwell 1972).

Without dispersal, habitat-specific stochastic effects determine species compositions because individuals of different species cannot recolonize a habitat. With dispersal (Fig. 9), colonists can restore local populations of their species. When the species is competitively subordinate, a permanent recovery is unlikely. Recovery of a competitively dominant population, however, has a significant effect on community composition. If dispersal is frequent enough, dominant species can establish in all patches and, on average, overcome the

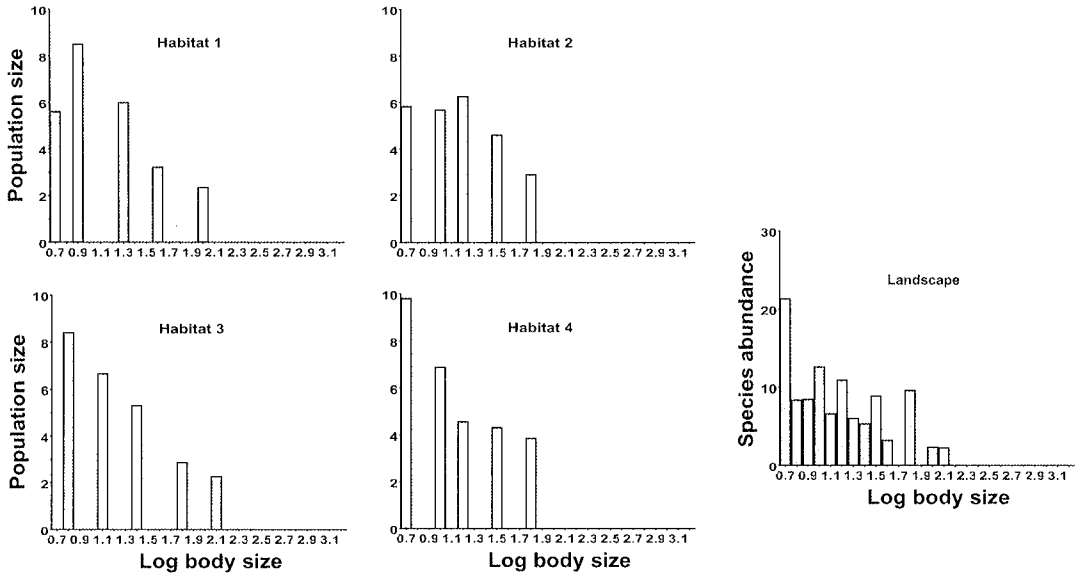

FIG. 8.—Typical sizes of all populations in different patches (habitats) and in entire landscape with interspecific competition and both demographic stochasticity and catastrophic stochasticity. Patterns emerging from combining the 2 stochasticities reflect their joint effect. First, discontinuities of body sizes are relatively large because of the way demographic stochasticity affects community structure. Second, the largest populations disappear because of the effect of catastrophic stochasticity on community structure.

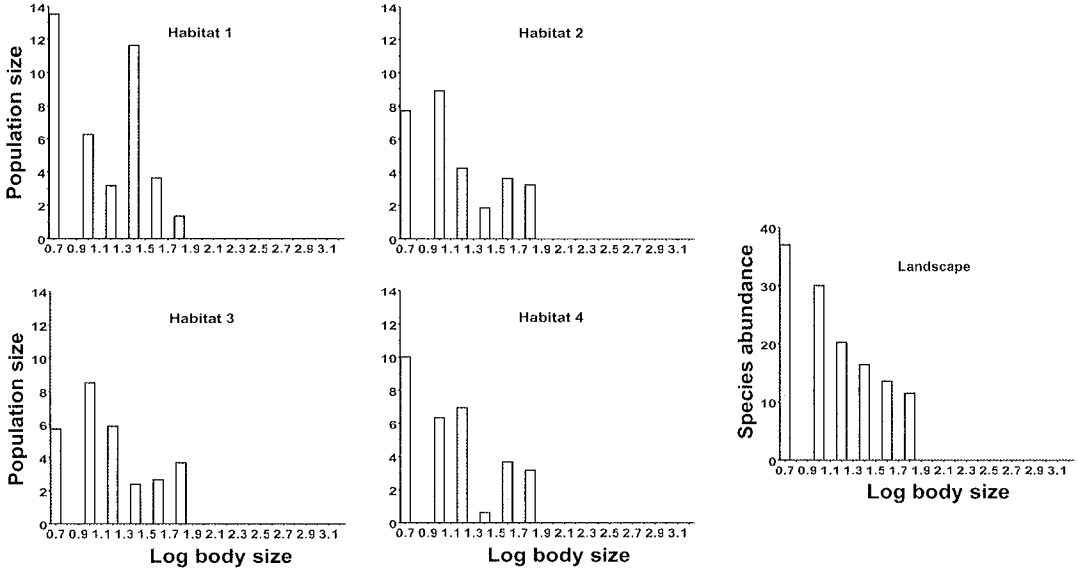

FIG. 9.—Typical sizes of all populations in different patches (habitats) and in entire landscape with interspecific competition, demographic and catastrophic stochasticities, and dispersal. Dispersal allows dominant populations that became extinct from a particular patch due to a chance event (any stochasticity) to recolonize that patch and increase in numbers. As a result, dominant species in the landscape reestablish their populations in all patches and, on average, overcome stochastic effects that might produce locally different patterns.

stochastic effects that tend to produce locally different patterns.

Knowing the outcomes (or fingerprints) of the different processes (competition, catastrophic stochasticity, and demographic stochasticity) as well as the joint outcome of demographic stochasticity and catastrophic stochasticity, we can now detect the fingerprints of the different processes, including dispersal, on the patterns shown in Fig. 6. As before, demographic and catastrophic stochasticities are responsible for larger discontinuities of body sizes and for disappearance of the largest species from the landscape (local extinction of the largest species from all patches deprives them of colonists that could otherwise restore extinct populations). The opportunity created by dispersal for the dominant species to recolonize patches in which they have become extinct results in all habitats having the same species. At the landscape scale, the presence of dispersal together with demographic and catastrophic stochasticities and interspecific competition produces the lowest species diversity (5.08 ± 0.598). The main reason for this low species diversity is the continuous disappearance of small populations that usually belong to large species.

Discussion

This paper presents a new approach to the study of large-scale ecological processes and patterns by providing nontrivial predictions on combination of spatial heterogeneity and multiple-process interactions. Simulation results show that mammalian body size and species abundance will have a log-normal relationship. Additionally, the results predict that geographic range will increase nonlinearly with log of body size. These patterns are consistent with those observed in natural systems studied to date (Brown and Maurer 1989), providing confidence in the model results. The model also allows us to explain these patterns using underlying processes of the model. Both patterns emerge from the existence of habitat heterogeneity, with some habitats being more suitable and others being less suitable for certain species. Larger species occupy more habitats, and within a particular habitat, larger species have lower abundances. In the log-normal relationship of body size and abundance, larger species have lower abundances because their populations have lower sizes everywhere. Smaller species have lower abundances because they occupy only a fraction of the habitats in the landscape (Ziv 2000). These results suggest that neither dispersal nor stochasticity of any kind is a necessary condition to produce the body size–abundance pattern because neither of them was invoked during the simulation runs. It is important to point out that although the model's results are consistent with the qualitative pattern of the relationship between body size and species abundance, they somewhat deviate from existing empirical data (Brown 1995; Brown and Maurer 1989; and see Brown et al. 1993; Kelt 1997 for optimal body-size consideration). I suggest that the many parameters of the model as well as the use of only empirically allometric exponents (but not the coefficients) force the model's results to depart quantitatively from empirical data.

The results of the model as described here allow me to point confidently to specific outcomes (fingerprints) that characterize specific processes affecting body size–dependent community structure. Once fingerprints are known, we can find them also in complex interactions (the combination of demographic and catastrophic stochasticities with interspecific competition). We can then compare the joint effects of multiple processes with the single-process effects. The overall effects were not simply additive but rather included effects that resulted from interaction between processes.

By itself, interspecific competition results in clear patterns of body-size discontinuities. This is not a new result, however; a perfectly deterministic environment implies stability, and stability reduces variability and promotes similarity (May 1974). This,

in turn, should lead to competitive exclusion. However, this result serves as a basis for comparison with the more complex interactions that also involve interspecific competition.

Stochasticity depresses mean population sizes. Hence, it opens opportunities for species to avoid competitive exclusion. Also, stochasticity 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 stochasticity and catastrophic stochasticity, 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 the largest species disappear. Combined, each of the 2 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 local populations of their species. Thus, dispersal neutralizes the randomness of assemblages produced by stochasticity. As a result, each habitat tends toward the same set of species. Even with dispersal, however, stochasticity eliminates the largest species and produces large discontinuities in body-size distribution. Loss of randomness in the assemblages means that, at the landscape scale, dispersal reduces species diversity.

The novel predictions 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 better understand natural systems.

Common modeling approaches deal with a single- or 2-species community and with 1 or 2 processes only. When other processes are studied, usually a different set of simulations is constructed without building on processes studied earlier. Because the current model makes predictions from interactions between multiple processes, its predictions may contradict those of other models. For example, metapopulation dynamics (Hanski and Gilpin 1997) postulates that stochastic events reduce species diversity by increasing probability of extinction and that dispersal saves some species from global extinction. Hence, we might conclude that stochasticity is bad and dispersal is good for species diversity. When interacting species are affected by catastrophic and demographic stochasticity and can move from one habitat to another in a heterogeneous landscape, however, dispersal and stochasticity have different effects. Both types of stochasticity increase overall species diversity by wiping out low-density large species, while dispersal decreases the overall species diversity by homogenizing the set of species that succeed in different habitats.

Another example of the contribution of this model to understanding multiple-process interactions involves conservation biology. Conservation biologists commonly argue for the use of wildlife corridors in management (Hudson 1991). The current model, however, suggests that corridors may interfere with conservation of a rare species by encouraging dispersal between reserves. Dispersal may result in a higher negative effect of demographic stochasticity. Small populations may become even smaller after dispersal, becoming more vulnerable to random sampling effects that promote extinction. Theoretical work (Kunin and Gaston 1997) suggests that we should distinguish between species that are naturally rare and species that are naturally common but become rare as a result of hu-

man impact. We may hope that through evolutionary time the former group has developed certain mechanisms to deal with rarity. The naturally common species that become rare because of human impact, however, may drastically suffer from dispersal between reserves that makes their local populations even smaller.

The modeling approach I suggest here may promote better understanding of the effect of multiple processes interacting in a heterogeneous landscape on species-diversity patterns. The results are consistent with observed patterns. They also produce reasonable predictions for interaction of multiple processes in heterogeneous landscapes. However, these are merely predictions. The model cannot eliminate field studies to test whether or not these predictions are realistic and what the natural conditions are that are likely to affect them. Given the high degree of complexity existing in ecological structures, the current approach allows us to generate testable predictions for future observational and experimental studies addressing the effect of multiple processes operating in heterogeneous landscapes on species-diversity patterns.

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