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The effect of habitat heterogeneity on species diversity patterns: a community-level approach using an object-oriented landscape simulation model (SHALOM)

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Abstract

Major progress has been made recently in our understanding of large-scale ecological processes and patterns. Here, a spatially explicit, multi-species, process-based, object-oriented landscape simulation model (SHALOM) is described that is built upon major lessons from fields such as metapopulation dynamics and landscape ecology. Consistent with the current landscape ecology terminology, SHALOM has physical classes (landscape, habitat, cell, patch) and biological classes (population, species, community). Each class has functions and characteristics that are strongly based on ecological realism. Processes of SHALOM are modelled on local and global scales. At the local scale, populations grow continuously, and are affected by: (1) a community-level saturation effect (ratio between energy consumed by all populations in a patch and the energy offered by that patch); (2) a species-habitat match (match between a species' niche space and the patch's habitat space); and (3) demographic stochasticity (inverse population-size dependent residuals from deterministic birth and death rates). The global-scale processes of the model include fitness-optimizing migration and catastrophic stochasticity (disturbance) that can be controlled for its probability, intensity, and spatial range. The processes of the model use allometric relationships and energy as a common currency to bridge differences between species of different body sizes located in habitats of different productivities. These processes also allow both intraspecific and interspecific effects to take place simultaneously without assuming a specific relationship between the two. Hence, SHALOM, with its functions and procedures, opens new opportunities to study combined ecosystem, community and population processes. Simulation results given in the paper on species composition and diversity show that the integration of interspecific competition, demographic stochasticity and dispersal revealed different predictions when different combinations of these processes were used. One novel prediction was that the complex relationship between dispersal and demographic stochasticity caused the global extinction of the largest species. This, in turn, might have further implications for conservation. Overall, the model represents a synthetic approach that provides ways to explore high-level ecological complexity and suggests predictions for future studies of macroecological questions.

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1. Introduction

Exploring large-scale ecological patterns and processes is a major current interest in ecology (Brown, 1995; Hansson et al., 1995; Rosenzweig, 1995). It is commonly recognized that large-scale processes strongly influence both population-level phenomena (Levin, 1974; Dunning et al., 1992; Johnson et al., 1992; Pulliam et al., 1992) and especially species diversity patterns (Brown and Maurer, 1989; Rosenzweig, 1992; Hanski et al., 1993; Holt, 1996a,b; Hanski and Gyllenberg, 1997). Fields such as metapopulation dynamics (Levins, 1969, 1970; Hanski and Gilpin, 1991, 1997), landscape ecology (Turner, 1989; Forman, 1995; Pickett and Cadenasso, 1995), and patch dynamics (Pickett and White, 1985; Collins and Glenn, 1991; Levin et al., 1993) focus on the effect of the environment and large-scale processes on single-species distributions as well as species-diversity patterns.

Population-level and species-diversity patterns may depend on the temporal and spatial scales at which they are described. For example, the species-area relationship has been shown to subsume four different relationships. Each emerges from processes that depend on the spatial scale (from a specific locality to the entire world) and the temporal scale (from short-term ecological periods to evolutionary time) (Rosenzweig, 1995). Ecological scaling becomes important when different processes affect populations and species at different spatio-temporal dimensions (Ricklefs, 1987; Fahrig, 1992; Wiens et al., 1993). For example, a local scale is restricted to one habitat area, or patch. It may include the processes of competition, the match between the species niche and the habitat, and aggregation. In contrast, a landscape scale includes a relatively large area having many different patches (Forman and Godron, 1986). Here, processes may include migration and extinction. These scales represent two extremes on a continuous axis. Intermediate scales may reflect other processes (see Dunning et al., 1992; Holt, 1993 for different landscape processes). For example, predation by a generalist predator that occupies a wide range of local patches of its prey may represent an intermediate-scale process affecting the prey species (Holt, 1996b). The relative contribution of each process may also depend on the specific characteristics of the species. For example, With (1994) showed that three grasshopper species responded differently to the same micro-landscape structures.

In addition to the scaling effect, habitat heterogeneity (Turner, 1987; Kolasa and Pickett, 1991; Hansson et al., 1995) also affects a variety of ecological aspects, such as species interactions (Pacala and Roughgarden, 1982; Danielson, 1991), foraging (Roese et al., 1991), dispersal (Levin, 1974; Gardner et al., 1989; Johnson et al., 1992), and disturbance (Pickett and White, 1985; Turner 1987). In particular, the number of different habitats (hereafter, habitat diversity), the size of each habitat's patch (hereafter, habitat size), and the patchy distribution of the different habitats' patches in the landscape (hereafter, habitat patchiness) may affect habitat heterogeneity (Holt, 1992; Loehle and Wein, 1994):

- Habitat diversity affects communities because different species may specialize on different habitat types. In the presence of new habitats, more species can exist (MacArthur, 1972). The presence of new habitats may also change the habitat selection of a species and may create more opportunities for coexistence (Rosenzweig, 1991). Hence, a larger area with more habitats has more species (Fox, 1983; Douglas and Lake, 1994).
- Habitat size affects communities because species may have a higher probability of escaping extinction when their populations are larger, and larger habitats support more individuals. Population size is the key factor in the vulnera-

bility of a population to local extinction (MacArthur and Wilson, 1967; Richter-Dyn and Goel, 1972; Leigh, 1981; Goodman, 1987; Pimm et al., 1988). Rare species may disappear due to environmental stochasticity, demographic stochasticity, and disturbances (Shaffer and Samson, 1985; Pimm et al., 1988). Overall, larger habitats will have lower extinction rates (Schoener and Schoener, 1981).

- Habitat patchiness affects communities because sub-populations of a species may escape local extinction in a few patches and recolonize those patches later on (Levins, 1969; Hanski, 1982, 1991; Harrison, 1991; Holt, 1992; Hanski, 1994). The greater the patchiness, the higher the probability that some individuals of a given population escape extinction in an entire area (den Boer, 1968). This may result in lower extinction rates. On the other hand, relative to a single-patched habitat with a larger area, habitat patchiness will result in a lower per-patch population size. Hence, each patch's population will have a higher probability of extinction due to low population size (see 'habitat size' above). This may result in overall higher extinction rates. Taken together, the relationship between the effect of low population size and the disturbance-colonization effect will determine the rate of extinction for a particular population.

Kolasa and Rollo (1991) showed that the scaling effect and environmental heterogeneity are not independent. In turn, 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. For example, Morris (1987) suggested that an organism that does not respond to a particular heterogeneity presented at one scale may respond (e.g. show differential habitat use) to the heterogeneity presented at another scale. This concept has led many ecologists to accept the idea that ecological processes and patterns are not fixed, but rather depend on the scale under study (Addicott et al., 1987; Kotliar and Wiens, 1990; Dunning et al., 1992; Wiens et al., 1993). For example, Ricklefs (1987) demonstrated that species diversity is affected by different ecological processes at different scales. Hence, the distribution of species and communities at a given scale depends on the overall processes operating at this scale, and these depend on the habitat heterogeneity (the patchiness of different habitats with different sizes) at this scale.

Biological heterogeneity, such as different body mass (Brown and Maurer, 1989; Holling, 1992) and different movement modes (With, 1994), may also play a role in the way different scales of environmental heterogeneity affect different species (Levin, 1992). For example, Robinson et al. (1992) showed that three small mammal species differing in body size (*Sigmodon hispidus*, 135 g; *Microtus ochogaster*, 43 g; *Peromyscus maniculatus*, 22 g), experience different persistence times and have different population sizes in habitat patches of various sizes. Because communities are assemblages of potentially interacting species, the community characteristics of a given spatio-temporal scale may depend on the scale and the structure of the environment.

Overall, scaling effects and environmental and biological heterogeneity should create a higher-level complexity that affects ecological systems from single-species population dynamics to large-scale species diversity patterns. Indeed, Levin (1976) suggested that we may expect newly emergent species-diversity patterns on some scales that are not observed and cannot be studied on others. Hence, the understanding of large-scale species diversity patterns and processes cannot be simply deduced from the understanding of local-scale patterns and processes. We need to explore large-scale species diversity patterns and processes in the context of their occurrence, given the relevant multi-scale processes and the heterogeneity of the environment in question.

The fact that experimentation is impossible at large scales and that without clear predictions observed data might not be very helpful either, makes modelling the major tool to explore large-scale ecological patterns (Turner, 1989; Turner and Gardner, 1991; Dunning et al., 1995; Turner et al., 1995). Two directions characterize current progress in landscape ecology and large-scale modelling: (1) focusing on population, community and landscape processes; and (2) using spatially explicit population models.

Recent studies (Kotliar and Wiens, 1990; Dunning et al., 1992; Wiens et al., 1993; Forman, 1995) have emphasized the importance of applying a process-based approach when studying landscape ecology because processes drive observed population and community dynamics. Additionally, because processes are affected by environmental heterogeneity, they add realism to studies of landscape patterns. A process-based approach might help to deal with the complexity of scaling in ecological structures because the relative importance of a given process may depend on the spatial scale.

Spatially-explicit population models (SEPM; Dunning et al., 1995) provide a realistic way to model heterogeneous landscapes by clearly representing the distribution of both physical and biological components. They allow one to deal with the different factors and processes affecting organisms given the number of habitats, patchiness, and size of each patch's habitat in the landscape. Hence, different ecological consequences can be explored and the overall effect of a given landscape matrix can be studied using SEPM.

2. Rationale

Given the potential of having higher-level complexity and having an interaction between scaling effects and environmental and biological heterogeneity, a realistic model should consider: (1) the incorporation of landscape-scale processes with local-scale processes; (2) the consideration of scale-dependent processes and organisimal characteristics; and (3) the integration of the three habitat factors that may affect heterogeneity: habitat diversity, habitat size, and habitat patchiness.

Much knowledge about these three aspects results from previous models of the relationship between habitat heterogeneity and community characteristics (see above). However, many models of landscape ecology deal with limited subsets of the potential complexity. Most models deal with only one or two heterogeneity factors, but not all three of them (Fahrig, 1992; Doak et al., 1992). The models usually apply a descriptive approach (Holt, 1992) rather than a process approach. They deal with only one community characteristic, usually species diversity (Hastings, 1991), or with one ecological process, such as dispersal (Kareiva, 1982). Finally, they usually deal with a single species (Hanski, 1991) or two-species community (Wu and Levin, 1994) rather than with a more diverse community. In general, the different models might not represent a broad generality. Ecologists sometimes oppose models that do not explore a specific system and, hence, might not be realistic (Levin et al., 1997). However, as noted by Levins (1966), specificity may come at the expense of generality which is required for establishing null hypotheses or predictions.

Interestingly, the extensive study of general ecological large-scale patterns (MacArthur, 1972; Brown, 1995; Rosenzweig, 1995; Polis and Winemiller, 1996) is treated separately from the study of landscape ecology, although they represent two sides of the same coin. Landscape ecology deals with the heterogeneity of a landscape and its affected processes; macroecology deals with general patterns observed at a large spatio-temporal scale and usually speculates on their driving processes. It is our challenge to unify these studies. In addition, if indeed observed patterns of species diversity at large scales result from some higher-level complexity, then we must not reduce ecological complexity when we explore these patterns. We therefore should have the capability to run simulations using multiple ecological processes that may operate in different ways at different scales possessing different heterogeneities.

Here I describe a process-based, multi-species, object-oriented computer simulation model that allows the exploration of the effect of environmental heterogeneity on community structure and species diversity patterns at different scales. The model incorporates different processes that are widely accepted to affect populations and communities at two major scales. The model achieves considerable ecological realism, mainly by using a mechanistic approach and allometrically based functions. I embedded the model in new software called SHALOM (species-habitat arrangement-landscape oriented model). In the following sec-

tion I will describe the design of the model, together with the options given by the software regarding different ecological processes and the landscape structure. I will use the term 'model' both for the theoretical design and for the software.

Our current ecological knowledge, combined with recently suggested modelling approaches and modern computer techniques, challenge us to take a risky but reasonable step toward more comprehensive simulation models that permit better understanding of general large-scale processes and patterns in ecology. I intend SHALOM to be such a step.

3. Model design

3.1. General

An object-oriented design (Booch, 1991; Martin, 1995) was used for my model, designing the different components of ecological structure (e.g. species, habitats) as classes of objects. I coded the model in C++ (Stroustrup, 1995). Object-oriented design may be a useful tool for ecological modelling (Sequeira et al., 1991; Baveco and Lingeman, 1992; Malley and Caswell, 1993; Ferreira, 1995). It allows one to model natural systems realistically because different components of a model can be designed and coded 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. Objects are individual instances of that class that have specific values. The characterization of particular components as whole units that encapsulate both functions and characteristics is similar to the real world. This is the case with population, species, community, cell, habitat and patch being classes of objects in the present model. For example, a species can be programmed as one unit encapsulating its data (e.g. body size) and its functions (e.g. resource consumption) to represent its 'identity'. In addition, the containment option of object-oriented programming allows class objects to contain and use the data and the functions from related objects of a different class that depend on the first class. Containment also helps to create an hierarchical spatial structure: a landscape (the coarse grain of the model) contains patches, and each patch contains cells (the fine grain of the model). Patches vary in area, so populations of the same species in different patches may have different carrying capacities. The built-in definitions of classes and objects make an object-oriented language a tool ready for relatively easy programming of complex relationships (Booch, 1991).

It is important to emphasize that although I found object-oriented design to be powerful for my work, it is a technical and a practical convenience rather than a scientific one. The functions and data structures mentioned in this paper could have been programmed with procedural computer languages as well. Hence, the use of object-oriented design in this model represents my personal speciality and desire to use the available object-oriented approach.

3.2. Realism

The model strives for ecological realism. First, it is process-based. It explicitly defines the processes affecting species, populations and communities. In most cases it goes beyond the simple description of a process to characterize it by its mechanics. For example, a species' body size and its physical/physiological constraints determine its preferred resource(s).

Second, SHALOM relies on empirical ecological findings. It avoids arbitrary functions and arbitrary value assignments. For example, the carrying capacity of a population emerges from comparing the energy consumption of all the populations' individuals (i.e., their metabolic rates) with the energy flow supplied by the patch (i.e. patch productivity).

Third, many of the processes' coefficients depend on body size via allometric equations. Parameters for these equations come from the empirical literature (Peters, 1983; Schmidt-

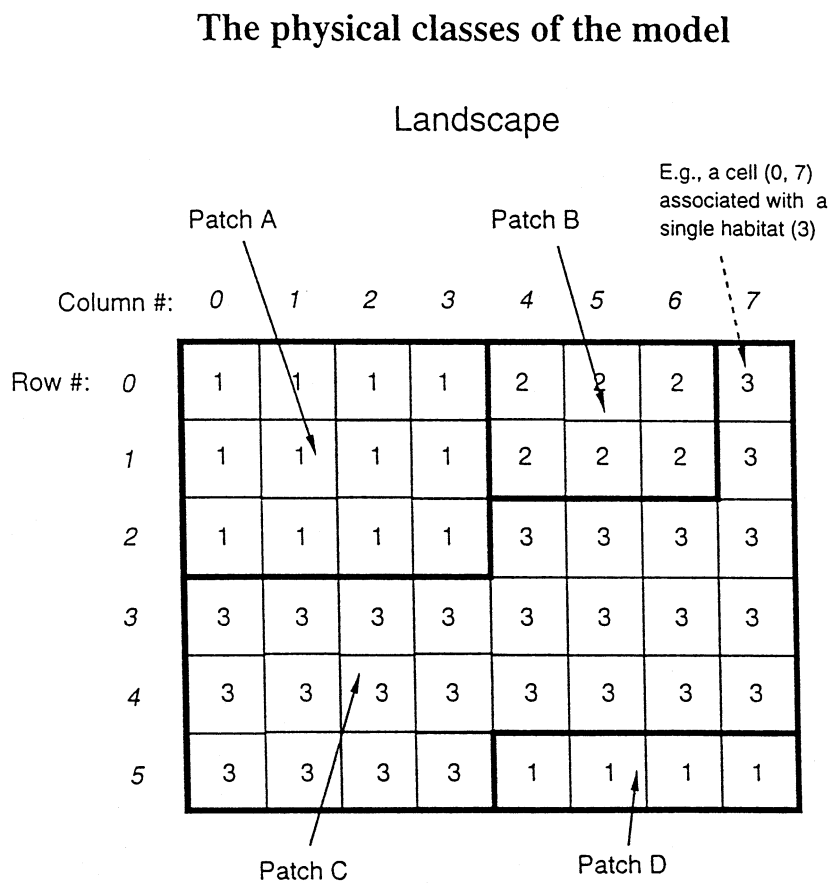

Fig. 1. The physical classes of the model. The small squares in the landscape matrix are cells. Each cell is characterized by a single habitat, given by the number inside each cell. All adjacent cells sharing a similar habitat create a patch (patches in the figure surrounded by a thick line).

Nielsen, 1984; Calder, 1996). For example, the power coefficient of the metabolic-rate function of mammals is ≈ 0.75 (Kleiber, 1961) with $\approx 10\%$ increase for field metabolism (Nagy, 1987). Hence, it is likely that values for many processes of the model are realistic.

Finally, the model permits different values to be entered manually, allowing for user-defined landscapes.

In the following sections, the details of the model's design are provided. First, the model's classes and their characteristics are described. Second, the model's processes, both at the local scale and the landscape scale are described and finally, the model's mechanics and dynamics are described.

3.3. Model's classes and their characteristics

3.3.1. Classes

I defined seven classes, that represent the biological components (population, species, community) and physical components (cell, patch, habitat, landscape) that produce an ecological structure and adopted the current terminology of landscape ecology (Forman and Godron, 1986; Turner, 1989) for the terms used here. Fig. 1 shows graphically the definitions of the physical classes of the model.

A landscape is the entire area under study. It is a row-by-column matrix (or grid) of cells (i.e. a two-dimensional array). For modelling purposes, in an object-oriented design, a landscape is an

abstract class that serves as the system controller (Martin, 1995). It controls the list of patches and cells, and it invokes the landscape-scale process, i.e. dispersal and catastrophic stochasticity (see 'model's processes' below). It is the coarse grain of the model.

A cell is a square (or a raster) in the landscape matrix that serves technically to produce patches. It may allow later for producing patches from a coordinate-based map or a satellite image consisting of a pixel structure used for geographical information systems (Haines-Young et al., 1993). This will permit integrating the model with currently available landscape-oriented representations. Each cell contains a single habitat type.

A habitat is defined as a place relatively homogeneous for physical and biological attributes. All adjacent cells sharing a habitat type create a patch. (The model defines two cells of the same habitat that touch only at corners to be different patches.)

A patch is what organisms see and respond to. Local-scale processes, such as population growth and demographic stochasticity (see 'model's processes' below), take place within each patch's borders. The model assumes that individuals of a species in one patch (hereafter, a population) interact among themselves independently of individuals in adjacent patches. However, potentially rapid across-landscape movement (dispersal) on a continuous time axis of individuals does connect the patches.

A species is the set of individuals in the landscape that share biological and physical characteristics. Individuals of a species may reproduce. However, all breeding occurs within a patch's borders. Hence, a species is a metapopulation.

A community is the set of non-zero populations in a patch.

3.3.2. Characteristics

Each class has its own set of characteristics. Appendix A gives the symbols used in the text and their meaning. Table 1 lists the class characteristics of the model.

- The class 'landscape' is an abstract class (i.e. a class with no objects or instances; Martin, 1995). It serves as a system controller. It controls the cell-object list, the habitat-object list, the patch-object list, and the species-object list. It ensures that the model's functions and their variables behave according to the system's defined processes. Two processes are directly controlled by the landscape: 'catastrophic stochasticity' and 'dispersal' (see below 'model's processes'). 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.
- The class 'cell' may have many objects (hereafter, cells). Its position in the landscape is defined by its 'row' and 'column' numbers. Each cell has an 'area' and a single 'habitat'. The model allows for cells with different areas by explicitly inserting a 'width' and a 'length' for each cell.
- The class 'habitat' may have many objects (hereafter, habitats). It has physical and biological characteristics. The physical characteristics are 'temperature', 'precipitation', and 'substrate'. I assume that temperature and precipitation play an important role in characterizing the physical environment from the point of view of the organisms (Scheiner and Rey-Benayas, 1994). At large scales, the combination of temperature and precipitation distinguishes particular ecosystems and biomes (Holdridge, 1947, 1967; 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). I assume that the temperature and precipitation characteristics can be combined in a bi-uniform distribution to represent a habitat (hereafter, 'habitat space').
- The biological characteristics of a habitat are the list of 'resources' it offers and the 'resource-proportion distribution' of each of these resources. Resources are assumed to be discrete (i.e. resource # 1, resource # 2, etc.). 'Resource-proportion distribution' represents the proportion of each resource in the habitat. For example, if two resources occur equally in a particular habitat, each has a resource-proportion of 0.5.

Table 1
Class characteristics and functions

Type of class	Class	Name	Role	Type	Comments
Physical (abstract class; system controller)	Landscape	Number of rows	Characteristic	Integer	Number of rows × number of columns' gives number of cells in landscape
		Number of columns	Characteristic	Integer	of columns' gives the cells in the landscape
		List of cells	Characteristic	Character array	List of objects
		List of habitats	Characteristic	Character array	List of objects
		List of patches	Characteristic	Character array	List of objects
		List of species	Characteristic	Character array	List of objects
		Catastrophic stochasticity (CS):	Function		(See Table 2)
		CS threshold	Characteristic	Real	Probability of getting hit by CS
		Population loss:			
		Lower limit	Characteristic	Real	Minimum % of population loss
		Upper limit	Characteristic	Real	Maximum % of population loss
		Scale of occurrence:			
		Lower limit	Characteristic	Real	Minimum number of cells
		Upper limit	Characteristic	Real	Maximum number of cells
		Dispersal	Function		(See Table 2)
Physical (Technical)	Cell	Row	Characteristic	Integer	
		Column	Characteristic	Integer	
		Width	Characteristic	Integer	
		Length	Characteristic	Integer	
		Habitat	Characteristic	Character	Contained object
Physical	Habitat	Name	Characteristic	Character	
		Precipitation:			
		mean	Characteristic	Integer	
		Standard deviation	Characteristic	Real	
		Temperature:			
		Mean	Characteristic	Integer	
		Standard deviation	Characteristic	Real	
		Substrate	Characteristic	Integer	
		Productivity	Characteristic	Real	
		Resources	Characteristic	Integer	
		Resource-proportion distribution	Characteristic	Real array	

Table 1 (*Continued*)

Type of class	Class	Name	Role	Type	Comments
Physical	Patch	Name	Characteristic	Character	
		List of cells	Characteristic	Character array	Contained list of objects
		Habitat	Characteristic	Character	Contained object taken from its cells
		Area	Characteristic	Integer	Taken from its list of cells
		Energy supply	Characteristics	Real	
		Resource-proportion energy supply	Characteristic	Real array	Taken from its cells and habitat
		Community	Characteristic	Character	Contained object
Biological	Species	Name	Characteristic	Character	
		Body size	Characteristic	Integer	
		Birth rate	Characteristic	Real	May depend on body-size
		Death rate	Characteristic	Real	May depend on body-size
		Metabolic rate	Characteristic	Real	Depends on body size; Use coefficients a and b
		Coefficient a	Characteristic	Real	
		Coefficient b	Characteristic	Real	
		Niche position:			
		Habitat utilization:			
		Precipitation:			
		Mean	Characteristic	Integer	
		Standard deviation	Characteristic	Real	
		Temperature:			
		Mean	Characteristic	Integer	
		Standard deviation	Characteristic	Real	
		Resource utilization:			
		Resources	Characteristic	Integer	May depend on resource consumption
		Resource-proportion use	Characteristic	Real array	May depend on resource consumption
		Resource consumption:	Function		May depend on body size
		Coefficient a	Characteristic	Real	Coefficients a and b determine the peak resource
		Coefficient b	Characteristic	Real	
		Coefficient c	Characteristic	Real	Coefficient c and d determine the resource proportion use
		Coefficient d	Characteristic	Real	
		Dispersal coefficient	Characteristic	Real	
		List of populations	Characteristic	Character array	Contained list of objects

Table 1 (*Continued*)

Type of class	Class	Name	Role	Type	Comments
Biological	Population	Name	Characteristic	Character	Taken from its species' name and its patch's name
		Species name	Characteristic	Character	The species it belongs to
		Patch name	Characteristic	Character	The patch it occupies
		Intrinsic rate of increase	Characteristic	Real	Taken from its species' birth and death rates and its species-habitat match
		Initial population size	Characteristic	Real	
		Final population size	Characteristic	Real	Output
		Resources	Characteristic	Integer	Taken from its species' resource proportion use and its patch's resource-proportion energy supply
		Resource-proportion use	Characteristic	Real array	Taken from its species' resource proportion use and its patch's resource-proportion energy supply
		Carrying capacity	Characteristic	Real	Taken from its species' birth and death rates its patch's resource-proportion energy supply and its species-habitat match
		Population growth	Function		(See Table 2)
		Species-habitat match	Function		(See Table 2)
		Community-level saturation effect	Function		(See Table 2)
		Demographic stochasticity:	Function		(See Table 2)
		Gamma	Characteristic	Real	

Table 1 (*Continued*)

Type of class	Class	Name	Role	Type	Comments
Biological	Community	Name	Characteristics	Character	Taken from the patch's name
		Patch name	Characteristic	Character	The patch it occupies
		List of populations	Characteristic	Character array	Contained list of objects
		Number of non-zero populations	Characteristic	Integer	Output
		Fisher's alpha for diversity	Characteristic	Real	Output
		Simpson's index for diversity	Characteristic	Real	Output

General comments:
(1) Characteristics derived from other characteristics within a given class are not included; e.g. the species' intrinsic rate of increase is a simple subtraction of the species' death rate from the species' birth rate and therefore is not included in the characteristics list. In contrast, the population's intrinsic rate of increase is calculated from the contained species' intrinsic rate of increase and the species-habitat match, and, hence, is included in the list.
(2) When objects of a class are contained in another class (e.g. 'populations' in 'species'), all characteristics and functions of those objects are known to the containing class. Hence, a given species knows the information of all its population objects.
(3) Some characteristics of different classes are identical to allow for matching between classes (e.g. the precipitation and temperature characteristics of a habitat are matched with the precipitation and temperature characteristics of a species to calculate the species-habitat match of a population which belongs to the species occurring in the patch's habitat).

- The class 'patch' may have many objects (hereafter, 'patches'). Each patch contains a list of cell objects and a habitat object. The patch takes on all its cells' information and its habitat's information. Some of this information produces patch-specific characteristics: 'energy supply' and 'resource-proportion productivity'. Productivity correlates with temperature and precipitation (Rosenzweig, 1968; Lieth and Whittaker, 1975). For simplicity, the model sets productivity as a linear function of the product temperature $(T) \times$ precipitation (P) (i.e. $E_p = aP \cdot T$, where E_p is productivity, and a is the coefficient that translates the product $P \cdot T$, into units of productivity) (Leigh, 1965; Lieth and Whittaker, 1975; Wright et al., 1993). The temperature and precipitation of a patch are set by its habitat type. The area of the patch is the sum of the areas of its cells. Hence, 'energy supply' is the amount of energy per unit of time for the entire area of the patch. '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 set by the patch's habitat, and each resource's share of the total comes from multiplying its proportion in that habitat by the energy supply available in the patch.
- The class 'species' may have many objects (hereafter, species). Each species has 'body size', 'niche position' (defined by habitat and resource utilization axes; see below), and 'dispersal coefficient'. Body size plays an important role in the model. Many variables and functions depend on body-size. 'Birth rate' and 'death rate' can be body-size dependent. For example, for eutherian mammals, birth rate correlates with the power coefficient -0.33 (i.e. $b \propto M^{-0.33}$, where M is body size), and death rate correlates with the power coefficient -0.56 (i.e. $d \propto M^{-0.56}$) (Calder, 1996). 'Metabolic rate' can also be body-size dependent, requiring two coefficients for its allometric power equation (i.e. $E_M = aM^b$, where E_M is metabolic rate of species with body size M, and a and b are coefficients). For example, the field metabolic-rate coefficients, a and b, of mammals are 3.35 and 0.81, respectively (Nagy, 1987). (However, the model allows one to use body-size-independent values for all variables and functions.)
- Habitat utilization and resource utilization usually play important roles in a species' niche position. These utilizations resemble the physical and biological characteristics of a habitat (see above). 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. For simplicity, these two characteristics determine the species' niche. As in class 'habitat', the temperature and precipitation requirements of a species are set by their 'mean' and 'standard deviation'. I assume that the mean represents the value at which a species reproduces best. The standard deviation represents the species' tolerance to values that are different from the mean. A trade-off between maximum performance and tolerance is assumed: the higher the standard deviation, the worse it does at each point in its niche. This trade-off allows for tolerance-intolerance community organization (Colwell and Fuentes, 1975; Rosenzweig, 1991; Wilson and Yoshimura, 1994). Temperature and precipitation are not independent and may not affect organisms directly. Instead, they work through several independent factors correlated with these two (e.g. water availability and evaporation). I assume that each can be represented by a bi-normal distribution according to the 'central limit theorem' (Durrett, 1991). Hence, a species' niche is characterized by a binormal space, shaped by the temperature and precipitation's mean and standard deviation. (To be practical, each characteristic's range was truncated by two standard deviations on each side of the mean. This covers about 90% of the distribution.)
- The lists of 'resources' and 'resource-proportion use' set the resource utilization of a species. As in class 'habitat', resources are distributed discretely. Resources associated

with smaller numbers are smaller or easier to consume than resources were assumed to be associated with larger numbers. A 'resource-consumption function' may determine the list of 'resources' and each 'resource-proportion use'. The 'resource-consumption function' consists of two functions. One determines the preferred resource for the species (hereafter, 'pick-resource utility function'). The other determines its proportional use of resources different from the preferred one (hereafter, 'fundamental-resource utility function'). The use of the terms 'preferred' and 'fundamental' is relevant because a species' population might utilize only a subset of its fundamental resources, without even utilizing its preferred one; this can arise from interspecific pressures (apparent preference; Abramsky et al., 1990).

- The 'pick-resource utility function' requires two species-specific coefficients in an allometric equation (i.e. $R_p(M) = aM^b + 1$, where $R_p(M)$ is the pick resource of species with body size M, a and b are coefficients, and 1 is added to ensure that no resource has a value of 0). The 'pick-resource utility function' relies on two main assumptions. First, it assumes that species with different body sizes require different resources. This is based on a commonly found body size-resource partitioning relationship that may also promote species coexistence (Giller, 1984). Second, it assumes that resource preference changes faster for smaller species than larger ones. This is based on the fact that many biologically-related processes change with body size in an allometric fashion (Peters, 1983; Calder, 1996).
- The 'fundamental-resource utility function' requires two species-specific coefficients and generates an asymmetrical curve. The curve describes the decline in the proportional use of the resources away from the preferred one. A body-size dependent function describes the decline in the proportional use of resources smaller (left-hand side of the curve) than the preferred one (i.e. $R_f(M, i) = e^{-(ci\log(M))}$, where $R_f(M, i)$ is the proportional use of a resource with a position i less than the preferred one for a species with body size M, and coefficient c). Note that because the position of the preferred resource is zero, its proportional use always takes a value of one. A body-size independent function describes the decline in the proportional use of resources larger (right-hand side of the curve) than the preferred one, with the original coefficient c multiplied by another coefficient, d (d > 1), to model a faster decline for the larger resources (i.e., $R_f(i) = e^{-(cdi)}$, where $R_f(i)$ is the proportional use of a resource with a position i larger than the preferred one, and coefficients c and d).
- The 'fundamental-resource utility function' relies on two main assumptions whose roots lie in foraging theory (Stephens and Krebs, 1986). First, it assumes that, when possible, organisms tend to consume those resources that allow them to gain the highest net benefit (assumed here to be positively correlated to resource value) within their actual range of resources (Rosenzweig and Sterner, 1970). Second, it assumes that some physiological/mechanical/energetic constraints limit the ability of an organism to consume resources that are too large, causing a relatively steep reduction in the use of resources as they grow larger.
- As an alternative, the model allows for fixed resources with a fixed resource-proportion use. This avoids the 'resource-consumption function' (with its 'pick-resource utility function' and 'fundamental-resource utility function'). Therefore, a user can decide to assign a fixed 'number of resources', each with a fixed 'resource-proportional use'. Alternatively, a user can fix a 'pick resource' value but use the 'fundamental-resource utility function' to determine the 'resource-proportional use' from the set of coefficients (the above c and d). It allows one to examine how different community types of organization (Rosenzweig, 1991) affect community structure and species diversity.
- Each species has a 'dispersal coefficient'. It determines the intensity of dispersal when and if it is invoked (see below). 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 simulation runs.

A species also has a list of its populations.

- The class 'population' may have many objects (hereafter, populations). 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'). (Hence, Table 1 omits them). 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 inter-specific competitors) is calculated by subtracting the species' death rate from its habitat-specific birth rate. The habitat-specific birth rate is obtained by multiplying the species-habitat match value (see below 'model's processes') 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; Shorrocks and Bingley, 1994). 'Final population size' is the output of a run.
- The list of 'resources' used by a population results from the resources used by its species and the resources available in the patch. For example, if a species can use resources 3, 4, 5, 6, and 7, and a patch offers resources 6, 7, 8, 9, and 10, then the population in that patch uses resources 6 and 7 only. 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. If, in this example, resources 6 and 7 have fundamental proportions 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.
- The 'carrying capacity' of a population is its population size at equilibrium in the absence of stochasticity. The carrying capacity is calculated by solving the local population dynamics (see below, 'model's processes') and finding the population size at which the derivative equals zero.
- A population is affected by four processes: 'population growth'; 'species-habitat match'; 'community-level saturation effect'; and 'demographic stochasticity'.

3.4. Model's processes

Ecological processes were simulated on two scales, local and landscape (global), 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 multi-scale 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. Landscape-scale processes may also have additional costs (e.g. moving costs) compared to local ones. Table 2 describes the different processes of the model.

3.4.1. Local-scale processes

In this section the processes are descibed first, then combined to produce the local population dynamics equation.

3.4.1.1. Process description. Continuous-time population growth (dynamics): I used a differential equation for population growth. Although natural populations rarely grow continuously, differential equations provide practical advantages. First, differential equations tend to smooth nonlinear curves. This, in turn, may allow us to distinguish between population growth and other processes as causes of stepwise dynamic behaviours. Second, differential equations of one dimension do not produce chaotic dynamics (May, 1974; Hassell and May, 1990), difference equations can. In complex models and with stochastic events, chaotic behaviour might cause patterns that are difficult to explain and are sensi-

Table 2
Model's processes

Process	Symbol	Mechanics	General equation
Local:			
Population growth	dN_j/dt	Growing populations on a continuos time	$N_j b_i \{F_{(b)}\} - N_j d_i \cdot \{F_{(d)}\}$
Community-level saturation effect	$f_{(s)}$	The ratio between the energy consumed (metabolic rate) by all populations in a patch and the energy (energy supply) offered by that patch	$\Sigma_{k=1}^{K} \Sigma_{l=1}^{S} \frac{(\mathrm{RPU}_{kl} N_l E_{Mi})}{\mathrm{RPP}_k}$
Species-habitat match	$f_{(m)}$	The match between the species niche space and the patch's habitat space given their precipitation and temperature attributes	$\frac{\int_{X_{hT}-2\mathrm{SD}_{hT}}^{X_{hT}+2\mathrm{SD}_{hT}} \int_{X_{hP}-2\mathrm{SD}_{hP}}^{X_{hP}+2\mathrm{SD}_{hP}} D_1(X_{iT}, \mathrm{SD}_{iT}, X_{sP}, \mathrm{SD}_{sP}, p)}{D_2(\mathrm{SD}_{hT}, \mathrm{SD}_{hP})}$
Demographic stochasticity		Inverse population-size dependent residuals from deterministic birth and death rates	$z_i \pm \frac{\varepsilon(0.5 z_i)}{\gamma N_i}$
Global:			
Dispersal	$f_{(d)}$	The movement of individuals between patches according to an Ideal Free Distribution	$D_i\left[\left(\frac{dN_j}{dt\, N_j}\right) - \left(\frac{dN_1}{dt\, N_1}\right)\right]$
Catastrophic stochasticity		The population-size independent loss of individuals or populations due to random disturbances	Random-number generating procedure that allows for changing the probability, the intensity and the range of the stochastic effects

tive to initial conditions (May, 1974). In these models, reducing additional difficult-to-explain effects is important.

The population growth process handles birth rate and death rate 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. In contrast, the logistic equation ($dN/dt = rN(1-(N/K))$, where r is intrinsic rate of increase, N is population size and K is carrying capacity) does not make this separation. Moreover, the logistic equation might introduce a problem when used with spatial heterogeneity. Multiplying an oversaturated population's value (i.e. $1 - N/K < 0$) by a declining population's value (i.e. $r < 0$) produces a population with a positive growth rate! Thus, landscape ecologists should be careful of using a single fixed value to represent dependent birth and death rates.

To simulate local-scale growth I use:

$$\frac{dN_j}{dt} = N_j b_i \{F_{(b)}\} - N_j d_i \{F_{(d)}\} \quad (1)$$

where N_j is the size of population j, b_i and d_i are the birth and death rate of species i to which population j belongs, and $F_{(b)}$ and $F_{(d)}$ are the grouped processes affecting birth and death separately.

Community-level saturation effect, $f_{(s)}$: The community-level saturation effect is analogous to the carrying-capacity feedback function of the logistic equation. However, the model does not assume an arbitrary value for carrying capacity. Instead, carrying capacity comes from calculating the equilibrium of a population. This happens at full saturation (see below). 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 inter-specific density dependence.

The community-level saturation effect's mechanics build 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. The species-specific energy consumption of a particular population is calculated by multiplying the metabolic rate of the species to which the population belongs by the number of individuals of that population.

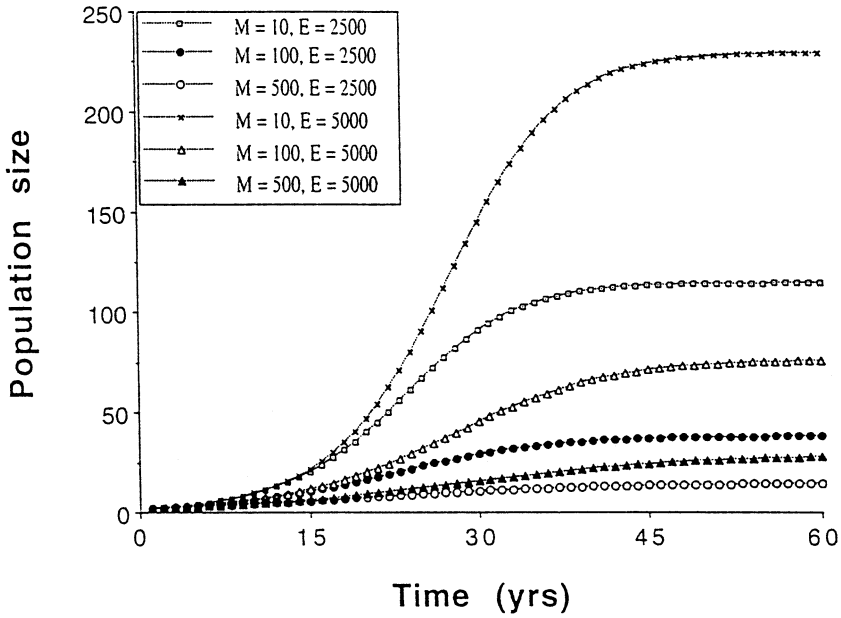

Fig. 2. Logistic growth using the saturation-effect feedback function of six populations that have different body sizes (M) and energy supplies (E).

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 between 0 (i.e. no individuals at all) and any positive value. At carrying capacity, populations use energy for maintenance equal to the energy supplied by the patch.

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

$$f_{(s)j} = \sum_{l=1}^{S} \frac{(\mathrm{RPU}_{kl} N_l E_{Mi})}{\mathrm{RPP}_k} \qquad (2a)$$

where: j is the population for which the effect is calculated; l is a population selected from all S existing populations in a patch; $\mathrm{RPU_{kl}}$ 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; RPP_k is the resource-proportion energy supply of resource k in a patch. Note that because Eq. (2a) describes the community-level saturation effect for one resource, the resource-proportion use of resource k by population l, RPU_{kl}, represents only the use of the single resource by each population relative to the other existing populations in the patch. Likewise, because only one resource exists, the resource-proportion energy supply of resource k in the patch, RPU_{kl}, is the energy supply of that patch.

Of course, 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 (see above). Each resource's energy in a patch is determined by its proportion (resource-proportion energy supply; see above) 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:

$$f_{(s)} = \sum_{k=1}^{K} \sum_{l=1}^{S} \frac{(\mathrm{RPU}_{kl} N_l E_{Mi})}{\mathrm{RPP}_k} \qquad (2b)$$

Fig. 2 shows the density-dependent population dynamics of hypothetical populations using the saturation-effect as a feedback function.

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 bi-normal curve of the species and the temperature-precipitation bi-uniform curve of the habitat (see above). Specifically, the population's niche space, D_1, is given by the following bi-normal distribution equation:

$$D_1 = \frac{e^{(-0.5[1/(1-p^2)((x-X_{iT}/SD_{iT})^2 - 2p(x-X_{iT}/SD_{it})(y-X_{iP}/SD_{iP}) + (y-X_{iP}/SD_{iP})^2])}}{2\pi SD_{iP} SD_{iT}\sqrt{(1-p^2)}} \quad (3)$$

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; X_{iP} is the species' precipitation requirement's standard deviation; p is a covariance between the species temperature and precipitation.

The patch's habitat space, D_2, is given by a bi-uniform distribution equation:

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

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; 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:

$$f_{(m)j} = \frac{\int_{X_{hT}-2SD_{hT}}^{X_{hT}+2SD_{hT}} \int_{X_{hP}-2SD_{hP}}^{X_{hP}+2SDhP} D_1(X_{iT}, SD_{iT}, X_{iP}, SD_{iP}, p)}{D_2(SD_{hT}, SD_{hP})} \quad (5)$$

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. In practice, a population can never achieve a match of 1, because this requires a $SD = 0$ for the habitat's temperature and precipitation characteristics.

I chose the above particular form of calculating species-habitat match because it 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 (Fig. 3b).

Second, the lower the standard deviation of the habitat's precipitation and temperature characteristics, the higher the species-habitat match (Fig. 3a). 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.

Notice that the way the species-habitat match above was calculated so it does not affect the consequences of the expressed species-habitat match in the local population dynamics equation (see below) directly. In other words, the population dynamics equation uses a value for the species-habitat match that can be generated by other functions. 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 does in the available habitats.

Demographic stochasticity: demographic stochasticity means any change in population size caused by a chance event independent of a biological process. It results from sampling errors. It tends to have critical effects when populations sizes are low. For example, the chance of a 2-female population having no females in the next

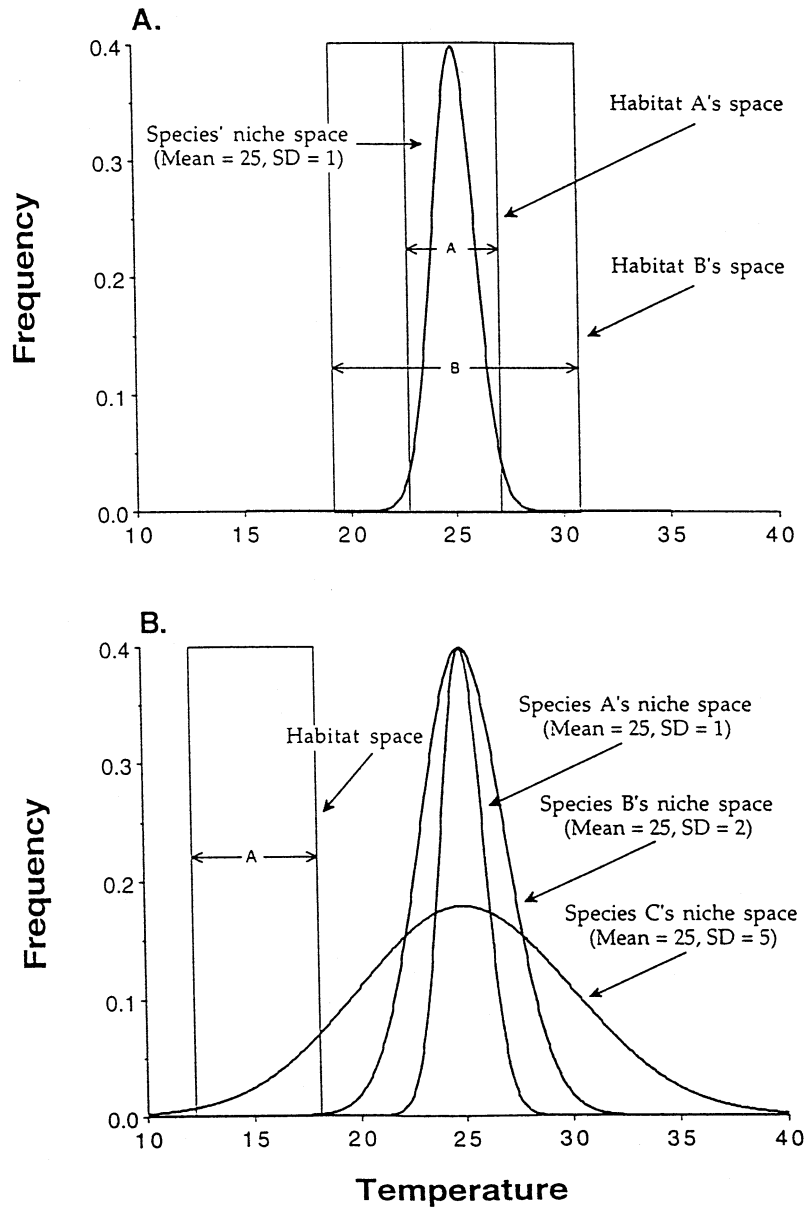

Fig. 3. A one-dimensional representation of the species-habitat match. (Species-habitat match is calculated by dividing the population's niche space nested within the patch's entire habitat space). A species' niche space is shown by a normal curve while a habitat is shown by a uniform curve. (A) The species-habitat match of the population belonging to the shown species in a patch of habitat A is higher than that species' population in patch of habitat B, because, relatively more area of the species' niche space is nested within habitat A. (B) A population of species C, a more tolerant species, has a higher species-habitat match with a patch of a habitat far away from the species mean value.

generation due to the birth of males only (and hence extinction) is higher than in a 10-female population.

I 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; i.e. 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 behaviour does follow the typical expectations of such stochasticity. The equation affects demographic parameters randomly and it is density-dependent (Shaffer, 1981; Shaffer and Samson, 1985; Pimm et al., 1988; Lande, 1993).

At this stage of the model, the demographic stochasticity function merely incorporates stochastic effects at the population level. These may affect species diversity in different habitat heterogeneities, but that does not explain them.

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

$$Z_j = z_i \pm \left(\frac{\varepsilon(0.5 z_i)}{\gamma N_j} \right) \quad (6)$$

where ε is a random number sampled from a Gaussian probability distribution with a mean of 0 and a symmetrical truncation of 2 standard deviations, of one unit each; $(0.5 z_i)$ 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 allowing for changing the 'intensity' of the effect; N_j is population size.

Fig. 4 shows different aspects of the demographic stochasticity function to demonstrate its consistency with the way it is thought to affect populations.

3.4.1.2. Local-scale population dynamics equation. The differential equation by which a given population grows in a patch without the effects of dispersal and catastrophic stochasticity is:

$$\frac{dN_j}{dt} = N_j b_i \{ f_{(m)j} (1 - f_{(s)j})_+ \} - N_j d_i \{ 1 + f_{(s)j} \} \quad (7)$$

where: $f_{(m)j}$ and $f_{(s)j}$ are the species-habitat match effect and the saturation effect, respectively, and $(1 - f_{(s)j})_+$ indicates that the latter term cannot take a value < 0 (Wiegert, 1979).

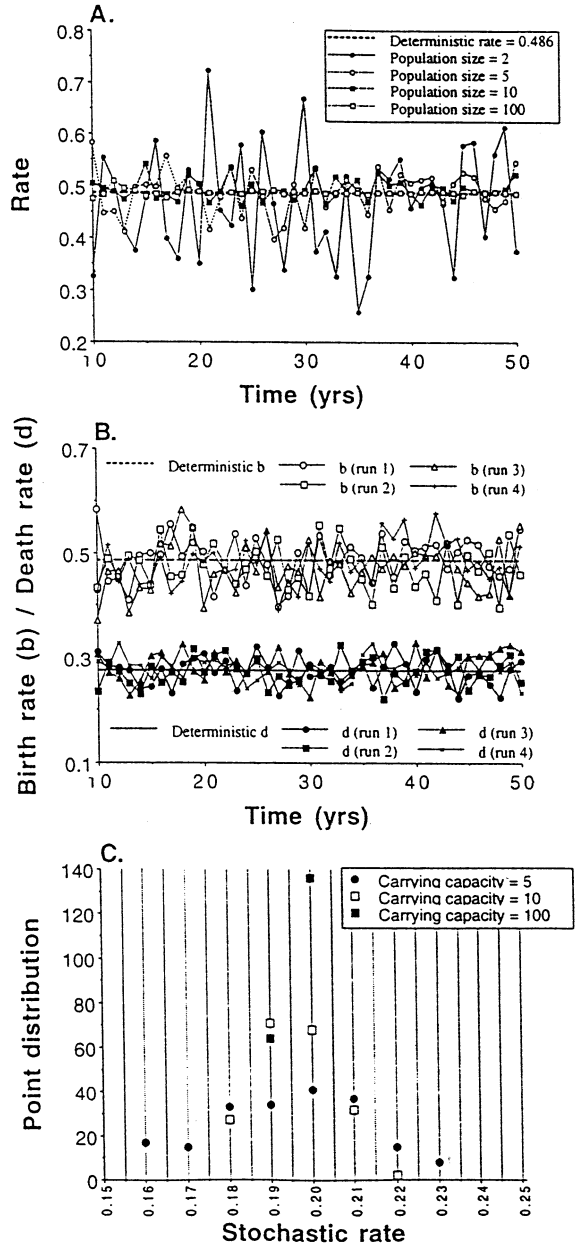

Fig. 4. Different aspects of the demographic stochasticity function. (A) Higher population sizes have lower stochastic residuals from their deterministic rate. Additionally, the higher the population size, the more points are closer to the deterministic, long-term expected rate. (B) Different runs generating stochastic birth and death rates do not co-vary. The range of the stochastic birth and death rates' values is similar for the populations of the same size. The higher the deterministic rate (for example, here, birth rate is higher than death rate), the larger the range of the stochastic values (see text).

The community-level saturation effect ($f_{(s)j}$) enters the equation twice. First, subtract the community-level saturation effect from 1 as in the carrying-capacity feedback function of the logistic equation (i.e. $1-N/K$). The new term models the effect of the community saturation on birth. Assume (as in the logistic equation) that birth decreases linearly with an increase in community density. Oversaturation (i.e. $1-f_{(s)j}<0$) results in no birth. Second, add 1 to the community-level saturation effect to model the effect of the community saturation on death. Here also, assume that death increases linearly with increase in community density. Also assume that the match between the species and the habitat affects fecundity (i.e. birth rate) but not mortality (i.e. death rate). Mathematically, we should get similar qualitative results if a species-habitat match affects mortality at a lower value than it affects fecundity. Hence, the assumption can be broadly summarized by stating that species-habitat match has a higher effect on fecundity than mortality.

In general, because the community-level saturation includes all non-zero populations of a given patch, the above population-dynamics equation is similar to the Lotka-Volterra additive equation (Lotka, 1925; Volterra, 1926). Hence, it makes the assumptions and produces the outcomes known for the latter. One is that species coexistence cannot occur without differences between the populations' resources. Coexistence between populations in a given patch depends on resource partitioning (see above).

The local-scale population dynamics equation with its analytical solution and outcomes for body-size dependent habitat specificity are found in Ziv, 1998.

3.4.2. Global-scale processes

Dispersal (movement, migration; Levin, 1974; Doak et al., 1992; Johnson et al., 1992; Lavorel et al., 1995) and disturbance-induced extinction (hereafter, catastrophic stochasticity; Levin and Paine, 1974; Pickett and White, 1985; Turner et al., 1989; Gilpin, 1990) are two important processes that determine the distribution and abundance of populations and communities at large scales.

3.4.2.1. Process description. Dispersal, $f_{(d)}$: dispersal is the movement of individuals from one patch to another. 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 intra-specific density-dependent habitat selection suggested by Fretwell and Lucas (1969); ideal free distribution). 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 and Lucas, 1969).

Using Eq. (7), we can calculate the per-capita movement of population j, given the difference between its per-capita growth rate and the per-capita growth rate of an adjacent population l, $f_{(d)jl}$:

$$f_{(d)jl}=D_i\left[\left(\frac{\mathrm{d}N_j}{\mathrm{d}tN_j}\right)-\left(\frac{\mathrm{d}N_l}{\mathrm{d}tN_l}\right)\right] \tag{8}$$

where: D_i is the populations' dispersal coefficient. SHALOM invokes the dispersal process between each population and adjacent populations of the same species. It assumes that individuals do not take into account the instantaneous change after a fraction of its population moves to another patch. Hence, within a given time step of the model, dispersal occurs according to the growth rate values at the end of the previous time step. In turn, this prevents any bias due to a particular order of calculating dispersal with adjacent populations.

Dispersal occurs on a continuous-time scale. Hence, dispersal from a given patch to patches that are not adjacent to that patch can happen fast in appropriate conditions (e.g. some patches of low potential fitness and a patch of a very high potential fitness). However, because individuals

need to cross the adjacent patches first, and because each population in the different patches experiences population change due to other processes, there is an implicit distance effect. 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: catastrophic stochasticity, or disturbance-induced extinction, 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 their 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 (Turner et al., 1989).

The catastrophic stochasticity of 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 seeding value of the random number generator;
- the threshold (fraction between 0 and 1) below which catastrophic stochasticity is not invoked;
- the lower and the upper limits (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;
- the spatial distribution (either a random or a fixed distribution on a cell, or patch, or the entire landscape) of the catastrophic stochasticity.

3.4.2.2. Global-scale population dynamics equation. The two global-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 Eq. (7) as $F_{(l)j}$, the overall population growth, including dispersal, is:

$$\frac{dN_j}{dt} = F_{(l)j} + \sum_{l=1}^{AP} (f_{(d)jl} N_{j_{(-)}} / l_{(+)}) \quad (9)$$

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 one.

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.

3.5. Model's mechanics

Fig. 5 describes the relationship between the different classes and the position of the different processes between the different classes according to the way they are modelled. Note the hierarchical structure of the model: the global-scale processes are invoked by the class landscape directly, while the local-scale processes are invoked at the patch-population level.

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, which are what organisms see in the real world. Having patches and species in the landscape, populations

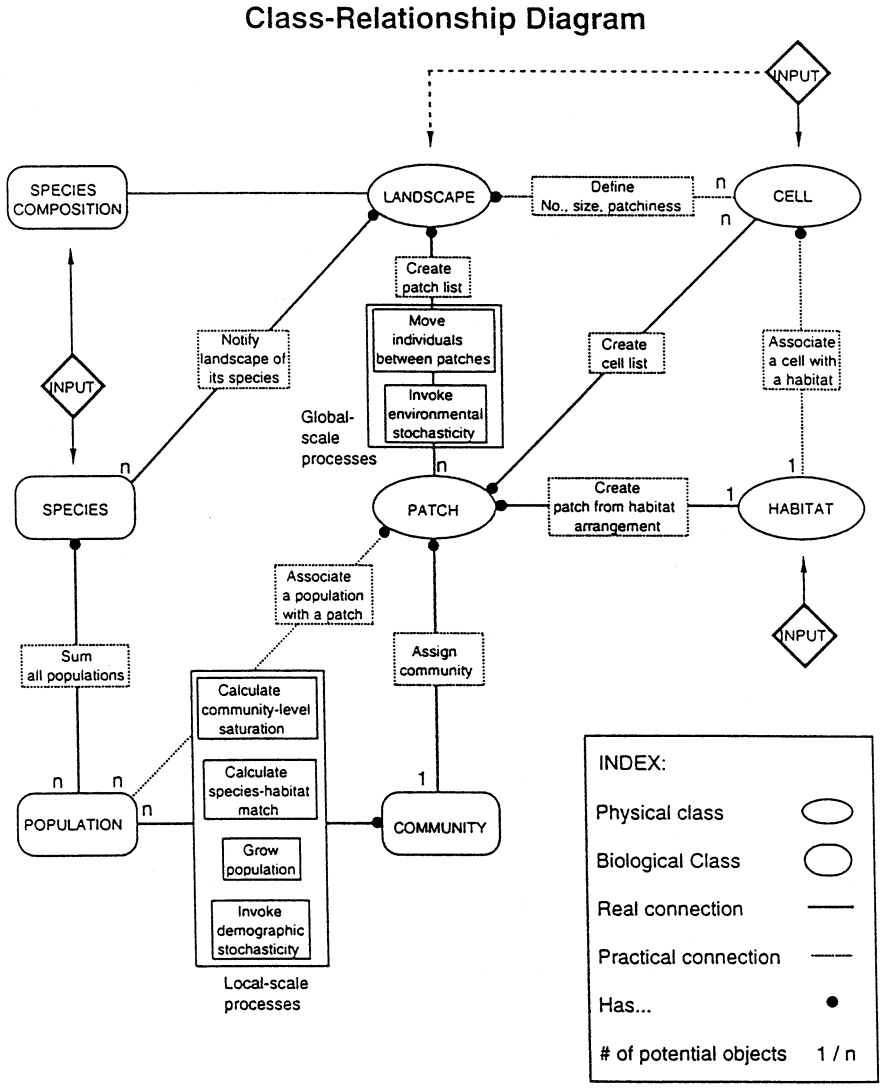

Fig. 5. The class-relationship diagram of the model. Notice that, consistent with the multi-scale design of the model, the global-scale processes are positioned between the landscape and the patch classes, while the local-scale processes are positioned at the population-community level.

are created. The species-habitat match of a population is 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 community-level indices. At this point, patches, communities, and populations are defined, including the local-scale process functions which are nested as function members within the class population.

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 intensity and the range of the

density-independent loss of individuals and populations. 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) integrates the small steps ($dt = 0.001$ year) on a continuous time axis. Without dispersal, at each time step each population grows according to the local-scale processes given by Eq. (7). However, if populations disperse between patches, each population grows according to the local-scale processes and the migration-related movement of individuals given by 10.

The model returns the value of population size for each population in the different patches every 100 time steps (i.e. 0.1 year). 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).

4. Some questions that can be asked of the model

SHALOM allows one to test how the arrangement of habitats in a particular landscape affects different aspects of community structure and species-diversity patterns. For example, a user can model different habitat diversities by including different types of habitats; or a user can model different habitat sizes by changing the number of cells of each habitat; or a user can model different degrees of patchiness by incorporating different habitats in different configurations. In addition, by applying values that do not allow any population to persist in some cells or patches, a user can model different shapes of the landscape, including habitat fragmentation.

SHALOM incorporates different ecological processes at different scales, based on the rationale that observed large-scale patterns are the products of interactive relationships between local and landscape processes. For example, dispersal across patches in the landscape affects population sizes within patches, which, in turn, should affect local density-dependent processes (e.g. community-level saturation effect). However, to enable the user to understand such patterns, SHALOM allows the complexity of the modelled landscape to gradually be increased. The user adds different processes/functions/modules (e.g. species and habitats) one at a time. This represents a major advantage of the current model: landscapes can be studied by comparing predictions of different runs (i.e. simulation results) with and without a particular process. This is especially important when an ecological structure introduces some higher-level complexity: a nested design may allow one to pick up differences that correspond to a particular process.

The incorporation of several aspects of ecological structure in a single model presents another major advantage of SHALOM. It allows one to predict the influence of different large-scale ecological issues with one comprehensive model. For example, several studies deal with dispersal or movement across a landscape (Doak et al., 1992; Lavorel et al., 1995). Others deal with the effect of disturbance on species persistence (Pickett and White, 1985; Turner, 1987). However, SHALOM let us predict the effect of disturbance on dispersal in landscapes of different patterns. Thus, we can study the interactions and relative importance of different processes like dispersal and disturbance.

Additionally, changing dispersal regime and extinction (i.e. catastrophic and demographic stochasticity) may help explore how metapopulation dynamics (Hanski and Gilpin, 1997) affect single-species distributions as well as patterns of species diversity. Reducing the percentage of habitats that can support any population, together with subsequent simulations of changing metapopulation structure, may provide a way to assess the effect of habitat fragmentation and habitat loss on community structure. Therefore, SHALOM may be used as a first-stage policy making tool in conservation.

SHALOM provides a framework for modelling species with different attributes (or identities). For example, we can model species with different body sizes to explore questions regarding body-size related species diversity (e.g. geographical ranges and species abundance) (Lawton, 1991; Gaston, 1996; Hanski and Gyllenberg, 1997). We can also model species with similar body sizes but different resource use and resource range to explore how resource generalist-specialist trade-offs affect community organization (e.g. competitive dominance, tolerance ability, and included niches). An exploration of these questions in landscapes with different habitats may help us understand the competitive advantage of particular species.

The existence of productivity (or energy supply for the entire patch) as a variable that controls the size of populations may allow us to explore how productivity affects different species-diversity patterns (Rosenzweig and Abramsky, 1993). For example, we can model landscapes with similar simulation designs but with an increase of 10% in the productivity of each habitat to detect how increase in productivity affects species richness and evenness. We can reduce productivity in landscapes that are similar to those observed in nature and predict the effects of desertification on communities.

5. Example for the model's contribution

In the following section, examples of community structure and species diversity predictions that the model has produced are given. My example intentionally uses a very simple landscape design (i.e. four cell-habitat configuration). However, as will be shown later, even with such simple design, joint effects of multiple ecological processes (such as those mentioned above) reveal complicated patterns that can be understood only with a modelling approach such as the one used here. This is because the inclusion of additional processes in a particular community structure may result in a completely different outcome.

Start with a simple simulation run and characterize its results. Then add another process and compare the new results with those of the previous one, and so on. By doing so, one can explain not only the single process effect, but, more importantly, its interactive effect with other processes, keeping in mind that natural systems result from multiple-process interactions.

5.1. Simulation design

A landscape was simulated with 2×2 cells, each having its own unique habitat type (total of four habitats). (Note that in this simulation, patch and habitat are synonyms). An area of 250 m^2 was assigned to each cell.

All habitats shared the same mean annual precipitation and temperature: 250 mm and 25°C. Such values represent semi-arid environments, such as the ecotone between the Mediterranean and the desert regions in Israel (Ziv, unpublished data). Having the same mean precipitation and temperature, all patches have the same productivity (see above). Hence, there is no possibility that productivity can indirectly affect the results. However, habitats did differ in their standard deviation of precipitation and temperature. Standard deviations for the precipitation in habitat 1, 2, 3, and 4 were 5, 10, 15, and 20, respectively. Standard deviations for the temperature in habitat 1, 2, 3, and 4 were 0.5, 1.0, 1.5, and 2.0, respectively. Each habitat offered ten different resources to allow for competitive coexistence between the modelled species (see below). For simplicity, all resources had an equal resource-proportion distribution.

A total of ten species were simulated. Species differed in only one characteristic, body size. Body size ranged between 2.29 and 3981 g, corresponding to log values of body size ranging between 0.36 and 3.6. (The smallest is species 1, while the largest is species 10.) Mean and standard deviation values of annual precipitation and temperature requirements for all the species were similar: 250 ± 20 mm and 25 ± 2°C. The lower the standard deviation of a particular habitat, the higher the corresponding species-habitat match, and hence, the better it is for the species (see above). Additionally, the similar assignment of the species' mean precipitation and temperature

values implies that all species enjoy higher fitness in similar habitats (shared-preferences habitat selection; Rosenzweig, 1991). A unique preferred resource was assigned 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 one; each of these had a resource-proportion use of 0.25 (e.g. species 4 is able to consume resources 3, 4, and 5 with a resource-proportion use of 0.25:0.5:0.25, species 5 is able to consume resources 4, 5, and 6 with a resource-proportion use of 0.25:0.5:0.25, and so on). From preliminary simulations it was found that this resource allocation was enough to produce a competitive relationship with resource partitioning, without assuming any complex resource-use function.

I used the allometric coefficients for the birth rate (b), death rate (d), and field metabolic rate (E) of eutherian mammals (i.e. $b \propto M^{-0.33}$, $d \propto M^{-0.56}$, $E \propto M^{0.81}$, where M is body size; Calder, 1996). 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 large-scale body-size dependent patterns that emerge, will result only from the basic rules described here.

The combination of ten species and four patches created 40 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 influence the extinction (catastrophic stochasticity) and the movement (dispersal) of populations across patches.

Demographic stochasticity was modelled with three intensities: low ($\gamma = 1$), moderate ($\gamma = 0.5$), and high ($\gamma = 0.25$). These intensity values were chosen after preliminarily and independently testing different values and exploring how they affected the probability of survival of species. For the present examples regarding the contribution of the model to understanding community structure, it is important to consider these intensities as low, moderate and high.

Fifty simulation runs were run for each simulation design that involved any kind of stochasticity (e.g. interspecific competition with demographic stochasticity) and each simulation run for 10000 years. For each of the simulations, 10000 years. was long enough to achieve either an equilibrial state or a steady state trajectory between the fluctuating points.

In the results, I will report the statistical value that takes into account all 50 simulation runs. However, I will show one pattern emerging from one of the runs that most typically represent the distribution of the results of that design. As mentioned before, the results in this paper are only examples of how community structure and species diversity patterns can be explored by using the current model. They do not represent a complete study of these processes and their complexity.

5.2. Results

5.2.1. Carrying capacities

Without interspecific competition or any other process, all species persisted in the landscape (Fig. 6E). However, the persistence of populations in the different habitats depended on the quality of the habitat (Fig. 6A–D). While populations of all species persisted in habitat 1 (the best habitat; see above), only populations of larger species persisted in the other habitats. The worse the habitat, the fewer populations that could persist. Larger species were more habitat generalist than smaller species (for full mathematical development of the relationship between habitat specificity and body size, and some related large-scale patterns see Ziv, 1998. As expected, population sizes were always higher in the higher-quality habitats.

5.2.2. Interspecific competition

The inclusion of interspecific competition drives some species to extinction, leaving a discontinuous distribution of body size. Even the best habitat, 1, had only six species at equilibrium (Fig. 6F). The species composition in all habitats resulted from the combination of the disappearance of smaller species from lower-quality habitats and competitive exclusion of some species that could persist otherwise (Fig. 6F–I).

In general, larger species had a competitive advantage over smaller species. This outcome was

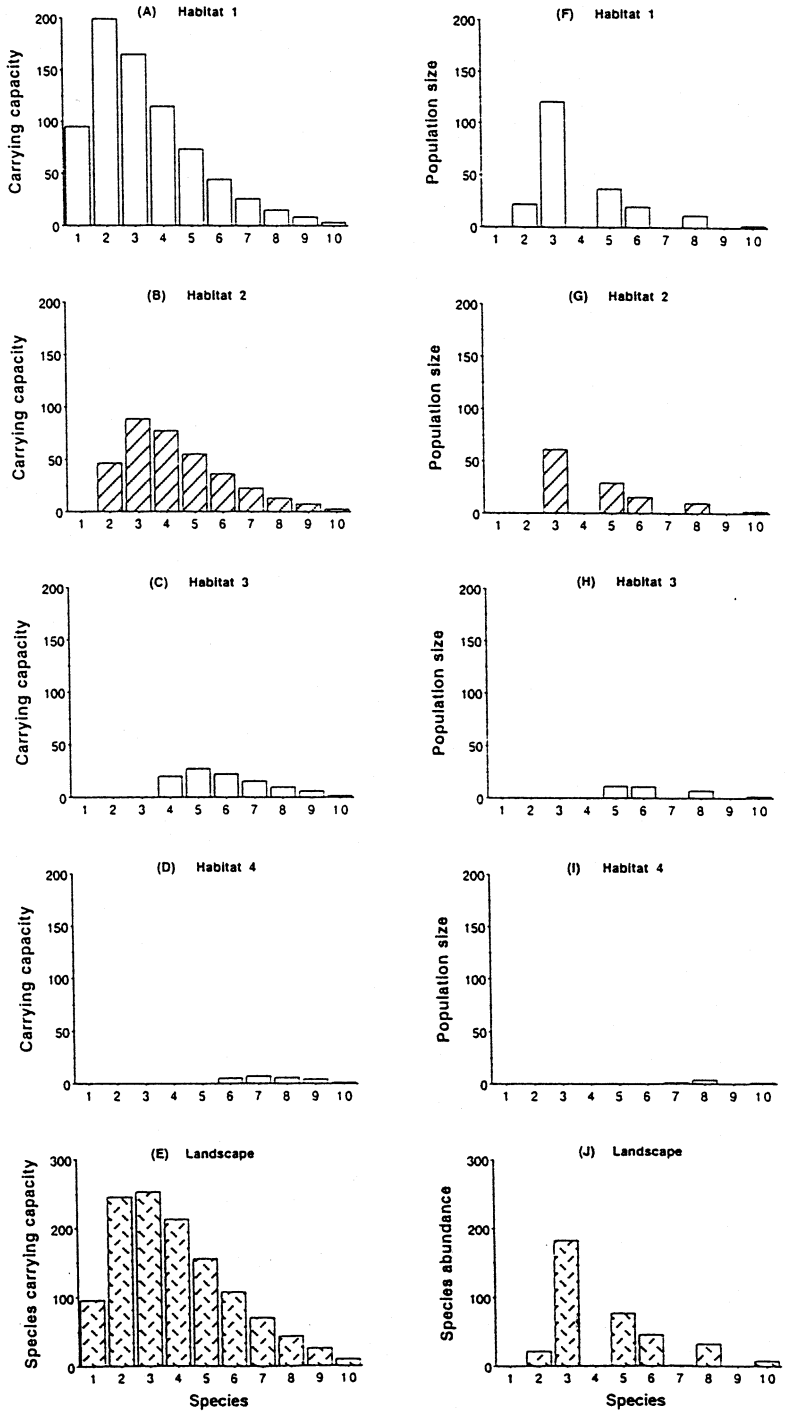

Fig. 6. Carrying capacities (A–E) and population sizes driven by interspecific competition (F–J) of all populations in the four habitats and in entire landscape. Body size increases with species number; the smallest is species 1, while the largest is species 10.

caused by the lower death rates of larger species. Regardless of the specific mechanism, this larger-species competitive advantage was consistent with competitive outcomes observed in many real systems (Kotler and Brown, 1988).

The absence of particular species depended on an 'intra-trophic level cascading effect': Because they had a competitive advantage, the largest species (species 10) depressed the second largest species' (species 9) population size. Although the second largest species had a competitive advantage over the third largest species (species 8), the small effect of the third largest species on the second largest species was enough to depress the former further to local extinction. The third largest species, which did not share resources with the largest one (species shared resources only with the species closest in body size; see above), was saved from the potentially dominating effect of the second largest species because the latter became extinct. The process repeated with species 7, 6, and 5, and so on. Because all interactions between all species were taking place simultaneously, the overall effect on the different species often resulted in an absence of a species of a particular body size in-between two coexisting species, each having close body sizes. Coexistence in this system occurred because the larger could consume its most preferred resource better, as well as having a competitive advantage, while the smaller benefited from the other resource that was no longer used by the species smaller than it that went extinct. Interestingly, the pairwise association of species within a single community observed here is consistent with MacArthur's (MacArthur, 1972) prediction regarding the effect of diffuse competition on a middle species' similarity to one of its competitors.

The joint effect of habitat generality by large species, interspecific dominance by large species, and overall lower population sizes in lower-quality habitats, resulted in another interesting outcome. While species 7 could not persist in habitats 1, 2, and 3, it could persist only in habitat 4, where it was rescued due to the inability of species 6 to persist there. As a result, the entire landscape consisted of 7 species (Fig. 6J), more species than occurred in habitat 1 (the best habitat) alone.

5.2.3. Interspecific competition and demographic stochasticity

With demographic stochasticity, populations of lower densities were more likely to become extinct, but the particular population that ended up extinct was determined randomly. Additionally, the likelihood of a species to become extinct increased with higher demographic stochasticity. However, once these extinctions took place, the community structure in each habitat was determined competitively by those large species' populations that escaped extinction. As a result, the higher the demographic stochasticity, the more dissimilar the community structure in each habitat was compared to the one expected deterministically from interspecific competition alone. Demographic stochasticity affected each species independent of the others. However, because closely body-sized species competed with each other, the extinction of one promoted a higher density of the other, which in turn, made the latter less vulnerable to demographic stochasticity. Hence, demographic stochasticity caused the disappearance of a few populations, but, at the same time, indirectly rescued others ('apparent negative autocorrelation').

On one hand, higher dissimilarity with higher demographic stochasticity potentially allowed for higher overall species diversity. On the other hand, higher demographic stochasticity caused an additional loss of species, potentially decreasing species diversity. Taken together, the overall species diversity in the simulation with interspecific competition and moderate demographic stochasticity (average of 7.28 ± 0.171; Fig. 7J) was higher than with interspecific competition alone (Fig. 6J). This result is consistent with a different set of simulations (Ziv, 1998), where I have shown that the dissimilarity between community structures in different habitats enhanced by demographic stochasticity also increased the overall species diversity in the landscape relative to that of interspecific competition alone.

5.2.4. Interspecific competition, demographic stochasticity and dispersal

With dispersal, species were able to move from one habitat to another. Without demographic

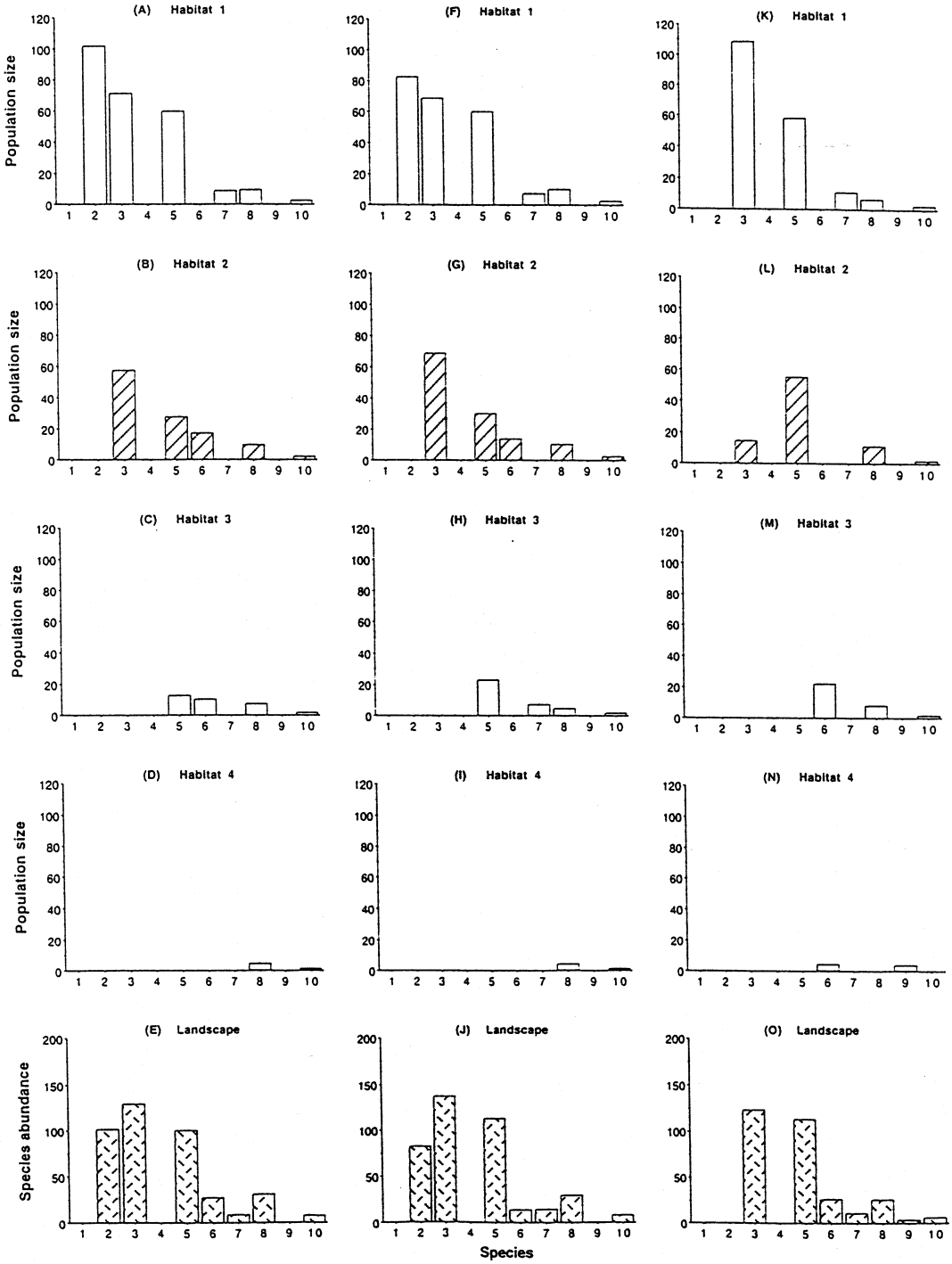

Fig. 7. Typical sizes of all populations in the four habitats and in the entire landscape with interspecific competition and different demographic stochastics (high (A–E), moderate (F–J), and low (K–O)) (see text). Body size increases with species number; the smallest is species 1, while the largest is species 10.

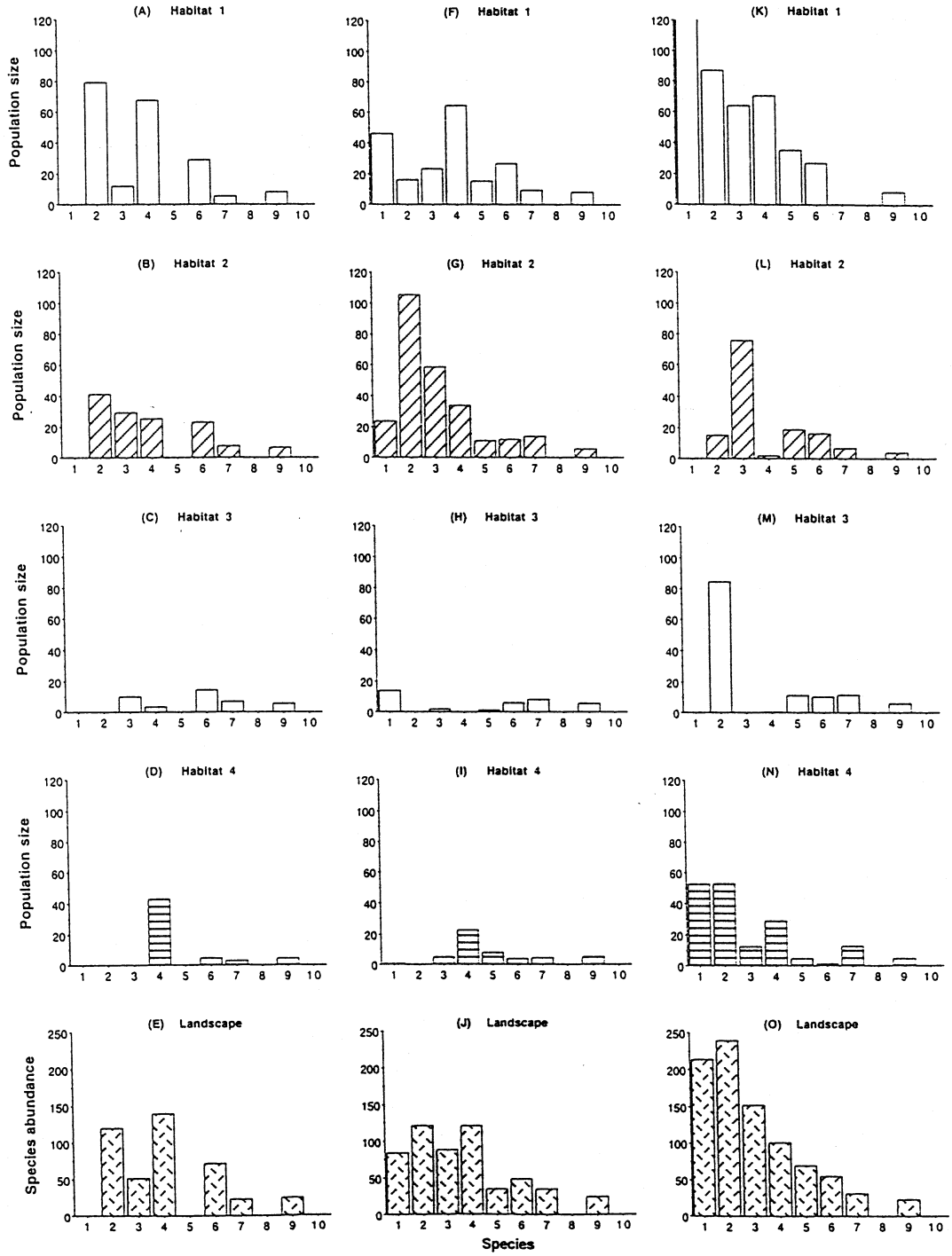

Fig. 8. Typical sizes of all populations in the four habitats and in the entire landscape with interspecific competition, different demographic stochastics (high (A–E), moderate (F–J), and low (K–O)), and dispersal (see text). Body size increases with species number; the smallest is species 1, while the largest is species 10.

stochasticity (or any other stochastic process), dispersal had no real effect, because at equilibrial states populations equalized their per-capita growth rate (= 0), and did not disperse anymore. Hence, dispersal had an effect on species diversity and community structure only in the presence of stochasticity. The most profound joint effect of interspecific competition, demographic stochasticity and dispersal was the occurrence of sink populations of species in some habitats where they would be absent otherwise (e.g. species 3 and 4 in habitat 4; Fig. 8I). The occurrence of sink populations resulted from the dynamic of demographic stochasticity. In some years demographic stochasticity caused a reduced intrinsic rate of increase (birth − death) of a particular population. However, in other years demographic stochasticity promoted a higher intrinsic rate of increase by causing, just by chance, higher birth rate and lower death rate. In those years, that particular population experienced an overshot of population density (i.e. population size that is higher than the one expected without stochasticity). Overshot of one or more populations resulted in oversaturation of that habitat's community. Once oversaturation occurred, populations in that habitat (even the best habitats) experienced negative per-capita growth rate. At this point, individuals moved to other habitats, including those habitats that provided negative per-capita growth rates higher than those negative per-capita growth rates in the oversaturated habitat.

In addition, the joint effect of demographic stochasticity and dispersal was not one directional, but rather depended on the intensity of demographic stochasticity. In general, while demographic stochasticity enhanced variability and dissimilarity between habitat communities due to the random disappearance of different species' populations, dispersal preserved the similarity between those communities by allowing the dominant species to recover their populations.

Low demographic stochasticity was not enough to affect the similarity (or dissimilarity) between community structure in the different habitats. Because dispersal allowed the dominant species to recover their populations after stochastic extinctions, the same dominant species kept pushing the other species toward extinction in all habitats. However, even low demographic stochasticity together with dispersal promoted the occurrence of sink populations.

The highest overall species diversity (average of 7.74 ± 0.07 species; Fig. 8J) was found with moderate demographic stochasticity. In this case, not only more species had sink populations in the lower-quality habitats, but more species were able to coexist in the higher-quality habitats as a result of a competitive release promoted by the demographic stochasticity effect. Similar results were observed for high demographic stochasticity (average of 7.58 ± 0.23 species). However, with the high demographic stochasticity, species diversity in the worse habitat (Fig. 8N) equalized to that of the best habitat (Fig. 8K).

An important result which characterized all the combined interspecific competition, demographic stochasticity (low, moderate, and high) and dispersal simulations was the consistent disappearance of the largest species, 10. As has been mentioned earlier, although the largest species was able to persist in all habitats, its population sizes were always the lowest. Therefore, species 10 was vulnerable to demographic stochasticity (e.g. Figure IC, DS = 0.25). Dispersal tended to move individuals of the largest species to the habitat where that species' population became locally extinct. As a result, after each local extinction of the largest species' population, the other populations of that species became even smaller (because some of their individuals dispersed to the extinct one), making them even more vulnerable to extinction, and so on. After long periods of time, no one population of the largest species survived to globally rescue the species. This large species effect is not coincidental. Elsewhere (Ziv, 1998), I have shown that in a 26-species pool, three large species became globally extinct due to the same joint effect of stochasticity and dispersal.

5.3. Conclusions

The purpose of this part of the paper is to demonstrate the contribution of the current model to our understanding of ecological complexity on large scales. The example given here is not in-

tended to give a full description and exhaustive results on many multi-process effects, but rather to emphasize the importance of understanding interactive effects and their consequences for community structure and species diversity in more realistic communities. Hence, in the following sections I only focus on a few points that could serve to demonstrate the model's potential contribution. A more complete description of results including competition, different stochastic effects, and dispersal is described elsewhere (Ziv, 1998).

Interspecific competition alone revealed a deterministic community structure with uniform body-size discontinuity. The highest species diversity was found in the best habitat, with species existing in the other habitats nested within the set of species found in the best habitat. The inclusion of demographic stochasticity lead to an extinction of low-density populations, shifting the interspecific dominance within each habitat according to the species that became extinct. As a result, a different, but still well-organized community occurred in each habitat ('multi-states communities'). Hence, demographic stochasticity built up dissimilarity in the system. More importantly, in one case (Fig. 7J; Ziv, 1998) demographic stochasticity increased overall species diversity in the system.

Dispersal complicated the interactive effects of the different processes. Sink populations started to be established due to community oversaturation promoted by demographic stochasticity on one hand, and by the populations' ability to move to different habitats with higher per-capita growth rate on the other hand. At the same time, demographic stochasticity allowed some species to recover their populations after extinction and apparently coexist with dominant species in habitats where they could not otherwise do so without dispersal. In contrast, the largest species became globally extinct because dispersal kept reducing its population sizes further by moving to the other habitat after local extinction there. In turn, its populations were even more vulnerable to demographic stochasticity until they went extinct everywhere.

The latter result (i.e. the disappearance of the largest species from the system) may best demonstrate the importance of including more realistic combinations of processes as opposed to treating only one or two processes at a time. Dispersal alone did not have a significant effect, or only recovered some of the populations that went locally extinct (a result not presented here). Indeed, dispersal is usually considered a 'good' process enhancing species diversity. However, the combination of dispersal with demographic stochasticity created a situation where a rare species which is already highly vulnerable to stochastic extinction 'made' itself even more vulnerable to stochastic events by losing some individuals due to dispersal. This finding is not merely theoretical, rather, it has immediate implications to conservation biology. It suggests that under more realistic ecological complexity, in some situations we may not want to open corridors or allow dispersal of a rare species. This is not to say that this should always be recommended, but that we must be alert to joint-process effects that may produce outcomes opposite to what we would have expected had we not taken complexity into account.

6. Concluding remarks

The main goal of this paper has been to describe a new modelling approach to the study of large-scale ecology. This approach incorporates several well-accepted processes, affecting local populations within and across patches, with the option of using realistic parameter values taken from field studies. In addition, this approach uses energy as a common currency to bridge intra and inter-specific effects. To deal with the high-level complexity of ecological systems, the model allows one to simulate each process at a time and then add them together to explore the emergent effects of these processes on species composition and species diversity patterns. In the examples given here, different predictions were obtained from the inclusion of additional processes to the analysis. In some cases, the new predictions countered the proposed predictions of simpler, less realistic landscapes. More importantly, the new predictions could be easily explained by the consequences of the different processes were considered (e.g. the effect of demographic stochasticity on

community structure and its tendency to cause a global extinction of a rare species with dispersal). Elsewhere (Ziv, 1998), it is shown that incorporating catastrophic stochasticity as another stochastic event revealed predictions that differ from those of demographic stochasticity. The knowledge of the effect of each type of stochasticity allowed me to recognize this effect ('signature'; Ziv, 1998) when both were incorporated. The advantage of this approach is that it allows us to explore species diversity patterns under a relatively realistic set of conditions without losing those effects that are relevant only when high-level complexity exists. Hence, the model becomes an important tool to uncover multi-process effects buried under high ecological complexity.

In addition to the multi-process effect, I have been able to show in another paper (Ziv, 1998 MSb) that the model allows one to look for scale effects by comparing species diversity patterns in different habitats with those in the entire landscape. By studying the relationship between geographic range, species abundance and body size, I have shown that the relationship between species abundance and geographic range could be simply explained as a large-scale averaging phenomenon rather than as a product of metapopulation dynamics (e.g. Hanski and Gyllenberg, 1997).

In general, the multi-species, process-based, spatially-explicit simulation model described here may have major importance in exploring the high complexity of macroecological scales. It may provide us with testable predictions that are largely missing when we come to explore large-scale processes and patterns. The real significance of this model will be known after its predictions are tested and further explored with appropriate observations.

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Appendix A. Nomenclature

a	A coefficient (dimensionless, or units depend on the multiplied variables)
AP	Number of adjacent patches (dimensionless)
b	A coefficient (dimensionless, or units depend on the multiplied variables)
b	Birth rate (1/time; e.g. 1/year)
c	A coefficient (dimensionless)
d	A coefficient (dimensionless)
d	Death rate (1/time; e.g. 1/year)
D	Dispersal coefficient (dimensionless)
D_1	A population's species niche space (dimensionless)
D_2	A patch's habitat space (dimensionless)
E_M	Metabolic rate (energy/time; e.g. Kcal/day)
E_p	Productivity (energy/time per area^2; e.g. Kcal/year per m^2)
$f_{(d)}$	Dispersal (dimensionless)
$f_{(m)}$	Species-habitat match (dimensionless)
$f_{(s)}$	Community-level saturation effect (dimensionless)
F	Grouped processes (dimensionless)
h	A habitat type (dimensionless)
i	Position of a particular resource from the pick resource (dimensionless), or, a species (dimensionless)
j	A population (dimensionless)

k	A resource (dimensionless)
K	Carrying capacity (number of individuals); or, number of resources (dimensionless)
l	A population (dimensionless)
M	Body size (mass; e.g. g)
N	Population size (number of individuals)
p	Covariance (dimensionless)
P	Precipitation (volume; mm)
r	Intrinsic rate of increase (1/time; e.g. 1/year)
R_f	Proportional use of a resource (dimensionless)
R_p	Pick (preferred) resource (dimensionless)
RPP	Resource-proportion energy supply (energy/time; e.g. Kcal/year)
RPU	Resource-proportion use (dimensionless)
S	Number of species (dimensionless)
SD	Standard deviation (units depend on the variable it represents)
t	Time (e.g. year)
T	Temperature (°C)
x	A variable representing a value of temperature (°C)
X	Mean (units depend on the variable it represents)
y	A variable representing a value of precipitation (volume; mm)
z	Rate (1/time; e.g. 1/year)
Z	Stochastic rate (1/time; e.g. 1/year)
ε	Random number sampled from a Gaussian probability distribution (dimensionless)
γ	Demographic stochasticity coefficient (dimensionless)

Units are given in parentheses

References

Abramsky, Z., Rosenzweig, M.L., Pinshow, B., Brown, J.S., Kotler, B.P., Mitchell, W.A., 1990. Habitat selection: an experimental field test with two gerbil species. Ecology 71, 2358–2369.

Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S., Soluk, D.A., 1987. Ecological neighbourhoods: scaling environmental patterns. Oikos 49, 340–346.

Baveco, J.M., Lingeman, R., 1992. An object oriented tool for individual-oriented simulation: host-parasitoid system application. Ecol. Model. 61, 267–286.

Begon, M., Harper, J.L., Townsend, C.R., 1986. Ecology: Individuals, Populations and Communities. Sinauer Associates, Sunderland.

Booch, G., 1991. Object-Oriented Design with Applications. Benjamin/Cummings, Redwood City.

Brown, J.H., 1995. Macroecology. The University of Chicago Press, Chicago.

Brown, J.H., Maurer, B.A., 1989. Macroecology: the division of food and space among species on continents. Science 243, 1145–1150.

Calder, W.A. III., 1996. Size, Function, and Life History. Dover, New York.

Collins, S.L., Glenn, S.M., 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72, 654–664.

Colwell, R.K., Fuentes, E.R., 1975. Experimental studies of the niche. Annu. Rev. Ecol. Syst. 6, 281–310.

Danielson, B.J., 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. Am. Natur. 138, 1105–1120.

den Boer, P.J., 1968. Spreading of risk and stabilizing of animal numbers. Acta Biotheor. 18, 165–194.

Doak, D.F., Marino, P.C., Kareiva, P.M., 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conversation. Theor. Popul. Biol. 41, 315–336.

Douglas, M., Lake, P.S., 1994. Species richness of stream stones: an investigation of the mechanisms generating the species-area relationship. Oikos 69, 387–396.

Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–174.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H., Stevens, E.E., 1995. Spatially explicit population models: current forms and future uses. Ecol. Appl. 5, 3–11.

Durrett, R., 1991. Probability: Theory and Examples. Wadsworth and Brooks/Cole, Pacific Grove.

Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. Theor. Popul. Biol. 41, 300–314.

Ferreira, J.G., 1995. ECOWIN-an object-oriented ecological model for aquatic ecosystems. Ecol. Model. 79, 21–34.

Fisher, R.A., Corbet, A.S., Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample from an animal population. J. Anim. Ecol. 12, 42–58.

Forman, R.T.T., 1995. Some general principles of landscape and regional ecology. Landsc. Ecol. 10, 133–142.

Forman, R.T.T., Godron, M., 1986. Landscape Ecology. Wiley, New York.

Fox, B.J., 1983. Mammal species diversity in Australian heathlands: the importance of pyric succession and habitat diversity. In: Kruger, F.J., Mitchell, D.T., Jarvis, J.U.M. (Eds.), Mediterranean-Type Ecosystems: The Role of Nutrients. Springer-Verlag, New York, pp. 473–489.

Fretwell, S.D., Lucas, H.L.J., 1969. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19, 16–36.

Gardner, R.H., O'Neill, R.V., Turner, M.G., Dale, V.H., 1989. Quantifying scale-dependent effects of animal movement with simple percolation model. Landsc. Ecol. 3, 217–228.

Gaston, K.J., 1996. The multiple forms of the interspecific abundance-distribution relationship. Oikos 76, 211–220.

Giller, P.S., 1984. Community Structure and the Niche. Chapman and Hall, London.

Gilpin, M.E., 1990. Extinction of finite metapopulations in correlated environments. In: Sharrocks, B., Swingland, I.R. (Eds.), Living in a Patchy Environment. Oxford University Press, Oxford, pp. 177–186.

Goodman, D., 1987. How do any species persist? Lessons for conservation biology. Conserv. Biol. 1, 59–62.

Haines-Young, R., Green, D.R., Cousins, S.H., 1993. Landscape Ecology and Geographic Information Systems. Taylor and Francis, London.

Hanski, I., 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38, 210–221.

Hanski, I., 1991. Single-species metapopulation dynamics: concepts, models and observations. In: Gilpin, M., Hanski, I. (Eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, San Diego, pp. 17–38.

Hanski, I., 1994. Patch-occupancy dynamics in fragmented landscapes. Tr. Ecol. Evol. 9, 131–135.

Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain. In: Gilpin, M., Hanski, I. (Eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, San Diego, pp. 3–16.

Hanski, I., Gilpin, M.E., 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, San Diego.

Hanski, I., Gyllenberg, M., 1997. Uniting two general patterns in the distribution of species. Science 275, 397–400.

Hanski, I., Kouki, J., Halkka, A., 1993. Three explanations of the positive relationship between distribution and abundance of species. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. Chicago University Press, Chicago, pp. 108–116.

Hansson, L., Fahrig, L., Merriam, G., 1995. Mosaic Landscapes and Ecological Processes. Chapman and Hall, London.

Harrison, S., 1991. Local extinction in metapopulation context: an empirical evaluation. In: Gilpin, M., Hanski, I. (Eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, San Diego, pp. 73–88.

Hassell, M.P., May, R.M., 1990. Population Regulation and Dynamics. Cambridge University Press, Cambridge.

Hastings, A., 1991. Structured models of metapopulation dynamics. Biol. J. Linn. Soc. 42, 57–71.

Holdridge, L.R., 1947. Determination of world plant formations from simple climatic data. Science 105, 367–368.

Holdridge, L.R., 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.

Holling, C.S., 1992. Cross–scale morphology, geometry, and dynamics of ecosystems. Ecol. Monogr. 62, 447–502.

Holt, R.D., 1992. A neglected facet of island biogeography: the role of internal spatial dynamics in area effects. Theor. Popul. Biol. 41, 354–371.

Holt, R.D., 1993. Ecology at the mesoscale: the influence of regional processes on local communities. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. University of Chicago Press, Chicago, pp. 77–88.

Holt, R.D., 1996a. Temporal and spatial aspects of food web structure and dynamics. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, pp. 255–257.

Holt, R.D., 1996b. Food webs in space: an island biogeographic perspective. In: Polis, G.A., Winemiller, K.O. (Eds.), Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York, pp. 313–323.

Johnson, A.R., Wiens, J.A., Milne, B.T., Crist, T.O., 1992. Animal movements and population dynamics in heterogeneous landscapes. Landsc. Ecol. 7, 63–75.

Kareiva, P., 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. Ecol. Monogr. 52, 261–282.

Kleiber, M., 1961. The Fire of Life: An Introduction to Animal Energetics. Wiley, New York.

Kolasa, J., Pickett, S.T.A., 1991. Ecological Heterogeneity. Springer-Verlag, New York.

Kolasa, J., Rollo, C.D., 1991. The heterogeneity of heterogeneity: a glossary. In: Kolasa, J., Pickett, S.T.A. (Eds.), Ecological Heterogeneity. Springer-Verlag, New York, pp. 1–23.

Kotler, B.P., Brown, J.S., 1998. Environmental heterogeneity and the coexistence of desert rodent communities. Ann. Rev. Ecol. Syst. 19, 281–307.

Kotliar, N.B., Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59, 253–260.

Lande, R.L., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nartur. 142, 911–927.

Lavorel, S., Gardner, R.H., O'Neill, R.V., 1995. Dispersal of annual plants in hierarchically structured landscapes. Landsc. Ecol. 10, 277–289.

Lawton, J.H., 1991. Species richness, population abundances, and body sizes in insect communities: tropical versus temperate comparisons. In: Price, P.W., Lewinsohn, T.M., Fernandes, W.G., Benson, W.W. (Eds.), Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions. Wiley, New York, pp. 71–89.

Leigh, E.G., 1981. The average lifetime of a population in a varying environment. J. Theor. Biol. 90, 213–239.
Leigh, E.G., 1965. On the relationship between productivity, biomass diversity and stability of a community. Proc. Natl. Acad. Sci. USA 53, 777–783.
Levin, S.A., 1974. Dispersion and population interactions. Am. Natur. 108, 207–228.
Levin, S.A., 1976. Population dynamic model in heterogeneous environments. Annu. Rev. Ecol. Syst 7, 287–310.
Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.
Levin, S.A., Grenfell, B., Hastings, A., Perelson, A.S., 1997. Mathematical and computational challenges in population biology and ecosystems science. Science 275, 334–343.
Levin, S.A., Paine, R.T., 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. USA 71, 2744–2747.
Levin, S.A., Powell, T., Steele, J.H., 1993. Patch Dynamics. Springer-Verlag, New York.
Levins, R., 1966. The strategy of model building in population biology. Am. Sci 54, 421–431.
Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull. Ent. Soc. Am. 15, 237–240.
Levins, R., 1970. Extinction. In: Gesternhaber, G. (Ed.), Some Mathematical Problems in Biology. American Mathematical Society, Providence, pp. 77–107.
Lieth, H., Whittaker, R.H., 1975. Primary Productivity of the Biosphere. Springer-Verlag, New York.
Loehle, C., Wein, G., 1994. Landscape habitat diversity: a multiscale information theory approach. Ecol. Model. 73, 311–329.
Lotka, A.J., 1925. Elements of Physical Biology. Dover, New York.
MacArthur, R.H., 1972. Geographical Ecology. Harper and Row, New York.
MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.
Malley, C.C., Caswell, H., 1993. Implication *i*-state configuration models for population dynamics: an object-oriented programming approach. Ecol. Model. 68, 75–89.
Martin, R.C., 1995. Designing Object-Oriented C + + Applications Using the Booch Method. Prentice Hall, Englewood Cliffs.
May, R.M., 1974. Biological populations with non-overlapping generations: stable points, stable cycles, and chaos. Science 186, 645–647.
Morris, D.W., 1987. Ecological scale and habitat use. Ecology 68, 362–369.
Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. Ecol. Monogr. 57, 111–128.
Pacala, S.W., Roughgarden, J., 1982. Spatial heterogeneity and interspecific competition. Theor. Popul. Biol. 21, 92–113.
Peters, R.H., 1983. The Ecological Implications of Body Size. Cambridge University Press, Cambridge.
Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269, 331–334.
Pickett, S.T.A, White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.
Pimm, S.L., Jones, H.L., Diamond, J., 1988. On the risk of extinction. Am. Natur. 132, 757–785.
Polis, G.A., Winemiller, K.O., 1996. Food Webs: Integration of Patterns and Dynamics. Chapman and Hall, New York.
Press, W.H., Teukolsky, S.A., Vetterling, W.T., Flannery, B.P., 1995. Numerical Recipes in C, edition 2. Cambridge University Press, Cambridge.
Pulliam, H.R., Dunning, J.B., Liu, J., 1992. Population dynamics in complex landscapes: a case study. Ecol. Appl. 2, 165–177.
Quinn, J.F., Robinson, G.R., 1987. The effects of experimental subdivision of flowering plant diversity in a California annual grassland. J. Ecol. 75, 837–856.
Richter-Dyn, N., Goel, N.S., 1972. On the extinction of a colonizing species. Popul. Biol. 3, 406–433.
Ricklefs, R.E., 1987. Community diversity: relative roles of local and regional processes. Science 235, 167–171.
Robinson, G.R., Holt, R.D., Gaines, M.S., et al., 1992. Diverse and contrasting effects of habitat fragmentation. Science 257, 524–526.
Roese, J.H., Risenhoover, K.L., Folse, L.J., 1991. Habitat heterogeneity and foraging efficiency: an individual-based model. Ecol. Model. 57, 133–143.
Rosenzweig, M.L., 1968. Net primary productivity of terrestrial environments: predictions from climatological data. Am. Natur. 102, 67–84.
Rosenzweig, M.L., 1991. Habitat selection and population interactions: the search for mechanism. Am. Natur. 137, S5–S28.
Rosenzweig, M.L., 1992. Species diversity gradients: we know more and less than we thought. J. Mammal. 73, 715–730.
Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.
Rosenzweig, M.L., Abramsky, Z., 1993. How are diversity and productivity related? In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. University of Chicago Press, Chicago, pp. 52–65.
Rosenzweig, M.L., Sterner, P.W., 1970. Population ecology of desert rodent communities: body size and seed husking as bases for heteromyid coexistence. Ecology 51, 217–224.
Scheiner, S.M., Rey-Benayas, J.M., 1994. Global patterns of plant diversity. Evol. Ecol. 8, 331–347.
Schmidt-Nielsen, K., 1984. Scaling: Why is Animal Size So Important? Cambridge University Press, Cambridge.
Schoener, A., Schoener, T.W., 1981. The dynamics of the species-area relation in marine fouling systems: 1. Biological correlates of changes in the species-area slope. Am. Natur. 118, 339–360.
Sequeira, R.A., Sharpe, P.J.H., Stone, N.D., El-Zik, K.M., Makela, M.E., 1991. Object-oriented simulation: plant growth and discrete organ interactions. Ecol. Model. 58, 55–89.

Shaffer, M.L., 1981. Minimum population sizes for species conservation. BioScience 31, 131–134.

Shaffer, M.L., Samson, F.B., 1985. Population size and extinction: a note on determining critical population sizes. Am. Natur. 125, 144–152.

Shorrocks, B., Bingley, M., 1994. Priority effects and species coexistence: experiments with fungal-breeding Drosophila. J. Anim. Ecol. 63, 799–806.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton.

Stroustrup, B., 1995. The C++ Programming Language, edition 2. Addison Wesley, Reading.

Turner, M.G., 1987. Landscape Heterogeneity and Disturbance. Springer-Verlag, New York.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20, 171–197.

Turner, M.G., Arthaud, G.J., Engstrom, R.T., et al., 1995. Usefulness of spatially explicit population models in land management. Ecol. Appl. 5, 12–16.

Turner, M.G., Gardner, R.H., Dale, V.H., O'Neill, R.V., 1989. Predicting the spread of disturbance across heterogeneous landscapes. Oikos 55, 121–129.

Turner, M.G., Gardner, R.H., 1991. Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York.

Vogel, S., 1994. Life in Moving Fluids: The Physical Biology of Flow, edition 2. Princeton University Press, Princeton.

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118, 558–560.

Whittaker, R.H., Levin, S.A., 1977. The role of mosaic phenomena in natural communities. Theor. Popul. Biol. 12, 117–139.

Wiegert, R.G., 1979. Population models: experimental tools for analysis of ecosystems. In: Horn, D.J., Stairs, G.R., Mitchell, R.D. (Eds.), Analysis of Ecological Systems. Ohio State University Press, Columbus.

Wiens, J.A., 1989. Spatial scales in ecology. Func. Ecol. 3, 385–397.

Wiens, J.A., Stenseth, N.C., Van Horne, B., Ims, R.A., 1993. Ecological mechanisms and landscape ecology. Oikos 66, 369–380.

Wilson, D.S., Yoshimura, J., 1994. On the coexistence of specialists and generalists. Am. Natur. 144, 692–707.

With, K.A., 1994. Using fractal analysis to assess how species perceive landscape structure. Landsc. Ecol. 9, 37–46.

Wright, D.H., Currie, D.J., Maurer, B.A., 1993. Energy supply and patterns of species richness on local and regional scales. In: Ricklefs, R.E., Schluter, D. (Eds.), Species Diversity in Ecological Communities. University of Chicago Press, Chicago, pp. 66–74.

Wu, J., Levin, S.A., 1994. A spatial patch dynamic modelling approach to pattern and process in an annual grassland. Ecol. Monogr. 64, 47–464.

Ziv, Y., 1998. Effects of environmental heterogeneity on species diversity: a new process-based, multi–species, landscape simulation model (SHALOM). Ph.D. dissertation, University of Arizona.