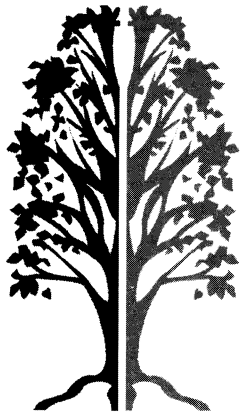

LANDSCAPE DIVERSITY

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GLOSSARY

alpha landscape diversity Number and dominance of patch types within a landscape.
corridor Strip of land or water that differs from the adjacent landscape on both sides.
gamma landscape diversity Total number of patch types contained within a geographic region.
landscape Spatially heterogeneous area composed of a mosaic of interacting components (patches, corridors, and area of matrix).
matrix Background landform, habitat, or ecosystem in a landscape, characterized by extensive area, high connectivity, and major control over landscape dynamics.
patch Area that is relatively homogeneous with respect to the characteristics being examined, and that differs from its surroundings.
region Large geographic area that contains more than one landscape.

LANDSCAPE DIVERSITY IS A DESCRIPTION OF THE NUMBER AND DOMINANCE OF DIFFERENT PATCH TYPES contained within a spatially heterogeneous area. This article describes landscape diversity and its importance, as well as its relationship to species diversity.

I. INTRODUCTION

While biodiversity is usually considered at the species level, maintenance of biodiversity requires management at higher levels of organization, particularly at the landscape scale. It is difficult to manage for each threatened species individually. Alternatively, management can focus on the ecosystems that contain these species, and on the landscapes in which ecosystems are found. The relatively new discipline of landscape ecology provides insight into both landscape diversity and species diversity, and suggests a theoretical and practical basis for conservation planning.

There are three basic characteristics of landscapes that affect their diversity: structure, function, and dynamics. Structure is the most well-understood element of landscapes. It is also the most obvious—nearly any

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aerial view will show a mixture of different landforms, habitats, or vegetation types. The patch is the basic unit of landscape structure. The characteristics of patches and the spatial relationships among patches are important components of landscapes. The distributions of energy, materials, and species among patches differing in size, shape, abundance, and configuration are particularly important to patterns in diversity at the landscape scale. The other two elements of landscapes go beyond a description of spatial heterogeneity. Function is concerned with interactions among the spatial elements of a landscape, including flows of energy, materials, and species among patches. Landscape dynamics includes characteristics of both structure and function in order to examine changes in pattern and process over time. The conservation and management of biodiversity require understanding of all three elements, including the effects of human activities on the system. This article discusses each element in turn, and also considers the underlying determinants of landscape structure, including environmental heterogeneity and disturbance patterns. We then discuss classical and current issues in biodiversity management, and conclude with a case study of landscape diversity at the Sevilleta National Wildlife Refuge Long-Term Ecological Research site in central New Mexico, United States.

It is essential to keep the concept of "scale" in mind when considering landscape diversity. Spatial scale has two elements: grain and extent. Grain is the minimum resolution sampled, usually the cell size or quadrat size for ecological studies. The extent is the domain of the study, which is typically the size of the study area. Ecological processes often have characteristic spatial and temporal scales. This means that the grain and extent of sampling in both space and time may strongly affect the results of a study. For example, as quadrat size (grain) increases, species richness may increase, yet diversity of patch types within a landscape may decrease since fewer large quadrats can be found within a given area (Fig. 1a). As landscape size (extent) increases, more species and more patches of a constant size may be found that would increase both species and landscape diversity (Fig. 1b).

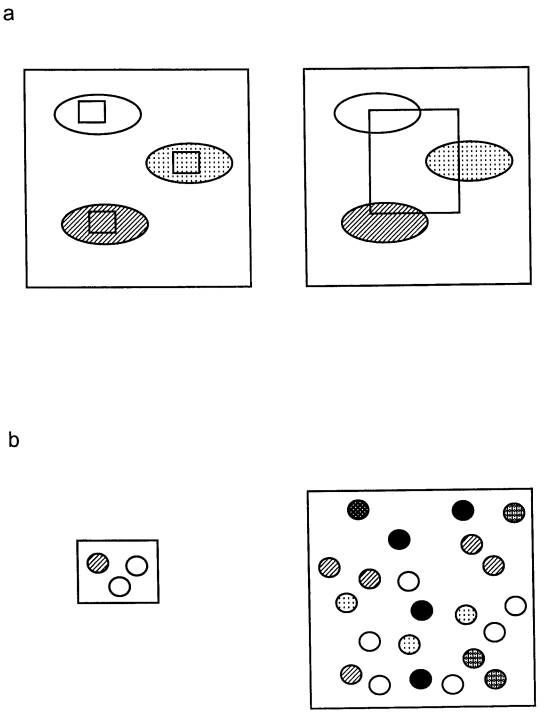

FIGURE 1 Landscape grain and extent: (a) as the grain or quadrat size of a landscape increases, yet the extent remains the same, the diversity of patch types decreases since fewer quadrats can be found in the same area; (b) as landscape extent or size increases, more species and more patch types of the same size can be found that result in higher landscape diversity.

II. DESCRIPTION OF LANDSCAPE STRUCTURE

Landscape structure can be most easily described at two hierarchical spatial levels, both of which are relevant to landscape diversity as well as to species diversity. At the lower level, the focus is on the attributes of individual patches, particularly size and shape. Description at the higher spatial level is concerned with the composition and pattern of the entire landscape and its mosaic of patches. The ability to quantify landscape structure at both levels allows the comparison of different landscapes. More importantly, interactions between landscape structure and function have implications for both species and landscape diversity.

A. Patch Description

A patch is a relatively homogeneous nonlinear area that differs from its surroundings. The definition and identification of individual patches and their boundaries are important steps in characterizing the structure of a landscape. In some systems, boundaries may be easily identified, such as between patches of agricultural field and adjacent woodland in human-dominated systems. In many cases, however, the boundary is not so

clear, and patches are more difficult to delineate. Most methods of patch identification combine qualitative and quantitative approaches. A subjective determination of how different two areas must be in order for them to be considered separate patches is often needed. A number of quantitative techniques have been developed to group similar cells into homogeneous patches or to identify repeating patterns across a landscape (Turner and Gardner, 1990). Approaches such as blocking techniques, spectral analysis, and nearest-neighbor analysis are commonly used. Other techniques rely on the detection of edges or boundaries rather than identifying patches directly. These methods include moving window analysis and image analysis to characterize landscapes with sharp transitions.

Patch identification provides an excellent example of the importance of the spatial scale of the observer. From inside a forest, clumps of trees and grass-dominated openings appear to be separate patches with different vegetation and resource availability. From an aerial view, the entire forest appears to be a single patch. This illustrates the importance of the selection of spatial scale based on study objectives prior to the determination of patches and their edges.

Once the patches in a landscape have been identified, there are many ways to describe and quantify them (Riiters *et al.*, 1995). Only patch size and shape will be discussed here, since the relevance of these two attributes for species diversity is the most well understood. The relationship between patch size and species richness goes beyond the familiar species–area curve (Fig. 2). Although the number of species present in a patch tends to increase with patch size up to a certain limit, the kinds of species found also tend to vary with size. Two general types of species can be distinguished. Interior species are found primarily in the interior of large patches. These species often have very specific habitat requirements and are relatively rare. Migratory songbirds that are particularly sensitive to patch size and adversely affected by habitat fragmentation are interior species. By contrast, edge species are found near the edges of large patches and throughout small patches that consist mostly of edge habitats. Edge species are commonly occurring generalists that can use various habitat types, and are often introduced species. Because small patches consist mostly of edge with little interior area, they often have the highest species densities, but contain few or no rare species. Large patches, on the other hand, are mostly interior area with lower species densities per unit area, but they contain more rare species and a higher total number of species.

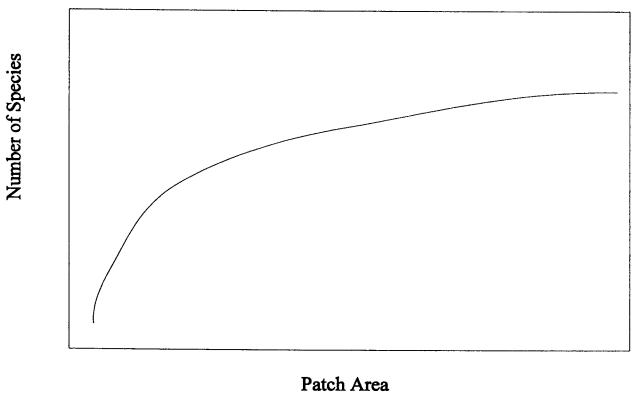

FIGURE 2 Species–area curve showing the increase in species number with increasing patch size tending toward a regional limit.

In an important study of tropical deforestation in the Amazon rain forest, species in patches of various sizes were compared to evaluate the importance of patch size to species number (Lovejoy *et al.*, 1984, 1986). Large patches were richest in species and small patches were found to contain only edge conditions. Patch size had important effects on different species, including trees, insects, birds, and mammals, that were noticeable in a short time. This study is one of the few where patch size was experimentally manipulated to allow comparison with pretreatment conditions as well as control patches.

A simple measure of patch shape is the perimeter : area ratio. This measure is often standardized so that the most compact possible form, either a square or circle, is equal to 1. More complex shapes have increasingly higher numbers. Another common index of shape complexity is the fractal dimension, which is also derived from the perimeter and area of a patch. The fractal dimension of a patch is between 1 and 2; a simple shape will have a lower fractal dimension than a more complex shape. Figure 3 illustrates the amount of interior area available in patches of different shapes. Both patches have an area of 25, but the perimeter of shape a is 20 while the perimeter of shape b is 32. Using a scaled perimeter : area ratio, a has a value of 1 and b has a value of 1.6. Assuming that interior area is at least 1 unit from any patch edge, a has an interior area of 9, but b has an interior area of only 2. Thus, a is more compact and less convoluted than b, where more of the area is closer to its edge and can interact with the area surrounding the patch. This suggests that the overall flow of species and resources between b and its surroundings is higher than that between a and its sur-

roundings. It is also expected that a would have higher richness of interior species than b, which would have higher richness of edge species.

B. Landscape Description

At the landscape level, there are two basic components of structure: composition and pattern. Composition refers to the parts (i.e., patch types) that make up the landscape, and pattern refers to how these patches are arranged. Though these two components are conceptually different, in practice they are often related. For example, the pattern of agricultural fields on a landscape is likely to be different from the pattern of undisturbed woodland.

Landscape composition can be measured in ways analogous to measurements of species composition (Romme, 1982). The most straightforward approach is landscape richness or the number of different patch types in a landscape. Another approach includes the relative abundance or dominance of different patch types along with richness. These landscape indices were derived from information theory and are closely related to species diversity measures, such as the Shannon–Wiener and Simpson indices, which are used to describe alpha species diversity (Turner, 1989; Huston, 1994). Using one of these indices, a landscape containing many small patches of different types would have a higher diversity value than a landscape consisting of one large patch and several smaller patches, even if the total number of patches is the same for both landscapes. Landscape measures of richness and evenness were used in a study conducted in different patch types in Yellowstone National Park (Romme, 1982). Changes in landscape diversity through time were related to fire frequency, and were hypothesized to have important effects on species diversity as well as wildlife habitat (Romme and Knight, 1982).

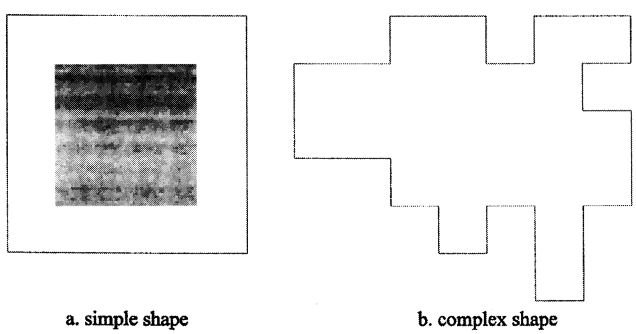

FIGURE 3 A simple shape and a more complex shape of equal area. The interior area is shaded.

Measurements of landscape diversity are analogous to common measurements of species diversity (Whittaker, 1960, 1972). Alpha species diversity is a measurement of species richness (number) and evenness (dominance or distribution) within a patch. Similarly, alpha landscape diversity is a measure of the number of patch types in a region (O'Neill *et al.*, 1988). Large-scale species diversity is called gamma diversity. Gamma landscape diversity of ecosystems is sometimes called ecodiversity (Rowe, 1992; Lapin and Barnes, 1995). The third form of species diversity, beta diversity, describes species turnover along a gradient. Beta diversity has no analog at the landscape level, but is sometimes estimated as gamma diversity/alpha diversity, which gives an average regional beta diversity.

Because different patch types provide different habitats and species compositions, one might expect that the total number of species in a landscape would increase as landscape richness increases. This idea was supported by a study that compared plant species richness in Rhode Island Audubon refuges varying in terrain and soil properties (geomorphological measures) (Nichols *et al.*, 1998). In a related study of one landscape, the diversity of trees and shrubs was higher on plots with the greatest geomorphological heterogeneity, indicating an important connection between landscape diversity and species diversity (Burnett *et al.*, 1998). Although this simple relationship between landscape and species diversity is generally true, the interactions between landscape composition and species diversity are more complex, in part because of species preferences to edge or interior types of habitats. The species found in a diverse landscape with many small patches are mostly edge species. Interior species are found only in landscapes with large patches, even though these landscapes have a lower diversity. The total number of interior species increases with the number of large patches on a landscape, similar to the species–area relationship in Fig. 2. Thus, the type of species that increases with increasing landscape diversity depends on the change in the size and configuration of patches within the landscape.

Landscape pattern, or the spatial arrangement of patches, can be measured in a number of ways, some of which are extensions of the patch-level metrics already discussed. These measures focus on patch abundance without regard to location in the landscape. The distribution of patch sizes can be determined within a landscape and used as information in the management of

habitat patches for species that are sensitive to patch size or spatial arrangement, such as the spotted owl in the Pacific Northwest. The effects of forest clear-cutting on changes in patch structure and implications for interior and edge species provide another example of the importance of these measures. Shape complexities and boundaries can also be scaled up from the patch to the landscape level using the fractal dimension and perimeter : area ratio (Milne, 1988).

The second type of measurement for landscape pattern explicitly considers the location of patches relative to each other and includes patch abundance as well. Dispersion indicates the tendency of patches of one type to be distributed either uniformly, randomly, or aggregated. Contagion describes the tendency of patches of two different types to be near each other. Connectedness can be quantified using nearest-neighbor probabilities that reflect the degree of fragmentation in the landscape. All three of these indices have implications for the flow of species and resources between patches of the same and different types, and thus have important effects on species diversity.

Two additional structural elements other than patches may be recognized in many landscapes. The second element is the matrix or the background landform, habitat, or ecosystem in a landscape. The matrix is characterized by extensive cover, high connectivity, and major control over landscape dynamics. Forest patches contained within a matrix of subdivisions are functionally very different from forest patches surrounded by agricultural land. Corridors, strips that differ from the adjacent landscape on both sides, are the third element of landscapes. Corridors are usually linear and always highly connected; stream networks and roadways are common examples. Corridors may also connect larger patches of a similar type, such as a stream flowing between two lakes.

The patch–matrix–corridor model of landscape structure is illustrated in Fig. 4. Corridors may be particularly important for preserving species diversity by allowing movements of species across diverse landscapes. Corridors can also adversely affect species diversity by allowing nonnative or exotic species to invade and reduce the number of native species in an area. An example is the extensive spread of cheatgrass, an annual introduced to North America in shipments of grain from Asia and Europe in the 1880s (Mack, 1981). Movement of cheatgrass seed along railroad and cattle trail corridors in the early 1900s spread this grass throughout much of the northwestern United States, resulting in changes in species composition and dominance as well as losses of diversity.

III. CONTROLS ON LANDSCAPE DIVERSITY

Heterogeneity or diversity of landscape structure arises from a number of factors. Patches can be produced

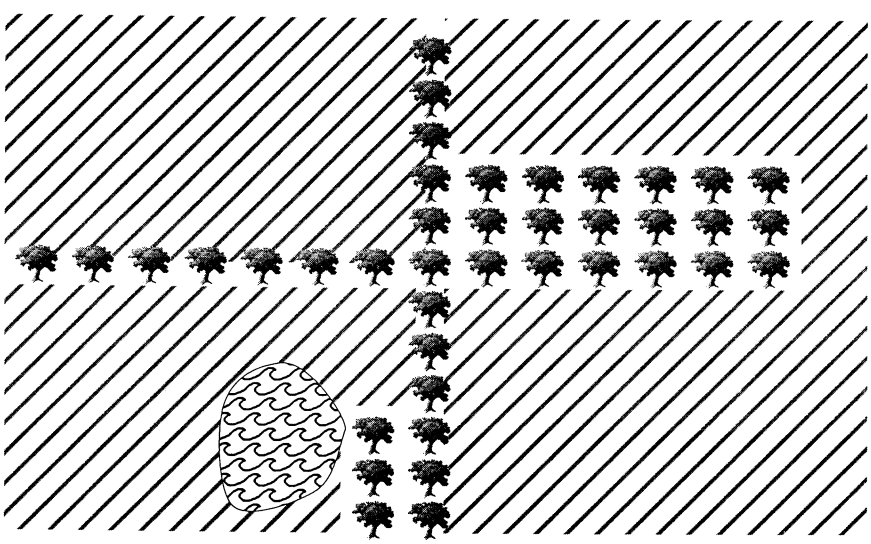

FIGURE 4 A matrix of agricultural land with patches of two types: woodlots and a farm pond. Windbreaks of trees act as corridors connecting the woodlots. Hedgerows and wooded windbreaks often create travel routes for wildlife.

through biotic or abiotic causes, including natural- or human-caused disturbance, fragmentation, regeneration, and persistent differences in environmental resources. Once a patch is formed, environmental conditions or interactions among organisms may change through time, leading to successional dynamics on the patch. A landscape consisting of patches in various successional stages is called a "shifting mosaic" (Bormann and Likens, 1979). The spatial pattern of patch formation and the changes within patches are collectively called "patch dynamics" (Pickett and White, 1985). The patch dynamic mosaic is part of the broader landscape transformation that includes changes in corridors and the matrix, as well as in the dynamics of species and ecosystem processes. These dynamics are discussed in Section V.

Biotic causes of patch generation include the local dispersal of seeds into a landscape, such as by an invasive weed, and the spatial segregation of populations or communities as a result of competition. Spatial structure can also be generated by differences between species in their dispersal abilities and rates of mortality. Naturally occurring and human-created disturbances are common causes of patch formation. A wide variety of natural disturbances are possible, including mud slides, avalanches, windstorms, ice storms, herbivore outbreaks, animal grazing, trampling, and digging, as well as fire. Mounds produced by badger digging activities in tallgrass prairie are an example of patch-producing disturbances that have important influences on patch structure as well as species diversity (Platt, 1975). Human activities, such as forest cutting, altered fire regimes, cultivation, urban development, introduction of pests, and strip mining for surface coal and minerals, also produce disturbance patches. Many landscapes are influenced by both natural- and human-caused disturbances, and distinguishing the separate effects on landscape diversity can be difficult. In a recent study, pollen and charcoal were collected from small lakes in Massachusetts in order to reconstruct long-term vegetation dynamics as related to disturbance history (Fuller *et al.*, 1998). This reconstruction over the past 1000 years included the period of time prior to European settlement when the primary disturbances were fire and wind. Landscape patterns in forest composition following settlement by Europeans were largely influenced by clearing of forests for agricultural purposes and timber. These researchers found that the past history of disturbance as a result of settlement has persistent effects on current landscape patterns.

Landscape fragmentation is closely related to disturbance. Many forms of disturbance effectively break up large patches into smaller pieces. Decreases in patch size, connections between patches, and total interior area as a result of fragmentation have important implications for species and landscape diversity. As landscapes become more fragmented, patch diversity increases with subsequent increases in edge species, exotic species, and generalists. Richness in interior species tends to decrease. Fragmentation of landscapes by human activities is considered a major threat to biodiversity worldwide (Saunders *et al.*, 1991; Bierregaard *et al.*, 1992). A major focus of the field of conservation biology is the design of nature reserves to maximize the likelihood of species existence and to minimize the loss of species to extinction. These processes are discussed in Section VI.

Another cause of patch formation is environmental heterogeneity, which refers to variation in soils, topography, and other landform features. This variation in the physical environmental leads to heterogeneous or patchy spatial distribution of resources, including water, nutrients, and light. Plant species found in a resource patch can differ from species in other patches containing different levels of resources. The importance of spatial heterogenity to species diversity has been well documented, and is most closely related to beta species diversity. The extension of these ideas to landscape diversity has occurred more recently, and several studies have linked measures of alpha and beta species diversity with landscape diversity (Romme, 1982; Lapin and Barnes, 1995). Large-scale gradients in landscape diversity can also be related to broad-scale patterns in the envionment. For example, spatial variation in climate, topography, and soils was found to be strongly related to latitudinal gradients in richness of land cover types across the continental United States (Wickham *et al.*, 1995).

IV. LANDSCAPE FUNCTION

Interactions among the spatial elements of a landscape are the major components of landscape function. These flows of energy, materials, and species among patches, or among patches, corridors, and the surrounding matrix, are at least as important to the maintenance of diversity as patch size and configuration. However, these flows have not been as well studied as landscape structure. An example of flows among different patch types is the dispersal of seeds from forest patches into clear-cuts, which has important effects on vegetation dynamics in these open areas. Boundaries or edges between patches or between patches and the mosaic often

control the strength of interactions or the amount and kinds of materials that can move between the landscape elements. Because of the importance of edges, boundaries of patches can have very different characteristics than interiors. For example, edges of recently disturbed tropical forest patches have greater tree mortality and increased recruitment of early-successional species compared to interior areas (Bierregaard *et al.*, 1992). Boundaries can also change location through time with resulting effects on landscape structure. In contrast to boundaries, where movement is generally restricted, corridors linking similar landscape elements tend to improve or enhance flows. Movements of organisms through corridors become increasingly important as the landscape becomes more fragmented (Saunders and Hobbs, 1991).

There have been several studies of the influences of landscape structure on flows of organisms and materials. Patchy environments in Yellowstone National Park were found to be more resistant to large fires than were homogeneous landscapes, and after burning they had a greater ability to maintain water quality (Knight and Wallace, 1989). Historical migration patterns of wild ungulates, such as wildebeest in the Serengeti of Africa and bison in North America, were mostly related to patterns of rainfall that were spatially variable both locally and regionally (reviewed in Coughenour, 1991). Changes in landscape structure through fencing and urbanization have restricted migration patterns and resulted in animal overabundance and overgrazing in wildlife preserves. Biogeochemical fluxes, such as CO_2 and various forms of nitrogen, can also be affected by patches within a mosaic structure created by human land use. Gene flow and metapopulation dynamics are other examples of processes that respond to spatial structure in a landscape. A population that is spatially subdivided into patches that are connected through dispersal is called a metapopulation. Movement of individuals between subpopulations can reduce the risk of local extinction of species within small isolated patches.

V. LANDSCAPE DYNAMICS

Landscape structure and function can change for many reasons and in many ways. Changes can happen over very small or very large areas, and over short or long time spans. The gap caused by a single tree falling in the forest during a storm is small and temporary, while an entire forest may be leveled by a hurricane and take decades to centuries to recover.

Vulnerability or sensitivity to change varies from landscape to landscape. This vulnerability (or, conversely, stability) is traditionally divided into two components: resistance and resilience. Resistance is the ability of a patch or landscape to remain unaffected by a disturbance. A grassland is much more resistant to wind damage than a forest, since grasses can bend with the wind without breaking. Resilience is the ability of a patch or landscape to recover after a disturbance. Temperate forests recover after clearing much more quickly than tropical forests (which may never recover) owing to differences in soil depth and fertility.

Change in a patch or landscape can be caused by any number of factors. Some of these are intrinsic to the population being studied, including recruitment, growth, mortality, and spread or migration, which can lead to invasions or extinctions as well as changes in patch boundaries. Other causes are extrinsic to the ecosystem and are imposed by outside forces, such as climate change and disturbance events. Human transformations of the landscape include deforestation and reforestation, urbanization, corridor construction, and agricultural conversion. The effects of consumer, pathogens, and especially people can be considered either intrinsic or extrinsic depending on the particular point of view. The potential causes of change may be interrelated in complex ways. A drought may make a forest more vulnerable to pathogens, or a new clearing may increase the vulnerability of adjacent trees to windthrow.

Changes in landscape structure can have several spatial and temporal forms. Patches can shrink or expand, or be lost entirely. Successional dynamics on patches can lead to a shifting mosaic of patch types through time. Species interactions with other species and with their environment, as well as dispersal of new species into patches, are primary determinats of the regrowth of plants on these successional patches. Changes in patch size and shape can occur along edges, such as the clearing of forest to increase the size of a cultivated field (Fig. 5a). A new patch type may spread outward from a corridor (Fig. 5b). For example, housing developments often spread from the course of new roads. Alternatively, a patch type may spread out from a nucleus that could be a remnant of a previous vegetation type, or an introduction site for a new patch type (Fig. 5c). Some changes are nearly instantaneous and occur over very short periods of time, such as the effect of fire. Other changes occur slowly and take a longer period of time to develop, such as suburbanization and desertification.

Patch configuration on a landscape can also change. Patches can become perforated by other patch types,

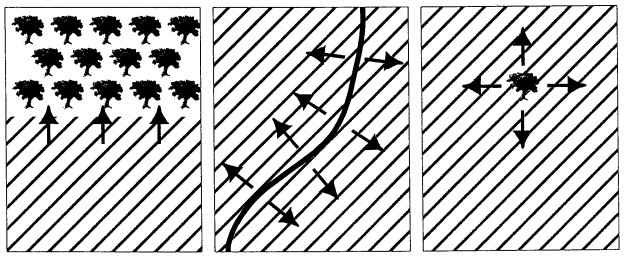

FIGURE 5 Three common patterns of landscape change. Arrows indicate the direction of spread. (a) An edge where agricultural land encroaches on forest along a field boundary. (b) A corridor where development spreads outward from a new road. (c) A point where reforestation proceeds outward from an isolated forest patch.

TABLE I

Transition Matrix for a Hypothetical Landscape with Three Land Use Types[a]

	Forest	Agriculture	Developed
Forest	60	25	15
Agriculture	10	75	15
Developed	0	2	98

[a] Each cell shows the percentage of the landscape area that changed from the patch type in that row to the patch type in that column over a single time step. For example, 25% of the original forest land was cleared for agriculture and 15% was developed. Figure 6 shows this projected change over 25 time steps.

and large patches can be fragmented into several smaller patches. Landscape fragmentation, particularly in the tropics, is having severe effects on species biodiversity. Some of the potential consequences of fragmentation include the loss of patch types and their characteristic species, decreased connectivity with its repercussions for species movements, and decreased interior area. The biggest consequence for species diversity is the associated loss of interior species and the increase of generalist or edge species.

Landscape-level dynamics are often studied with ecological models since the temporal scales of interest are often greater than the human life span, and experiments are difficult to perform at large spatial scales. There are four general classes of models that are used to predict landscape dynamics: transition probability models, individual-based models, ecosystem process models, and biogeographic models. Transition process models are useful when the factors causing landscape change are not represented mechanistically. For example, assume that a landscape with three patch types was sampled twice, before and after an event. A table can be constructed showing the percentage of each patch type that stayed the same or that was transformed into a different patch type in this hypothetical landscape (Table I). Each row shows the fate of a particular patch type. Over a single time step, 60% of the forest land remained forested, 25% was converted to agricultural uses, and 15% was developed. These transition probabilities can be used to extrapolate into the future by individual time steps. Figure 6 shows the projected change over 25 time steps if this original landscape had 50 units of forest, 25 units of agriculture, and 10 units of developed land. This landscape will stabilize with a high proportion of developed land and a very small forest area. Transition analyses are very simple to conduct and can be useful for examining the effects of various probabilities and initial conditions. In the simple form presented here, no allowance was made for variations in the rate of change, and no specific spatial component was included.

Individual-based simulation models are useful when information is known about the mechanisms underlying changes in landscape structure. These models incorporate life-history traits of individuals and the mechanisms by which they interact with their environment in order to predict landscape-level dynamics. Landscapes are simulated by linking plots together in a grid or transect. Plots are spatially interactive through processes such as seed dispersal. Spatially interactive individual-based models can represent a variety of environmental conditions, including differences in soil properties, climate, and disturbance regime (Coffin and Lauenroth, 1994). These models are most commonly used for evaluating changes in the diversity of groups of similar species (i.e., functional types) rather than species diversity.

A third class of models simulates ecological processes, including rates of nutrient cycling, water balance, and primary production. These models have been linked with geographic information systems (GIS) to simulate large regions. Effects of climate, soil texture, and management on soil organic carbon dynamics were simulated for the central grasslands of the United States (Burke *et al.*, 1991). Across this large region, soil organic carbon increased with precipitation and decreased with temperature and percentage sand content. Biogeographic models are a fourth class of models that can be used to investigate vegetation responses to environmental heterogeneity. These models incorporate large-scale variations in climate and soils, as well as water

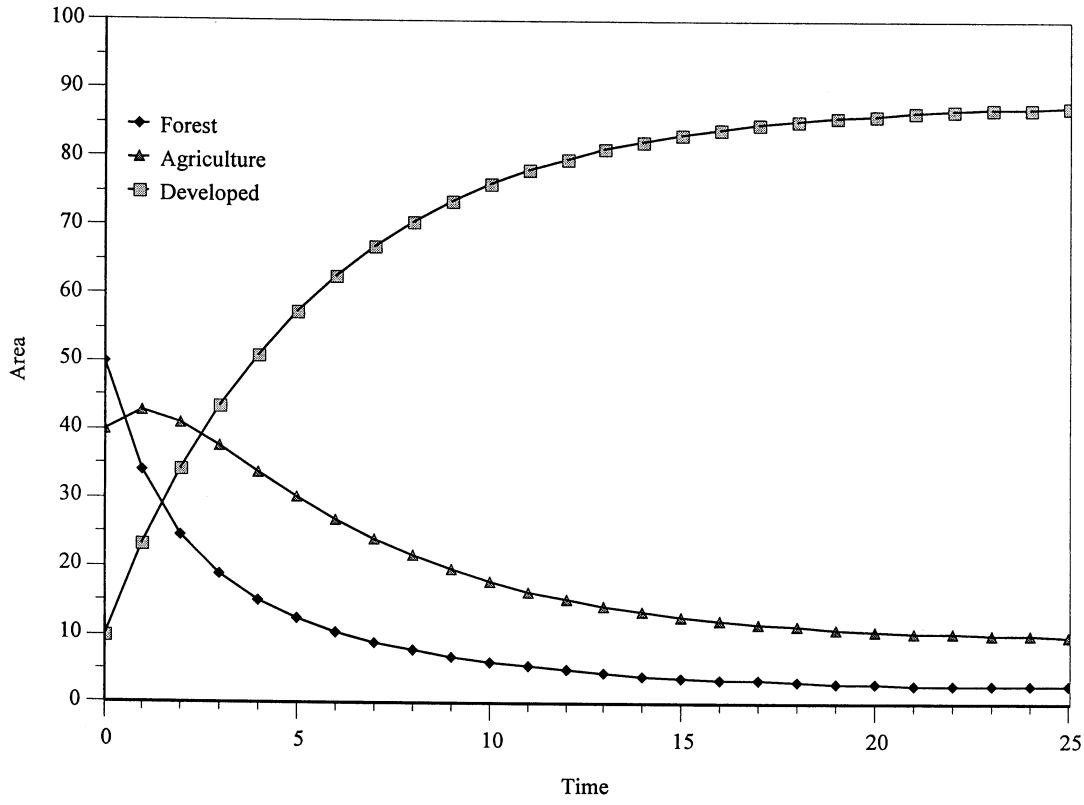

FIGURE 6 Transition matrix analysis of a hypothetical landscape with three patch types of differing abundance: forest, 50 units; agriculture, 25 units; and developed, 10 units. Transition probabilities are shown in Table I.

and energy constraints on plant growth, to simulate continental and global patterns in vegetation. Biogeographic models are most useful for simulating responses of plant functional types at large spatial scales, to either equilibrium or transient environmental conditions (Prentice *et al.*, 1992; Neilson and Drapek, 1998). These models do not explicitly incorporate landscape-scale processes or flows among patches.

Although each of these types of models has traditionally been used independently, the linking of different models together is a recent development that has considerable potential for addressing issues related to landscape diversity. Because of important feedbacks between species and rates of ecosystem processes (Schulze and Mooney, 1994), linking a spatially interactive individual-based model with an ecosystem model has a large potential for simulating the dynamics of landscape structure and function as well as changes in species diversity. An important first step was illustrated by connecting a nonspatial individual-based model with a nutrient cycling model to examine the importance of soil heterogeneity to forest responses to global climate change (Pastor and Post, 1988). The incorporation of landscape-scale flows of water, carbon, and nutrients into a spatially interactive individual-based model is an important research area for predicting landscape diversity dynamics. Recent linkages between biogeochemical and biogeographic models are another area of potential application to landscape diversity, especially if the plant functional types become more resolved and landscape-scale processes, such as disturbance regime, are included.

VI. BIODIVERSITY PLANNING AT THE LANDSCAPE LEVEL

To preserve species diversity most effectively, management plans must preserve the habitats and landscape structures needed by the target species, rather than simply preserving the species in isolation from the larger, potentially changing environment. Management practices aimed directly at a particular species run the risk of losing ecosystem functions that might actually be crucial for the target species, but that were unknown

when the management plan was created. Furthermore, maximizing benefits for one species may threaten others. The ideal is to preserve overall ecosystem health, including species diversity. Unfortunately, this is easier said than done. Much of the effort of conservation biologists has been directed toward learning how to manage ecosystems, at both theoretical and practical levels.

One of the classic debates in conservation biology centers around the "best" reserve design. If limited resources are available to purchase land, is it better to establish one big reserve or a few smaller ones? This has become such a famous and controversial issue that it has its own acronym, SLOSS (single large or several small). A large reserve provides the most potential habitat for interior species, which are usually the ones most in need of protection. However, a single reserve is vulnerable to all sorts of disasters. If a major hurricane or a pathogen hits that reserve, there are no other reserves to take its place. The establishment of several smaller reserves minimizes the risk of losing everything at the same time. However, a minimum size is needed to sustain populations of interior species as well as to preserve the characteristic species diversity and species composition of the ecosystem. Furthermore, reserves do not operate like isolated islands, thus connections between reserves and the surrounding habitats are also important.

A related concept involved in determining the optimum size of a nature reserve is the minimum dynamic area (Pickett and Thompson, 1978). Assuming the disturbance regime of an area is known, the frequency, areal extent, and recovery time can be used to determine the smallest reserve area in which there will always be some mature patch types to provide a species source for the rest of the area as it recovers from disturbance. If a patch is smaller than this minimum dynamic area, it will likely be eliminated through time simply from natural disturbances.

Given the large number of species on the planet, it is impossible, or at best impractical, to manage for every one of them. Instead, conservation biologists are now trying to identify ways to simplify the task of landscape-level management. The most promising methods identify one or a few important species, and concentrate on their management. One tactic is to manage keystone species, those on which important ecosystem functions or other species depend. Another approach is to target umbrella species, those with large ranges or broad habitat requirements. Managing for these species will automatically save many other species with smaller or less inclusive requirments. A similar method identifies a set of focal species, each of which is sensitive to a particular aspect of landscape structure or function. One of the focal species might be especially vulnerable to habitat fragmentation, whereas another might require a high level of connectivity. The protection of this set of sensitive species provides the management goals. When the requirements of the sensitive species are met, other species will be provided for as well.

VII. CASE STUDY: SEVILLETA NATIONAL WILDLIFE REFUGE

The Sevilleta National Wildlife Refuge (SNWR; 34.5°N, 106.9°W), located approximately 75 km south of Albuquerque, New Mexico, provides an excellent example of landscape diversity and its relationship to species diversity. This 100,000-ha wildlife refuge was established in 1973 and is currently managed by the United States Fish and Wildlife Service. The refuge is also a Long-Term Ecological Research site funded by the U.S. National Science Foundation. The climate at the SNWR is semiarid to arid, with low amounts of precipitation and high temperatures during the April to October growing season. Mean annual precipitation over the past 65 years was 23.4 cm. (sd = 70.4 cm) and average annual temperature was 14.1°C (sd = 0.7°C).

The SNWR is uniquely located at the ecotonal boundary between four major grassland–shrubland biomes found within the continental United States. Two of these biomes, shortgrass steppe ecosystems and Chihuahuan desert grasslands, form transition zones in the eastern part of the refuge (Figs. 7a and 7b). Patches of variable size (<10 m^2 to >1000 m^2) and shape occur and result in high landscape diversity (Fig. 7b). These patches can be differentiated into one of two patch types based on the cover of the dominant plant species (Gosz, 1995; Kröel-Dulay *et al.*, 1997). The vegetation of some patches consists mostly of blue grama (*Bouteloua gracilis*), the dominant species in shortgrass steppe ecosystems. A second patch type occurs where the majority of cover is black grama (*Bouteloua eriopoda*), a dominant grass in Chihuahuan desert ecosystems. Species richness is similar for both patch types, although the cover of plants is higher in black grama compared to blue grama patches (Coffin, 1997). A transect across the conceptual landscape shown in Fig. 7b goes through each patch type as well as the matrix vegetation where similar cover of both species occurs (Fig. 7c).

Within each patch, a smaller scale of heterogeneity also exists due to disturbances associated with the burrowing activities of bannertail kangaroo rats (see Fig.

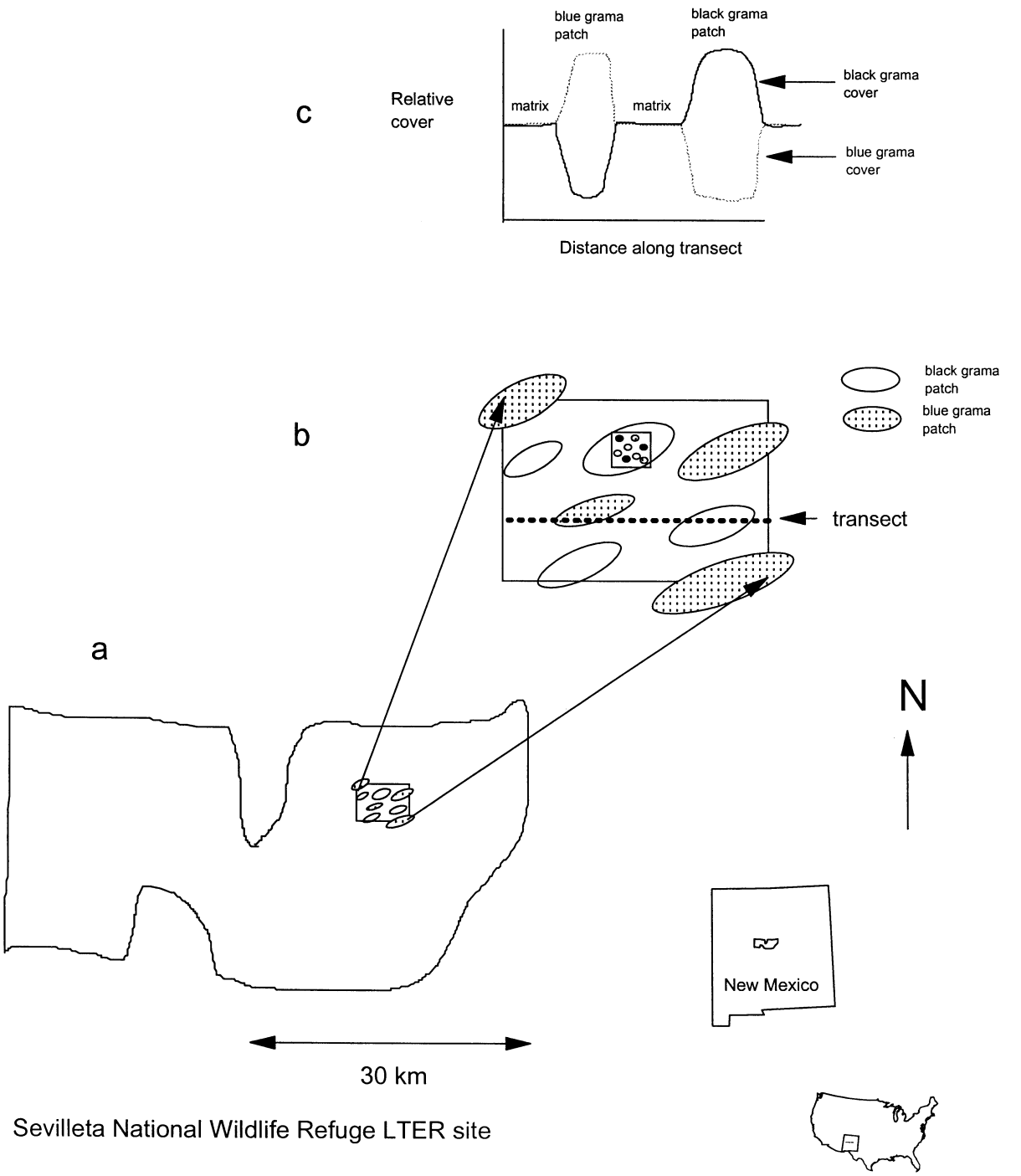

FIGURE 7 Patch types at the Sevilleta National Wildlife Refuge LTER site (SNWR). (a) Location of the SNWR in central New Mexico, United States, and location of patch types in the eastern part of the refuge. (b) Location of two patch types on the landscape. The transect across the landscape goes through patches dominated by either blue grama, black grama, or the matrix containing both species. (c) Cover of blue grama and black grama along the transect, showing one approach to identifying and delineating patches.

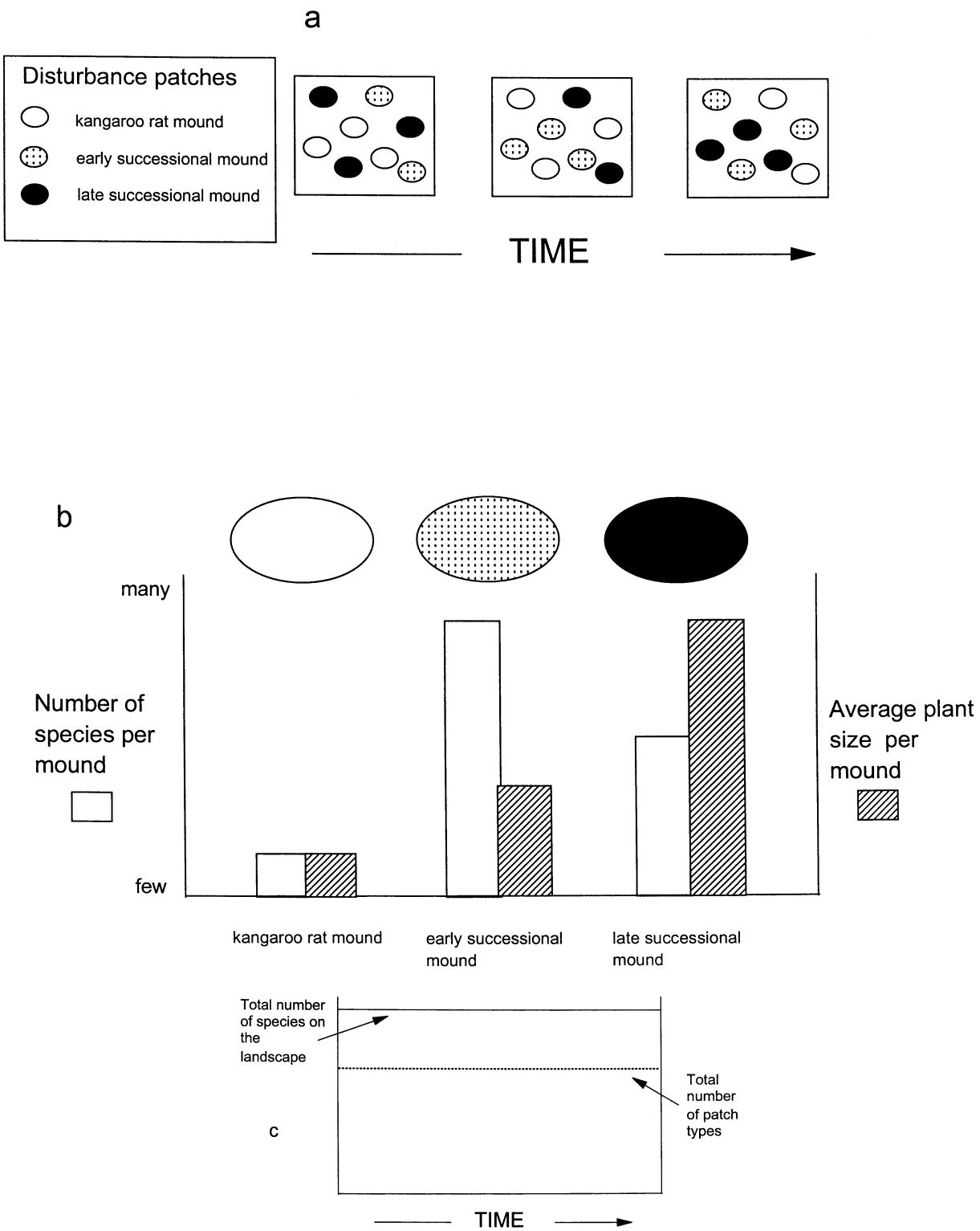

FIGURE 8 Small-scale heterogeneity within one black grama patch from Fig. 7b. Three types of mounds can be defined based on plant species composition and burrowing activities of bannertail kangaroo rats. (a) Mounds change from one type to another through time as kangaroo rats abandon some mounds and invade others. (b) Number of plant species and average plant size for each mound type. (c) Because the number of mounds within each of the three types is constant in this hypothetical landscape, the total number of species found on the landscape is also constant.

7b). Mounds can be distinguished into one of three types based on plant species diversity as well as composition (Fig. 8a). Active mounds are the site of frequent burrowing, thus only plant species well adapted to disturbance can survive there. Typically this vegetation consists of small plants representing few species (Fig. 8b). After mounds are abandoned and burrowing activities cease, more plant species can survive to larger sizes on these early-successional mounds. Through time, competition among plants typically reduces the number of species, although plant sizes can be quite large as one or a few plants come to dominate late-successional mounds. This invasion–abandonment cycle results in a shifting mosaic of mound types through time across the landscape (Fig. 8a). Although the species diversity on mounds changes through time, and the location of mound types varies spatially across the landscape, the total numbers of species and patch types remain constant on the scale of the landscape (Fig. 8c). Therefore, landscape diversity both reflects and determines patterns in diversity at smaller levels of organization, and in particular species diversity.

VIII. CONCLUSIONS

Although much of the current emphasis on biodiversity has been at the level of species, landscape diversity is also important. The preservation and maintenance of multiple levels of organization, including species, populations, communities, and ecosystems, require an understanding of how these various levels interact with their environment across a range of spatial scales. Maintenance of landscape diversity provides a spatial template for the preservation of these smaller levels of organization, and in particular for species biodiversity. Changes in landscape structure and function through time have important effects on the distribution of resources, with resulting influences on the survival of species. Because of the overwhelming numbers of species, it may be impractical to attempt to conserve species diversity per se. By focusing on landscape diversity and the perpetuation of dynamic processes across multiple scales, an attempt can be made to preserve entire ecosystems with their full complement of genetic diversity.

See Also the Following Articles

DEFORESTATION AND LAND CLEARING • DESERTIFICATION • LAND USE ISSUES • KEYSTONE SPECIES • RANGE ECOLOGY • TEMPERATRE GRASSLAND AND SHRUBLAND ECOSYSTEMS

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