

APPLYING SPECIES DIVERSITY THEORY TO LAND MANAGEMENT

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Abstract. Many theories, hypotheses, and empirical studies seek to explain patterns of species richness, turnover, and distribution/abundance (i.e., diversity patterns) at various scales, but it is often not clear how these ideas relate to one another, or how they apply across scales. Consequently, it has been difficult to use diversity theory as a basis for understanding patterns at the intermediate (landscape) scales at which biodiversity is managed. Here, we present a framework for the study and management of diversity based on the ecological processes that influence the distribution of species at different scales. We use this framework to organize diversity theories into several classes based upon how the theories link patterns of habitat occupancy, landscape distribution, and geographic range for a variety of taxa. The processes contributing to diversity patterns depend on the characteristics of the taxa considered, the spatial scales at which organisms respond to environment, and the scales and other characteristics of the particular environments in which investigators hope to explain variation in diversity. At the scales traditionally considered by land managers and conservation biologists, biodiversity is determined by processes addressed by several bodies of theory. Of necessity, management decisions aimed at biodiversity as a whole are based either implicitly or explicitly on only a subset of biodiversity (e.g., single species or functional groups). We suggest that the translation of diversity theory into conservation practice can be achieved, at present, by considering a set of questions for each case: (1) which groups of organisms will be considered, (2) how do their domains of scale relate to the land area under consideration, (3) what processes are likely to be important determinants of species distribution at management scales, and (4) how will the proposed management activities interact with these processes? We illustrate this process using an example from the Chihuahuan Desert. We emphasize the value of considering species diversity theories in a pluralistic and case-specific way.

Key words: Chihuahuan Desert; competition; conservation; dispersal limitation; geographic range; habitat selection; land management; landscape ecology; macroecology; natural resources management; species diversity.

INTRODUCTION

Change in species diversity (the number, identity, and relative abundances of species) across space and time is one of the oldest and best studied subjects in ecology. Despite this, there is little agreement about the underlying causes of many diversity patterns (MacArthur 1972, Rosenzweig 1995, Whittaker et al. 2001). Understanding the causes of diversity involves addressing three fundamental questions: (1) How does diversity arise (Erwin 1991)? (2) How is diversity distributed in space (Flather et al. 1997, Myers et al. 2000)? (3) How is diversity maintained (Lande 1988)? Initially, these questions were largely of academic interest, but growing concerns over the adverse effects of human activities on biodiversity and the services it provides have broadened their scope considerably (Steffen et al. 1992). Promoting species diversity has

become a national and global research and management priority.

Consequently, our understanding of the causes of species diversity has matured in recent years. Although early studies emphasized the preeminent role of competition in determining variation in diversity at local scales, we now recognize that many factors, including competition, dispersal, predation, variation in the physical environment, and historical factors, interact to determine diversity patterns across a range of scales (Rosenzweig 1995). These patterns, in turn, interact. In particular, ecologists are rapidly expanding our understanding of the relationships between local and regional diversity patterns (Cornell and Lawton 1992, Huston 1999). Generally, our current working concept of the causes of diversity emphasizes that regional diversity (i.e., the “species pool”) may be constrained by environmentally governed rates of speciation, migration from adjacent regions, and extinction (Ricklefs and Schluter 1993). This diversity is filtered to varying degrees by a combination of local biotic and abiotic factors (Zobel 1997) to create variation in diversity among

Manuscript received 14 March 2002; revised 24 January 2003; accepted 7 February 2003; final version received 19 March 2003.
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local communities within a region (e.g., varying degrees or levels of community saturation; Wiens 1989a, Cornell and Lawton 1992).

Between the scales of regional species pools and local communities, diversity exhibits patterning that is the focus of a great deal of management activity (Lambeck 1999, Bureau of Land Management 2001, Rogers et al. 2001). Holt (1993:77) referred to this mesoscale as “the gray zone between the local mechanisms that are the traditional concern of community ecologists and the large-scale processes that are the province of biogeographers and systematists.” Within this gray zone (e.g., 1–1000 km²), the relationship between movement and dispersal patterns, extinction and recolonization, and the gradient or mosaic structure of environmental properties mediates how regional variation in the species pool is translated into patterns of diversity in local communities (Caswell and Cohen 1993). Understanding and managing species diversity depends critically on our ability to interpret and manipulate the “filtering” effects of landscape (mesoscale) patterns.

Land-use strategies aimed at biodiversity conservation, in turn, should be based on local, landscape, and regional processes, in addition to social, political, and practical issues. Management actions to promote biodiversity occur at many scales for both biological and policy reasons (Dale et al. 2000). Nonetheless, land-use decisions are often weakly linked to contemporary ideas about species diversity. As it is now organized, species diversity theory seems to be incapable of helping overcome this difficulty (Havstad and Peters 1999, Prendergast et al. 1999).

A key issue complicating the interpretation of species diversity theory is that the processes affecting diversity may operate at different spatial scales for different species, but ecologists tend to view them from a human perspective rather than from the perspective of the organisms being studied (Wiens 1989b). That is, the kinds and scales of environmental variation that managers recognize may differ sharply from those that determine the distribution and abundance of many species they wish to manage. In order to provide a foundation for managing landscapes for the conservation of many kinds of organisms, we need to consider at least some of the details of the species involved (e.g., Lambeck 1997, Lindenmayer et al. 2002) rather than focusing on fixed (and restricted) spatial scales.

Our objective is to examine the relationships among species diversity theories and underscore key insights that may be of use to land managers. To do this, we first argue for the need to adopt a species-centered perspective to understand diversity (He and Legendre 2002), even though this necessarily involves consideration of only a subset of total diversity. Second, we develop a simple framework for relating theories that address various kinds of diversity patterns (e.g., richness, species turnover) at different scales to one another. Specifically, we suggest that managers consider

three fundamental characteristics that determine species distribution at fine to broad scales: habitat occupancy, landscape distribution, and the location of the geographic range. These characteristics define species-specific scale domains (Wiens 1989b) that can be used as a logical basis for an organizing framework. Third, we use the framework as the basis for categorizing diversity theories and recognizing their complementarity. Finally, we show how a consideration of various explanations within the framework can facilitate an understanding of diversity patterns at the spatial scales at which biodiversity is usually managed.

USING SPECIES DISTRIBUTIONS TO UNDERSTAND SPECIES DIVERSITY

As a whole, biodiversity is regulated by a daunting variety of life-history traits and environmental features. Consider the wide range in body sizes of organisms. Body size alone influences many attributes such as energy use, space requirements, and dispersal distances (Brown 1995, Enquist et al. 1998). As a consequence of these and other features, different species view environments through different “windows” of environmental grain and extent, and therefore react to heterogeneity and landscapes in different ways (Wiens 2000).

This means that at the kilometer-wide scales at which humans commonly perceive landscapes, many biological processes and environmental features simultaneously contribute to biodiversity. In a 10-ha study plot, for example, the patchy ground cover that determines dispersal patterns of smaller organisms such as beetles are dealt with by larger organisms such as ungulates in momentary foraging decisions. The selection of a predetermined spatial extent based on human perceptions complicates attempts to relate measured heterogeneity (that which we as investigators recognize and define) to functional heterogeneity (which is defined by responses of the organisms; Kolasa and Rollo 1991). Functional heterogeneity determines species distribution, and measured and functional heterogeneity converge only when investigators use species' responses to define important environmental features and then measure these features at appropriate scales.

Few may disagree with these arguments, but from a practical standpoint, how can we account for functional heterogeneity when managing many species? One common approach is to focus on groups of species that react to similar kinds and scales of heterogeneity, and to identify the sources of that heterogeneity. We do this by breaking biodiversity up into taxonomic, trophic, functional, or body size groups (e.g., MacArthur 1972, Andersen 1995, Hubbell 2001). Ultimately, the accuracy of the picture of biodiversity we create (and manage by) is built on the numbers and kinds of groups we consider.

Even when such approaches are used, we often group species together that differ widely in body size, ecology, and the kinds and scales of environmental vari-

Sites	Species				
	A	B	C	D	E
1	X	X			
2	X	X	X		
3	X		X		
4	X		X	X	
5			X	X	X

FIG. 1. The relationship between species distribution and site diversity showing the distribution of species (A–E) across sites (1–5). Site 4 contains three species.

ation to which they respond (Huston 1999). In such cases we often fail to identify significant sources of heterogeneity in statistical analyses. Ecologists and managers have much to gain from natural history data in grouping sets of species that respond to environmental variation at similar scales, especially with respect to lesser known, but ecologically diverse taxa such as beetles or spiders.

Once we have successfully identified suitable sets of organisms to consider simultaneously, experiments and statistical analyses can reveal similarities in the causes of distribution patterns of component species. We can then begin to understand the causes of diversity patterns because site diversity and species distribution can be viewed as two perspectives of the same phenomenon (Fig. 1). In the strict sense, site diversity is the number of species (or an index describing the relative abundance of species) within a defined area. Orthogonal to this view, species distribution is the presence (or abundance) of species across a series of sites, which together may correspond to a landscape or region. In this sense, understanding variation in species diversity requires that we identify the factors regulating species distributions at various scales (e.g., Colwell and Lees 2000, He and Legendre 2002).

THE FRAMEWORK: RELATING SPECIES-SPECIFIC SCALE DOMAINS TO DIVERSITY THEORIES

Even after we have distilled our view of biodiversity to several groups of species, we still face a great variety of perspectives and scales. Given this variety, how can general theories aid management endeavors? We suggest that a focus on common, scale-independent characteristics of species can be used to draw upon diversity theories to generate scale-specific, management-oriented questions. Specifically, there are three characteristics that determine species distributions across all scales: habitat requirements, dispersal capabilities, and the size and location of the geographic range. The geo-

graphic range is partly a function of habitat and dispersal ability, but is also determined by the time since speciation, historical events, and the geographic location of a species' origin. Thus, it is treated as a distinct characteristic here. Hereafter, we refer to species-defined scales as the habitat, landscape, and geographic domains (sensu Wiens 1989b). Several processes are associated with each characteristic that can be detected at different spatial and temporal scales (Fig. 2; see also Ricklefs and Schluter 1993). The domains and associated processes are the basis of our framework.

The framework examines linkages between three measurable patterns associated with each domain and the realized niche (Hutchinson 1957) to classify theories (Fig. 3). First, the habitat domain represents the finest species-defined scales. Within it, potential habitat occupancy is a consequence of the physiological limitations of a species combined with the effects of competitors, predators, and pathogens (i.e., the realized

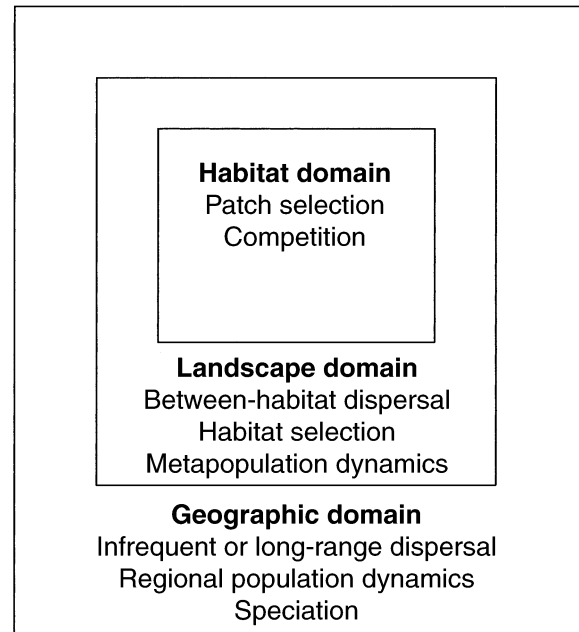


FIG. 2. Hierarchical relationships among three domains of scale, and the processes that distinguish them for a given species. The habitat domain refers to the scale at which a species exploits resources and reproduces (e.g., a microsite or home range). The expression of habitat preferences is based upon the value of patches (e.g., for foraging and nesting) that may be determined by interactions with other organisms. The landscape domain includes the scales at which landscape heterogeneity may be perceived by species, including both the habitats that a species prefers and less suitable habitat types. Both natal dispersal and relocation of the home range occur within this domain and may contribute to source-sink or metapopulation dynamics. The geographic domain refers to the extent and location of the distribution of a species. Infrequent, long-range dispersal and the geographic context of speciation events ultimately determine the location of the geographic range and thus the potential for range expansion or contraction.

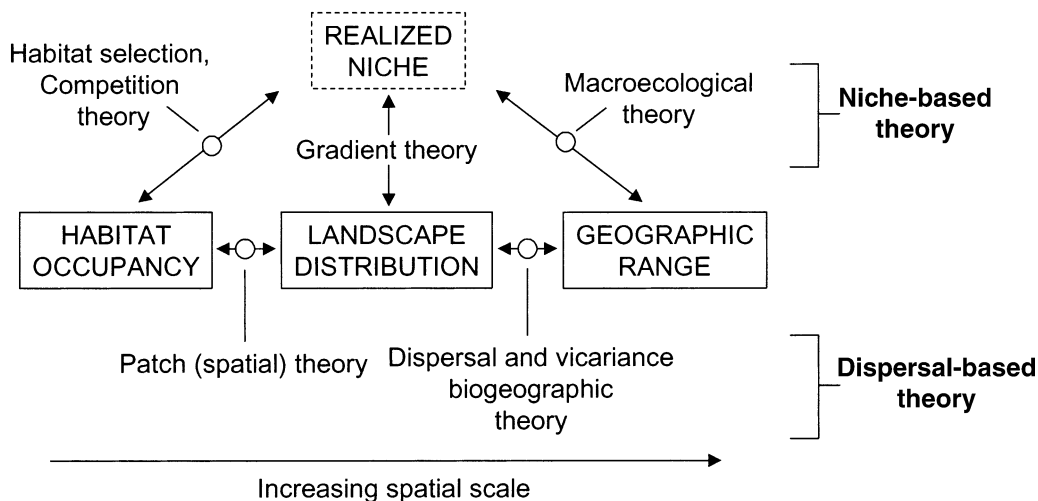


FIG. 3. This diagram shows the framework for relating five bodies of theory that explain patterns of species diversity and distribution. Theories are classified according to the species' features that they link together. Habitat occupancy, landscape distribution, and geographic range are expressed at increasing spatial scale relative to a species, whereas the effects of a species' realized niche are expressed at all scales. Niche-based theories link the realized niche to species' features (vertical, diagonal arrows), whereas dispersal-based theories link species' features at different scales (horizontal arrows).

niche). Second, scaling up to the landscape domain, the landscape distribution of a species depends upon the abundance and spatial distribution of habitats and interacting species. The ability of species to disperse among habitat patches additionally determines how much suitable (or unsuitable) habitat is occupied. Finally, scaling up again, a species' geographic range is determined by dispersal barriers between landscapes containing suitable habitat, time lags associated with colonization, or by limits to suitable habitat imposed by factors such as climate (Udvardy 1969).

Different bodies of diversity theory address different linkages among these patterns and with the realized niche. These linkages fall into two broad categories. Niche-based theories, including habitat selection, competition, gradient, and macroecological theory, focus on the abundance, availability, selection, and richness of habitats as a function of the spatial distribution of biotic and abiotic factors. Dispersal-based theories, including patch (or spatial theory sensu O'Neill 1999) and dispersal and vicariance biogeography theory (Myers and Giller 1988), emphasize the importance of dispersal in determining habitat occupancy and richness as a function of the context, spatial arrangement, and historical events occurring in patches (see also Belyea and Lancaster 1999). Together, these bodies of theory highlight some key relationships between domains that can be useful for developing questions in land management and conservation planning (summarized in Table 1). We discuss these points in *Insights for land management from species diversity theories*. There are many significant relationships we do not discuss because we did not wish to undertake an exhaustive review of them here (see Wiens 1989a, Palmer 1994,

Huston 1999, Blackburn and Gaston 2001 for partial reviews).

INSIGHTS FOR LAND MANAGEMENT FROM SPECIES DIVERSITY THEORIES

Viewing general theories through this framework provides two conceptual tools for land managers. First, it focuses attention on the complementarity of various explanations of diversity and distribution patterns across scales. For example, it is well known that the importance of different explanatory variables is scale dependent. Patterns at fine grain sizes may be dominated by competitive interactions, whereas by expanding grain size, the variation due to competition may be averaged out and the effects of landscape or regional gradients become apparent (e.g., Reed et al. 1993).

For land managers, a less well-known and especially useful way of looking at scale-dependent complementarity in theory is to examine how and why species distribution, richness, or composition changes with increasing distance between equal-area samples (Underwood and Chapman 1996). This question underlies the evaluation of land areas or comparisons between "impacted" and "reference" areas. Variation in community dissimilarity with increasing distance between samples is a function of both organismal attributes, such as dispersal ability and niche breadth, and site characteristics, such as the rate of change in environmental variables in space and the spatial configuration of habitat patches (Nekola and White 1999). In terms of variance partitioning, we might observe that several processes explain a differing percentage of the variance in richness or composition among samples at different spatial scales (Fig. 4). Over a relatively fine study ex-

TABLE 1. A categorization of diversity theory highlighting the major processes that affect the distribution and abundance of species and some important effects on patterns of diversity.

Class and body of theory	Processes affecting distribution/abundance	Resulting diversity patterns	References
Niche-based			
Habitat selection	Intraspecific competition increases habitat breadth at high population density.	Richness may be inflated in a habitat patch at high densities.†	Fretwell and Lucas (1969), Wiens (1989a)
Competition	Interspecific competition reduces habitat breadth.	Dominance may reduce richness in habitat patch.‡	Paine (1996)
	Interspecific competition increases habitat breadth.	Dominance may inflate richness in a habitat patch.	Wiens (1989a)
Gradient	Disturbance/heterogeneity inhibits dominance/exclusion.	Richness maintained by disturbance/heterogeneity.	reviewed in Palmer (1994)
	Trade-offs produce unimodal distributions on environmental gradients.	Steeper gradients have higher richness and turnover.	Gauch and Whittaker (1972), ter Braak (1994)
Macroecology	Competitors inhibit expression of habitat preference (alters mode position or number).	Gradient steepness may be unrelated to richness or turnover.	Mueller-Dombois and Ellenberg (1974), Austin (1985)
	High energy/large area promotes speciation and inhibits extinction.	High energy/large areas maintain large species pools.	Rosenzweig (1995), Blackburn and Gaston (2001)
	Climate changes increases or reduces habitat area depending on continental position.	Regional richness may increase or decrease with climate or land-use change.	Vrba (1992), Rosenzweig (2002)
Dispersal-based			
Patch (spatial)	Dispersal rate/success determines distributions.	Local richness increased and turnover reduced with high dispersal rates.	Loreau and Mouquet (1999)
		Local richness reduced due to dispersal limitation.	Krasnov and Shenbrot (1998)
		Local richness favored by dispersal limitation of competitors.	Tilman (1994), Hubbell et al (1999)
Dispersal or vicariance biogeography	Geographic isolation promotes speciation.	Regional richness higher in areas of rapid geologic change.	Mayr (1963), Cracraft (1985)

Note: The list is not exhaustive. It emphasizes processes that may be useful for land managers to consider.

† By “inflated” we mean that richness may be higher in a habitat type than is typically observed.

‡ By “reduce” we mean that richness may be lower in a habitat type than is typically observed.

tent (i.e., the scale over which samples are distributed), variance in the abundance of strong competitors might be the most important variable explaining differences in diversity. Samples distributed over broader extent might reveal the influence of both soil type and the characteristics of the matrix in which these soil types are embedded. At the broadest extents, the position of mountain ranges between groups of samples might explain the majority of the variance in composition or richness. Moving the position of an extent across space would alter the variance explained by different factors (i.e., a mountain range may be present in one but not the other extent). Any generalizations within an extent, however, would be statistical abstractions; any two individual land areas within the extent that a manager considers could vary in their diversity for different reasons.

Second, the framework reminds us that the land units we manage (e.g., tens to thousands of hectares) en-

compass many different species-defined domains of scale and perceptions of heterogeneity (Kolasa and Waltho 1998). Depending upon the group of species, scale, and type of landscape that is considered, different processes and related explanatory variables will explain diversity (Table 1). We review some of the conditions in which different theories and processes should be considered by managers, note problems and unexpected consequences presented by the processes, and suggest guidelines to deal with them.

Issues within the landscape domain

Management decisions are usually focused within the landscape domain because management scales are often larger than those of most species' home range sizes but smaller than their geographic ranges (Fig. 3). At these species-defined scales, environmental heterogeneity can be conceptualized as a patch-matrix or mosaic pattern, and movement or dispersal between hab-

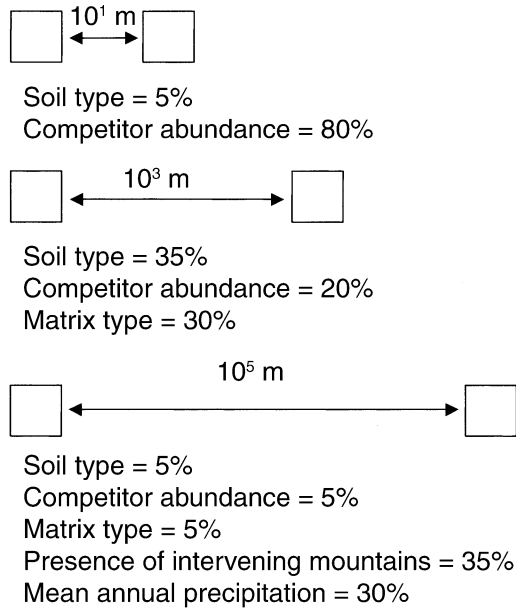


FIG. 4. Hypothetical examples of the relative contributions of different factors to variance in species composition or richness among sets of sites distributed over different spatial scales. Plots (squares) are of equal area, and the average distance between plots is indicated.

itats (or combinations of habitat types) is of central concern (e.g., Harrison et al. 1999; patch theory, Table 1). Alternatively, environmental heterogeneity may be conceptualized as one or more gradients (gradient theory). The patch approach is crucial when considering species whose dispersal is limited due to species' traits and/or landscape structure. The gradient approach may be appropriate when dispersal limitation is deemed unimportant because patchiness is not pronounced or between-patch barriers are easily overcome. In this case, species richness should be coupled to measurable abiotic and/or biotic features, if we can identify them. Even environmental features that exhibit a patchy structure in space can be represented using the gradient approach (Austin 1985, Krasnov and Shenbrot 1998).

When patchiness in landscapes is important, local communities are often capable of supporting more individuals or species than they actually do at particular times due to dispersal limitation. This affects correlations between environmental measures available to managers and species distribution or richness. Habitat quality or value as determined by correlations or experiments may relate poorly to the true value of a patch if it is uncolonized when measurements are taken (Fonseca and Hart 2001). This means that when dispersal limitation is strong, within-patch variables alone will be insufficient to explain variation in species abundance or diversity (e.g., He et al. 1996). The inclusion of landscape configuration metrics that relate to dispersal, such as patch size, distance to nearest patch, or matrix type, may improve the accuracy of statistical

models (e.g., Mazerolle and Villard 1999, Miller and Cale 2000). Such approaches may help to identify important source habitats (defined by both patch characteristics and landscape context) that maintain richness across landscapes (but see Fauth et al. 2000).

In other cases, the consequences of spatial pattern may be minor because dispersal is not strongly limited within a given spatial extent (e.g., birds and many ants within desert grassland/shrubland mosaics). Then, richness and abundance may track landscape gradients. A key issue likely to confront managers is to decide which among the many gradients present in a landscape are most important. When using field data to create models, it is useful to gain a broad-scale view of species associations in order to tease apart the effects of gradients that may frequently (but not always) parallel one another (Bestelmeyer and Wiens 2001). Multivariate techniques (e.g., ordination) can be employed in this context to measure the strength of various environmental variables across scales for producing changes in species richness or turnover (Kremen et al. 1999, Boone and Krohn 2000). Unfortunately, the amount of variance in species abundances explained using environmental gradient approaches is often lower than expected, perhaps reflecting the importance of spatial pattern or the omission of other important environmental variables (e.g., competitor abundance).

Both environmental gradients and the effects of habitat patchiness on dispersal are likely to be important in most study systems. For example, variation in the richness of serpentine-endemic herbaceous plants among patches and areas of continuous habitat can be explained by both patch size and underlying gradients of calcium levels (Harrison 1999). The amount of variance explained by patch metrics or gradients in habitat variables within the same system may be scale dependent. At fine scales within patches, birds may respond in a continuous way to patch edge characteristics (Campi and MacNally 2001), but respond to spatial organization of patches at larger scales (Jokimaki and Huhta 1996). This means that the effects of habitat patchiness (e.g., forest fragmentation) should not be considered independently of less obvious, but potentially important, sources of variation underlying the patches that managers recognize. Similarly, it is important to recognize the influence of patchiness and gradients in land-use policy and human behaviors and their interactions with biological patterns (Kremen et al. 1999).

Issues within the habitat domain

The recognition of important landscape gradients or habitat patches requires information on species responses within the habitat domain. The emphasis here is on identifying key habitat elements and life history requirements that define habitats (e.g., multistemmed yuccas for nesting of Aplomado Falcons, *Falco femoralis*). When dispersal limitation is unimportant, occurrence or density data may provide an indication of

relative habitat quality (as defined by population persistence, e.g., Rodriguez et al. 2000), provided that a sufficient range of habitat variation has been sampled (Aberg et al. 2000).

Even when dispersal limitation is not an issue, the use of abundance or density to indicate habitat quality can be unreliable for a variety of reasons (Morrison 2001). The major contribution of theory in this regard has been to alert us to the role of intra- and interspecific competitive dominance in inhibiting the expression of habitat preferences (Van Horne 1983, Chamberlain and Fuller 1999). Dominance may depress richness and abundance in valuable habitats and increase them in poorer habitats (Wiens 1989a).

When evaluating and comparing the diversity of habitats, managers should consider whether territoriality or interspecific interactions are likely to be important in the species group considered (e.g., some birds) and whether variation in the strength of these interactions is responsible for variation in abundance or richness at a particular scale. The role of competitive interactions will depend in part on the mitigating effects of structural heterogeneity or disturbances at scales relevant to a species group. It is widely recognized that spatial structure, for example, can promote richness. The role of disturbance regimes such as fire (McPherson 1995) and herbivore grazing (Fuhlendorf and Engle 2001), on the other hand, are controversial in many management settings, and have been understudied. Although competition theory provides strong support for manipulating disturbance regimes to enhance richness, relatively subtle differences in disturbance type, timing, and intensity may result in decreases of even desirable species (Drewa and Havstad 2001).

Issues within the geographic domain

Theories addressing the geographic domain direct attention to the fact that managed landscapes vary in their geographic context and that this context determines species richness (MacArthur and Wilson 1967). The recognition of species endemism (e.g., "hotspots"; Myers et al. 2000) and the maintenance of endemism and regional richness relies, in part, on understanding the forces promoting speciation or inhibiting regional extinction. Dispersal and vicariance biogeography theory indicate that particular areas (e.g., geologically active areas and transition zones) may be responsible for the production of a great deal of a region's biodiversity (e.g., Riddle et al. 2000). Macroecological theory emphasizes that the maintenance of this diversity in any one landscape depends upon factors affecting component species throughout their geographic range (Rosenzweig 2002). One fundamental guideline is to maintain productive ecosystems that capture energy and make it available to support food webs (Wright 1990, Brown 1995). These ideas underscore the need for communication and coordination among managers working in different landscapes and with different resources

(e.g., wildlife biologists, agricultural extension agents, and private land owners). Without region-wide planning, even excellent landscape-level plans may fail.

The coordinated management of a regional species pool requires an understanding of past region-wide disturbances (e.g., glaciation, historical or pre-historical deforestation). This is because the unmeasured, historical loss of vulnerable species may constrain how contemporary assemblages respond to subsequent environmental changes (Monkkonen and Welsh 1994, Balmford 1996). Regional assemblages that have already lost species that would have been sensitive to habitat loss, for instance, may appear to benefit little from measures aimed at restoring habitat. On the other hand, assemblages in regions where historical losses have not yet occurred would benefit greatly from improved management. This suggests that (1) a consideration of history is needed when interpreting the responses of species groups to a management strategy, (2) it may not be appropriate to "export" interpretations about the importance of land-use effects, even among environmentally similar regions, and (3) it should be a priority to identify and allocate management resources to areas where regional losses have not yet occurred (Balmford 1996).

Geographic-scale studies also tell us that species persistence at regional scales will depend on the longevity of habitats in the face of climate change and the presence of ecological transitions or dispersal barriers (Vrba 1992, Davis et al. 2000). The size and location of habitats may shift with climate change, leading to the loss of desired species from areas located near biome transitions, mountain ranges, or rivers. Of particular concern, highly diverse ecological transition zones tend to be selected in some reserve design algorithms but these marginal areas may have limited value as long-term refugia (Gaston et al. 2001). In a similar way, the long-term capacity of species to respond to gradual climate changes by migrating or evolving will depend upon the availability of suitable "substrate" on which habitat and species can respond and the ability of species to track these changes via dispersal and habitat generalism (Warren et al. 2001). Land uses that constrain the capacity of vegetation and dependent species to respond naturally to climate (e.g., some urbanized land, cropland, or degraded rangeland) and that limit dispersal along climate-change gradients threaten the long-term, regional persistence of species. Regional planners should consider the potential for interactions between climate dynamics, landscape composition, and dispersal.

Integrating species-groups, domains, and processes

We have emphasized that biodiversity is managed at several (albeit restricted) spatial and temporal scales and that management decisions interact across scales. The collective perceptions of many organisms and qualitatively different kinds of processes operate within



PLATE 1. Recent changes in the structure of a rangeland on a gravelly sandy loam soil in southwestern New Mexico, near Lake Valley, Sierra County. (Left) In this rangeland-trend photograph taken by the Bureau of Land Management in November 1971, grasses are largely black grama (*Bouteloua eriopoda*) and tobosa (*Pleuraphis mutica*). Individuals of viscid acacia (*Acacia neovernicosa*) are present. (Right) This photograph was taken in June 2003. Long-lived perennial grasses are absent, and acacia cover and height have increased dramatically. (Photograph by Harvey Brockman.)

and among human-defined scales. Despite this complexity, management decisions aimed at maintaining biological diversity necessarily involve the consideration of limited numbers and kinds of species, depending upon the politics motivating the decisions and the availability of scientific resources. The degree of success will depend upon how the selected species and groups approximate the overall relationships between species diversity and environment in a particular setting (Oliver et al. 1998).

Given these contingencies and limitations, our framework provides a way to begin attacking the problem of multi-species management by directing our attention to some common questions: (1) Which groups of organisms will be considered, (2) how do their domains of scale relate to one another and the land area under consideration, (3) what processes are likely to be important determinants of species distribution at management scales, and (4) how will the proposed management activities interact with these processes? Understanding the determinants of species diversity (question 3) can be aided by answering the following questions: (3a) Do the groups of species considered together in diversity or abundance measures respond similarly to environmental variation? (3b) Which environmental gradients determine the distribution and richness of those groups, and have they been identified? (3c) How might the spatial patterning of these gradients across landscapes influence species–environment relationships? (3d) How might historical variation in environments or disturbances with time lags alter species–environment relationships and the effects of spatial patterning? (3e) How do regional gradients and discontinuities cause variation in the response of species groups to environmental pattern within different landscapes? The value of species diversity theory for managers, then, is not to provide “general answers to specific questions. . . , but to reverse the process, and

seek many different special answers to each general question” (Bartholomew 1982). Concepts can be assembled in different ways to explain species diversity in particular instances (see Caughley 1994).

An example

An example from the Chihuahuan Desert grasslands of southern New Mexico can be used to illustrate some of the points we have raised. In this ecosystem, concern about biodiversity is centered on the direct and indirect effects of livestock grazing, fire suppression, and climate change that results in loss of grasslands and the encroachment of shrublands. Much of the grassland area in the region was converted to shrubland over the last century, but shrub encroachment is ongoing in many remaining grasslands (Gibbens et al. 1992; see Plate 1). Recovering grasslands from shrublands is difficult and costly, where it is possible at all. Key questions for land managers (e.g., the United States Bureau of Land Management) include: How much, if any, livestock grazing should be conducted on individual parcels of public land? Where should shrub control measures be implemented to recover grasslands?

In the United States, single endangered species (following the Endangered Species Act of 1973) can be primary drivers of management decisions. In Chihuahuan Desert grasslands, the Northern Aplomado Falcon (*Falco femoralis septentrionalis*) is increasingly playing this role. Despite the fact that the falcon was not selected as a surrogate for biodiversity as a whole, it has been argued that preservation of falcon habitat will sustain desert grassland biodiversity (Forest Guardians 2002). This argument stems from some ideas about the falcon’s local ecology, including: (1) a preference to nest in multistemmed soaptree yuccas (*Yucca elata*, a stem succulent) associated with grassland habitat types, and (2) the requirement to hunt birds, ro-

dents, and insects in open grassland habitat types (Montoya et al. 1997, Keddy-Hector 2000).

If the management of Chihuahuan Desert grassland biodiversity is to be based largely upon the needs of the Aplomado Falcon, we can ask: (1) To what degree do the Aplomado Falcon and other species groups perceive similar environmental gradients and patchiness at similar scales (questions 1, 2, and 3a)? (2) How do geographic-scale features such as long-distance dispersal, climate and land-use variation, and biome distribution mediate these species' responses to landscape pattern (questions 3b–3e), and (3) where should changes to livestock management and shrub control be considered to promote desert grassland biodiversity (question 4)?

Published studies of different species groups from landscapes identified as containing superior habitat for the Aplomado Falcon (Forest Guardians 2002) add a variety of perspectives about environmental variation. Richness and turnover patterns within a group of 22 bird species indicated a higher richness in shrubland types than in grassland and substantial differences in species abundances among grasslands and a variety of shrubland types (Pidgeon et al. 2001). The basis for these patterns in several cases appears to be related to the details of nesting biology. Several species are able to nest in shrubs and fewer may require grasslands. Although we have not considered the potential for some shrubland habitat occurrences to be affected by competitive interactions or "spill-over" from adjacent grasslands (Whitford 1997), it is clear that overall landscape bird richness is supported by shrub diversity.

The relatively low richness of grassland habitats in this study may be a consequence of the spatial configuration and the historical, geographic context of the patches. Grassland patches may have been too small to support occupancy by area-sensitive grassland species such as Grasshopper Sparrows (*Ammodramus saviannarum*) and Lark Buntings (*Calamospiza melanocorys*), whether or not the vegetation within the patches was shrub-free (Pidgeon et al. 2001). Through this mechanism, historical overgrazing may have extirpated several grassland species from the region that would have added richness to current grassland patches. It is possible that the restoration of extensive grassland patches would eventually increase regional richness by promoting colonization of additional species.

A study of 41 desert grassland ants in several of the same habitat types revealed similarities and differences to the desert grassland bird study (Bestelmeyer and Wiens 2001). Within the Jornada Basin, a shrubland type had the highest richness and a relatively distinct species composition when compared with grassland types. Like the birds, several ant species nest exclusively in certain shrub species and contribute to the shrubland's high richness (e.g., *Crematogaster larreae*, *C. depilis*). Unlike the birds, some ant species nested in coarsely textured soils, independent of whether

shrubs or grasses occurred on them (e.g., *Pogonomyrmex imberbiculus*, *Pheidole* sp. J1). The ants revealed the importance of a distinct landscape gradient that can produce habitat heterogeneity within vegetation-based habitats.

The available data indicate distinct management directions as well as the need for additional data. Certainly, there is a need for better data on falcon biology. The Chihuahuan Desert grasslands represent the northern extent of the falcon's geographic range; because the falcon can disperse widely (up to 300 km; Keddy-Hector 2000), its population dynamics in New Mexican desert grasslands may depend to some degree on habitat changes occurring outside of New Mexico. These relationships are not understood. Nonetheless, there is a clear need to maintain and restore grasslands because extensive grasslands are relatively rare in the region, and several species depend on them. The size and context of grassland patches is a potentially important and poorly understood factor: Many small patches may have less value for biodiversity than a few patches above a critical size. Furthermore, the landscape and geographic position of grassland patches determines their size and longevity. The preservation and restoration of large grassland patches in the face of land-use and climate change is more likely to be successful in some regions and soil types than in others (Bestelmeyer et al. 2003). Managers can use these ideas to prioritize management actions.

The data also reveal "hidden heterogeneity" within the grassland–shrubland dichotomy. Different shrubland types and different soils (irrespective of vegetation) support different elements of biodiversity. As Pidgeon et al. (2001) point out, there is no regional shortage of shrublands. Nonetheless, there is little accounting of the value of soil types occurring within shrublands, nor of the threats posed to rare soil types by destructive shrub control measures or ceding land to housing developments. Besides this, there is interest in promoting richness at local scales near to human communities (Miller and Hobbs 2002). The maintenance of grasslands may be important for maintaining regional biodiversity, but landowners and land users might wish to experience a high local diversity of birds, for example. In this case, maintaining a diversity of shrubland types would be desirable. This means that some shrub encroachment battles may not be worth the effort (Belsky 1996). The more we consider different species groups, processes, and scales, the better decisions we will make.

A theory-based framework can help land managers put their decision making into a broader, ecological context. In our example, answers to the questions we asked indicate new directions and data needs: (1) Habitats other than grasslands are worth recognizing and the value of grasslands will depend on their size and location, (2) promoting grassland biodiversity within the management area requires data about species that

may not be present and data from habitats well outside the management area, and (3) changes to grassland management and shrub control efforts can be prioritized according to the local richness of shrubland types, the rarity of soils, and the regional position and size of grasslands. The framework indicates the potential importance of processes and relationships that may not be addressed in management datasets and that might otherwise be overlooked.

CONCLUSIONS

Land managers have a difficult job. Whereas ecologists may spend entire careers on a few concepts, organisms, and scales, land managers are called upon to make decisions that are based on many organisms and concepts, in addition to human wants and needs. Ecologists and managers should continue to pull their ideas together to support this task. Our framework is one attempt to do so. The body of theory on which this framework is based reveals the contingency of different explanations for various species, scales, and situations (Shrader-Frechette and McCoy 1993). In this way, the management of biodiversity is the set of case studies of species groups (Caughley 1994). The more case studies we have, the better. Nonetheless, theory also shows that generalities exist in the kinds of patterns and processes we look for in the species groups we examine. Although institutional resources are usually not great, managers can use those that are available much more effectively once they know the right questions to ask.

ACKNOWLEDGMENTS

Thanks to Joan Herbers, Boris Kondratieff, Bill Lauenroth, Deb Peters, Stephanie Bestelmeyer, Alan Andersen, and an anonymous reviewer for their comments.

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