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DISSERTATION

A MULTI-SCALE PERSPECTIVE ON ANT DIVERSITY IN SEMIARID LANDSCAPES

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

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Fort Collins, Colorado

Spring 2000

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Brandon T. Bestelmeyer

30 November 1999

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY BRANDON THOMAS BESTELMEYER ENTITLED A MULTI-SCALE PERSPECTIVE ON ANT DIVERSITY IN SEMIARID LANDSCAPES BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

COMMITTEE ON GRADUATE WORK

Advisor

Department Head

ABSTRACT OF DISSERTATION

A MULTI-SCALE PERSPECTIVE ON ANT DIVERSITY IN SEMIARID LANDSCAPES

Documenting biodiversity patterns and understanding the multiscale processes that create them is an important front of progress in both landscape ecology and conservation biology. One problem in understanding such patterns centers on the differences between how landscapes are perceived by investigators and land managers on the one hand, and the variety of organisms that they are trying to manage, on the other. Are these perceptions concordant? I address this question and related issues by examining the correlates of variation in ant diversity, species composition, and their contributions to the redistribution of scavenged materials with respect to 1) habitat variation defined by ecologists according to grazing management and natural shifts in vegetation within 100-km^2 landscapes at three Long-Term Ecological Research (LTER) sites, and 2) a biome transition from the shortgrass steppe to the Chihuahuan desert grassland biome that is represented by changes in dominant vegetation at the LTER sites. I also considered ant community variation at fine scales with respect to shrub microhabitats in a landscape dominated by Sonoran thornscrub. Grazing was the dominant land use in the LTER landscapes, and had large effects on vegetation. Despite this, ant communities and scavenging patterns were relatively little affected by grazing. Instead, soil characteristics were shown to be the most consistent correlate of ant composition at the LTER sites. Vegetation contrasts between grasslands and shrublands sometimes paralleled soil contrasts, and sometimes did not. Some ant species were associated directly with particular plants that defined vegetation types, and some others could be linked to particular soil textural characteristics. Across the biome transition, ant composition and the representation of ant faunal complexes changed, but not in step with vegetation. Contrary to predictions, ant diversity was not greatest at the vegetation-defined biome transition. Overall, ants responded to variation in soils and climate in ways that were distinct from those of vegetation. These results support the notion that patterns from several, functionally-distinct focal taxa will be required to characterize landscape species diversity adequately. Existing techniques that rely on vegetation pattern to characterize landscapes may be limited in their capacity to represent habitat variation for some taxa.

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CHAPTER I

OVERVIEW

In a broad sense, species diversity refers to the numbers, abundances, and composition of species occupying an area. The central questions underlying this research are, How is species diversity distributed? What are the causes of its distribution? These questions are fundamental to ecology, and form the basis for the subdiscipline of community ecology. Historically, community ecology has considered how groups of related species covary in their distribution in space and time, and has focused upon the role of species interactions in mediating these patterns (Wiens 1989). The failure of community ecology to approach diversity in an intellectually satisfying way, due in part to an overemphasis on the role of competitive interactions coupled with its inability to explain many diversity patterns (Wiens 1989), led to a dormancy of the subdiscipline through much of the 1980s (e.g. Rosenzweig 1993). Recently, however, explaining species diversity patterns has returned to the forefront of ecology, in part due to the use of "biodiversity" as a currency in ecosystem management (Franklin 1993) and conservation reserve selection (van Jaarsveld et al. 1998). Areas with a large number of species, or with a unique or distinct species composition, are considered to be valuable and reductions in the number of species occupying an area due to human activities are to be avoided. Thus, explaining why species diversity varies, and the degree to which the presence or abundance of species covaries, continue to be important problems in ecology.

The renewed emphasis on the distribution of biodiversity underscores the need to understand patterns and processes operating at the scales of human-defined landscapes. There has been little theoretical development in this area, and broad-scale empirical studies of many taxa are still rare. We have only begun to focus on ecological studies in the human-dominated ecosystems that harbor an increasing amount of the Earth's remaining biodiversity (Pimentel et al. 1992), and decisions to conserve or destroy biodiversity in these ecosystems are applied at the scales of landscapes. Despite the large number of theories and hypotheses proposed to explain diversity patterns, we lack a general framework for studying species diversity in landscapes.

In Chapter 2, I review and classify several theories and ideas that attempt to explain patterns of species distribution and diversity, and offer some thoughts about how this body of work can be applied to the study of species diversity in landscapes. Because landscapes are, in a hierarchical sense, sandwiched between a series of complex processes operating at smaller, within-patch scales and larger, regional scales, I conclude that a pluralistic view that acknowledges the simultaneous influence of several processes emerging from different spatial scales will be required to represent the mechanisms by which biodiversity is structured in landscapes. Furthermore, not all of these processes act in all cases (Huston 1994). Different taxonomic groups will differ in important characteristics, and the landscapes and regions in which they exist also vary. There are likely to be many combinations of these features, but we may reasonably expect that we can identify a limited number of the kinds of processes that translate this variability into variation in species diversity. This suggests that a 'contingent theory' of diversity would be useful and appropriate, and that we can classify the process elements creating the patterns we observe to communicate them in a general way. We can provide a framework through which we can approach the study of species diversity in landscapes. A number of these elements are already well-understood; we simply need to put them together in the right way, given a particular situation. I emphasize that the intelligent assembly of these ideas requires that we know the natural history of our study organisms and the environments in which they exist. We need to know about their environmental requisites, the distribution and dynamics of these requisites in a landscape, a taxon's dispersal abilities and the challenges to dispersal that exist in a landscape, and we need to understand the relationships among these features.

To examine these issues empirically, I documented patterns of diversity in ant communities (Hymenoptera: Formicidae) at different spatial scales in three semiarid landscapes located along a climatic, regional gradient from the shortgrass steppe of Colorado to the Chihuahuan desert of New Mexico (Fig. 1.1). These landscapes are representatives of grasslands and shrublands that occupy much of the western United States, that harbor substantial biodiversity, but that receive comparatively little attention from conservation biologists when compared to forested areas (Noss and Cooperrider 1994). I focus on insects because they constitute the single largest group of organisms on Earth (May 1988), and comprise almost all of what we refer to as "biodiversity." Nonetheless, insects, whether in forested areas or grasslands, are seldom considered by community ecologists, conservation biologists and land managers (Dingle et al. 1997).

Among insects, ants are particularly well-suited for studies of species diversity in semiarid landscapes. Their ecology and taxonomy are relatively well-known, they are abundant, species rich, easily sampled, and they exhibit strong responses to environmental variation at different scales (Andersen 1997). The number of species and lifestyles that they exhibit, however, is not so large as to be intractable for a study of limited duration. Thus, ants are in a favorable position to provide an insect's perspective on variation within and among landscapes and regions, and may ultimately prove to be a useful part of a suite of focal animal taxa for use in the conservation evaluation of landscapes in North America, as they have in semiarid Australia (Andersen et al. 1998, Majer and Nichols 1998).

By examining patterns of ant diversity and distribution on different spatial scales, I sought to elucidate the relationships between variation in climate and local, within-landscape variation in soils, natural vegetation, and land use, all of which combine to determine the structure and composition of ant communities. The ants in this study are aerial dispersers, and I chose study landscapes that did not contain any obvious potential dispersal barriers. Thus, I considered the responses of ants to only environmental and spatial variables, but not to patch/matrix characteristics or landscape metrics (e.g. Wiens et al. 1993). The validity of this approach is supported by the high degree of correlation between environmental and spatial variables and variation in ant community structure in this study.

In Chapter 3, I focused on the response of ant diversity and composition within landscapes to distinct classes of environmental variation: 1) variation within grasslands due to differences in grazing management, and 2) variation within natural vegetation due to characteristics of soil texture and other factors. My objectives were to 1) compare the influence of these two classes of factors within landscapes, and thus ascertain the threat posed by grazing to ant diversity; 2) to evaluate how well a vegetation-based habitat typology, whether based on grazing effects or natural differences, represented environmental variation that creates ant diversity patterns; and 3) determine how variation among regions affects these patterns. The results of this work have implications for how we evaluate environmental degradation, as well as how we evaluate habitats for biodiversity conservation.

In Chapter 4, I shift the focus to patterns of variation at the regional scale, and ask how ants respond to climatic variation within similar, vegetation-defined habitat types occurring in different regions. Specifically, I ask whether the location of a phytogeographic transition between shortgrass steppe and Chihuahuan desert vegetation at a central site along the regional gradient corresponds to a zoogeographic transition in the ant fauna. These results contribute to our understanding of how patterns of diversity in landscapes covary regionally among different kinds of organisms.

In Chapter 5, I consider patterns of ant composition and diversity at a small scale, on the order of tens of meters, to determine how patchiness in vegetation affects a semiarid ant assemblage. In this study, Bob Schooley and I used a different site from those considered in the rest of the chapters. The site had similar precipitation levels to the others, but was located in Sonora, Mexico at a desert-thornscrub transition zone. This location provided strong, small-scale contrasts between habitats under large trees and shrubs and open, bare-ground areas. I first sought to describe this previously unknown ant community type, and then asked if the variation between open and tree/shrub habitats affected ant composition. The results illustrate the importance of recognizing particular, fine-scale elements within semiarid habitats.

Finally, in Chapter 6, I turn away from patterns of ant richness and species composition to investigate another aspect of ant biodiversity: what ant species do in the ecosystems that they inhabit (Lawton 1993). Several authors have recognized the important effects that ants have on other organisms, but their role in the redistribution of nutrients by scavenging has received little attention to date. I investigated the ecology of scavenging by ants at the study areas in the United States, and asked how the rates and patterns of redistribution of dead arthropod material on the ground surface differed among regions, among habitats, among different times of day, and among species. The redistribution of nutrients may have important consequences for soil nutrient levels, and this study provides an initial step toward the investigation of the relationship between ant species and scavenging function.

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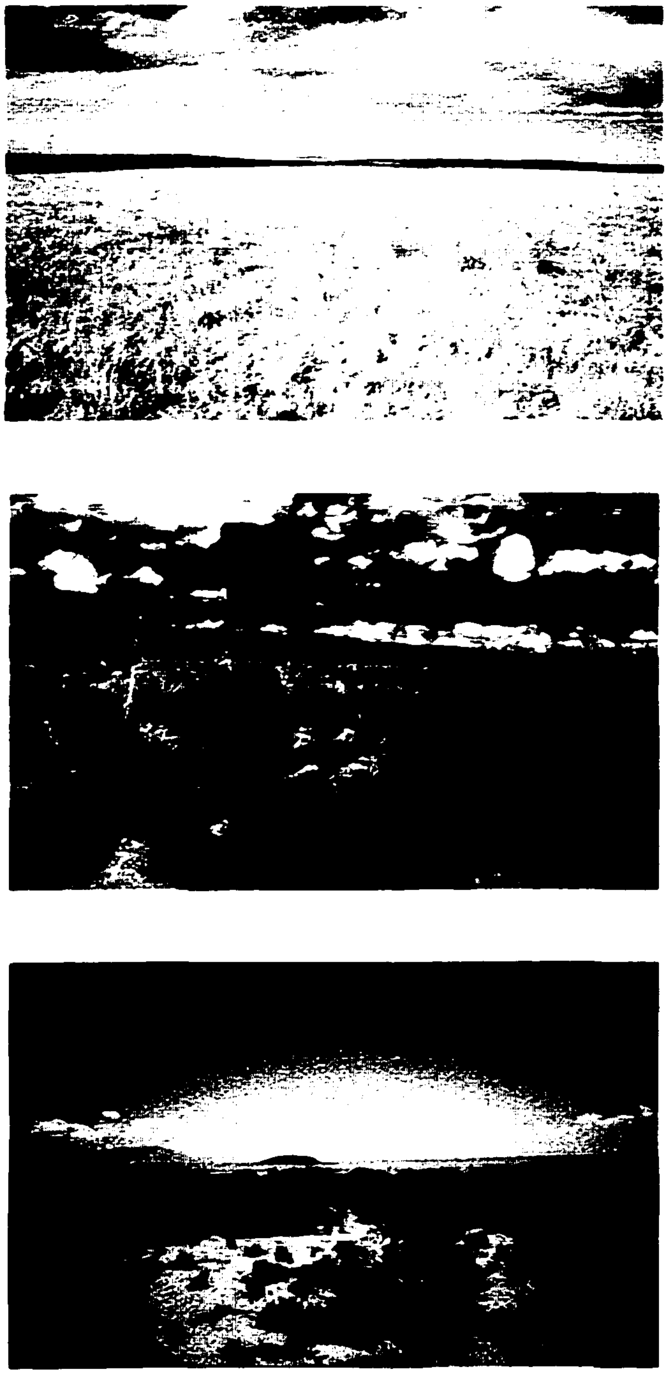

Fig. 1.1. Moderately-grazed blue grama grassland at the Central Plains Experimental Range, Shortgrass Steppe LTER in Weld County, CO (top), that typifies shortgrass steppe habitats, and ungrazed black grama grassland (middle) and creosotebush shrubland (bottom) at the Sevilleta National Wildlife Refuge, Sevilleta LTER, Socorro County, NM; typical desert grassland habitats.

"The process of rediscovery might be as follows: a young, inquisitive, and original man might one morning find a fissure in the traditional technique of thinking. Through this fissure he might look out and a find a new external world around him. In his excitement a few disciples would cluster about him and look again at the world they knew and find it fresh. From this nucleus there would develop a frantic new seeing and a cult of new seers who, finding some traditional knowledge incorrect, would throw out the whole structure and start afresh. Then, the human mind being what it is, evaluation, taxonomy, arrangement, pattern making would succeed the first excited seeing. Gradually the structure would become complete, and men would go to this structure rather than to the external world until eventually something like but not identical with the earlier picture would have been built. From such architectures or patterns of knowledge, disciplines, ethics, even manners exude. The building would be complete again and no one would look beyond it—until one day a young, inquisitive, and original man might find a fissure in the pattern and look through it and find a new world. This seems to have happened again and again in the slow history of human thought and knowledge."

John Steinbeck, 1948
Foreword to *Between Pacific Tides*, 2nd ed., E. F. Rickets and J. Calvin.
Stanford University Press, Stanford, CA, USA

"The complications inherent in most studies of ecological communities are unfortunately such that it can be hard to keep a balanced view of all the relevant factors and contending hypotheses. Although this danger is present in all the sciences, the unconscious temptation to superimpose one's prejudices upon the data is more easily yielded by virtue of these complexities".

Robert May, 1984
An Overview, Real and Apparent Patterns in Community Structure, in *Ecological Communities: Conceptual Issues and Evidence*, D. Strong et al., eds. Princeton University Press, Princeton, NJ, USA.

CHAPTER II

A SCALE-BASED, ORGANISM-CENTERED APPROACH TO THE STUDY OF SPECIES DIVERSITY IN LANDSCAPES

Abstract

There are many theories and hypotheses proposed to explain patterns of species diversity and distribution/abundance. Many of these theories represent processes and patterns centered on different spatial scales. A coherent framework relating these ideas to one another has yet to emerge. I present such a framework and use it to synthesize several classes of diversity theories. The framework is based on the notion that the processes contributing to diversity pattern are context-dependent with respect to the characteristics of the organisms considered, spatial scale as defined by organismal responses, and the characteristics of the particular environments in which diversity is observed. At the scales traditionally considered by land managers and conservation biologists, the diversity of different kinds of organisms is determined by the interactions of different processes. I argue that broad-scale studies of several focal taxa that differ in their attributes will be required to characterize overall species diversity patterns for the management of landscapes .

Introduction

What determines patterns of species diversity? This question is among the oldest and best studied in ecology. The last century has witnessed the evolution of species-diversity studies from a focus on pattern description and identifying the abiotic determinants of geographic distribution patterns, to an emphasis on diversity regulation by competitive interactions in communities at equilibrium (McIntosh 1985), to a recognition that non-equilibrium due to environmental fluctuations (Wiens 1984) and variation in speciation rates at regional scales (Ricklefs 1987) may be primary determinants of local diversity patterns. Recent syntheses have shown that the importance of the factors determining species diversity depends upon the scale at which patterns are observed, and have brought to the forefront that multiple processes act across scales (Ricklefs and Schluter 1993, Rosenzweig 1995, Huston 1994). Consideration of species diversity often addresses different aspects, each leading to a focus on different factors and determinants. This variety of approaches may be summarized in three questions; 1) how does diversity arise, 2) how is diversity distributed, and 3) how is diversity maintained?

As both professional ecologists and the public have come to realize the staggering loss of species diversity due to human activities, interest in the questions asked above has increased. Under the term of "biodiversity conservation," there is increasing scientific concern for the identification and preservation of the evolutionary processes that create species diversity (Erwin 1991), for identifying and conserving diversity hotspots within regions (Prendergast et al. 1993) and across the globe (Mares 1992), and for understanding how species populations are lost (Lande 1988) and how this loss affects ecosystems (Tilman et al. 1997). The increasing frequency with which articles dealing with these issues appear in general science journals such as *Science* and *Nature*, as well as the emergence of biodiversity conservation as an issue in international politics (Steffen et al. 1992), suggests that the study of species diversity has become a global research priority.

Traditionally, emphasis has been placed on understanding species diversity patterns at local scales. This was initially approached by exploring the effects of small-scale processes, such as competition, through manipulative experiments (Ricklefs and Schluter 1993). More recently, emphasis has shifted to documenting the role of regional processes in controlling variation in local diversity (Cornell and Lawton 1992, Caley and Schluter 1997). Regional diversity is filtered by biotic and abiotic processes (Zobel 1997) to create diversity patterns in target communities (Wiens 1989a). In between the scales of regional species pools and local communities lies what Holt (1993) referred to as the mesoscale, "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, the relationship between movement and dispersal patterns, disturbance, and the mosaic structure of landscapes mediates the influence of regional variation in species production on the occurrence of species in local communities (Caswell and Cohen 1993, Zobel 1997). Thus, understanding patterns and dynamics at intermediate scales may be critical to understanding local-regional relationships (contra Lawton 1999).

Besides contributing to our understanding of the relationships between local and regional diversity, documenting and understanding the distribution of species in landscapes and their responses to human disturbance are necessary components of biodiversity conservation. This is because decisions that bear on the sacrifice or preservation of biodiversity are usually applied at the scales of human-defined landscapes (Forman 1995). One objective of landscape ecology is to provide both theory and practical tools to aid land managers in their efforts to promote biodiversity in landscapes.

To this end, landscape ecologists have emphasized the importance of the spatial geometry and composition of habitat (O' Neill 1999) for populations and communities of organisms. Haines-Young (1999) argued, however, that landscape ecologists often have little understanding of the significance of the general patterns that they document. This may result from considering spatial patterns from human perspectives rather than examining the perceptions and reactions of the organisms studied, as well as a lack of understanding about how different organisms are distributed across landscapes (e.g. Tuomisto et al. 1995), or the variety of factors that determine the diversity patterns of different organisms.

I argue that a scale-based, organism-centered approach is required to understand diversity patterns in landscapes. This approach needs to consider the domains and interelationships of the various factors currently known to determine biodiversity patterns. Here, I describe how hierarchies of scale, scale-dependence in spatial heterogeneity, and differing organismal perspectives relate to provide a framework for classifying several types of theory that address diversity patterns. My objectives are to characterize the common elements of theories that address diversity patterns at different scales, and to identify research priorities for diversity studies on the scales traditionally considered by land managers. Finally, I will argue for the utility of considering ecological theory in a case-contingent and pluralistic way.

What is Species Diversity?

The concepts of species diversity and species distribution are closely related, but the theories created to explain their patterns are usually treated separately. For the purpose of broadening my discussion of theories and hypotheses about biodiversity, I consider species diversity and distribution as two reflections of the same phenomenon. Their unity can best be visualized as an ecological data matrix, or species-site matrix (Fig. 2.1). This matrix can be considered from two different perspectives. Species diversity is the presence or abundance of various species within a site of defined area. A site's richness refers to presence-absence data within the cells; if abundance is considered, then information measures such as the logseries-α (Magurran 1988), can also characterize diversity. 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 multivariate analysis of community composition, these two perspectives correspond to Q-mode (relationships among sites in species composition) versus R-mode (relationships among species based on their distribution among sites) analyses, respectively (Legendre and Legendre 1998). Thus, variation in species diversity can be conceptualized and measured in two distinct ways; as variation in the number of species among areas, and as variation in the composition of species among areas when species identity is considered (i.e. beta diversity or species turnover; Whittaker 1972). There are different aspects to species diversity, and their patterns can be defined at different spatial scales, and are determined by the same processes.

Scale, Heterogeneity, and Diversity

Patterns of environmental heterogeneity and species distributions vary with changing spatial scale, but these changes can occur in two distinct ways. In some cases, changes in patterns of species abundance, distribution, or diversity covary directly with changes in their habitat. That is, distributional changes are simply due to a quantitative rescaling of the environment, but distribution-environment associations are consistent across scales, and determined by the same mechanism (Allen 1998). Alternatively, distribution-environment relationships may be determined by qualitatively different mechanisms at different scales (Urban et al. 1987, Morton 1993). In this case, changing distribution-environment relationships represent emergent properties at different scales (Allen 1998, King 1999). For example, Pinel Alloul (1995) demonstrated that marine zooplanktonic distribution on relatively fine scales is predominantly affected by plankton behavioral reactions to depth, whereas large-scale distributions are primarily affected by the movement of water. Such shifts in dominant mechanisms need not involve large changes in spatial scale. Morris (1992) showed that deer mouse (*Peromyscus*) movements related to foraging occurred within a range of 60 m, whereas movement for dispersal was within 140 m.

I often think of the cause-effect relationships determining diversity or distribution as being concordant in space, time , and scale. Hierarchy theory (O'Neill et al. 1986), however, tells us that distribution patterns observed on one scale may be determined by the interaction of processes operating on adjacent scales. Behavioral responses of individual animals to resources on small scales may influence patterns of population density on larger scales (Crist and Wiens 1995, Stapp and Van Horne 1997), while the distribution of resources on large scales may constrain individual behavior on smaller scales (Orians and Wittenberger 1991). Explaining the distribution of organisms on one scale therefore requires a knowledge of processes operating on several scales (Conroy and Noon 1996).

Cutting across species distributions, diversity patterns are subject to the same principles. Diversity may increase systematically with increases in the number of habitat types in landscapes (Wagner et al., in press). Alternatively, MacArthur and Wilson's (1967) island biogeographic theory holds that local-scale diversity is determined by an interaction of processes emerging from distinct spatial scales. An excellent example is provided by Cole (1983), who showed experimentally that competitive interactions in local communities are constrained by regional variation in colonization probabilities. At the scale of continents, the effect of climate or energy on the rate of species production may constrain variation in local community diversity (Wright 1983, Vrba 1992, Morton 1993). In some situations, these hierarchical relationships may become decoupled. Dispersal barriers can prevent the species produced in a region from colonizing suitable local communities (Brown and Lomolino 1998), in which case local processes might predominate. Even when dispersal is possible, local processes may be so strong as to override any regional effects (i.e. community saturation; Cody 1966, Diamond 1975, Terborg and Faaborg 1980). These themes reinforce my view that a general approach to the study of diversity patterns must consider how processes occurring within local communities, across landscapes, and across continents and the globe vary in their importance and interactions.

Organisms Define Scale and Heterogeneity

Determining how processes defining distribution-environment relationships correspond to spatial scales requires an organism-centered perspective (Levins 1968, Wiens 1989b). Organisms exhibit several kinds of characteristics that determine the "operative environment" with which they interact (MacMahon et al. 1981). Body size is a particularly important characteristic because it exerts a strong influence on many other features, such as: 1) physiology and environmental tolerance, and thus the nature of the resources and conditions that organisms require (Brown 1984, Brown and Nicoletto 1991); 2) movement and vagility, and thus the scales over which organisms acquire these resources (McNab 1963, Holling 1992, Brown 1995); and 3) sensory ability, perception, and behavior (or *umwelt*; von Uexküll [1909]) which ultimately determine how individuals distribute themselves with respect to environment (Lima and Zollner 1996).

Irrespective of differences in characteristics such as body size, all organisms have in common three fundamental attributes that are necessary for us to understand their distribution: habitat requirements, dispersal capabilities, and the location of the geographic range. These attributes are expressed at different spatial scales relative to an organism, and these domains of scale (*sensu* Wiens 1989b) are generally referred to here as the habitat, landscape, and geographic domains (Fig. 2.2). The habitat domain refers to the scales at which habitat features and species interactions determine the capacity of an organism to survive and reproduce. Spatially, this corresponds to the home range of a mobile organism or the microsite of a sessile one. The landscape domain reflects the scales at which macrohabitat heterogeneity may be perceived. Different kinds of macrohabitats often exhibit a mosaic structure at these scales, and patches of suitable habitat may be interspersed with less suitable habitat types (Wiens et al. 1993). Between-habitat dispersal is an important organismal attribute acting within this domain. Between-habitat dispersal may represent the relocation of an organism's home range (e.g. the "environmental dispersal" of Howard (1960)) or the dispersal of propagules or offspring to other habitats. The geographic domain refers to the scale within which the distribution of a species occurs. Predominant organismal attributes include innate dispersal (Howard 1960), outbreeding, and gene flow, which may occur over temporal scales that are often much longer than the life span of individuals. In addition, long-range dispersal such as the "jump dispersal" of Pielou (1979) may be important. These processes may often operate across continents and are usually addressed by biogeographers (Brown and Lomolino 1998).

The nature of the relationship of organismal attributes to environmental heterogeneity determines how domains of scale translate into spatial scales. The use of fixed quantitative criteria (e.g. Forman 1995) or vegetation units (e.g. biomes; Urban et al. 1987) to discuss scale-dependent processes in a general way ignores or makes unfounded assumptions about the way different organisms perceive environmental variation (Kotliar and Wiens 1990). For example, the regional domain of a thermophilic archaea might be a set of hot springs occurring over several hundred square meters, and a habitat patch might represent a single pool (Brown et al. 1996).

If we shift perspectives from the scales defined by organisms to those defined by humans, several kinds of processes can be important determinants of species diversity in the kilometers-wide landscapes of (Forman 1995). For example, in a 1-km^2 study plot, smaller organisms such as ants may interact with the heterogeneity we observe through between-patch dispersal, whereas larger organisms such as ungulates may respond to the same patches through momentary foraging decisions. This variety of processes complicates our ability to relate measured heterogeneity (that which we as investigators recognize and define) and functional heterogeneity (that is defined by responses of the organisms; Kolasa and Rollo 1991). It is functional heterogeneity that determines organismal distribution, and measured and functional heterogeneity converge only when investigators use organismal responses to define important environmental features and then measure these features at appropriate scales.

MacArthur (1972) noted that our search for explicable, general patterns is aided by a focus on particular taxa, and "no one has ever claimed to find a diversity pattern in which birds plus butterflies made more sense than either one alone". Without realizing it, community ecologists usually consider diversity patterns within taxonomically-defined groups in order to minimize differences in functional heterogeneity and scaling among community members. Animal species belonging to the same family or genus may respond to heterogeneity on similar scales and in similar ways, and multitaxon guilds can be defined based upon the similarities of the resources to which different animals react

(Root 1972). A similar logic underlies the use of functional groups in plant and invertebrate communities (Keddy 1992, Andersen 1995).

Relationships Among Scale Domains and Species Diversity Theories

There are a dizzying number of theories, hypotheses, and concepts that are used to explain species diversity patterns. Several attempts have been made to organize these ideas by categorizing them, although this has proven to be a difficult task (Palmer 1994). The recognition that the processes invoked by different hypotheses operate or explain patterns at different spatial scales has figured prominently in such efforts (Brown 1988). Ricklefs and Schluter's (1993) framework, for example, distinguished local versus regional effects on diversity patterns. This framework is hierarchical: diversity may be defined at several spatial scales and processes emerging from one spatial scale interplay with processes operating within adjacent levels. Following Cornell and Lawton (1992), important influences either add species to, or remove them from, a system. Augmenting influences emerge from the regional scale (speciation and biotic interchange) and may influence diversity at the local scale, where species may be removed by competitive or predatory exclusion or stochastic extinction. This framework forms the basis for recent assessments of the degree to which local species communities are "saturated," due to the limitations imposed by local-scale competitive interactions, versus "open," determined by variation in regional-scale diversity (e.g. Caley and Schluter 1997).

In contrast, Palmer (1994) recognized that diversity patterns exist as a continuous gradient across a range of spatial scales, not simply "local" or "regional." No matter which spatial scale is considered, diversity is determined by factors operating both within and outside of species communities. Thus, Palmer focused on the dichotomy between those hypotheses that consider the processes that lead to the origin of species richness in communities, such as speciation, versus those dealing with the maintenance of richness, i.e., patterns of coexistence. He organized this latter class of hypotheses by categorizing them with respect to violations of different assumptions of the competitive exclusion principle of Gause (1937).

I extend upon these previous syntheses to introduce another general framework that includes the relationships between hypotheses addressing the origin and maintenance of species diversity, and in addition, considers diversity patterns across a range of spatial scales. Although Palmer (1994) argued that the processes determining diversity patterns operate across a continuum of scales, and should not be considered according to arbitrary categories, the organism-defined domains of scale provide discrete categories that can be used as logical basis for an organizing framework. Because diversity and distribution reflect different aspects of the same phenomenon, we can consider the theories addressing them within the same framework.

In considering this framework, diversity must be defined with respect to more-or-less functionally-homogeneous species groups whose distributions respond to similar processes at similar spatial scales. A lack of concordance between the processes and scales at which community diversity and component species' distributions are determined indicate the limitations of species diversity theory. Some communities may be composed of species that are too different from one another to consider together in any meaningful way (e.g. MacArthur 1972).

The processes that affect species distribution and diversity at the finest organism-defined scales fall within the habitat domain. These processes determine what constitutes suitable habitat and the quality of this habitat, and thus potential *habitat occupancy* (Fig. 2.3). Potential habitat occupancy is a direct consequence of the fundamental niche (Hutchinson 1957) that is defined by the physiological limitations of a species and, more proximately, by the *realized niche* which is determined by the distribution of competitors and predators with respect to requisite abiotic conditions. Actual habitat occupancy, of course, depends upon whether or not dispersing individuals of a species have reached a particular suitable habitat. At a broader spatial scale, within the landscape domain, suitable habitat patches may be separated by a matrix of less suitable habitat, or habitats may vary in quality in a continuous way. The *landscape distribution* of species is thus determined by patterns of dispersal between suitable habitat patches (Harrison and Taylor 1997) or simply by variation in the availability or quality of suitable habitat irrespective of dispersal. At the broadest possible organism-defined scales, a species' *geographic range* is determined by dispersal barriers between landscapes containing suitable habitat or because suitable habitat reaches a geographic limit imposed by gradually-varying factors such as climate (Udvardy 1969).

Existing bodies of theory address relationships between distinct components of diversity and distribution patterns. These relationships fall into two broad categories (Fig. 2.3). Niche-based theory links patterns at different scales to the presence and abundance of suitable habitat. Dispersal-based theory emphasizes the importance of patchiness, the spatial arrangement of habitats, and movement in mediating the relationship between species distribution and the distribution of suitable habitat. My objective here is to review briefly how the fundamental premises of several theories relate to this framework and to one another, without undertaking a complete review of their predictions.

Niche-based Theory

I identify four bodies of niche-based theory (Table 2.1). First, habitat selection theory and competition theory address how characteristics of the realized niche translate into patterns of habitat occupancy. Habitat-selection theory, such as the Fretwell-Lucas (1969) model, is generally not considered in addressing patterns of species diversity. Nonetheless, habitat-selection models show that interactions among conspecifics can affect the habitat distribution of a species, and therefore these models bear on local-scale diversity patterns. For example, the Fretwell-Lucas model predicts that the habitat breadth of a species will be greater where the density of individuals is higher (Wiens 1989a). Individuals occupy less-suitable habitats when the best habitats are saturated or dominated by superior competitors at low densities. This would result in increased species richness in a less suitable habitats relative to the same kind of habitats in the context of lower overall densities. In contrast, competition theory addresses patterns of richness within communities. In manner similar to the Fretwell-Lucas model, competitively dominant species may displace species from their preferred habitat to occupy less suitable habitats, and thus, increase their diversity (Austin 1985, Wiens 1989a). Most competition theory, however, focuses how variation in features such as within-habitat heterogeneity, local-scale disturbance, resource availability, or predation pressure mediate the potential for competitive exclusion to reduce diversity in habitats (see Palmer [1994] for a review).

At the intermediate scales of landscapes, gradient theory relates the realized niche to distribution among elements of a landscape. Gradient theory is founded in the continuum concept of plant ecology (Austin 1985), which states that species respond to environmental gradients independently of one another, according to their individual niche requirements. As a consequence, species composition changes more or less gradually along gradients, rather than responding to environmental variation as integrated community units. Gradient theory holds that environmental variation is the primary determinant of species distribution and abundance patterns above relatively fine scales (ter Braak 1994). Because patterns at intermediate scales are often contingent on variation in environmental conditions (Lawton 1999, Wiens 1999), this theory is not usually applied in a predictive manner. One broad prediction underlying the gradient approach, however, is that there is a unimodal relationship between species abundance and important environmental variables (Gauch and Whittaker 1972, ter Braak and Prentice 1988). This emerges from what Rosenzweig (1995) called the "tradeoff principle," that species tend to specialize upon a subset of the available environmental conditions. Further, Mueller-Dombois and Ellenberg (1974) specify that physiological optima (i.e. fundamental niche) and resulting abundance-response curves along ecological gradients should be bell-shaped, but that observed response curves may vary in shape due to the distribution of superior competitors. When a superior competitor is present in a landscape, the ecological optimum of an inferior competitor may not match its physiological optimum, and it may exhibit non-modal patterns, or bimodal patterns (Austin 1985). This vegetation-based model relates closely to the habitat selection models developed for animals (e.g. Fretwell and Lucas 1969). A null hypothesis derived from gradient theory is that species are randomly distributed with respect to environmental gradients. A secondary hypothesis may ask whether non-random patterns are determined solely by physiological relationships, or by the interaction of competition and physiology (Austin 1985). From the point of view of diversity, we may hypothesize that the species diversity of an area is positively related to the steepness of the environmental gradients that it contains (Gillison 1983, Burnett et al. 1998) because, all else being equal, species abundance curves rise and fall more rapidly along steep gradients and, consequently, more species will be represented per unit area.

At the broadest scales, macroecological theory examines how various aspects of the realized niche, such as physiology and resource utilization, are related to properties of the geographic range (Brown 1995). These ideas are currently receiving a great deal of attention (Lawton 1999). Macroecological theory draws upon the field of ecological biogeography (Myers and Giller 1988, Brown et al. 1996), which considers how gradual changes in niche parameters at large scales limit species ranges and create biogeographic patterns. Both McNaughton and Wolf (1970) and Brown (1984) recognized that there may be a positive relationship between niche breadth and geographic distribution. A species' niche breadth may also be determined by seasonal or historical variation in environmental conditions along latitudinal gradients, which, in turn, may determine range size and diversity patterns (i.e. Rapoport's rule; Stevens 1989). More recently, Brown and Maurer (1989; Brown 1995) argued that the physiological characteristics of species that determine reproductive power, i.e. the rate at which energy can be converted into offspring, may determine both the geographic distribution of species as well as the diversity of different taxa. Several other theories focus on the role of large-scale variation in the distribution of the environmental conditions to which species are adapted, and how this affects speciation and extinction rates (Table 2.1). Increased population sizes associated with increased habitat area, energy availability, primary productivity, and climatic favorability may lead to increased speciation and/or decreased extinction rates and determine large-scale diversity patterns. Large-scale temporal dynamics may interact with the geographic distribution of environmental conditions to affect diversity and distribution. The habitat theory of Vrba (1992), for example, asserts that the location of environmental zones on continental land masses determines whether these zones expand, contract, or disappear in the face of climate change, and thus determines speciation and extinction rates (via the effects of area).

Dispersal-based Theory

I identify two forms of dispersal-based theory. Spatial theory (*sensu* O'Neill 1999) considers how the spatial distribution and geometry of suitable habitat with respect to other, less suitable habitats affect the relationship between habitat occupancy, and landscape distribution/diversity patterns. In contrast to gradient approaches, suitable habitats are thought to occur in discrete patches embedded in a matrix of less suitable habitat. Dispersal and colonization may link populations inhabiting patches to varying degrees depending on the range of distances between patches or variation in the characteristics of the matrix elements (Wiens 1995). If the occupancy of suitable patches varies due to within-landscape variation in disturbance frequencies or demographic accidents (i.e., there is a metapopulation structure), then dispersal may govern the distribution and abundance of species in a landscape (Levins 1969, Hanski 1982, Harrison and Taylor 1997). Metapopulation modeling efforts suggest, all else being equal, that species exhibiting high dispersal rates may be more widespread in landscapes than those with low dispersal rates (Hanski et al. 1993, and see Tokeshi 1992). Dispersal from nearby habitat patches may also affect local diversity (Holt 1997). The presence of some species in an unsuitable habitat patch may be supported by source-sink relationships (Pulliam 1988), and this effect may lead to increasing local diversity and similarity in species composition where distinct habitat patches are closer together and/or the probability of between-patch dispersal is greater (the mass effect; Shmida and Wilson 1985, Nekola and White, in press).

At a broader scale, spatial patterning and dispersal determine the relationship between the distribution of species across landscapes and geographic distribution. Vicariance and dispersal biogeography (Myers and Giller 1988) address how the presence of dispersal barriers within landscapes limits the geographic distribution of species. In the case of vicariance, dispersal barriers emerge within a species range and fragment it, whereas in dispersal biogeography long-distance migrants overcome an existing dispersal barrier, but not frequently enough to establish gene flow between two populations (Myers and Giller 1988). Vicariance and dispersal biogeography can be viewed as a modification of between-habitat dispersal in which barriers to gene flow separate populations occupying suitable habitats and allopatric speciation ensues (Mayr 1963). By this process, geographic isolation leads to increasing diversity in regional species pools. The lithospheric complexity hypothesis of Cracraft (1985) predicts that regions with relatively rapid rates of geological change have a high frequency of isolation events, and this leads to relatively high species diversity.

Disturbance and Change

The temporal dynamics imposed by disturbances and other changes to habitats affect processes operating at any spatial scale (Urban et al. 1987) and play a role in both niche-based and dispersal-based theories. Disturbances to vegetation may change the environmental conditions to which animals are exposed within a habitat, and disturbances that remove individuals may alter the constraints imposed by competitors or predators (Paine 1966, Connell 1978). At broader scales, disturbances that cause local extinction within habitat patches and may contribute to metapopulation dynamics, or they may alter the characteristics of the matrix through which organisms disperse between patches (Wiens 1994). At the broadest spatial and temporal scales, climatic change and (e.g. Pleistocene glaciations) may leave a lasting imprint on diversity patterns between regions. Such change is a critical component of Vrba's (1992) habitat theory. Climate change may also induce vicariance events that lead to speciation. Eggleton et al. (1994), for example, attribute continental variation in termite generic diversity to differences in the degree of fragmentation among tropical forests during Quaternary climatic changes. This effect appears to override variation in productivity between regions. On the other hand, the impact of severe climate change or other catastrophic disturbances may vary depending upon the breadth of a taxon's geographic range, and this can produce variation in mass extinction patterns (Westrop 1991).

Linking Diversity Theory Across Scales

It is apparent from the theories represented in Figure 2.3 that an area's geographic location, the environmental characteristics and spatial patterning of habitat, and the characteristics of the taxon that constitute the community in question interact to create variation in diversity. These theories can produce complementary explanations of diversity patterns. For example, Collins and Glenn (1997) showed that, as scale increased, distribution-abundance patterns of tallgrass prairie plants conformed less to Hanski's (1982) metapopulation-based model and more to Brown's (1984) ecological specialization model. At a particular spatial scale, patterns might conform to either model, depending upon the body size and dispersal abilities of the focal taxa. Reed et al. (1993) showed that the degree to which vegetation composition is related to environmental variation may depend upon the grain (i.e. quadrat size) of the samples. At a finer grain size, pattern may be dominated by competitive interactions, whereas at broader scales the variation due to competition may be averaged out and the effects of broader-scale environmental heterogeneity become apparent.

Another way of looking at variation in diversity patterns with scale is to examine how and why species numbers or species composition change with increasing distance between equal-area samples. For example, Nekola and White (in press) suggested that variation in the rate of loss of community similarity with 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 and spatial configuration of habitat patches. In terms of variance partitioning, we might observe that several processes explain a differing percentages of the variance in richness or composition among samples at different spatial scales (Fig. 2.4). Over relatively fine scales, variance in the abundance of strong competitors might be the most important variable explaining differences in diversity. Samples distributed over broader scales might reveal the influence of both soil type and the characteristics of the matrix in which these soil types are embedded. At the broadest scales, the position of mountain ranges between groups of samples might explain the majority of the variance in composition or richness. Such generalizations, however, would be statistical; any two individual samples might vary in their diversity for different reasons.

The example above illustrates the need to understand a taxon's natural history, the nature of environmental variation at the target spatial scale, and important historical events that took place in the study area (e.g. Lonsdale 1999). The utility of particular species diversity theories will be contingent upon the locations, organisms, and scales we consider (Wiens 1999). Some features (e.g. variation in dispersal rates through a matrix or historical events) are more difficult to measure than others, and are often not considered when they should be. In these cases, we should not expect to explain much of the variation in species diversity. This, however, does not indicate that community theory is weak (contra Lawton 1999), but perhaps it is our tools or our judgments that are often weak. Existing theories offer us guidance only if we consider them with respect to spatial scale and species natural history.

The Application of Diversity Theory in Landscape Ecology

Studies of species diversity at fine scales often emphasize the role of interspecific competition in determining patterns (Reed et al. 1993, Andersen and Patel 1994), whereas continental-scale studies have focused on the effects of climate or energy (Currie 1991, Kaspari et al., in press). At the intermediate scales traditionally considered in landscape ecology, the consequences of habitat heterogeneity are believed to be the preeminent factors contributing to diversity patterns (Shmida and Wilson 1985, Turner 1989).

The consideration of habitat heterogeneity in landscapes has taken two forms. Habitats have been considered as discrete entities that exist together in a patch-matrix or mosaic pattern, and movement or dispersal between habitats is of central concern (Wiens 1995, Fig. 2.3). Applications of this concept in diversity studies have focused on how the spatial location and context of a habitat patch influence its occupancy by species, and thus, community structure (i.e. the metacommunity; Holt 1997). This approach may be important when dispersal is limited and local communities are capable of supporting many more species than they actually do (Tilman 1997). In these cases, the processes that promote or inhibit dispersal can lead to variation in diversity. Two consequences of dispersal limitation are, 1) spatial variation in local diversity patterns may be decoupled from local environmental features because some species do not occupy suitable habitats, and 2) this decoupling may inhibit competitive exclusion and promote landscape diversity because superior competitors do not reach suitable habitats (Hubbell et al. 1999). At fine scales, these processes may interact with competition via priority effects

(Cole 1983, Connolly and Roughgarden 1998). The degree to which diversity increases when dispersal limitation to a patch is alleviated by the removal of a barrier should depend upon the characteristics of the species already occupying the patch relative to those of potential invaders. At broader scales, dispersal limitation may explain cases of unusually low diversity within an isolated habitat patch (Krasnov and Shenbrot 1998). Overall, when dispersal limitation is strong, environmental patterns alone will be insufficient for predicting variation in species diversity (e.g. He et al. 1996).

In other communities and landscapes, dispersal limitation may be less important because barriers do not exist and species diversity may be strongly coupled to local environmental features. In these cases, habitat heterogeneity may be considered according to niche-based approaches such as gradient theory (Fig. 2.3). Even when particular environmental features exhibit a patchy structure in space, they can be modeled in "environmental space" using gradient approaches (Austin 1985, Krasnov and Shenbrot 1998). In particular, several studies illustrate the importance of gradients in geologic, topographic, and edaphic characteristics in driving landscape diversity patterns (Lapin and Barnes 1995, Fraser 1998). Burnett et al. (1998) formalized this idea by proposing the "geomorphological heterogeneity" hypothesis—species diversity in landscapes is positively correlated with aggregate measures of heterogeneity in soil properties, drainage, and slope and aspect. Modifications to environments by humans, such as through cultivation or grazing, may also contribute to landscape heterogeneity (Forman 1995). In some cases, geomorphological heterogeneity may be more important than land-use generated disturbances in determining diversity pattern (Nichols et al. 1995). In the case of Mesoamerican forests, however, Clark et al. (1995) found that local variation in palm tree species distributions required an understanding of soil and topographic variation as well as the activity of historical human activities, such as palm cultivation. Historical anthropogenic effects may be very important, Nabhan (1994) reports that the distribution of the rare *Agave murpheyi* is due almost entirely to their persistence in areas where they were historically cultivated by human populations.

It is likely that both habitat patchiness and environmental gradients are important in many study systems. On the one hand, environmental gradients may create habitat patchiness and create the potential for metapopulation dynamics. Crist (1998) found that topographic gradients and associated drainage patterns drove variation in the densities of shrubs that are habitat patches for termites. Whether or not gradient or patchy patterns of habitat heterogeneity are relevant will depend upon the scale at which that heterogeneity is perceived by the focal organism. At one spatial scale, a species' response to habitat variation might be best modeled as a gradient, but smaller organisms may recognize a patch-matrix structure at finer scales (Solon 1999), and attention to dispersal dynamics would be required. Beyond this, patchiness with respect to one set of variables may be superimposed upon gradients in other variables. The interaction between spatial and niche-related factors was revealed by Harrison (1999), who showed that variation in the richness of serpentine-endemic herbaceous plants among patches and areas within continuous habitat was determined by both the influence of patch size and by underlying gradients of calcium levels. Thus, the effects of habitat patchiness (e.g. forest fragmentation) should not be considered independently of undetected, but potentially important, sources of variation underlying the patches that humans recognize.

Promoting a Multiscale, Multi-organism Perspective on Diversity in Landscapes

Thus far, I have maintained an organism-centric perspective on the processes, scales, and environmental features that produce diversity patterns In order to utilize this perspective in management action, however, we must adopt an anthropocentric perspective. Biodiversity conservation and management are actuated at the relatively fixed spatial scales of hectares to kilometers, so land use decisions therefore encompass many different kinds of organismal responses to environmental variation.

The variety and contingency of the responses of functionally distinct taxa to landscape variation generates a great deal of variance in the properties of ecological communities as a whole. Lawton (1999) argued that we should abandon the complexity of community ecology in order to focus on the pursuit of generality offered at broad spatial scales. Unfortunately, it will contribute little to land management if we all became macroecologists. Conservation would be easier if we could choose between one or the other end of the latitudinal diversity gradient, but it is not this simple.

The reality is that we must continue to find ways to improve our understanding of diversity patterns within particular landscapes and regions and acknowledge that they vary in important ways in their species composition, histories, and environments. Studies that consider diversity of several kinds of organisms at multiple scales are an important front of progress. The work of Woinarski et al. (1999) illustrates one such approach. They compared the responses of birds, reptiles, amphibians, and mammals to variation in soil texture in landscapes arrayed along a regional gradient of varying precipitation in the tropical savannas of northern Australia. They found that taxa differed in their responses to soil texture, and these responses varied along the precipitation gradient. Overall, changes in species composition with variation in rainfall depended upon soil type and its spatial arrangement. Where a soil type was rare, its fauna was relatively impoverished and was similar to the site's spatially dominant soil types. Thus, the nature of local landscape variation is contingent upon the taxon examined, the spatial patterning of habitat, and the regional context. Nevertheless, the patterns that Woinarski et al. (1999) observed emerge from a few, well-understood processes (Fig. 2.3), including responses to soils (gradient theory), area and mass effects (spatial theory), and climate (macroecological theory).

A second multiscale approach considers variation among landscapes from a macroecological perspective. The influence of broad-scale processes may be identified by analyzing the constraints that they impose on the distribution of observations in a data cloud (Brown 1995). Another way of looking at this cloud that may be useful for comparing landscapes is to focus upon individual data points and ask, why do these points vary in their deviation from the constraints imposed by macroecological processes? For example, Currie (1991) examined mammalian species richness in 336 quadrats covering all of North America north of Mexico, identifying a trend of increasing richness with decreasing latitude. He found that this pattern was best explained by increasing energy availability (measured as potential evapotranspiration, PET), and concluded that energy availability imposed an upper limit on mammalian richness. The relationship revealed considerable scatter at high PET values, which Kerr and Packer (1997) interpreted as a shift in the control of richness from energy to habitat heterogeneity at high PET values. In contrast, R. L. Schooley and B. T. Bestelmeyer (unpublished) employed a constraint-line approach to identify an increasing upper limit to species richness across the full range of PET values, and considered why quadrats varied in their deviation from this constraint. Some points had strong negative deviations from the upper constraint because they were located in areas that are dominated by habitats to which species-rich mammalian taxa are poorly adapted (e.g. burrowing rodents *vis a vis* swamps). Thus, the clearest explanation of mammalian diversity patterns at both quadrat and continental scales required an understanding of both local and regional environmental variation with respect to species natural history. Further, a macroecological framework provided a useful basis with which to compare quadrats occurring within similar values of PET.

Finally, studies conducted at ecotones and biogeographic transitions can be used to tease apart the effects of different kinds of processes acting at different scales. Krasnov and Shenbrot (1998) examined how different animal groups responded to environmental variation across an ecotonal area of ca. 40 km that is situated at a biome transition between Irano-Turanian steppe and Saharo-Arabian desert vegetation in Israel. They found that the ecotone corresponded with a zoogeographic transition between distinct faunal complexes (i.e. taxa that had a similar geographic range) for tenebrionid beetles but not for rodents or lizards. Thus, the relationship between landscape and biogeographic variation differed among taxa, reflecting their distinct ecologies and histories. At a finer scale, the work of Harrison (1999) on serpentine-endemic plants described above illustrates how the transitions from continuous to patchy habitats that are often observed across ecotones (Gosz 1993) can be used to examine how broader-scale gradients in environment and the effects finer-scale patchiness on dispersal interact to determine diversity patterns. Despite the potential utility of multiple-scale studies across ecotones, a recent review suggests that these studies are still rare (Kent et al. 1997).

Concluding Remarks

Sagoff (1993) identified two ways that ecologists think about biodiversity. One is to search for general and predictable patterns using case studies that are tests of general hypotheses; general results are viewed as intellectually satisfying (MacArthur 1972, Lawton 1999). The other is to focus upon the variety of patterns emerging from the case studies themselves, "to insist upon what MacArthur calls 'tedious case histories'. This approach appreciates the individuality and contingency of particular things and claims these as the proper objects of knowledge" (Sagoff 1993). Does this mean that we need exhibit "an almost suicidal tendency...to celebrate complexity and detail at the expense of bold, first-order phenomena" (Lawton 1999)? No, there is a middle ground. Bartholomew (1982) recognized the value of generality, but not necessarily for seeking "general answers to specific questions..., but to reverse the process, and seek many special answers to each general question." General concepts and theories can be assembled in different ways to explain the species diversity in particular instances.

How do we approach the diversity of biodiversity studies in human-defined landscapes with contingent theory? One element should be a refocus of the question 'why can so many species coexist in this community' to 'why and how do richness and composition vary within this set of samples.' This orients our efforts away from single-scale, competition-based explanations of community patterns to a scale-encompassing, contingent process-driven view of diversity. We should also focus our efforts to predict diversity patterns in landscapes to interpolating rather than extrapolating sampling results (Haila and Margules 1996). In doing so, we acknowledge that landscapes are variable and essentially unpredictable from place to place. Sampling design should strive to reveal the breadth of the relationships between species composition and environment occurring within an area of specified extent in order to maximize the study's capacity to characterize biodiversity patterns. The use of gradient-oriented transects (i.e. gradsects; Gillison 1983) and stratified sampling designs can accomplish this. But how do we deal with the seemingly insurmountable variety of natural history and organismal scalings that produces the complexity that so concerned Lawton (1999)? We can at least partly overcome the logistical problems involved in characterizing the responses of different species occupying a landscape by examining a few focal taxa that represent other species with similar functional attributes (Conroy and Noon 1996). Body size and trophic level are two features that vary broadly across taxa and can be used to select focal taxa, in addition to non-functional considerations such as taxon richness (Andersen 1997) or conservation concern (Berger 1997). The assessment of landscape variation in diversity can then be informed by the responses of taxa bearing several, different organismal perspectives (Pearson et al. 1996). Ultimately, our perspective on landscapes will be contingent on the organisms and landscapes we consider, guided by an understanding of general processes. Such contingent generality may not conform to the MacArthurian ideal, but it is better than broad, but useless generality, or no generalities at all.

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Table 2.1. Theories and hypotheses explaining patterns of species diversity or distribution arranged according to theory class (based on relationships between environment and the realized niche or to dispersal) and theory group (see Fig. 3). The type of pattern addressed, some of the dominant processes used to explain the pattern, and authors of the idea are presented.

Theory type **Theory group**	Theory/Hypothesis	Pattern that varies	Causal processes	Author(s)
Niche-based				
Habitat selection	Ideal-free	Distribution/abundance	Competition Habitat selection	Fretwell&Lucas 1969
Competition	Niche diversity	Richness	Competition Within-habitat heterogeneity	MacArthur & MacArthur 1961
	Intermediate disturbance	Richness	Competition Local disturbance	Levin & Paine 1974, Connell 1978
	Intermediate productivity	Richness	Competition Resource availability	Whittaker & Niering 1975
	Density-dependent predation	Richness	Competition Predation	Paine 1966, Connell 1975
Gradient	Gradient	Distribution/abundance	Competition Abiotic tolerance	Gauch and Whittaker 1972, Mueller-Dombois &Ellenberg 1974
Macroecological	Ecological specialization	Distribution/abundance	Niche breadth	McNaughton & Wolf 1970, Brown 1984
	Range of tolerance	Distribution/abundance	Adaptation to variation in abiotic variables	Janzen 1967, Monkonnen & Welsh 1994

Table 2.1 continued.

	Habitat theory	Richness	Climate occillations Extinction/speciation	Vrba 1992
	"Habitat commoness"	Richness	Habitat area Speciation/extinction	Denslow 1980, Rosenzweig 1995
	Species-energy	Richness	Energy apportionment Speciation	Wright 1983, Currie 1991
	Climatic favorableness	Richness	Abiotic tolerances Speciation/extinction	Terborgh 1973
	Productivity	Richness	Population size Extinction probability	Rosenzweig & Abramsky 1993

Dispersal-based				
Spatial	Core-satellite	Distribution/abundance	Dispersal Habitat change Stochastic extinction	Hanski 1982, Tokeshi 1992
	Metapopulation dynamics	Richness	as above	Hanski et al. 1993
	Mass effect	Richness	Dispersal Source-sink dynamics	Shmida & Wilson 1985
Vicariance	Geographic isolation	Richness	Dispersal Speciation	Mayr 1963
	Lithospheric complexity	Richness	Geologic change Speciation	Ross 1972, Cracraft 1985

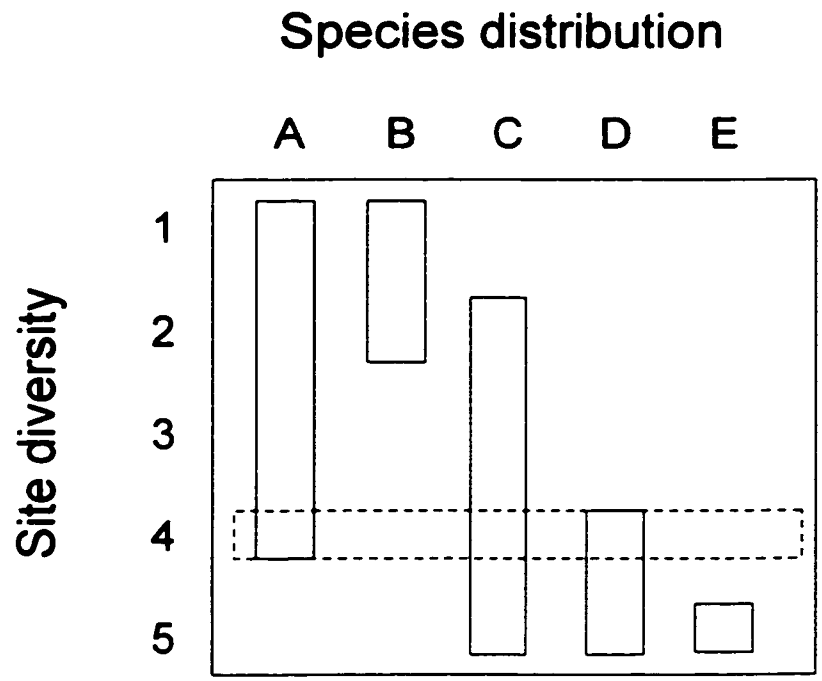

Fig. 2.1. The relationship between species distribution and site diversity. The distribution of species (A-E) across sites (1-5). Site 4 contains 3 species.

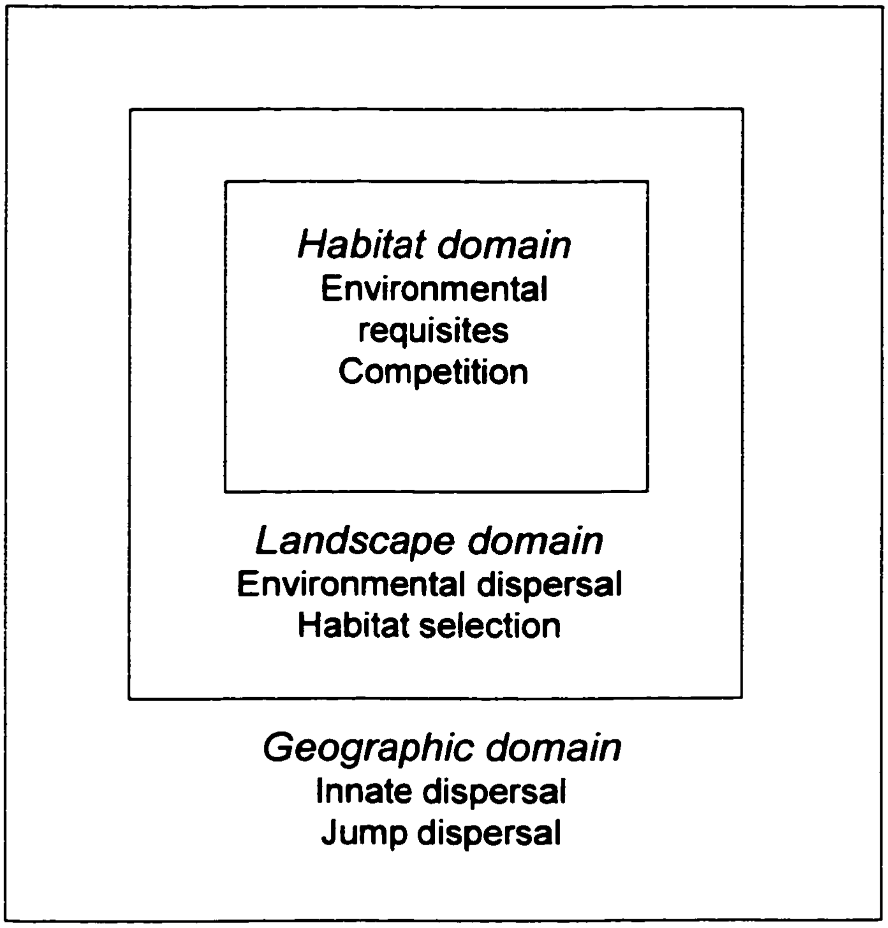

Fig. 2.2. Hierarchical relationhips among three domains of scale, and the processes that distinguish them. Adapted from Ricklefs and Schluter (1993).

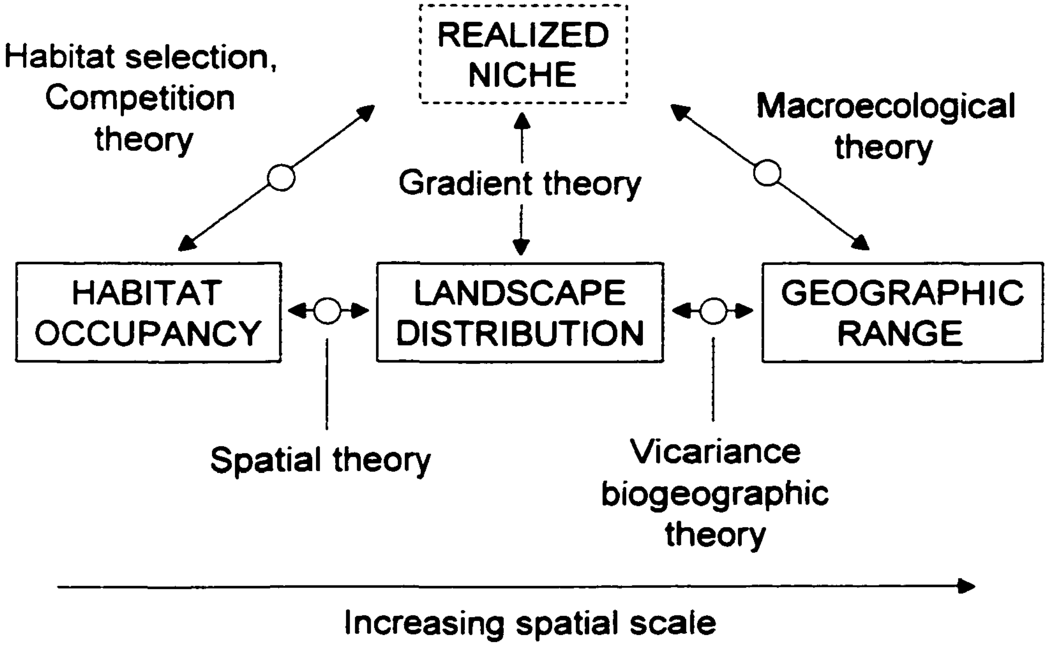

Fig. 2.3. A framework for relating five bodies of theory that explain patterns of species diversity and distribution. Theories are classified according to the organismal features that they link together (see text). Habitat occupancy, landscape distribution, and geographic range are expressed at increasing spatial scale relative to an organism, whereas the effects of an organism's realized niche are expressed at all scales. Niche-based theories link the realized niche to organismal features (vertical, diagonal arrows), whereas dispersal-based theories link organismal features at different scales (horizontal arrows).

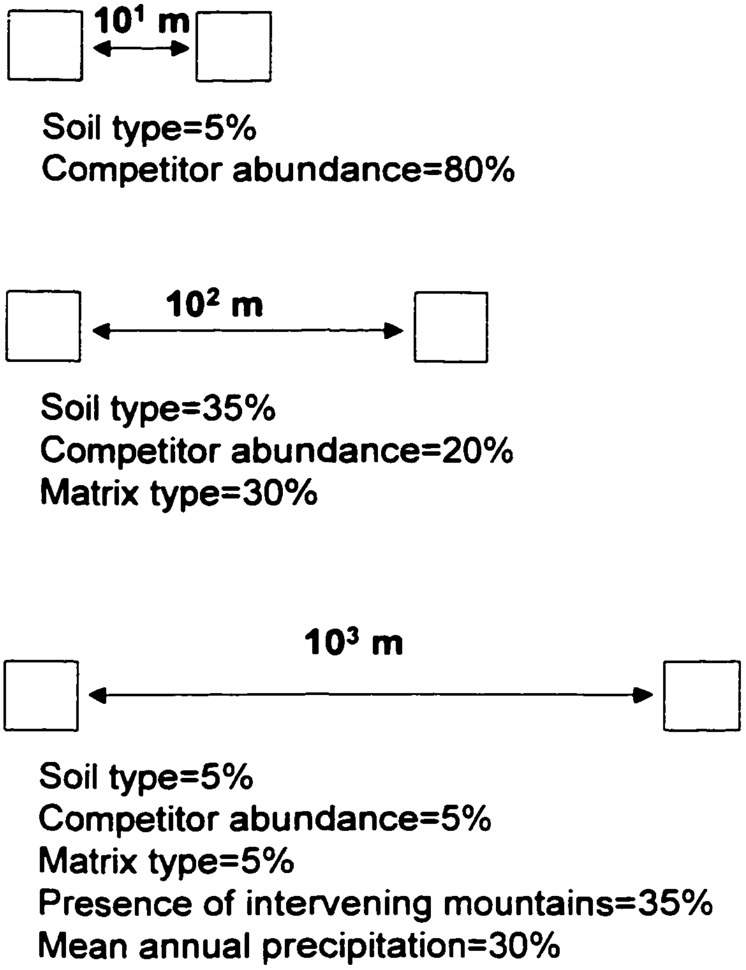

Fig. 2.4. Hypothetical results from analyses determining the relative contribution of different factors to variance in species composition or richness among sets of sites distributed over different spatial scales. Plots (squares) are of equal area and the average distance between plots is indicated. See text.

The Vantage Point

If tired of trees I seek again mankind,
    Well I know where to hie me—in the dawn,
    To a slope where the cattle keep the lawn.
There amid lolling juniper reclined,
Myself unseen, I see in white defined
    Far off the homes of men, and farther still,
    The graves of men on an opposing hill,
Living or dead, whichever are to mind.

And if by noon I have too much of these,
    I have but to turn on my arm, and lo,
    The sun-burned hillside sets my face aglow,
My breathing shakes the bluet like a breeze,
    I smell the earth, I smell the bruisèd plant,
    I look into the crater of the ant.

Robert Frost, 1949
Complete Poems of Robert Frost.
Holt, Rinehart, and Winston, New
York, NY, USA

Chapter III

ANT BIODIVERSITY IN SEMIARID LANDSCAPE MOSAICS: THE CONSEQUENCES OF GRAZING VS. NATURAL HETEROGENEITY

Abstract

The conservation of biodiversity in landscape mosaics requires an understanding of the impacts of human land use within mosaic elements and an evaluation of the biological uniqueness of different elements. I address these issues by examining patterns of ant diversity in three semiarid rangeland landscapes used predominantly for grazing. These landscapes lie along a regional gradient from shortgrass steppe through a transitional zone to desert grassland, along which climate and ant species composition vary. Within each landscape, I compared the effects of grazing and natural variation in soils and vegetation on ant diversity and community composition. Grazing had little effect on ant richness, diversity, or composition at the transitional zone or the desert grassland site, but ungrazed areas at the shortgrass steppe site had a higher overall richness and favored the abundance of some species. Some samples of saltbush (*Atriplex canescens*) shrubland were similar in richness and species composition to ungrazed samples. In both the transitional zone and the desert grassland, creosotebush (*Larrea tridentata*) dominated habitats harbored comparatively species rich and distinct ant communities. In addition, mesquite (*Prosopis glandulosa*) coppice dunes at the desert grassland site favored the abundance of several species that were rare across the site. Canonical correspondence analysis revealed that variation in soil hardness and texture best explained community variation at the shortgrass steppe site, whereas soil texture and associated differences in shrub density best explained differences in composition at the transitional and desert grassland sites. The characterization of habitats based upon vegetation classification did not adequately reflect environmental variation that was important to ants in shortgrass steppe, but reflected important soil textural variation in the transitional and desert grassland sites. These results suggest that ant conservation in these semiarid rangelands should emphasize the conservation of different soil types. The results add to a growing consensus that a variety of variables determined by the responses of several focal taxa may be needed to characterize biodiversity patterns.

Introduction

In a world increasingly dominated by human activities, a central focus of modern conservation biology is the maintenance of species diversity in landscape mosaics composed of areas of varying land use and natural habitat features (Lubchenco et al. 1991, Steffen et al. 1992). Two objectives supporting this broad goal include the identification and preservation of mosaic elements that maximize biodiversity (Prendergast et al. 1993, Wagner et al. in press) and the evaluation and minimization of negative impacts to biodiversity within mosaic elements that are exploited by humans (Pimentel et al. 1992, Wiens 1994).

Livestock grazing is one of the most extensive forms of land use. About 26% of the Earth's land surface (FAO 1996) and 70% of land in the 11 western United States (Fleishner 1994) is used primarily for grazing. Where grazing pressure is poorly managed, desertification can result in the loss of grasslands and associated species (Graetz 1994). Mabbutt (1984) estimates that 62% of the world's grasslands, and 42% of grasslands in North America, are desertified. At both regional and global scales, the magnitude of grazing-induced environmental change may be great (Wright 1990, Fleishner 1994, Wuerthner 1994), and Cooperrider (1991) considered grazing to be "one of the primary threats to biological diversity".

Ecologists and environmentalists, however, have recently debated the impacts of grazing (Brussard et al. 1994, Brown and MacDonald 1995, Curtin 1995, Fleishner 1995, Noss 1995, Wuerthner 1995). For example, some authors (Milchunas et al. 1998, Perevotsky and Seligman 1998) contend that "undergrazing" carries negative consequences for biodiversity in some situations. Several points have emerged from this debate. First, the response of biodiversity to grazing is not easily generalizable; species respond in different ways depending upon their adaptations and the environmental and historical context in which these adaptations evolved (Milchunas and Lauenroth 1993). Second, the effects of grazing on the environmental variables that underlie species' responses vary among ecosystems (Lauenroth and Milchunas 1991, Perevotsky and Seligman 1998). Finally, comparisons of biodiversity responses to grazing are often complicated by such factors as the size, position, availability, and representativeness of grazing treatments, temporal variability in grazing effects, the methods used to select study sites, the methods used to assess grazing intensity, and the measurements used to characterize biodiversity (Fleishner 1994, Brussard et al. 1995, Brown and MacDonald 1995). Clearly, there is an urgent need for carefully designed studies of grazing impacts on different taxa in different regional settings (e.g. Landsberg et al. 1997). These studies should consider the range of grazing intensities most often observed in a region and employ a variety of measures to characterize the responses of species communities.

Anthropogenic effects upon biodiversity operate within a context of naturally occurring landscape variation in soils, vegetation, and topography. Such variation may have important consequences for the distribution of biodiversity and its management (e.g. Tuomisto et al. 1995), yet we know very little about them or their relationships to human influences in most ecological systems. Because grazing management and conservation decisions are implemented at relatively large scales (Turner et al. 1995), management areas often include habitats other than the economically-important rangeland vegetation. These habitats may contain unique biotic communities that complement the overall biodiversity of landscape mosaics (Wagner et al., in press). Rangeland conservation strategies should explicitly consider the conservation value of less exploited habitats adjacent to the areas of more intense economic use (Forman 1995).

A landscape perspective may also aid our understanding of the indicator properties of focal taxa. The use of focal taxa to characterize the effects of human activities on other, unconsidered species (Kremen et al. 1993) has been necessary because exhaustive biodiversity studies are usually impossible within reasonable timeframes (Scott et al. 1993). Such focal or indicator taxa should be sensitive to a wide range of environmental variation and their ecology should be relatively well understood. If a potential indicator taxon reveals little response to anthropogenic environmental change, this may be due to its general insensitivity to environmental variation in a region (Whitford et al. 1998). Alternatively, a small response by an otherwise sensitive focal taxon may suggest that an anthropogenic change is relatively unimportant to other, similar kinds of organisms at that site. Comparing the responses of focal taxa across a range of environmental variation occurring at a site can assist in our evaluation of a focal taxon's utility (e.g. Haila and Margules 1996).

Here, I address these issues by examining the effects of different grazing regimes on ant communities (Hymenoptera: Formicidae) at three Long-Term Ecological Research (LTER) sites occurring in shortgrass steppe and desert grassland biomes of the United States. Ants have been used extensively as focal taxa in studies of human impacts throughout the world (e.g. Perfecto and Snelling 1995, Bestelmeyer and Wiens 1996, Andersen 1997, Majer and Nichols 1998) because their responses may indicate environmental patterns that determine the distribution of other organisms over a wide range of scales and environments (Andersen 1997). This may be especially true for invertebrates (Andersen et al. 1998), which constitute the bulk of animal biodiversity but seldom enter into conservation decision making (Dingle et al. 1997). Furthermore, ants are important components of ecosystems in their own right (Elmes 1991, Catangui et al. 1996). Previous studies have demonstrated that ants respond in ecologically-interpretable ways to grazing (Scougall et al. 1993, Bestelmeyer and Wiens 1996, Landsberg et al. 1997).

My approach was to examine the consequences of grazing activities in relation to natural sources of heterogeneity in soils and vegetation that may contribute to diversity patterns across landscapes (Forman 1995). In contrast to some other studies, grazing treatments were chosen to reflect the dominant rangeland management that I observed in each landscape rather than selecting highly degraded but spatially limited areas (see Brussard et al. 1995, Brown and MacDonald 1995). I compared these treatments to one another, to ungrazed areas, and to other, previously recognized vegetation types occurring within each LTER site. Instead of relying solely on land-type categorizations, I also measured the effects of grazing and natural processes on several environmental variables that are believed to affect ant distributions. Specifically, I asked 1) do general measures of ant diversity and community composition change with grazing and how do these effects vary between regions, 2) is variation in ant diversity or composition due to grazing more or less important than that generated by natural processes acting at landscape scales, and 3) do vegetation-type categorizations correspond well to the primary sources of environmental variation affecting ant community structure?

Study Areas and Methods

Study Sites, Grazing Treatments, and Vegetation Types

This work was conducted in and around the Shortgrass Steppe (SGS), Sevilleta (SEV) and Jornada (JRN) LTER sites (see Fig. 4.1). These sites span a transition from the shortgrass steppe biome (SGS) to the Chihuahuan desert biome (JRN). Grassland is the dominant vegetation type in these regions and cattle grazing is the dominant land use (Holechek et al. 1994, Lauenroth and Milchunas 1991). At each site, I sampled ants and environmental variables along 20 transects, located in areas of different grazing management within the dominant grassland type and in other, less dominant vegetation types (mostly shrublands) that were recognized in previous studies at each site. Four transects were located in each of five grazing or vegetation types (collectively referred to as 'habitats') in each site. To maintain control over variables such as climate and to facilitate regional comparisons, all transects were distributed within a 100-km^2 area in each site.

Sufficient replication, and thus precise statistical inference, is difficult at broad spatial scales (Hargrove and Pickering 1992). In order to maximize the generality of my assessments within each site, grazing and vegetation types considered in this study were selected to represent the dominant categories of vegetation and grazing management recorded by maps as well as the prevalent conditions that I observed while driving all roads in and around the 100-km^2 areas. Elevation at the transects within a site varied by no more than 58 m and I located transects away from the confounding influences of major topographic relief and watercourses. Overall, grazing types fell into the following categories: a) ungrazed areas in exclosures or reserves, b) moderate-managed grazed areas as determined by rangeland research protocols in U.S. Department of Agriculture-Agricultural Research Service sites (USDA-ARS; see Holechek et al. 1994, Milchunas et al. 1998), and c) public-leased or private lands with varied grazing management. Study areas situated in public-leased and private lands were located as near as possible to other grazing types.

Areas along networks of roads passing through the study areas were categorized according to the five habitats I studied at a site. Within a habitat, the four transects were allocated among road sections (ca. 0.5-5 km) so that the sections were as evenly distributed as possible within the study area. Most transects were then placed 100 m from the road at a randomly determined location along each section. Transects located on the other side of cattle fences from the road were placed 300 m from the fenceline in order to avoid the influence of the fence on cattle activity patterns. Transect locations that fell upon unusual terrain, such as in flooded depressions or areas near to water points (see Brown and MacDonald 1995), were avoided because they represented a minute area within the habitat and were likely to experience atypical grazing pressures. Ungrazed exclosures were selected to be interspersed with transects located in moderate-grazed treatments. Interspersion was not possible for treatments found exclusively in different administrative units, such as private land, or for other vegetation types. The grazing and vegetation types sampled in each LTER site are described below.

SGS was located in the USDA-ARS Central Plains Experimental Range (CPER) and Pawnee National Grasslands (PNG) near Nunn, Weld County, Colorado. The area receives ca. 320 mm of precipitation/yr. The shortgrass steppe vegetation is dominated by blue grama grass (*Bouteloua gracilis*). Within the CPER, I sampled moderately summer-grazed pastures and 1-ha exclosures that had not been grazed since 1939. The PNG is administered by the US Forest Service. Grazing intensity across the PNG is managed at moderate levels based on the protocols used at the CPER (R. Peterson, USDA, personal communication). Two shrubland types were sampled in the CPER: 1) patches of saltbush (*Atriplex canescens*) that typically occupy low-lying areas (Stapp 1997), and 2) soapweed yucca (*Yucca glauca*)-dominated patches often found on stony hillocks or ridges. These sites were moderately grazed in winter and spring.

SEV was located in the Sevilleta National Wildlife Refuge and on adjacent privately-owned land in Socorro County, New Mexico. The area receives ca. 265 mm precipitation/yr, and represents a transitional zone between shortgrass steppe and Chihuahuan desert grassland biomes (Gosz 1992). I sampled sites in the MacKenzie Flats area of the refuge that were dominated by black grama grass (*Bouteloua eriopoda*). The refuge has been ungrazed since 1973. The grazed transects were located in privately-owned land to the north of MacKenzie Flats. I also sampled in blue grama grasslands near the foot of the Los Piños range, creosotebush stands (*Larrea tridentata*), and ecotonal areas between creosotebush and black grama grassland.

JRN was located largely in New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC; elsewhere referred to as the College Ranch), and in the USDA-ARS Jornada Experimental Range (JER) and on Bureau of Land Management (BLM) land near Las Cruces, Doña Ana County, New Mexico. The area receives ca. 232 mm of precipitation/yr. The grassland transects were characterized by black grama and mesa dropseed (*Sporobolus flexuosa*); shrubs such as honey mesquite (*Prosopis glandulosa*) and *Yucca elata* were often common. Grazing exclosures (1-2 ha) that had been ungrazed since 1946 and moderately-grazed grassland were sampled within CDRRC and JER, and more heavily grazed areas with a greater cover of honey mesquite were sampled in the BLM land (see Holechek et al. 1994). I also sampled creosotebush shrublands along a gently-sloping bajada, as well as honey mesquite-dominated coppice dunes that often represent an irreversible transformation from grassland to shrubland due to a combination of grazing and drought (Hennessy et al. 1983, Schlesinger et al. 1990).

Sampling of Environmental Variables and Ant Communities

Features of ant communities and environmental features were measured at a maximum of 10 stations (subsamples) along each transect (10-m spacing). I measured environmental variables that are known to influence the distribution and abundance of ants. Soil texture may determine where ants nest (Johnson 1992) and may vary strongly at broad scales . Soil cores were collected at four of the 10 transect stations, so that each sample was separated by 30 m. Soil samples were collected to a depth of 24 cm using a 1-inch diameter probe. The samples were homogenized for soil texture analyses and thus represented the average soil properties encountered by ants with nest structures occurring from near the surface to a 24-cm depth. Soil texture was determined following the hydrometer method and calculations presented in Gee and Bauder (1986). For each sample, I calculated the percentage of coarse sand (particles >500 um), fine sand (53-500 um), silt, and clay. Values for the four samples were averaged to obtain values for transects.

Basal cover, the vertical complexity of vegetation, and soil strength were recorded around each station of each transect. Cover and vegetative complexity determine the microclimates to which ants are exposed (Perfecto and Vandermeer 1996) as well as nesting sites and food abundance. Soil strength may determine where ants nest. Cover and complexity of vegetation may be altered by grazing (Milchunas and Lauenroth 1989) and soil strength may increase in grazed areas due to soil compaction from livestock trampling (Bryant et al. 1972).

Basal cover at the ground surface and vertical complexity were recorded at five points along each of four 2-m long rays placed at 90° angles around each station. Points on each ray were located at 0.25, 0.5, 1.0, 1.5, and 2.0 m from the station. Cover was classified as bare ground, grass, shrub, halfshrub, forb, litter, and other. Bare ground was further subdivided into stones/pebbles (2-64 mm) and small particles (<2 mm). Percent cover was calculated for each station and then averaged across stations to obtain values for transects. Prior to analysis, cover values were arcsine-square root transformed following recommendations in Zar (1997).

Vertical complexity was measured as the number of touches of vegetation to a 1-cm diameter pole held perpendicular to the ground surface at 0-50 and 50-100 cm height intervals. Thus, areas with sparse grass cover and with short-statured grasses tend to have low complexity values, whereas areas with abundant tall-statured grasses and shrubs tend to have higher values, particularly in the 0-50-cm stratum. Vertical complexity values were summed across points within stations and averaged across stations to obtain transect values.

Soil strength was measured as the pressure (kg/cm^2) required for the end of a soil penetrometer (Pocket Penetrometer, Forestry Suppliers, Inc., Jackson, MS, USA) to penetrate the soil to a depth of ca. 6.5 mm. Soil strength was measured at four points located 0.25 cm from the sample point along each ray. Soil strength values were averaged across points within stations and averaged across stations. All soil strength measures when the surface was dry.

Ant species composition and abundance were measured using pitfall traps. Pitfall traps were polypropylene sample containers (65 mm diameter, 100 mm deep) filled with 40 ml of a propylene glycol/ethanol mixture. Pitfall traps were buried in the soil with lids on for at least 72 h to allow ants to reestablish foraging trails and become accustomed to the disturbance (Greenslade 1973). Traps within a site were operated simultaneously for 72 h during a trapping session. Trapping sessions occurred in the dry (October/November at SGS, April at SEV and JRN) and wet (June at SGS, July/August at SEV and JRN) seasons of each site over 2 years (6/96-6/98) during periods when temperatures were high enough for ants to be active. This ensured that ants with different seasonal activity would be recorded. Following trapping, pitfall traps were capped and removed to the laboratory for processing. Ant specimens in each trap were counted and identified to species or morphospecies. Most species identifications were verified by Roy R. Snelling of the Los Angeles County Museum, James Trager of the Shaw Arboretum, and William MacKay of the University of Texas, El Paso. Nomenclature follows Bolton (1995).

For each sampling period, ant abundances were ln-transformed at the trap level in order to reduce the wide variance in capture rates due to differences in the proximity of traps to nests, differences in capture rates due to the effects of varying substrate on forager movement, and differential species responses to traps (Bestelmeyer et al. in press). Furthermore, species that are poorly sampled by pitfall trapping techniques, including legionary (*Neivamyrmex*), obligate slave-making (*Polyergus*), and subterranean ants (*Hypoponera*), were excluded from analyses. The ln-transformed trap abundance values were summed to obtain transect values. These values represent scaled estimates of ant activity that may provide less biased comparisons between samples than those based on raw abundance values (Andersen 1991).

Species richness analyses considered the number of species recorded at transects over all sampling periods. For diversity and multivariate analyses (see below), the scaled transect abundance values were summed over the four sampling periods. Summing across seasons results in a sample that is less affected by seasonal or weather-induced differences in ant foraging activity than a single-season sample and thus better represents ant community characteristics at points in space (see Krasnov and Shenbrot 1998). Most colonies of ant species in this study are sessile, but their activity above ground may vary greatly depending upon season or weather events (Whitford 1978). Thus, even when ant species are unrecorded within a seasonal sample, they are likely to be present below ground and thus constitute a component of the community with respect to the characterization of a site's biodiversity (Andersen, pers. comm.). There was considerable seasonal variation in ant activity, which I consider elsewhere.

Data Analysis

I compared overall differences in environment conditions between habitats using MANOVA (Proc GLM; SAS 1996). All environmental variables, including both the soil and vegetation-related variables, were tested simultaneously. When overall tests were significant, individual variables were evaluated for differences among habitats.

Species diversity (measured as species richness and Fisher's logseries-α) were compared among habitats within sites at two spatial scales. Values were compared statistically using general linear models at the transect scale (n=4 replicates per habitat). Habitat-scale values (considering all four transects together) were unreplicated. Additionally, I used species richness extrapolation techniques (EstimateS 5.0.1; Robert Colwell) based on trap-level data (n=40 per habitat) to obtain estimates of true habitat-scale richness given that habitats may have varied in the completeness of the species sampling. Because ant abundances in traps are aggregated due to their colonial structure, only incidence-based estimators were examined (Chao 2, Incidence-based Coverage Estimator [ICE], Jacknife 1 and 2); of these, ICE was used for comparisons because its asymptote appeared most stable (see Colwell and Coddington 1994 for description). Differences among ant richness and diversity values at the transect scale were analyzed using generalized linear models (GLM; SAS 1996).

I tested for differences in species composition among habitats using the multiresponse permutation procedure (MRPP; McCune and Mefford 1999). MRPP is a nonparametric procedure for testing the hypothesis of no differences in species composition among two or more groups of samples (Zimmerman et al. 1985). The test is based upon a distance measure between samples, and I used Sørenson's distance, calculated as:

$$1 - \frac{2w}{A + B}$$

where A and B are the number of species in two samples and w is the number of species shared between the samples. This distance measure performs similarly to the more commonly used Euclidian distance, but has the advantage of de-emphasizing outliers (McCune and Mefford 1999). Tests of significance were based upon an approximated P-value from a Pearson type III distribution of the test statistic (McCune and Mefford 1999)

Correspondence analysis (CA; CANOCO 4.0; ter Braak and Smilauer 1998) was used to examine variation in community composition among habitats within sites independently of *a priori* land-type categorizations. CA is an indirect ordination technique that extracts the primary gradients in species composition/abundance patterns, independently of measured environmental variation. Specifically, I sought to assess whether or not gradients in species composition corresponded to land-type categorizations.

I used the canonical form of CA, canonical correspondence analysis (CCA), to examine how the relationships between species and significant environmental variables corresponded to land-type categorizations and to synthetic gradients observed in the species data using CA. By comparing the results of CA with those of CCA, we can evaluate how well that patterns in the species data can be explained by measured environmental variables. Congruent configurations of samples in CA and CCA ordinations increase my confidence that the important environmental variables have been measured (Økland 1996). CCA is a modification of CA in which the ordination axes are constrained to be linear combinations of measured environmental variables (i.e. direct ordination; Jongman et al. 1995). The ordination diagram reflects patterns of species composition with respect to measured environmental gradients. Significant environmental variables were selected through stepwise forward-selection procedures in CANOCO. Variables explaining a significant ($P<0.05$) amount of variation in Monte Carlo permutation tests (199 random permutations of the samples in the species data) were included in the CCA analyses. Rare species were downweighted in CANOCO. Biplot scaling was used and the CCA plots were focused on intersample distances (see ter Braak and Smilauer 1998 for discussion) using sample scores that are linear combinations of the environmental variables (ter Braak 1994). Thus, distances between sample (transect) positions in this CCA indicate chi-square distances in an ordination space defined by the environmental variables (McCune 1997). Only species for which the ordination explained $\geq$ 40% of variation in their abundance were plotted on the diagram for clarity.

I measured the degree of association of individual species with particular habitats using indicator species analysis (i.e. the indicator value method (IndVal); Dufrêne and Legendre 1997) Species were assigned indicator values for each habitat that were greatest when 1) all individuals of a species occurred in only one habitat and 2) all samples within one habitat contained an occurrence by that species. Values for each habitat varied from zero (no indication) to 100 (perfect indication). I evaluated the statistical significance of the maximum indicator values for each species using Monte Carlo randomization tests in which species abundance data was randomized among habitats (1000 iterations; McCune and Mefford 1997). Observed indicator values were then directly compared to a distribution of these values generated from randomized communities. The P-value reported is the proportion of randomized trials with values equal to or exceeding the observed values.

Results

Environmental Variables

Together, grazing-induced and natural habitat variation had significant effects on environmental variables at SGS (Wilk's λ=0.0005; F=3.84; df=40, 24.6; P=0.0004), SEV (Wilk's λ=.00015; F=5.55; df=40, 24.6; P=0.0001) and JRN (Wilk's λ=0.00004; F=6.32; df=44, 21.08, P=0.0001) sites. Below, comparisons of habitats with respect to structural variables (Table 3.1) and soil variables (Table 3.2) are discussed.

Grazing contrasts—Grazing reduced vertical complexity between the ungrazed and moderately-grazed treatments and decreased the cover of non-grass plant species at SGS (Table 3.1). Bare ground cover was greatest in both the ungrazed and public-lands grazed sites. Soil strength was lower in ungrazed exclosures than in both moderately-grazed treatments, suggesting that trampling by cattle was an important factor here (Table 3.2). The percent cover of litter, shrubs, and grass as well as soil texture did not differ among grazing treatments.

Grazing greatly reduced vertical complexity at SEV and decreased litter with an increase in bare ground. Grass basal cover was also unaffected despite the apparently large differences between the two treatments, due largely to the increased dominance of small burrograss (*Scleropogon brevifolius*) plants that were evenly distributed across the ground (personal observations). Woody plants and forbs were mostly absent from these samples. In contrast to SGS, soil strength was unaffected by grazing. Soil texture, in particular the percent of clay, differed between the grazing treatments. This is probably due to the coincidence of the fenceline between the treatments with a natural transition in soil conditions.

As at SEV, grazing tended to reduce vertical complexity at JRN and reduced litter cover while increasing the cover of bare ground. Additionally, however, the cover of grass decreased with grazing intensity and the density of mesquite shrubs was greater in the BLM land than in either CDRRC grazed or ungrazed treatments. Again, soil strength did not differ among treatments but soil texture did. The percent of coarse sand was greater in the ungrazed exclosures than in the BLM land. This may reflect a gradient in soil variation between the more southerly exclosures and the BLM transects to the north.

Natural contrasts—At SGS, both *Atriplex* and *Yucca* shrublands had similar densities of shrubs whereas few shrubs were observed in the grassland sites (Table 3.1). The cover of bare ground in the *Yucca* shrubland was greater than anywhere else, and vertical complexity was lower there than in the *Atriplex* shrubland or ungrazed grassland. Vertical complexity was similar between *Atriplex* shrubland and ungrazed grassland, due in part to the taller stature of the grasses present in this shrubland. Soil texture did not differ in any systematic way between grassland and shrubland sites, nor between the two shrubland sites (Table 3.2). *Yucca* sites were, however, more often found on well-drained ridges with a more stony soil surface. The soil strength of the *Atriplex* habitat was similar to that found in ungrazed exclosures and lower than that in other habitats.

The blue grama grassland of SEV was structurally similar to grazed black grama grassland, although this habitat had a greater proportion of coarse sand and less fine sand than the others. The *Larrea*/grassland ecotone had ground cover that was similar to the grazed and ungrazed habitats, except that vertical complexity and litter cover were intermediate between them and stone cover was greater than in either. Shrub density at the ecotone was variable and less dense than in pure *Larrea* shrublands. *Larrea* shrublands had less grass cover, greater stone cover, and lower vertical complexity than any of the other habitats. The soils of both *Larrea* habitats had a lower proportion of coarse sand than in any other habitat.

Coppice dune habitats at JRN exhibited similar bare ground cover, litter cover, grass cover and vertical complexity values to those observed in moderate and heavily grazed grasslands. Shrub densities were as high as those observed in heavily grazed grasslands. The soil texture of the coppice dunes was indistinguishable from that of the grasslands. Ground cover in the *Larrea* shrubland was similar to that in the coppice dunes, but shrub density and vertical complexity were higher. Vertical complexity was similar to that in ungrazed exclosures, due in part to large bush muhly plants (*Muhlenbergia porteri*) growing at the bases of *Larrea* shrubs. In contrast to SEV, the *Larrea* shrublands here had a higher proportion of coarse sand and less fine sand than the other sites.

Overall then, there were important, measurable differences between habitats within a site, but the nature of these differences varied greatly among sites. For example, grazing in dominant grasslands caused reductions in vertical complexity at all sites but caused decreases in grass cover only at the most arid (JRN) site, where heavy grazing also resulted in increased mesquite shrub density. Similarly, transitions between different grasslands and from grasslands to shrublands may be accompanied by changes in surface-soil texture, as with a shift to *Larrea* shrublands and blue grama grassland, or not, as with shifts to *Atriplex* and coppice-dune habitats.

Ant Communities

Ant richness and diversity—Over the duration of my sampling, I recorded 35, 39, and 41 ant species in pitfall traps at SGS, SEV, and JRN, respectively. If we restrict attention to the grazing treatments in dominant grassland, grazing had no measurable effect on transect-scale ant richness or logseries-α at any of the sites (Figs 3.1, 3.2, all P>0.10). Measured habitat-scale richness differed little among grazing treatments at SEV and JRN, but was higher in the ungrazed habitat than the other grasslands at SGS. Estimated richness (ICE), generally followed measured patterns at SGS, was slightly higher in the ungrazed than grazed habitat at SEV, and was similar among grassland habitats at JRN. Habitat-scale logseries-α differed little among the dominant grassland habitats at all three sites.

If we consider both grazing treatments and natural habitats together at each site, transect-scale richness was significantly higher in the *Larrea* habitat at JRN than the others (F=4.05; df=4, 15; P=0.020; Fig 1). Transect-scale logseries-α was higher in the *Larrea* habitat here than in either of the grazed habitats (F=2.78; df=4, 15; P=0.065; Fig 3.2). Transect-scale richness or logseries-α did not differ among habitats at either SGS or SEV (all P>0.10). Both measured and estimated habitat-scale richness and logseries-α were highest in the *Larrea* habitat at both JRN and SEV, but differed little among the other habitats. At SGS, measured and estimated habitat-scale richness and logseries-α were highest in the *Atriplex* and *Yucca* habitats.

At all sites, diversity at the habitat-scale tended to be highest in natural habitat variants. At JRN, this tendency was also found at the transect level. Grazing affected diversity measures only at the habitat scale at SGS.

<u>Ant community composition</u>—MRPP analyses revealed significant differences in species composition among habitats at SGS (T=-2.06; P=0.028), SEV (T=-6.21; P=0.000), and JRN (T=-4.27; P=0.000). Subsequent pairwise tests revealed that grazing treatments

differed significantly in species composition only at SGS, where the PNG grazed habitat differed from the ungrazed habitat, but the CPER grazed did not (Table 3.3). At SGS, the *Yucca* habitat was distinct from all but the CPER grazed habitat, and the *Larrea* habitat was distinct from all other habitats at SEV and JRN. At JRN, the coppice dune habitat was distinct from all but the CDRRC grazed habitat. Overall, differences in species composition among habitats that differed naturally (e.g. grasslands vs. shrubland) were more often significant than among grazing treatments within dominant grassland types.

For all sites, patterns of segregation of the habitat types in the space formed by the first two axes of CA were largely consistent with the results of the MRPP. At SGS, the primary axis of variation in species composition described a gradient from ungrazed and *Atriplex* transects to grazed and then *Yucca* transects (Fig. 3.3). Axis 2 corresponded to variation among sites within the shrublands. At SEV, axis 1 revealed a gradient in species composition from *Larrea*, through the *Larrea*/grassland ecotone, to black grama grassland, to blue grama grassland (Fig. 3.4). Axis 2 largely described variation within blue grama grassland transects. At JRN, *Larrea* transects were separated from grassland and coppice dune transects along axis 1, and axis 2 separated the coppice dune transects from most of the grassland transects (Fig. 3.5). Differences between the coppice dune and BLM grazed habitats found in MRPP were not reflected in the CA ordination. There was good separation of the coppice dune transects from the BLM grazed transects on axis 3, and this is likely responsible for the discrepancy.

CCA revealed significant relationships between species composition and 2 to 4 environmental variables at each site. In all three cases, both the first canonical axis and the overall relationship between species and environmental variables (all canonical axes) were significantly different from those derived from randomized data (Table 3.4).

At SGS, soil strength was negatively correlated (-0.79) with CCA axis 1 (i.e. the 'inter-set' correlation; ter Braak 1994); and increasing % clay and a decrease in the % fine sand were correlated with variation in species abundance along axis 2 (0.82 and -0.65, respectively; Fig. 3.5). The ordination shows that the relatively low values of soil strength (cf. Table 3.2) at two *Atriplex* transects and three ungrazed transects were related to their distinct species composition. Variation along axis 2 mainly separated an *Atriplex* transect with relatively high clay content from sandier *Yucca* and *Atriplex* transects. Additionally, increasing surface stone cover, poorly correlated with either axis, was related to the separation of the *Yucca* transects and a CPER grazed transect along a diagonal (cf. Table 3.3a). Variation at SEV along axis 1 was best correlated with increasing shrub density (0.92) and decreasing % of coarse sand (0.72; Fig. 3.6). Variation at JRN on axis 1 was best correlated with decreasing % fine sand (0.94) and increasing shrub density (0.77; Fig. 3.7). Shrub density was also positively correlated with axis 2 (0.46), reflecting the influence of some shrubbier BLM grazed and coppice dune sites on species composition. Overall, environmental variables related to natural habitat variation were significant descriptors of variation in species composition at all three sites, and one variable, soil hardness, was related to both grazing induced and natural habitat differences at SGS.

The percentage of variation in species composition explained by the first two axes of the CA and CCA ordinations was identical at SGS, but the percentage explained by the CCAs at the SEV and JRN was lower (14-16 %) than in the CAs (Table 3.4). Within each site, the ordinations of transects derived from CA and CCA ordinations were similar along axis 1, reinforcing my confidence that the environmental variables identified in the forward selection were related to the primary axis of variation in the species data. The results for axis 2 were less satisfactory. I did not identify an environmental variable that could explain the distinct species composition of one distant *Yucca* transect at SGS detected by CA (Fig. 3), nor for two blue grama transects at SEV (Fig. 3.4) and three coppice dune transects at JRN (Fig. 3.5).

Tests of association between individual species and habitats using the IndVal method revealed that grazing treatments, and dominant grasslands in general, possessed relatively few strong associates whereas other habitats, shrublands in particular, had many strong associates (Table 3.5). Associations of species with habitats at SGS were generally weak. *Formica densiventris* was associated with the *Atriplex* habitat and two other species with grasslands in general. No species was significantly associated with the grazing types. Because the MRPP revealed an effect of grazing, but CCA revealed that some ungrazed transects were similar to *Atriplex* transects at SGS, I performed ANOVAs to test whether the abundance of any species was affected by grazing. Only one was significantly affected by grazing, *Formica lasiodes* (F=8.04; df=2, 9; P=0.02) and was more abundant in the ungrazed habitat than the others.

In contrast to the situationat SGS, many species at SEV and JRN were strongly associated with particular habitats. At SEV, 2 species were associated with the dominant grassland, 8 with the blue grama grassland, and 8 with the shrublands. Most of the shrubland species exhibited their greatest indicator values when the combined *Larrea* and *Larrea*/grass ecotone habitats were compared with the grassland habitats, but 2 species were most strongly associated with pure *Larrea* stands. Patterns at JRN were similar to those observed at SEV. In the grassland/shrubland contrast, 3 species were associated with grassland and 9 species with shrublands. Within shrublands, 4 species were associated with coppice dunes and 10 species with *Larrea* shrublands. Within the dominant grassland type, however, few species were associated with particular grazing treatments at either SEV or JRN. At SEV, 1 species was associated with the grazed, and 1 with the ungrazed habitat. At JRN, 1 species was associated with the ungrazed habitat but none with the other grazing treatments.

A comparison of the results from the gradient-based analysis techniques (CA, CCA) with techniques based upon the *a priori* designation of habitat types (MRPP and IndVal) illustrate that the environmental variation to which ant composition responded did not always differ systematically among habitats. For example, at SGS, relatively high abundances of species such as *Formica obscuripes, F. limata*, and *F. lasiodes* were related to low soil strength values (Fig. 3.6), but transects with low soil strength were present in both ungrazed and *Atriplex* habitats. Further, another *Atriplex* transect exhibiting high clay content had high abundances of species such as *Monomorium minimum* and *Tapinoma sessile*.

In contrast, environmental variables important to ants differed among habitat types at both SEV and JRN. At SEV only 1 of the 8 species displayed in the CCA did not associate with an *a priori* habitat. At JRN, 1 species of 7 did not associate with a habitat. In contrast, only 3 of 11 species displayed at SGS revealed habitat associations using IndVal.

Discussion

The Effects of Grazing

The effects of grazing on the dominant grassland environments examined here were great, and correspond well with results found in previous studies at JRN (Holechek et al 1994) and SGS (Milchunas and Lauenroth 1989, Milchunas et al. 1989) sites. In general, grazing resulted in a simplified vegetation structure; at all three sites foliage complexity was significantly and substantially reduced by grazing. There were important differences, however, in other impacts of grazing among the sites. The maximum impact of grazing on vertical complexity increased along the aridity gradient, from a 40% reduction at SGS to 62% at SEV to 77% at JRN (Table 3.1). This reduction was accompanied by a reduction in grass cover at JRN but not at SEV or SGS. Grazing appeared to result in soil compaction at SGS, but not at the more southerly sites. At JRN, heavier grazing resulted in increased shrub densities but this effect was not observed at SEV and might even have been reversed at SGS where woody halfshrubs increased in ungrazed exclosures (Milchunas et al. 1989; Table 3.1).

Despite the strong effects of grazing on soil properties and/or vegetation, an effect of grazing on ant diversity was observed only at SGS, where habitat-scale richness was higher in the ungrazed habitat (Figs 3.1 and 3.2). There were no effects on richness or logseries-α at any site at transect scales. The results at SEV and JRN are consistent with those found in other studies that have considered grazing impacts on ants. Both Bestelmeyer and Wiens (1996) and Landsberg et al. (1997) found little effect of grazing on overall ant species richness in the semiarid woodlands of northern Argentina and central Australia, respectively. Both of these studies, however, detected important changes in species composition with differences in grazing intensity. In this study, changes in species composition were detected only at SGS (Table 3.3). Nonetheless, the variable composition of the ungrazed treatments apparent in CA and CCA (Figs 3.3 and 3.6) indicate that the effects of grazing exclosures were not consistent. Of 35 species, only *Formica lasiodes* exhibited a significant response to grazing. Additionally, the large, conspicuous nests of the thatching ant, *F. obscuripes*, occurred only in three of the ungrazed exclosures in the grassland (one nest per exclosure). I never observed these nests in grazed grasslands at the site.

The mechanisms by which *F. lasiodes* and *F. obscuripes* responded to grazing at SGS differed. It is unclear why *F. lasiodes* was more abundant in ungrazed sites, although its response may be related to a preference for nesting in less compact soils (Fig. 3.3). My observations of *F. obscuripes* suggest that its local distribution may be limited by the availability of woody plant material with which to build its large nests. The presence of this species in only the *Atriplex*, *Yucca*, and ungrazed habitat is consistent with this suggestion. In the ungrazed habitat, the woody parts of halfshrubs and forbs that were favored there, such as *Artemisia frigida*, were used as building materials (BTB, personal observations).

Why were there no responses to grazing at either SEV or JRN, despite the profound changes in vegetation cover? Two explanations come to mind, based upon hypothesized mechanisms that mediate the effects of grazing on ant populations,. First, the changes in vegetative cover or stature may not significantly alter the microclimates to which foraging ants are exposed. Thus, even though grazing at JRN dramatically increased the cover of bare ground, bare ground was still the dominant cover type in ungrazed grassland (Table 3.1). Diurnally-foraging ants will likely be exposed to unshaded, dangerously hot microclimates (e.g. Marsh 1985) while foraging in desert grassland environments, irrespective of differences in grass cover. Second, ant species nesting in vegetation may be flexible with respect to the type of vegetation in which they nest. Workers of *Forelius pruinosus* at JRN, for example, nested most frequently at the bases of grasses in the ungrazed habitat but nested more often under mesquite shrubs and snakeweed (*Xanthocephalum* spp.) in the BLM grazed area (Chapter 6).

The desert grassland ant fauna has been exposed to large temporal variations in environmental conditions throughout the Holocene (Van Devender 1995). Gibbens and Beck (1988) report that the worst drought at JRN in 350 years occurred in the 1950s, leading to great reductions in the basal cover of black grama grass. Thus, the ant species persisting at JRN have probably been exposed to and tolerate relatively desertified conditions. In general, drought events have a greater impact on patterns of grass cover than does grazing (Herbel et al. 1972, Gibbens and Beck 1988) and may also have acted as a climatic extinction filter (*sensu* Balmford 1996) and eliminated those species which would be sensitive to contemporary grazing impacts. Janzen (1967) first recognized that organismal adaptation to spatial heterogeneity may be closely linked to adaptations to temporal variation in environmental conditions (see also Mönkkönen and Welsh 1994). Understanding and predicting the consequences of anthropogenic impacts on biodiversity requires a knowledge of the range of environmental conditions to which species are exposed in space and time.

The Role of Natural Landscape Heterogeneity

Natural environmental features, in particular soil texture and associated changes in vegetation cover, were often better correlates of variation in ant richness and composition than was grazing-induced variation. This was clearly true at SEV and JRN. At both sites, habitat-scale species richness was greatest in the *Larrea* habitat, as was transect-scale richness at JRN. This pattern was paralleled by relatively large shifts in species composition between the *Larrea* sites and the others. Indicator species analysis revealed that many more species were strongly associated with particular natural habitat variants, especially *Larrea* shrublands, than with grazing-treatment variants.

At SGS, both grazing and natural environmental variation were important. The *Atriplex* and *Yucca* habitats were the most species rich at the habitat scale and the *Yucca* habitat differed from most other habitats in species abundances (Table 3.3). Variation in soil texture was related to patterns of species abundance. The most important component of environmental variation affecting species composition (i.e. soil strength), however, may have resulted from both grazing-induced and natural processes. Two of the low soil strength *Atriplex* transects had relatively high values of % fine sand (Fig. 3.3), thus both the resistance of sandier soils to compaction and a lack of grazing may effect species composition in similar ways.

The processes affecting ant diversity at the coppice dunes at JRN may also be interpreted as a combination of anthropogenic (grazing) and natural (drought) effects (Buffington and Herbel 1965, Hennessy et al. 1983). I failed to measure an environmental variable that mediated the differences in species composition observed between the coppice dune and the BLM grazed and ungrazed habitats. It is possible that soil characteristics below 24 cm, differing patterns of surface water runoff, or differences in vegetation patch size (Schlesinger et al. 1990, Ludwig et al. 1994) may affect ant nest-site characteristics. For example, Snelling (1976) noted that *Myrmecocystus romainei*, an indicator species of the coppice dunes (Table 5), exhibited a peculiar nest structure, relative to other members of the genus, that is presumably an adaptation to nesting in deep, soft sand. The association of *Trachymyrmex smithi* with coppice dunes, on the other hand, is clearly related to the presence of large mesquite patches that provide both shade and abundant litter for fungus cultivation (Schumaker and Whitford 1974).

Environmental Variation and Habitat Typology

The environmental variables emerging from the CCA were often able to explain the differences in ant composition between habitats that were detected by MRPP and IndVal; the exception was the coppice dune habitat at JRN discussed above. The most important variation in species-environment relationships often corresponded well to the *a priori* typology of natural habitats based upon vegetation characteristics (i.e. grassland/ shrubland types) at the SEV and JRN, but this matching was less apparent at the SGS site. The *Atriplex* transects, for example, varied widely in their characteristics, ranging from moderate to high soil strength and from relatively clay soils to sandy soils. In addition, one *Yucca* transect located in a 'blowout' harbored a high abundance of two species (*Lasius neoniger* and *Formica bradleyi*) not recorded elsewhere at the SGS site. As with the coppice dune habitat, the depth and looseness of the sand is an important feature for ants such as *F. bradleyi* (Halverson et al. 1976), but these features were not quantified in this study. The small number of species exhibiting significant habitat associations with IndVal at SGS is another indication of the incongruence between what ants recognize as important environmental variation and a vegetation-based habitat typology.

The idea plant and animal communities may not be tightly associated is not new. Charles Elton recognized this over 70 years ago (McIntosh 1985). Nonetheless, this observation has critical importance for modern efforts to conserve biodiversity. Landscape pattern inferred from remote sensing of vegetation formations (e.g. from LANDSAT imagery; Scott et al. 1993) may not adequately reflect the variation that is important to some animal taxa (Short and Hestbeck 1995). Such a lack of congruence can occur in animals that are directly affected by features such as soil texture, and respond to variation in soil texture differently from plant communities. Another problem that may be of particular relevance to small animals such as arthropods is that important environmental variation occurring below the resolution of vegetation maps may be ignored (Edwards et al. 1996). Recognizing the uniqueness of small patches of sandy-blowout habitat at SGS might be precluded by both of the problems mentioned above.

In other cases, however, the distribution of plant communities may covary with animal distributions. This may occur when there are parallel responses to variation in soil properties or when the distribution of animal species is directly linked to that of particular plants. Part of the strong relationship between plant-defined and ant communities at SGS and JRN, for example, is due to ants such as *Crematogaster larreae* (Table 3.5) that nest exclusively at the base of creosotebush shrubs (so far as is known; Buren 1968). Other species, such as *C. depilis*, are more catholic with respect to shrub species, also nesting in woody shrubs.

Even when plant and animal distributions are concordant within one landscape, this association may break down across a region. Indicator species analysis results for *Pogonomyrmex imberbiculus* revealed that this ant was associated with creosotebush at JRN and blue grama at SEV. These habitats occurred on soils with a high percentage of coarse sand (Table 3.2), whereas at SEV, creosotebush shrublands occurred on soils with a low percentage of coarse sand. Thus, it appears that the abundance of *P. imberbiculus* is favored by coarse sand (Figs 3.7 and 3.8), but varying plant-soil relationships between SEV and JRN led to differing plant community-ant associations between these sites. It is clear that animal species differ in the nature of their responses to landscape heterogeneity, and a broad-scale understanding of species distribution and natural history is necessary to assess biodiversity-habitat relationships (Ingham and Samways 1996).

Implications for Biodiversity Conservation and Bioindication

Cooperrider (1991) stated that the "available evidence indicates that livestock grazing has profound ecological costs", among them, "...reductions in species richness, and changing community organization." This statement is not supported by the results presented here. At most, grazing affected the abundances of some taxa, but did not result in a great degree of species turnover or loss. Clearly, species vary in their sensitivity to grazing, but ants are not unique in their resistance to grazing impacts in the landscapes studied here. Working at SGS, Milchunas et al. (1998) reported that the composition of some taxa, such as birds and macroarthropods were responsive to grazing, but others, including plants, soil microarthropods, and nematodes, were little affected. At JRN, one mammal species, the banner-tailed kangaroo rat (*Dipodomys spectabilis*), declined in abundance in areas transformed from black grama grassland to mesquite-dominated coppice dunes, but the richness and relative abundances of other mammals and breeding bird species were not adversely affected (Whitford 1997).

It is possible that grazing-induced heterogeneity may increase biodiversity in these semiarid landscapes. For example, in shortgrass steppe the mountain plover (*Charadrius montanus*), a bird species that is Federally listed as threatened, nests primarily in heavily grazed areas, whereas increases in plant species richness in ungrazed areas are due to exotic, weedy species (Milchunas et al. 1998). Whitford (1997) reported that the species richness of both birds and mammals was higher in shrublands, and shrubland communities included those species found in grasslands. Several ant species that are otherwise rare at JRN are also found in coppice dune sites.

Nonetheless, the lack of response by ants to grazing-induced changes in vegetation led Whitford et al. (1999) to conclude that ants were not useful indicators of faunal diversity patterns in rangeland ecosystems. There is evidence that most non-ant taxa so far examined do not exhibit strong responses to grazing at JRN either (Whitford 1997). Ants do, however, respond to gradients in soil texture and vegetation that are potentially important to other taxa. Other authors have indicated that variation in soil texture may have important effects on arthropod diversity patterns in steppe and desert grasslands (Crawford 1988, Crist and Wiens 1996, Stapp 1997). The value of shrubs for maintaining both arthropod (Stapp 1997, Bestelmeyer and Schooley 1999) and vertebrate (Stapp and Van Horne 1997, Whitford 1997) biodiversity has also been recognized. An evaluation of the utility of ants as bioindicators in rangelands awaits parallel studies of the responses of ants and other taxa to different soil texture and vegetation gradients.

The perception of ecological degradation in many rangelands may be rooted in a paradigm that assumes the existence of some set of 'normal,' equilibrial, and desirable ecological conditions (Sullivan 1996). The temperate forest systems for which this paradigm was developed may conform to this notion (Wiens 1984); animal diversity patterns may be closely linked to vegetation structure because vegetation structure is relatively stable over time. This is clearly not the case in semiarid rangelands, where periodic changes in vegetation, due to drought (Herbel et al. 1972) or bison grazing (Milchunas et al. 1988) may be the rule rather than the exception, and the dynamics of animal and plant populations are decoupled (Wiens and Rotenberry 1981, Westoby et al. 1989). A focus on vegetation patterns colors not only how we perceive environmental degradation, but how we evaluate biodiversity within what humans recognize as different environments.

Ecologists must qualify both the recognition of degradation and the evaluation of habitat heterogeneity from the perspective of their study organisms (Levins 1968, Kolasa and Rollo 1991). From this perspective, "human transformations of nature merge with natural processes: there are no absolute standards to distinguish between human-induced and natural change" (Haila and Margules 1996). A focus on the correlations between the composition of different taxa and carefully-selected environmental variables at broad scales can aid our understanding of the relationships between human-induced and natural variation. An evaluation of the impact of this variation on patterns of biodiversity may need to be based upon the responses of a variety of fundamentally different organisms, and consensus may, or may not, be reached. The ants of the shortgrass steppe and desert grassland sites I examined tell us that variation in soil properties, whether of human or natural origin, is of paramount importance.

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Table 3.1. Mean values (1 SE in parenthesis) of habitat structural variables measured at transects (n=4) in each habitat of each site (see text). Grazing contrasts are italicized, other habitat types are not. Superscript letters within columns indicate that a variable differed significantly among habitats within a site (ANOVA, $p < 0.05$); values with different letters are significantly different at $p < 0.05$ (LSD). The units for vertical complexity are number of hits/station (see text) and shrub density is the number of shrubs within 5 m of a station. Vertical complexity at 0.5-1 m was not analyzed at the SGS and SEV sites because too few hits were recorded in that stratum.

Site	Ground cover (%)					Shrub	Vertical complexity	
Habitat	Total bare	Stones	Grass	Forb/Subshrub	Litter	density	0-0.5 m	0.5-1 m
Shortgrass Steppe								
PNG grazed	8.0 (1.7)^{b}	0^{b}	46.8 (8.3)	0^{c}	40.8 (7.5)	0^{b}	56.5 (3.2)^{c}	---
CPER grazed	3.3 (0.9)^{c}	0^{b}	58.9 (0.9)	1.0 (0.4)^{ab}	34.1 (0.7)	0^{b}	63.5 (2.3)^{bc}	---
Ungrazed	4.6 (1.1)^{bc}	0.1 (0.1)^{b}	48.4 (11.3)	1.6 (0.6)^{a}	41.5 (9.9)	0.19 (0.19)^{b}	94.4 (5.1)^{a}	---
Atriplex shrub	3.0 (0.5)^{c}	0^{b}	37.9 (6.4)	0.4 (0.2)^{bc}	55.4 (6.8)	16.2 (4.7)^{a}	83.6 (14.5)^{ab}	---
Yucca	21.3 (3.3)^{a}	1.5 (0.5)^{a}	28.8 (1.5)	0.6 (0.5)^{abc}	43.6 (4.2)	22.7 (2.2)^{a}	57.2 (6.1)^{c}	---
Sevilleta								
Grazed	63.3 (5.5)^{abc}	0.3 (0.1)^{c}	9.1 (1.9)^{ab}	0	21.5 (2.2)^{c}	0.5 (0.2)^{b}	34.3 (2.0)^{cd}	---
Ungrazed	53.4 (6.7)^{c}	0.7 (0.3)^{c}	8.6 (2.8)^{ab}	0	36.0 (5.2)^{a}	0.9 (0.5)^{b}	88.9 (10.6)^{a}	---
Blue grama	66.9 (2.2)^{ab}	1.0 (0.4)^{bc}	10 (1.4)^{a}	0.1 (0.1)	21.1 (3.3)^{c}	0.6 (0.4)^{b}	51.2 (6.5)^{bc}	---
Larrea/grass	58.9 (2.6)^{bc}	2.1 (0.4)^{b}	4.8 (1.2)^{b}	0.5 (0.2)	32.9 (2.4)^{ab}	11.9 (5.5)^{b}	56.5 (5.7)^{b}	---
Larrea shrub	72.6 (2.7)^{a}	4.2 (0.7)^{a}	0.4 (0.2)^{c}	0.1 (0.1)	25.0 (2.7)^{bc}	38.8 (8.0)^{a}	28.1 (3.0)^{d}	---
Jornada								
BLM grazed	75.3 (2.5)^{a}	0.2 (0.1)	1.3 (0.3)^{b}	0.3 (0.1)	21.9 (2.9)^{b}	6.1 (1.4)^{b}	16.5 (1.9)^{b}	4.2 (1.4)^{b}
CDRRC grazed	59.1 (5.8)^{bc}	0.6 (0.2)	3.9 (2.4)^{ab}	0.1 (0.1)	36.3 (5.6)^{ab}	2.7 (0.5)^{c}	33.1 (8.6)^{ab}	3.2 (1.3)^{b}
Ungrazed	46 (3.9)^{c}	1.7 (0.7)	7.0 (2.1)^{a}	0	45.3 (3.0)^{a}	2.0 (0.4)^{c}	70.6 (14.2)^{a}	1.0 (0.8)^{b}
Coppice dune	68.0 (7.3)^{ab}	0.3 (0.2)	0.5 (0.2)^{b}	0.3 (0.1)	29.5 (7.5)^{b}	6.0 (1.1)^{b}	22.0 (2.7)^{b}	8.2 (2.5)^{b}
Larrea shrub	70.1 (5.3)^{ab}	1.5 (1.3)	2.0 (1.4)^{b}	0.1 (0.1)	24.6 (5.0)^{b}	16.3 (0.7)^{a}	70.9 (29.8)^{a}	18.4 (5.7)^{a}

Table 3.2. Mean values (1 SE in parenthesis) of soil variables measured at transects (n=4) in each habitat of each site (see text). Grazing contrasts are italicized, other habitat types are not. Superscript letters within columns indicate that a variable differed significantly among habitats within a site (ANOVA, $p < 0.05$), values with different letters are significantly different at $p < 0.05$ (LSD). Soil strength is reported in kg/cm^2.

Site	Soil texture (%)			
Habitat	Coarse sand	Fine sand	Clay	Soil strength
Shortgrass Steppe				
PNG grazed	6.3 (1.8)	60.2 (4.3)	20.0 (2.5)	3.5 (0.4)^{a}
CPER grazed	4.3 (1.0)	63.3 (2.0)	20.3 (1.5)	3.4 (0.1)^{a}
Ungrazed	6.6 (1.7)	63.6 (2.1)	18.5 (0.9)	2.2 (0.3)^{b}
Atriplex shrub	6.7 (3.0)	57.4 (11.3)	20.0 (7.3)	2.3 (0.4)^{b}
Yucca	9.1 (2.7)	62.0 (5.6)	17.6 (2.6)	2.8 (0.1)^{ab}
Sevilleta				
Grazed	15.3 (3.2)^{b}	49.6 (4.8)^{a}	20.6 (2.4)^{a}	1.3 (0.3)
Ungrazed	19.3 (3.3)^{b}	58.0 (5.4)^{a}	13.4 (0.9)^{b}	0.8 (0.0)
Blue grama	28.6 (0.9)^{a}	31.1 (0.9)^{b}	21.7 (2.3)^{a}	1.2 (0.1)
Larrea/grass	8.1 (1.9)^{c}	48.7 (1.1)^{a}	22.8 (1.6)^{a}	0.7 (0.3)
Larrea shrub	8.3 (1.7)^{c}	48.9 (1.6)^{a}	21.5 (0.6)^{a}	0.5 (0.3)
Jornada				
BLM grazed	5.2 (1.0)^{c}	77.3 (2.7)^{a}	10.9 (0.9)^{b}	0.2 (0.0)
CDRRC grazed	7.8 (1.8)^{bc}	73.1 (3.4)^{a}	11.8 (1.3)^{ab}	0.3 (0.1)
Ungrazed	9.8 (0.8)^{b}	69.8 (2.3)^{a}	11.7 (1.0)^{ab}	0.2 (0.0)
Coppice dune	7.5 (1.0)^{bc}	76.9 (2.4)^{a}	9.9 (1.6)^{b}	0.2 (0.0)
Larrea shrub	25.5 (3.8)^{a}	45.2 (1.8)^{b}	15.7 (1.2)^{a}	0.5 (0.2)

Table 3.3. The results of multiresponse permutation procedure (MRPP) analyses testing the hypothesis that transects grouped by habitat type differed significantly from one another in species composition. Overall tests for between group heterogeneity were highly significant (see text). The value in the top cell of each contrast is the T statistic (see text) and the value in parentheses indicates the probability that the observed segregation of groups based on Sørensen distances could be observed in randomized data. Bold indicates significance at $P < 0.05$, italics indicate marginal significance at $P < 0.07$. N= 4 for all groups.

a) Shortgrass Steppe

Habitat	PNG grazed	CPER grazed	Ungrazed	Atriplex
CPER grazed	1.13	-----		
	(0.905)			
Ungrazed	-2.30	-0.53	-----	
	(0.020)	(0.272)		
Atriplex	-1.68	-0.20	1.09	-----
	(0.057)	(0.394)	(0.873)	
Yucca	-2.72	-0.65	-2.53	-2.06
	(0.012)	(0.234)	**(0.009)**	**(0.026)**

b) Sevilleta

Habitat	Grazed	Ungrazed	Blue grama	Larrea/grass
Ungrazed	-0.02	-----		
	(0.422)			
Blue grama	-0.59	-1.44	-----	
	(0.242)	(0.088)		
Larrea/grass	-1.68	-1.32	-3.67	-----
	(0.064)	(0.099)	**(0.006)**	
Larrea	-3.61	-4.09	-4.15	-4.00
	(0.006)	**(0.006)**	**(0.006)**	**(0.005)**

c) Jornada

Habitat	BLM grazed	CDRRC grazed	Ungrazed	Coppice dune
CDRRC grazed	-1.35	-----		
	(0.100)			
Ungrazed	-1.11	0.31	-----	
	(0.134)	(0.574)		
Mesquite dune	-2.32	-0.68	-2.20	-----
	(0.033)	(0.242)	**(0.024)**	
Larrea	-2.80	-1.95	-3.23	-3.15
	(0.013)	**(0.035)**	**(0.005)**	**(0.008)**

Table 3.4. The percentage of variation in the species abundance data explained by the first two ordination axes in correspondence analysis (CA) and canonical correspondence analysis (CCA), and F-statistics for significance tests of the first canonical axis and all canonical axes. All tests were significant at the P=0.005 level (Monte Carlo permutation tests).

Site	% of species variation explained in CA	% of species variation explained in CCA	F of CCA axis 1 test	F of CCA all axes test
SGS	30.1	30.4	3.121	2.847
SEV	52.4	36.4	5.925	4.870
JRN	41.2	27.2	3.822	3.169

Table 3.5. Indicator species (see text) of habitat types for which indicator values (IndVal) were significantly different from that expected from randomized data, organized by site. Values reported are those for the habitat type where maximum indicator values were attained. Two sets of analyses were performed: first grouping transects of related habitat types into broader categories (usually grassland vs. shrubland) and then analyzing them grouped by their narrower habitat type (italics). When a species exhibited significant indicator properties in both analyses, the species name appears in bold next to the grouping in which its maximum IndVal was attained. Relative abundance = the average abundance of a species in the habitat type divided by the average abundance of that species in all habitat types. Relative frequency = the percentage of transects in the habitat type in which a species was present (both expressed as percentages). The P value denotes the proportion of randomized data sets that had a greater maximum indicator value.

Site	Habitat type	Indicator species	Relative abundance	Relative frequency	Maximum IndVal	P
SGS	Grassland	*Lasius crypticus*	72	100	72.2	0.004
		Tapinoma sessile	71	100	70.7	0.021
	Atriplex	*Formica densiventris*	83	75	62.3	0.031
SEV	Grassland	*Pheidole longula*	55	100	55.3	0.022
		Pogonomyrmex maricopa	90	88	79.1	0.000
	Grazed	*Pogonomyrmex maricopa*	45	100	45.1	0.040
	Ungrazed	*Myrmecocystus navajo*	42	100	42.0	0.019
	Blue grama	*Brachymyrmex minutus*	100	50	50	0.026
		Crematogaster punctulata	98	75	73.3	0.009
		Crematogaster navajoa	100	50	50	0.037
		Dorymyrmex smithi	100	50	50	0.027
		Pheidole cerebrosior	73	75	55.1	0.040
		Pheidole sp. J1	95	75	70.9	0.008
		Pogonomyrmex imberbiculus	75	100	74.6	0.005

Table 3.5 continued

		Pogonomyrmex apache	100	50	50	0.033
	Shrubland	***Crematogaster depilis***	100	88	87.5	0.001
		Dorymyrmex insanus	59	100	59.3	0.006
		***Dorymyrmex* sp. S1**	100	63	62.5	0.031
		Forelius mccooki	77	100	77.1	0.000
		Leptothorax olbiquicanthus	77	100	77.3	0.000
		Leptothorax sp. J1	95	50	47.3	0.050
		Myrmecocystus placodops	79	100	79	0.002
		Pheidole soritis	81	100	70.9	0.008
	Larrea/grass	*Leptothorax olbiquicanthus*	58	100	58.1	0.001
	Larrea	*Crematogaster depilis*	60	100	60.4	0.015
		Dorymyrmex insanus	47	100	46.5	0.000
		Dorymyrmex sp. S1	79	75	58.9	0.046
		Forelius mccooki	52	100	52.4	0.005
		***Leptothorax* sp. J1**	95	100	94.7	0.000
		Pheidole soritis	73	100	72.6	0.000
		Pheidole tepicana?	77	75	57.9	0.027
JRN	Grassland	*Myrmecocystus mimicus*	72	100	72.1	0.004
		Pogonomyrmex desertorum	72	100	71.8	0.003
		Solenopsis krockowi	80	100	80.3	0.002
	Ungrazed	*Monomorium minimum*	48	100	48.3	0.016
	Shrubland	*Crematogaster depilis*	94	50	46.9	0.041
		Crematogaster larreae	100	50	50	0.013

Table 3.5 continued

	Dorymyrmex insanus	84	75	63.1	0.031
	Myrmecocystus depilis	66	100	66	0.033
	Pheidole sciophila	98	75	73.5	0.002
	Pheidole tusconica	100	38	37.5	0.047
	Pogonomyrmex californicus	84	100	84.2	0.002
	Tetramorium spinosum	100	50	50	0.013
	Trachymyrmex smithi	89	63	55.3	0.025
Coppice dunes	*Myrmecocystus romainei*	74	100	73.8	0.004
	Pogonomyrmex californicus	43	100	42.7	0.039
	Pogonomyrmex maricopa	68	100	67.6	0.022
	Trachymyrmex smithi	83	100	82.9	0.002
Larrea	***Crematogaster depilis***	91	100	91.0	0.000
	Crematogaster larreae	100	100	100	0.000
	Dorymyrmex insanus	72	100	72.0	0.000
	Pogonomyrmex imberbiculus	43	100	43.3	0.009
	Leptothorax carinatus	86	75	64.8	0.028
	Myrmecocystus depilis	35	100	34.8	0.039
	Pheidole sp. J1	60	100	60	0.012
	Pheidole sciophila	89	100	89.2	0.005
	Pheidole tucsonica	100	75	75	0.018
	Tetramorium spinosum	100	100	100	0.000

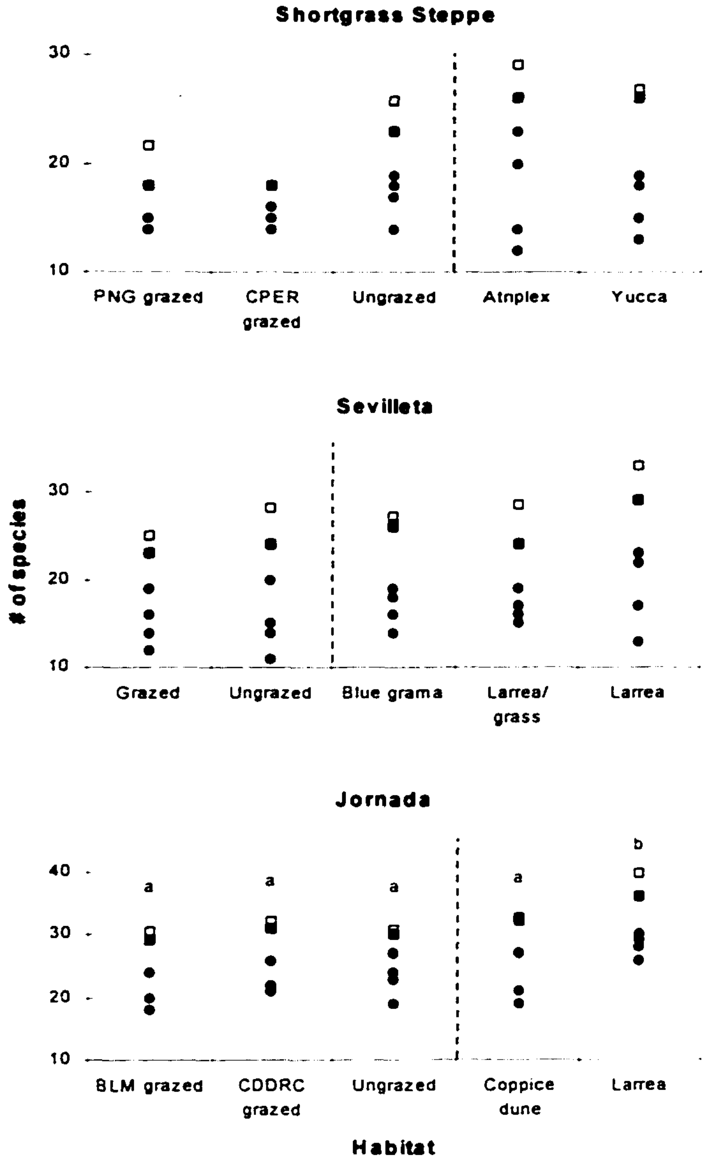

Fig. 3.1. Species richness patterns at the SGS, SEV, and JRN sites. Grazing contrasts are on the left side of the dashed line. Measured richness values at transects (n=4; solid circles), at the habitat scale (solid square), and a habitat-scale richness estimate (incidence-based estimator (see text); open square) are presented for each habitat at each site. Habitats sharing letters are not signficantly different in post-hoc tests of richness at transect-scale (LSD).

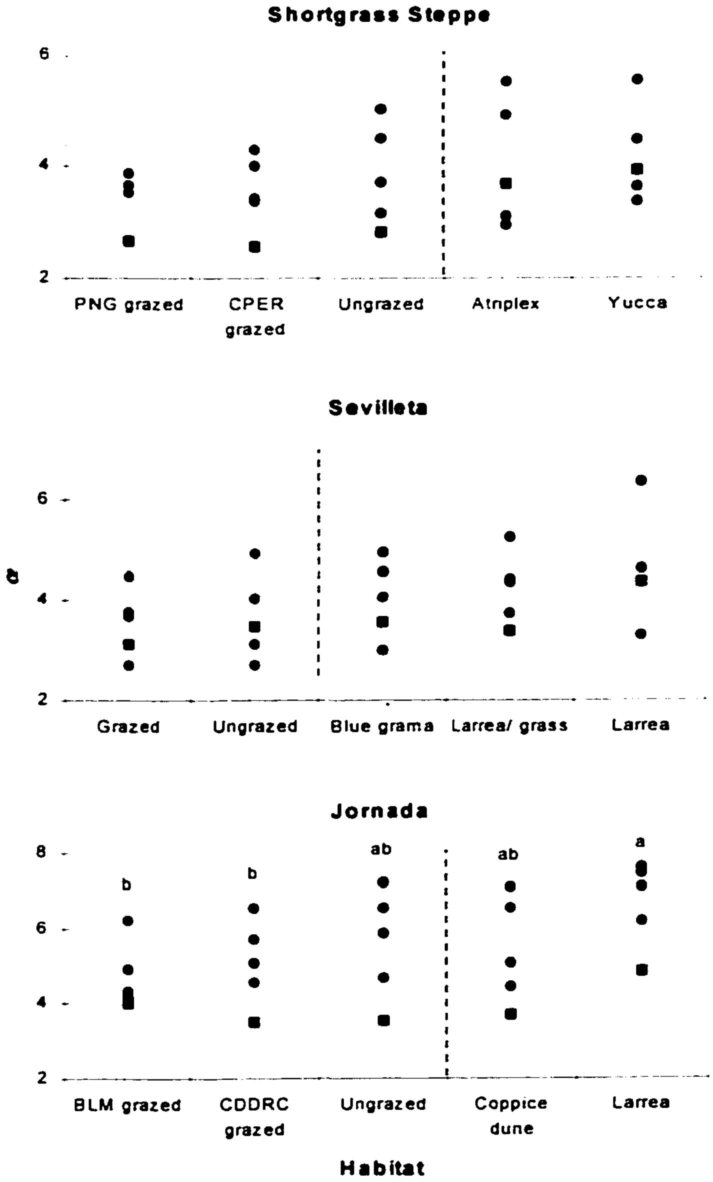

Fig. 3.2. Logseries-α patterns at the SGS, SEV, and JRN sites (symbols as in Fig. 3.1).

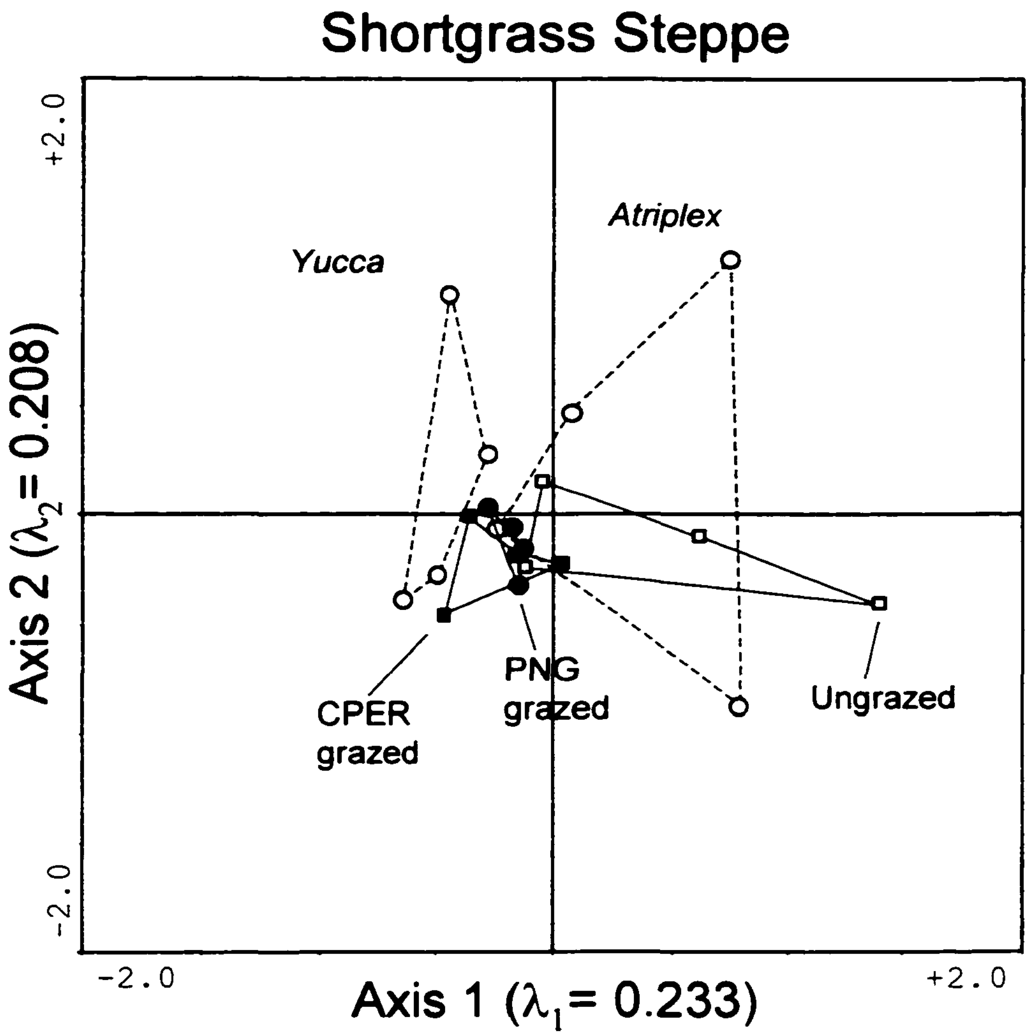

Fig. 3.3. Correspondence analysis ordination of transects at the SGS site. Site scores of transects belonging to the same habitat are joined by lines; solid lines indicate grazing treatments within the dominant grassland type and dashed lines indicate natural habitat types. Adjacent to each axis, eigenvalues are reported.

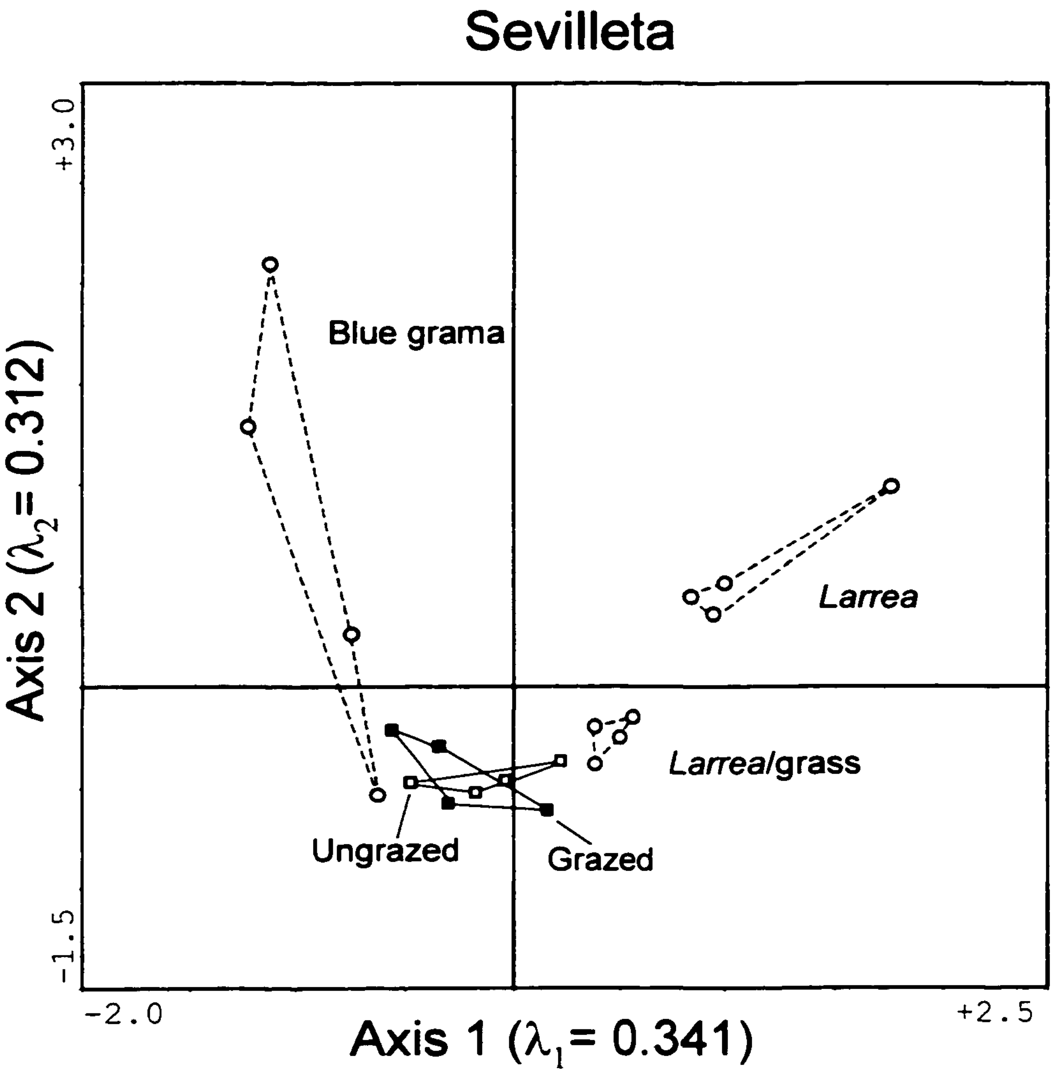

Fig. 3.4. Correspondence analysis ordination of transects at the SEV site, interpretations follows Fig. 3.3.

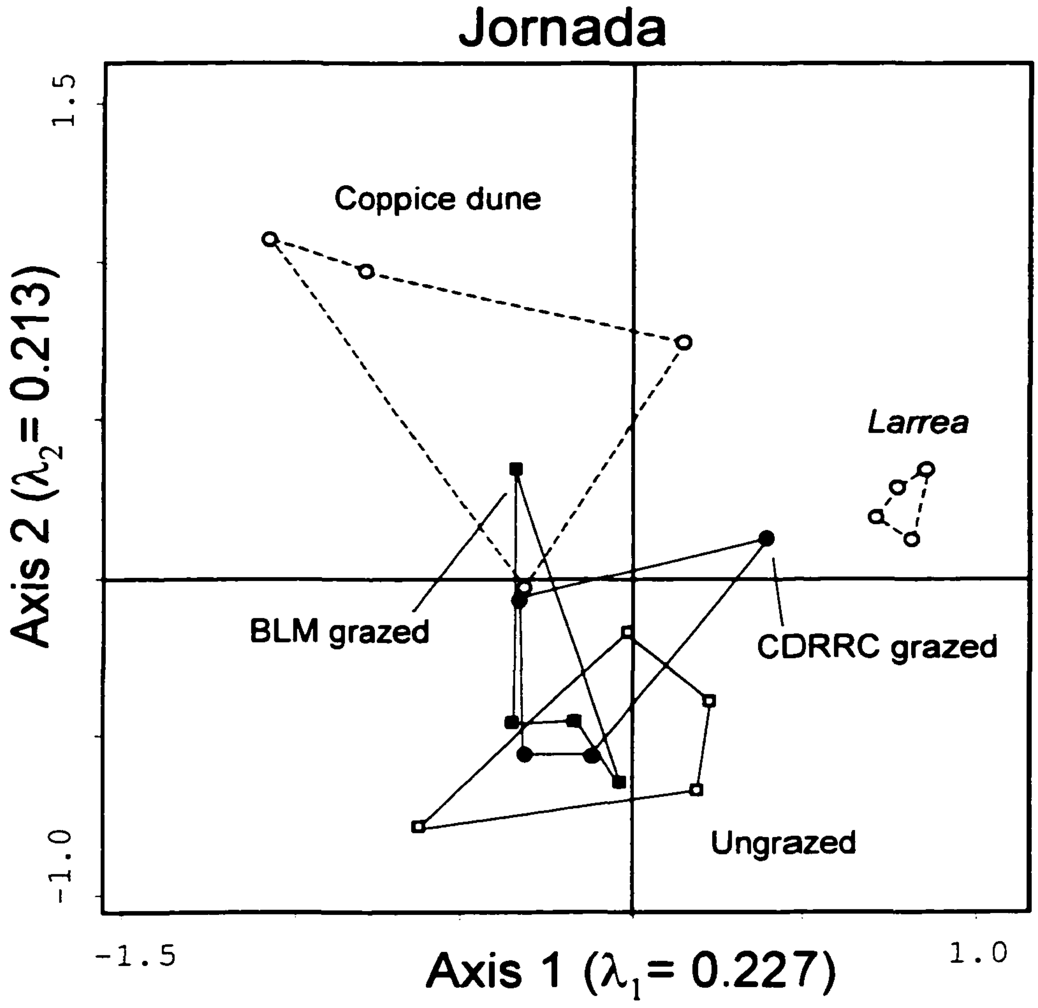

Fig. 3.5. Correspondence analysis ordination of transects at the JRN site, interpretations follows Fig. 3.3.

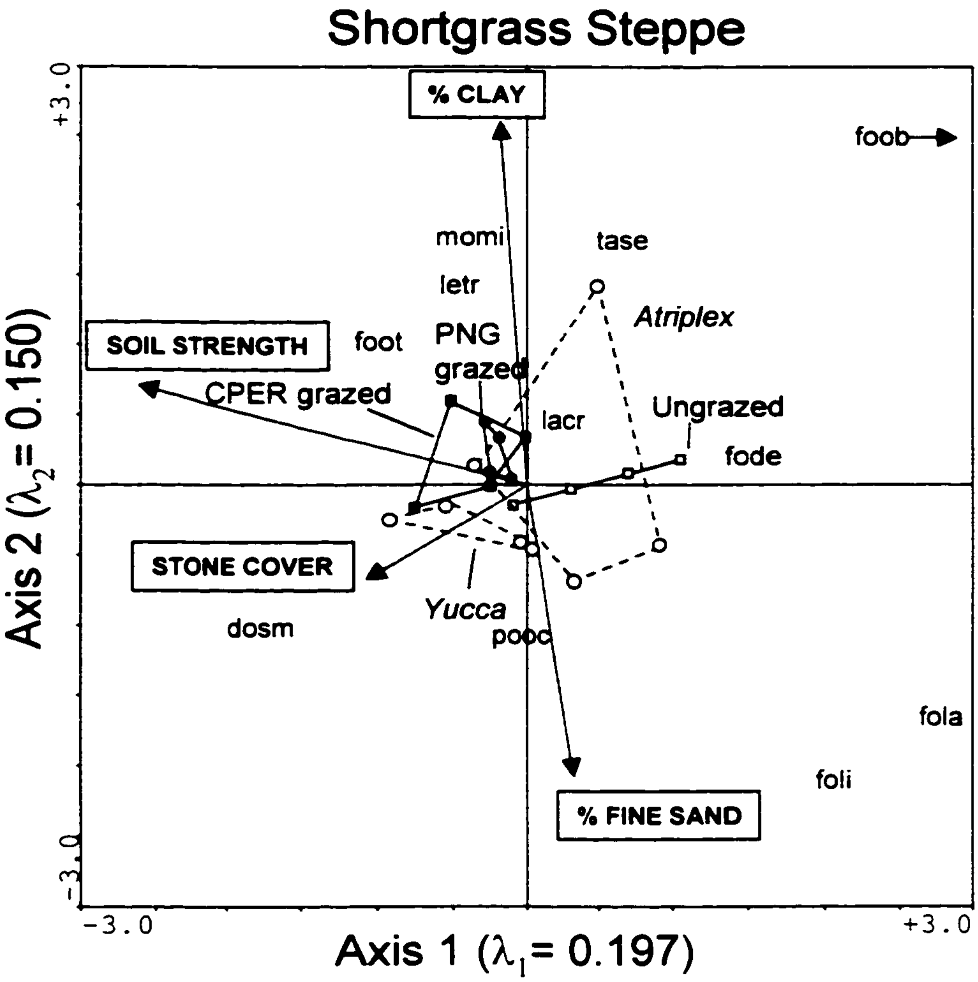

Fig. 3.6. Canonical correspondence analysis ordination of transects at the SGS site. Site scores of transects belonging to the same habitat are joined by lines; solid lines indicate grazing treatments within the dominant grassland type and dashed lines indicate natural habitat types. Species scores are indicated by lowercase codes; only species for which the ordination explained > 40 % of variation in their abundance are shown for clarity. dosm=*Dorymyrmex smithi*, fode=*Formica densiventris*, fola=*F. lasiodes*, foli=*F. limata*, foob=*F. obscuripes*, foot=*F. obtusopilosa*, lacr=*Lasius crypticus*, letr=*Leptothorax tricarinatus*, momi=*Monomorium minimum*, pooc=*Pogonomyrmex occidentalis*, and tase=*Tapinoma sessile*. The interpretation of environmental arrows in the CCA diagram, following ter Braak and Verdonschot (1995), is that the arrow represents the vector of maximum change in the values of the environmental variable, with length of the arrow indicates the rate of change in the variable. The rank of the transects with respect to an environmental variable is approximated by projecting the the transect point in the diagram perpendicularly onto the environmental arrow. The origin (0,0) is the mean for each environmental variable, so that transects projecting onto the axis of, but on the side

opposite of, the arrow are inferred to exhibit a lower than average value of the variable. Species scores that occur close to a transect point are inferred to have a relatively high abundance at that transect. Adjacent to each axis, eigenvalues are reported.

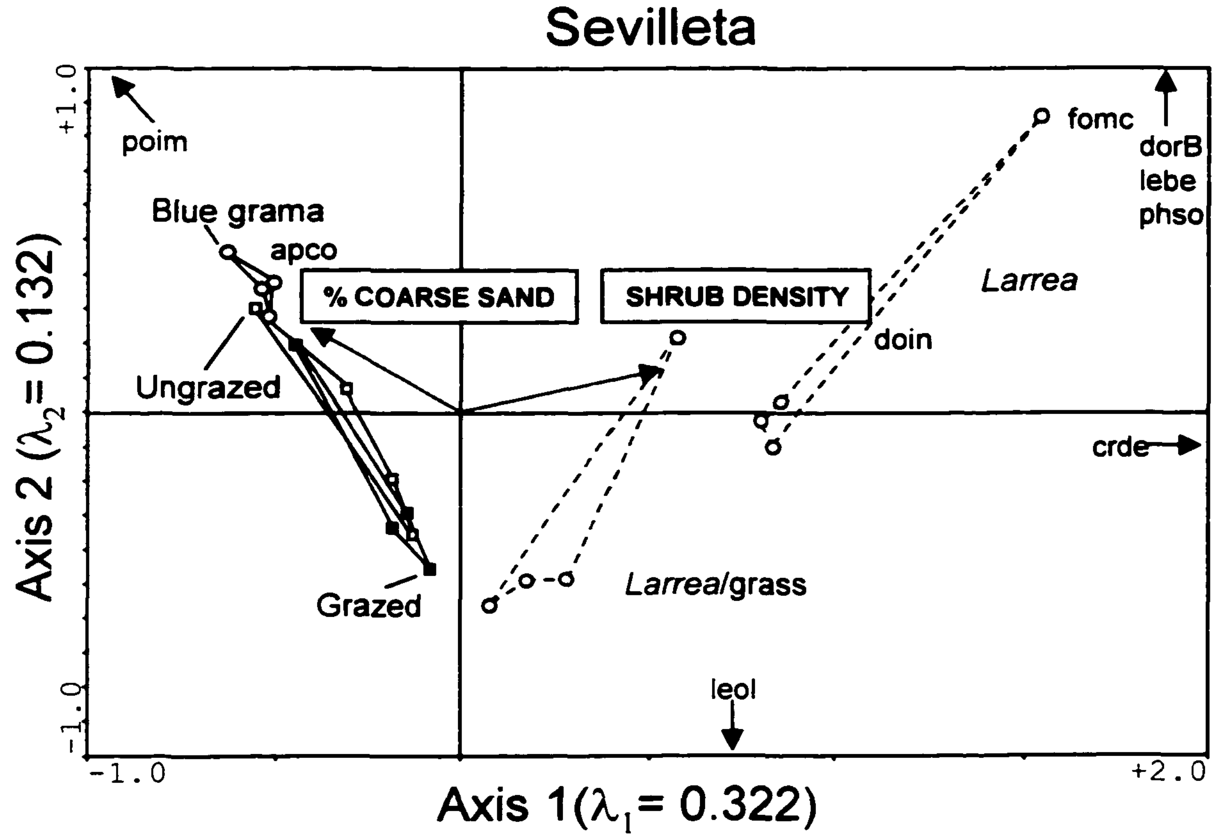

Fig. 3.7. CCA of the SEV site. Interpretation as in Fig. 3.6. apco=*Aphaenogaster cockerelli*, crde=*Crematogaster depilis*, dorb=*Dorymyrmex* sp. B, doin=*Dorymyrmex insanus*, fomc=*Forelius mccooki*, lebe=*Leptothorax* sp. J1, leol=*Leptothorax olbiquicanthus*, phso=*Pheidole soritis*, poim=*Pogonomyrmex imberbiculus*.

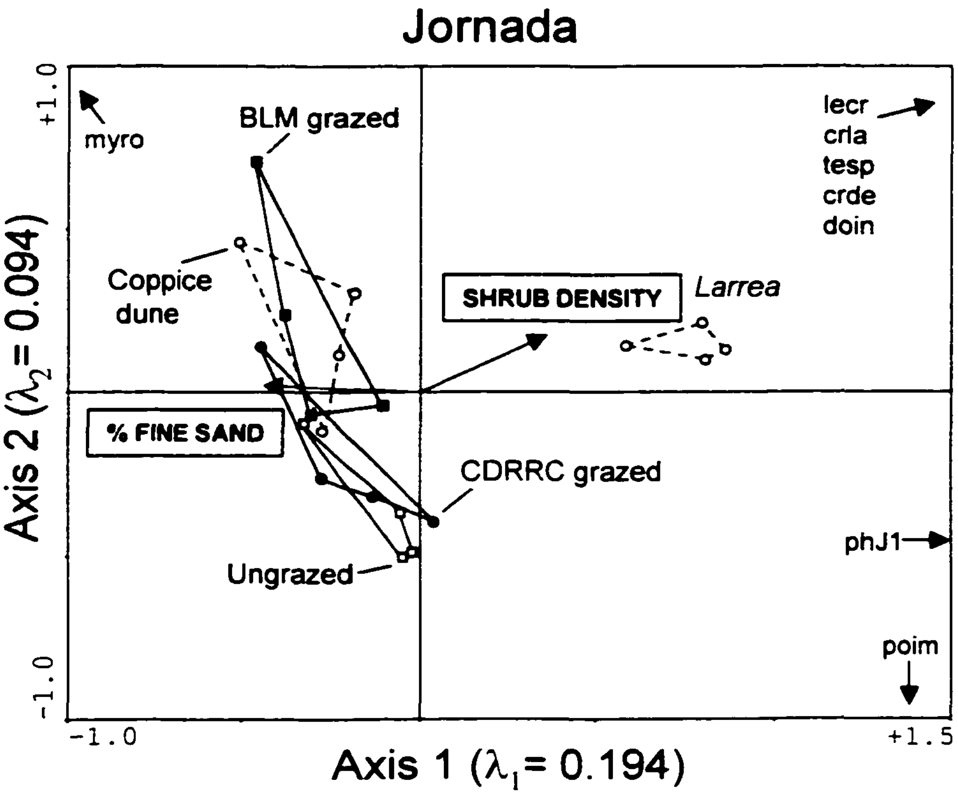

Fig. 3.8. CCA of the JRN site. Interpretation as in Fig. 3.6. crde=*Crematogaster depilis*, crla=*C. larreae*, doin=*Dorymyrmex insanus*, lecr=*Leptothorax carinatus*, myro=*Myrmecocystus romainei*, phJ1=*Pheidole* sp. J1, poim=*Pogonomyrmex imberbiculus*, tesp=*Tetramorium spinosum*.

"Our own interest lay in relationships of animal to animal. If one observes in this relational sense, it seems apparent that species are only commas in a sentence, that each species is at once a point and the base of a pyramid, that all life is relational to the point where an Einsteinian relativity seems to emerge. And then not only the meaning but the feeling about species grows misty. One merges into another, groups melt into ecological groups until the time when what we know as life meets and enters what we think of as non-life: barnacle and rock, rock and earth, earth and tree, tree and rain and air. And the units nestle into the whole and are inseparable from it. Then one can come back to the microscope and the tide pool and the aquarium. But the little animals are found to be changed, no longer set apart and alone. And it is a strange thing that most of the feeling we call religious, most of the mystical outcrying which is one of the most prized and used and desired reactions of our species, is really the understanding and attempt to say that man is related to the whole thing, related inextricably to all reality, known and unknowable. This is a simple thing to say, but the profound feeling of it made a Jesus, a St. Augustine, a St. Francis, a Roger Bacon, a Charles Darwin, and an Einstein. Each of them in his own tempo and with his own voice discovered and reaffirmed with astonishment that all things are one thing and that one thing is all things—plankton, a shimmering phosphorescence on the sea and the spinning planets and an expanding universe, all bound together by the elastic string of time. It is advisable to look up from the tide pool to the stars and then back to the tide pool again."

John Steinbeck and Edward Ricketts, 1941. *The Sea of Cortez*. Viking Penguin, Inc., New York, NY, USA.

CHAPTER IV

MULTISCALE RESPONSE OF ANT DIVERSITY TO A SEMIARID BIOME TRANSITION

Abstract

The locations of biome transitions and ecotones are frequently defined by the rapid shift from one form of dominant vegetation to another. The composition of other taxa is predicted to shift in parallel with that of dominant plants and species diversity is predicted to be greater in transitional zones than in adjacent areas. I asked whether ant species diversity and composition supported these predictions across a biome transition between shortgrass steppe and Chihuahuan desert vegetation and across a grassland-shrubland ecotone within a landscape at the biome transition. Neither species richness nor diversity was highest at the biome transition landscape as a whole, or within habitats in the biome transition or in ecotonal habitats. The biome transition landscape was not intermediate in ant species composition or in the representation of different faunal complexes. A spatial gradient in vegetation within the biome transition landscape was related to gradients in ant species composition, but changes in ant composition at this scale did not involve different faunal complexes. A zoogeographic transition for ants may occur to the north of the phytogeographic transition and may be coincident with the

northern limits of monsoonal precipitation patterns. In contrast, the phytogeographic transition may be related to less extreme climatic variation within the monsoonal region.

Introduction

At the scales of regions and continents, biotic assemblages exhibit a mosaic pattern and the characteristics of local communities may change abruptly in space. Documenting and understanding the processes underlying such transitions are key to explaining biogeographic patterns in species diversity (Gosz 1992). Biome transitions are often defined by a shift in the dominance of particular life forms or generalist taxa in response to climatic variation across a region (Gosz and Sharpe 1989). The location of this shift, or tension zone (Curtis 1959, Gosz and Sharpe 1989), may be determined by the steepness of climatic gradients or because of nonlinear, threshold responses of taxa to changing interactions between climate and other environmental variables across a region. These interactions occur across spatial scales, such as between broad-scale climatic variation and fine-scale variation in topography or soil texture (Gosz 1992). Fine-scale processes, such as soil textural or microtopographic variation in moisture availability, may induce a mosaic structure in plant communities at a biome transition (Gosz 1993, Kent et al. 1997).

Tension zones between plant communities at finer spatial scales, within or away from biome transitions, are often manifested as ecotones. At these scales, climate does not vary, so community variation is controlled by local features such as microtopography or soils (Gosz 1992). Kent et al. (1997) referred to zones of changing plant community structure generally as transitional areas because community transitions may vary in their abruptness, forming either ecotones or more gradual ecoclines (van der Maarel 1990), depending upon the steepness of environmental gradients. At the limits of biomes, transitional areas exist on a continuum of spatial scales (Gosz 1993) and may manifest themselves as gradients, mosaics, or ecotones depending upon the scale at which they are observed (Solon 1999).

Transitional areas are predicted to have a higher species diversity than adjacent areas because they harbor species from two or more community types (Odum 1971, Risser 1995). This is due to an increase in the number of distinct habitat types in an area, and to increases in the number of species within habitats due to dispersal from distinct habitats (i.e. mass effects; Shmida and Wilson 1985, Nekola and White, in press) emerging from the proximity of these habitats. Transitional areas should also exhibit greater functional diversity due to the mixing of different life forms. For some taxa, transitional areas may represent distinct habitats and may favor some species found in lower abundance in adjacent habitats (Hansen and Urban 1992). There have been few studies of species diversity patterns across ecotones (Risser 1995), so it is unclear how different taxa compare in their responses to changing environmental conditions across landscapes and regions.

Biome transitions and ecotones are usually defined by the responses of plant communities. Animal communities, which are usually circumscribed by taxonomic affiliation, may respond to changes in plant communities to varying degrees, depending upon their characteristics. Many bird species forage and nest in vegetation, and small mammals may depend upon particular plant life forms, such as shrubs, for food or cover.

Thus, their assemblages might be expected to exhibit parallel responses to changing plant-community structure in transitional areas. On the other hand, some animal groups, such as soil-dwelling invertebrates, might respond to environmental variation, including soil texture, independently of plant composition.

Krasnov and Shenbrot (1998) asked how different animal taxa responded to a desert-steppe phytogeographic boundary by considering two questions. First, they asked whether the assemblages found on either side of the boundary differed. If they differed, they then evaluated whether the assemblages belonged to different faunal complexes (i.e. have similar geographic ranges that are distinct from those of other complexes) or if the assemblages represented different groupings within the same faunal complex. They sought to determine how well phytogeographic classification represented the zoogeographic patterns of different animal groups.

In this study, I ask the same questions as Krasnov and Shenbrot (1998) with respect to the response of ant assemblages to a biome transition between North American shortgrass steppe and Chihuahuan desert biomes. Ants are abundant and diverse animals in these environments. Furthermore, ants are an interesting group with which to consider how animals respond to phytogeographic transitions because ant species vary in their direct dependence upon plants for food and shelter, and because their populations respond to similar environmental variables as do plants, including soil texture (Johnson 1992) and microclimate (Perfecto and Vandermeer 1996). This convergence is due to the fact that ants are colonial and their colonies are generally sessile. Ant colonies are often rooted in the soil but ant workers compete for resources above ground, so ant colonies and plants may respond to their environments and to each other in broadly similar ways (Andersen 1991).

The Sevilleta Long-Term Ecological Research (LTER) site in central New Mexico contains a phytogeographic boundary between the shortgrass steppe and Chihuahuan desert biomes. The shortgrass steppe biome extends north and east from this point through northwest Texas, western Kansas, eastern Colorado, to eastern Wyoming and southern Montana of the United States.(Fig. 4.1). The Chihuahuan desert extends south and east from the Sevilleta (SEV) through western Texas into the states of Chihuahua, Durango, and Coahuila, Mexico. The biome transition is defined by the shift in the dominant vegetation from blue grama (*Bouteloua gracilis*) grasslands that characterizes the shortgrass steppe to the black grama (*Bouteloua eriopoda*)-dominated grasslands interspersed with more xeric creosotebush (*Larrea tridentata*) shrublands that characterize the Chihuahuan desert. Within the SEV, blue and black grama co-dominate (Minnick and Coffin 1999). At the regional scale, the location of the biome transition in central New Mexico is caused by shifts in the seasonality of precipitation (Gosz 1992). The location of the biome transition within the boundaries of the SEV may be determined by the impedance of spring weather systems caused by local topography, which may also determine the position of finer scale ecotones.

Here, I examined the response of ant assemblages to both the broad-scale biome transition as well as smaller-scale transitions between vegetation-defined habitat types within the biome transition zone. I tested the hypothesis that SEV would have greater ant species diversity than adjacent sites occurring entirely within the shortgrass steppe and Chihuahuan desert biomes. At a finer scale, I hypothesized that an ecotonal habitat within the SEV would have greater ant diversity than would pure habitat types. I also compared matched habitat types occurring within the biome transition zone with those habitats occurring in regions away from the transition to determine if local habitats, in the context of a biome transition, would have greater ant diversity due to the mixing of faunal complexes.

I then asked whether the ant fauna of the biome transition was intermediate in species composition and in the representation of different faunal complexes at a regional scale. I hypothesized that matched habitats occurring in different regions would be more similar to one another in species composition than to distinct habitats within the same region. Within SEV, I asked whether ant communities responded to spatial gradients in habitat and ecotones between habitat types and, if so, did the different ant assemblages represent distinct faunal complexes or different groups of species within a single faunal complex? I bring together the answers to these questions to determine if the Sevilleta area is located at a zoogeographic transition for ants and, if so, does this transition correspond to a climatic discontinuity?

Materials and Methods

Study areas

Field work was conducted within the SEV and two other LTER sites located well within the shortgrass steppe and Chihuahuan desert biomes (Fig. 4.1). SEV is located in the Sevilleta National Wildlife Refuge in Socorro County, New Mexico. The area receives ca. 265 mm precipitation/yr. I sampled sites in the eastern half of this refuge, which has been ungrazed since 1973. Black grama grasslands in the MacKenzie Flats area, blue grama grasslands near the foot of the Los Piños range, and creosotebush stands and ecotonal areas between creosotebush and black grama grassland were sampled in the Five-Points area (Fig. 4.2).

To represent the shortgrass steppe, I examined ant assemblages within the Shortgrass Steppe (SGS) LTER site located in the USDA-ARS Central Plains Experimental Range near Nunn, Weld County, Colorado. This area is wetter than SEV, receiving ca. 320 mm of precipitation/yr. This site is dominated by blue grama grassland. In order to represent blue grama grasslands under similar conditions to those found at SEV, I sampled within 1-ha exclosures that had not been grazed since 1939. Creosotebush shrublands do not occur at SGS, so I sampled the two most common shrubland types to balance the effects of landscape heterogeneity among sites for overall regional comparisons. The shrublands constituted patches of saltbush (*Atriplex canescens*) that typically occupy low-lying areas (Stapp 1997), and soapweed yucca (*Yucca glauca*)-dominated patches often found on stony hillocks or ridges.

Chihuahuan desert was represented by the Jornada (JRN) LTER site, located in New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC; elsewhere referred to as the College Ranch), and in the USDA-ARS Jornada Experimental Range (JER) near Las Cruces, Doña Ana County, New Mexico. This area is drier than SEV, receiving ca. 232 mm of precipitation/yr. Black grama/mesa dropseed (*Sporobolus flexuosa*) grasslands are abundant here and were sampled within grazing exclosures (1-2 ha) that had been ungrazed since 1946. These grasslands also included shrubs such as honey mesquite (*Prosopis glandulosa*) and *Yucca elata.* I also sampled creosotebush shrublands along a gently-sloping bajada near Mount Summerford, as well as in honey mesquite-dominated coppice dunes that represent an irreversible transformation from grassland to shrubland due to a combination of grazing and drought (Hennessy et al. 1983, Schlesinger et al. 1990).

Ant Sampling

Ant species composition and abundance were sampled at each site at 10 stations along 90-m transects (10-m spacing). Within each habitat type at each site, four transects were placed following the methods described in Chapter 3. Transect locations were recorded with GPS. Pitfall traps were polypropylene sample containers (65 mm diameter, 100 mm deep) filled with 40 ml of a propylene glycol/ethanol mixture. Pitfall traps were buried in the soil with lids on for at least 72 h prior to operation in order to allow the ants to reestablish foraging trails and become accustomed to the disturbance (Greenslade 1973). Traps within a site were operated simultaneously for 72 h during a trapping session. Trapping was performed at two times per year to coincide with the driest and wettest months during which temperatures would be sufficiently high for ants to be active. Dry periods included October/November at SGS, and April at SEV and JRN. Wet periods included June at SGS, and July/August at SEV and JRN. This sampling design ensured that ants with different seasonal activity would be recorded. Ants were sampled over two years (1996-98) to improve my estimates of ant-community composition at the sites given annual variation in ant activity above ground in arid environments (Whitford 1978).

Following trapping, pitfall traps were capped and removed to the laboratory for processing. Ant specimens in each trap were counted and identified to species or morphospecies. Most species identifications were verified by Roy R. Snelling of the Los Angeles County Museum, James Trager of the Shaw Arboretum, and William MacKay of the University of Texas, El Paso. Nomenclature follows Bolton (1995).

For each sampling period, ant abundances were ln-transformed at the trap level in order to reduce the wide variance in capture rates due to differences in the proximity of traps to nests, differences in capture rates due to the effects of varying substrate on forager movement, and differential species responses to traps (Bestelmeyer et al. in press). Furthermore, species that are poorly sampled by pitfall trapping techniques, including legionary (*Neivamyrmex*), obligate slave-making (*Polyergus*), and subterranean ants (*Hypoponera*), were excluded from analyses. The ln-transformed trap abundance values were summed to obtain transect values. These values represent scaled estimates of ant activity that may provide less biased comparisons between samples than those based on raw abundance values (Andersen 1991).

Characterization of Faunal Complexes and Biogeographic Analysis

Ant genera occurring within the three study areas and represented by more than one species were classified into three faunal complexes based upon previous studies of biogeographic patterns in North American ants (Gregg 1963, Brown 1973). Three groups were identified, including 1) holarctic genera that are restricted to the north temperate and boreal regions of the United States, Canada, Europe, and Asia; 2) New World xeric genera that inhabit arid and semiarid regions within the Neotropical (e.g. western Chaco woodlands and Monte/Atacama deserts of South America) and/or Nearctic biogeographic realms (in the Great Basin, Mojave, Sonoran, and Chihuahuan deserts), and 3) pantropical genera that are abundant within most tropical zones of the world.

To broaden my consideration of biogeographic patterns between the shortgrass steppe and Chihuahuan desert regions, I documented the regional distributions of ant species found within my study areas and tallied the number of species per ant genus in a belt encompassing both biomes as well as the northern mixed prairie found to the north of shortgrass steppe (Lauenroth and Milchunas 1991). I considered records in prairie and steppe in eastern Wyoming, eastern Colorado, and northwestern Texas, and in Chihuahuan desert-dominated regions in western Texas and a site in the state of Durango, Mexico, using previously published species lists. Distribution data for Wyoming were recorded at the county level (Wheeler and Wheeler 1988), so the eastern counties in which prairie exists were divided into three groups based upon differences in their latitude (Fig. 4.3). Colorado records included mapped locations of collection localities (Gregg 1963), so records in areas dominated by shortgrass steppe were divided into 1°-latitude blocks extending from the eastern border to the foothills of the Rocky Mountains. Texas records were also mapped (Moody and Francke 1982, Cokendolpher and Francke 1990) and shortgrass steppe records (referred to as Great Plains grassland; Moody and Francke 1982) and Chihuahuan desert records (located in the Trans-Pecos region of west Texas) were determined using regional maps and habitat records found within the publications. Finally, all records for the Mapimi Biosphere Reserve in Durango were in Chihuahuan desert vegetation (Rojas-Fernandez and Fragoso 1994). In all cases, I attempted to ascertain from the publications whether the species occurred within the appropriate habitat type.

Data Analysis

Species diversity was characterized as both species richness and logseries-α diversity, which includes a measure of the distribution of abundance among species (Magurran 1988). Richness and diversity values at the transect-level, for which there were four replicates per habitat, were compared between habitats within (at SEV) and between regions using Wilcoxon rank-sum tests and Kruskal-Wallis tests where appropriate. Richness and diversity at the habitat level within sites and at the level of the entire site were unreplicated and compared directly. I also report incidence-based coverage estimators (ICE; EstimateS 5.01; Robert Colwell) of site-scale and habitat-scale richness to compare estimates of true species richness, given that there may have been differences in sampling efficiency among the sites (Colwell and Coddington 1994).

I compared the abundances of individuals within genera that belonged to different faunal complexes among each of the study sites. I then compared patterns of species composition between matched habitat pairs using correspondence analysis (CA; ter Braak 1994). This analysis was used to test whether patterns of association of species with particular habitats were stronger than between-site variation in species composition. CA is an indirect gradient analysis technique in which abundance patterns of species among a set of sites are used to ordinate the sites (and species) in the space defined by one or more axes. The range of scores on the first axis encompasses the greatest amount variation in species abundances that can be explained on a single axis; subsequent axes explain a decreasing proportion of the remaining variation, subject to the constraint of being uncorrelated with the first axis. Thus, in the space formed by two axes, the strongest gradient of variation will separate samples and species along axis 1 and a secondary gradient separates samples on axis 2. According to my hypothesis, I expected that axis 1 should segregate transects located in different habitat types, and variation due to between site differences might be apparent on axis 2.

Variation in species composition across habitats and ecotones within SEV was evaluated using canonical correspondence analysis (CCA). CCA is a modification of CA in which the ordination axes are constrained to be linear combinations of a set of environmental or spatial variables (i.e. direct ordination; Jongman et al. 1995). Thus, the ordination diagram reflects patterns of species composition with respect to measured gradients. In this analysis, I sought to evaluate how variation in species composition at SEV related to a spatial gradient in habitat that runs from creosotebush in the western part of the study area, through an area dominated by black grama, to blue grama in the east (Fig. 4.2). I evaluated the influence of several spatial variables using stepwise forward-selection procedures in CANOCO 4.0 (ter Braak and Smilaur 1998). I followed Borcard et al. (1992) in considering x and y coordinates (UTM), their squares, cubes, and the products between all of these terms in order to examine both linear and non-linear or patchy spatial relationships. Variables explaining a significant ($P<0.05$) amount of variation in Monte Carlo permutation tests (199 random permutations of the samples in the species data) were included in the CCA analyses. Rare species were downweighted in CANOCO. Biplot scaling was used and the CCA plots were focused on intersample distances using sample scores that are linear combinations of the environmental variables (ter Braak 1994). Thus, distances between sample (transect) positions in this CCA indicate chi-square distances in an ordination space defined by the included spatial variables (McCune 1997).

I used detrended correspondence analysis (DCA) to examine gradients in species turnover from Wyoming shortgrass steppe to Mexican Chihuahuan desert within a group of ant species that were found within the study sites and that had also been recorded outside of a study area. Restricting the analysis to this set of species helps to ensure that 1) the records for species gleaned from the literature pertain to species that occur within shortgrass steppe and Chihuahuan desert habitats (and not, for example, in forested patches in areas otherwise dominated by steppe vegetation), and 2) the species records are not accidental occurrences or misidentifications. In DCA, axes are scaled in units of the average standard deviation (SD) of species turnover, such that there is a complete turnover in species composition along axis 1 over ca. 4 SD, and a 50% turnover occurs within about 1-1.4 SD (Gauch 1982). The length of the first DCA axis is thus a suitable measure of the length of a principal ecological gradient and turnover along it (Legendre and Legendre 1998). I used DCA axis 1 scores to look for discontinuities, in particular an increase in slope, along the north-south latitudinal gradient from shortgrass steppe to Chihuahuan desert. The presence of SEV at such a discontinuity would support its characterization as a zoogeographic transition for ants (e.g. Gosz and Sharpe 1989). In addition, I compared the number of species belonging to different faunal complexes along the gradient using all records from the literature sources, provided that the species were believed to occur in the appropriate habitats.

Results

Diversity Patterns

I recorded 33, 39, and 40 ant species within the dominant, ungrazed grassland type and the two other most dominant habitat types at SGS, SEV and JRN, respectively. Estimated total richness values (ICE) were similar (SGS, 41.7; SEV, 42.7; JRN, 40.6). Within the blue grama habitat, neither transect-scale richness (Wilcoxon rank sum=18.5; n=4, 4; P=1.00) nor logseries-α (Wilcoxon rank sum=18.0; n=4, 4; P=1.000) differed between SGS and SEV (Fig. 4.4). Observed habitat-scale richness and diversity were higher at SEV, although estimated richness was only slightly so. Within the Chihuahuan desert habitats, transect-scale richness (Wilcoxon rank sum=11; n=4, 4; P=0.06) and logseries-α (Wilcoxon rank sum=11; n=4, 4; P=0.06) within black grama grassland were greater at JRN than at SEV (Fig. 4.5). Habitat-scale richness, both observed and estimated, was higher in JRN, although habitat-scale logseries-α was not. In creosotebush shrubland, transect-scale richness was also higher at JRN than SEV (Wilcoxon rank sum=20; n=4, 4; P=0.03), but logseries-α was not (Wilcoxon rank sum=24; n=4, 4; P=0.11; Fig. 4.6). Estimated and observed habitat-scale richness and logseries-α followed this pattern. Within the SEV, neither transect-scale richness (Kruskal-Wallis, χ^2=1.93; df=2; P=0.38) nor logseries-α (χ^2=2.81; df=2; P=0.25) differed among black grama, ecotonal, or creosotebush habitats (Fig. 4.7). Estimated and observed habitat-scale richness and logseries-α were similar between black grama and ecotonal areas and higher in the creosotebush habitat. Thus, at a site scale, at habitat scales, and at transect scales within habitats, SEV did not possess a more diverse ant fauna than either the SGS or JRN.

Patterns of Species Composition

Holarctic genera, including *Formica*, *Lasius*, and *Myrmica*, were abundant at SGS (Fig. 4.8) but were completely absent from SEV and only one occurrence of *Formica* was recorded at JRN (*F. perpilosa*; Appendix 4.1). In particular, the abundance of *Formica* at SGS was greater than that of any genus at any site in this study. The abundance of xeric genera increased from SGS to JRN. *Forelius* was found only once at SGS and *Myrmecocystus* was absent. *Dorymyrmex* and *Pogonomyrmex* were abundant at SGS. Results for the tropical genera were mixed. Some genera (*Leptothorax* and *Tapinoma*) decreased in abundance from SGS toward JRN, whereas others were absent at SGS and abundant at SEV and JRN (*Aphaenogaster* and *Crematogaster*), or were least abundant at SEV (*Solenopsis*). *Pheidole* was abundant at all sites and increased from SGS to SEV and JRN. Overall, the SGS site can be distinguished from SEV and JRN by the abundance of holarctic genera, whereas SEV and JRN are comparatively similar to one another, and are dominated by the genus *Pheidole*.

The SGS site was most distinct in species composition from the others, sharing only 7 species with SEV (19.4% of species; Jaccard's index) and 3 species with JRN (8.2%). On the other hand, SEV and JRN shared 26 species (65.8%). Within the blue grama habitat, only four species were shared between the SGS and SEV (16.5%), revealing the relative importance of variation in species composition between sites. The CA of desert habitats at SEV and JRN showed that the primary axis separated the sites, and the second axis separated black grama from creosotebush habitats within sites (Fig. 4.9). This indicates that variation among sites was more important than between-habitat variation. Further, differences in species composition between the desert habitats were stronger at SEV than at JRN along axis 2.

Within SEV, CCA revealed the presence of a spatial gradient separating creosotebush and creosotebush/grassland ecotonal areas in the west, through black grama habitat, to blue grama habitat in the east (Fig. 4.10). Of nine spatial variables examined, only the east-west spatial coordinates explained a significant amount of variation in species abundances in the forward selection. The first (and only) constrained axis was significantly different from that expected from randomized data (F=3.97; P=0.005), and the spatially-constrained axis was highly correlated with the unconstrained (i.e. representing derived gradients from only the species-abundance data) CA axis (0.901), confirming that the spatial gradient is related to the primary gradient in the species data. Nonetheless, a considerable amount of variation in species abundances was unexplained by the east-west spatial axis, and axis 2 explained a greater amount of variation than axis 1 (26% and 22.1%, respectively). Specifically, axis 2 separated creosotebush habitats from ecotonal habitats (Fig. 4.10) that are located close together and interspersed in space (Fig. 4.2). Axis 2 also revealed strong variation within the blue grama habitat.

By considering the identity of the transects and comparing their locations in actual (Fig. 4.2) and CCA ordination (Fig. 4.10) space, two within-habitat gradients are apparent. First, there is a clear east-west gradient within the black grama habitat such that the eastern transects are similar to the blue grama transects, and the western transects are more similar to the ecotonal areas. Second, the gradient within the blue grama habitat suggests a segregation of the transects closest to the Los Piños mountains from transects located farther away.

Several species were abundant in blue grama habitats including *Aphaenogaster cockerelli*, *Dorymyrmex smithi*, *Pheidole cerebrosior*, *P.* sp. J1, *P. xerophila*, and *Pogonomyrmex imberbiculus* (Fig. 4.10). Of these, only *D. smithi* was also recorded at the SGS in blue grama habitat. Other species that were present at the SGS site within blue grama (Appendix 1), including *Pheidole longula*, *Leptothorax olbiquicanthus*, and *Dorymyrmex insanus* are most abundant at SEV in black grama grassland, the creosotebush-grass ecotone, and creosotebush shrubland, respectively. Species such as *P. longula* that were abundant in black grama at SEV (in fact, this ant was the most abundant species at SEV) were completely absent from JRN (Appendix 1).

Species turnover within the ant fauna recorded at the study sites was variable along the latitudinal gradient from Wyoming to Durango (Fig. 4.11). The correlation of the distances along the first DCA axis with the relative Euclidean distances in the original distance matrix was high (R^2=0.851), indicating that much of the variation in the ant composition was represented in the DCA axis 1 scores. There was relatively little change in the composition of the ant assemblage from Wyoming through northern Colorado and from JRN to Durango. These patterns are, in part, an artefact of using the LTER sites to define the regional fauna. Because there were not sites to the north of the SGS or south of JRN defining the ant assemblage, species present at SGS and JRN were progressively lost to the north and south, respectively, and no new species appeared. This results in little change in DCA scores. The more relevant part of the gradient for my question lies between northern Colorado and JRN. This part of the gradient reflected a continuous change in ant composition south through Colorado with an increasing representation of Chihuahuan desert species. If SEV were located at a compositional threshold, we would expect it to have a higher, more intermediate DCA score and to be flanked by much higher and much lower scores on each side. In fact, SEV is not intermediate in composition and is instead most similar to JRN.

The proportion of the species belonging to different faunal complexes also exhibited continuous change to the south along the latitudinal gradient (Fig. 4.12; Appendix 4.2). Throughout Wyoming and northern Colorado, holarctic species predominate, and their representation declines rapidly through Colorado. By the time SEV is reached, all but one holarctic species has disappeared. A few holarctic taxa persist in the shortgrass steppe of Texas.

Discussion

Diversity Patterns

Contrary to the hypothesized peak in richness expected at a biome transition, species richness was not greatest at SEV at the site scale nor within habitats. Along the north-south gradient, measured richness increased from SGS to SEV and JRN, but estimated richness values were similar across the sites. This is surprising considering that ants are thermophilic animals. Cold temperatures have been identified as an important stress affecting both ant composition and richness patterns at local (Gregg 1963, Andersen 1997) and global (Brown 1973, Andersen 1995) scales and the duration of winter temperatures decreases from SGS to JRN. Precipitation, however, also decreases, and this may also have a negative effect on ant richness (Davidson 1977, Marsh 1985). It is possible that these factors act antagonistically and lead to similarities in regional ant richness among the sites.

Within the blue grama habitat, richness did not differ between the SGS and SEV. The pool of species available to colonize blue grama habitats is almost completely different between SGS and SEV, so a role for regional-scale faunal mixing or mass effects in increasing richness in SEV's blue grama habitat does not apply. Local richness levels in the two regions may be governed by similar factors.

In both Chihuahuan desert habitats, however, richness decreased from JRN to SEV. It is possible that, because these habitats were located at the extreme northern extent of their distribution, they may be less suitable for many Chihuahuan ant species found deeper within the biome. Many ants may exhibit a greater sensitivity to the changing environmental factors that limit the northward distribution of dominant plant taxa at SEV. This process, coupled with a lack of faunal mixing or mass effects, may lead to a depression in within-habitat richness at a plant-defined biome transition. Whitford (in press; personal communication) also recorded unusually low ant richness at a Chihuahuan desert-oak savanna transition zone in eastern New Mexico, and this may be due to this combination of processes.

In a similar fashion, the ecotone between grassland and creosotebush shrubland at a finer scale within SEV failed to exhibit greater ant richness than pure habitats. Again, we observe that the conditions required for a diversity peak in a transition zone are violated. Many ant species are found on both sides of the ecotone. This fact, coupled with a high variation in richness due to local environmental factors, likely inhibits the predicted response of richness to the ecotone.

Patterns of Species Composition

Many different factors may determine ant diversity patterns at local scales, so species and life-form composition are perhaps most important in characterizing a zoogeographic transition for ants. SEV was not intermediate in either the abundance of different faunal complexes (Fig. 4.8) or consequently, in species composition. Thus, the shift in the composition of dominant life-forms observed among the plants that determines the physical structure of these environments is not reflected in a shift in life-forms in ants. As noted previously, the ants inhabiting blue grama habitats at SEV are largely distinct from those found at SGS, indicating that the environmental features governing the distributions of ants and blue grama differ and do not covary between regions. Even when regional pools are more similar, such as between SEV and JRN, regional differences in species composition continue to predominate.

In studies comparing the relationship between local and regional determinants of diversity patterns, it is common to witness an overriding influence of regional variation on features of community structure (Cornell and Lawton 1992, Medel 1995, Caley and Schluter 1997). Many of these results are likely due to the fact that regional variation also includes a great deal of unmeasured local variation, depending upon how "habitat" is defined. In Chapter 3, I showed that habitat types based on vegetation, such as creosotebush shrubland, may encompass areas that differ in soil characteristics between regions and that many ant species may respond directly to this latter source of variation.

The use of incorrect criteria to define the habitat of a taxon (Kolasa and Rollo 1991) will confound regional comparisons, and insofar as human-defined habitats occurring in different regions also differ in other important ways, controlled comparisons of the role of local versus regional effects will be difficult.

Nonetheless, some components of the ant community did respond to the contrast between grassland and creosotebush shrubland in parallel between SEV and JRN (Fig. 4.8; axis 2). This effect is due to the influence of species such as *Crematogaster depilis*, *Forelius mccooki*, and *Leptothorax* sp. J1 that are associated with creosotebush in both sites, as well as species such as *Aphaenogaster cockerelli* and *Myrmecocystus mimicus* that were associated with grasslands across the sites.

The response of ant-community composition to variation between grasslands and shrublands was greater at SEV than at JRN. This is consistent with the suggestion that the sensitivity of assemblage structure to local environmental variation is heightened at biome transitions due to an increased variability in climate, and thus an increasing role for climate-by-environment interactions (Gosz and Sharpe 1989). As noted above, however, the habitats vary in soil texture between the regions, so it is not possible to isolate the effects of climatic and local environmental variation.

At a finer scale, both soil texture and climate may combine to produce spatial structure in ant composition within SEV. The west-east spatial gradient (Fig. 4.10) is highly positively correlated with the percentage of coarse sand in the top 24 cm of soil (adjusted $R^2=0.95$; $F=268.15$; $df=1, 14$; $P=0.000$), which I found to be the dominant environmental correlate of variation in ant composition at the site (Chapter 3). This soil textural gradient is paralleled by a west-east gradient of increasing precipitation in the study area (Gosz et al. 1995). The combination of these factors is likely responsible for the creosotebush shrubland-black grama grassland and black grama-blue grama vegetation transitions, as well as gradients in ant composition. This gradient is apparent even within the black grama grassland samples (compare Fig. 4.2 to Fig. 4.10).

Despite the close spatial proximity of the creosotebush shrubland and ecotonal transects, there were consistent differences in ant composition between them (Fig. 4.10; axis 2). These sites did not differ in soil texture (Chapter 3), so either variation in plant cover and/or other factors such as drainage or unmeasured soil properties that vary on fine scales are responsible for their differences.

Fine scale variation was also important at the eastern side of the SEV study area, in blue grama grassland. The compositional differences between the blue grama samples closest to the Los Piños mountains from those farther away was not related to an increase in the steepness of the soil texture gradient (Fig. 3.7). The community variation among these samples might be due to the effects of precipitation runon near to the mountains.

Where is the Zoogeographic Transition?

My results are similar to those of Krasnov and Shenbrot (1998), and indicate that there are strong ecotonal effects on ant composition at SEV, but these ecotones, and the SEV site as whole, do not correspond to a zoogeographic transition for ants. Where, then, is the transition for ants? Patterns of variation in species composition (Fig. 4.11), and the proportion of species belonging to different faunal complexes (Fig. 4.12), suggest that an important transitional zone for ants occurs north of SEV. Unfortunately, ant distributional data are lacking for northern New Mexico, but it is likely that nearly all holarctic species occurring in southern Colorado west of the eastern New Mexico border terminate their distributions in extreme southern Colorado or northeast New Mexico.

The location of the postulated zoogeogeographic transition in ant faunal complexes at the Colorado/New Mexico border is concordant with a climatic transition from a monsoonal precipitation pattern (summer rainfall peak) to a Midwestern pattern (spring rainfall peak) in southern Colorado that has been identified by Comrie and Glenn (1998; Fig. 4.13). This threshold is based upon a multivariate regionalization of precipitation patterns in the southwestern United States and northern Mexico. While such a regionalization imposes an artificially discrete structure to continuous variation in climate, their results suggest the presence of a relatively steep gradient in climate across the northern New Mexico-southern Colorado region that may be an important determinant of ant composition. A similar transition in may occur within the panhandle of Texas (Figs 4.12, 4.13). More detailed surveys of ant abundance and precipitation patterns across these region will be necessary to test this proposition.

Comrie and Glenn (1998) also identified a secondary set of climatic subregions within the large monsoonal region (Fig. 4.13). The junction of three of these subregions corresponds roughly with the location of SEV. This observation suggests that major shifts in the life-forms of plants and ants occur in response to different kinds of climatic variation. Increasingly spring-dominated precipitation and decreasing winter temperatures to the north may determine the location of a vegetation transition, but ants may respond independently of plants to climatic variation occurring farther to the north. At this point, little information is available to suggest potential mechanisms for these differences. One likely candidate, however, is that precipitation patterns directly determine the distribution of ant taxa because the seasonality and amount of rainfall are known to affect the timing of reproduction of ant species (Hölldobler and Wilson 1990).

My results illustrate how different processes operating at different spatial scales structure biotic assemblages (Wiens et al. 1987). The recognition of these processes, and the spatial patterns they create, vary depending upon the characteristics of the study organisms (Wiens 1989b, Conroy and Noon 1997). In some cases, the abiotic processes determining the distribution patterns of different taxa may be linked and covary in space. In other cases, they may not. Given the variability of species characteristics and the environmental variables to which they respond (e.g. van Jaarsveld et al. 1998, Woinarski et al. 1999), untangling and documenting patterns of biodiversity will likely require surveys of many different organisms (Haila and Margules 1996) using organism-specific definitions of habitats and regions. The task ahead of us is formidable and we should allocate our scientific resources accordingly.

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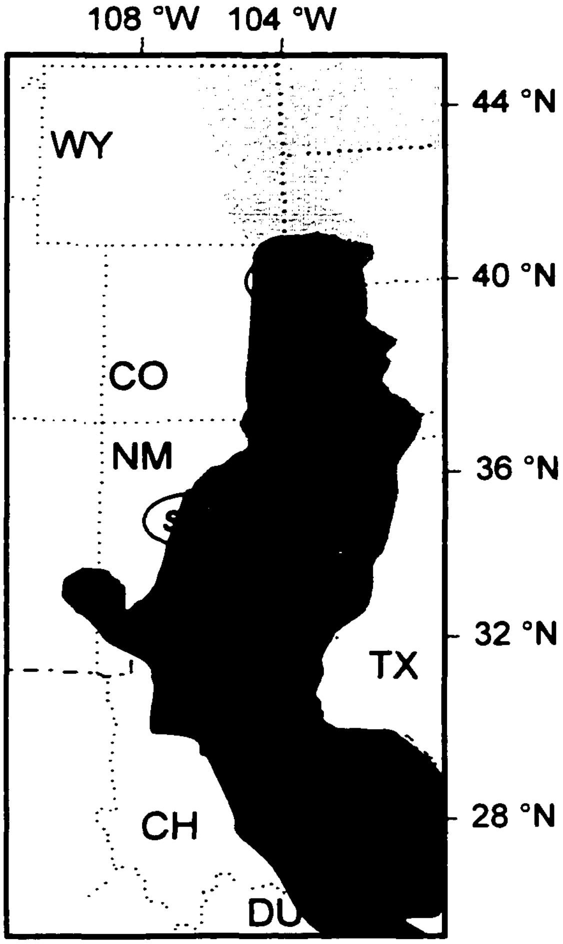

Fig. 4.1. Approximate distribution of northern mixed prairie vegetation (top), shortgrass steppe vegetation (middle) and Chihuahuan desert vegetation in Wyoming (WY), Colorado (CO), New Mexico (NM), United States, and Chihuahua (CH), Coahuila (CO), and Durango (DU), Mexico. Detail in WY and CO adapted from Lauenroth and Milchunas (1991) and within NM from Gosz (1992). The locations of the study sites are also given; SGS=Shortgrass Steppe Long-Term Ecological Research (LTER) site, SEV=Sevilleta LTER, and JRN=Jornada LTER.

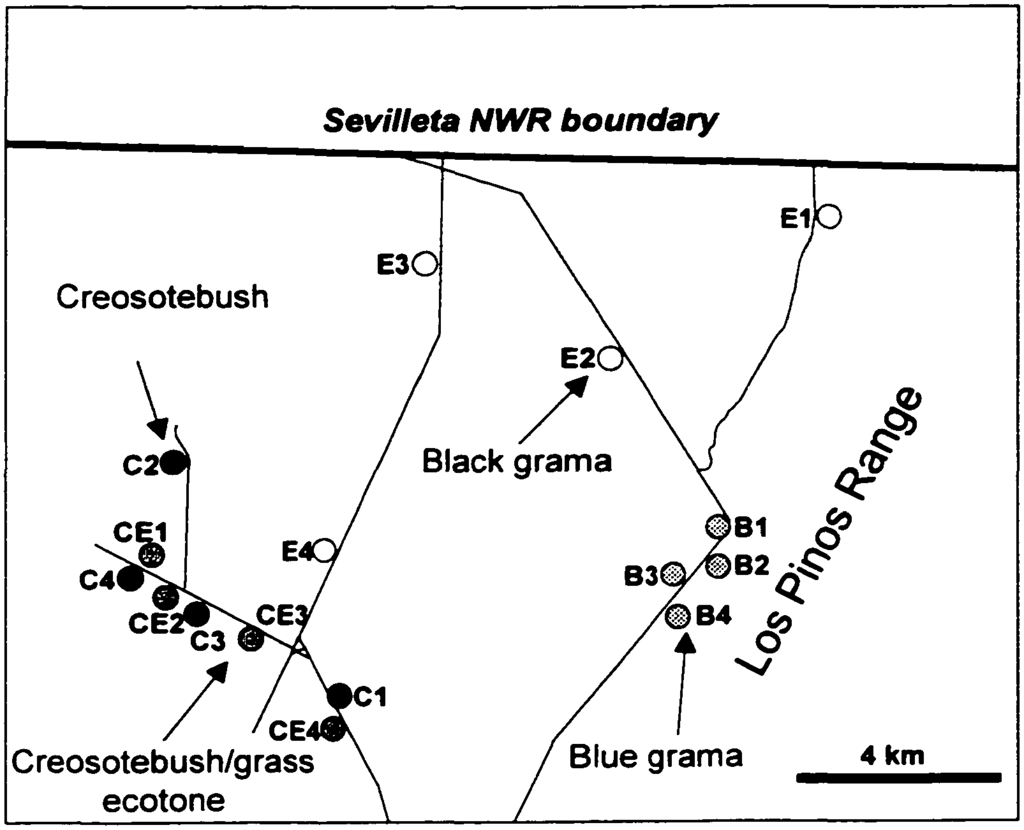

Fig. 4.2. The locations of ant-sampling transects within the SEV site, and the habitat types that they represent. Thin lines are roads and the thick line is the reserve boundary.

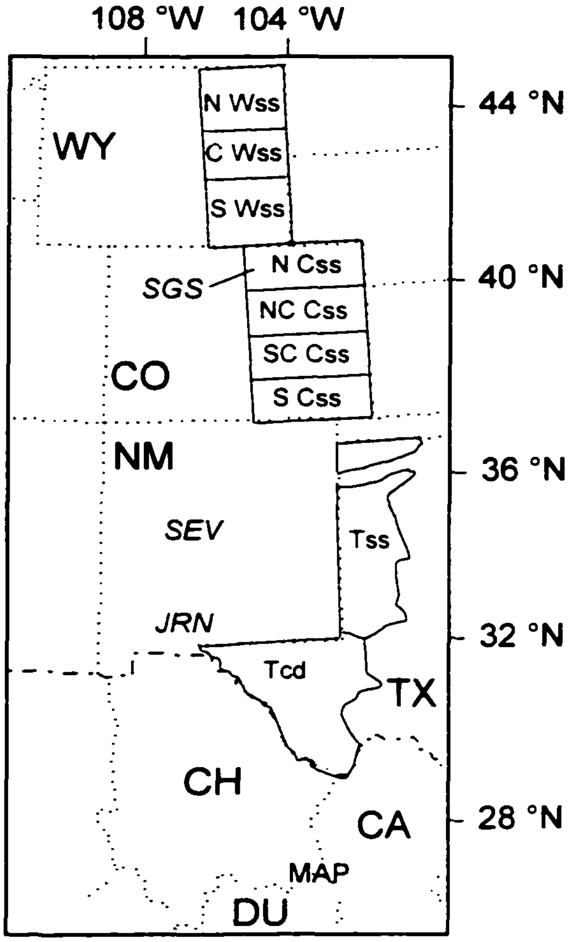

Fig. 4.3. The locations of geographic areas used to ascertain the distribution of ant species using previously published records (see text). N, NC, C, SC, S=north, north-central, central, south central, and south, respectively. Prefix W, C, T=Wyoming, Colorado, and Texas, respectively. Suffix ss= shortgrass steppe habitat, and cd=Chihuahuan desert habitat. MAP=Mapimi Biosphere Reserve.

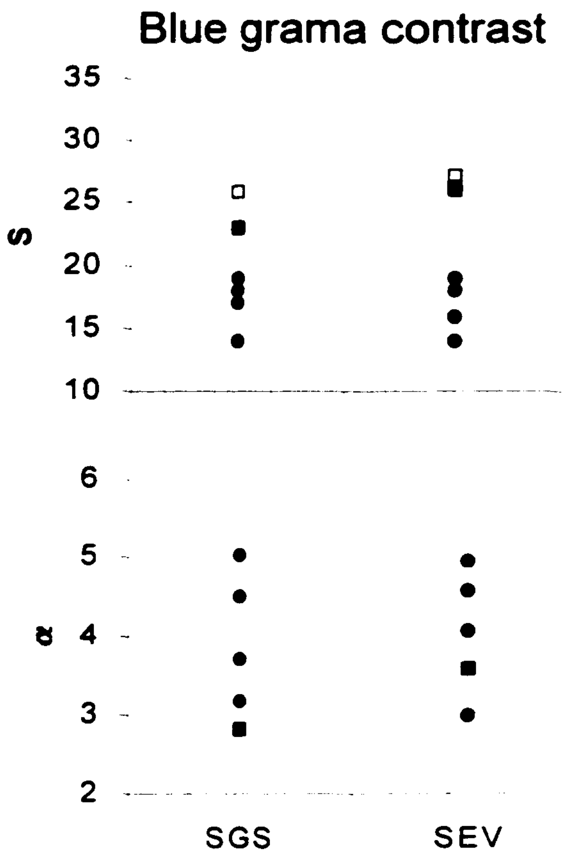

Fig. 4.4. Species richness (S) and logseries-α diversity (α) patterns in blue grama habitats at the SGS and SEV sites. Measured richness/diversity values at transects (n=4; solid circles), at the habitat scale (solid square), and a habitat-scale richness estimate (incidence-based estimator; open square) are presented. Transect-scale differences were not significant.

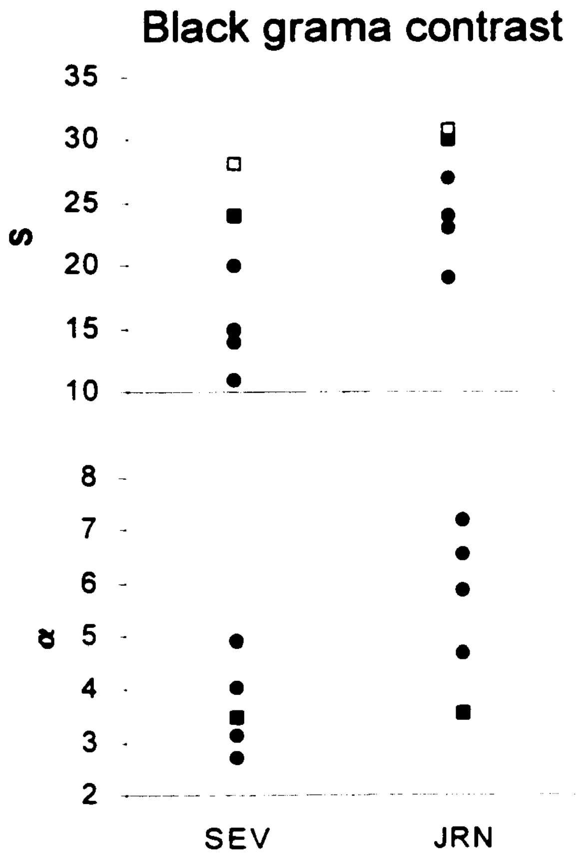

Fig. 4.5. Black-grama contrast of SEV and JRN, as in Fig. 4.4. Transect-scale differences were significant.

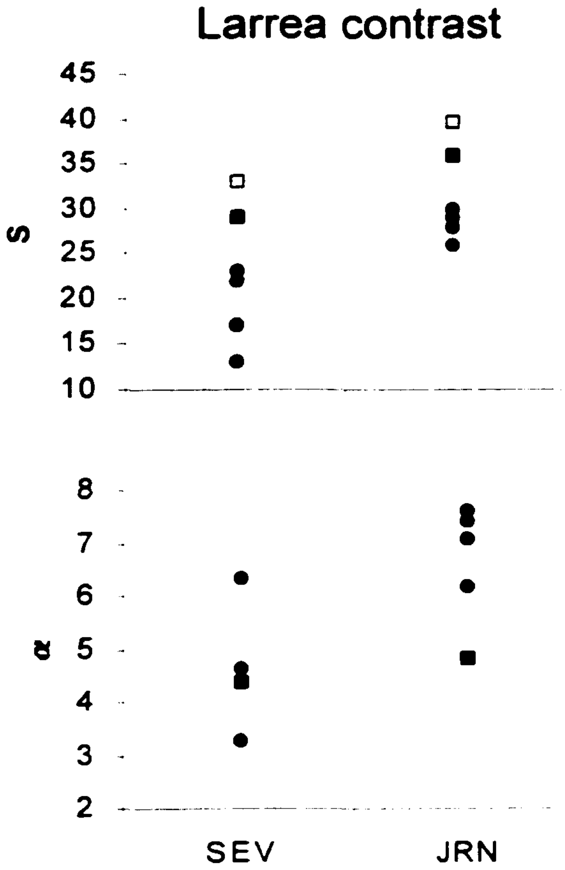

Fig. 4.6. Creosotebush contrast of SEV and JRN, as in Fig. 4.4. Transect-scale differences were significant.

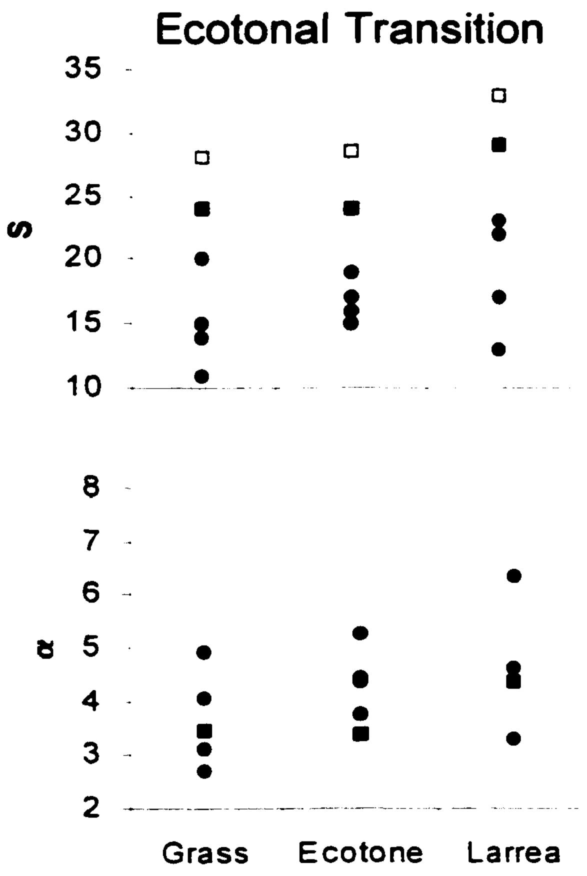

Fig. 4.7. Contrast of habitats within SEV, as in Fig. 4.4. Transect-scale differences were not significant.

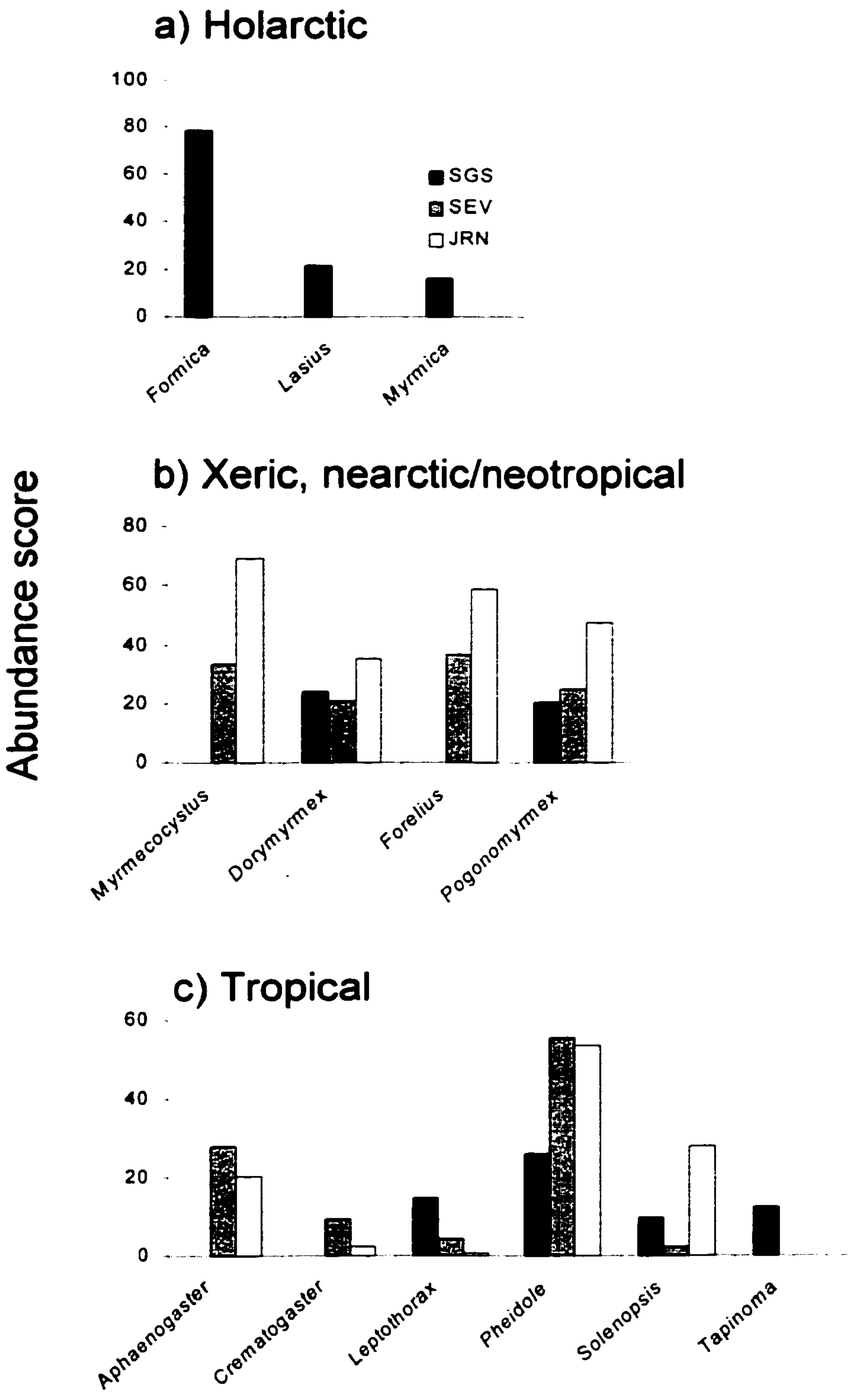

Fig. 4.8. The abundance of general belonging to different faunal complexes at the three study sites.

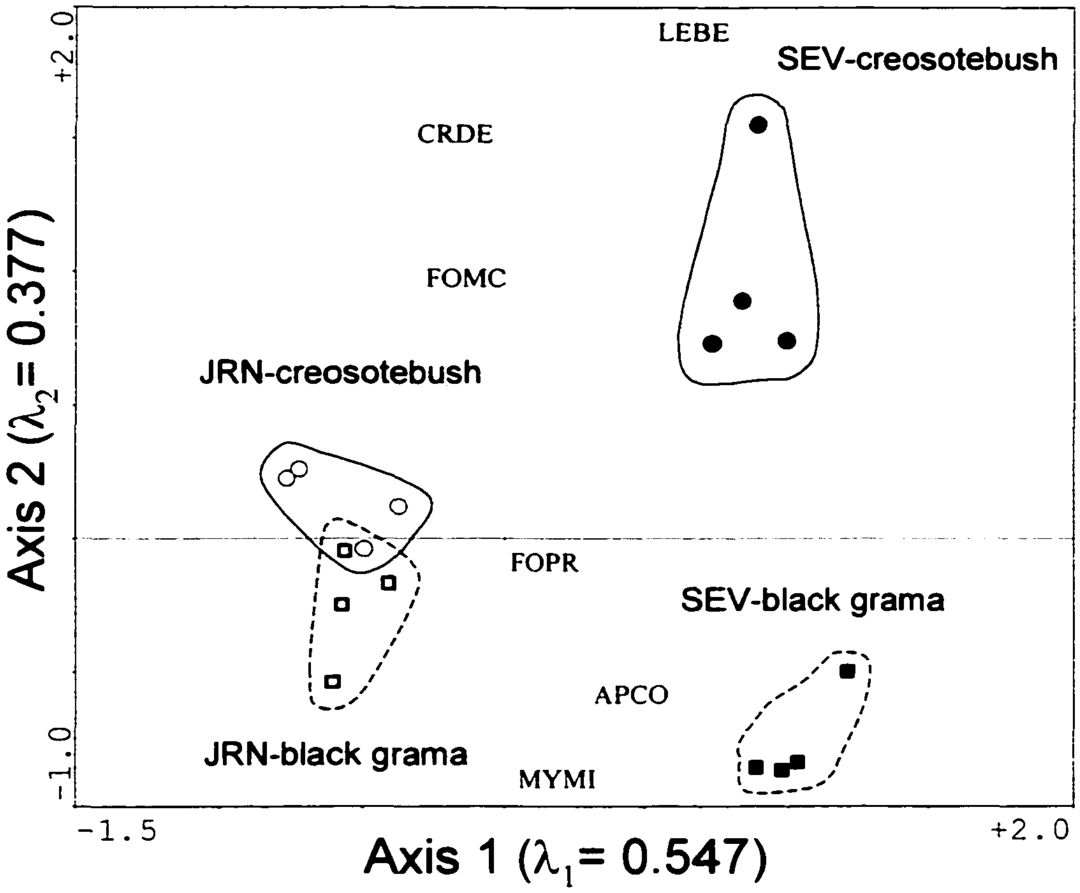

Fig. 4.9. Correspondence analysis of ant species composition at transects located in creosotebush shrubland and black grama grassland at the SEV and JRN sites. Species found in both SEV and JRN and that drive covariation on axis 2 are shown; apco=*Aphaenogaster cockerelli*, crde=*Crematogaster depilis*, doin=*Dorymyrmex insanus*, fomc=*Forelius mccooki*, fopr=*F. pruinosus*, lebe=*Leptothorax* sp. J1, mymi=*Myrmecocystus mimicus*.

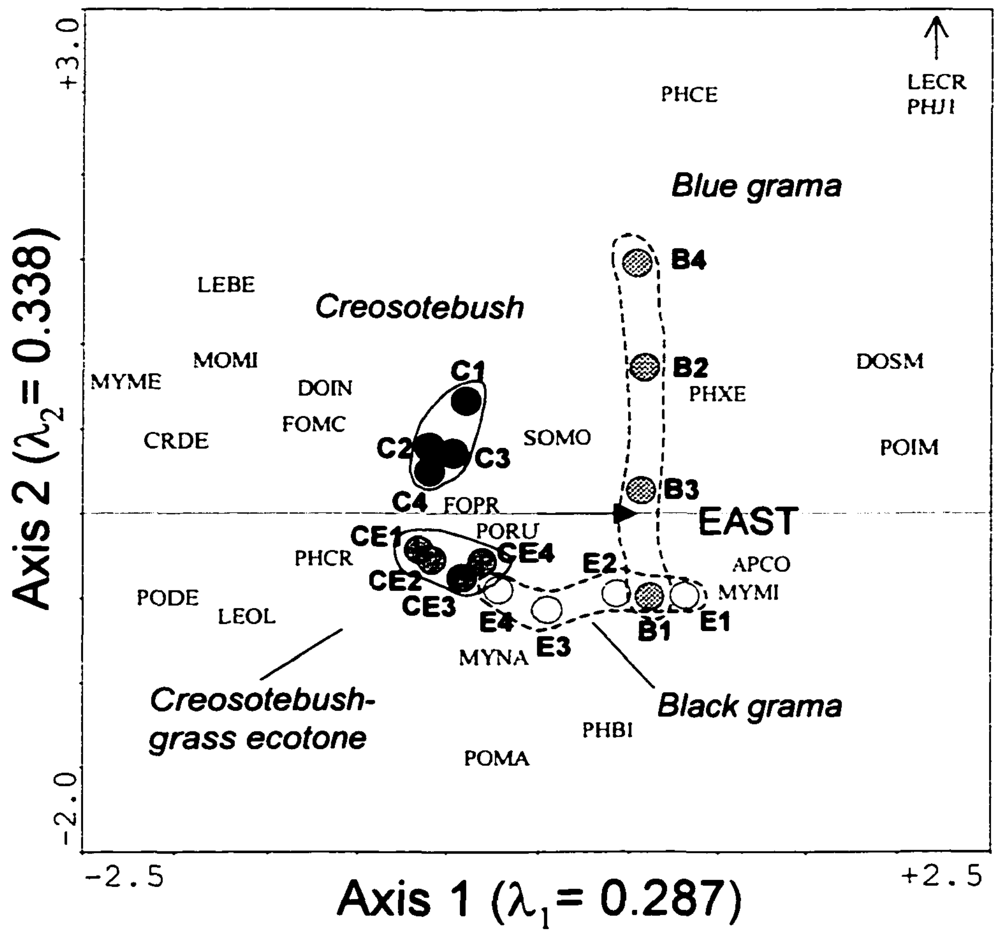

Fig. 4.10. Canonical correspondence analysis (CCA) of transects located in different habitat types with the SEV. Of nine spatial variables tested, only east-west coordinates explained a significant amount of variation in ant composition in forward selection procedures and is presented. Consult Fig. 2.6. for the rules for interpreting CCA plots. apco=*Aphaenogaster cockerelli*, crde=*Crematogaster depilis*, doin=*Dorymyrmex insanus*, dosm=*D. smithi*, fomc=*Forelius mccooki*, fopr=*F. pruinosus*, lebe=*Leptothorax* sp. J1, lecr=*L. carinatus*, leol=*L. olbiquicanthus*, momi=*Monomorium minimum*, myna=*Myrmecocystus navajo*, myme=*M. mexicanus*, mymi=*M. mimicus*, phce=*Pheidole cerebrosior*, phcr=*P. crassicornis*, phJ1=*P. sp.* J1, phxe=*P. xerophila*, pode=*Pogonomyrmex desertorum*, poim=*P. imberbiculus*, poru=*P. rugosus*, somo=*Solenopsis molesta*,

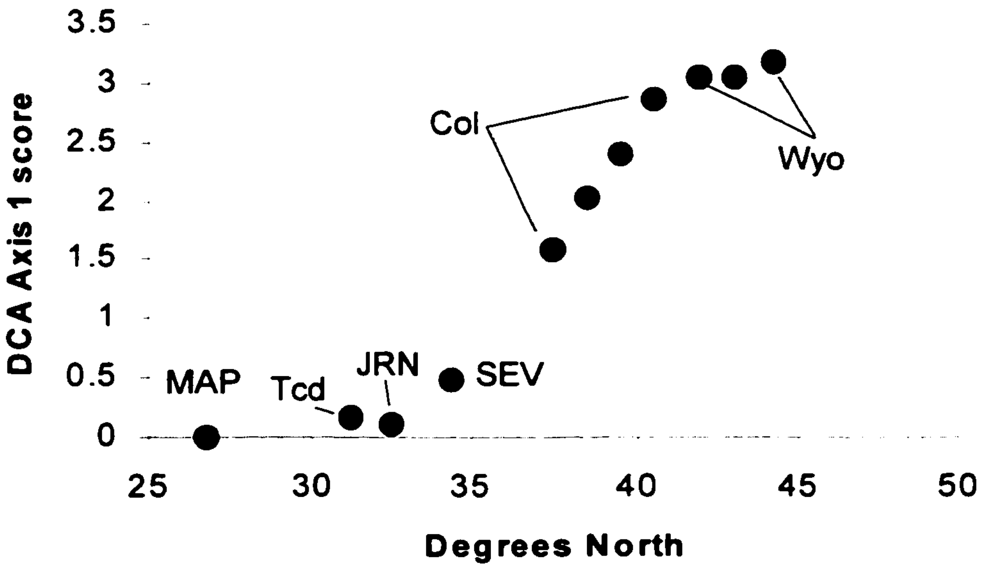

Fig. 4.11. Variation in DCA axis 1 scores based upon an ordination of presence-absence data of the distribution of a set of common ant species (see text) among geographic areas (see Fig. 4.3). Latitude values are at the center of geographic areas.

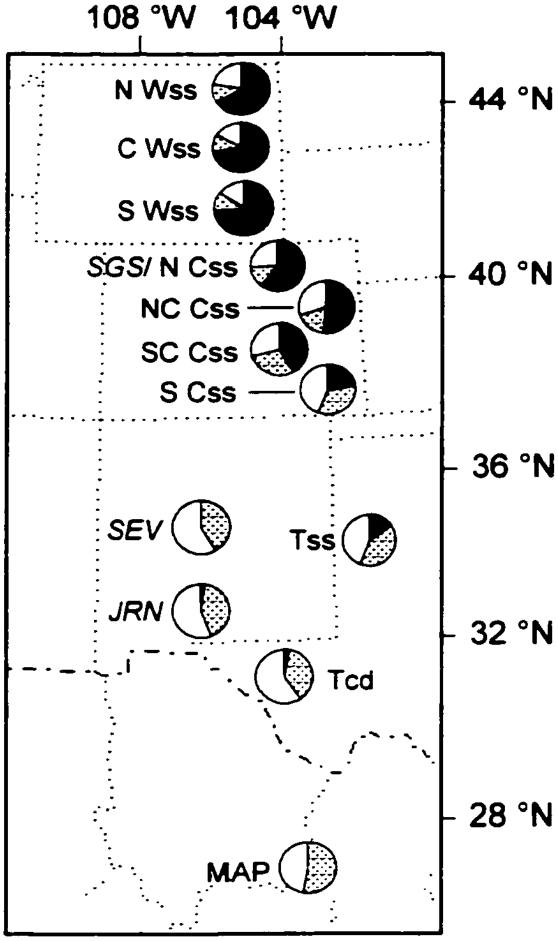

Fig. 4.12. The proportion of shortgrass steppe and Chihuahuan desert ant species occurring in each geographic area that belong to holarctic (black), xeric (stippled), and tropical (white) faunal complexes.

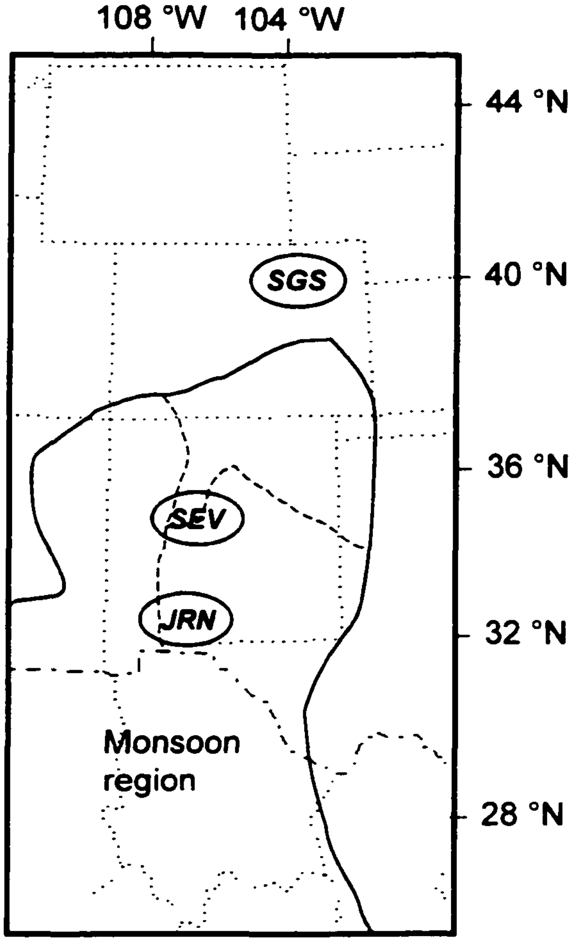

Fig. 4.13. The northern limit of the monsoonal precipitation region (solid line) and the division between three subregions within the monsoonal region of New Mexico (dashed lines), based upon a multivariate (principal components analysis) regionalization of precipitation seasonality and annual variability in the southwestern United States and northern Mexico (adapted from Comrie and Glenn 1998). In this plot, regional delineations were defined by different principal components, and depict the maximum-loading approach in which each of the 309 weather stations studied was assigned to the component upon which it loaded most highly (Fig. 4b in Comrie and Glenn 1998). All of the regionalization methods Comrie and Glenn tried yielded similar results.

Appendix 4.1. Ant species recorded in all the habitat types examined at the Shortgrass Steppe, Sevilleta, and Jornada LTER sites. OT= Pitfall trapped in a habitat other than that examined in this study, incuding grazing treatments within in dominant grassland types. HC = hand collected only. Species collected outside of stated habitats or hand-collected were not considered in diversity or multivariate analyses in this chapter, but were used for distributional information.

Subfamily Species	**SGS**	**SEV**	**JRN**
Ponerinae			
Hypoponera opacior (Forel)	OT		
Ecitoninae			
Neivamyrmex carolinensis (Emery)	HC		
Neivamyrmex nigrescens (Cresson)		x	
Neivamyrmex texanus Watkins		x	x
Myrmicinae			
Aphaenogaster cockerelli André		x	x
Aphaenogaster huachucana Creighton		HC	
Crematogaster depilis Wheeler		x	x
Crematogaster larreae Buren			x
Crematogaster navajoa Buren		x	HC
Crematogaster punctulata Emery		x	HC
Crematogaster sp. S1		x	
Leptothorax sp. J1*		x	x
Leptothorax carinatus Cole		x	x
Leptothorax olbiquicanthus Cole	x	x	x
Leptothorax schmitti (Wheeler)	x		
Leptothorax sp. C1	x		
Leptothorax sp. S1		x	
Monomorium minimum (Buckley)	x	x	x
Myrmica emeryana Cole	x		
Myrmica sp. C1	x		
Myrmica sp. C2	HC		
Pheidole cerebrosior Wheeler		x	x
Pheidole coloradensis Emery	x		
Pheidole crassicornis Emery		x	x
Pheidole desertorum Wheeler		HC	
Pheidole hyatti Emery		x	x
Pheidole longula Emery	x	x	
Pheidole militicida Wheeler			x
Pheidole rugulosa Gregg			x
Pheidole sciophila Wheeler			x

Pheidole soritis Wheeler		x	
Pheidole sp. C1	x		
Pheidole sp. J1		x	x
Pheidole sp. J2			x
Pheidole sp. S1		x	
Pheidole tepicana? Pergande		x	
Pheidole tucsonica Wheeler		x	x
Pheidole xerophila Wheeler		x	x
Pogonomyrmex apache Wheeler		x	HC
Pogonomyrmex californicus (Buckley)			x
Pogonomyrmex desertorum Wheeler		x	x
Pogonomyrmex imberbiculus Wheeler		x	x
Pogonomyrmex maricopa Wheeler		x	x
Pogonomyrmex occidentalis (Cresson)	x		
Pogonomyrmex rugosus Emery		x	x
Pogonomyrmex texanus Francke&Merickel		x	x
Solenopsis amblychila Wheeler			x
Solenopsis krockowi Wheeler			x
Solenopsis molesta sp.	x	x	
Solenopsis sp. J1			x
Solenopsis xyloni McCook			x
Tetramorium spinosum (Pergande)			x
Trachymyrmex smithi Buren			x
Dolichoderinae			
Dorymyrmex c.f. *flavus* McCook			x
Dorymyrmex insanus (Buckley)	x	x	x
Dorymyrmex smithi Cole	x	x	
Dorymyrmex sp. S1		x	
Dorymyrmex bicolor Wheeler			x
Forelius mccooki McCook		x	x
Forelius pruinosus (Roger)	x	x	x
Tapinoma sessile (Say)	x		
Formicinae			
Acanthomyops coloradensis (Wheeler)	HC		
Brachymyrmex sp. S1		x	
Camponotus festinatus (Buckley)			x
Camponotus noveboracensis (Fitch)	x		
Camponotus vicinus Mayr		x	
Formica argentea Wheeler	HC		
Formica bradleyi Wheeler	x		
Formica dakotensis Emery	x		
Formica densiventris Viereck	x		
Formica fossaceps Buren	x		
Formica integroides sp.	x		

Formica lasiodes Emery	x		
Formica limata Wheeler	x		
Formica mucescens Wheeler	x		
Formica neoclara Emery	HC		
Formica neogagates Viereck	x		
Formica obscuripes Forel	x		
Formica obtusopilosa Emery	x		
Formica occulta Francouer	x		
Formica oreas Wheeler	x		
Formica perpilosa Wheeler			OT
Formica wheeleri Stitz	x		
Lasius crypticus Wilson	x		
Lasius neoniger Emery	x		
Lasius pallitarsus (Provancher)	HC		
Lasius sitiens Wilson	x		
Lasius sp. C1	OT		
Lasius subumbratus Viereck	HC		
Myrmecocystus depilis Forel		x	x
Myrmecocystus mexicanus Wesmael		x	x
Myrmecocystus mimicus Wheeler		x	x
Myrmecocystus navajo Wheeler		x	x
Myrmecocystus placodops Forel		x	
Myrmecocystus romainei Snelling			x
Paratrechina terricola (Buckley)			HC
Polyergus breviceps Emery	OT		

**L. bestelmeyeri*, sp. nov.;W. M. MacKay, in press.

Appendix 4.2. The number of species per genus recorded in geographic areas (see Fig. 3.3), organized by faunal complex. Genus codes (italics) are the first four letters of the generic name, except for Myrc (= *Myrmecocystus*).

Geographic area	**Holarctic**			**Xeric**				**Tropical**				
	Form	*Lasi*	*Myrm*	*Myrc*	*Dory*	*Fore*	*Pogo*	*Apha*	*Crem*	*Lept*	*Phei*	*Sole*
N Wss	10	5	3	0	1	1	1	2	0	2	2	0
C Wss	11	4	3	0	1	1	1	0	0	2	2	0
S Wss	11	4	4	0	1	1	1	0	0	2	2	0
N Css	17	4	2	1	1	1	2	0	1	3	3	2
NC Css	13	4	1	1	1	1	2	0	1	3	4	2
SC Css	11	4	0	2	1	2	5	0	2	2	4	2
S Css	5	3	0	3	1	2	5	0	3	3	6	3
SEV	0	0	0	5	3	2	6	1	4	4	11	3
Tss	4	1	0	3	3	2	6	2	2	1	7	4
JRN	1	0	0	5	3	2	7	1	4	3	10	4
Tcd	2	0	0	4	3	2	7	1	4	1	12	5
MAP	0	0	0	3	1	2	5	1	1	1	5	2

"Y allá, sobre el tope de las piedras, está el grito del hombre, llamando al viento para que detenga el viaje de las nubes y las haga llorar sobre su campo: --¡Vientooo! ¡Vientooo! ¡Traéme aguacero...!"

Atahualpa Yupanqui
Aires Indios. Ediciónes
Siglo Viente, Buenos
Aires, Argentina.

CHAPTER V

THE ANTS OF THE SOUTHERN SONORAN DESERT: COMMUNITY STRUCTURE AND THE ROLE OF TREES.

Bestelmeyer, B. T., and R. L. Schooley. 1999. Biodiversity and Conservation 8: 643-657

Abstract

In contrast to other North American deserts, the southern Sonoran desert is dominated by trees that provide shaded microhabitats necessary for the establishment and survival of several plant species. Near the southern limit of the Sonoran desert in Sonora, Mexico, we evaluated the role that tree microhabitats may play in structuring ant communities. We recorded 39 species and 21 genera of ants from a 9.7-ha area. Total species richness was estimated to be between 47 and 49 species, a much greater species richness than that reported for other North American arid-zone habitats. Although species richness did not differ between open ground and tree-shaded microhabitats, species composition did. Opportunistic species, *Camponotus* species, *Pheidole sciophila* and *P. titanis* were more common near trees, whereas *Pheidole* sp. A and granivorous species were more active in open areas. The imperilment of trees in the Sonoran desert due to commercial cutting and

the spread of buffelgrass *Pennisetum ciliare* may alter the existing composition of ant communities.

Introduction

Ants (Hymenoptera: Formicidae) are conspicuous, diverse, and functionally-important elements of arid and semiarid ecosystems throughout the world (Kusnesov 1963, Andersen 1983, MacKay 1991, Andersen and Clay 1996, Bestelmeyer and Wiens 1996). However, relatively few ecological studies have been undertaken in North American arid zones (MacKay 1991). Although the Great Basin (Wheeler and Wheeler 1986), Chihuahuan (Schumaker and Whitford 1975, Whitford 1978) and Mojave deserts (Wheeler and Wheeler 1973) have received some attention, the ant communities of the Sonoran desert remain largely undescribed. Furthermore, much of the existing information on desert ant communities addresses specific ecological questions or subsets of communities (e.g. Davidson 1977) and cannot be compared directly. Studies of ecological communities based on standardized methods are essential if we are to begin to understand patterns in the distribution of biodiversity.

The dominance of trees and large shrubs in the southern portion of the Sonoran desert distinguishes it from other North American deserts (MacMahon and Wagner 1985, Brown 1994, Búrquez et al. in press). Trees are important habitat elements in deserts because they harbor critical resources for a variety of animals (MacMahon and Wagner 1985). In general, trees and shrubs provide critical nesting sites (Schumacher and Whitford 1974), microclimates (Cole 1932, Bestelmeyer 1997), and food resources

(Andersen 1983, Van Zee et al. 1997) for ants and for other arthropods (Crawford 1991, Stapp 1997) in arid environments. The distinct and favorable microclimates found beneath trees such as ironwood (*Olneya tesota*) contribute to habitat heterogeneity and support perennial plant species not found in other desert microhabitats (Búrquez and Quintana 1994). For these and other reasons, ironwood has been considered a keystone species in the Sonoran desert (Nabhan and Carr 1994).

Ants and other arthropods may react to the microhabitat heterogeneity produced by trees in the Sonoran desert, although little is known of these relationships. Because of their great abundance, ecological diversity, high local species richness, and environmental sensitivity, ants have frequently been used as focal taxa in studies of the response of biodiversity to environmental variation and disturbances (Andersen 1991a, Perfecto and Snelling 1995, Bestelmeyer and Wiens 1996, Catangui et al. 1996). Ants may be especially valuable as focal taxa in arid zones because they are abundant and species-rich even when compared to other ground-foraging arthropods.

Here, we document the ant fauna at a site near the southern limit of the Sonoran desert. We describe several characteristics of the ant community and draw comparisons to other arid-zone ant communities. We also focus on the role of trees in generating habitat heterogeneity for ant species and functional groups.

Methods

Study Area

The study was conducted in a 9.7-ha area within Rancho Los Horcones, 4 km E of La Colorada on highway 16 in Sonora, Mexico (Fig. 5.1). The area is semiarid and receives an average of 346 mm of precipitation annually; elevation is ca. 400 m (Búrquez et al. in press). The topography of the sample area is flat and the soil surface consists predominantly of coarse sand. The vegetation at the site is typical of the Plains of Sonora division of the Sonoran desert (Búrquez et al., in press). Dominant trees and shrubs includes *Olneya tesota*, *Cercidium microphyllum*, *Acacia constricta*, *Jatropha cardiophylla*, *Mimosa laxiflora*, *Caesalpinia pumilla*, *Calliandra eriophylla*, *Opuntia arbuscola*, and *Encelia farinosa*. The sparse grass cover is dominated by *Cathestecum erectum* (M. Miller, pers. comm.). The vegetation in the region is quite variable, however, and changes between desert scrub and thornscrub depending upon elevation and aspect (Búrquez et al. in press). The site had not been grazed for 1.5 years at the time of the study.

Ant and Vegetation Sampling

In July 1995, we sampled ants and vegetation at points along four transects (20 stations each, 10-m spacing; 80 traps total). Transects were parallel and separated by 150 m. Ants were sampled at each point using one pitfall trap. Although data from pitfall traps may provide biased estimates of ant colony density, pitfall traps effectively represent ant forager activity in open habitats such as deserts (Greenslade 1973, Andersen 1991b, Bestelmeyer et al. in press). Traps were polypropylene sample cups (60 mm diameter. 73 mm deep) filled with 40 ml of propylene-glycol-based antifreeze. We placed traps in the ground with the upper margin flush to the soil surface and allowed them to settle for 24 hr prior to opening them. Traps remained open for ca. 72 hours. Air temperatures ranged from 25 to 41 °C and unshaded soil-surface temperatures ranged from 26 to 61 °C during trapping. One trap was destroyed by animals and was excluded from the analyses. In addition to trapping, casual hand-collection was performed throughout the study area to reveal the presence of species that are undersampled using pitfall traps (e.g. legionary ants; Ecitoninae).

We sampled basal vegetation cover around each station along four 1.5-m line-intercept rays placed at 90° angles from one another. Vertical complexity of vegetation, recorded as the number of times a rod held perpendicular to the ground surface touched vegetation in 0-50 cm, 50-100 cm, and 100-150 cm intervals, was measured at four points located 50 cm away from each station.

Most voucher specimens of the ants were identified by Roy R. Snelling of the Los Angeles County Museum of Natural History and are housed in the C. P. Gillete Museum of Arthropod Diversity at Colorado State University.

Data Analysis

Only pitfall-trap records were used in these analyses because hand collections were not performed in a systematic way and cannot be compared directly with the pitfall data. We constructed a species accumulation curve by subsampling our 79 pitfall samples up to 500 times (depending upon the number of different subsamples possible) for each subsample size, and calculated mean numbers of species for each subsample size (McCune and Mefford 1997; see also Colwell and Coddington 1994). We generated estimates of total ant species richness from our samples using first-order and second-order jackknife estimators (Burnham and Overton 1979; McCune and Mefford 1997). Both of these estimators provide adequate bias reduction for large numbers of samples (i.e. > 50; Colwell and Coddington 1994). Species that were hand-collected were added to the jackknife estimates.

We analyzed the relationship between ant species composition and environmental variables using canonical correspondence analysis (CCA) and indicator species analysis. CCA is a direct-gradient ordination technique in which the weighted averages of species abundances are constrained to be linear combinations of a set of provided environmental variables. The resulting ordination diagram expresses both patterns of species composition (as in conventional ordination techniques) and the relationships between samples, species and environmental variables. This second feature is similar to regression (see Jongman et al. 1995). The abundances of ant species from individual pitfall traps were used in the ordination, and these were related to three environmental variables measured around each trap that describe the contrast between open-ground and tree-shaded microhabitats: 1) the proportion of ground cover that was bare, 2) the proportion of ground covered with litter, and 3) the mean vertical complexity of vegetation ($n=4$ rays) from 0.5-1.5 m above ground. Proportions were arcsine-square-root transformed prior to analysis, and species abundances were log-transformed to reduce the variance associated with high capture rates when traps were near to ant nests. The statistical significance of axis eigenvalues and species-environment correlations (i.e. the correlation between sample scores for an axis derived from species data and sample scores that are linear combinations of the environmental variables; Jongman et al. 1995) was ascertained with a Monte Carlo randomization test (McCune and Mefford 1997) using 100 iterations. The randomization procedure was performed by randomly reassigning species abundance values among samples. Observed eigenvalues and correlations were then directly compared to a distribution of these values generated from randomized communities. The P value reported is the proportion of randomized trials with values equal to or exceeding the observed values.

We evaluated associations of species with either open-ground or tree-shaded microhabitats with indicator species analysis (i.e. the indicator value method (IndVal); Dufrêne and Legendre 1997). Trap points were considered to be in the tree-shaded microhabitat if >33 % of the ground cover was leaf litter and the mean vegetation complexity/ray was >1.5 in the 0.5-1.5-m strata (20 trap points), and we categorized all other trap points as open (59). This threshold was chosen because most values were either much greater or less than this value. IndVal was used to describe the capacity of different species for indicating particular habitats or environmental conditions. Species were assigned indicator values for each microhabitat that were greatest when 1) all individuals of a species occurred in only one microhabitat and 2) all samples within one microhabitat contained an occurrence by that species. Values for each habitat varied from zero (no indication) to 100 (perfect indication). We evaluated the statistical significance of the maximum indicator values for each species using Monte Carlo randomization tests in which species abundance data were randomized among microhabitats (1000 iterations; McCune and Mefford 1997).

For a broader level of analysis, we assigned species to functional groups (Appendix 5.1) following Andersen (1992, 1997) with modifications from Bestelmeyer and Wiens (1996). The use of functional groups provides a means of evaluating the responses of ants to environmental variation with respect to aspects of their ecology without requiring detailed knowledge of their natural history. Six functional groups were abundant enough for analysis: 1) *thermophiles* are largely or entirely diurnal and are active when soil-surface temperatures are too high for most other ant species to maintain activity; 2) *generalized myrmicines* are widespread, aggressive, and have workers that mass-recruit to food sources but do not tolerate extremely high temperatures; 3) *opportunists* are behaviorally submissive and are often common in disturbed habitats; 4) members of the genus *Camponotus* are usually nocturnal and arboreal; 5) *attines*, members of a myrmicine tribe, use plant matter and detritus to cultivate fungus; and 6) *granivores* are largely seed-specialists. The log-transformed abundances of functional groups were compared at stations occurring in open ground and tree-shaded microhabitats using multivariate analysis of variance (MANOVA). Only species captured in pitfall traps were considered in these analyses.

We used PC-ORD 3.0 (McCune and Mefford 1997) to generate species-accumulation curves, estimate species richness and perform CCA and indicator species analysis. All other analyses were performed in SAS 6.1 (SAS Institute Inc. 1989).

Results

Community Structure

We recorded 21 genera and a total of 39 species of ants from pitfall traps (35 spp.) and hand collections (4 additional spp.; Appendix 5.1). Of 79 traps containing 5503 specimens, *Forelius* sp. *pruinosum* group occurred in 94% of traps and constituted over 60% of all individual ants. In addition, *Monomorium* sp. A, *Tetramorium spinosum*, *Cyphomyrmex wheeleri*, *Solenopsis aurea*, and four *Pheidole* spp. all occurred in >30% of the pitfall traps and together constituted 26% of the individual ants. The most species-rich genera were *Pheidole* (10 spp.), *Camponotus* (3) and *Solenopsis* (3).

The species-accumulation curve (Fig. 5.2) does not reveal an asymptote, suggesting that the community was inadequately sampled. Of the species caught in pitfall traps, seven were represented by only one or two individuals. A first-order jackknife estimate of the total species richness at the site (based on the number of species found in only one sample) was 43 and the second-order jackknife estimate (based on the number of species found in one and two samples) was 45 species. Adding species observed only from hand collections to these estimates yields 47 and 49 species, respectively.

The Role of Trees

Neither species richness (t=0.06; df=77; P=0.94) nor diversity (Shannon-Weiner diversity indices: t=0.33; df=77; P= 0.73) within traps differed between open ground and tree-shaded microhabitats. Nine species were captured exclusively in open ground traps and five species exclusively in tree-shaded traps.

CCA revealed that ant species abundance and composition were related to the measured environmental variation (Fig. 5.3). Although the eigenvalue of axis 1 was low (0.175), indicating that most (93%) of the variation in species abundances remained unexplained by the ordination, the eigenvalue was significantly higher than that generated from randomized data (P=0.01). Furthermore, the species-environment correlation on axis 1 was high (Pearson correlation=0.80) and significantly greater than that expected from randomized data (P=0.01), indicating that patterns in the variation of species abundances were correlated with environmental variation along axis 1. In particular, axis 1 corresponded to the contrast between trap stations in open areas with a high proportion of bare ground and traps under trees with greater litter cover and vertical structure of vegetation.

IndVal revealed that four species were significantly more likely to indicate a particular habitat than expected by chance (Table 5.1; P<0.05). *Camponotus atriceps*, *Pheidole sciophila*, and *Pheidole titanis* were associated with tree habitats, whereas *Pheidole* sp. A was associated with open areas. The positions of these species in the ordination are highlighted in Fig. 5.3 and agree with the IndVal results. In addition to these species, *Camponotus vafer* was associated with high values of vertical structure and *Messor pergandei* and *Forelius mccooki* with bare ground, although these species did not reveal significant associations using IndVal.

Overall, the activity of functional groups differed between open ground and tree-shaded microhabitats (Wilks' λ=0.80; df=6, 72; P=0.01; Fig. 5.4). Opportunists (F=3.85; P=0.05) and *Camponotus* (F=3.28; P=0.07) were more active in tree-shaded microhabitats, whereas granivores (F=7.59; P=0.007) were more active in the open ground areas (all df=1, 77).

Discussion

Community Structure

The species richness of our southern Sonoran site is similar to or exceeds that of all other North American desert sites so far documented, despite the relatively limited spatial extent and duration of our study. Although few complete or systematic surveys of arid-zone ant faunas over defined or comparable spatial scales are available for comparison, species richness values at some sites may be compared with caution. Rojas-Fernandez and Fragoso (1994) recorded 32 species from the Mapimi Biosphere Reserve, which included different soil and vegetation types within the Chihuahuan desert. Wheeler and Wheeler (1973) recorded 27 species from Mojave and Sonoran desert-scrub habitats occurring within Deep Canyon, California. In the Chihuahuan desert grassland of southern New Mexico, Schooley et al. (unpubl.) recorded 29 species over a 10-ha area and Bestelmeyer and Wiens (unpubl.) recorded 37 spp. across an area of 100 km^2 containing different soil types.

A likely explanation for the comparatively high relative richness of the Sonoran site may be that the site receives greater annual precipitation (346 mm) than the Chihuahuan desert (284 mm), Mojave desert (150 mm), or Chihuahuan desert grassland (222 mm) sites mentioned above. Ant diversity tends to increase with increasing rainfall in arid zones (Davidson 1977, Marsh 1986, Andersen and Clay 1996). In addition, the minimum annual temperatures are generally higher in the Sonoran desert than in other North American deserts (MacMahon and Wagner 1985). Andersen (1995) suggested that low temperature is the principal abiotic stress affecting ant community structure and it may limit the diversity of many ant taxa.

Another reason that our site is relatively species rich may be its proximity to tropical dry forests in the region. The Sonoran desert differs from other North American deserts in the relative abundance of the arboreal *Camponotus* and fungus-growing attines such as *Atta* and *Cyphomyrmex* and the presence of the specialist predator *Odontomachus* and arboreal *Pseudomyrmex* (see also Andersen 1997), all of which are well represented in neotropical habitats. In fact, two species recorded here, *Camponotus atriceps* and *Cyphomyrmex flavidus*, have published records only as far north as Guatemala and Nayarít, Mexico, respectively (Kempf 1972, Brandão 1991). MacMahon and Wagner (1985) and Burquez et al. (in press) note a similar enrichment of the southern Sonoran desert flora by tropical plant taxa.

The Role of Trees

Most species of ants at our site did not differ in activity between areas under trees and in the open. This is not surprising considering that most of the recorded species are common inhabitants of desert regions in which trees and shrubs are sparse or absent (see Wheeler and Wheeler 1973). Many of these ants possess adaptations such as thermal-respiting behavior (Bestelmeyer 1997) or nocturnality (Snelling 1976) that permit them to tolerate or avoid harsh microclimates and utilize unshaded areas. *Forelius* spp., for example, were observed to travel along the stolons and leaves of grasses at midday and make quick forays onto the ground surface from these cooler microclimates. Because shaded microclimates probably represent less stressful environments than open ground for desert ants in general, especially during midday, ants possessing adaptations for foraging at high temperatures should be microhabitat generalists unless they are competitively excluded from shaded areas (Bestelmeyer 1997, Cerdá et al. 1997).

Several species, however, exhibited differences in activity between the open and canopy habitats. *Camponotus atriceps* nested at the base of trees and foraged along tree branches, and so may be closely tied to vegetation structure. This association is apparent from the proximity of this ant to the vertical-structure axis in the ordination diagram (Fig. 5.3). *Pheidole sciophila* and *Pheidole titanis* were not observed foraging in trees and may forage or nest in leaf litter under trees in this area, although little is known of the natural history of these ants. Similarly, nothing is known of the ecology of the unidentified species of *Pheidole* that was more active in open areas. Possible explanations for this pattern are competitive exclusion from canopy habitats or preferences for food items such as grass seeds that are found in the open. In addition, the specialist predator *Odontomachus* and arboreal *Pseudomyrmex* may also rely on trees, although their rarity made this impossible to determine. Some ant species that forage in open areas may require trees in which to nest. *Forelius* sp. were very active in open areas at a Chihuahuan desert site, but most nests occurred near to the bases of shrubs or half-shrubs (Bestelmeyer, unpublished data). Information on ant nesting behaviors greatly complements pitfall trap data in ant community studies.

When ants were grouped by ecological traits, additional responses to environmental heterogeneity became apparent. The opportunist group, largely

Tetramorium and *Dorymyrmex*, may have been more active under shrubs due to their relatively unspecialized characteristics (Andersen 1992), which limited their use of harsher microclimates, or because they were better able to avoid encounters with behaviorally-dominant thermophiles such as *Forelius* in the more complex litter habitats. At a broader scale, Andersen (1997) found that the abundance of opportunists increased with increasing shrub and tree cover along an elevation gradient from desert to woodland in southeastern Arizona. As discussed previously, the arboreal *Camponotus* ants may respond to vegetation structure, although little is known of the second species in this group, *Camponotus vafer*. Like *Pheidole* sp. A, the granivore group, including *Pogonomyrmex*, *Messor*, and *Ephebomyrmex*, may have preferred open areas because the seeds that they favor were more available there. The patterns presented here identify several ant species that would make fruitful subjects for more intensive studies. Such studies would most likely point to a variety of mechanisms that determine the response of ants to tree-induced heterogeneity, including the distribution of food, nest-site and abiotic limitation, and competition.

Environmental heterogeneity imposed by small-scale variation in vegetation structure has important effects on patterns of diversity in ants (Heatwole 1996, Bestelmeyer 1997, Cros et al. 1997) as well as other arthropods (MacKay et al. 1986, Stapp 1997, Herrera 1997) in arid ecosystems. The responses of this ant community to trees emphasize the important role that trees play in creating heterogeneity in the Sonoran desert. There is growing concern that tree populations in the Sonoran desert are declining due to commercial uses (Suzán et al. 1997) and land conversion (Yetman and Búrquez 1994). These changes may threaten populations of other plant species (Búrquez and

Quintana 1994, Suzán et al. 1994) and may alter the structure and composition of ant communities as well.

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Table 5.1. Indicator values (see text) of species for which values were significantly different from that expected from randomized data. For each habitat, relative abundance = the average abundance of a species in tree-shaded and open ground traps divided by the average abundance of that species in all traps. Relative frequency = the percentage of traps in tree-shaded and open ground microhabitats where a species was present (both expressed as percentages). Habitat affinity is the habitat in which a species had the highest indicator value, and the indicator value = relative abundance*relative frequency (*100) for the habitat in which the highest value was observed. The P value denotes the proportion of randomized data sets that had a greater maximum indicator value.

Species	Relative abundance		Relative frequency		Habitat affinity	Indicator value	P
	Tree	Open	Tree	Open			
Camponotus atriceps	96	4	22	5	Tree	21	0.029
Pheidole sciophila	97	3	43	5	Tree	42	0.000
Pheidole titanis	93	7	43	27	Tree	41	0.011
Pheidole sp. A	0	100	0	52	Open	52	0.001

Fig. 5.1. The extent of the Sonoran desert and the location of the study site.

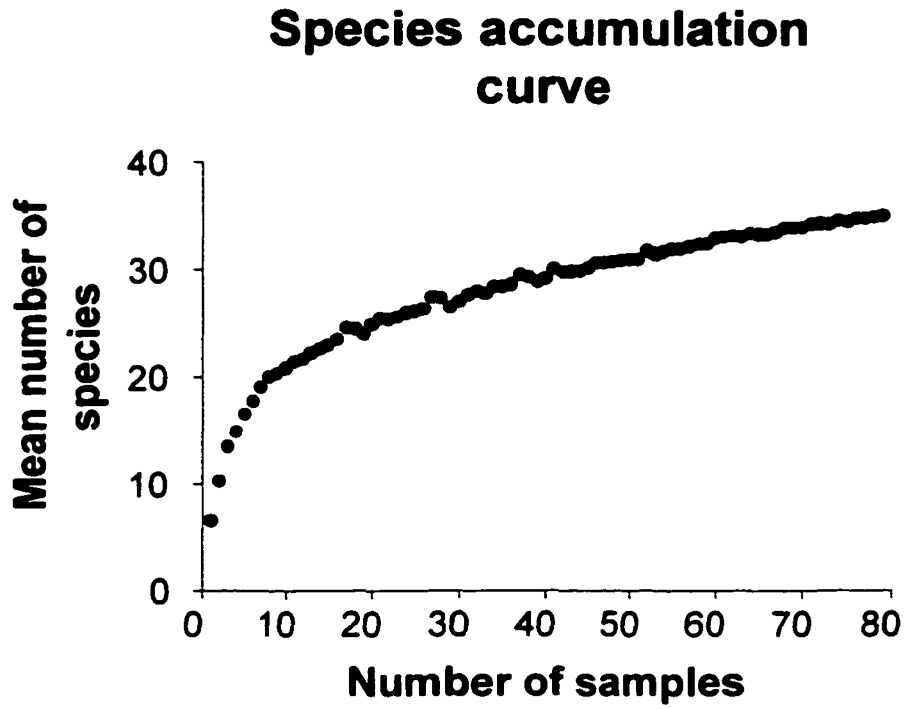

Fig. 5.2. A species accumulation curve representing all pitfall samples at the site. Each point represents the mean number of species in ≤ 500 subsamples of a given sample size.

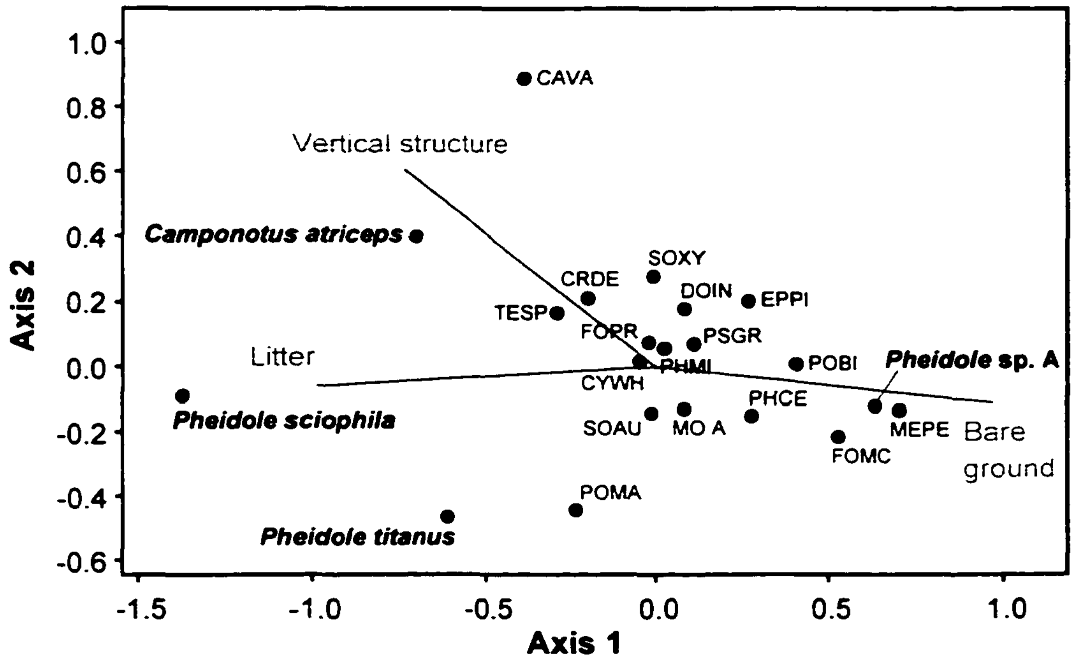

Fig. 5.3. A canonical correspondence analysis ordination of pitfall traps and species at the site. Vectors are environmental variables and points are species. Trap positions and species with less than three records are not shown to clarify presentation. Full species names indicate those species which had statistically significant indicator values (Table 1), all other species codes are the first two letters of the genus and the first two letters of the species names (Appendix 1). In the case of unidentified morphospecies, the single-letter morphospecies designation is used instead of the species name (e.g. *Monomorium* sp. A=MO A).

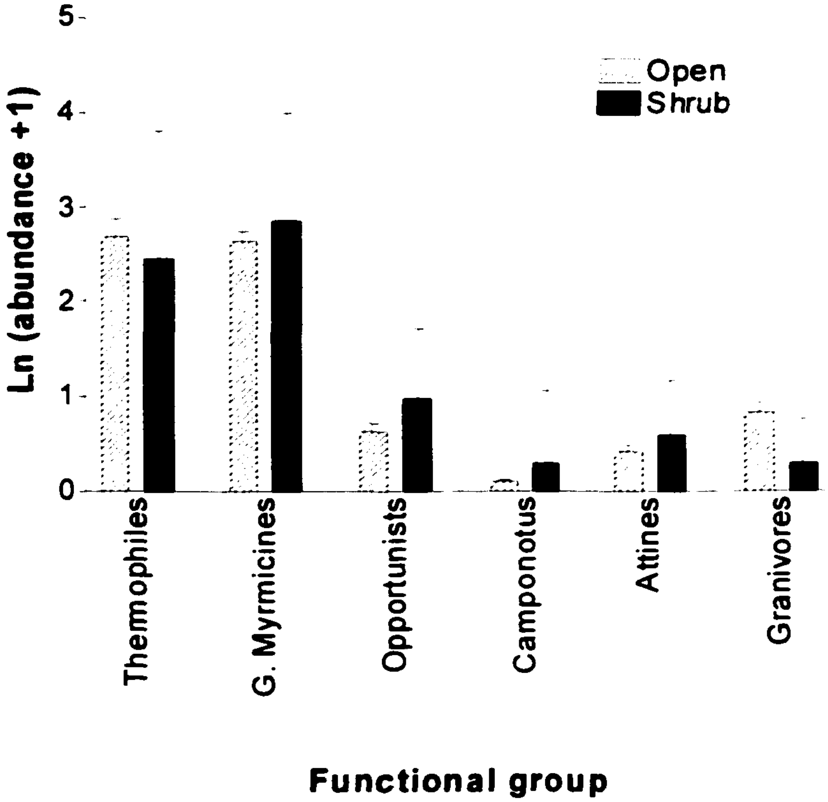

Fig. 5.4. The log-transformed abundance values (+ 1 SE) of functional groups in traps from open ground and tree-shaded microhabitats.

Appendix 5.1. The ant species recorded in this study, their functional group[a], their frequency of capture (% of traps), and the proportion of individuals captured (% of total). Raw values are in parenthesis. HC= recorded in hand collections only. Most species determinations were by Roy. R. Snelling, Los Angeles County Museum of Natural History.

Subfamily Species	Group	Frequency	Abundance
Ponerinae			
Odontomachus clarus Wheeler	P	1.3 (1)	0.04 (2)
Ecitoninae			
Neivamyrmex nigrescens (Cresson)	L	HC	
Pseudomyrmicinae			
Pseudomyrmex gracilis (Fabricius)	A	3.8 (3)	0.05 (3)
Myrmicinae			
Aphaenogaster albisetosus (Mayr)	O	HC	
Atta mexicana (F. Smith)	At	1.3 (1)	0.02 (1)
Crematogaster depilis Wheeler	M	16.5 (13)	0.29 (16)
Cyphomyrmex wheeleri Forel	At	41.8 (33)	1.20 (66)
Cyphomyrmex flavidus (Pergande)	At	2.5 (2)	0.04 (2)
Ephebomyrmex pima Wheeler	G	26.6 (21)	0.65 (36)
Leptothorax (Macromischa) sp. A	?	1.3 (1)	0.02 (1)
Messor pergandei (Mayr)	G	11.4 (9)	1.11 (61)
Monomorium sp. A	M	60.8 (48)	3.63 (200)
Pheidole cerebrosior Wheeler?	M	41.8 (33)	3.18 (175)
Pheidole hyatti Emery	M	2.5 (2)	0.14 (8)
Pheidole cf. *micula* Wheeler	M	39.2 (31)	2.40 (132)
Pheidole sciophila Wheeler	M	16.5 (13)	1.47 (81)
Pheidole titanis Wheeler	M	31.7 (25)	6.65 (366)
Pheidole tucsonica Wheeler	M	1.3 (1)	0.05 (3)
Pheidole vistana Forel	M	2.5 (2)	0.14 (8)
Pheidole sp. A	M	36.7 (29)	2.96 (163)
Pheidole sp. J	M	1.3 (1)	0.04 (2)
Pheidole sp. K	M	1.3 (1)	0.02 (1)
Pogonomymex bicolor Cole	G	21.5 (17)	0.69 (38)
Pogonomyrmex maricopa Wheeler	G	12.7 (10)	0.29 (16)
Solenopsis aurea Wheeler	M	40.5 (32)	4.36 (240)
Solenopsis xyloni McCook	M	26.6 (21)	5.69 (313)
Solenopsis (*Diplorhoptrum*) sp.	Cr	1.3 (1)	0.02 (1)
Tetramorium hispidum Wheeler	O	HC	

Tetramorium spinosum (Pergande)	O	51.9 (41)	1.38 (76)
Trachymyrmex desertorum (Wheeler)	At	2.5 (2)	0.04 (2)
Dolichoderinae			
Dorymyrmex insanus (Buckley)	O	29.1 (23)	0.95 (52)
Forelius mccooki McCook	T	15.2 (12)	1.29 (71)
Forelius sp. *pruinosum* group	T	93.7 (74)	60.44 (3326)
Formicinae			
Camponotus atriceps (F. Smith)	C	10.1 (8)	0.55 (30)
Camponotus festinatus (Buckley)	C	HC	
Camponotus vafer Wheeler	C	6.3 (5)	0.11 (6)
Myrmecocystus kennedyi Snelling	T	1.3 (1)	0.02 (1)
Myrmecocystus nequazcatl Snelling	T	2.5 (2)	0.04 (2)
Paratrechina terricola (Buckley)	?	2.5 (2)	0.04 (2)

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[a] A=Arboreal, At=Attini, C=*Camponotus*, Cr=Cryptic species, G=Granivore, L=Legionary, M=Generalized Myrmicines, O=Opportunist, P=Predator, T=Thermophile.

"...scavenging should be seen as among the most ancient and decent professions, one that has been needed as long as waste has been generated in this world. Scavengers, as I see it, are those who turn the upward curve of consumption back onto itself. They help complete the loop that helps the rest of us go on living".

Gary Paul Nabhan, 1994
Desert Legends: Re-storying the Sonoran Borderlands.
Henry Holt & Co., New York, NY, USA.

"I wish we had time to bury them fellas".
"To hell with them fellas. Buzzards gotta eat, same as worms".

The Outlaw Josey Wales, 1976

CHAPTER VI

ANT SCAVENGING PATTERNS IN NORTH AMERICAN SEMIARID GRASSLANDS: REGIONAL, HABITAT, AND MICROCLIMATIC EFFECTS.

Abstract

The redistribution and concentration of nutrients by ants into the soil around their nests is a potentially important ecosystem function in semiarid grasslands. The scavenging of arthropod carrion and other materials by ants is perhaps the most important mechanism of nutrient redistribution. I documented the composition and behavior of ants that scavenged arthropod carrion from the ground surface in three grassland sites spanning a north-south gradient from shortgrass steppe through a transitional zone to Chihuahuan desert grassland. I compared the rates that small-insect baits were removed by scavengers and the distances that the baits were removed between sites, habitats and grazing treatments within sites, and under different microclimatic conditions. Additionally, I compared the numbers of baits removed to different microhabitats among grazing treatments at each site. From 10 to 16 species of ants were observed scavenging at each site, and 3-4 species removed ca. 75% of baits. Bait removal rates were highest, and bait removal distances lowest, in the shortgrass steppe. Within sites, habitat variation affected scavenging rates only at the transitional site and affected removal distances only at the Chihuahuan desert site. Microclimatic variation affected both removal rates and removal distances by determining which species foraged upon baits. Species varied widely in the distances that they removed baits to nests; generally, species with large-bodied workers and thermophilic species removed baits the farthest. Overall, this resulted in a positive relationship between removal distance and temperature. Grazing-induced habitat variation affected the fate of baits only at the Chihuahuan desert site, where baits were removed frequently to mesquite shrubs in heavily grazed areas and more often to grass clumps in the ungrazed habitat. Scavenging patterns at regional and habitat scales were best explained by variation in species composition and activity, which may have important consequences for nutrient redistribution patterns in semiarid grasslands.

Introduction

Lawton (1994) asked “what do species do in ecosystems?” There has been considerable progress in answering this question; for example, the composition and diversity of plant species has been shown to affect ecosystem properties such as soil-nutrient status (Tilman et al. 1997, Hooper and Vitousek 1997). There is increasing recognition that animals also play important roles in the structuring of terrestrial ecosystems (Jones et al. 1994). The redistribution of nutrients by animals may influence landscape characteristics (Turner 1989). Disruption of the functions contributed by abundant and diverse animal taxa such as insects may have important negative repercussions, including reductions in rates of decomposition (Klein 1989), plant reproduction (Aizen and Feinsinger 1994), and the control of pests (Didham et al. 1996).

Ants (Hymenoptera: Formicidae) are among the most abundant and active animals in most terrestrial environments (Wilson 1987). Ants are colonial, nesting animals, and the activity of tens to thousands of individuals concentrates both materials and other changes around nest sites. Consequently, ants can have important influences on ecosystem structure by altering soil-nutrient properties (Petal 1992, Whitford and DiMarco 1995, Dean et al. 1997, Wagner et al. 1997), redistributing and consuming seeds (Kaspari 1993a, Crist and Wiens 1994, Andersen and Morrison 1998), and by creating patchiness in vegetation (Coffin and Lauenroth 1991).

The transfer of organic matter from the surface to below ground by ants alters soil-nutrient levels (Petal et al. 1992). Most ant species are scavengers (Carroll and Janzen 1973), and the redistribution of material by scavenging is among the most important activities mediating the influence of ants on soil nutrients and other organisms (Gentry and Stiritz 1972, Laakso and Setala 1998). Scavenging ants may consume as much as 59% to 100% of dead arthropod material from the ground (Jeanne 1979, Fellers and Fellers 1982, Retana et al. 1991) and they may consume vertebrate carrion as well (Clark and Blom 1991). Scavenging ants are also dominant predators of living arthropods (Kajak et al. 1972, Kalule-Sabiti 1980, Risch and Carroll 1982). Together, these observations suggest that scavenging by ants may be a significant ecosystem function in many regions.

The contributions of ants to nutrient cycling and redistribution in arid and semiarid habitats may be especially great. Animal carrion is rich in nutrients such as nitrogen and phosphorus, and these nutrients are often limiting in arid and semiarid zones (Noy-Meir 1985, Schlesinger et al. 1990, Burke et al. 1997). These nutrients may accumulate in nest mounds in the form of waste products and result in increased plant growth (Gentry and Stirtitz 1972). The contribution of ants to nutrient cycling may be especially great in comparatively nutrient-poor habitats (Petal 1992).

Patterns of seed removal by ants are affected by both species composition (Hughes and Westoby 1992, Gorb and Gorb 1999) and environmental variation, such as that caused by changes to vegetation structure (Crist and Wiens 1994, Andersen and Morrison 1998). Variation in microclimate may determine removal patterns by affecting species foraging behavior (Traniello et al. 1984, Retana et al. 1991). The body size of ant workers may also influence removal patterns by determining how ants react to environmental heterogeneity (Kaspari and Weiser 1999). Differences in the availability of nest sites also affect patterns of species composition and behavior in arid landscapes (Schumaker and Whitford 1974) and may determine the fate of removed materials. For example, the shaded areas provided by shrubs that invade desertified habitats (Gibbens and Beck 1988) may provide attractive nesting sites for some ant species and, consequently, serve to concentrate scavenged materials in the soil beneath shrubs.

Despite the potentially important roles that scavenging ants play in North American semiarid and arid habitats (MacKay 1991), no studies have yet examined how species composition or environmental variation mediate ant-scavenging activities. I address this by documenting the composition of organisms scavenging arthropod carrion from the ground surface and how this material is redistributed in different habitats in three semiarid grassland sites. These sites lie along a north-south regional gradient from shortgrass steppe to Chihuahuan desert grassland and vary in habitat structure and in composition and ant species composition. These areas are also used extensively for cattle grazing, which can have profound effects on habitat structure and biota (Cooperrider 1991) and may adversely affect ecosystem functioning (Fleishner 1994). I examined the relationship between environmental variation and ant scavenging by testing four hypotheses; 1) differences in species composition and/or habitat composition among sites result in differing rates of scavenging and patterns of redistribution, 2) within sites, habitats subjected to differing grazing intensity or that differ naturally will differ in ant-scavenging patterns, 3) variation in species activity due to microclimatic variation will affect overall scavenging patterns, and 4) habitats subjected to different grazing intensities will differ in the microhabitats to which scavenged material is removed.

Materials and Methods

Study Areas

This study was conducted at three grassland Long-Term Ecological Research (LTER) sites. At the north end of the gradient is the Shortgrass Steppe LTER site, located in the USDA-ARS Central Plains Experimental Range (CPER) and Pawnee National Grasslands (PNG) near Nunn, Weld County Colorado. Vegetation is classified as shortgrass steppe, and the dominant grass cover is blue grama, *Bouteloua gracilis*. In low-lying areas, saltbush (*Atriplex canescens*) shrublands are also common. The middle site is the Sevilleta LTER, located in the Sevilleta National Wildlife Refuge and on adjacent privately-owned land in Socorro County, New Mexico. This site represents a biome transition from shortgrass steppe and Chihuahuan desert grassland (Gosz 1992). The dominant grass cover here is black grama, *Bouteloua eriopoda*, which is characteristic of desert grassland. Blue grama also occurs in large patches on coarse soils, and creosotebush (*Larrea tridentata*) occurs on relatively fine soils here (Chapter 3). The southern site is the Jornada LTER, located largely in New Mexico State University's Chihuahuan Desert Rangeland Research Center (CDRRC; elsewhere referred to as the College Ranch) and Bureau of Land Management (BLM) land near Las Cruces, Doña Ana County, New Mexico. This site is mostly desert grassland, and creosotebush-dominated shrublands occur in areas of coarse sand on a fan apron at the base of Mount Summerford (Wondzell et al. 1996).

In each site, ant scavenging was observed in four habitat types, including both grazing treatments within the dominant grassland type and other, common, natural habitat variants on areas of differing soil texture. At the SGS, habitat types included ungrazed areas in exclosures, moderately grazed areas within the CPER, moderately grazed areas in the PNG, and grassland areas with saltbush. Moderate grazing at SGS reduced grass stature but not grass cover (Chapter 3). The most extensive habitat in the study area was CPER grazed grassland. At the SEV, habitat types included a large ungrazed pasture, a grazed pasture on privately-owned land, an area dominated by blue grama, and a creosotebush shrubland. As at the SGS, grazing reduces grass stature but not grass cover (Chapter 3). The most extensive habitat in the SEV study area was ungrazed grassland. At the JRN, habitats included ungrazed areas in exclosures, moderately-grazed areas in the CDRRC, heavily grazed areas in BLM land, and creosotebush shrublands. The effect of grazing on habitat structure here was more pronounced, including reductions in grass cover, increased bare ground cover, and increases in the density of honey mesquite

(*Prosopis glandulosa*) shrubs (Chapter 3). The most extensive habitat in JRN study area was CDRRC grazed grassland.

Scavenging Observations

I used halves of freshly-killed termite workers (Rhinotermitidae, Termitidae) or whole fruit flies (*Drosophila*) as baits to simulate small, naturally-occurring arthropod carrion that most ant species at the sites can gather individually (following Fellers and Fellers 1982, Retana et al. 1991). Baits were always ca. 2 mm in length. During June-August 1997, baits were placed on the ground in randomly-selected locations in the vicinity of permanent transects used for pitfall trapping studies in each habitat type (Chapter 3). Areas inside large, dense grass clumps or in the center of shrubs were avoided because baits would not have been observable.

I placed 7-10 baits in each habitat during each of three time periods during which microclimates differed and different ant species may be active: morning or afternoon (soil-surface temperatures 20-30 °C), midday (33-45 °C), and night (10-25 °C). Baits were dusted with chemically-inert orange fluorescent powder (Radiant Color, Richmond, California) to facilitate observations during the day and at night with the use of a fluorescent lantern outfitted with an ultraviolet bulb (General Electric Company, #F6T5). Preliminary observations suggested that the powder did not affect the response of ants to the baits. Upon bait placement, time, soil -surface temperature (HH-23 Digital Thermometer, type J thermocouple, Omega Engineering, Inc., Stamford CT, USA), and relative humidity at the soil surface (RH-30C Digital Humidity Meter with RH-30-3 Humidity Sensor, Omega Engineering, Inc., Stamford CT, USA) were recorded adjacent to baits. The observer then sat motionless watching the bait continuously until the bait was discovered and removed or until 20 min elapsed, at which point observations ceased. This time limit was selected because preliminary trials suggested that if baits were not recovered within 20 min, they would usually not be recovered for 60+ min, perhaps because they were away from ant foraging routes. Upon bait removal, the observer followed scavenging ants to their nests. Some ants never arrived at nests with baits because the ants were disturbed or their location lost by the observer, their baits robbed by other ant species (Hölldobler 1986), or they were preyed upon by spiders. During nocturnal trials, observers were careful not to occlude view of the sky from ants at baits because this appeared to cause disorientation in nocturnally-foraging ant species (i.e. *Myrmecocystus navajo*, *Dorymyrmex flavus*).

A voucher specimen from the colony was collected to confirm field identification upon arrival at the nest. The distance from the nest entrance to the point of bait placement and the type of nest microhabitat was recorded (open ground, grass clump, half-shrub, or shrub). Body lengths (measured from the frons to the tip of the outstretched gaster) of voucher specimens (n=3-10) of scavenging ant species were measured using a stereo microscope outfitted with an ocular micrometer. To supplement information gathered on nest microhabitats of common, mass-recruiting scavenging ant species, tuna baits were used to follow ant foraging trails to nest sites in the same areas where insect baits were used.

Statistical analyses focused upon two response variables, the probability of bait removal within 20 min (modeled as a binary variable), and the distance (cm) that a bait was transported to a nest entrance upon removal. The former variable is considered as an estimate of scavenging rates, whereas the latter estimates the distance that scavenged material (and nutrients) is removed to below ground. Log-transformation of distance values normalized the data. Most relationships between the response variables and species identity, site, habitat type within sites, and microclimate were examined using general linear models (Proc GENMOD, SAS Institute, Inc, 1996). I used quantile (i.e. least absolute deviation) regression (Blossom software; Slauson et al. 1994) to examine the relationship between distance and microclimate. In contrast to least-squares regression approaches, quantile regression may be used to investigate relationships at the limits of the distribution of two variables (Cade et al. 1999). Quantile regression using the median (50th) quantile is analogous to traditional least-squares regression but with the advantage of de-emphasizing extreme outlying data points and performing well with sparse data sets (Scharf et al. 1998). In addition to the 50th regression quantile, I examined patterns at the limits of the microclimate-distance relationship using the 80th and 20th quantiles. These quantiles were chosen because more extreme quantiles would have given unreliable estimates of variance for regression coefficients given our sample sizes (see Sharf et al. 1998). Statistical tests for non-zero slope were performed using Monte Carlo permutation test procedures.

Because small arthropods such as ants are sensitive to variation in both temperature and humidity, microclimate was characterized by vapor pressure deficits (VPD) that measure the drying power of the air (Kaspari 1993b). VPDs were calculated from temperature and relative humidity using formulae in Campbell (1977). In this study, soil-surface temperature was highly correlated with VPD.

Results

Among-site Comparisons

The number of ant species observed scavenging baits at each site was 13 at SGS, 10 at SEV, and 16 at JRN (Appendix 6.1). Ants scavenged all baits at SGS and JRN, and one of 61 baits was removed by an unidentified mite (Acari) at SEV.

The probability that a bait would be removed within 20 min differed significantly among sites (χ^2=19.36; df=2; P=0.0001). Subsequent contrasts revealed that the probability of removal was higher at SGS (80.5 % of baits removed) than at either SEV (54.5%; χ^2=16.72; df=1; P=0.001) or JRN (58.8%; χ^2=7.97; P=0.003). Removal rates at SEV and JRN did not differ (χ^2=1.67; P=0.184). If variation in VPD among sites is controlled, significant differences among sites are still detected (χ^2=6.93; df=2; P=0.019) and the probability of discovery remains higher at SGS than at JRN (χ^2=6.79; P=0.007). Focusing only upon the most common grassland habitats at each LTER site, overall differences in removal rates were observed (χ^2=7.25; df=2; P=0.027), which were due to higher removal rates at SGS than at SEV and JRN ($P \leq 0.05$). When VPD was controlled in this comparison, however, the differences disappeared (χ^2=4.19; df=2; P=0.12).

The distance baits were removed by ants to nest sites also differed among sites (habitats nested within sites; F=4.05; df=2, 9; P=0.055). Contrasts of least-squares means (Fig 6.1) revealed significant differences between SGS and JRN; SEV was intermediate. This pattern remained significant when differences in VPD were controlled among sites (F=5.10; df=2,9; P=0.033). The distance baits were removed within the most common grassland habitat at each site, however, did not differ (F=0.25; P=0.78) even after controlling for variation in VPD (F=0.93; df=2, 38; P=0.40). Habitats other than the dominant grassland are thus responsible for the among-site differences in distances of bait transport.

Only one taxon was present in more than one site and had a sufficient number of removal distance records for comparison. Removal distances for *Forelius* spp. occurring at SEV and JRN did not differ (F=0.49; df=1, 20; P=0.49).

Habitat Effects

After controlling for variation in VPD among habitats, differences among grazing treatments or habitats in the probability of bait discovery within 20 min were observed only at SEV (χ^2=8.06; df=3; P=0.045; Fig. 6.2). These differences were due to a relatively high discovery rate in the blue grama habitat, coupled with a low discovery rate in the creosotebush habitat. Grazing within black grama grassland had little effect.

The distance of bait removal was affected by grazing and natural habitat differences only at JRN (F=3.41; df=3, 41; P=0.026; Fig. 6.3). There, removal distances in the ungrazed habitat were greater than those in CDRRC grazed habitat, and distances in the creosotebush habitat were greater than in the BLM or CDRRC grazed habitat. I conducted an additional analysis examining the effect of habitat and species identity on removal distances to determine if the mean distances of bait removal by individual species differed among habitats. The habitat-by-species interaction term was not significant (F=1.64; df=11,27; P=0.142), indicating that behavioral differences among species in bait removal did not contribute to the overall differences among habitats.

Microclimate Effects on Scavenging

Controlling for differences among habitats, VPD had statistically significant effects on the probability of bait discovery only at SEV (χ^2=5.91; df=1; P=0.015), although the trends were similar at all three sites (Fig. 6.4). The probability of bait discovery was highest at intermediate VPD values and lowest during the driest times of day (midday).

The median (50th) quantile regressions all revealed significant, positive relationships between VPD and the distance baits were removed (Fig. 6.5). These relationships were highly variable; the coefficient of determination for SGS was 0.06, 0.20 for SEV, and 0.08 for JRN. Regressions at more extreme quantiles revealed that the relationship between VPD and removal distance differed depending upon the distance values. At SGS, a significant positive slope was observed at the 80th quantile but not at the 20th quantile. At SEV and JRN, positive slopes were observed only at the 20th quantile. Thus, the maximum distance that baits were removed increased with VPD at SGS, whereas the minimum distance baits were removed increased with VPD at SEV and JRN.

Scavenger Species Composition and Characteristics

Generally, several ant species removed baits in each site; the dominant scavenger removed no more than about one third of the total baits removed in each site (Table 6.1). At SGS, *Myrmica emeryana*, *Formica neogagates*, *Dorymyrmex insanus*, and *F. obtusopilosa* together removed 71.4% of the baits. At SEV, *Pheidole* spp. (mostly *longula*), *Forelius* spp., and *D. insanus* removed 76.7% of the baits, and at JRN *Forelius* spp., *D. bicolor*, *D. flavus*, and *Pheidole* spp. (mostly *xerophila*) removed 73.3% of baits.

In each site, different groups of ant species scavenged baits under different microclimatic conditions (Fig. 6.6). At SGS, *F. obtusopilosa*, *Pogonomyrmex occidentalis*, *Leptothorax* sp. C1, and *F. neogagates* removed baits at relatively high VPDs, whereas *M. emeryana*, *Lasius crypticus*, and *D. insanus* foraged at lower VPDs. At SEV, *Forelius* spp. took baits at relatively high VPDs and *Pheidole* spp., *D. insanus*, and *Aphaenogaster cockerelli* foraged at lower VPDs. At JRN, *Forelius* spp. and *Myrmecocystus* spp. were active at high VPDs, *Pogonomyrmex desertorum* and *Dorymyrmex bicolor* foraged at intermediate VPDs, and *Pheidole* spp., *Dorymyrmex flavus*, and *A. cockerelli* foraged at the lowest VPDs.

Species at each site also differed in the distances that they removed baits to their nests (Fig. 6.6). Part of these differences can be attributed to differences in body length; there was a positive relationship between average worker length and the distance that species removed baits (R^2=0.45; F=13.49; df=1, 14; P=0.003). The large *P. occidentalis* at SGS and *A. cockerelli* at SEV and JRN removed baits over the longest distances, whereas smaller species such as *Lasius* or *Pheidole* removed baits only over short distances. The body length of the species, however, is not sufficient by itself to explain differences in removal distances among sites. I observed no differences among sites in species' body lengths weighted by the number of distance observations (F=0.67; df=2, 15; P=0.89). Thus, there were no systematic differences in the contributions of different-sized species to scavenging among the sites. Furthermore, some ants that scavenged many baits deviated from the positive body length-removal distance relationship. *M. emeryana*, for example, is a relatively large ant that removed baits over short distances.

There was no significant relationship between the body length of species and the average VPD at which species removed baits (F=0.17; df=2,14; P=0.69). Inspection of Fig. 6.6, however, suggests that, with the exception of *Forelius*, species removing baits at high VPDs were often large. Species at each site for which there were >5 distance observations were tested individually to assess the effect of VPD on the distance moved by individuals within species. Of nine tests, only *Forelius* at SEV exhibited a significant, positive relationship at the Bonferroni-adjusted alpha level of 0.0055 (R^2=0.96; F=137.63; df=1,6; P=0.0001). Thus, VPD can affect the distance that baits are moved by affecting the composition and characteristics of species removing baits as well as by affecting the behavior of individuals of certain species.

Microhabitat Fate of Scavenged Baits

Ants at the SGS and SEV sites were observed removing baits exclusively to either grass or bare-ground microhabitats. I could not detect differences in the frequency of removal to these microhabitats among grazing treatments at SGS (two-tailed Fisher's exact test; P=0.691) or at SEV (P=0.180). Ants at JRN removed baits to grass, bare ground, shrub and infrequently, to half-shrub (*Xanthocephalum* spp.) microhabitats. The frequency of bait removal to bare ground, grass, and shrub microhabitats differed significantly among grazing treatments (two-tailed Fisher' exact test; P=0.047). Baits were removed to mesquite shrub microhabitats more frequently in the BLM grazed habitat than in either the CDRRC grazed or ungrazed habitats (Fig. 6.7). One species at JRN, *Forelius* spp., was abundant enough at tuna baits to evaluate differences in the location of their nests between the BLM-grazed and ungrazed treatments. Nests of *Forelius* spp. were more often found under shrubs or half-shrubs in the BLM grazed habitat (23 nests in shrubs vs. 2 in grass) and more often in grass clumps in ungrazed areas (3 nests in shrub, 7 in grass, 1 in bare ground; two-tailed Fisher's exact test; P=0.0001).

Discussion

The small insect carrion examined in this study were scavenged almost exclusively by ants. Studies in other habitat types and regions, including North American temperate deciduous forest (Fellers and Fellers 1982) and Mediterranean temperate grassland (Retana et al. 1991), also found that arthropod carrion was scavenged exclusively by ants. From temperate to tropical areas, the impact of ants as predators and scavengers may increase (Jeanne 1979). The number of comparable scavenging studies is still very small, but the important roles of ants in ecologically-distinct temperate habitats and their increasing impact in tropical areas suggest that ants may be the dominant scavengers of small arthropod remains in much of the world.

My results suggest clear differences in ant scavenging rates and patterns of redistribution of scavenged material among semiarid grassland regions. A higher discovery rate of insect carrion at SGS was coupled with a relatively low redistribution distance when compared to the most arid site (JRN). Both patterns are consistent with higher ant-colony densities at SGS, perhaps due to the greater coverage of grass (Chapter 3). The maximum number of ant nests along transects that intersect different habitat types at the SGS is higher than at either SEV or JRN (Kaspari, pers. comm.).

Differences in removal rates within the most extensive grassland habitats of each site, paralleled among-site differences. Removal distances in these grasslands, however, did not differ among sites. This suggests that the presence of non-grassland habitat types, such as creosotebush shrublands at JRN (Fig. 6.3), are largely responsible for the overall differences among sites. The relatively large differences in vegetation structure between creosotebush shrublands and grasslands (Chapter 3) may affect the foraging behavior of ants and determine removal patterns. In Great Basin shrub steppe, Fewell (1988) found that *Pogonomyrmex occidentalis* traveled farther to search for seeds on routes with lower vegetation cover. Differences in microclimate among habitats and sites might also have influenced bait removal patterns (Morehead and Feener 1998, see below). I observed differences in scavenging patterns between habitats at JRN and among sites when microclimate variation was controlled, and this suggests that microclimatic differences did not contribute to among habitat or among site variation.

Differences in removal rates among habitat types within sites were found only at SEV, where rates were comparatively high in the blue grama habitat and low in the creosotebush shrubland (Fig. 6.2). Differences in scavenging rates at SEV were probably not due to differences in ant abundance or richness among habitats, as contemporaneous pitfall-trapping data from transects located in bait sampling areas indicate that neither richness (F=0.21; df=3, 8; P=0.88) nor ant forager abundance (F=1.21; df=3,8; P=0.36) differed among the habitats. The pattern might be due to differences in the reliance of local ant assemblages on arthropod carrion (as opposed to homopteran exudates, for example). Decreased removal rates in creosotebush might be also be due to altered foraging activity due to an increased risk of predation by horned lizards. Predation by horned lizards may depress ant foraging activity where they are common (Crist and Wiens 1994). Both round-tailed (*Phrynosoma modestum*) and short (*P. douglassi*) horned lizards were frequently observed in the creosotebush habitat, but were seldom seen in grassland habitats at SEV.

Differences in scavenging patterns attributable to grazing were found only at JRN. The lack of response at SGS and SEV may be related to the similarity in grass cover between grazing treatments at these sites. Grazing could indirectly reduce nest site availability and/or increase the foraging range of ant workers (Fewell 1988) by reducing grass cover, but the reduction in grass *stature* observed at SGS and SEV may be unimportant to the movement of small organisms such as ants. This is because both short and tall grass likely present similar obstacles for ants (see Kaspari and Weiser 1999), so changes in grass cover, but not necessarily stature, should be most important. Indeed, grass cover was reduced by grazing at JRN. If increased environmental patchiness due to reduction of grass cover produced greater patchiness in ant nests and more continuous cover of bare ground, we would expect this to result in increased removal distances in grazed sites. In fact, removal distances did not differ between the ungrazed and the most heavily grazed habitats, but was least in the moderately-grazed habitat (Fig. 6.3). Within-species heterogeneity in the removal distances among habitats at JRN was not detected, so species responses to differing environmental patchiness is probably not significant.

Differences in removal distances at both habitat and regional scales are most likely due to variation in the species composition scavengers. In the moderately grazed habitat at JRN, most baits were taken by *D. bicolor* (Table 6.1), which removed baits over shorter distances than ants such as *Forelius*, *P. desertorum*, or *A. cockerelli* (Fig.

6.6). These species were more common scavengers in the heavily grazed and ungrazed habitats. The contributions of *A. cockerelli* and *Myrmecocystus* in the creosotebush habitat led to relatively large removal distances in this habitat. Both of these species nest in open-ground habitats between vegetation patches or shrubs, countering the hypothesis that vegetation patchiness determined removal distances by affecting ant nest site density. At the regional scale, many baits at SGS and SEV were removed by species that remove baits over short distances, such as *M. emeryana* and *Pheidole* spp., respectively. At JRN, many baits were removed by species that moved baits over larger distances, such as *Forelius*.

Scavenging ant species partition foraging times due to differential tolerance to microclimate conditions and interference competition (Cerdá et al. 1997, Bestelmeyer 1997). Microclimatic variation therefore affects species activity patterns, and thus bait removal rates and removal distances. Overall, relatively few baits were removed by ants at the highest VPDs (Fig. 6.4) in this study because conditions were too harsh for much activity by even thermophilic species such as *Forelius* or *Formica obtusopilosa*. In contrast, Retana et al. (1991) found that removal rates increased at relatively high soil-surface temperatures due to increased activity by highly specialized scavenging species. At high VPDs in shortgrass steppe and desert grassland, relatively thermophilic species often forage or move upon vegetation that provides cooler microclimates (Kay and Whitford 1978, pers. obs.), which may decrease foraging efficiency for baits located on the ground.

Species that removed baits at high VPDs tended to remove baits over longer distances than most species active at lower VPDs (Fig. 6.6). Consequently, I observed positive relationships between VPD and removal distances at all three sites (Fig 6.5). Which ant traits might mediate this relationship? Ant worker size is one candidate; larger ant species tended to move baits farther (see also Crist et al., 1992) and Kaspari (1993b) found that larger ant species were generally more tolerant of higher VPDs than were smaller ones. In contrast, I did not observe an overall relationship between a species' body length and the VPDs at which species removed baits.

The relationship between species body length, VPD, and removal distance depends upon whether the maximum or minimum distance values are considered (Fig 6.5, 6.6). The minimum distances (20th quantile) that baits were moved by ants increased with VPD only at SEV and JRN, and this pattern was not related to increasing body size (Fig. 6.6). No relationship between VPD and removal distance was observed at the 80th quantile at SEV or JRN because a large-bodied species (*A. cockerelli*) removed baits over long distances at low VPD values. These patterns were inverted at SGS. The lack of a VPD-removal distance relationship at the 20th quantile can be attributed to the activity of species that removed baits over short distances across a range of VPD values. The significant, positive relationship at the 80th quantile is due to the activity of larger species at high VPDs.

Part of the positive relationship between VPD and removal distance at SEV was caused by an increase in removal distance by *Forelius* individuals with increasing VPD. Morehead and Feener (1998) showed that the running speed of *Pogonomyrmex* increased with increasing temperature, which may explain why both thermophilic ant species and *Forelius* individuals foraging at high VPDs (at SEV) removed baits over longer distances in this study. Given similar path tortuosity, net displacement is positively related to movement rate (Wiens et al. 1997). At high VPDs, movement rates may increase due either to the direct effects of increased temperature on ant metabolism (Nielsen 1986) or to a minimization of the time spent in stressful microclimates on the soil surface and/or increasing convective cooling (Marsh 1985). For these reasons, ants active at higher temperatures may often be relatively large (Rissing and Pollock 1984). Their longer legs permit rapid movement and elevate their bodies from the hot soil surface (Christian and Morton 1992). Relatively large bodies heat up more slowly (Christian and Morton 1992) and lose water less rapidly (Lighton et al. 1994). Small size, however, has advantages for thermophilic ants in desert environments; smaller bodies cool more quickly and intercept less incident radiation than larger bodies (Christian and Morton 1992).

To summarize, I suspect that the positive relationship between VPD and removal distance is determined by increased movement rates at high temperatures. Large body size, thermophily, and the effects of increasing VPD on individual behavior have similar effects on movement rates and redistribution patterns. but there are not consistent relationships among these factors in different assemblages. Species active at high VPDs may or may not have large body sizes, and VPD may or may not increase removal rates by individual species. In any case, the net result is a general increase of removal distance with increasing VPD.

What are the consequences of variation in species composition and behavior on the fate of scavenged material? At a regional scale, my results suggest that the capacity of ants to capture and recycle nutrients is greater in shortgrass steppe than in desert grassland. I expect that other consumers or abiotic vectors such as wind may play a more important role in desert grassland environments because ants capture materials there at a lower rate (see also Retana et al. 1991). The role of ants may also depend upon the time of day that material appears on the ground (Fig. 6.4).

My results also suggest that nutrients are redistributed by ants at a finer scale in shortgrass steppe than in desert grassland. Vegetation patchiness in the more mesic shortgrass steppe appears to be more finely textured than in desert grassland (i.e. smaller patches of both grass and bare ground; see Ludwig et al., in press; personal observations), and this may generate relatively finer nutrient redistribution by both abiotic mechanisms, such as fluvial runoff-runon (Ludwig and Tongway 1995), as well as by affecting ant behavior and community composition.

At finer scales, changes in vegetation patchiness due to livestock grazing or other processes may also alter the composition or behavior of ant foragers and the fate of nutrients redistributed by ants. In particular, ant nesting behavior is an important determinant of the fate of scavenged material. The destinations of scavenged baits shifted from grass clumps to shrubs with increased grazing intensity at JRN (Fig. 6.7), suggesting that the "islands of fertility" phenomenon, whereby nutrients are concentrated under shrubs due to abiotic processes in desertified environments (Schlesinger et al. 1990), may also be promoted by ant activity. A positive feedback mechanism may exist in which shrubs provide exceptional habitat for ants (Ludwig and Tongway 1995) which serves to concentrate ant activity under shrubs and contribute to resource island development (Dean et al. 1999). In addition, several ant species nest exclusively in bare ground, inter-plant spaces, such as *Myrmecocystus* and *Aphaenogaster cockerelli*. These ants may promote homogenization of soil nutrient distributions in desert ecosystems.

Clearly, the species composition of ant communities influences scavenging patterns. The next step is to quantify the impact of nutrient redistribution and concentration by ants on soil-nutrient levels and plant growth in semiarid ecosystems. This study identified several ant species that should be targeted in this effort and raises several questions that can be addressed in future studies. What is the proportion of fine-scale variance in nutrient concentrations that can be attributed to ants? How do the nutrients concentrated by different ant species differ in their availability to decomposers or plants? Ant colonies vary widely in worker population size and dispersion due to factors such as nest-site availability (Herbers and Greico 1994) or social structure (e.g. polygyny; Porter and Savignano 1990); how do ant worker population size and nest dispersion affect the concentration of nutrients by ant colonies? Finally, do ant foraging activities contribute to the retention of nutrients in ecosystems? Such studies will greatly enhance our understanding of the role of ants in the structure and functioning of semiarid ecosystems.

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Table 6.1. The percentages of the total baits removed in each habitat (n) by different ant groups. Groups are displayed in descending rank of the percentage of baits that they removed in a region.

Shortgrass steppe	PNG grazed	CPER grazed	Ungrazed	Saltbush	Total
n	*14*	*27*	*23*	*27*	*91*
M. emeryana	21.4	37.0	21.7	40.7	31.9
F. neogagates gp.	21.4	14.8	30.4	3.7	16.4
D. insanus	21.4	22.2	0	3.7	12.1
F. obtusopilosa	7.1	3.7	13	18.5	11.0
L. crypticus	0.0	3.7	17.4	0.0	5.5
Leptothorax sp.	7.1	3.7	4.3	7.4	5.5
P. pilifera	0.0	7.4	8.7	0.0	5.5
T. sessile	7.1	3.7	0.0	11.1	4.4
P. occidentalis	0.0	0.0	4.3	7.4	3.3
F. obscuripes	0.0	0.0	4.3	3.7	2.2
M. minimum	0.0	3.7	0.0	3.7	2.2

Sevilleta	Grazed	Ungrazed	Blue grama	Creosotebush	Total
n	*15*	*15*	*18*	*12*	*60*
Pheidole	33.3	40.0	22.2	25.0	30.0
Forelius	6.7	33.3	33.3	25.0	25.0
D. insanus	40	0.0	5.6	50.0	21.7
A. cockerelli	6.7	20.0	22.2	0.0	13.3
Myrmecocystus	13.3	6.7	5.6	0.0	6.6
Crematogaster	0.0	0.0	11.1	0.0	3.3

Jornada	BLM grazed	CDRRC grazed	Ungrazed	Creosotebush	Total
n	*20*	*20*	*19*	*12*	*71*
Forelius	55.0	10.0	21.0	18.2	26.8
D. bicolor	15.0	50.0	10.5	0.0	21.1
D. flavus	15.0	15.0	10.5	9.0	12.7
Pheidole	15.0	10.0	15.8	9.0	12.7
P. desertorum	0.0	5.0	21.0	9.0	8.4
Myrmecocystus	0.0	5.0	5.3	27.3	7.0
A. cockerelli	0.0	0.0	10.5	18.2	5.6
M. minimum	0.0	0.0	5.3	9.0	2.8
P. imberbiculus	0.0	5.0	0.0	0.0	1
T. spinosum	0.0	0.0	0.0	9.0	1

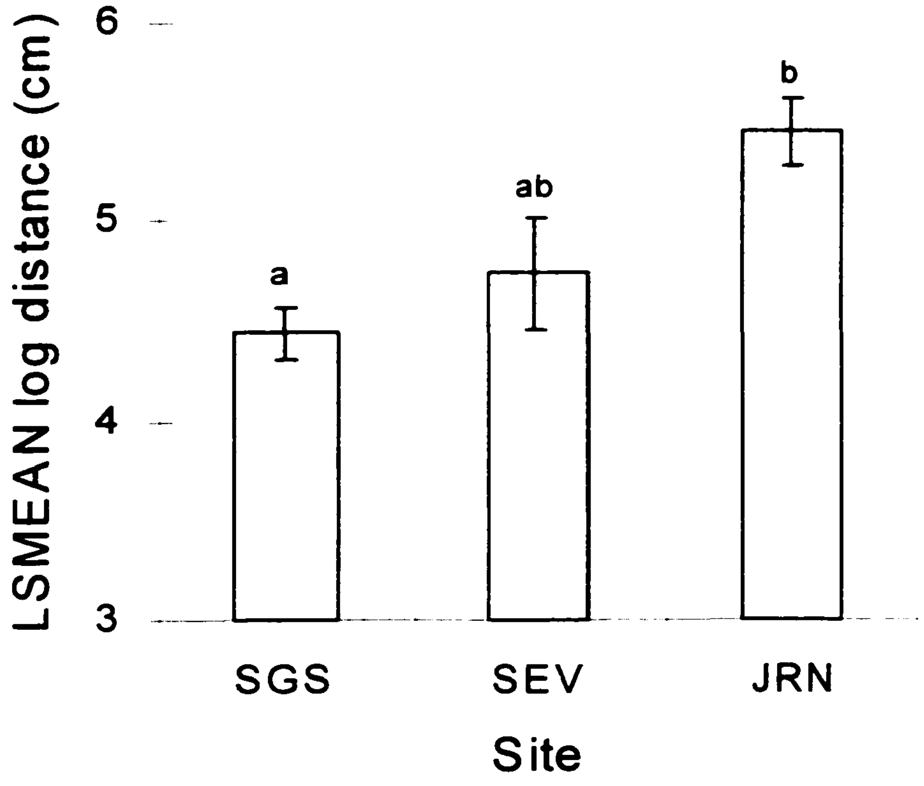

Fig. 6.1. Least-squares estimates (+1 SE) of ln-transformed bait-removal distance values adjusted for habitat composition and between-site variation in vapor pressure deficit (VPD). Sites with differing letters above the bar differed significantly in *post-hoc* contrasts of least-squares means (LSD).

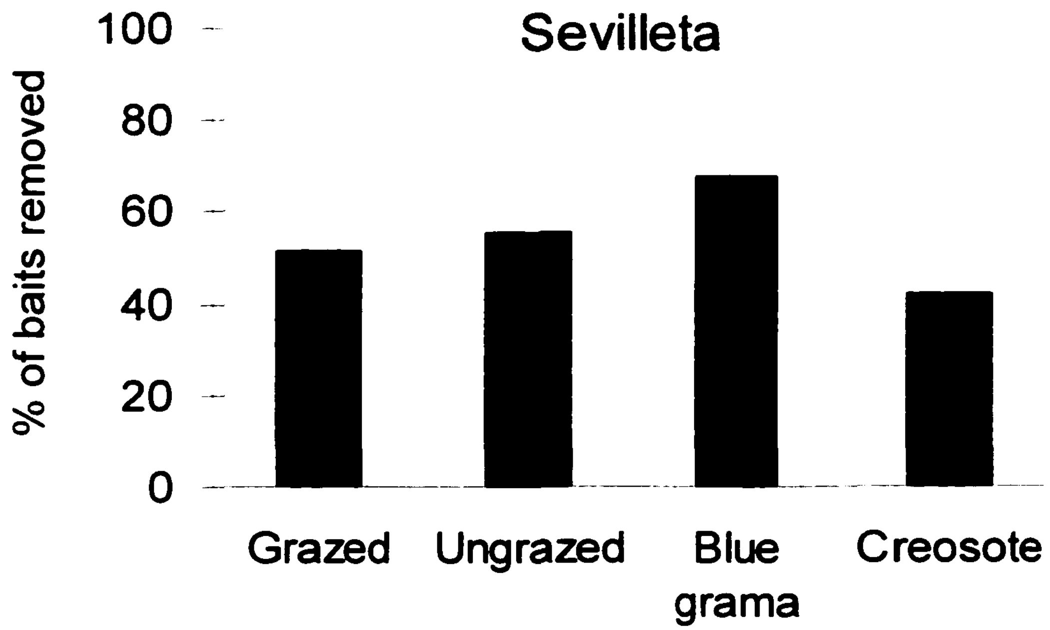

Fig. 6.2. The percentage of baits removed by ants from different habitats at the Sevilleta LTER.

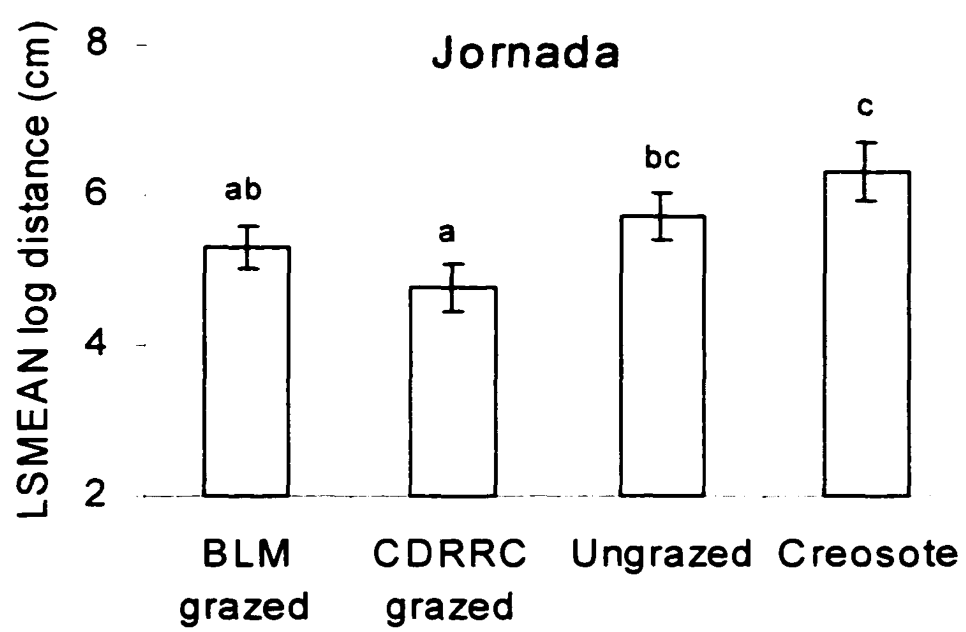

Fig. 6.3. Least-squares estimates (+ 1 SE) of ln-transformed bait-removal distance values adjusted for between-habitat variation in VPD at the Jornada LTER. Habitats with differing letters above the points differed significantly in *post-hoc* contrasts of least-squares means.

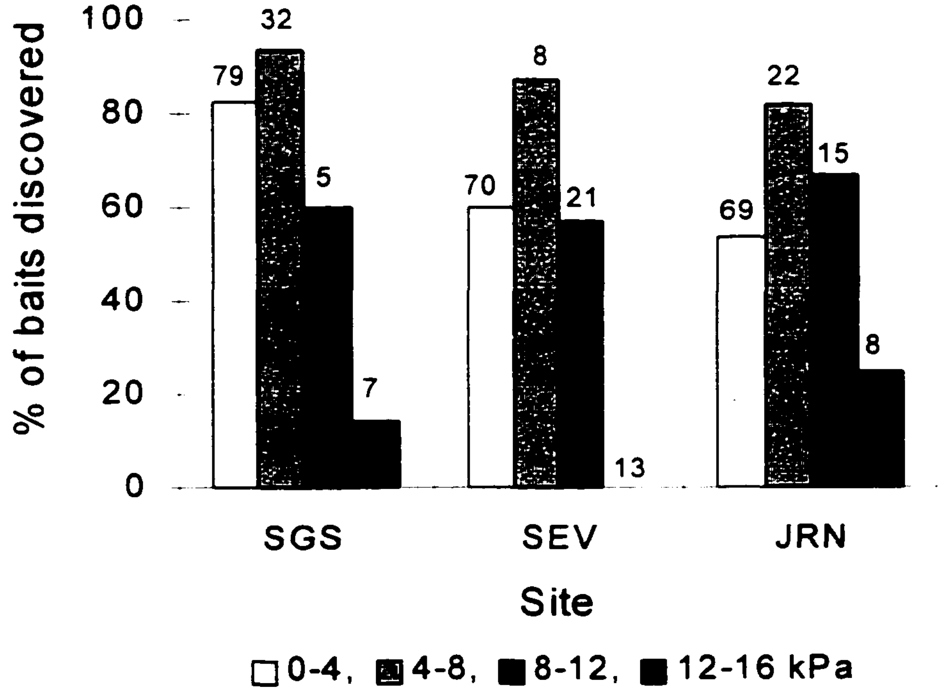

Fig. 6.4. The percentage of baits discovered by ants in different vapor pressure deficit (VPD) classes at each LTER site. The number above bar is the number of observations in each VPD class.

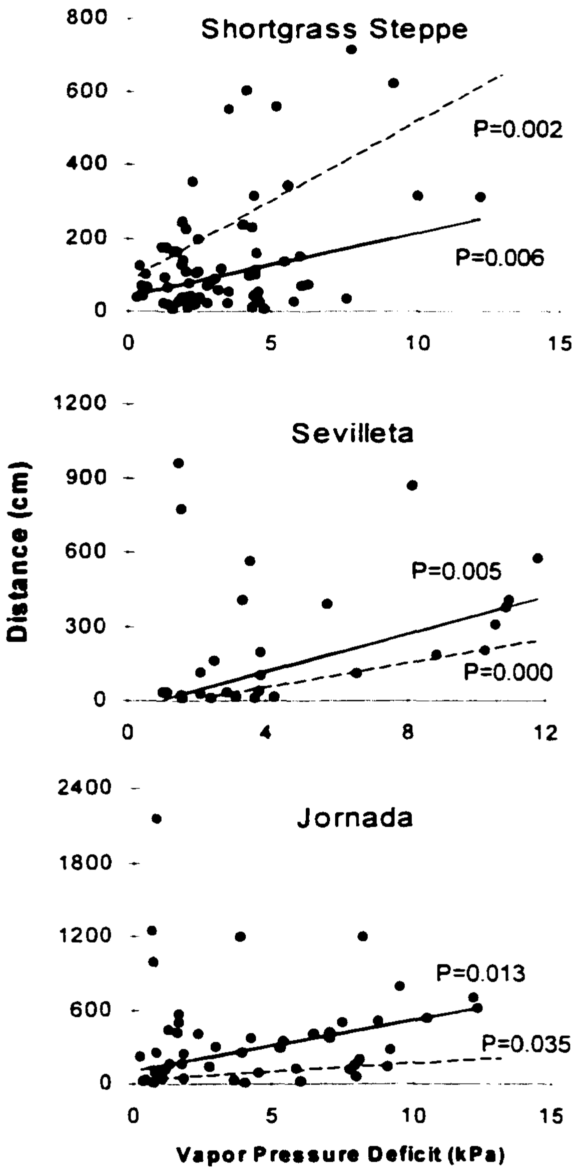

Fig. 6.5. Quantile regressions of bait removal distance on vapor pressure deficit at each site. The solid lines are 50th regression quantile estimates, dashed lines above the solid line are 80th regression quantile estimates, and dashed lines below the solid line 20th regression quantile estimates (only estimates from statistically significant regressions are shown).

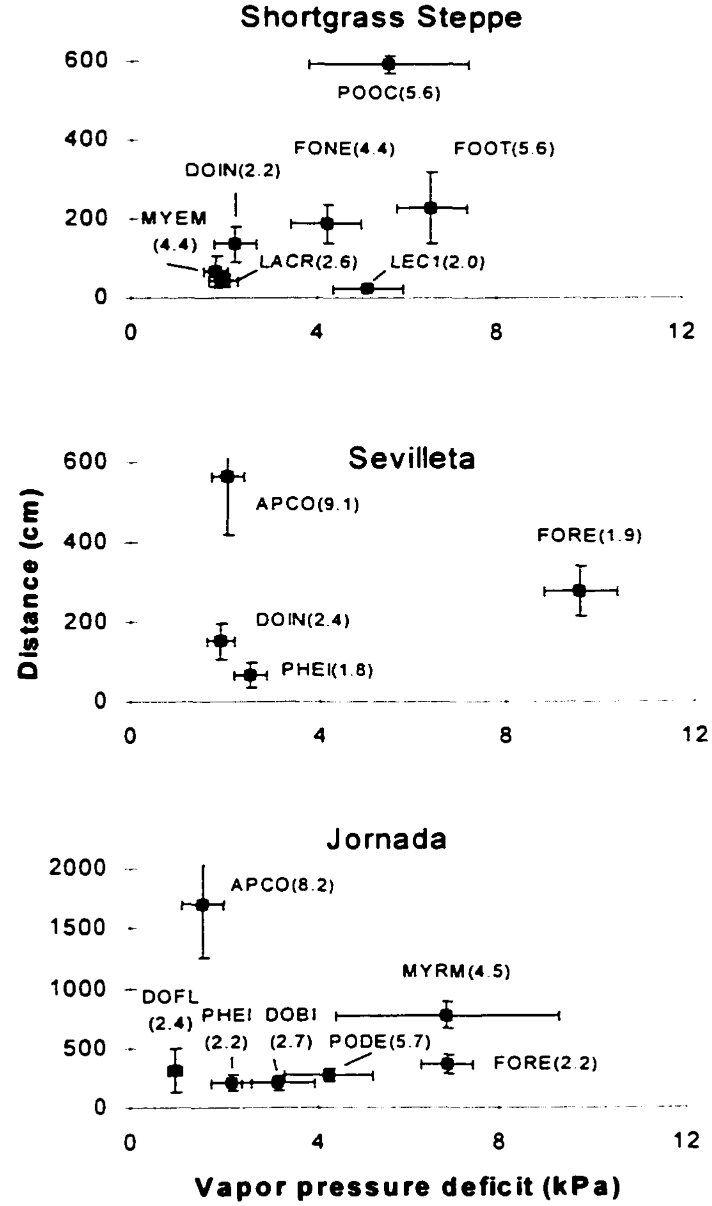

Fig. 6.6. Means and standard errors for removal distances and vapor pressure deficits at which baits were removed for ant taxa. APCO=*Aphaenogaster cockerelli*, DOIN=*Dorymyrmex insanus*, DOFL=*Dorymyrmex* c.f. *flavus*, FONE=*Formica neogagates*, FOOT=*F. obtusopilosa*, FORE=*Forelius* spp., LACR=*Lasius crypticus*, LEC1=*Leptothorax* sp. C1, MYEM=*Myrmica emeryana*, MYRM=*Myrmecocystus* spp., PHEI=*Pheidole* spp., PODE=*Pogonomyrmex desertorum*, and POOC=*P. occidentalis*.

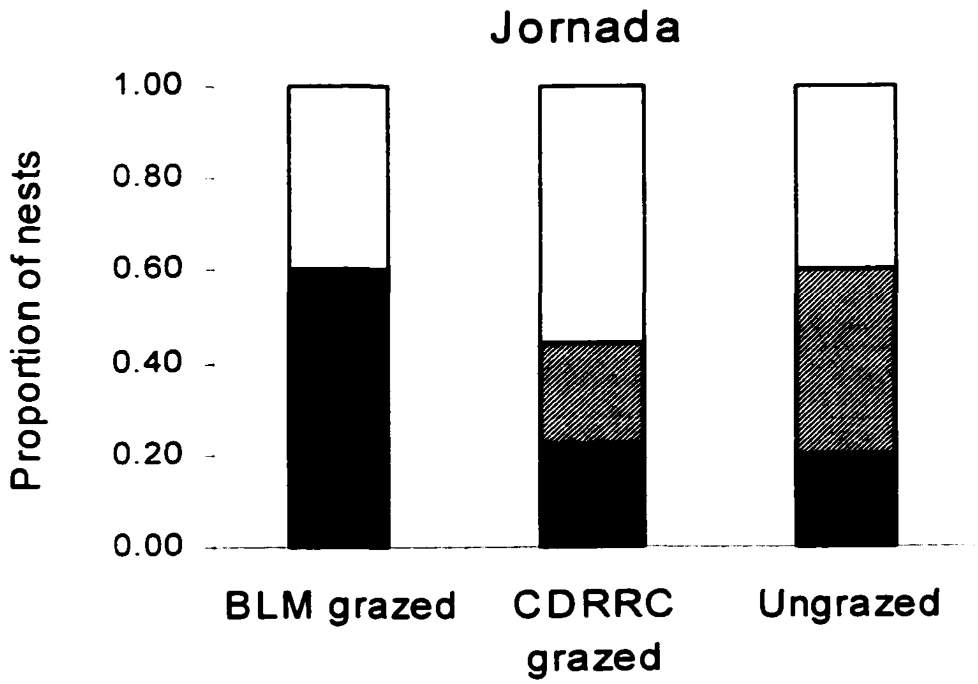

Fig. 6.7. The proportion of ant nests to which baits were taken in different grazing treatments at the Jornada LTER, NM.

Appendix 6.1. The ant species observed removing insect baits in each region.

Shortgrass Steppe
Dorymyrmex insanus (Buckley)
Dorymyrmex smithi Cole
Formica neogagates Viereck
Formica obscuripes Forel
Formica obtusopilosa Emery
Formica limata Wheeler
Lasius crypticus Wilson
Leptothorax sp. C1
Monomorium minimum (Buckley)
Myrmica emeryana Cole
Pheidole coloradensis Emery
Pogonomyrmex occidentalis (Cresson)
Tapinoma sessile (Say)

Sevilleta
Aphaenogaster cockerelli André
Crematogaster navajoa Buren
Dorymyrmex insanus (Buckley)
Forelius pruinosus (Roger)
Forelius mccooki McCook
Myrmecocystus mimicus Wheeler
Myrmecocystus navajo Wheeler
Pheidole longula Emery
Pheidole soritis Wheeler
Pheidole sp. J1

Jornada
Aphaenogaster cockerelli André
Dorymyrmex bicolor Wheeler
Dorymyrmex c.f. *flavus* McCook
Pogonomyrmex imberbiculus Wheeler
Forelius pruinosus (Roger)
Forelius mccooki McCook
Monomorium minimum (Buckley)
Myrmecocystus depilis Forel
Myrmecocystus mimicus Wheeler
Pheidole crassicornis Emery
Pheidole militicida Wheeler
Pheidole rugulosa Gregg
Pheidole hyatti Emery
Pheidole xerophila Wheeler
Pogonomyrmex desertorum Wheeler
Tetramorium spinosum (Pergande)

CHAPTER VII

SYNTHESIS: ANT AND HUMAN PERSPECTIVES ON SEMIARID LANDSCAPES

I argue that we will need to conduct broad-scale studies of several, different taxa in different landscapes in order to understand patterns of diversity within particular landscapes and to continue the development of general approaches in landscape studies of diversity (Chapter 2). Humans generally perceive landscapes and regions with respect to the distribution and abundance of dominant plants, and seek to establish linkages between animal distributions and this perception. Here, I summarize a view of some semiarid landscapes from the perspective of ant communities. What does this perspective tell us about landscapes and about how we should practice landscape ecology?

In the semiarid landscapes I examined, ant diversity was generally not sensitive to contemporary grazing effects upon vegetation structure within grasslands (Chapter 3). This is because ant diversity is apparently not strongly linked to the abundance of the grasses that dominate the structure of these environments from a human perspective. As a consequence, ant abundance and composition do not vary with grass cover or stature. This result is paralleled in the scavenging functions performed by ants (Chapter 6).

If we extend consideration of grazing effects to their contribution to historical desertification and mesquite invasion, then there was plant-mediated effect of grazing on ant diversity. In contrast to the anticipated negative impact, however, the effect seems to have been positive, at least at the habitat scale, due to the association of some ants with mesquite shrubs (Chapter 3). Thus, although mesquite invasion is regarded as an environmental problem for rangeland managers (Burgess 1995), it may actually benefit many species (J. Van Zee, personal communication). Contrast this attitude with the concern over the loss and removal of similar shrubs from the Sonoran desert where grasses are naturally sparse and exotic species are being introduced as cattle forage (Yetman and Búrquez 1994). Alberto Búrquez refers to this as "grasslandification." Here, the microhabitats provided by shrubs and trees were shown to be important elements for ants (Chapter 5), and they are also regarded as integral for other desert organisms. Human attitudes about landscapes may be more variable than the responses of ant communities to landscape structure.

In contrast to the generally low variation in ant diversity produced by grazing effects on grass cover within grasslands, variation in ant richness and community composition were consistently associated with gradients in soil conditions (Chapter 3). The effect of grazing on ants observed at SGS was related to soil hardness, not to grass cover. Ant species were sometimes strongly associated with habitat types defined by natural plant communities, depending upon the presence of the particular plants used to define the habitat and their relationships to underlying variation in soil conditions. The shift in the relationship between soil texture and creosotebush at SEV and JRN revealed that some species were linked directly to soil-texture gradients, whereas others appeared to be linked to creosotebush. This suggests that the conservation of ant diversity in the landscapes I considered would be best served by preserving areas with varying soil texture, but that grazing at reasonable levels can be accomodated.

Regional variation in ant communities within a plant community type is likely due to climatic effects in addition to variation in other local features such as soil texture. Within particular vegetation-vdefined habitats, ant composition differed between regions to varying degrees depending upon geographic distance and, consequently, the magnitude of the climatic differences between regions (Chapter 4). In any case, regional variation always overshadowed variation among habitats with respect to patterns of species composition as well as scavenging function (Chapter 6).

Turning to broader-scale patterns of ant faunal variation between biomes, I found that shifts in dominant life-forms along the north-south latitudinal gradient did not correspond to a shift in the representation of different ant faunal complexes (Chapter 4). Ants and dominant plants appeared to be responding to different kinds of climatic variation occurring in different geographic locations.

Overall, these results suggest that human perceptions of landscapes and biomes differ somewhat from those of ant species, considered together as a group. Some components of the ant community are associated with the vegetation that defines the habitats that humans recognize and manage, whereas others are not, responding instead to the effects of soils and climate directly and in ways different from those of plants.

These specific insights have several, more general implications for how we approach an integrated view of species diversity with landscapes. First, this study adds to a growing consensus among ecologists that single indicator taxa, including the vegetation classifications that are the foundation of remote-sensing approaches to habitat identification, are insufficient to detect variation that is important to a broad array of organisms (Landres et al. 1988, Launer and Murphy 1994, Edwards et al. 1996, Niemi et al. 1997, Simberloff 1998). Thus, it is imperative that ecologists and land managers consider several taxa within the same study areas in order to compare their responses to environmental variation and evaluate habitats for biodiversity conservation. Adding taxa to landscape studies increases the logistical burden considerably, so an important question is, how many taxa do we need to examine? A select group of taxa may be able to represent the bulk of species responses, at least for the practical purpose of evaluating land areas. It will be crucial to develop a set of criteria to guide researchers in the selection of the members of this group, given the limited resources generally available to researchers.

Second, my results illustrate the value of considering the responses of taxa to variation at different spatial scales, from patches, to landscapes, to climatic regions. For example, small scale associations of ant species with particular plants, soils, or microclimates may determine the responses of ant communities to landscape patterns, whereas biogeographic-scale variation in the ecological characteristics of higher taxa may constrain the responses of communities to local environmental variation. One consequence of these cross-scale interactions is that changes in ant community composition in response to grazing may vary considerably among regions for different reasons (Fig. 7.1). Changes may be minor in desert grasslands because desert ants are tolerant of changes to microclimate, moderate in shortgrass steppe due to the effects of grazing on soils and the nest materials of thatch-nesters, and great in thornscrub due to the effects of changes in microclimates and litter cover on tropical ants (Bestelmeyer and Wiens 1996). Broad-scale, comparative studies can be used to determine the nature of species-habitat associations and may aid our local-scale interpretations.

Many of these general points may be summarized by saying, first, that students of species diversity in landscapes should focus first and foremost on the natural history and environments of their chosen study organisms, and, second, they should consider this information in the context of general theories or ideas, but not the other way around. Organisms, not theories, matter. Theories are abstractions of nature meant to represent it for us in simpler terms, but we should not let them deceive us into thinking that nature is simple (May 1984). Like Lawton (1999), I feel it is doubtful that a *general explanation* of species diversity patterns in landscapes will emerge. Unlike Lawton (1999), however, I feel that we must strengthen research in community ecology despite a lack of general explanations. Community ecology and the questions it addresses are too important to ignore. Progress can be achieved through detailed, broad-scale studies of well-chosen focal taxa that consider the relationship between species characteristics and environments with respect to a set of *general processes*. Understanding how these processes interact in different contexts and at different scales is the next phase of research in community ecology. Community ecology, with the aid of its younger siblings, landscape ecology and macroecology, is alive and well!

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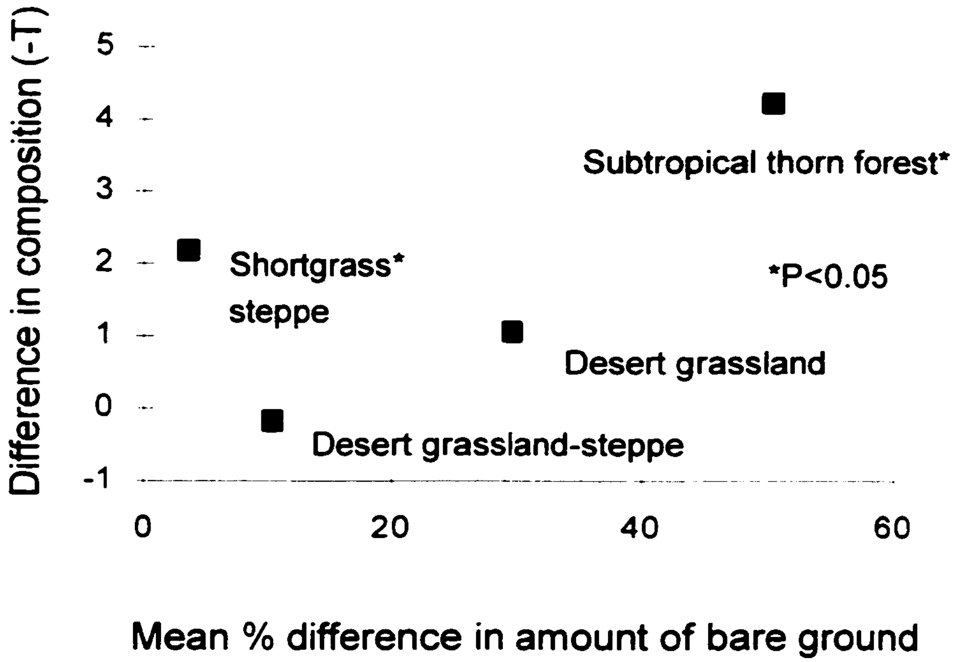

Fig. 7.1. The mean percent difference in bare ground (used here as an index of grazing impact on vegetation) between the ungrazed areas and areas where grazing impacts were greatest versus the difference in ant community composition (n=4 samples per treatment) determined by the T statistic from multiresponse permutation procedure (an index of group separation). Sites are shortgrass steppe (SGS), desert-grassland/steppe (SEV), desert grassland (JRN), and South American Chaco thornscrub (Bestelmeyer and Wiens 1996) vegetation. Asterisks indicate significant differences between grazed and ungrazed ant communities.

"ANTS AND MAN. Among ants we find weavers, butchers, cattle-rearers, masons, road-makers, harvesters, bakers, mushroom-farmers, excellent nurses of various kinds, gardeners, warriors, pacifists, slave-makers, thieves, brigands and parasites, but we find no professors, orators, governors, bureaucrats or generals, nor even corporals, nor do we find capitalists, speculators, or mere swindlers. Think carefully about that dear reader, and it will give you the key to the mystery".

Auguste Forel, 1929
The Social World of the Ants, Vol. 2. Albert and Charles Boni, New York, NY, USA

APPENDIX

Species keys or names of taxonomic authorities for ant genera occurring within the LTER study sites* and adjacent desert areas, including the Sonoran desert (based in part on MacKay and Vinson 1989). Previously used, but invalid, generic names are given in parenthesis. Problems with keys, including their age, the systematic status of the genera, or the comprehensivness of the keys are also evaluated. Superscripts indicate a footnote at bottom. Current locations of taxonomic authorities are LACM=Los Angeles County Museum of Natural History; MCZ=Museum of Comparative Zoology, Harvard University; SA=Shaw Arboretum, Gray Summit, Missouri; UCD=Entomology Department, University of California, Davis; UTEP=Centennial Museum, University of Texas at El Paso.

Genus	Keys/taxonomic resources	Problems
Acanthomyops	Wheeler and Wheeler 1986, Wing 1968	
Aphaenogaster *(Novomessor)*	Wheeler and Wheeler 1986, Creighton 1950	Needs revision
Brachymyrmex	Creighton 1950	Needs revision
Camponotus[1]	Wheeler and Wheeler 1986, Snelling 1988, Creighton 1950, Roy Snelling (LACM)	Difficult
Crematogaster	Buren 1968, Wheeler and Wheeler 1986	Difficult
Cyphomyrmex	Wheeler and Wheeler 1986	
Dorymyrmex[2] *(Conomyrma)*	Snelling 1995	Undescribed spp.
(Ephebomyrmex)	still used but see *Pogonomyrmex*	
Forelius[3] *(Iridomyrmex)*	Wheeler and Wheeler 1986	Needs revision Probably more spp.
Formica[4]	Wheeler and Wheeler 1986 for spp. group, *fusca* group; Francoeur 1973 or Wheeler and	

	Wheeler 1986; *rufa* group, James Trager or Wheeler and Wheeler 1986; *sanguinea* group, Snelling and Buren 1985, James Trager (SA); *neogagates* group, Wheeler and Wheeler 1986, but some inconsistencies	
Leptothorax[5]	Creighton 1950, William MacKay (UTEP)	In revision
Lasius	Wilson 1955, Wheeler and Wheeler 1977/1986	
Messor (Veromessor)	Wheeler and Wheeler 1986	
Monomorium	DuBois 1986	
Myrmecocystus	Snelling 1976, 1982, Wheeler and Wheeler 1986	
Myrmica[6]	Creighton 1950, Wheeler and Wheeler 1977 Andre Francoeur (?)	In revision
Neivamyrmex	Watkins 1985	
Odontomachus	Brown 1976	
Paratrechina	Trager 1984	
Pheidole	Wheeler and Wheeler 1986, Gregg 1958, Edward Wilson (MCZ)	In revision, key by Wilson and W. L. Brown nr. completion
Pogonomyrmex[7]	Wheeler and Wheeler 1986, Mackay et al. 1985	
Pseudomyrmex	Phil Ward (UCD)	
Solenopsis[8]	Trager 1991 (*geminata* group), Creighton 1950 (others)	Needs revision, difficult
Tetramorium	Bolton 1979	
Trachymyrmex	Creighton 1950	

* Georeferenced ant data sets at Long-Term Ecological Research Sites will be made available online, http://lternet.edu (follow links to databases at Shortgrass Steppe, Sevilleta, and Jornada sites).

1. I recorded *C. vicinus* (CV) at the Sevilleta, and *C. noveboracensis* (CN) at Shortgrass Steppe. CN was found nesting only under rocks at CYU 1 (only 2 nests). I am not confident with this identification. The characters distinguishing the subgenus to which CV belongs, *Tanaemyrmex*, from the subgenus to which CN belongs (*Camponotus*), is the whether the clypeal carina forms an edge and the scape is flattened, or the carina is weak and the scape is rounded, respectively. Otherwise, CV and CN are very similar. It is possible that the CN specimens are in fact CV, but with slightly flattened clypeal carinae and more rounded scapes. James Trager thought that the record of CN at the Shortgrass Steppe was unusual because it is generally a forest-inhabiting ant in the east.

2. A couplet in a recent key by Snelling (1995) separated *Dorymyrmex insanus* and *D. flavus* from *D. bicolor* and *D. smithi*, based upon morphology of the head capsule. Some of my observations at tuna baits suggest that behavioral characteristics parallel these morphological differences. Specifically, *D. flavus* and *D. insanus* are quite timid and subordinate in interactions, and their colonies appear monodomous. In contrast, both *D. smithi* and *D. bicolor* are very aggressive and appear to have polydomous colony structure. A reciprocal transplant experiment of *D. bicolor* individuals among different colony entrances at JRN (which should be interpreted with caution; Steve Rissing. personal communication) suggest that colonies may be related that are up to 90 m apart.

3. There is a lot of color variation in the two species of this genus, in the LTER sites ranging from chocolate brown (SEV) to the usually yellowish, to bicolored. Some individuals currently identified as *pruinosus* inhabiting creosotebush shrub at SEV and JRN are clearly bicolored, and are red anteriorly, yellow posteriorly. This distinct form may represent another species.

4. James Trager should be consulted for identifications from the *sanguinea* group, despite the existence of a key. There are some inconsistencies in descriptions of species of the *neogagates* group, which are very common at SGS. In particular, the specimens identified here as *F. limata* have setae on the pronotum, in contrast to some descriptions in keys, and some *F. neogagates* may also have few hairs on the pronotum. Another character than can be used at SGS is the size of the eyes, which are larger in *F. limata* than in *neogagates*. This was noted by W. M. Wheeler early in the last century, but Creighton (1950) disagreed. Further, my limited observations suggest that *F. limata* was largely nocturnal in summer, and *F. neogagates* was active at all times of day.

5. *Leptothorax* is a mess, so much so that experienced taxonomists give different names to what appear to me to be the same species. Many of the individuals at SGS grade from one form (shiny, smooth pronotum/mesonotum) to another (rugulose). Species identifications of *L. schmitti* and *L.* sp. C1 should not be considered to be reliable.

6. Like *Leptothorax, Myrmica* specimens are exceedingly difficult to identify reliably at this point. Roy Snelling identified the most abundant species at SGS as *M. emeryana*. Previous work indicates that the most abundant species in shortgrass steppe was *M. americana*. It is likely that these records represent the same ant species, unless a remarkable change in *Myrmica* dominance has occurred over the last few decades. Rumor had it that Andre Francouer was revising this genus, but it is unclear whether this is nearing completion.

7. *Pogonomyrmex texanus* was described in 1985, and would previously have keyed to *P. apache*. Thus, many previous records of (or current ones if researchers are not aware of this new species) of *P. apache* may represent *P. texanus*. I have recorded this ant near Pueblo, Colorado, where Gregg (1963) recorded *P. apache*.

8. *Solenopsis amblychila* at JRN co-occurs with completely reddish forms of *S. xyloni* (sometimes referred to as *maniosa*), with which it may be confused easily. James Trager pointed me to the number of hairs on the thorax as a good character, they are comparatively few in *S. amblychila*.

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