

ECOLOGICAL CONSEQUENCES OF LANDSCAPE FRAGMENTATION ON THE
LIZARD COMMUNITY IN THE MESCALERO-MONAHAN'S SHINNERY SANDS

A Dissertation

by

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ABSTRACT

Landscape fragmentation poses a major threat to biodiversity world-wide. The goal of my dissertation research was to determine the effects of landscape fragmentation on a lizard community in the Mescalero-Monahans shinnery sands, New Mexico and the extent to which conservation efforts might protect biodiversity in this ecosystem. My research relied heavily on data collected from a large-scale spatially-replicated comparative study. The purpose of this study was to evaluate the impacts of landscape fragmentation as a result of oil and gas development on the dunes sagebrush lizard (*Sceloporus arenicolus*).

Results from analysis of lizard community structure indicate that fragmented sites are less diverse than non-fragmented sites. In particular, two species are found in lower density and occupancy in the fragmented locations (*Holbrookia maculata* and *Sceloporus arenicolus*). Analysis of landscape configuration at the scale of a trapping grid indicated that sand dune blowout shape and size differed between fragmented and non-fragmented locations. Differences in landscape pattern were associated with reduced lizard diversity. Because of this association between lower diversity and altered landscape pattern, extensive alterations to landscape pattern may cause disassembly at the ecosystem level. The maintenance of existing landscape pattern may be important to the maintenance of diversity in this ecosystem.

Evaluations of habitat use patterns of the lizards in this community demonstrate that a few species have narrow preferences for certain habitats. In particular, *H.*

maculata, *Phrynosoma cornutum*, and *S. arenicolus* all demonstrated narrow habitat use patterns. Effect size of fragmentation for each species indicated that the same three species showed a large effect when comparing their average abundances between fragmented and non-fragmented locations. Thus species that are most likely to benefit or be harmed by landscape fragmentation are those with the most specific habitat requirements.

Umbrella species represent one of many approaches to conservation using surrogate species. I used data on ants, beetles, small mammals, lizards, and endemic species to test the use of the dunes sagebrush lizard (*Sceloporus arenicolus*) as an umbrella for endemism and biodiversity of the Mescalero-Monahans shinnery sands ecosystem. I applied a comparative approach at three spatial scales to examine how conservation practices at different scales may affect biodiversity and endemism in this ecosystem. At the largest scale, the frequency of occurrence for endemic species increased though no other patterns emerged because *S. arenicolus* was present at all sites and there were no relationships between relative abundances of *S. arenicolus* and the other taxonomic groups. At the smallest scale, both beetle species richness, diversity, and endemic species richness were higher in the presence of *S. arenicolus*. To protect biodiversity in this ecosystem, conservation efforts should focus on protection at the scale of the species distribution rather than on the small-scale placement of individual well pads.

DEDICATION

I dedicate this work to: my parents, Darrell Gene and Dionne Elaine Leavitt of Cumberland Head, New York, USA for nurturing my interests in life; to Missy, Greg, Mark, Raymond, Joe, and Allison of Big Bend National Park, Texas, USA for encouraging me to learn more about the natural world; and to Gabriel Theodore Leavitt of New York, New York, USA for being a consistent sounding board for my ideas no matter how far-reaching.

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CHAPTER I

INTRODUCTION TO DISSERTATION, ECOSYSTEM, AND STUDY DESIGN

Introduction

Landscape fragmentation results in discontinuities in a landscape and is a known driver of biodiversity loss worldwide (Fahrig 2003). Fragmentation research has traditionally examined landscapes with a clear distinction between patch and matrix (Fischer and Lindenmayer 2006, Didham et al. 2012). Based on the theory of island biogeography (MacArthur and Wilson 1967) the traditional fragmentation model viewed forest remnants or habitat patches as essentially isolated within an inhospitable matrix (e.g. Laurance 1991). Not surprisingly, many studies of fragmentation such as that of Laurance (1991) have found species-area and species-isolation relationships to be similar between fragments and islands (Debinski and Holt 2000). Further, the majority of what we know about ecological community response to fragmentation is derived from studies conducted in forest ecosystems (Laurance 1991, Sarre 1995, Laurance et al. 1998, Laurance et al. 2001, Laurance et al. 2002, Bell and Donnelly 2006, Watling and Donnelly 2006, Feeley and Terborgh 2008, Watling et al. 2009) and most of these fit the traditional model of isolated fragments surrounded by an inhospitable matrix.

However, it is clear that not all landscapes are fragmented in the same way. There are a variety of “landscape modification states” (*sensu* Fischer and Lindenmayer 2007) that a given landscape could be in and each state corresponds with an amount of remaining intact vegetation and the degree to which the habitat is modified (Fig. 1). As

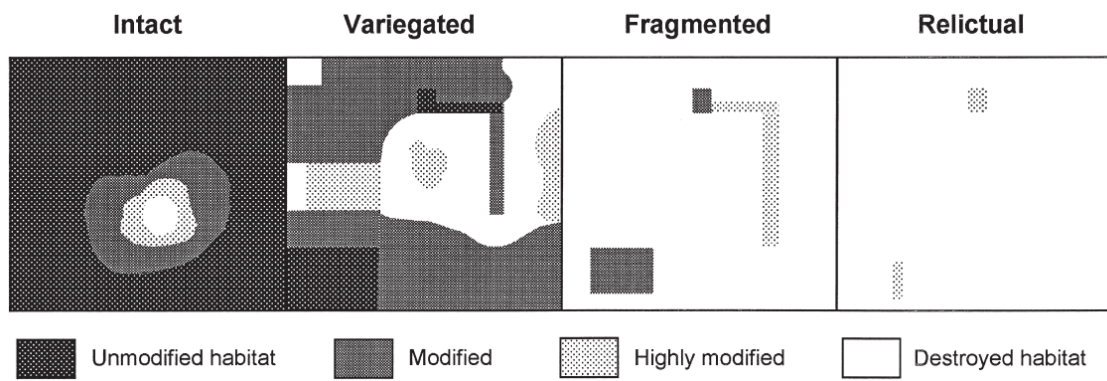


Figure 1. Four landscape modification states in fragmentation studies (from McIntyre and Hobbs 1999)

these states range from intact to relictual the amount of unmodified and destroyed habitat varies. Due to disparities such as these, the continuum model was introduced to fragmentation research to explain species distributions in studies where the traditional model does not fit with the landscape configuration (Fischer and Lindenmayer 2006). The continuum model differs from the traditional fragmentation model in regards to five major issues. First, the continuum model does not assume a clear contrast exists between the patch and matrix, rather the landscape maintains environmental gradients on which species are sorted. Second, human-defined “patches” in the traditional fragmentation model correspond with animal-perceived patch boundaries, in the continuum model species respond to environmental gradients and may not perceive the same edge for a given patch as humans do. Third, fragmentation models generally are applied to single species or multiple species with similar requirements whereas the continuum model can allow for the consideration of multiple species with difference resource requirements. Fourth, species distributions in the fragmentation model should correspond with the patch and matrix in the continuum model distributions are complex and assorted in continuous ways. Finally, the fragmentation model assumes that landscape pattern can serve as a proxy for ecological process whereas the continuum model examines ecological processes directly. These perceptions of the types of fragmentation have caused some to refer to fragmentation research as a pantheon, because the term, fragmentation, is too broadly inclusive to explain all possible landscape variations that may fall under its definition. (Lindenmayer and Fischer 2007).

Meanwhile it has been argued, that fragmentation research has not kept pace with our understanding of species response to landscape change (Didham et al. 2012). Differences between the two aforementioned models are similar to those that separate niche and neutral perspectives for the maintenance of diversity (Leibold and McPeck 2006). It is important to note that perspectives which separate the effects of habitat loss from habitat fragmentation (Fahrig 2003) may do a disservice to gaining an understanding of fragmentation or landscape modification. This is possible because of the dependant and correlated effects of habitat loss and fragmentation (Didham et al. 2012). Thus the “integrated community” (IC) model for fragmentation research has been suggested for fragmentation research (Didham et al. 2012). Integration of the two models suggests some species covary in their response to fragmentation but not all species respond in the same way therefore IC is a blend of the two perspectives.

Because fragmentation research has been flagged as falling behind our understanding of landscape change, it is of utmost importance that general predictions regarding species response to fragmentation should be evaluated to discern whether they fit better with the fragmentation, continuum, or integrated models. Understanding the susceptibility of species to landscape fragmentation requires an understanding of individual natural history, species abundance, and environmental resource needs (Henle et al. 2004, Ewers and Didham 2006, Fischer and Lindenmayer 2007). For example, specialist species are predicted to be more susceptible to changes in isolation, fragment area, and/or matrix contrast than more generalized species (Laurance 1991, Ewers and Didham 2006, Fischer and Lindenmayer 2007). Specialization on a resource is defined

as the restricted niche breadth or use of a resource by a species (Futuyma and Moreno 1988). Species that are dependent on patchily distributed resources are more extinction prone than more generalist species (Patterson 1987, Foufopoulos and Ives 1999). Thus, if a species' needs are disrupted by habitat alteration they are more likely to demonstrate a population level response (positive or negative). This suggests a level of interdependence of species in response to fragmentation as suggested by either the continuum or IC models.

My research evaluates the effects of landscape fragmentation on the structure of communities. I examine community structural differences using current theory regarding species niches in fragmented landscapes. Further, because one of the species in this community is a species of conservation concern (Chan et al. 2009, Fitzgerald and Painter 2009, Smolensky and Fitzgerald 2011, Leavitt 2012), I ask if protecting this species will result in umbrella protection of other types of biodiversity in the ecosystem. The objectives of my dissertation research were to examine the effects of landscape fragmentation associated with oil and gas development on the lizard community of the Mescalero-Monahans shinnery sands and to explore the effectiveness of *Sceloporus arenicolus* as a conservation umbrella for the biodiversity of this ecosystem. The three main objectives of my dissertation are:

- 1) Examine the effect of landscape fragmentation on lizard community structure.
- 2) Examine habitat preferences of lizards to determine if that is an indicator of response to fragmentation

- 3) Explore the use of *Sceloporus arenicolus* as an umbrella species for endemism and biodiversity protection

Ecosystem

Hereafter, I use the term Mescalero-Monahans shinnery sands (MMSS) to describe this ecosystem because it is geographically, biologically, and geologically descriptive. Terms such as “Mescalero Sands” or “Monahans Sandhills” are place names and should not suggest that they are separate geomorphological features. According to the most recent research on sand depositions these landforms share a similar history (Hall and Goble 2011, Rich and Stokes 2011). The term “shinnery sands” refers to the predominance of the two main characters in this ecosystem, shinnery oak (*Quercus havardii*) and quartz sands. These two characters (shinnery oak and sand) bind east and west for this ecosystem. The winds that deposited the sands 43- 204 ka blew in from the desert southwest (Rich and Stokes 2011) and the shinnery oak ranges from this ecosystem to the southern high plains to the east (Peterson and Boyd 1998).

The MMSS is situated on a transition zone between temperate grasslands of the southern high plains and arid shrubland of the Chihuahuan desert in North America. This narrow band of sandy shrub-land occurs between 31° N and 34° N in southeastern New Mexico and west Texas (Fig. 2). On its periphery are the cities and towns of Elida, Plains, Andrews, Odessa, Crane, Monahans, Kermit, Jal, Carlsbad, Artesia, and Roswell (clockwise from north). Many of these cities are built on economies related to ranching, agriculture, and/or oil and gas extraction. Because each of these human practices may

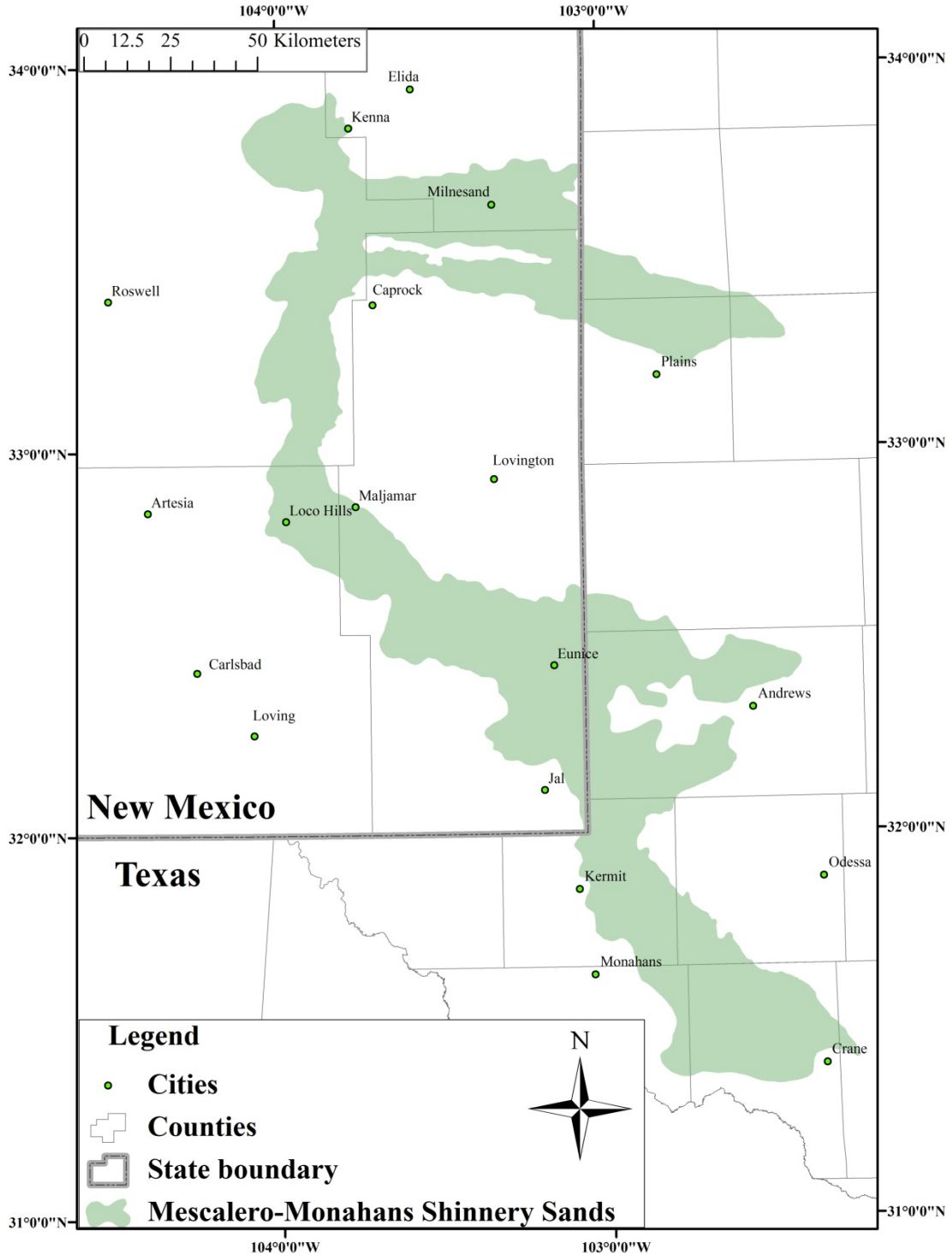


Figure 2. The Mescalero-Monahans shinnery sands ecosystem of southeastern New Mexico and west Texas (Griffith et al. 2004, Griffith et al. 2006).

alter ecosystem structure (Chapin et al. 2002), I will describe ecosystem structure based on state factors (*sensu* Amundson and Jenny 1997) that may control processes in the ecosystem. One human practice that creates concern for the long-term stability of the ecosystem as a whole is oil and gas extraction (Leavitt 2012).

Climate— The climate of the MMSS is typified by low average annual rainfall (330 - 460 mm), hot summers (avg. July temp: 27° C), mild winters (avg. Jan. temp: 6° C), and strong late winter and early spring winds (Stout and Arimoto 2010). Monthly normal climate records in temperature and precipitation from Elida, Andrews, Artesia, and Crane from 1981-2010 demonstrate weather trends for the limits of the ecosystem (Fig. 3). During this time, the northern station in Elida, NM was the coolest and wettest, Artesia, NM was the driest and had the largest variability in monthly temperatures, Andrews, TX was average in climate and Crane, TX was the hottest station, fairly moist, and the least variable in monthly temperatures. The peak in rainfall for the ecosystem is in mid-to late summer when temperatures are either at their peak or on the downward-slide. The early spring is a dry time of year and aquifer recharge should not be expected to take place until the fall. Wind patterns in the MMSS have been evaluated recently by Stout and Arimoto (2010). Yearly trends suggest the strongest winds occur in late winter and spring out of the southwest. Daily trends suggest peak wind activity mid-day between noon and four PM.

Soils—The parent material of the soils can include as many as four layers. From the top down, one encounters an upper aeolian sand unit, a mid aeolian sand unit, a lower aeolian sand unit, and these sit atop a caliche paleosol unit. The upper aeolian unit

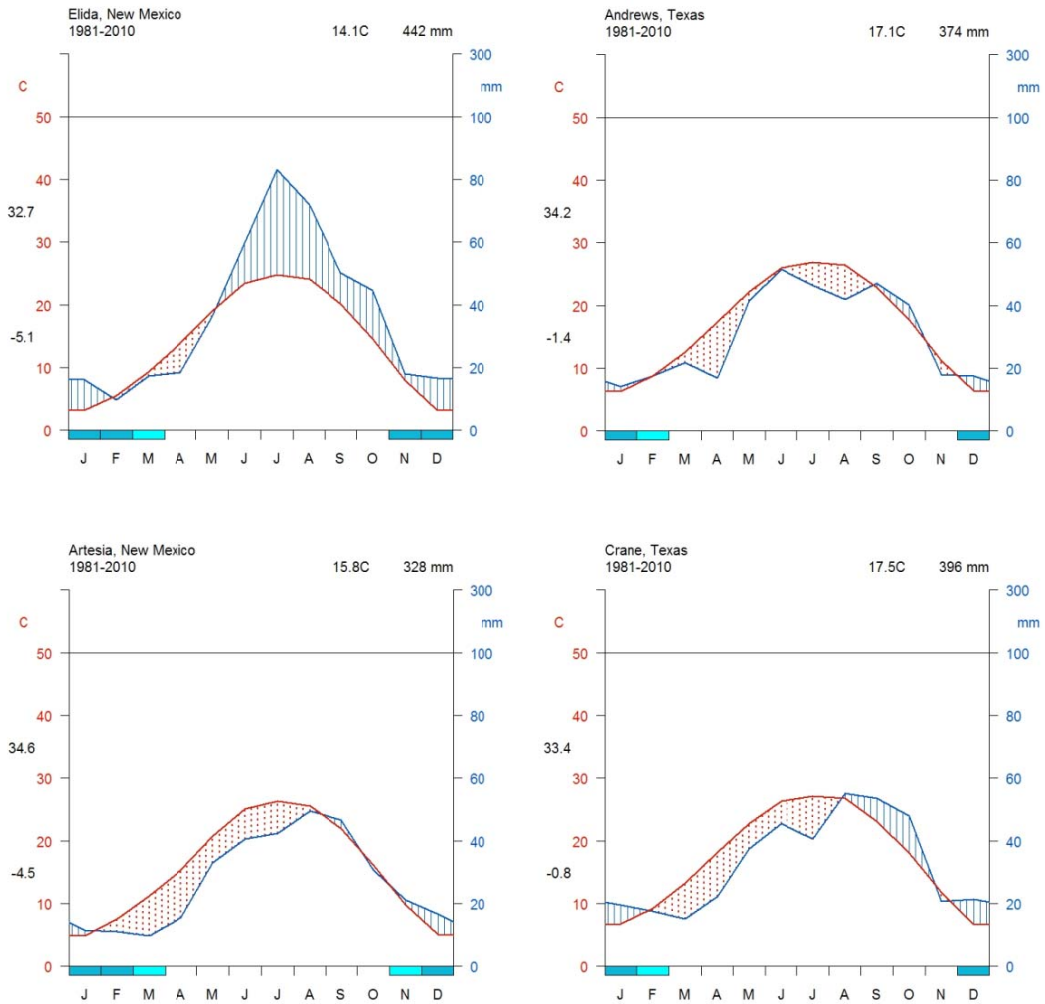


Figure 3. Climate graphs (average monthly precipitation and temperatures) for four locations surrounding the Mescalero-Monahans shinnery sands ecosystem between 1981 and 2010 (NOAA, data accessed online January 17, 2011).

was deposited between 0.08 - 7.5ka it was most recently active during the “dust bowl” as evidenced from optically dated sediments (Rich and Stokes 2011). These sands are part of a highly variable surface sand sheet that is similar to those found on the southern high plains in New Mexico and Texas (Hall and Goble 2006, 2011, Rich and Stokes 2011). The mid aeolian sand unit is not easily distinguishable and, depending on location, could be comprised of two layers of aeolian sand with distinct clay bands. These two lower layers of aeolian deposits accreted 2.0 - 13.0 ka and 15.0 - 29.0 ka. The lower aeolian sand unit, also known as the Blackwater Draw Formation, is a heavily compacted aeolian deposit which accreted 43.0 - 204.0 ka. The caliche paleosol unit (a hard-packed rock composed of calcium carbonate; Hall and Goble 2006) sits below these sand layers. This unit developed before aeolian deposition began and sits atop eroded Pleistocene, Cretaceous, Triassic, and Permian deposits (Hall and Goble 2008, 2011) thus it is thought to have formed sometime between 204.0 - 639.0 ka (Hall and Goble 2006). Below this lies the Permian Basin fossil petroleum deposits, reservoir deposits of ancient organic material which sit atop or are embedded within sandstone, shale, or dolomite from the paleozoic era. Discovery of these deposits in the early twentieth century gave rise to a booming oil and gas industry in the region.

Topographic complexity— In aeolian systems, topographic complexity arises due to prevailing winds, vegetation patterns, sand grain sizes, and parent material (Cooke and Warren 1973). At the southern end of the MMSS sand sheet the surface elevation is approximately 720 m and where the sheet climbs the llano estacado near Caprock, NM it is 1320 m. The sand sheet holds variable amounts of vegetative cover

which translates to localized changes in micro-topography. The largest active dunes exist between Monahans, TX and Jal, NM, however many smaller active dunes exist throughout the MMSS. Exposure of these active dunes to winds results in elevation variation in places of over 25 m (Machenberg 1984). Areas of vegetated (inactive) dunes exist in greater extent ecosystem-wide. Other dune types observed in the MMSS include barchanoid, parabolic, coppice, blowouts, akle, and transverse ridges. Both vegetated parabolic and coppice dunes are thought to be a product of intensive grazing during historic times (Hall and Goble 2011).

Biota—The plant communities occurring within this ecosystem are co-dominated by shrubs and grasses, with shinnery oak (*Quercus havardii*) being the most common plant (Dick-Peddie et al. 1993, Peterson and Boyd 1998, Powell 1998, Mills 2001). There are potentially as few as six (Mills 2001) or as many as 11 (Neville et al. 2007) plant associations found within the ecosystem. These plant associations vary due to spatio-temporal patterns of sand deposition, soil moisture, and human land-use. In my study sites *Q. havardii* was the most dominant plant (59.8%), followed by Purple threeawn (*Aristida purpuraea*) (6.9 %), Little bluestem (*Schizachyrium scoparium*) (6.8 %), Thin paspallum (*Paspallum setaceum*) (4.6 %), Sand sagebrush (*Artemesia filifolia*) (2.6 %), and Giant dropseed (*Sporabolus giganteus*) (2.6 %). Between 2008 and 2011 all species of plants encountered on study sites were identified (a full list of the 89 species of plants encountered is provided in Appendix A). A great diversity of animal life exists within the MMSS (Henderson 2006). Between 2008 and 2011 all species encountered and captured on study sites were identified (a full list is provided in

Appendix B). Over that time, I identified 80 species of arthropod, 6 amphibians, 20 reptiles, and 24 mammals. There are at least 17 known endemic animal species or sub-species found in the MMSS (Table 1) of these I observed or captured 11 in the region between Loco Hills and Maljamar, NM.

Study design

Research described in the following research chapters was conducted in the MMSS between the towns of Loco Hills and Maljamar, New Mexico (Fig. 2). Between April and September of 2009, 2010, and 2011 I conducted a large-scale spatially-replicated study to investigate the impacts of landscape fragmentation on the dunes sagebrush lizard (*Sceloporus arenicolus*). The project was designed as a hierarchical before-after control-intervention type study (Stewart-Oaten et al. 1986, Fitzgerald proposal to BLM). Three levels of study unit were created for the hierarchy: sites ($n = 9$), trapping grids ($n = 27$), and trapping locations ($n = 810$; Fig. 4). In early 2009, site selection was undertaken to insure the historic presence of *S. arenicolus* as determined from voucher specimens from the Museum of Southwestern Biology at the University of New Mexico (MSB) accessed online 19 November, 2008 at HerpNet (<http://www.herpnet.org>). The nine sites were separated into three categories: non-fragmented, experimental, and fragmented (Fig. 5). Non-fragmented sites were selected because they had fewer than 3 well pads per section (249 ha.). Experimental sites were selected based on their proximity to recently active oil and gas wells and expert advice

Table 1. Species endemic to the Mescalero-Monahans shinnery sands ecosystem.

Latin name	Common name
<i>Ammobaenetes mescalero</i>	Mescalero camel cricket
<i>Anomala suavis</i>	Mescalero-Monahans shining leaf chafer
<i>Arethaea Mescalero</i>	Mescalero thread-legged katydid
<i>Ceuthophilus</i> sp.	Mescalero-Monahans spotted camel cricket
<i>Cicindela formosa rutilovirescens</i>	Big sand tiger beetle
<i>Epitragosoma arenaria</i>	Mescalero-Monahans epitragini
<i>Eupompha viridis</i>	Green blister beetle
<i>Graphops comosa</i>	Monahans sandhills chrysomelid
<i>Nicagus occultus</i>	Monahans stag beetle
<i>Polyphylla monahansensis</i>	Monahans ten-lined June beetle
<i>Polyphylla pottsorum</i>	Mescalero-Monahans June beetle
<i>Plagiostira mescaleroensis</i>	Mescalero shield-backed katydid
<i>Prionus arenarius</i>	Longhorn beetle
<i>Prionus spinipennis</i>	Longhorn beetle
<i>Sceloporus arenicolus</i>	Dunes sagebrush lizard
<i>Stenopelmatus mescaleroensis</i>	Mescalero sands Jerusalem cricket
<i>Trigonoscutoides texanus</i>	Monahans oak weevil

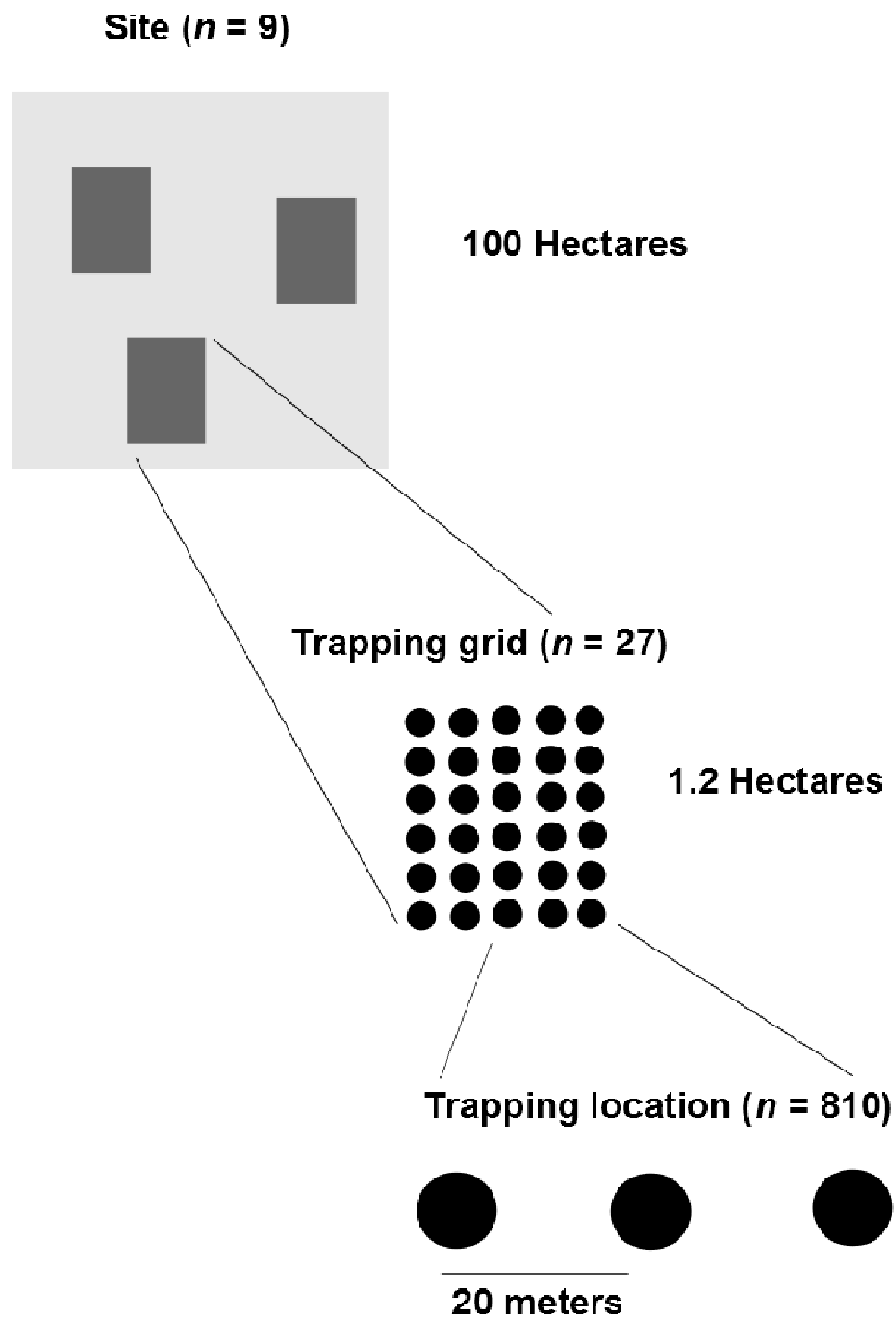


Figure 4. Summary of the hierarchical study design used for research on the effects of fragmentation in the Mescalero-Monahans shinnery sands, New Mexico.

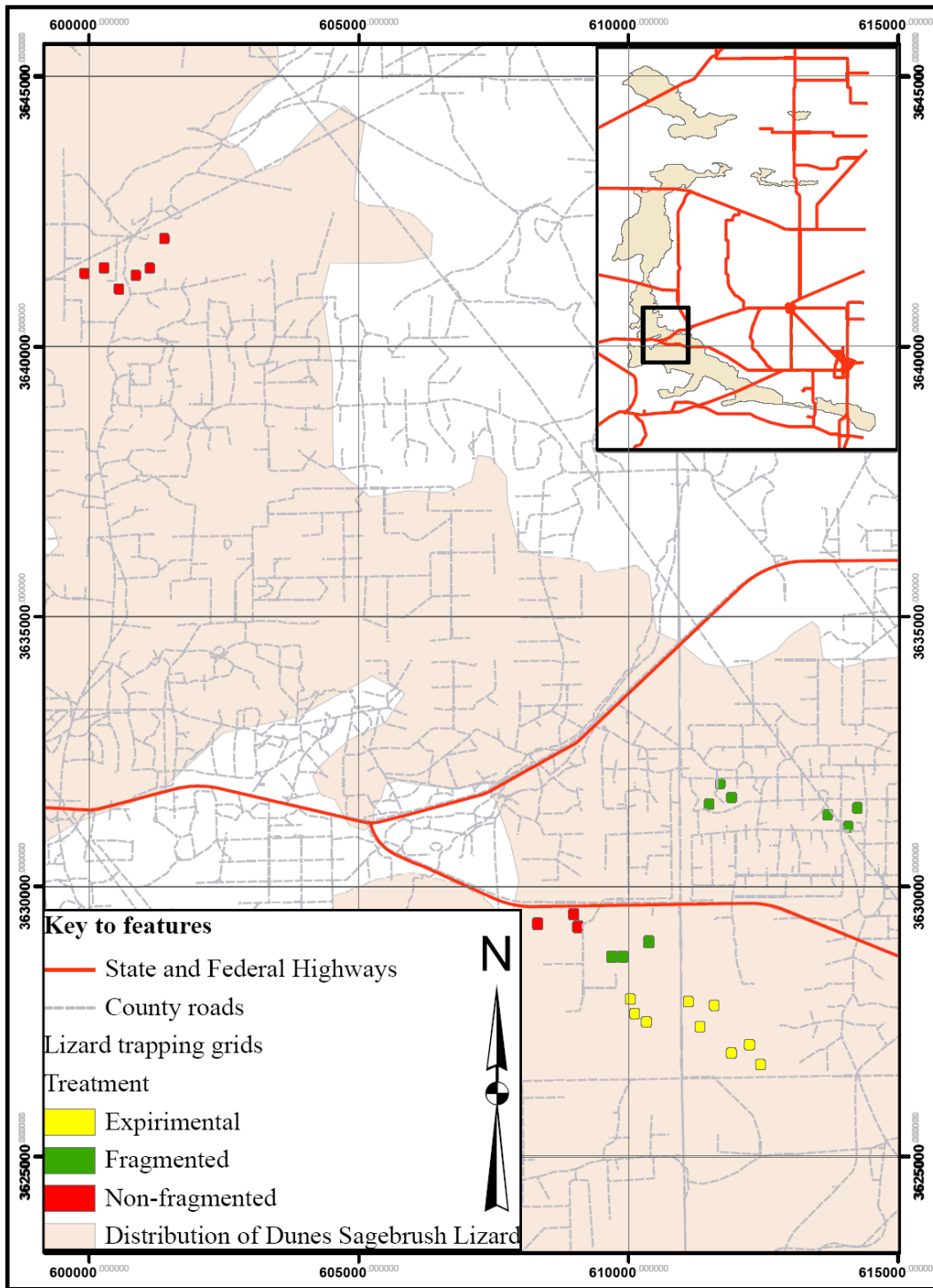


Figure. 5. Map of study area and trapping grids within the Mescalero-Monahans shinnery sands, New Mexico. Twenty seven trapping grids divided equally into three separate experimental treatments (listed in map key) can be shown.

(Ty Allen, BLM biologist; currently US FWS). Fragmented sites had more than 13 well pads per section, a criteria recommended by conservation managers in the region (Painter et al. 1999). The research design called for the experimental sites to be fragmented following the second year of research. However, oil and gas development and road-building has yet to occur in the experimental sites, and as of September 2011, these 3 sites still have fewer than 3 well pads per section.

Within each of the nine sites, three lizard trapping grids were selected based on random number generation in Microsoft Excel and were spaced at least 100 m apart. At each lizard trapping grid I established 30 permanent pit traps. These traps were established in a 5 by 6 grid spaced 20 m apart. At a corner of each trapping grid I placed a 1.2 m green t-post. Each pit trap was a 20 l (5-gallon) plastic bucket with a plywood lid propped < 2 cm off the bucket lid when open. Each grid was sampled three times in 2009 and six times each in 2010 and 2011. Between September and April of each year, traps were closed with permanent lids and/or turn upside down to insure no animals were accidentally captured and trapped while no person was attending to them. Between April and September of each year, I opened traps according to a randomly selected schedule. Sampling sessions lasted for four full 24 hour cycle days (thus I insured that traps were closed on the last day within an hour of the time that they were opened on during the first day). On the third trap day of each session, all arthropods were collected from three randomly selected trapping locations at each trapping grid. All arthropods were placed in vials for later identification and sorting. In 2010 and 2011, the middle four rows (20 traps) of each trapping grid were sampled for small mammals. On these

occasions I sampled small mammals for 4 consecutive nights using Sherman traps baited with rolled oats. I sampled environmental variability at each trapping location using techniques similar to the point-quarter method (Cottam et al. 1953).

Using this study design, I evaluate trends in lizard abundances and occupancy patterns in a fragmented landscape to discern whether there is a noticeable effect of fragmentation. In addition, I examine landscape structure and environmental variability between non-fragmented and fragmented areas. I explore each lizard species use of habitat based on the environmental conditions surrounding the trapping locations where I caught them. I partner these data with capture abundances to explore whether niche breadth may predict response to fragmentation. Finally, I examine *Sceloporus arenicolus* as a potential umbrella species for the biodiversity of the Mescalero-Monahans shinnery sands ecosystem by evaluating patterns in co-occurrence for ants, beetles, small mammals, and lizards.

CHAPTER II
DISASSEMBLY OF A DUNE-DWELLING LIZARD COMMUNITY DUE TO
LANDSCAPE FRAGMENTATION

Overview

In fragmented landscapes ecological dynamics are influenced by landscape pattern among other factors. Community disassembly, a process of community change due to nonrandom species losses and declines, is occurring in ecosystems worldwide as a result of landscape fragmentation, habitat loss, and habitat degradation. I established a comparative study to investigate how fragmentation at the landscape scale influences community structure in a dune-dwelling lizard community. Patterns of relative abundance and occurrence in lizard communities in non-fragmented sites showed a pattern of nested community structure. Conversely, lizard communities fragmented by oil and gas development had consistently lower abundance of two species and these communities demonstrated random structure due to species loss and low abundance, thereby suggesting disassembly. Two species, the dunes sagebrush lizard (*Sceloporus arenicolus*; an ecological specialist) and the lesser earless lizard (*Holbrookia maculata*), were found in most non-fragmented habitats. Neither species was found in more than half of the fragmented trapping grids, nor did they exist in abundances similar to those in non-fragmented trapping grids. Changes to landscape configuration at the patch-scale were associated with reduced lizard diversity. In particular, configuration (both size and shape) of sand dune blowouts varied between non-fragmented and fragmented sites.

Thus landscape-scale fragmentation directly influenced patch-scale landscape configuration and drove community disassembly.

Introduction

Landscape fragmentation is a process by which natural landscapes are modified in a manner that produces variegated, fragmented, or relictual states (Fischer and Lindenmayer 2007) and is one of the leading causes of worldwide loss of biodiversity (Tilman 1994, Vitousek et al. 1997, McGarigal and Cushman 2002, Fahrig 2003). Some biodiversity loss can be attributed to changes in the rates of species turnover and extinction in ecological communities (Laurance et al. 1998, Boulinier et al. 2001, Leidner et al. 2010). However, not all species respond to landscape fragmentation (Ewers and Didham 2006, Devictor et al. 2008) nor does landscape fragmentation occur in a predictable way or result in a typical pattern. The configuration of patches of habitat on a landscape following fragmentation, known as “realized landscape configuration” (*sensu* Turner et al. 2001) is context dependent (Watling et al. 2011, Didham et al. 2012). Landscape configuration often drives ecological dynamics in heterogeneous habitats (Watling et al. 2011). For instance, Valladares et al. (2006) found the trophic interactions of herbivory and parasitism to be not only dependant on the size of the woodland remnant but also dependent on distance from the edge of the habitat. However, the variety of landscape patterns examined in fragmentation studies can be problematic when building a theoretical and predictive understanding of the ecological consequences of landscape fragmentation (Lindenmayer and Fischer 2007, Didham et al.

2012).

The landscape continuum model considers both spatial and temporal dimensions of landscape fragmentation (McIntyre and Hobbs 1999) and serves as an alternative to the traditional fragmentation model (Fischer and Lindenmayer 2006). The traditional fragmentation model was derived from the theory of island biogeography (MacArthur and Wilson 1967) and assumes a clear distinction exists between patches and the matrix within which they are embedded, and that all species will respond equally to fragmentation (Fischer and Lindenmayer 2006). Much of our understanding regarding the effects of fragmentation on community structure comes from studies conducted in forest fragments (e.g. Laurance et al. 1998, Vallan 2000, Boulinier et al. 2001, Leidner et al. 2010). In such cases, a clear delineation of patches in the matrix is evident and the landscapes fit well with the traditional views of fragmentation for most species. In heterogeneous landscapes, it is difficult to determine boundaries between habitat patches and the surrounding matrix for many species. When there is no distinct edge or patch for a community, the traditional fragmentation model does not suffice in its assumptions regarding species distributions (Fischer et al. 2005).

Assumptions of species being restricted to patches are relaxed in the continuum model, and this perspective considers species to be distributed in complex and continuous ways (Fischer and Lindenmayer 2006). The “integrated community” (IC) concept proposed by Lortie et al. (2004) and incorporated into fragmentation theory by Didham et al. (2012) helps advance understanding of fragmentation processes. This model synthesizes the expectations of traditional fragmentation theory and the

continuum model by considering both interdependence of landscape effects on species and the interdependence of species response to landscape change. This perspective challenges us to consider the multiple interacting drivers of fragmentation and the multiple interacting species responding to landscape change on a case-by-case basis (Didham et al. 2012). Community structure in the IC model is determined by stochastic processes, species specific responses to abiotic conditions, and direct or indirect interactions between species (Lortie et al. 2004).

The purpose of this study is to examine how landscape fragmentation influences community structure and species loss in a heterogeneous landscape where fragmentation is obvious, but boundaries between patches and their surrounding matrix are unclear. Heterogeneity in the landscape can result in the maintenance of diversity at the regional scale (Fischer et al. 2005, Bell and Donnelly 2006). For instance, Fischer et al. (2005) found lizards responded individually to environmental gradients in a fragmented landscape and there was no overall species loss. However at the local scale, we should expect a reduction in overall diversity due to fragmentation because of loss of species habitat over time (Tilman et al. 1994). Even moderate habitat destruction may create an extinction debt, in which deterministic local extinctions are time lagged occurring over the course of generations. Together, these ideas suggest that, in an ecosystem characterized by heterogeneity and subjected to fragmentation, community structure may be shaped by deterministic processes. Studies that can examine and disentangle drivers of species loss in fragmented landscapes will assist our understanding of the processes important to the maintenance of diversity and thus guide conservation efforts.

The Mescalero-Monahans shinnery sands (MMSS) ecosystem is a naturally patchy landscape comprised of expanses of wind-blown, sand dune blowouts (depressions) and vegetated flats dominated by shinnery oak (*Quercus havardii*). The ecosystem exists atop the Permian Basin oil fields where extraction of oil and gas over the past century has resulted in landscape fragmentation due to construction of roads, well pads, and other structures. Fragmentation by roads and well pads results in habitat loss, subdivision, degradation, and isolation, all of which have consequences for the resident species (Fahrig 2003, Henle et al. 2004).

To examine the local community-level consequences of landscape fragmentation, I quantified relative abundance and occupancy patterns of lizards in a region of the MMSS where oil and gas development is prevalent. I established a spatially replicated comparative study to examine these patterns in fragmented and non-fragmented locations. The purpose of this investigation was to assess the impacts of recent landscape fragmentation on MMSS lizard community structure and associated environmental structure. Specifically, I investigated the following questions. First, how does community structure differ between fragmented and non-fragmented communities? The IC concept predicts that species respond individually to fragmentation and the resultant pattern would demonstrate a process of progressive species declines and losses consistent with the notion of community disassembly (*sensu* Zavaleta et al. 2009). Second, how does environmental structure differ between non-fragmented and fragmented trapping grids? At a scale larger than the trapping grids, roads and well pads clearly alter environmental structure on the landscape. As such, I predict that landscape

change at relatively large regional scales (beyond the scale of trapping grids) will correlate with landscape metrics that indicate habitat quality for lizard species. To evaluate whether large-scale processes affect small scale patterns of environmental structure, I compared environmental variability between fragmented and non-fragmented trapping grids. I predict that large scale environmental change due to fragmentation will influence smaller-scale landscape configuration. Finally, I predict that small-scale environmental structure is associated with diversity patterns observed in lizard communities.

Methods

Study area - The MMSS is on a transitional zone between the temperate grasslands of the Southern High Plains and the arid shrubland of the Chihuahuan Desert in North America. This narrow band of sandy shrubland exists between 31° N and 34° N in southeastern New Mexico and western Texas (Fig. 1). The ecosystem experiences low average annual rainfall (330 - 460 mm), hot summers (avg. July temp: 27° C), mild winters (avg. Jan. temp: 6° C), and strong late winter and early spring winds (Stout and Arimoto 2010). Surface soils are comprised of three to four layers of material including: the Mescalero paleosol (a hard-packed rock composed of calcium carbonate; Hall and Goble 2006), two layers of eolian sand with distinct clay bands, and a highly variable surface sand sheet (Hall and Goble 2006). The plant communities of this ecosystem are co-dominated by shrubs and grasses, with shinny oak being the most common plant (Peterson and Boyd 1998, Mills 2001). There are potentially as few as six (Mills 2001)

or as many as 11 (Neville et al. 2007) plant associations found within the MMSS. These plant associations are encountered throughout the ecosystem and most likely vary due to spatio-temporal patterns of sand deposition, soil moisture, and cattle grazing. The regional pool of lizards includes 1 scincid (*Plestiodon obsoletus*), 2 teiids (*Aspidoscelis marmorata* and *A. sexlineata*), 5 phrynosomatids (*Holbrookia maculata*, *Phrynosoma cornutum*, *Sceloporus arenicolus*, *S. consobrinus*, and *Uta stansburiana*) and 2 crotaphytids (*Crotaphytus collaris* and *Gambelia wislizenii*).

Lizard sampling - I sampled the lizard communities of nine fragmented and eighteen non-fragmented trapping grids ($n = 27$) from April-September of 2009, 2010, and 2011 (Fig. 5). Trapping grids were categorized as fragmented if they occurred in a landscape with more than 13 oil well pads per section (2.59 km^2). This value was chosen due to its predicted effect on lizards in this system (Sias and Snell 1998) and its practical use among natural resource agencies (Painter et al. 1999). Non-fragmented sites had fewer than three oil well pads per section. Trapping locations were chosen based on the historic presence of the dunes sagebrush lizard (*S. arenicolus*), which is endemic to this ecosystem (Fitzgerald et al. 1997, Fitzgerald and Painter 2009, Laurencio and Fitzgerald 2010). Historic presence of *S. arenicolus* was determined using geo-referenced locations for voucher specimens from the Museum of Southwestern Biology at the University of New Mexico (MSB) accessed online 19 November, 2008 at HerpNet (<http://www.herpnet.org>). At each of the 27 trapping grids, lizards were captured in a 5 by 6 grid of 30 pit traps (20 l plastic buckets), making a total of 810 traps. Traps were spaced 20 m apart; thus, each trapping grid sampled an

area of 1.2 ha. Sampling periods consisted of 4 trap-days, and each site was sampled three times in 2009 and six times each in 2010 and 2011. In total, lizards were sampled at each site for 1,800 trap-days for a grand total of 48,600 trap-days.

Environmental variation – Three variables (mean soil compaction, percent leaf litter, and percent relative cover) were quantified at the location of each trap following the centered-point quarter method (Cottam et al. 1953). To assess landscape configuration, I clipped a 1.2 ha area corresponding to the location of each trapping grid from a landcover layer in ArcGIS 9.3 (ESRI 2008, Redlands, CA). The landcover layer was derived from satellite imagery (Neville et al. 2007), and classification of sand-dune blowouts was derived from 1 m digitally rectified orthoquarterquads. I used the program FRAGSTATS (McGarigal et al. 2002) to calculate five class metrics (percent land cover, number of patches, total area, aggregation index, and perimeter area ratio) for “blowout” (open sand) and “shinnery oak duneland” (shinnery oak dominated vegetation) classes and one landscape metric (total edge) for each trapping location.

Statistical analyses - I calculated species richness, total captures, and diversity (Δ_1 : Hurlbert 1971, Olszewski 2004) at each trapping grid for comparisons between non-fragmented and fragmented groups. I conducted analysis of similarity (ANOSIM: Clarke 1993) on log-transformed lizard abundance at each trapping grid to determine if lizard community structure was different between non-fragmented and fragmented groups (one species, *P. obsoletus*, was removed because it was only present at two trapping grids). For this analysis, I selected the Bray-Curtis dissimilarity metric because it ignores shared absences between trapping grids (Field et al. 1982). I used non-metric

multidimensional scaling (NMDS) on log-transformed lizard abundance to visualize the differences between non-fragmented and fragmented groups. I conducted Spearman rank correlations between the NMDS axes and species richness, total captures, diversity, or lizard abundance to determine which of these factors contributed to the overall pattern in the ordinated data. Data for species richness, total captures, diversity, lizard abundance, and environmental variation did not always meet assumptions of normality and homogeneity of variance required for parametric tests, and standard transformations did not result in normality or homogeneity. Therefore, comparisons of these variables between groups were tested with Wilcoxon rank sum tests.

Analyses of community structure were conducted separately for non-fragmented and fragmented groups using the “elements of metacommunity structure” (EMS) script designed by Presley et al. (2009) for MATLAB (version R2010b). The analysis computes an ordination of the site by species incidence matrices with reciprocal averaging (RA), in this case to align trapping grids along a similarity gradient. Resulting site and species scores were used to order the incidence matrix for null model permutations of coherence, turnover, and boundary clumping. I evaluated two RA axes separately for both the non-fragmented and the fragmented incidence matrices. Null matrices were assembled using the Random0 option, a conservative approach that holds the total number of species at a site fixed but allows equiprobable opportunity for any species to be in a location (Ulrich et al. 2009). This option made sense for my data because it was clear that, after three years of intensive trapping, the species present at each site was known. I ran 1000 iterative comparisons between the observed and null

matrices to evaluate structure of these communities as compared to a random set of alternatives. I compared embedded absences (to evaluate coherence), replacements (to evaluate turnover), and similarity of matrix components (to evaluate boundary clumping) to the null alternatives (see: Leibold and Mikkelsen 2002, Presley et al. 2010).

I conducted a multivariate analysis of variance (MANOVA) to test the null hypothesis of no significant variation in environmental variables between non-fragmented and fragmented groups. I used discriminant analysis (DA) to examine the separation between the environmental variables on non-fragmented and fragmented trapping grids. A new function created by the DA combined some of the original variables that best distinguished between the two groups and indicated which of these variables contributed most strongly to the separation of the groups. I used the R programming platform (R Development Core Team 2011) and the package *vegan* (Oksanen et al. 2009) to calculate ANOSIM, NMDS, Wilcoxon rank sum tests, and Spearman rank correlations. I used PAST (Hammer et al. 2001) to calculate MANOVA and DA.

Results

A total of 11,995 lizards of 8 species were captured over the three seasons. More than three quarters of all captures (79%) were of one species, *U. stansburiana*. *Sceloporus arenicolus* was the next most common species in the community making up 8.8% of all captures. *Aspidoscelis marmorata*, *A. sexlineata*, *H. maculata*, *P. cornutum*, *P. obsoletus*, and *S. consobrinus* made up the remainder of captures (12.2%). There was

no difference in species richness or total captures between non-fragmented and fragmented groups (Table 2). On the contrary, diversity (Δ_1) was higher in the non-fragmented group compared to the fragmented group. This pattern was marked by higher average captures per site for two species in the non-fragmented group, *S. arenicolus* and *H. maculata* (Table 2). Nearly all species were captured in lower numbers in the fragmented group.

Community structure differed between the non-fragmented and fragmented groups (ANOSIM: $R = 0.20$, $p = 0.02$). Non-metric multidimensional scaling based on species abundances at each trapping grid revealed similarities and differences between lizard communities of the two landscapes (Fig. 6). Trapping grids on fragmented landscapes generally had positive values on NMDS axis 1 and higher capture rates for *A. marmorata* and *U. stansburiana* than trapping grids on non-fragmented landscapes. Trapping grids in non-fragmented areas differed from those on fragmented landscapes on NMDS axis 2 as well, and was correlated with captures of *H. maculata*, *S. arenicolus*, total captures, and Δ_1 . Species richness, Δ_1 , *S. arenicolus*, and *S. consobrinus* were negatively correlated with NMDS axis 1 (Table 3). Total captures and *U. stansburiana* captures were positively correlated with NMDS axis 1 (Table 3). Total captures, Δ_1 , *A. marmorata*, *H. maculata*, and *S. arenicolus* were negatively correlated with NMDS axis 2 (Table 3). The NMDS axis 2 shows the greatest spread between the non-fragmented and fragmented groups and this pattern is driven by Δ_1 and *S. arenicolus* captures (Fig. 6, Table 3).

Table 2. Wilcoxon rank sum tests for difference in mean (\pm SD) values of species richness, total captures, diversity, and captures of each species of lizard by trapping grid in non-fragmented and fragmented groups in the Mescalero-Monahans shinnery sands ecosystem, New Mexico. Significant ($P \leq 0.05$) results are shown in bold.

	Non-fragmented ($n = 18$)	Fragmented ($n = 9$)	W	P
Species richness	6.2 (\pm 0.7)	5.8 (\pm 1.5)	76	0.82
Total captures	452 (\pm 118.1)	429 (\pm 84.2)	73.5	0.71
Diversity (Δ_1)	0.40 (\pm 0.1)	0.22 (\pm 0.1)	8	< 0.001
<i>Aspidoscelis marmorata</i>	30.5 (\pm 22.7)	29.8 (\pm 22.1)	73.5	0.72
<i>Aspidoscelis sexlineata</i>	7.2 (\pm 3.7)	8.0 (\pm 3.3)	66	0.45
<i>Holbrookia maculata</i>	10.1 (\pm 10.6)	3.2 (\pm 5.7)	129	0.01
<i>Phrynosoma cornutum</i>	0.9 (\pm 1.3)	2.1 (\pm 2.7)	52	0.12
<i>Sceloporus arenicolus</i>	57.0 (\pm 46.2)	3.2 (\pm 4.4)	156	<0.001
<i>Sceloporus consobrinus</i>	8.3 (\pm 6.2)	5.2 (\pm 4.7)	100.5	0.32
<i>Uta stansburiana</i>	337.9 (\pm 77.1)	376.8 (\pm 78.9)	60	0.29

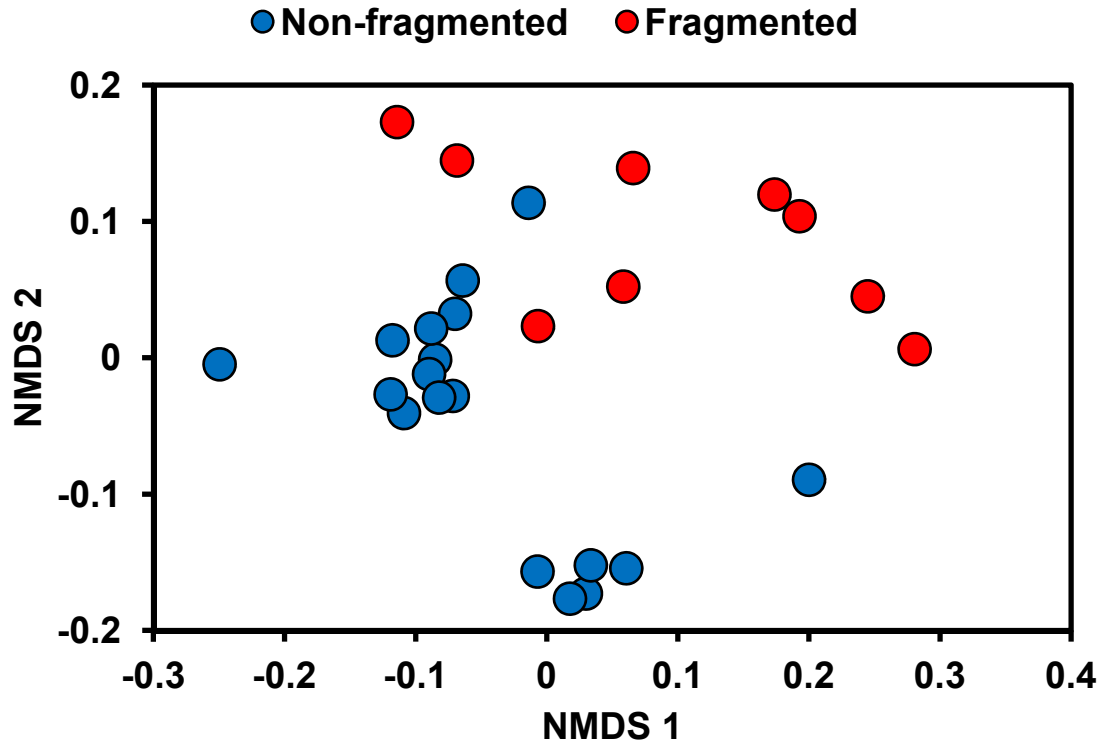


Figure 6. Two-dimensional ordination of 27 lizard communities from a non-metric multidimensional scaling of Bray-Curtis dissimilarity values of species relative abundances by trapping grid in the Mescalero-Monahans shinnery sands ecosystem, New Mexico. Stress = 0.12.

Table 3. Spearman’s rho value (ρ) and significance of rank correlations between axes in a non-metric multidimensional scaling and measures of species richness, total captures, diversity, and individual species abundances in the Mescalero-Monahans shinnery sands ecosystem, New Mexico. Significant ($P \leq 0.05$) results are in bold.

	NMDS1		NMDS2	
	ρ	P	ρ	P
Species richness	-0.51	<0.01	0.06	0.76
Total captures	0.56	<0.01	-0.63	<0.001
Diversity (Δ_1)	-0.49	0.02	-0.82	<0.001
<i>Aspidoscelis marmorata</i>	0.77	<0.001	-0.50	<0.01
<i>Aspidoscelis sexlineata</i>	-0.10	0.61	0.22	0.27
<i>Holbrookia maculata</i>	-0.26	0.20	-0.60	<0.001
<i>Phrynosoma cornutum</i>	0.15	0.46	-0.03	0.87
<i>Sceloporus arenicolus</i>	-0.55	<0.01	-0.75	<0.001
<i>Sceloporus consobrinus</i>	-0.79	<0.001	0.29	0.14
<i>Uta stansburiana</i>	0.74	<0.001	-0.33	0.08

Because lizard communities of fragmented and non-fragmented landscapes were distinctive, subsequent analyses of community structure were conducted separately for these groups. Both RA axes that were derived from site by species incidence matrices for the non-fragmented landscape demonstrated positive coherence, whereas, both axes for the fragmented landscape were classified as random due to the lack of coherence (Table 4). The pattern of the first non-fragmented group axis suggested less turnover in this community than random and clumped species range boundaries, indicative of the nested subsets model of community structure and suggestive of clumped species occurrence on non-fragmented sites (*sensu* Presley et al. 2010). The second axis for the non-fragmented group demonstrated less species turnover in this community (albeit non-significantly) than random, and randomly dispersed species range boundaries (Table 4) suggestive of a quasi-nested subsets model (*sensu* Presley et al. 2010). Five distinct subsets of lizard communities were identified in the non-fragmented axis RA1. Three of the seven lizard species occurring on the non-fragmented sites were absent from a few trapping grids. *Holbrookia maculata*, *S. consobrinus*, and *P. cornutum* were not found on 1, 5, and 10 of the 18 grids, respectively. Therefore it was the absences of these 3 species on some of the grids that ordered the species and site RA scores. Four species were absent from the fragmented communities. The endemic specialist, *S. arenicolus*, was ubiquitous to the non-fragmented trapping grids but was absent from four of the nine fragmented trapping grids. Other species absent from fragmented areas that

Table 4. Assessments of coherence, species turnover, and boundary clumping for the non-fragmented and fragmented groups and the idealized pattern of metacommunity structure that is suggested. Significant ($P \leq 0.05$) results are bold.

Treatment	Axis	Coherence			Species turnover			Boundary clumping		Idealized pattern Structure
		Abs	<i>P</i>	Mean \pm SD	Rep	<i>P</i>	Mean \pm SD	<i>I</i>	<i>P</i>	
Non-fragmented	1	3	<0.01	7.5 \pm 1.7	19	0.05	43.1 \pm 12.2	2.19	<0.001	Nested Subsets
Non-fragmented	2	7	0.05	10.2 \pm 1.6	8	0.54	11.3 \pm 5.4	1.33	0.22	Quasi-nested
Fragmented	1	3	0.52	3.8 \pm 1.3	8	0.46	13.9 \pm 8.0	0.71	0.32	Random
Fragmented	2	4	0.06	6.6 \pm 1.4	8	0.36	16.2 \pm 8.9	1.11	0.29	Random

contributed to the lack of coherence included *S. consobrinus*, *H. maculata*, and *P. cornutum*.

The MANOVA on environmental variables showed significant differences exist on non-fragmented and fragmented landscapes (Wilks' $\lambda = 0.14$, $F_{17,9} = 3.34$, $P = 0.03$). The number of patches, patch density, and perimeter area ratio of the blowout cover class were all significantly higher for the non-fragmented landscapes (Table 5). Total area and aggregation index (a measure of the number and compactness of patches) for blowouts were significantly higher for the fragmented areas (Table 5). Differences between trapping grids on the fragmented and non-fragmented areas with regard to general shape and patch counts for the blowout cover class are congruent with the results from the DA. The DA correctly classified all but 2 of the 18 non-fragmented and 2 of the 9 fragmented trapping grids (Fig. 7). Visual comparison of extreme trapping grids demonstrates total area and aggregation index trends between trapping grids in non-fragmented and fragmented areas (Fig. 7A). The blowouts in the far left (fragmented) landscape model are connected and create large patches as compared with those of the far right (non-fragmented) landscape model where blowouts are small compact and not connected (Fig. 7A). The large patch of blowout adjacent to the caliche cover class at the bottom center of the fragmented trapping grid is the result of sand that was pushed aside in the creation of a nearby oil well pad. The far right landscape model depicts the other extreme of an undisturbed landscape in the non-fragmented areas. Importantly, patch density of blowout and perimeter area ratio for blowouts loaded high for the non-fragmented areas (0.001 and 0.0004, respectively) and total edge and patch density for

Table 5. Wilcoxon rank sum tests for difference in mean (\pm SD) values for ecosystem properties and landscape configuration variables in non-fragmented and fragmented sites in the Mescalero-Monahans shinnery sands, New Mexico. Significant ($P \leq 0.05$) results are bold.

Environmental variable	Non-fragmented ($n = 18$)	Fragmented ($n = 9$)	W	P
Patch density – blowout α	3752 (\pm 1039)	2971 (\pm 1083)	32.5	0.01
Patch density – shinnery oak α	905 (\pm 458)	1558 (\pm 666)	116	0.08
Percent land cover – blowout α	24.2 (\pm 6.7)	28.6 (\pm 11.1)	64	0.40
Percent land cover – shinnery oak α	68.5 (\pm 10.4)	49.3 (\pm 15.7)	64	0.40
Number of patches – blowout α	84.1 (\pm 23.3)	66.6 (\pm 24.3)	139	0.002
Number of patches – shinnery oak α	20.3 (\pm 10.3)	34.9 (\pm 14.9)	116	0.08
Total area – blowout α	0.5 (\pm 0.2)	0.6 (\pm 0.3)	33	0.01
Total area- shinnery oak α	1.5 (\pm 0.2)	1.1 (\pm 0.4)	64	0.40
Aggregation index – blowout α	87.2 (\pm 2.5)	87.9 (\pm 3.2)	139	0.002
Aggregation index – shinnery oak α	95.4 (\pm 0.9)	93.2 (\pm 1.8)	63	0.38

Table 5. Continued.

Environmental variable	Non-fragmented (<i>n</i> = 18)	Fragmented (<i>n</i> = 9)	W	P
Perimeter area ratio – blowout α	23629 (\pm 3294)	23245 (\pm 2493)	143	<0.001
Perimeter area ratio – shinnery oak α	24863 (\pm 3294)	23698 (\pm 4276)	90	0.67
Total edge α	2956 (\pm 486)	3321 (\pm 339)	46	0.08
Percent leaf litter†	23.4 (\pm 7.3)	21.5 (\pm 5.0)	46	0.08
Mean soil compaction†	2.7 (\pm 2.3)	3.1 (\pm 2.0)	95	0.50
Percent relative cover†	23.5 (\pm 7.8)	22.0 (\pm 5.5)	64	0.40

† Measured on site using centered point quarter method

α Calculated with FRAGSTATS

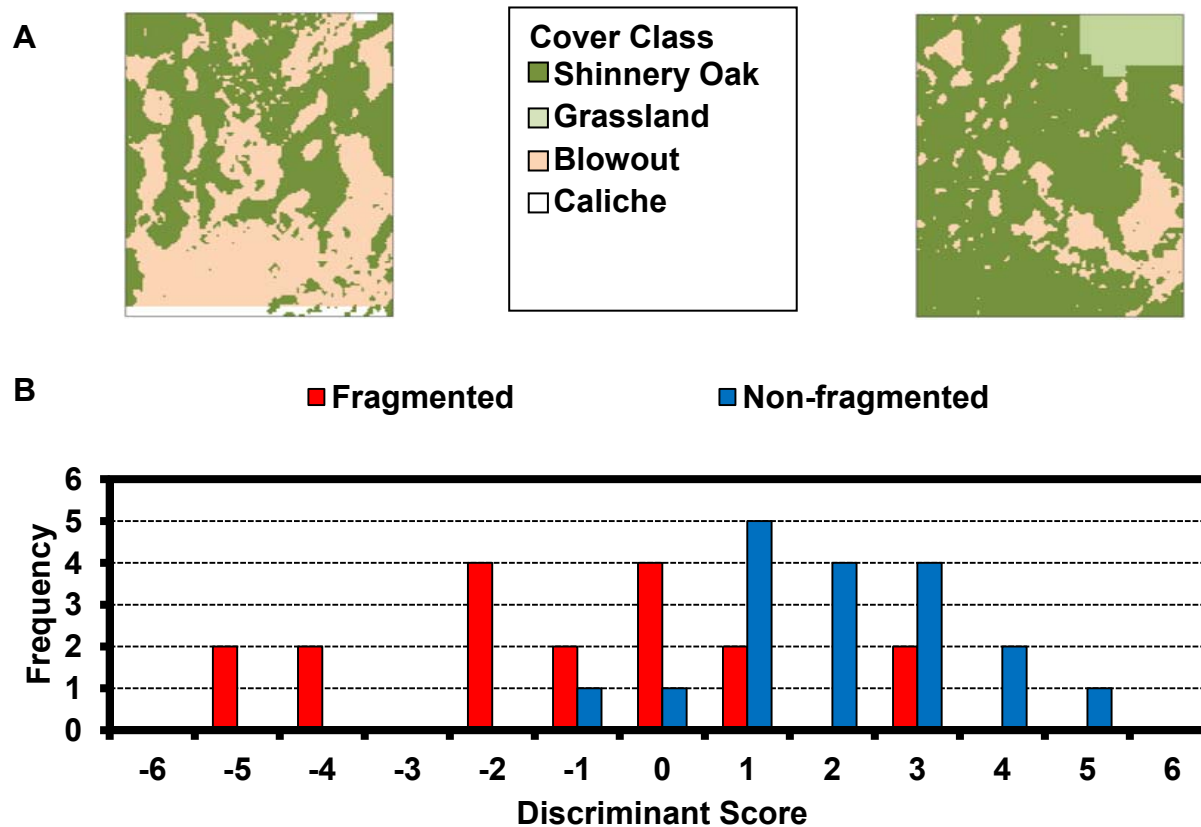


Figure 7. Examples of and frequency histogram for discriminant analysis (DA) of environmental variation between non-fragmented and fragmented areas. (A) Landscape models representing the trapping grids (1.2 ha) at the extreme end for each grouping in the DA (fragmented on left and non-fragmented on right) with a legend of cover classes. (B) Frequency histogram of discriminant scores for environmental variables from an analysis of 27 trapping grids separated into non-fragmented and fragmented groups.

shinnery oak loaded highest for fragmented grids (-0.003 and -0.002, respectively). To examine observed patterns in lizard community structure and environmental structure, I compared the Δ_1 values with the DA scores (Fig. 8). There was a significant positive correlation between these landscape pattern and lizard community diversity ($\rho = 0.47$; $p = 0.02$). None of the fragmented sites had Δ_1 values greater than 0.30, making the distinction clear between these trapping grids and those from the non-fragmented areas.

Discussion

The multiple impacts caused by landscape fragmentation on ecological communities can be complex and difficult to interpret (Davies et al. 2001, Gibbs and Stanton 2001, Fahrig 2003, Bell and Donnelly 2006, Ewers and Didham 2006, Devictor et al. 2008). My study provides an assessment of how landscape configuration can influence lizard community structure in a patchy environment. Differences in alpha diversity, community membership, and landscape pattern between non-fragmented and fragmented areas indicate that community disassembly is occurring where the MMSS landscape has become fragmented. Specifically, two species (*H. maculata* and *S. arenicolus*) consistently occurred in lower abundances and were captured at fewer trapping grids in fragmented landscapes (Table 2). The species that drive patterns of nested community structure (*H. maculata*, *P. cornutum*, and *S. consobrinus*) in non-fragmented areas were the same as those that drove the random community structure pattern in fragmented areas. At the same time, differences in small-scale habitat features

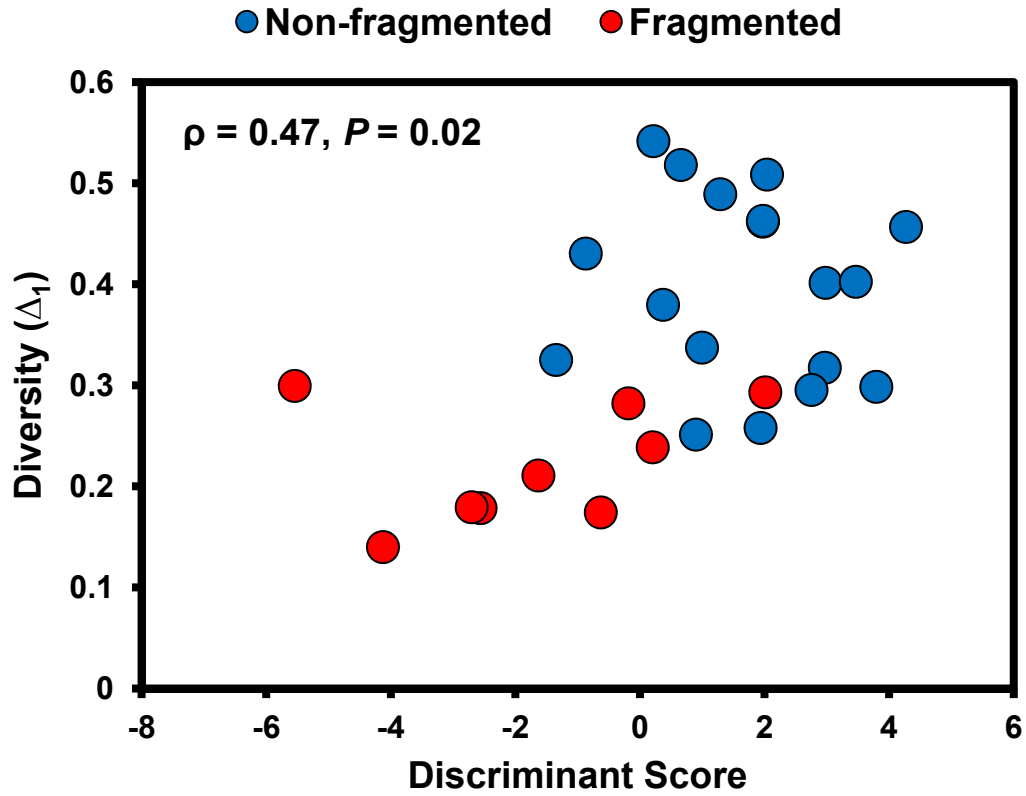


Figure 8. Correlation between discriminant scores and diversity (Δ_1) for fragmented and non-fragmented trapping grids in the Mescalero-Monahans shinnery sands, New Mexico.

between non-fragmented and fragmented areas created variation in patch density, number of patches, total area, aggregation index, and perimeter-area ratio for the blowout cover class (Fig. 7). Differences in landscape pattern at the small scale appear to be a result of large-scale changes (building caliche well pads and roads) associated with landscape fragmentation.

Results here are congruent with the findings of similar studies of fragmentation and community structure (Fischer et al. 2005, Bell and Donnelly 2006, Hamer et al. 2006). Specifically, regional species richness was not influenced by fragmentation however, Δ_1 was lower in fragmented areas than non-fragmented areas (Table 2). Similar patterns in disassembly have been observed in forest remnants for amphibians and reptiles (Fischer et al. 2005, Bell and Donnelly 2006), in grasslands with bird communities (Hamer et al. 2006), and for island mammal communities (Okie and Brown 2009). Four species (*A. marmorata*, *A. sexlineata*, *S. arenicolus*, and *U. stansburiana*) were present at every trapping grid located on non-fragmented landscapes, and with the exception of *S. arenicolus*, these four species were present at all fragmented trapping grids as well. These species seem to form the foundation of the regional lizard community. Community structure in non-fragmented areas was consistent with the nested subsets model in which “depauperate faunas should constitute a proper subset of those in richer faunas” (Patterson and Atmar 1986). Lower Δ_1 on fragmented trapping grids was driven by lower numbers and absences of *S. arenicolus* and *H. maculata*, suggests deterministic processes congruent with predictions of extinction debt (Tilman et al. 1994) and community disassembly (Zavaleta et al. 2009). In this circumstance, these

two species represent the early losers in the processes that follow fragmentation.

Whether these two species are the best competitors, as predicted by the extinction debt (Tilman et al. 1994), or are just vulnerable to landscape fragmentation (Zavaleta et al. 2009) remains to be determined. However, the fragmented communities demonstrated random structure (Table 4) that might be a result of the small sample size for this landscape category ($n = 9$) (Leibold and Mikkelson 2002).

Alterations to landscape patterns, beyond habitat loss, are known to cause shifts in occupancy patterns for animals (Lomolino and Perault 2000, Vega et al. 2000, Thrush et al. 2008) occasionally resulting in localized extinctions. Often community disassembly results from predictable responses of species to external drivers (Zavaleta et al. 2009). In this case, configuration, patch counts, and aggregation metrics of the blowout cover class explained reduced diversity on fragmented sites. The fragmented landscapes had more overall area and fewer patches for the blowout cover class than non-fragmented trapping grids (Table 5; Fig. 7). Some of the increase in blowout cover class area resulted from the creation of pipelines and the pushing aside of surface sands in areas under oil and gas development. The end result of these activities can be seen in the clipped image of a fragmented trapping grid in Fig. 7. While there are no roads or well pads within any trapping grids, multiple pipelines may cross them and many were adjacent to large patches of bull-dozed sand. In contrast, more small patches of the blowout cover class exist within the matrix of the shinnery oak duneland cover class in non-fragmented grids.

These differences in landscape features and configuration appear to be driving

community disassembly in this system. Certain species respond negatively where native habitats are bull-dozed and leveled. Temperature, vegetation, and other abiotic or biotic factors are likely to vary in accordance with these disturbances. The configuration and size of blowouts are expected to be important factors influencing activity and movements of lizards, with ramifications for population size and persistence. (Huey and Slatkin 1976, Overall 1994, Vega et al. 2000). *Sceloporus arenicolus* was sensitive to fragmentation and occurred in much lower abundance at fragmented sites. Blowout and edge (the transition from blowout to shinnery oak) habitat is preferred for *S. arenicolus* (Sartorius et al. 2002, Chan et al. 2009, Fitzgerald and Painter 2009, Smolensky and Fitzgerald 2011). This study demonstrated that fragmented areas have differently shaped blowouts as compared with non-fragmented areas. *Holbrookia maculata* also demonstrated reduced occupancy and lower abundance at fragmented sites. This species has a preference for flat areas with sparse cover (Jones and Ballinger 1987). In the MMSS, *H. maculata* are associated with vegetated flat habitat (CHAPTER III). There was no clear association between the observed landscape pattern and the lower numbers of *H. maculata* at the fragmented trapping grids.

Variation in lizard community structure was consistent with theoretical perspectives on the effects of landscape fragmentation on ecological communities (Fahrig 2003, Ewers and Didham 2006). In particular, some lizard species appear to have narrower niches than other species in the ecosystem (CHAPTER III). This trend agrees with the predictions of Ewers and Didham (2006) that more specialized species with narrower niches are more susceptible to fragmentation than generalists.

This work demonstrates how fragmentation resulting from networks of roads, well pads, and other structures associated with oil and gas development causes change in structure and composition of ecological communities. Future research in this system could examine thresholds of community change in response to aspects of habitat fragmentation. Ecological thresholds represent breakpoints for shifts in community structure (Huggett 2005). For instance, in the MMSS, it will be beneficial to examine the fragmentation thresholds for behavioral and demographic responses by *H. maculata* and *S. arenicolus*. The ecological dynamics responsible for reduced numbers for these species may not be the same, therefore it is important that each species be evaluated separately. Attempts have been made to integrate fragmentation theory to account for spatial and biological complexity (Didham et al. 2012). This study reveals how fragmentation at the landscape scale can influence smaller-scale dynamics in a heterogeneous environment. Examinations of conditions like those presented here can clarify our understanding of how community disassembly occurs.

CHAPTER III

LIZARD HABITAT BREADTH DICTATES RESPONSE TO LANDSCAPE

FRAGMENTATION

Overview

Landscape fragmentation is a major contributor to biodiversity loss and the processes of global change biology. Derived from the theory of island biogeography, the most common paradigm in fragmentation research treats habitat fragments as essentially isolated in an inhospitable matrix. However, in many cases traditional views of fragmentation do not fit with patterns observed on the ground. In regards to habitat use patterns, it is unclear whether theories stating that specialist species respond negatively to fragmentation are applicable to traditional patch-matrix models only or if they should be extended to continuum models. Alterations to the environment that influence factors beyond isolation and patch size may be important to our understanding of the interaction between species habitat use and landscape fragmentation. The Mescalero-Monahans shinnery sands ecosystem of New Mexico, USA has been fragmented by placement of well pads and roads during oil and gas development. The resultant landscape pattern is characterized by multiple small patches of heterogeneous environment separated by narrow roads and well pads. I evaluated lizard habitat use at a small scale to determine if narrow niche breadth can predict species response to landscape fragmentation. I quantified habitat use for seven species of lizards in the Mescalero-Monahans shinnery sands in areas varying in environmental conditions. Habitat use was variable among the

species with *Holbrookia maculata*, *Phrynosoma cornutum*, and *Sceloporus arenicolus* demonstrating the most narrow habitat use patterns. These same three species showed the largest effect sizes to landscape fragmentation. Interestingly, each of the three species responded to fragmentation uniquely. I examined relative abundances at the scale of a trapping grid to evaluate what landscape characteristics were associated with species responses to fragmentation. *Holbrookia maculata* and *S. arenicolus* declined in fragmented areas, but their declines were associated with different landscape patterns. For *H. maculata*, locations with more edge habitat were associated with fewer total captures. There was a positive association between *S. arenicolus* abundance and large patches of habitat. *Phrynosoma cornutum* responded positively to landscape fragmentation and this was most likely due to an increase in flat open habitats. These results from a non-traditional example of fragmentation fit the predictions regarding species response to fragmentation; specialized species demonstrate a greater susceptibility to fragmentation than do generalists.

Introduction

The spatial structure of the environment plays a critical role in species-species and species-environment interactions (Andrewartha and Birch 1954, Huffaker 1958). In addition, the spatial distribution of processes influencing resource availability (e.g.: predation, nutrient cycling, etc.) can shape the ways organisms use their landscape (Franklin 1993, Turner et al. 2001). Landscape modification and fragmentation are known causes of global biodiversity loss (2003) and these sources of landscape change

can alter ecological and environmental processes (Saunders et al. 1991). Yet, not all modified environments fit the traditional model of fragmentation derived from the theory of island biogeography (Fischer and Lindenmayer 2006, Fischer and Lindenmayer 2007, Didham et al. 2012).

Alternative perspectives help clarify the effects of landscape modification and fragmentation on patterns of species' habitat use. For instance, the continuum model proposed by Fischer and Lindenmayer (2006) differs from the traditional fragmentation model in that it emphasizes the importance of gradually changing environmental gradients, space-related ecological processes, and species individual responses to these factors. Species respond to environmental gradients and because landscape fragmentation may alter these gradients, distributions of species may in turn be disrupted (Fischer et al. 2005). One of the clear differences between the traditional model of fragmentation and the continuum model relates to the interdependence or independence of species responses to fragmentation (Didham et al. 2012).

Fragmentation takes place at the landscape level and results in modification of species' habitats through habitat reduction, increased edge, increased isolation of habitat patches, or the creation of novel habitats (Fahrig 2003). A vast majority of the studies on fragmentation evaluate biodiversity loss due the breaking apart of habitat into isolated, island-like forest fragments (Fischer and Lindenmayer 2006). In many of these cases, evaluations are of either one species or of multiple species with similar requirements. In contrast, the continuum model allows for consideration of multiple species with vastly different requirements. Integration of the traditional fragmentation

and continuum models (Didham et al. 2012) would suggest some species covary in their response to fragmentation but also recognize that not all species respond in the same way. Therefore, general predictions regarding species response to fragmentation should be evaluated to discern whether they fit better with the fragmentation, continuum, or integrated models.

Predictions regarding the susceptibility of species to landscape fragmentation, require an understanding of individual natural history, species abundance, and environmental resource needs (Henle et al. 2004, Ewers and Didham 2006, Fischer and Lindenmayer 2007). For example, specialist species are predicted to be more susceptible to changes in isolation, fragment area, and/or matrix contrast (Laurance 1991, Ewers and Didham 2006, Fischer and Lindenmayer 2007). Specialization on a resource is defined as the restricted niche breadth or use of a resource by a species (Futuyma and Moreno 1988). Species that are dependent on patchily distributed resources are more extinction prone than more generalist species (Patterson 1987, Foufopoulos and Ives 1999). Thus, if a species' needs are disrupted by habitat alteration they are more likely to demonstrate a response (positive or negative). This suggests a level of interdependence of species in response to fragmentation as suggested by either the continuum or integrated models. For instance in coastal dunes of Argentina, sympatric, congeneric lizard species showed responses to fragmentation and provide an example of how species may differ in their responses to fragmentation. *Liolaemus multimaclatus* is a specialist that lives among the grass *Spartina ciliata* in coastal dunes. Predictably, after a road was built through these dunes *L. multimaclatus* all but

disappeared in accordance with drastic reduction of *S. ciliata* (Vega et al. 2000). However the generalist, *Lioleamus gracilis*, remained equally abundant despite 50% reduction of its habitat. Cases such as this demonstrate how co-occurring species may respond very differently to fragmentation.

Landscape characteristics that may be important to understanding species response to fragmentation vary under the different models of fragmentation. Factors such as isolation and area are highly influential in the traditional fragmentation model, whereas factors such as matrix contrast are more influential in the continuum model. In their assessment of lizard distribution patterns in a fragmented environment Fischer et al. (2005) found species response to fragmentation to be reliant on environmental gradients. Specifically, lizards responded individualistically to ecological variables such as climate, space, shelter, and food in a fragmented environment. This should not be surprising due to our understanding of the relationship between the organism and its structural environment (Pianka 1966), and there are countless examples where structural modification of the environment has resulted in positive or negative conditions for a variety of species (Vega et al. 2000, Blouin-Demers and Weatherhead 2001, Jellinek et al. 2004, Santos et al. 2008). Thus, it would be likely that in the context of an ecological community, species will respond independently to fragmentation.

The aim of this study is to evaluate individual lizard responses to a fragmented heterogeneous landscape to assess to what degree lizards respond independently to fragmentation. In a heterogeneous landscape this naturally occurring pattern of patchiness may give rise to niche partitioning (MacArthur 1958). However, in most

assessments of fragmentation, heterogeneity is created after land modification. To address these ideas regarding species responses to fragmentation, I evaluated how fragmentation by roads and oil well pads influences habitat use and presence of lizard species in a sand dune ecosystem.

Using data on the environmental conditions surrounding 810 trapping locations, I inferred lizard habitat use from 48,600 trap/days for seven species of lizard. In doing so, I quantified each species' Grinnellian niche for use of habitat (Grinnell 1917, Devictor et al. 2010). By comparing species' habitat use with their abundances in fragmented and non-fragmented locations, I can test predictions regarding how niche breadth can influence species response to an altered environment. A few investigations of lizard response to habitat fragmentation have demonstrated that species response is dependent on niche requirements of the species (Smith et al. 1996, Jellinek et al. 2004, Fischer et al. 2005).

The Mescalero-Monahans shinnery sands (MMSS) is a patchy landscape consisting of expanses of windblown sand deposits within a shinnery oak (*Quercus havardi*) matrix (Leavitt 2012). Where patches of deep sand occur, large complexes of wind-hollowed depressions, termed blowouts, exist in the shinnery oak matrix. Places where patches of blowouts are not present the sands are generally shallow and vegetated with a mix of shinnery oak and sand sage (*Artemisia filifolia*); this is the most dominant land cover type in this ecosystem. Over the past century, oil and gas development in the MMSS has resulted in landscape modification and fragmentation (Smolensky and Fitzgerald 2011, Leavitt 2012). The resulting landscape pattern is best described as

variegated and does not lend itself easily to the traditional fragmentation model paradigm. Because human defined patches may not be perceived as patches to a lizard, nor to all the lizards in the community. None of the species of lizards in the MMSS are restricted to singular patches consisting only of shinnery oak or blowout habitats. Thus, each species utilizes different portions of this heterogeneous environment.

Evaluations of lizard occupancy and relative abundance at the local scale in the MMSS have shown that lizard diversity is lower in regions of high oil and gas development and where the landscape is fragmented (Chapter II). Fragmentation of the MMSS is concordant with the continuum model of landscape fragmentation, in that fragmentation does not result in the creation of isolated areas of habitat representing distant island-like patches in an inhospitable matrix. Rather, over time and space the MMSS may fit a variety of landscape modification states. Therefore, I expect that species response to human landscape modification to be dependent on individual resource use patterns.

In order to clarify how individual species respond to this landscape fragmentation, my first goal was to quantify habitat use of each species. This was conducted using techniques that evaluate habitat surrounding a trapping location (Simonetti 1989, Patterson et al. 1990, Poindexter et al. 2012). By characterizing the habitat use of these species at trapping locations, I can test the null hypothesis that these lizards use the landscape randomly. Then, I quantify each species' landscape level response to fragmentation testing the null hypothesis that species demonstrate no response to fragmentation. If either of these hypotheses were falsified, I ask whether

species habitat use breadth predicts their response to landscape fragmentation (Henle et al. 2004, Ewers and Didham 2006). I predict that specialized species will demonstrate a greater response to fragmentation than generalists. Further, I predict that specialized species will respond uniquely to patterns in landscape variability associated with fragmentation.

Methods

Lizard sampling—I sampled the lizard communities at three fragmented and six non-fragmented sites ($n = 9$ sites) from April-September of 2009, 2010, and 2011 in the MMSS. Sites were categorized as fragmented if they had more than 13 oil well pads per section (1 mi^2 ; 2.59 km^2). This value was chosen due to its predicted effect on lizards in this system and use among land managers (Painter et al. 1999). Non-fragmented sites had fewer than 3 oil well pads per section. All site locations were chosen based on the historic presence of the dunes sagebrush lizard (*Sceloporus arenicolus*), a species endemic to this ecosystem (Fitzgerald et al. 1997, Fitzgerald and Painter 2009, Laurencio and Fitzgerald 2010). Presence of *S. arenicolus* was determined using geo-referenced voucher specimens from the Museum of Southwestern Biology at the University of New Mexico (MSB) accessed online 19 November, 2008 at HerpNet (<http://www.herpnet.org>). Each site was 100 ha, and lizards were trapped in three randomly placed, 5 by 6 grids of 30 pit traps (20 l plastic buckets), making a total of 27 grids and 810 traps. Traps were spaced 20 m apart; thus, each trapping grid sampled an area of 1.2 ha. Sampling periods consisted of 4 trap-days, and each site was sampled

three times in 2009 and six times each in 2010 and 2011. In total, lizards were sampled at each site for 5,400 trap-days, for a grand total of 48,600 trap-days. Before release, lizards were sexed and permanently marked by toe-clip (Waichman 1992), standard measurements (SVL, TL, and mass) were taken, and reproductive condition was noted.

Habitat variability—Following methods similar to Poindexter et al. (2012) I quantified five environmental variables at each trapping location (Table 6). Environmental variables were determined using a 1m² frame positioned in a random direction 1m from the trap location. Land cover type was determined by identifying whether or not the 1 m² frame was positioned in either a blowout, matrix, or edge. Dominant vegetation was determined by identifying which plant species was most dominant (*Quercus havardii*, *Schizachyrium scoparium*, *Artemisia filifolia*, *Chamaesyce* sp., *Sporobolis giganteus*, or *Aristida purpurea*) within the 1 m² frame. Aspect was measured with a folding military lensatic compass (Brunton, Riverton, Wyoming) facing in the direction of the dominant slope. Slope was measured with a magnetic angle locator (Johnson Level & Tool Mfg. Co., Mequon, Wisconsin) placed on a flat piece of metal strap positioned on the dominant slope within the frame. Soil compaction was measured from the center of the furthest edge of the frame with a penetrometer (Lang Penetrometer, Inc., Gulf Shores, Alabama).

Table 6. Five environmental variables measured at the location of each trapping location ($n = 810$) in the Mescalero-Monahans shinnery sands, New Mexico.

Variable	Definition
Land cover type	Describes landscape cover type that surrounded the trapping location (Blowout, Matrix, Edge)
Dominant vegetation	Dominant species of plant that surrounded the trapping location (<i>Quercus havardii</i> , <i>Schizachyrium scoparium</i> , <i>Artemisia filifolia</i> , <i>Chamaesyce</i> sp., <i>Sporobolus giganteus</i> , <i>Aristida purpurea</i> .)
Aspect	Direction of the facing aspect of the dune
Slope	Steepness of the trapping location
Soil compaction	Compactness of the soils around a trapping location

Landscape variability—To characterize landscape pattern as a result of fragmentation, each 100 ha site was clipped from a landcover layer in ArcGIS 9.3 (ESRI 2008, Redlands, CA) derived from satellite imagery (Neville et al. 2007). I used the program FRAGSTATS (McGarigal et al. 2002) to calculate four landscape metrics related to general landscape configuration patterns. Landscape metrics chosen to assess variability in configuration were patch density (PD), largest patch index (LPI), total edge (TE), and landscape shape index (LSI). Patch density, largest patch index, and total edge are self-explanatory metrics. The landscape shape index is a measure of clumpiness or aggregation and is measured by dividing the total length of edge by the minimum total edge length for the landscape. Each of these metrics were calculated for both shinnery oak duneland and blowout cover classes.

Statistical analysis— I used contingency analysis (Zar 1999) to test lizard preferential use of habitat type. Expected values for each environmental variable were calculated by creating a proportional incidence matrix for each trapping grid. Because not all species were captured at all trapping grids, expected values for each species were calculated only from the trapping grids where they occurred. In order to conduct these enumeration analyses on observed habitat use, each of the quantitative variables was transformed into categorical variables. I chose to conduct enumeration analysis because it provides a means to compare all species and their habitat use. Aspect was divided categorically into four ordinal directions: northeast (1 - 90°), southeast (91 - 180°), southwest (181 - 270°), and northwest (271 - 360°). Slope was subdivided into steep (> 11.5°), moderate (11.5 – 5.0°), and flat (< 5.0°). Finally, soil compaction was

subdivided into loose (< 6 lbf), average (6 – 12 lbf), and hard (> 12 lbf). Multiple logistic regression was used to investigate if slope, aspect, or soil compaction were related to presence or absence of each species in the trapping locations. I modeled two-way interactions between variables and found that no significant two-way interactions existed. To determine which main effects were more or less important to model selection, I eliminated all non-significant variables. In all cases the significance level chosen was $p < 0.05$.

To quantify niche breadth, I conducted a principle coordinates analysis (PCoA) on the frequency of occurrence for land cover type and dominant vegetation and the mean value for slope, aspect, and soil compaction for each species. For this analysis, I selected the Gower dissimilarity metric to describe the pairwise distances between species in Euclidean space (Devictor et al. 2010). Levels of habitat use among lizard species were determined by calculating the Euclidean distance from origin for each species (a high Euclidean distance suggests narrow habitat use). I calculated the standardized effect size (Krebs 1999) for each species' difference in relative abundance between the two treatments (non-fragmented and fragmented) at nine sites to determine the effect of fragmentation on lizard abundances. Standardized effect size is the difference in means between two samples corrected for the standard deviation for the whole sample (Krebs 1999). To determine whether or not lizards with more narrow habitat affinities were more responsive to fragmentation, I compared the absolute effect size to the Euclidean distance from origin in the PCoA with linear regression (Zar 1999). Finally, because each lizard's response to fragmentation may depend on the observed

landscape pattern of fragmentation, I conducted a linear regression on the log-transformed site abundance of each species to the landscape metrics to explain the specific landscape features impacting each species. Because these were independent tests a Bonferroni correction was not required.

Results

Uta stansburiana occurred at all sites, grids, and in all but three of the trapping locations. They were followed in occurrence by *Aspidoscelis marmorata*, *S. arenicolus*, *A. sexlineata*, *S. consobrinus*, *Holbrookia maculata*, *Phrynosoma cornutum*, and *Plestiodon obsoletus* (Table 7). Because *P. obsoletus* only occurred at three trapping locations, they were excluded from further analysis. *Sceloporus arenicolus* was the second most common capture per site, but occurred in fewer traps than the third most common lizard, *A. marmorata*. Contingency analysis of land cover type, dominant vegetation, slope, and soil compaction demonstrated that the lizard community used each of these variables in a non-random way (Table 8). Lizard community usage of aspect did not differ from random (Table 8). Sub-dividing the contingency tables demonstrated that all species, with the exception of *U. stansburiana* and *P. cornutum*, selected for land cover type. Specifically, *S. arenicolus* preferred blowouts over matrix whereas *S. consobrinus* demonstrated the opposite pattern (Fig. 9a). None of the other lizard species in this community demonstrated a preference for land cover type. Only *S.*

Table 7. Total occurrence, frequency, and average captures per site for each species of lizard captured in traps ($n = 810$) in the Mescalero-Monahans shinnery sands, New Mexico.

Species	Occurrence	Frequency	Average per site
<i>Aspidoscelis marmorata</i>	361	44.6%	89.8
<i>Aspidoscelis sexlineata</i>	162	20.0%	22.2
<i>Holbrookia maculata</i>	130	16.0%	23.0
<i>Phrynosoma cornutum</i>	30	3.7%	3.8
<i>Plestiodon obsoletus</i>	3	0.4%	0.4
<i>Sceloporus arenicolus</i>	223	27.5%	112.9
<i>Sceloporus consobrinus</i>	145	17.9%	21.2
<i>Uta stansburiana</i>	807	99.6%	974.9

Table 8. Results of contingency analyses for lizard community use of land cover type, dominant vegetation, aspect, slope, and soil compaction in the Mescalero-Monahans shinnery sands, New Mexico.

Environmental variable	χ^2	DF	<i>P</i>
Land cover type	155.6	12	<0.001
Dominant vegetation	50.5	30	0.01
Aspect	21.7	18	0.25
Slope	50.7	12	<0.001
Soil compaction	65.0	12	<0.001

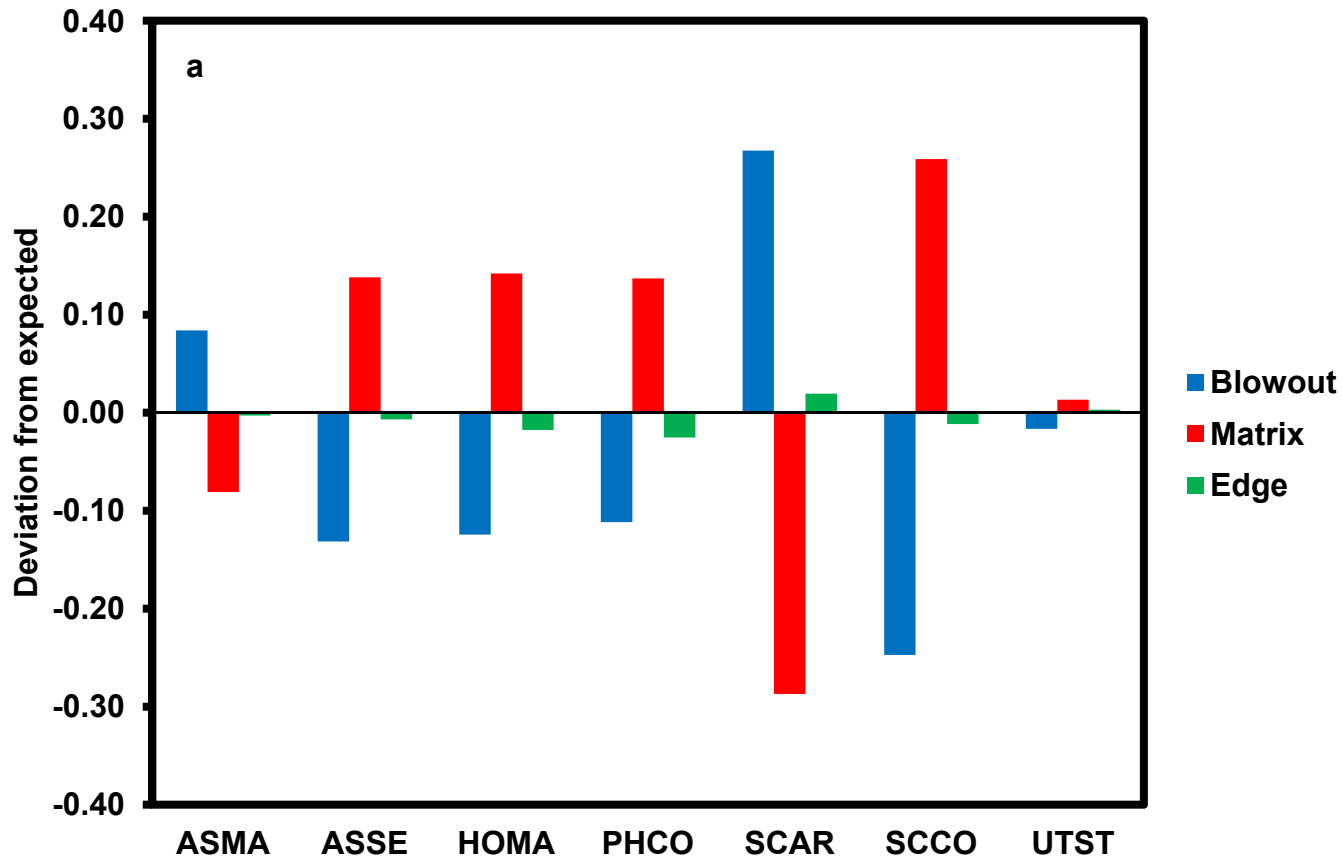
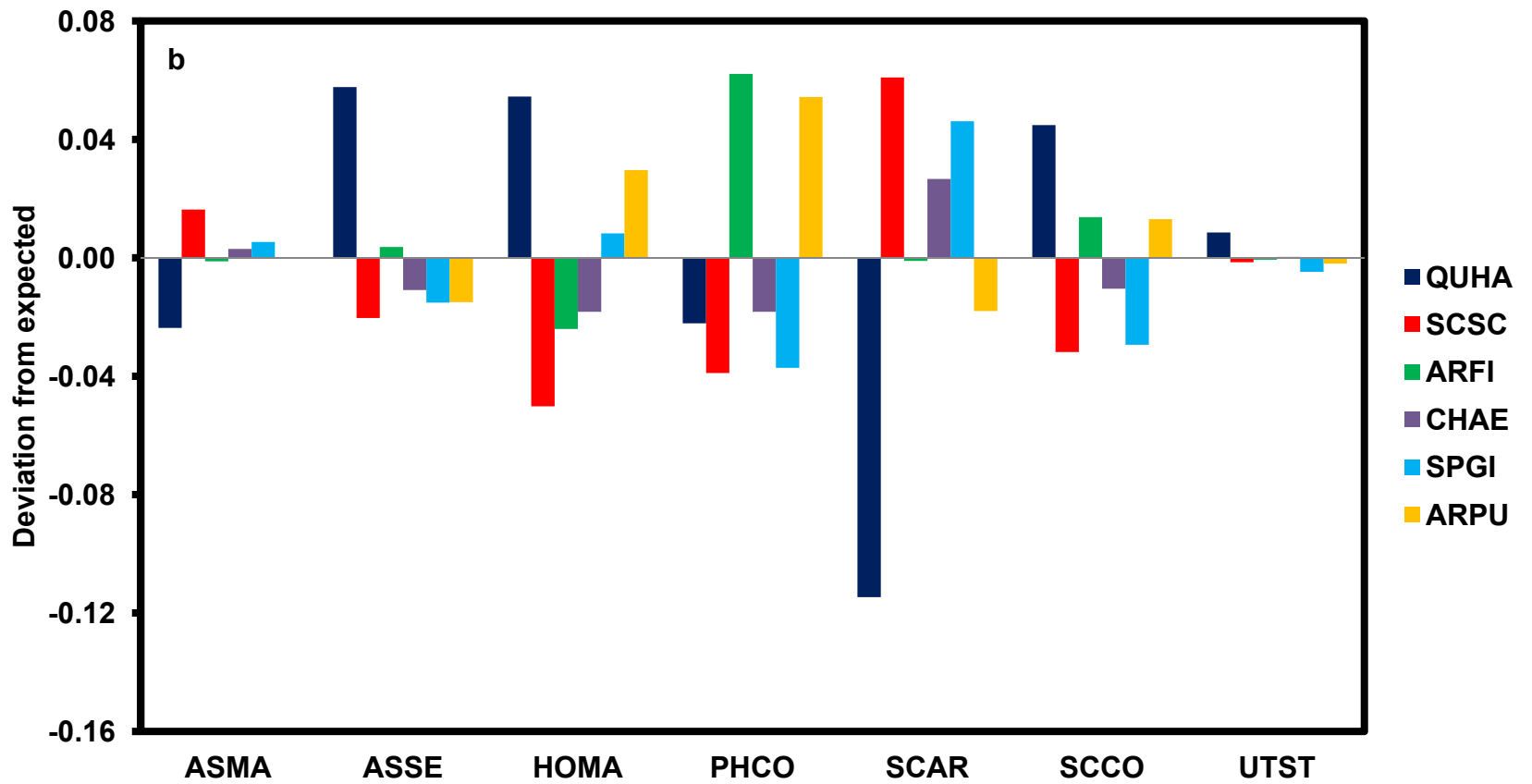


Figure 9. Proportional deviation from expected for each species of lizards' use of environmental variables calculated at each trapping location. Positive deviations beyond 0.00 suggest use and negative deviations suggest avoidance of a) land cover type, b) dominant vegetation, c) aspect, d) slope, and c) soil compaction in the Mescalero-Monahans shinnery sands, New Mexico. Species are ASMA: *Aspidoscelis marmorata*, ASSE: *Aspidoscelis sexlineata*, HOMA: *Holbrookia maculata*, PHCO: *Phrynosoma cornutum*, SCAR: *Sceloporus arenicolus*, SCCO: *Sceloporus consobrinus*, UTST: *Uta stansburiana*.



* Plant abbreviations: QUHA: *Quercus havardii*, SCSC: *Schizachyrium scoparium*, ARFI: *Artemisia filifolia*, CHAE: *Chamaesyce* sp., SPGI: *Sporobolus giganteus*, ARPU: *Aristida purpurea*.
Figure 9. Continued.

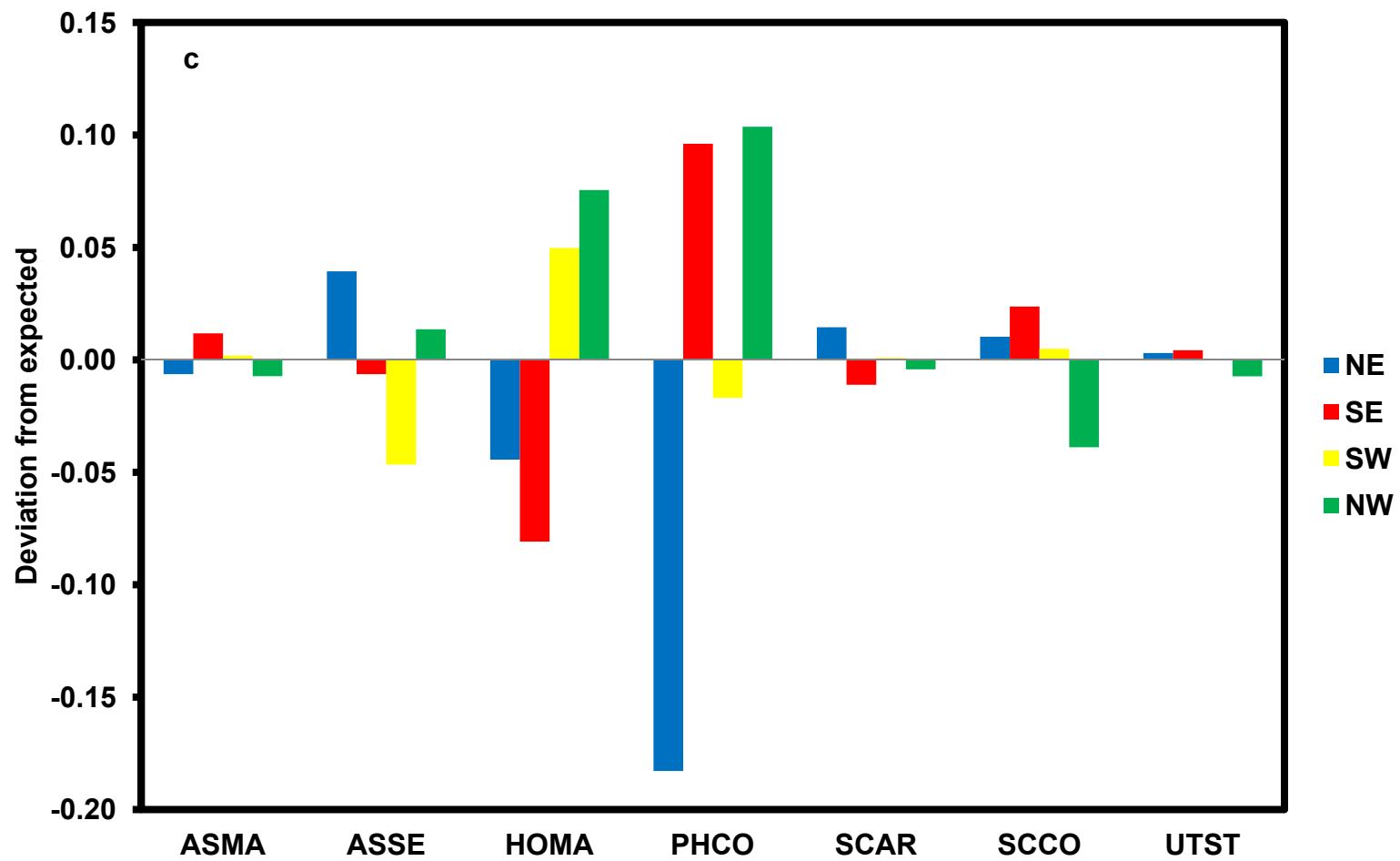


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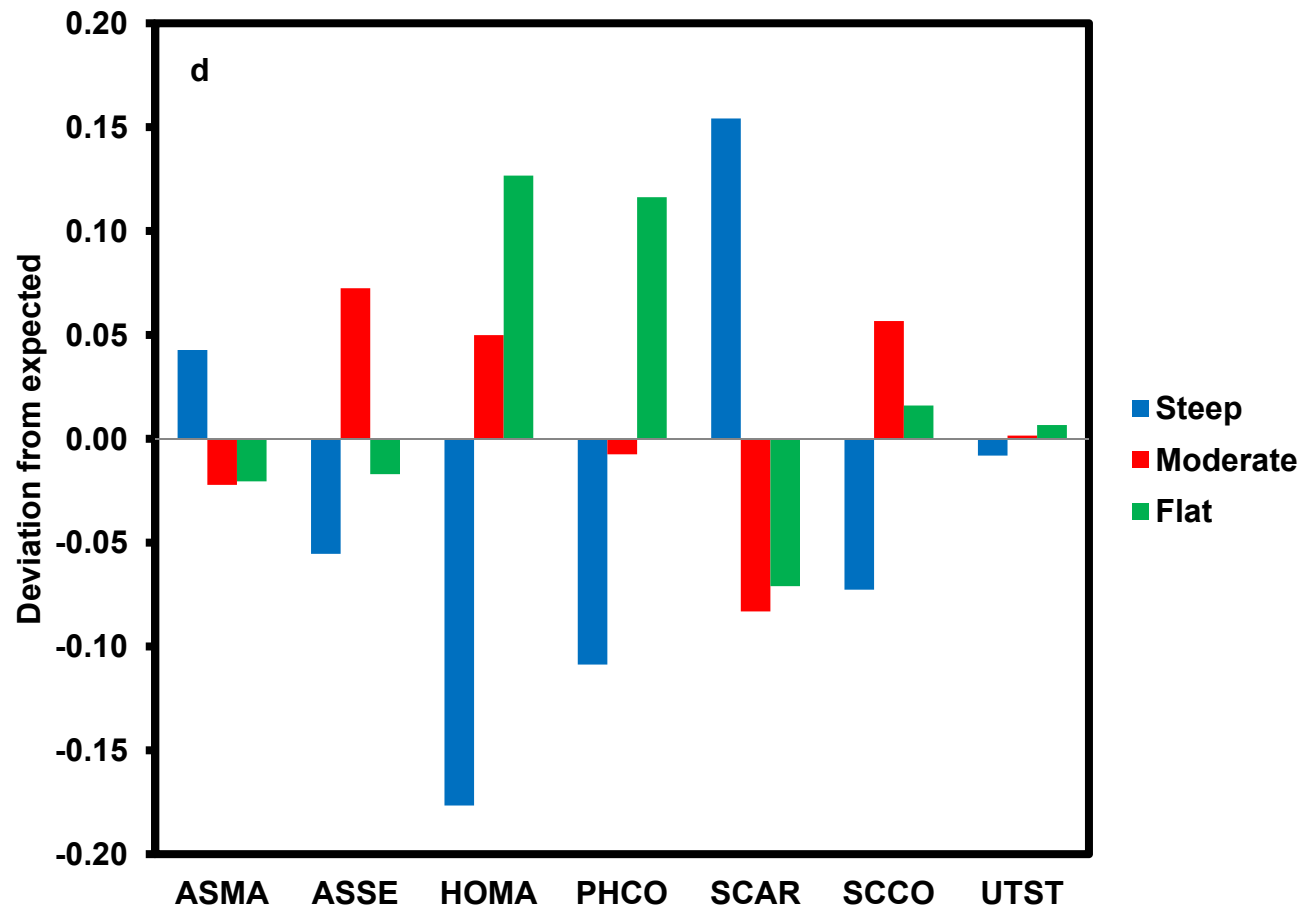


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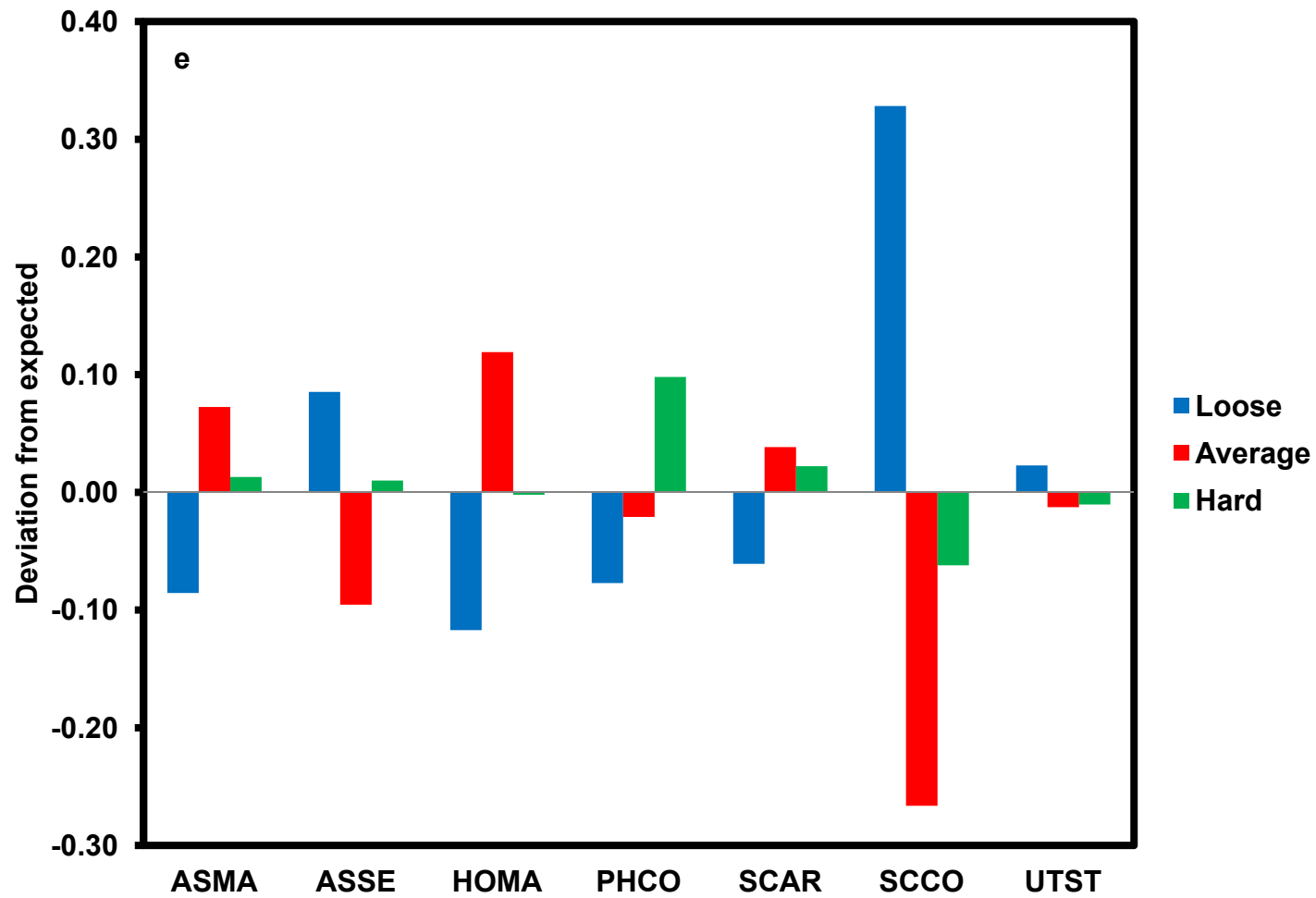


Figure 9. Continued.

arenicolus demonstrated a strong preference for dominant vegetation which was consistent with plants that grow in abundance in blowout habitats (*Schizachyrium scoparium* and *Sporobolus giganteus*; Fig 9b) and an avoidance of *Quercus havardii* which is consistent with their preferences in land cover type. While the contingency table suggested that there was no significant pattern in use of aspect for the lizards, *P. cornutum* demonstrated an aversion to northeastern facing slopes (Fig. 9c). Both *S. arenicolus* and *H. maculata* demonstrated a strong preference for slope (Fig 9d). However each species lay on different ends of that spectrum with *S. arenicolus* preferring steep slopes and *H. maculata* preferring flat slopes (Fig. 9d). Both *S. consobrinus* and *A. sexlineata* preferred loose soils whereas *A. marmorata*, *H. maculata*, *P. cornutum*, and *S. arenicolus* used harder soils (Fig 9e). Logistic regression models demonstrated that *A. marmorata*, *H. maculata*, and *S. arenicolus* presence or absence was associated with slope and soil compaction (Table 9). These analyses were congruent with the contingency analysis. In particular, *A. marmorata* preferred hard soils and steep slopes, *H. maculata* preferred hard soils and flat slopes, and *S. arenicolus* preferred hard soils and steep slopes (Fig 9d; 9e; Table 9). Additionally, *P. cornutum* presence/absence was associated with hard soils (Fig 9e; Table 9). Finally, *S. consobrinus* was more likely to occur where soils were flatter than steep (Fig 9d; Table 9). The first two axes of the PCoA on lizard habitat preference accounted for 79% of the variance in lizard habitat dissimilarities (Fig. 10). The first axis (56% of the total variation) separated *S. arenicolus* from *H. maculata*, *P. cornutum*, and *S. consobrinus*

Table 9. Multiple logistic regression models for species presence at traps in the Mescalero-Monahans shinnery sands, New Mexico.

Species	Term	Coefficient	SE	<i>p</i> -value
<i>Aspidoscelis marmorata</i>	(Intercept)	-1.20	0.16	< 0.001
	Slope	0.04	<0.01	< 0.001
	Soil compaction	0.18	0.03	< 0.001
<i>Aspidoscelis sexlineata</i>	(Intercept)	-1.25	0.12	< 0.001
	Soil compaction	-0.05	0.03	0.10
<i>Holbrookia maculata</i>	(Intercept)	-1.64	0.32	< 0.001
	Slope	-0.05	0.01	< 0.001
	Soil compaction	0.13	0.03	< 0.001
<i>Phrynosoma cornutum</i>	(Intercept)	-3.04	0.29	< 0.001
	Soil compaction	0.10	0.05	0.03
<i>Sceloporus arenicolus</i>	(Intercept)	-2.26	0.20	< 0.001
	Slope	0.08	0.01	< 0.001
	Soil compaction	0.19	0.03	< 0.001
<i>Sceloporus consobrinus</i>	(Intercept)	-0.80	0.16	< 0.001
	Slope	-0.04	0.01	< 0.001
<i>Uta stansburiana</i>	(Intercept)	11.18	4.67	< 0.001
	Aspect	-0.02	0.1	0.14

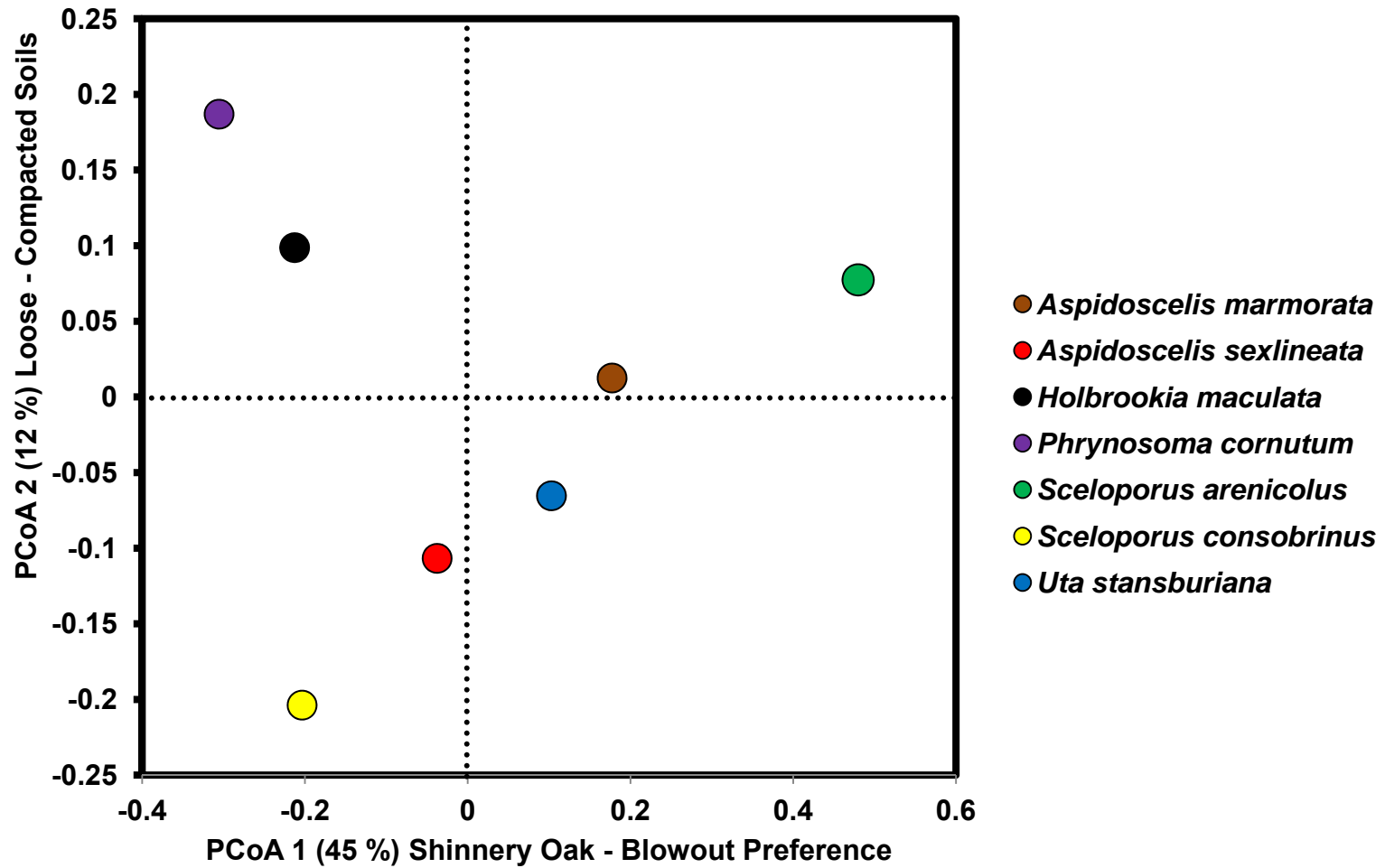


Figure 10. Principal coordinates ordination of lizard habitat use in the Mescalero-Monahans shinnery sands, New Mexico.

due to differences in preferred cover type, dominant vegetation, and slope. The second axis (23% of the total variance) separated *S. consobrinus* and *A. sexlineata* from *P. cornutum* and *H. maculata* due to differences in preferences for soil compaction. Euclidean distance from the origin (calculated for 6 axes of variation accounting for > 99.8% of the variation) on PCoA axes demonstrates that *S. arenicolus*, *P. cornutum*, and *H. maculata* had the most restricted habitat preferences of the lizard species in this community (Table 10). Likewise, species absolute effect size to fragmentation was highest for *S. arenicolus*, followed by *P. cornutum*, and *H. maculata* (Table 10). Regression of species-specific absolute effect size to fragmentation and the Euclidean distance from origin for each species in the PCoA demonstrated a strong interaction (Fig. 11; $R^2 = 0.75$, $P = 0.01$). Using the 0.8 effect size criteria of Cohen (1988) for large effect *S. arenicolus*, *P. cornutum*, and *H. maculata* were identified as demonstrating a large effect of fragmentation and being very specific with regard to habitat use (Fig. 11).

Sceloporus arenicolus had the largest absolute effect size of all the lizards in this study. Linear regression of *S. arenicolus* abundance to landscape variables demonstrated a positive association with each of them, but the strongest relationship existed where high abundances of *S. arenicolus* occurred at sites with large patches (LPI; Table 11). *Phrynosoma cornutum* had the second highest absolute effect size of the lizards in this study however their response to fragmentation was positive rather than negative and there were no distinct positive or negative relationship to landscape variability.

Table 10. Euclidean distance from origin in a PCoA for lizard habitat affinities and absolute species specific effect size to fragmentation in the Mescalero-Monahans shinnery sands, New Mexico.

Species	Euclidean distance from origin	Absolute species specific effect size
<i>Aspidoscelis marmorata</i>	0.18	0.04
<i>Aspidoscelis sexlineata</i>	0.13	0.51
<i>Holbrookia maculata</i>	0.25	0.85
<i>Phrynosoma cornutum</i>	0.37	1.15
<i>Sceloporus arenicolus</i>	0.49	1.44
<i>Sceloporus consobrinus</i>	0.29	0.55
<i>Uta stansburiana</i>	0.13	0.37

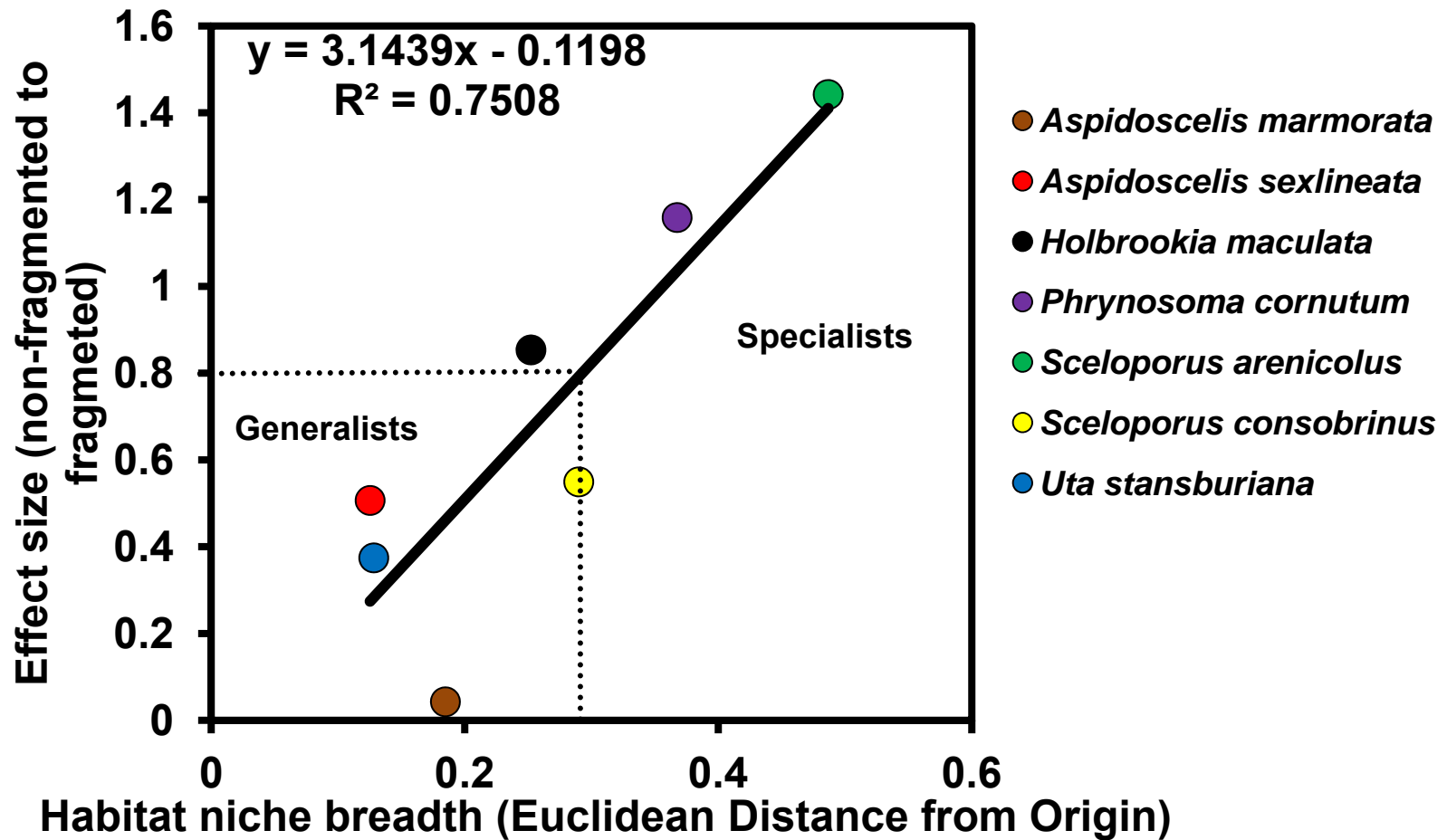


Figure 11. Effect size of fragmentation plotted against habitat niche breadth for lizard species in the Mescalero-Monahans shinnery sands, New Mexico. Dashed line represents 0.8 effect size and the corresponding niche breadth for habitat.

Table 11. Association between log-transformed abundances of lizards and landscape metrics per site (R^2 value; P value) in the Mescalero-Monahans shinnery sands, New Mexico.

Species	PD		LPI		TE		LSI	
	R^2	P	R^2	P	R^2	P	R^2	P
<i>Aspidoscelis marmorata</i>	0.01	0.86	0.01	0.97	0.20	0.23	0.16	0.29
<i>Aspidoscelis sexlineata</i>	0.01	0.87	0.03	0.64	0.19	0.25	0.18	0.26
<i>Holbrookia maculata</i>	0.63	0.01	0.63	0.01	0.67	<0.01	0.69	<0.01
<i>Phrynosoma cornutum</i>	0.01	0.77	0.03	0.68	0.01	0.76	0.01	0.78
<i>Sceloporus arenicolus</i>	0.60	0.01	0.65	<0.01	0.44	0.05	0.49	0.04
<i>Sceloporus consobrinus</i>	0.02	0.75	0.02	0.72	0.38	0.07	0.37	0.10
<i>Uta stansburiana</i>	0.08	0.47	0.10	0.40	0.02	0.69	0.01	0.84

Holbrookia maculata demonstrated the third highest absolute effect size and their relative abundance was lower at sites with more edge (TE, LSI; Table 11).

Discussion

As predicted, lizard species' used habitats differently. My analysis indicates that species with more specific habitat use patterns respond to landscape fragmentation more than generalized species. In accordance with similar theoretical and empirical studies (Smith et al. 1996, Andren et al. 1997, Henle et al. 2004, Ewers and Didham 2006), these analyses indicate that species with the narrowest habitat utilization patterns were affected by fragmentation the most and those with more generalist habitat use demonstrated little to no response. Because the three species that demonstrated a large effect to fragmentation did so in unique ways my analysis fits with predictions of the continuum and integration models regarding interdependence of species responses. Response to fragmentation was highlighted by two species showing marked declines and one species occurring in higher abundance in fragmented landscapes.

Differential response to landscape fragmentation by species is not an uncommon trend (Fischer et al. 2005, Rizkalla and Swihart 2006, Swihart et al. 2006, Klingbeil and Willig 2009, Kennedy et al. 2010, Pelegrin and Bucher 2012). A common driver of response to fragmentation is resource availability. However, the resources essential to maintaining stable populations should be different for each species. In Australian eucalypt forests fragmented by plantation, lizards with different resource needs responded to fragmentation individually (Fischer et al. 2005). Turtle assemblages

fragmented by agriculture in the Midwestern United States demonstrated differential responses, resulting in random community structure for the eight species occurring there (Rizkalla and Swihart 2006). In desertified regions of North Sinai, Egypt, lizards that specialized on dune systems increased in numbers when habitat was degraded by grazing and vegetation removal (Attum et al. 2006). Attum et al. (2006) hypothesized that in extreme environments specialists and generalists responses would be opposite to that of more productive environments. In the case presented here, two species decreased in areas affected by oil and gas development while one species increased. As such, species-specific response has more to do with what constitutes a productive environment for the individual species rather than the productivity of the environment as a whole as in my example. Swihart et al. (2006) evaluated this issue for rodents, bats, turtles, and amphibians and found that niche breadth and proximity to range boundary were the largest indicators of occupancy for vertebrates across the Wabash basin in Indiana, USA. For *H. maculata* and *S. arenicolus*, both niche breadth and proximity to range boundary could limit their ability to persist in increasingly fragmented habitats.

For *S. arenicolus*, proximity to range-boundary is most likely a result of narrow niche breadth. Here, I have shown that this species is narrowly focused on a particular habitat type, and it is well established that they are endemic to a small portion of a small ecosystem (Fitzgerald and Painter 2009, Laurencio and Fitzgerald 2010). Therefore, throughout their range they are comparatively close to their range boundary. Any alteration to their preferred habitat is likely to leave populations isolated, which could lead to localized extinction. Results of the regression analysis showed an interaction

between high capture rates and the LPI, suggesting that this species exists in higher numbers in large unspoiled tracts of habitat. Similarly, in a study on the population dynamics of *S. arenicolus*, Ryberg et al. (*in review*) explain that populations of this species are structured at small scales, or “neighborhoods”, and these scale up to influence metapopulation dynamics. Further, Smolensky and Fitzgerald (2011) showed that quantity and quality of shinnery dune habitat were positively correlated. Together these examples suggest that large tracts of habitat will result in high quality habitat for *S. arenicolus*, with greater potential for healthy metapopulations resilient to demographic stochasticity.

Holbrookia maculata occur over a vastly larger range than *S. arenicolus*; however, the MMSS is positioned near the southern boundary of their range (Rosenblum et al. 2009). This species demonstrated preference for flatter habitats in the shinnery oak matrix (Fig. 9d; Table 9). It would seem that this is typical throughout their range, given that this preference has been demonstrated in nearby habitats in New Mexico by Gennaro (1972) and in the sandhills of Nebraska (Jones and Droge 1980). In eastern New Mexico, this species is short lived and annual population turnover is near 80% (Gennaro 1974). This species demonstrated higher captures where there was more edge habitat (Table 11). Vegetative changes such as increases of non-native or weedy grasses along edge habitats, may have altered the preferred habitat for this species, and in the MMSS roadside grasses such as *Aristida purpurea* and *Eragrostis lehmanniana*, are increasing (pers. obs.). Ballinger and Watts (1995) reported on a population of *H. maculata* from the Arapahoe Plains of Nebraska that had become nearly extinct due to

the encroachment of grasses into their preferred open habitats. This study and others have now indicated that *H. maculata* populations are in decline in some regions across their range (Taggart 2006).

Phrynosoma cornutum was found in higher abundance in fragmented areas. This was likely due the creation of flat open patches more suitable for the lizard and their prey (Whiting et al. 1993, MacMahon et al. 2000). In this study, the species appeared to avoid northeastern facing slopes (Fig. 9c). *Phrynosoma cornutum* is a dietary specialist on *Pogonomyrmex* ants (Whitford and Bryant 1979). *Pogonomyrmex* are chiefly grass seed harvesters and found in areas of where their preferred food is in high abundance including areas of high disturbance (Whiting et al. 1993, Johnson 2000, MacMahon et al. 2000). This species responds favorably to the disturbance found on and around fragmented sites. Fragmented sites have more roads and well pads and more grasses (pers. obs.) than the non-fragmented sites. Future research could evaluate whether increases in prey may be driving this phenomenon of higher capture rates for *P. cornutum* in regions fragmented by oil and gas development.

The other species in this lizard community showed little response to landscape fragmentation. These species demonstrate patterns in resource use typical of generalist species, and this may be the ultimate reason why no apparent effect from landscape fragmentation was detected for these species (Smith et al. 1996, Andren et al. 1997). None of these species seemed to be using a specific habitat type, and their ability to persist in a range of habitat types is most likely the reason for their persistence.

Trends in habitat fragmentation have been examined in temperate and tropical forests, but there is little knowledge regarding how desert lizards respond to patterns of habitat loss and isolation. Studies that consider only the patch fragmentation model are challenged in that they often ignore the importance of matrix composition in metapopulation or metacommunity dynamics (Fischer and Lindenmayer 2006, Watling et al. 2011). Here I have demonstrated that species response to fragmentation depends on the way in which fragmentation of the landscape occurs. This study is unique because it demonstrates even where landscapes are fragmented in ways that may not fit the paradigm of isolated fragments in an inhospitable matrix, similar trends in species response are observed.

CHAPTER IV

IS *SCELOPORUS ARENICOLUS* AN UMBRELLA FOR ENDEMISM AND
BIODIVERSITY OF THE MESCALERO-MONAHANS SHINNERY SANDS
ECOSYSTEM?

Overview

Umbrella species are managed or protected species that confer protection to biodiversity in the ecosystem where they occur. Flagship, indicator, umbrella, endangered, and keystone species may all provide an effective means for biodiversity protection. Assessments of the usefulness of the umbrella species approach to conservation have highlighted some of the shortcomings in our understanding of how to best apply these conventions. Of these, there has been a tendency to evaluate the effectiveness of top predators, birds, and mammals as umbrella species in forest ecosystems. Here I use data on ants, beetles, small mammals, lizards, and endemic species to test whether the dunes sagebrush lizard (*Sceloporus arenicolus*) may serve as an umbrella species for protecting endemics, and biodiversity in general, in a sand-dune ecosystem. I applied a comparative approach to examine how conservation practices at different scales may affect biodiversity and endemism in the Mescalero-Monahans shinnery sands ecosystem. The scales chosen represent the home range of an individual lizard (small-scale: 1.2 ha), a functional population (large-scale: 100 ha), and the known distribution of the lizard. Current land management in this ecosystem takes place at many scales with the smallest being near 10 ha (the equivalent size of a oil well pad). I

used data on presence, relative abundance, and reproductive success of *S. arenicolus* to gain insight towards how these parameters may suggest different levels of association with co-occurring species. To examine other potential umbrella species in this ecosystem, I investigated the co-occurrence patterns for all lizards, small mammals, ants, and beetles to calculate an umbrella index that ranks all species. Rankings for the umbrella index identify which of them confer the greatest protection for co-occurring species. Range-wide, the frequency of occurrence for endemic species was higher than at smaller scales, though no other patterns emerged because *S. arenicolus* was present at all sites and there were no relationships between relative abundances and other species. At the small-scale, beetle species richness, beetle diversity, and species richness of endemics were higher in the presence of *S. arenicolus*. In addition, ant species richness was lower in the presence of *S. arenicolus* at the small-scale. Results indicate that *S. arenicolus* would serve as an umbrella to some, but not all, of the biodiversity and endemism in this ecosystem at the small-scale and protection of biodiversity increases with scale. I recommend that future efforts towards protecting endemism and biodiversity in this ecosystem be focused at larger scales and practices that would disturb *S. arenicolus* habitat be moved outside of the Mescalero-Monahans shinnery sands ecosystem.

Introduction

Conservation efforts are trailing behind the fast paced human-induced pressures that threaten biodiversity worldwide (Vitousek et al. 1997, Sala et al. 2000).

Conservation practitioners are challenged with reducing the needs of multispecies conservation in order to maximize the protection of ecosystem services and biodiversity while also cutting costs (Wiens et al. 2008). Naturally, evaluation of current approaches to biodiversity conservation is warranted. One method of reducing the complexity of biodiversity conservation and cutting costs is through the use of surrogate species for conservation (Caro and O'Doherty 1999). Surrogate species approaches are appealing because the protection of one species should result in the protection of many (Simberloff 1998). However, a considerable amount of uncertainty exists regarding the effectiveness of surrogate species approaches (Roberge and Angelstam 2004, Branton and Richardson 2010, Caro 2010, Cushman et al. 2010).

Surrogate species approaches used to protect ecosystem services or biodiversity include: indicator species (species indicative of environmental health), keystone species (species with a disproportionately large role in their ecosystem), flagship species (species that attract the attention of the public to conservation efforts), or umbrella species (species that through the protection of their distribution or home ranges results in the protection of other co-occurring species) (Simberloff 1998, Caro 2010). The umbrella species approach to biodiversity conservation may be viewed as a potential panacea for land managers wanting to maximize biodiversity conservation while cutting costs through focusing their efforts on protecting just one species. The idea is that an umbrella species will have a broad enough pattern in resource use or spatial requirements that many other species will be protected as well (Branton and Richardson 2010). As with any surrogate species, an umbrella species should reduce the amount of

time, money, and data required for conducting inventories of multiple species or ecosystem services (Favreau et al. 2006). Many cases for the conservation of a single species have cited the benefits of the umbrella species approach as a justification. For instance, Lammertink et al. (2009) assessed the current extent of population decline for great slaty woodpecker (*Mulleripicus pulverulentus*) and determined that their loss coincided with the loss of old-growth forest in Southeast Asia. As such, they suggest that protecting this species will provide umbrella protection for the biodiversity found in the old growth forests of Southeast Asia. However, the central question in any of these cases is which species make for good umbrellas and under what circumstances?

Recent reviews of the umbrella species approach to conservation have identified where bias exists in the literature. For instance, most analyses were biased towards mammal or bird umbrella species in forest ecosystems (Branton and Richardson 2010, Caro 2010). The bias towards ecological research in forest ecosystems appears to be part of a much larger trend in the fields of ecology and conservation biology research (Martin et al. 2012). An additional source of bias is that most umbrella species are upper level consumers and/or predators (Branton and Richardson 2010). There is a dearth of cases where middle or lower trophic level species, which are not a bird or mammal, are evaluated as umbrella species in ecosystems other than forests.

Selecting effective umbrella species *a priori* is challenging, and a variety of criteria to identify them have been proposed (Seddon and Leech 2008). However, in the practice of conservation, umbrella species are not typically chosen *a priori*. Species that fall under protection are default candidates to be umbrella species. Species that are not

protected cannot be umbrella species until they are designated as protected, and there are no cases of bestowing protected status to a species because of its potential as an umbrella species. Still, it is a useful endeavor to evaluate which species, if protected, would be the best umbrellas. A few factors are considered important traits in identifying potential umbrella species. Large home-range size, large body size, ecological specialization, co-occurrence with other species of concern, negative response to disturbance, ease in sampling, and a well-known natural history are the most common traits used in defining effective umbrella species (Seddon and Leech 2008, Branton and Richardson 2010). These characteristics are relevant in most circumstances. However, their importance may vary on a case-by-case basis due to factors such as: the scale of conservation, the ecosystem studied, or the taxonomic group of interest. Scale is especially important in regards to selection criteria such as home range size, co-occurrence with other species, and ease in sampling. For instance, early recommendations for umbrella species suggested that animals with large home ranges would serve as the best umbrellas for protection (Wilcox 1984).

To illustrate further this issue of choosing the appropriate scale, consider the following two cases where the umbrella species approach has been applied. Dunk et al. (2006) evaluated effectiveness of reserves established for northern spotted owls (*Strix occidentalis caurina*) to examine its effectiveness as an umbrella species for amphibian and mollusk diversity at the level of the Klamath Bioregion (2.2 million ha.). In this large region, randomly sampled co-occurring mollusk and amphibian diversity accounted for 83% and 91%, respectively, of the known species occurring in the reserves

(Dunk et al. 2006). In a second example, Launer and Murphy (1994) assessed the serpentine grasslands surrounding San Jose and Morgan Hill, California (30,000 ha.) to evaluate the effectiveness of the bay checkerspot butterfly (*Euphydryas editha bayensis*) as an umbrella species for native plants. They determined that 98% of the spring flowering plants would receive protection under the umbrella of the bay checkerspot butterfly. In both circumstances the species evaluated were determined to be effective umbrella species due to their co-occurrence with other species of conservation value. However, the differences in taxonomic groups, trophic levels assessed, and scale of assessment between these studies exemplify part of the confusion in determining what the preferred characteristics of an umbrella species should be. Therefore, it would be more effective to determine the scale of conservation focus prior to evaluating the effectiveness of an umbrella species rather than focusing on a species trophic position or taxonomy.

Additionally, assessment of any potential umbrella species may depend on the functional relatedness between the taxonomic groups being evaluated. For instance, Suter et al. (2002) evaluated the use of the grouse, Capercaillie (*Tetrao urogallus*) as an umbrella for conserving bird species in the Swiss Prealps. They found that Capercaillie were not an ideal umbrella because their habitat requirements were not broad enough to account for the habitat requirements of the bird communities of that region. Following a different approach, Hurme et al. (2008) evaluated the Siberian flying squirrel (*Pteromys volans*) in boreal forests of Finland as an umbrella species for biodiversity that was functionally tied to the same resources. The squirrel served as an effective umbrella

species for wood dependent species, and its presence may be indicative of habitat for a variety of species dependent on dead and live wood in these forests. Ideally an effective umbrella species should result in the protection of more than just the most functionally related species (Branton and Richardson 2010). For conservation practitioners to maximize the conservation value of protecting a single species, they should achieve higher levels of biodiversity protection than expected by virtue of functionality alone.

The dunes sagebrush lizard (*Sceloporus arenicolus*) is a psammophilic habitat specialist that occurs in the Mescalero-Monahans shinnery sands (MMSS) of southeastern New Mexico and west Texas (Degenhardt et al. 1996, Fitzgerald et al. 1997, Fitzgerald and Painter 2009). Within the ecosystem, *S. arenicolus* occupies only interconnected sand dune blowouts in parabolic dune formations and the fringes of active transverse dunes. *Sceloporus arenicolus* fits many of the general criteria of an umbrella species because it has a fairly well known natural history and ecology (Degenhardt et al. 1996, Fitzgerald and Painter 2009), it co-occurs with many other endemic species (Leavitt 2012), it demonstrates a response to disturbance, and it is easy to sample (Chapters II and III). Conservation measures for the species have been put into place throughout the range of the species (Federal Register June 19, 2012). It was proposed as an endangered species by the United States Fish and Wildlife Service primarily due to habitat loss and land conversion associated with oil and gas development and herbicide spraying (Federal Register December 14, 2010), and conservation measures were strengthened in order to avoid listing (Federal Register June 19, 2012). *Sceloporus arenicolus* is one of approximately 17 endemic species in the

MMSS (Hebard 1936, Tinkham 1961, O'Brien 1977, Tinkham 1979, Hovore 1981, Paulsen and Smith 2005, Fitzgerald and Painter 2009). The other sixteen endemics are arthropods associated with plants that are specialized on the sand dune blowouts or on shinnery oak (*Quercus havardii*). Endemic species are a global conservation priority due to typically small distributions and the threat of extinction (Lamoreux et al. 2006). Because *S. arenicolus* occurs in the same ecosystem as other endemic species and because they too are a species of concern in the region it has been suggested that protection for *S. arenicolus* would provide protection for the other species of importance in the ecosystem (Bailey and Painter 1994).

Most assessments of umbrella species status examine patterns of co-occurrence that employ presence-absence approaches. This level of generality may not be preferred in cases where an indication of habitat quality is sought. However, Van Horne (1983) suggests that habitat quality can be inferred with relative abundance with support from demographic data such as productivity. If associations exist between *S. arenicolus* and co-occurring species in locations that are productive for *S. arenicolus* then this would be suggestive of shared habitat preferences. The conservation value of any species proposed to function as a conservation surrogate or umbrella species should be evaluated rather than assumed (Cushman et al. 2010). Here, I evaluate the extent to which *S. arenicolus* may serve as an umbrella species for other lizards, beetles, ants, small mammals, and endemic species of the MMSS of New Mexico. The focal groups all maintain different functional roles in the MMSS ecosystem. Comparison among dissimilar functional groups provides insight to the effectiveness *S. arenicolus* as an

umbrella species. That is, if protection of *S. arenicolus* results in protection for functionally diverse species then it would be well suited as an umbrella species.

The Bureau of Land Management (BLM) is the largest land owner in the MMSS of New Mexico. Multiple land use practices are supported on BLM lands in the MMSS, including oil and gas extraction, cattle ranching, and off highway vehicle use. The ecosystem exists above the Permian Basin oil fields and oil and gas extraction is, by far, the most common land use. Current conservation efforts in the MMSS are focused on *S. arenicolus* and the lesser prairie chicken (*Typanuchus palidicinctus*) in New Mexico (U S Fish and Wildlife Service, 2008a, b) and only *S. arenicolus* in Texas (U S Fish and Wildlife Service, 2011). Practices put into place by the BLM in New Mexico to manage oil and gas extraction and *S. arenicolus* habitat conservation occur at a variety of scales ranging from the size of oil well pads (10 ha.) to the entire range of a species (U S Fish and Wildlife Service, 2008a, b). Because the BLM occasionally makes decisions at small-scales, the landscape is fragmented over time by the selective placement of multiple individual oil wells (Fig. 12). It is possible that this could continue if conservation management in this region is limited to a series of small-scale independent decisions. This issue is common to agencies that focus on multiple use management (Grumbine 1994). Here, I evaluate data from three spatial scales where the smallest scale relates to an approximation of the home range for an individual *S. arenicolus* and the smallest scale of land management (1.2 ha.), the medium scale analyzed is 100 ha, and at the scale of the entire known range for *S. arenicolus*. The extent of the known range in this case encompasses all potential habitat for *S. arenicolus* that lies within the

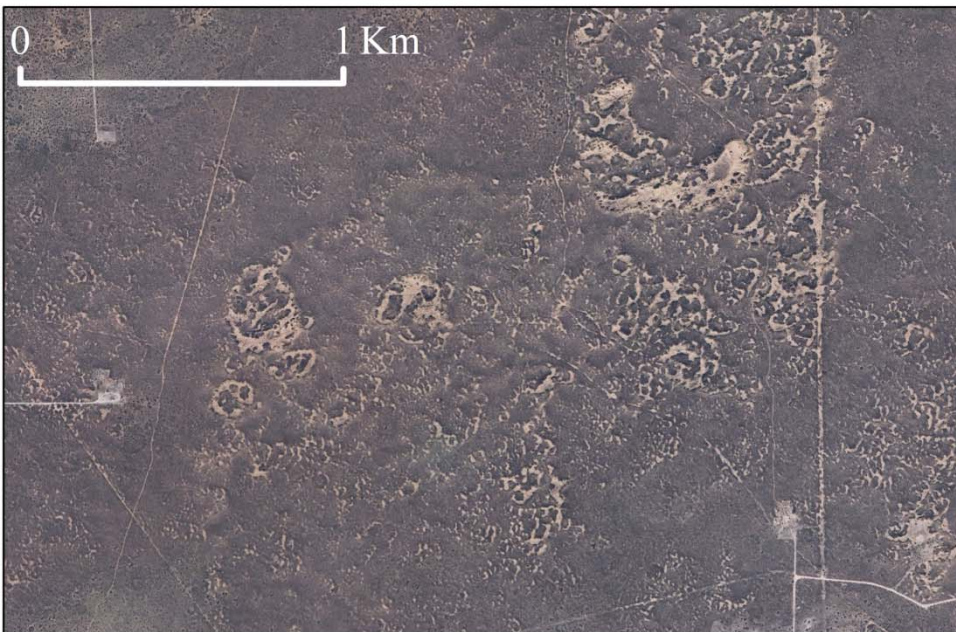


Figure 12. Satellite image of the Mescalero-Monahans shinnery sands, New Mexico. Above is a region fragmented by oil and gas development. In the upper image white squares and lines are well pads and roads used for oil and gas extraction. The landscape pictured below is not fragmented.

species' range boundary. Assessment of multiple scales is important because the future of protection for *S. arenicolus* is uncertain and the scale at which conservation occurs will affect land use, and hence patterns of biodiversity throughout the ecosystem.

This assessment is unique in that it evaluates the use of a reptile as an umbrella species in a desert ecosystem. It is additionally unique, because it is conducted at three spatial scales and evaluates multiple types of biodiversity that are functionally related to *S. arenicolus* in unique ways. I ask if sites where *S. arenicolus* are present hold higher richness for other endemic species, beetles, ants, small mammals, and lizards than sites where they are not. If so, which species or taxonomic groups tend to co-occur with *S. arenicolus* and at what scale? Because presence does not necessarily reflect long-term persistence of populations at a location, I ask these same questions where *S. arenicolus* maintained reproductive populations over three years as compared with sites where they did not. I continue this approach by comparing relative abundances for *S. arenicolus* with species richness for other endemic species, beetles, ants, small mammals, and lizards. If any clear trend emerges it would suggest that these locations were especially good for other biodiversity and it could indicate a functional link with *S. arenicolus*.

Methods

Study area— This study was conducted in Eddy and Lea Counties, New Mexico, USA in the MMSS ecosystem. The study area is bordered to the east by the caprock escarpment and the southern High Plains and to the west by the plains leading out of the Pecos river valley and the Chihuahuan desert. The vegetation of the MMSS is

dominated by shinnery oak (*Quercus havardii*). The study area contains large expanses of intact shinnery oak dunes and recent development by oil and gas extraction is prevalent throughout the MMSS (Fig. 12). Within the MMSS, *S. arenicolus* occupies nearly 20.5% of the area of the ecosystem (MMSS: 1,280,074 ha; *S. arenicolus*: 262,077 ha). The geographic distribution of *S. arenicolus* in New Mexico is estimated to be 223,158 ha (Laurencio and Fitzgerald 2010) and 38,919 ha in Texas (Fitzgerald et al. 2011, Federal Register June 19, 2012). Nine study sites 100 ha in size were selected based on the historic presence of *S. arenicolus* as determined from voucher specimens from the Museum of Southwestern Biology at the University of New Mexico (MSB) accessed online 19 November, 2008 at HerpNet (<http://www.herpnet.org>). Within each of the nine sites were three randomly selected trapping grids where I sampled biodiversity (Fig. 4,5).

Lizard presence— I sampled three lizard trapping grids nested within each of the nine sites between April-September of 2009, 2010, and 2011. At each of the 27 grids, lizards were trapped in a 5 by 6 grid of 30 pit traps (20 l plastic buckets), making a total of 810 traps. Traps were spaced 20 m apart; thus, each trapping grid sampled an area of 1.2 ha. Sampling periods consisted of 4 trap-days and each site was sampled three times in 2009 and six times each in 2010 and 2011. In total, lizards were sampled at each grid for 1,800 trap-days, for a grand total of 48,600 trap-days. When captured each lizard was identified to species and released at the site of capture.

Beetle and ant presence— At each lizard trapping grid, three randomly assigned traps were dedicated as sampling sites for beetles and ants. During each lizard sampling

period between April 2009 and April 2011, all beetles and ants were collected out of the pit traps to determine relative abundances and species presence. In total, beetles and ants were sampled for 810 trap-days. All beetles and ants were identified to the lowest level possible (at least to taxonomic order and often to species) and tallied per trap, grid, and site.

Small mammal presence— Small mammals were sampled for four consecutive nights on each trapping grid once in both 2010 and 2011. I sampled the middle 4 rows of each lizard trapping grid using Sherman live traps (H. B. Sherman Traps, Tallahassee, Florida; 23 x 9 x 7.5 cm) placed within 1 m of each pit trap location. Two hours before sunset, I baited traps with rolled oats and checked them at sunrise the following morning. All animals were identified to species (Schmidly 2004) and released. In total, small mammals were sampled for 4,320 trap/nights.

Statistical analysis— I calculated species diversity for each taxonomic or functional group (endemic species, beetles, ants, small mammals, and lizards). I used the Δ_1 measure (Hurlbert 1971) for my diversity metric due to its performance when sample sizes are small and uneven (Olszewski 2004). This measure is calculated as

$$\Delta_1 = (N/(N - 1))(1 - \sum(N_i/N)^2)$$

where N is the total number of individuals in the sample and N_i equals the number of individuals for species i . Values for Δ_1 range from 0 to 1 with values near 1 being the most even and values near 0 being dominated by a single species. To compare mean diversity and richness parameters, I conducted non-parametric Mann-Whitney U tests because variances were not homogeneous. I conducted separate tests between grids and

sites where *S. arenicolus* were present or not and also for grids and sites where *S. arenicolus* maintained reproductive populations. These locations were identified as any location where hatchlings (< 26 mm SVL) were captured in each of the three summer seasons. To compare relationships between relative abundances of *S. arenicolus* and species richness and diversity parameters, I conducted Spearman's rank correlations (Zar 1999). Any parameter means that were significantly higher in the presence of *S. arenicolus*, their reproductive populations, or locations with high abundance would be suggestive of their use as an effective umbrella species. To rank all species in this community as potential umbrella species, I used the cross-taxonomic umbrella index (UI) as modified by Berglund (2004). This index takes into account co-occurrence with other species in the community (PCS) and the species median rarity (R). For each species *j* mean percentage of co-occurring species is calculated:

$$PCS = \sum_{i=1}^1 \left[\frac{(S_i - l)}{(S_{max} - l)} \right] / N_j$$

where *l* is the number of locations (grids or sites) in the data set, *S_i* is the number of species present at location *i*, *S_{max}* is the total number of species present at all locations in the data set, and *N_j* is the number of locations at which species *j* occurs. Species median rarity is calculated as:

$$R = l - 2 * |(N_j/l) - 0.5|$$

and the umbrella index is calculated by adding PCS and R. Grid level data were aggregated to a site for site level analysis. To assess the effectiveness of *S. arenicolus* as an umbrella species in the MMSS, I aggregated data on co-occurrence and diversity at

all 9 sites. This allows a conservative estimate of biodiversity that co-occurs with *S. arenicolus* in the 262,077 ha distribution where it is known to occur. All statistical analyses were conducted in program R (R Development Core Team 2011).

Results

Sceloporus arenicolus was present at all nine sites and at 23 of the 27 grids. Because *S. arenicolus* occurred at all sites, aggregation of site-level data provides a conservative estimate of the species and diversity that co-occurs with *S. arenicolus* across its entire range. At the scale of its known distribution, *S. arenicolus* serves as an umbrella for this biodiversity in the 262,077 ha that comprise its potential and occupied habitat. I detected 7 species of lizards other than *S. arenicolus*, 8 species of small mammals, 39 species of beetles, and 22 species of ants in this study. This species list represents a low estimate for the number of species from each of these groups that co-occur with *S. arenicolus* range-wide. At the grid scale, *S. arenicolus* co-occurred with all seven species of lizards, all eight species of small mammals, 38 of 39 species of beetles, and 21 of 22 species of ants. Populations of *S. arenicolus* that were reproductive each of the three years were detected range-wide at 5 of the 9 sites and 8 of the 27 grids. Eight species, representing two taxonomic orders of endemic arthropod were captured in the study area (Table 12). Each of the endemic species was encountered at a greater frequency at the site scale than at the grid scale (Table 12). An additional nine endemic species are known to occur in this ecosystem however they were not recorded by this study (Table 1). *Ammobaenetes mescalero* and *Stenopelmatus mescaleroensis* were the

Table 12. Endemic species recorded in this study and frequency of occurrence at both grid and site scale in the Mescalero-Monahans shinnery sands, New Mexico.

<i>Order</i>	<i>Genus</i>	<i>Species</i>	Frequency of occurrence	
			Grid	Site
Coleoptera	<i>Cicindella</i>	<i>formosa rutilovirescens</i>	3.7	11.1
Coleoptera	<i>Epitragosoma</i>	<i>arenaria</i>	37.0	88.8
Coleoptera	<i>Eupompha</i>	<i>viridis</i>	7.4	22.2
Coleoptera	<i>Graphops</i>	<i>comosa</i>	11.1	33.3
Coleoptera	<i>Prionus</i>	<i>arenarius</i>	14.8	44.4
Orthoptera	<i>Ammobaenetes</i>	<i>mescalero</i>	100.0	100.0
Orthoptera	<i>Ceuthophilus</i>	sp.	7.4	22.2
Orthoptera	<i>Stenopelmatus</i>	<i>mescaleroensis</i>	77.7	100.0

most commonly captured endemic species. *Dipodomys ordii* was the most commonly captured small mammal, followed by *Onychomys leucogaster*, *Perognathus flavus*, *Perognathus flavescens*, *Neotoma micropus*, *Peromyscus leucopus*, *Spermophilus spilosoma*, and *Peromyscus maniculatus*. Among beetles, *Embaphion muricata* was the most commonly captured, followed by *Eleodes extricatus*, and *Pasimachus* sp. Ant communities were dominated by *Dorymyrmex* sp., followed by *Pogonomyrmex* sp., *Solenopsis* sp., and *Camponotus* sp. Of the seven species of lizards in addition to *S. arenicolus* captured in this study, *Uta stansburiana* was the most common, followed by *Aspidoscelis marmorata*, *Holbrookia maculata*, and *A. sexlineata*.

Species richness and diversity—At the site scale no differences were detected in species richness or diversity for any taxon group where *S. arenicolus* maintained reproductive populations (Table 13). Both endemic species and beetle richness were higher on grids where *S. arenicolus* was present than those where they were absent (Table 13). Ant species richness was higher on grids where *S. arenicolus* did not maintain reproductive populations than grids where they did. Interestingly counter to the species richness data, beetle diversity was significantly higher on grids where *S. arenicolus* was absent. At both the grid and site scale, and thus range-wide, no differences were detected in diversity measurements for any other taxon.

S. arenicolus relative abundance and occupancy— There were no significant relationships detected between *S. arenicolus* relative abundance and the species richness of any taxon group at the site scale (Table 14). Also, with the exception of beetles, there were no significant relationships detected between *S. arenicolus* and species richness at

Table 13. Comparison of species richness and diversity at sites and grids by presence of *S. arenicolus* or their reproductive populations over the course of three years in the Mescalero-Monahans shinnery sands, New Mexico. Mann Whitney U tests were used for comparison and all significant differences are in bold. (Present = Pres; Absent = Abs; Repro = reproductive population; Non = non-reproductive population)

		Site						Grid					
		Pres	Abs	P	Repro	Non	P	Pres	Abs	P	Repro	Non	P
Endemics	Richness	-	-	-	5.93	5.91	0.89	6.26	3.75	<0.01	6.88	5.47	0.46
	Diversity	-	-	-	0.72	0.75	0.19	0.73	0.74	0.78	0.80	0.70	0.18
Beetles	Richness	-	-	-	10.13	9.33	0.80	10.30	7.00	<0.01	10.25	9.63	0.34
	Diversity	-	-	-	0.21	0.17	0.19	0.17	0.29	<0.01	0.20	0.16	0.12
Ants	Richness	-	-	-	6.13	6.58	0.53	6.13	6.75	0.45	5.00	6.74	<0.01
	Diversity	-	-	-	0.46	0.32	0.11	0.41	0.34	0.77	0.55	0.33	0.07
Small mammals	Richness	-	-	-	3.27	3.25	0.16	3.09	4.00	0.17	3.38	3.16	0.72
	Diversity	-	-	-	0.29	0.31	0.73	0.27	0.48	0.17	0.27	0.31	0.74
Lizards	Richness	-	-	-	4.93	5.33	0.24	5.22	5.25	0.88	5.00	5.32	0.38
	Diversity	-	-	-	0.27	0.22	0.90	0.27	0.20	0.10	0.25	0.25	0.77

Table 14. Relationships between taxon group diversity and richness and *S. arenicolus* relative abundances in the Mescalero-Monahans shinnery sands, New Mexico at site and grid scale. Spearman rank correlations used for comparison significant associations in bold.

Taxon group	Diversity				Richness			
	Site		Grid		Site		Grid	
	ρ	P	ρ	P	ρ	P	ρ	P
Endemic	0.53	0.14	0.05	0.80	-0.18	0.63	0.01	0.95
Beetles	-0.40	0.29	-0.34	0.08	-0.10	0.79	0.46	0.02
Ants	0.28	0.46	0.34	0.08	-0.39	0.29	-0.32	0.10
Small mammals	-0.50	0.18	-0.04	0.82	0.62	0.07	-0.08	0.67
Lizards	-0.05	0.91	0.22	0.27	-0.25	0.52	-0.08	0.67

the grid scale. There was a positive relationship detected between beetle species richness and *S. arenicolus* relative abundance at the grid scale (Table 14; Fig. 13). No significant relationships were detected between *S. arenicolus* relative abundance and diversity measures for any taxonomic group at either scale (Table 14).

Umbrella index and co-occurrence—The UI calculated for 77 species of ants, beetles, small mammals, and lizards at the site and grid level provides umbrella rankings for the species in this ecosystem (Table 15). At the site level the white-footed mouse (*Peromyscus leucopus*) occurred at only 4 sites but had the highest UI rank. It was followed by the beetle (*Eusattus muricatus*), the ant (*Pogonomyrmex desertium*), the tiger beetle (*Cicindella scutellaris*), and the beetle (*Eusattus convexus*). At the grid level, two species of ants (*Formica* sp.1 and *Forelius* sp.2) had the highest UI ranking. They were followed in order by the fire ant (*Solenopsis* sp.1), the grasshopper mouse (*Onychomys leucogaster*), and the Texas horned lizard (*Phrynosoma cornutum*). At the site level, *S. arenicolus* was tied for the last rank due to its ubiquity and at the grid level it was ranked at thirty-three out of sixty eight for the same reason. For *S. arenicolus*, overall PCS was 50 % at the site scale and 30 % at the grid scale (Table 15).

Discussion

The results showed that at large landscape scales *S. arenicolus* may serve as an umbrella species for many endemic and native species of the MMSS. Current conservation initiatives to protect *S. arenicolus* would provide some umbrella protection

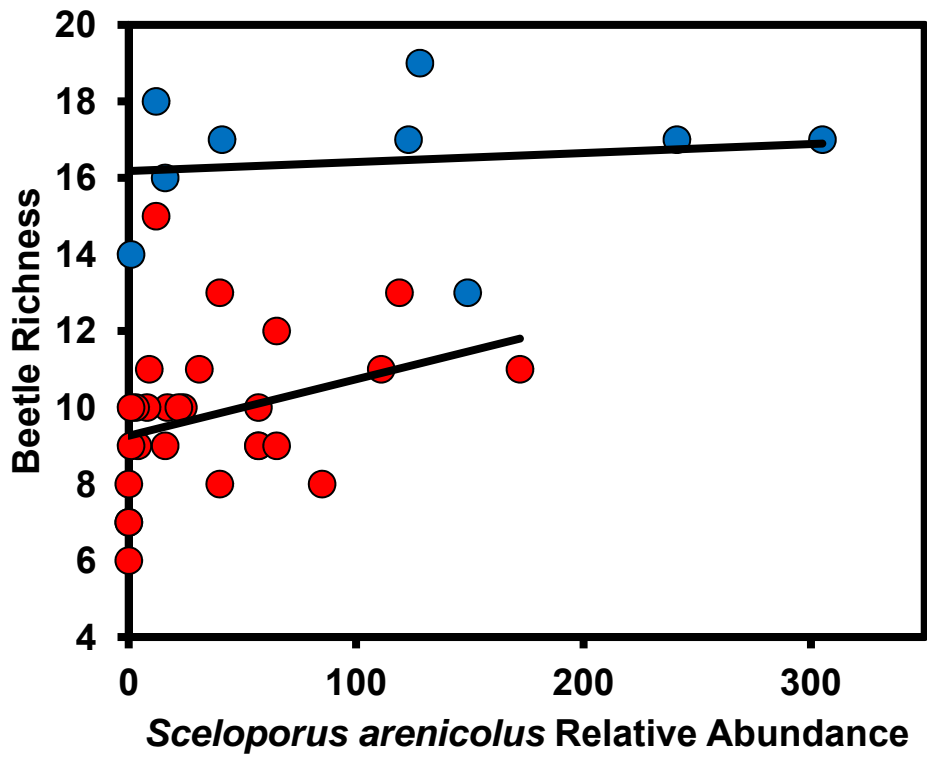


Figure 13. Relationships between beetle species richness and relative abundance of *Sceloporus arenicolus* at the grid scale (●) and the site scale (●) in the Mescalero-Monahans shinnery sands, New Mexico. Spearman rank correlations: grid $\rho = 0.46$, $P = 0.02$; site $\rho = -0.10$, $P = 0.79$.

Table 15. List of species of beetles, ants, small mammals, and lizards captured in the Mescalero-Monahans shinnery sands, New Mexico. The cross-taxonomic umbrella index (UI) is based on percent co-occurring species (PCS) and rarity (R). The species with the top ten umbrella index rankings are in bold for both the site and grid level.

Species	Site (<i>n</i> = 9)						Grid (<i>n</i> = 27)				
	Endemic	Presence	PCS	R	UI	Rank	Presence	PCS	R	UI	Rank
Beetles											
<i>Agrypnus</i> sp.		9	0.5	0.5	1.0	58	21	0.3	0.7	1.0	24
<i>Areoschizus</i> sp.		9	0.5	0.5	1.0	58	24	0.3	0.6	0.9	41
<i>Blapstinus</i> sp.		1	0.5	0.6	1.1	50	1	0.3	0.5	0.9	59
<i>Canthon</i> sp.		2	0.5	0.7	1.2	23	2	0.3	0.6	0.9	56
<i>Cicindella formosa rutilovirescens</i>	x	1	0.5	0.6	1.1	45	1	0.3	0.5	0.8	68
<i>Cicindella scutellaris</i>		5	0.6	0.9	1.5	4	7	0.3	0.8	1.1	14
Coleoptera sp.1		1	0.5	0.6	1.1	50	1	0.3	0.5	0.9	59
Coleoptera sp.2		1	0.6	0.6	1.2	30	1	0.4	0.5	0.9	42
Coleoptera sp.3		3	0.6	0.8	1.4	10	3	0.4	0.6	1.0	35
Coleoptera sp.4		1	0.6	0.6	1.2	30	1	0.4	0.5	0.9	42
Elateridae sp.		1	0.5	0.6	1.1	54	1	0.3	0.5	0.8	76
<i>Eleodes acutus</i>		3	0.6	0.8	1.4	9	4	0.4	0.6	1.0	27
<i>Eleodes extricatus</i>		9	0.5	0.5	1.0	58	24	0.3	0.6	0.9	47
<i>Eleodes hispilabrus</i>		8	0.5	0.6	1.1	40	17	0.3	0.9	1.2	8
<i>Eleodes longicollis</i>		3	0.5	0.8	1.4	13	3	0.3	0.6	0.9	46
<i>Eleodes trichostata</i>		9	0.5	0.5	1.0	58	10	0.3	0.9	1.2	9
<i>Embaphion muricata</i>		9	0.5	0.5	1.0	58	26	0.3	0.5	0.9	66
<i>Epitragosoma arenaria</i>	x	8	0.5	0.6	1.1	38	10	0.3	0.9	1.2	9
<i>Eupompha viridis</i>	x	2	0.5	0.7	1.2	34	2	0.3	0.6	0.9	64
<i>Eusattus convexus</i>		5	0.5	0.9	1.5	5	6	0.3	0.7	1.1	20
<i>Eusattus muricatus</i>		4	0.6	0.9	1.5	2	6	0.4	0.7	1.1	15
<i>Eusattus</i> sp.1		2	0.5	0.7	1.3	22	2	0.4	0.6	0.9	40
<i>Eusattus</i> sp.2		3	0.5	0.8	1.4	15	3	0.3	0.6	0.9	48

Table 15. Continued.

Species	Site (<i>n</i> = 9)						Grid (<i>n</i> = 27)					
	Endemic	Presence	PCS	R	UI	Rank	Presence	PCS	R	UI	Rank	
<i>Graphops comosa</i>	x	2	0.6	0.7	1.3	19	3	0.4	0.6	1.0	31	
Harpalinae sp.		2	0.6	0.7	1.3	21	2	0.3	0.6	0.9	49	
<i>Harpalus</i> sp.		1	0.6	0.6	1.2	30	1	0.4	0.5	0.9	42	
<i>Hybosorus illigeri</i>		1	0.6	0.6	1.2	24	1	0.4	0.5	0.9	54	
<i>Nicophorus</i> sp.		1	0.6	0.6	1.2	35	1	0.3	0.5	0.9	57	
<i>Omorgus nodosus</i>		9	0.5	0.5	1.0	58	20	0.3	0.8	1.1	17	
<i>Pasymachus</i> sp.		9	0.5	0.5	1.0	58	23	0.3	0.6	1.0	34	
<i>Philonthus</i> sp.		1	0.6	0.6	1.2	24	1	0.4	0.5	0.9	51	
<i>Poecilus</i> sp.		1	0.5	0.6	1.1	54	1	0.3	0.5	0.8	76	
<i>Prionus arenarius</i>	x	4	0.5	0.9	1.5	6	4	0.3	0.6	1.0	32	
<i>Rhadine</i> sp.		3	0.6	0.8	1.4	11	4	0.4	0.6	1.0	26	
Scydmaenidae sp.		5	0.5	0.9	1.5	7	5	0.3	0.7	1.0	30	
<i>Selenophorus</i> sp.		1	0.5	0.6	1.1	50	1	0.3	0.5	0.9	59	
<i>Serica</i> sp.		9	0.5	0.5	1.0	58	20	0.3	0.8	1.1	18	
Tenebrionidae sp.		2	0.6	0.7	1.3	16	2	0.4	0.6	1.0	38	
<i>Ulus</i> sp.		1	0.5	0.6	1.1	45	1	0.3	0.5	0.8	68	
Ants												
<i>Camponotus</i> sp.		9	0.5	0.5	1.0	58	22	0.3	0.7	1.0	28	
<i>Crematogaster</i> sp.		2	0.6	0.7	1.3	19	2	0.4	0.6	1.0	37	
<i>Dorymyrmex</i> sp.		9	0.5	0.5	1.0	58	20	0.3	0.8	1.1	16	
<i>Forelius</i> sp.1		2	0.6	0.7	1.3	18	3	0.4	0.6	1.0	35	
<i>Forelius</i> sp.2		8	0.5	0.6	1.1	37	12	0.3	0.9	1.3	2	
<i>Formica</i> sp.		8	0.5	0.6	1.1	38	13	0.3	1	1.3	1	
Formicidae sp.1		9	0.5	0.5	1.0	58	9	0.3	0.8	1.2	12	
Formicidae sp.2		1	0.6	0.6	1.2	24	1	0.4	0.5	0.9	51	
Formicidae sp.3		1	0.5	0.6	1.1	54	1	0.3	0.5	0.9	67	

Table 15. Continued.

Species	Site (<i>n</i> = 9)						Grid (<i>n</i> = 27)				
	Endemic	Presence	PCS	R	UI	Rank	Presence	PCS	R	UI	Rank
Formicidae sp.4		1	0.6	0.6	1.2	30	1	0.4	0.5	0.9	42
Formicidae sp.5		1	0.5	0.6	1.1	45	1	0.3	0.5	0.8	68
<i>Monomorium</i> sp.		2	0.5	0.7	1.2	29	2	0.3	0.6	0.9	58
<i>Myrmecosystus</i> sp.		6	0.5	0.8	1.3	17	6	0.3	0.7	1.0	25
<i>Phedole</i> sp.1		5	0.5	0.9	1.4	8	7	0.3	0.8	1.1	19
<i>Pheidole</i> sp.2		1	0.5	0.6	1.1	45	1	0.3	0.5	0.8	68
<i>Pheidole</i> sp.3		1	0.6	0.6	1.2	24	1	0.4	0.5	0.9	50
<i>Pogonomyrmex desortium</i>		4	0.6	0.9	1.5	3	5	0.4	0.7	1.0	21
<i>Pogonomyrmex</i> sp. 1		9	0.5	0.5	1.0	58	26	0.3	0.5	0.9	65
<i>Pogonomyrmex</i> sp.2		2	0.5	0.7	1.2	28	2	0.3	0.6	0.9	53
<i>Solenopsis</i> sp.1		8	0.5	0.6	1.1	40	15	0.3	0.9	1.3	3
<i>Solenopsis</i> sp.2		8	0.5	0.6	1.1	44	12	0.3	0.9	1.3	6
<i>Trachymyrmex</i> sp.		1	0.5	0.6	1.1	50	1	0.3	0.5	0.9	59
Small mammals											
<i>Dipodomys ordii</i>		9	0.5	0.5	1.0	58	27	0.3	0.5	0.8	72
<i>Neotoma micropus</i>		6	0.5	0.8	1.4	14	8	0.3	0.8	1.1	13
<i>Onychomys leucogaster</i>		9	0.5	0.5	1.0	58	15	0.3	0.9	1.3	4
<i>Perognathus flavescens</i>		8	0.5	0.6	1.1	49	12	0.3	0.9	1.3	6
<i>Perognathus flavus</i>		8	0.5	0.6	1.1	43	18	0.3	0.8	1.2	11
<i>Peromyscus leucopus</i>		4	0.6	0.9	1.5	1	4	0.3	0.6	1.0	29
<i>Peromyscus maniculatus</i>		1	0.6	0.6	1.2	35	1	0.3	0.5	0.9	59
<i>Spermophilus pilosoma</i>		1	0.5	0.6	1.1	54	2	0.3	0.6	0.9	55
Lizards											
<i>Aspidoscelis marmorata</i>		9	0.5	0.5	1.0	58	27	0.3	0.5	0.8	72
<i>Aspidoscelis sexlineata</i>		9	0.5	0.5	1.0	58	27	0.3	0.5	0.8	72
<i>Holbrookia maculata</i>		9	0.5	0.5	1.0	58	21	0.3	0.7	1.0	22

Table 15. Continued.

Species	Site ($n = 9$)						Grid ($n = 27$)				
	Endemic	Presence	PCS	R	UI	Rank	Presence	PCS	R	UI	Rank
<i>Phrynosoma cornutum</i>		8	0.5	0.6	1.1	40	15	0.3	0.9	1.3	5
<i>Plestiodon obsoleta</i>		3	0.6	0.8	1.4	12	3	0.3	0.6	0.9	39
<i>Sceloporus arenicolus</i>	x	9	0.5	0.5	1.0	58	23	0.3	0.6	1.0	33
<i>Sceloporus consobrinus</i>		9	0.5	0.5	1.0	58	21	0.3	0.7	1.0	23
<i>Uta stansburiana</i>		9	0.5	0.5	1.0	58	27	0.3	0.5	0.8	72

for endemism and biodiversity in the MMSS. However, the scale of protection will be an important consideration because land managers will make decisions regarding conservation at the scale of large landscapes as well as at the scale of where individual well pads and caliche roads may be placed. Beetle species richness was highest where *S. arenicolus* was present and had a positive association with *S. arenicolus* density at the smallest scale. Across its range, *S. arenicolus* would serve as an umbrella for a relatively large area, approximately 25% of the MMSS. The species' known range covers 262,077 ha of shinnery sands in southeastern New Mexico and west Texas. Because *S. arenicolus* is a habitat specialist that relies on the unique dune-blowout formations, it serves as a critical umbrella species for protection of these dunes and the biodiversity they contain, provided all of its potential and occupied habitat fall under protection. Thus, a caveat of umbrella protection is that not all locations within the 262,077 ha comprising the species' range, may be considered suitable for this habitat specialist species. If so, there is an un-quantified area in the MMSS that may not be protected if occupancy by *S. arenicolus* is the sole criterion for conservation of MMSS landscapes. Thus it is meaningful to consider the implications at the scales where individual land disturbances, such as from oil and gas development, take place.

At the grid scale, endemic species richness was higher where *S. arenicolus* was present versus where they were not. At this small scale these relationships demonstrate the importance of protecting *S. arenicolus*, because if current management continues as is, many independent land use decisions will take place at a small spatial scale, especially if oil fields are developed based on uncoordinated placement of individual

well pads. None of these trends were apparent at the site scale because the study design required that *S. arenicolus* occur at all sites thus we could expect that this would hold true at the largest range-wide scale as well. There were no clear disadvantages for small mammals, ants, or lizards as a result of not co-occurring along with *S. arenicolus* at any scale. Further, the umbrella index did not rank *S. arenicolus* high on the list of potential umbrella species among the other sympatric species. Under the scenario presented here, *S. arenicolus* would only serve as an umbrella species to some endemic species and beetles at the scale of grids in this ecosystem. Of course, the grids are samples from a broader contiguous landscape, and more protected land obviously translates into more biodiversity protected overall.

Sceloporus arenicolus fits some of the preferred characteristics of an effective umbrella species, such as relatively large body size, ecological specialization, co-occurrence with other species of concern, negative response to disturbance, ease in sampling, and a well-known natural history (Seddon and Leech 2008, Branton and Richardson 2010). They are a small bodied reptile (average snout-to-vent length 55 mm), however they are much larger than the other endemic species with which they co-occur. Some endemic species in this ecosystem are specialized on the same microhabitat as *Sc. arenicolus*, such as *A. mescalero* or *St. mescaleroensis*. Both species co-occurred with *S. arenicolus* at both the grid and site scale. The methods used to capture arthropods in this study were not sufficient to capture all species of endemics in the MMSS, however I did capture nearly half of the species known to occur in the ecosystem (Table 12). Distinct relationships between endemic species richness and

presence of *S. arenicolus* were apparent at the smallest scale making these locations, and by inference similar areas important for conservation of endemics in this ecosystem. However, the frequency of occurrence of endemic species was higher at the site scale than at the grid scale. To maximize endemic species richness and increase potential for endemic species occurrence, land conservation would be more effective if applied over large spatial scales rather than by a series of small-scale independent decisions.

There was a positive association detected between beetle species richness and the relative abundance of *S. arenicolus* at the grid scale. This suggests that high quality habitat for *S. arenicolus* may also be high quality for beetles. This may be due to beetle larvae sharing similar preferred habitats as required for nesting *S. arenicolus*. Many beetles have evolved behavioral and physiological adaptations that allow them to persist in desert environments, and many of these depend on soil moisture as a determinant for success (Cloudsley-Thompson 2001). *Sceloporus arenicolus* also shows signs of adaptation to the desert by taking advantage of deep soil moisture for their nesting habitat (Ryberg et al., *in review*). It is possible that the factors that limit *S. arenicolus*' distribution within this ecosystem, such as soil moisture, may also be limiting factors for beetles. Therefore, *S. arenicolus* may be an indicator of sites with relatively high beetle diversity in this ecosystem.

There were fewer species of ants found on grids where *S. arenicolus* maintained reproductive populations over the three years. This too may be related to habitat quality and *S. arenicolus*' nesting habits in the MMSS. Chihuahuan desert ant guilds are generally structured on plant productivity gradients (Whitford 1978), and there is a linear

relationship between plant and ant species richness. In the MMSS the abundance and diversity of grasses and forbs is higher in the shinnery oak flats outside of the sand dunes (Peterson and Boyd 1998). Thus, lower ant richness in the sand dunes may be due to sand dunes being less productive for plant species even though shinnery dunes are the habitat required by *S. arenicolus* (Fitzgerald and Painter 2009). *Sceloporus arenicolus*, like most small iguanid lizards, are known to eat ants (Fitzgerald and Painter 2009, pers. obs.) but effects of ant predation on structure of ant communities has not been studied.

There were no differences in small mammal or lizard communities with or without *S. arenicolus* at either scale. One of the earliest uses of the umbrella species approach indicated that large animals with large home ranges should serve as the best umbrella species due to the area of conservation (Wilcox 1984). In regards to *S. arenicolus*, most of the small mammals and lizards in the MMSS maintain similar home range and body sizes as compared to the ants, beetles, and other endemic species. Thus, the pattern that emerges when considering *S. arenicolus* as an umbrella for small mammal or lizard biodiversity is that they would be effective umbrellas in general. But this determination would have to be due to their ease in sampling as compared to trapping mammals or capturing other lizard species.

I used the UI introduced by Fleischman et al. (2000) to compare *S. arenicolus* with all other species captured in this study. I followed Berglind (2004) who adapted this measure to account for lack of information regarding sensitivity to disturbance for the species in this ecosystem. My use of this statistic demonstrates its scale sensitivity and presents a challenge to using it. Because the UI is a scale-dependent measure, it is

important to consider the scale of conservation effort in the system being evaluated. In the MMSS, the smallest scale of conservation for *S. arenicolus* relates to the placement of a single oil well pad (> 10 ha), and this was relevant to the grid scale in my analysis. At this scale, the species selected as good potential umbrellas (e.g. *O. leucogaster*) had high median rarity values. These high median rarity values are valuable when a random biodiversity sample is taken, however my assessment was conducted on a sample with known prior occurrence of *S. arenicolus*. This condition biased the UI assessment and placed more importance on median rarity than co-occurrence patterns. At the site scale, the measures of rarity and co-occurrence combined do not capture the factors that are important to determining an umbrella or indicator species either. This was because the scale was too large. For instance, *P. leucopus* only occurred at four of the nine sites yet it was ranked high among umbrella species. My use of this statistic without any data on sensitivity to disturbance undoubtedly highlighted different species than it would have with those type of data included for each species. Any further assessments using this tool in this system should be accompanied by information regarding each species sensitivity to disturbance.

The current scale of conservation management allows incidental “take” (harass, harm, pursue, shoot, wound, kill, trap, capture, or collect, or attempt to engage in any such conduct) of *S. arenicolus*. Current conservation of *S. arenicolus* is stipulated in several forms of Candidate Conservation Agreements, all of which are based on habitat avoidance, while allowing development of shinnery dunes in certain circumstances (US Fish and Wildlife Service, 2008a, b, US Fish and Wildlife Service, 2011). Mitigation

practices involve independent small-scale management decisions that may impact shinnery dunes habitat and result in landscape fragmentation of shinnery dunes and especially surrounding areas (Chapter II). Small scale management like this could result in loss of populations and potentially result in the loss of other biodiversity or endemism. An alternative to this would be to manage the distribution of known populations for *S. arenicolus* and thus much more biodiversity and endemism would be preserved. Although my analysis did not demonstrate significant associations between *S. arenicolus* and endemics or other biodiversity at the largest scale, it did demonstrate an overall increase in species richness. This trend should not be surprising given the species-area relationship a factor commonly used in the conservation reserve planning literature (Lahti and Ranta 1985). These ideas are long established, and the USFWS should consider efforts that would protect large tracts of *S. arenicolus* habitat in perpetuity. I recommend that managers throughout this ecoregion set aside large tracts of land that would encompass multiple populations of *S. arenicolus*, local endemic diversity, and other species.

CHAPTER V

SUMMARY AND CONCLUSIONS

Research on the effects of landscape fragmentation in ecological communities has typically followed a traditional model of fragmentation that considers habitat patches to be isolated and surrounded by an inhospitable matrix. My research objectives were three-fold: first I examined lizard community structure in fragmented and non-fragmented locations, second I asked if the resultant patterns from my first evaluation were due to the habitat breadth of each species, specifically asking if specialists are more susceptible to fragmentation than generalists, and finally I evaluated the potential use of the dunes sagebrush lizard (*Sceloporus arenicolus*) as an umbrella species for the protection of endemism and biodiversity of the Mescalero-Monahans shinnery sands ecosystem. My results emphasize that current land-use practices that fragment the landscape cause community disassembly. Further, the species that are most susceptible to the effects of landscape fragmentation are those that have the most narrow habitat use patterns. Finally, my evaluation of the dunes sagebrush lizard as an umbrella species for endemism and biodiversity of the Mescalero-Monahans shinnery sands suggests that land managers should focus conservation efforts on large tracts of land.

Comparisons of lizard community structure between fragmented and non-fragmented trapping grids revealed disassembly was occurring. Two species were captured at fewer trapping grids and occurred in lower relative abundances in the fragmented locations. Both *Sceloporus arenicolus* and *Holbrookia maculata* were

regular members of the non-fragmented lizard community. Discriminant analysis of environmental structure between fragmented and non-fragmented trapping grids revealed that the configuration of blowouts was different on the fragmented trapping grids. Specifically, fragmented trapping grids had fewer and larger blowouts in general. Further, a comparison between the discriminant function of environmental structure and diversity of the trapping grids revealed a pattern consistent with expectations, sites with fewer larger blowouts generally were less diverse.

Theory on species response to fragmentation suggests that the species most susceptible to fragmentation should have narrow niche breadths. I examined the habitat use patterns of the lizards in this community to determine if response to fragmentation was dependent on the lizards' breadth of habitat use. For each species, I examined use relative to available habitat preference for soil compaction, land cover, dominant plant, slope, and aspect. To calculate niche breadth, I conducted principal coordinates analysis on lizard habitat use and calculated the Euclidean distance to origin. As a proxy for species susceptibility to fragmentation, I calculated absolute effect size of difference in species abundance between fragmented and non-fragmented trapping grids. Finally, I compared the absolute effect sizes to the Euclidean distance to origin to determine if the species most susceptible to fragmentation were also those with the most narrow habitat use patterns. Three species (*H. maculata*, *P. cornutum*, and *S. arenicolus*) had effect sizes greater than 0.80 and these same three species also have the most narrow habitat use patterns.

Umbrella species are one of many surrogate species approaches to biodiversity conservation. Umbrella species are species that through their protection alone confer protection to co-occurring species. Often traits associated with effective umbrella species are large home range size, large body size, or high trophic position. I examined the co-occurrence patterns of *S. arenicolus* and ants, beetles, small mammals, and lizards of the Mescalero-Monahans shinnery sands at two spatial scales representing different biological entities and conservation possibilities. At the largest scale, the frequency of occurrence for endemic species increased though no other patterns emerged because *S. arenicolus* was present at all sites and there no relationships between relative abundances and other species. At the smallest scale, both beetle species richness, diversity, and endemic species richness were higher in the presence of *S. arenicolus*. In addition, ant species richness was lower in the presence of *S. arenicolus* at the smallest scale. Results indicate that *S. arenicolus* would serve as an umbrella to some, but not all, of the biodiversity and endemism in this ecosystem at the smallest scale and protection of biodiversity increases with scale. I recommend that future efforts towards protecting endemism and biodiversity in this ecosystem be focused at larger scales and practices that would disturb *S. arenicolus* habitat be moved outside of the ecosystem.

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APPENDIX A

LIST OF PLANTS ENCOUNTERED IN MESCALERO-MONAHANS SHINNERY

SANDS ECOSYSTEM, NEW MEXICO 2008-2011

Genus species	Common name
<i>Abronia fragrans</i>	Snowball sand verbena
<i>Acanthochiton wrightii</i>	Greenstripe
<i>Amaranthus (arenicola)</i>	(Sand amaranth)
<i>Ambrosia psilostachya</i>	Cuman ragweed
<i>Andropogon gerardii</i>	Big bluestem
<i>Aphanostephus ramossisimus</i>	Plains dozedaisy
<i>Aristida purpurea</i>	Purple threeawn
<i>Artemisia dracunculus</i>	Tarragon
<i>Artemisia filifolia</i>	Sand sagebrush
<i>Asclepias latifolia</i>	Broadleaf milkweed
<i>Asclepias subverticillata</i>	Horsetail milkweed
<i>Atriplex canescens</i>	Fourwing saltbush
<i>Bothriochloa laguroides</i>	Silver beardgrass
<i>Bouteloua curtipendula</i>	Sideoats grama
<i>Bouteloua eriopoda</i>	Black grama
<i>Bouteloua hirsuta</i>	Hairy grama
<i>Cenchrus spinifex</i>	Coastal sandbur
<i>Chaetopappa ericoides</i>	Rose heath
<i>Chamaesyce (carunculata)</i>	(Sanddune sandmat)
<i>Chenopodium sp.</i>	Goosefoot
<i>Commelina erecta</i>	Whitemouth dayflower
<i>Croton (dioicus)</i>	Grassland croton
<i>Cryptanthus cinerea</i>	James' cryptantha
<i>Cylindropuntia imbricata</i>	Cholla
<i>Dalea formosa</i>	Feather dalea
<i>Dalea lanata</i>	Wooly prairie clover
<i>Dasyochloa pulchella</i>	Low woolygrass
<i>Digitaria pubiflora</i>	Carolina crabgrass
<i>Dimorphocarpa wislizenii</i>	Spectacle pod
<i>Diodia teres</i>	Poorjoe
<i>Eragrostis trichodes</i>	Sand lovegrass

Genus species	Common name
<i>Eragrostis lehmanniana</i>	Lehmann's lovegrass
<i>Ericameria nauseosa</i>	Rubber rabbitbrush
<i>Erigeron divergens</i>	Spreading fleabane
<i>Eriogonum annuum</i>	Annual buckwheat
<i>Escobaria vivipara</i>	Spinystar
<i>Euphorbia (parryi)</i>	(Parry's sandmat)
<i>Evolvulus sericeus</i>	Silver dwarf morning-glory
<i>Gutierrezia sarothrae</i>	Broom snakeweed
<i>Hedyotis sp.</i>	Bluet
<i>Helianthus sp.</i>	Sunflower
<i>Heliotropium convolvulaceae</i>	Fragrant heliotrope
<i>Hibiscus coulteri</i>	Desert rose mallow
<i>Hoffmannseggia glauca</i>	Indian rushpea
<i>Hymenoppapus filifolius</i>	Fineleaf hymenopappus
<i>Lepidium montanum</i>	Mountain pepperweed
<i>Linum rigidum</i>	Stiffstem flax
<i>Lithospermum incisum</i>	Narrowleaf stoneseed
<i>Machaeranthera sp.</i>	Tansyaster
<i>Maurandya wislizenii</i>	Giant snapdragon
<i>Melampodium leucanthum</i>	Blackfoot daisy
<i>Mentzelia sp.</i>	Blazingstar
<i>Mimosa quadrivalvis</i>	Fourvalve mimosa
<i>Mirabilis albida</i>	White four o'clock
<i>Mollugo cerviana</i>	Threadstem carpetweed
<i>Monarda citriodora</i>	Lemon beebalm
<i>Munroa squarrosa</i>	False buffalograss
<i>Oenothera curtiflora</i>	Guara
<i>Oenothera hartwegii</i>	Sundrop
<i>Oenothera macrocarpa</i>	Lemon sunset
<i>Opuntia polyacantha</i>	Plains pricklypear
<i>Palafoxia sphaelata</i>	Othake
<i>Panicum havardii</i>	Havard's panicgrass
<i>Paspalum setaceum</i>	Thin paspalum
<i>Pectis angustifolia</i>	Lemonscent
<i>Penstemon buckleyi</i>	Buckley's beardtongue
<i>Penstemon ambiguus</i>	Gilia beartongue
<i>Phacelia integrifolia</i>	Gyp blue-curls

Genus species	Common name
<i>Phyllanthus sp.</i>	Leafflower
<i>Portulaca oleracea</i>	Common purslane
<i>Proboscidea parviflora</i>	Devil's claw
<i>Prosopis glandulosa</i>	Honey mesquite
<i>Psilostrophe tagentina</i>	Wooly paperflower
<i>Quercus havardii</i>	Havard oak
<i>Sapindus drummondii</i>	Western soapberry
<i>Schizachyrium scoparium</i>	Little bluestem
<i>Senecio riddellii</i>	Riddell's ragwort
<i>Senna bauhinioides</i>	Twinleaf senna
<i>Setaria leucopila</i>	Streambed bristlegrass
<i>Solanum elaeagnifolium</i>	Silverleaf nightshade
<i>Sorghastrum nutans</i>	Indiangrass
<i>Sporobolus contractus</i>	Spike dropseed
<i>Sporobolus cryptandrus</i>	Sand dropseed
<i>Sporobolus flexuosus</i>	Mesa dropseed
<i>Sporobolus giganteus</i>	Giant dropseed
<i>Stillingia sylvatica</i>	Queen's delight
<i>Thelesperma megapotamicum</i>	Hopi tea greanthread
<i>Tradescantia occidentalis</i>	Prairie spiderwort
<i>Yucca glauca</i>	Soapweed yucca

() parenthesis indicates uncertainty

APPENDIX B

LIST OF ANIMALS CAPTURED OR OBSERVED IN MESCALERO-MONAHANS

SHINNERY SANDS ECOSYSTEM, NEW MEXICO 2008-2011

Latin name	Common name
Phylum Arthropoda	
Class Arachnida – Arachnids	
<i>Centruroides vittatus</i>	Striped back scorpion
<i>Hogna coloradensis</i>	Wolf spider
<i>Geolycosa</i> sp.	Burrowing wolf spider
<i>Latrodectus mactans</i>	Southern black widow spider
<i>Paruroctonus utahensis</i>	Eastern sand scorpion
<i>Psilochorus</i> sp.	Daddy long-legs spider
<i>Steatoda</i> sp.	Cobweb spider
<i>Zelotes gertschi</i>	Ground spider
Class Chilopoda – Centipedes	
<i>Scolopendra</i> sp.	Centipede
Class Hexapoda - Hexapods (Insects)	
<i>Araeoschizus</i> sp.	Ant beetle
<i>Agrypnus</i> sp.	Click beetle
<i>Amblycheila cylindriformis</i>	Flightless tiger beetle
<i>Ammobaenetes mescalero</i>	Sand-treader cricket
<i>Apiomerus</i> sp.	Assassin bug
<i>Arenivaga</i> sp.	Sand cockroach
<i>Arethaea mescalero</i>	Mescalero thread-legged katydid
<i>Blapstinus</i> sp.	Darkling beetle
<i>Campanotus</i> sp.	Carpenter ant
<i>Campylacantha olivacea</i>	Fuzzy olive-green grasshopper
<i>Canthon</i> sp.	Dung beetle
<i>Ceuthophilus</i> sp.	Camel cricket
<i>Cicindela formosa rutilovirescens</i>	Big sand tiger beetle

Latin name	Common name
<i>Cicindela scutellaris</i>	Festive tiger beetle
<i>Crematogaster</i> sp.	Valentine ant
<i>Dactylotum bicolor</i>	Barber-pole grasshopper
<i>Dasymutilla asopus</i>	Velvet ant
<i>Dasymutilla bioculata</i>	Velvet ant
<i>Dasymutilla nigricauda</i>	Velvet ant
<i>Dasymutilla radkei</i>	Velvet ant
<i>Dorymyrmex</i> sp.	Cone ant
<i>Eleodes acutus</i>	Desert stink beetle
<i>Eleodes caudifera</i>	Pointy tenebrionid
<i>Eleodes extricatus</i>	Darkling beetle
<i>Eleodes hispilabris</i>	Prince of the dunes
<i>Eleodes longicollis</i>	Darkling beetle
<i>Eleodes suturalis</i>	King of the dunes
<i>Eleodes tricostata</i>	Three-ribbed darkling beetle
<i>Embaphion muricata</i>	Scalloped false wireworm beetle
<i>Epitragosoma arenaria</i>	Fuzzy epitragini
<i>Eremoblatta subdiaphana</i>	Sand cockroach
<i>Eupompha viridis</i>	Blister beetle
<i>Eusattus convexus</i>	Darkling beetle
<i>Eusattus muricatus</i>	Darkling beetle
<i>Formica</i> sp.	Field ant
<i>Forelius</i> sp.	Ant
<i>Gonatista grisea</i>	Grizzled mantis
<i>Gryllus</i> sp.	Cricket
<i>Graphops comosa</i>	Monahans sandhills chrysomelid
<i>Harpalus</i> sp.	Ground beetle
<i>Hybosorus illigeri</i>	European hybosorus scarab
<i>Monomorium</i> sp.	Ant
<i>Myrmecocystus</i> sp.	Honeypot ant
<i>Nicagus</i> sp.	Scarab beetle
<i>Nicrophorus</i> sp.	Burying beetle
<i>Omorgus nodosus</i>	Hastate hide beetle
<i>Parcoblatta</i> sp.	Wood roach
<i>Pasimachus</i> sp.	Pedunculate ground beetle
<i>Pediocetes</i> sp. 1	Shield-backed katydid
<i>Pediocetes</i> sp. 2	Shield-backed katydid

Latin name	Common name
<i>Pheidole</i> sp.	Big-headed ant
<i>Philonthus</i> sp.	Rove beetle
<i>Plagiostira mescaleroensis</i>	Mescalero shield-backed katydid
<i>Poecilus</i> sp.	Woodland ground beetle
<i>Pogonomyrmex</i> sp.	Harvester ant
<i>Pogonomyrmex desertorium</i>	Desert harvester ant
<i>Polypylla mescaleroensis</i>	Mescalero Lined June beetle
<i>Polypylla monahansensis</i>	Monahans 10-lined June beetle
<i>Polypylla pottsorum</i>	Lined June beetle
<i>Prionus arenarius</i>	Longhorn beetle
<i>Psuedomethoca bequaerti</i>	Velvet ant
<i>Psuedomethoca paludata</i>	Velvet ant
<i>Rhadine</i> sp.	Ground beetle
<i>Schistocerca</i> sp.	Bird grasshopper
<i>Selenophorus</i> sp.	Ground beetle
<i>Serica</i> sp.	June beetle
<i>Solenopsis</i> sp.	Thief ant
<i>Sphaerophthalma marpesia</i>	Velvet ant
<i>Stenopelmatus mescaleroensis</i>	Mescalero Jerusalem cricket
<i>Trachymyrmex</i> sp.	Ant
<i>Ulus</i> sp.	Darkling beetle

Phylum Chordata

Class Amphibia – Amphibians

<i>Ambystoma tigrinum</i>	Tiger salamander
<i>Anaxyrus cognatus</i>	Great plains toad
<i>Anaxyrus debilis</i>	Green toad
<i>Anaxyrus speciosus</i>	Texas toad
<i>Scaphiopus couchii</i>	Couch's spadefoot
<i>Spea bombifrons</i>	Plains spadefoot

Class Mammalia – Mammals

<i>Antilocapra americana</i>	Pronghorn antelope
<i>Canus latrans</i>	Coyote
<i>Dipodomys ordii</i>	Ord's kangaroo rat

Latin name	Common name
<i>Erithozon dorsatum</i>	Porcupine
<i>Geomys knoxjonesii</i>	Knox Jones' pocket gopher
<i>Lepus californicus</i>	Black-tailed jackrabbit
<i>Lynx rufus</i>	Bobcat
<i>Mephitis mephitis</i>	Striped skunk
<i>Neotoma micropus</i>	Southern plains woodrat
<i>Odocoileus hemionus</i>	Mule deer
<i>Onychomys leucogaster</i>	Northern grasshopper mouse
<i>Perognathus flavescens</i>	Plains pocket mouse
<i>Perognathus flavus</i>	Silky pocket mouse
<i>Peromyscus leucopus</i>	White-footed mouse
<i>Peromyscus maniculatus</i>	Deer mouse
<i>Reithrodontomys montanus</i>	Plains harvest mouse
<i>Spermophilus mexicanus</i>	Mexican ground squirrel
<i>Spermophilus spilosoma</i>	Spotted ground squirrel
<i>Spermophilus tridecimlineatus</i>	Thirteen-lined ground squirrel
<i>Sylvilagus audubonii</i>	Desert cottontail
<i>Taxidea taxus</i>	Badger
<i>Tayassu tajacu</i>	Collared peccary
<i>Thomomys bottae</i>	Botta's pocket gopher
<i>Urocyon cinereoargenteus</i>	Gray fox
Class Reptilia - Reptiles	
<i>Arizona elegans</i>	Kansas glossy snake
<i>Aspidoscelis marmorata</i>	Marbled whiptail
<i>Aspidoscelis sexlineata</i>	Six-lined racerunner
<i>Coluber flagellum</i>	Coachwhip
<i>Crotalus atrox</i>	Western diamond-back rattlesnake
<i>Crotalus viridis</i>	Prairie rattlesnake
<i>Holbrookia maculata</i>	Lesser earless lizard
<i>Kinosternon flavescens</i>	Yellow mud turtle
<i>Lampropeltis triangulum</i>	Milksnake
<i>Leptotyphlops dulcis</i>	Texas threadsnake
<i>Phrynosoma cornutum</i>	Texas horned lizard
<i>Pituophis catenifer</i>	Bullsnake
<i>Plestiodon obsoletus</i>	Great plains skink
<i>Rhinocheilus leconteii</i>	Long-nosed snake

Latin name	Common name
<i>Sceloporus arenicolus</i>	Dunes sagebrush lizard
<i>Sceloporus consobrinus</i>	Prairie lizard
<i>Sistrurus catenatus</i>	Massasauga
<i>Tantilla nigriceps</i>	Plains black-headed snake
<i>Terrapene ornata</i>	Ornate box turtle
<i>Uta stansburiana</i>	Side-blotched lizard

All endemic species are in bold type.