

Disassembly of a dune-dwelling lizard community due to landscape fragmentation

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Abstract. Landscape fragmentation alters patterns of landscape structure that affect quality and configuration of habitats, and disrupts population dynamics and persistence of species. Community disassembly, a process of community change due to nonrandom species losses and declines, is occurring worldwide as a result of landscape fragmentation, habitat loss, and habitat degradation. We carried out a comparative study at 27 trapping sites designed to characterize how fragmentation affects community structure in a dune-dwelling lizard community. Lizard communities in non-fragmented sites demonstrated nested community structure. Conversely, lizard communities at sites fragmented by roads and well pads from oil and gas development had consistently lower abundance of two species, and demonstrated random community structure. Species loss and lower abundance of species at fragmented sites suggested a pattern of community disassembly. The dunes sagebrush lizard (*Sceloporus arenicolus*), an ecological specialist, and the lesser earless lizard (*Holbrookia maculata*) were present on most non-fragmented sites. However, neither species was present on more than half of the fragmented sites, and their abundances were much lower than on non-fragmented sites. We attributed reduced species diversity on fragmented sites to quantitative differences in landscape configuration compared to non-fragmented sites. Specifically, both size and shape of sand dune blowouts differed between non-fragmented and fragmented sites. Fragmented sites possess more large patches of open sand and barren ground and fewer, smaller, and more dispersed shinnery dune blowouts. Patterns of occurrence and relative abundance suggest *S. arenicolus* and *H. maculata* were sensitive to these patch-scale attributes. In this ecosystem, landscape-scale fragmentation appears to influence landscape configuration and community disassembly at the patch-scale. Our findings allow us to disentangle drivers of species loss and enhance our understanding of the processes of community disassembly in fragmented landscapes.

Key words: community structure; diversity; dunes sagebrush lizard; ecological dynamics; elements of metacommunity structure; extinction debt; *Holbrookia maculata*; oil and gas development; *Phrynosoma cornutum*; richness; *Sceloporus arenicolus*.

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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 biodiversity loss (Tilman 1994, Vitousek et al.

1997, McGarigal and Cushman 2002, Fahrig 2003). Some biodiversity loss in fragmented landscapes 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 in a fragmented landscape, known as “realized landscape configuration” (sensu Turner et al. 2001), often drives ecological dynamics in heterogeneous habitats and is context dependent (Watling et al. 2011, Didham et al. 2012). For instance, Valladares et al. (2006) observed that herbivory and parasitism by insects on plants were influenced by the distance of the plant or host to the edge of the habitat patch. Because effects of fragmentation depend on ecological context, the variety of landscape patterns examined in fragmentation studies presents challenges to building a theoretical and predictive understanding of the ecological consequences of landscape fragmentation (Lindenmayer and Fischer 2007, Didham et al. 2012).

Two models exist that deal with these ecological consequences of landscape fragmentation. One is the landscape continuum model, which considers both spatial and temporal dimensions of landscape fragmentation (McIntyre and Hobbs 1999) and it serves as an alternative to the more traditional fragmentation model derived from the theory of island biogeography (MacArthur and Wilson 1967). The traditional fragmentation model assumes a clear distinction between patches and the matrix within which they are embedded, and that all species 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), and models based on the theory of island biogeography may apply in these cases. 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. However, in some heterogeneous land-

scapes, 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). In the continuum model, the assumption that species are restricted to isolated patches is relaxed and therefore species are expected 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) further advances understanding of ecological effects of fragmentation. The IC integrates expectations of traditional fragmentation theory and the continuum model by considering both interdependence of landscape effects on species and the interdependence of species’ responses to landscape change. Thus, identification of landscape change and responses of multiple interacting species due to landscape fragmentation can be examined on a case-by-case basis (Didham et al. 2012). Community structure in the IC model is evaluated and classified according to stochastic processes, species-specific responses to abiotic conditions, or direct and indirect interactions between species (Lortie et al. 2004).

The purpose of this study is to characterize how landscape pattern influences community structure in a landscape where fragmentation is obvious, but isolation of patches within the surrounding matrix is unclear. Heterogeneity of landscape pattern can result in the maintenance of species diversity at the regional scale (Fischer et al. 2005, Bell and Donnelly 2006). For instance, Fischer et al. (2005) found lizard species responded individually to environmental gradients in a fragmented landscape and there was no regional species loss. However at the local scale, we should expect a reduction in diversity because of loss of species’ habitat (Tilman et al. 1994). Furthermore, landscape configuration and habitat heterogeneity may also be directly linked to population dynamics (McCoy and Mushinsky 1999, Ryberg et al. 2013). The vigor of localized populations can vary with landscape configuration and changes in landscape condition due to fragmentation can result in localized population

sinks, even in continuous habitat (Ryberg et al. 2013). Species loss due to fragmentation is the final consequence of a process of diminishing populations. Thus, even moderate habitat destruction may create an extinction debt, leading to deterministic local extinctions over the course of generations.

The Mescalero-Monahans shinnery sands ecosystem is a naturally patchy landscape found in southeastern New Mexico and adjacent west Texas, USA, characterized by expanses of semi-vegetated dunes and hummocks with naturally occurring sandy depressions called sand dune blowouts. Dune blowouts are open patches in a matrix of vegetation dominated by shinnery oak (*Quercus havardii*) that are created and maintained by the interaction among sand, wind, and the growing shinnery oak. The ecosystem exists atop the Permian Basin where extraction of oil and gas over the past century has resulted in landscape fragmentation due to construction of “oil fields” comprised of well pads and structures inter-connected by extensive networks of roads. Fragmentation by roads and well pads results in habitat loss and subdivision, degradation, and isolation of habitat patches, all of which have consequences for the resident species (Smolensky and Fitzgerald 2011, Leavitt 2012).

To examine community-level consequences of landscape fragmentation, we quantified abundances of lizard species in a multi-site and spatially replicated study, in fragmented and non-fragmented locations. Our research design allowed us to quantify community structure, environmental variables, and landscape configuration on fragmented and non-fragmented sites and integrate findings to characterize how fragmentation of shinnery dunes landscapes impacts lizard communities. To address the first overarching question, “How does community structure differ between fragmented and non-fragmented communities?”, we tested several predictions derived from fragmentation theory. The IC concept predicts species respond individually to fragmentation via a process of progressive species declines and losses consistent with the notion of community disassembly (sensu Zavaleta et al. 2009). To test this, we applied analyses of metacommunity structure (Leibold and Mikkelson 2002) and identified patterns in terms of species loss, gain, and changes in

abundance. The second question to be answered was, “How does landscape configuration and variation in small-scale environmental variables differ between non-fragmented and fragmented areas?” At relatively large scales in the shinnery sand dune ecosystem, roads and well pads clearly alter environmental structure and landscape configuration. As such, we expected to find meaningful differences in patch characteristics and configuration of patches in the shinnery dune landscape between non-fragmented and fragmented sites. We predicted landscape change attributable to fragmentation at regional scales would correlate with landscape metrics that indicate habitat quality for lizard species. We also predicted large-scale environmental change due to fragmentation would influence smaller-scale landscape configuration. To test for such influences, we compared small-scale environmental variability between fragmented and non-fragmented areas. Finally, while anticipating lower diversity in fragmented areas, we predicted small-scale environmental structure would be associated with species diversity.

MATERIALS AND METHODS

Study area

The Mescalero-Monahans shinnery sands lies in 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 consist 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 shinnery oak being the most common plant (Peterson and Boyd 1998, Mills 2001, Leavitt 2012). There are potentially as few as six (Mills 2001) or as many as 11

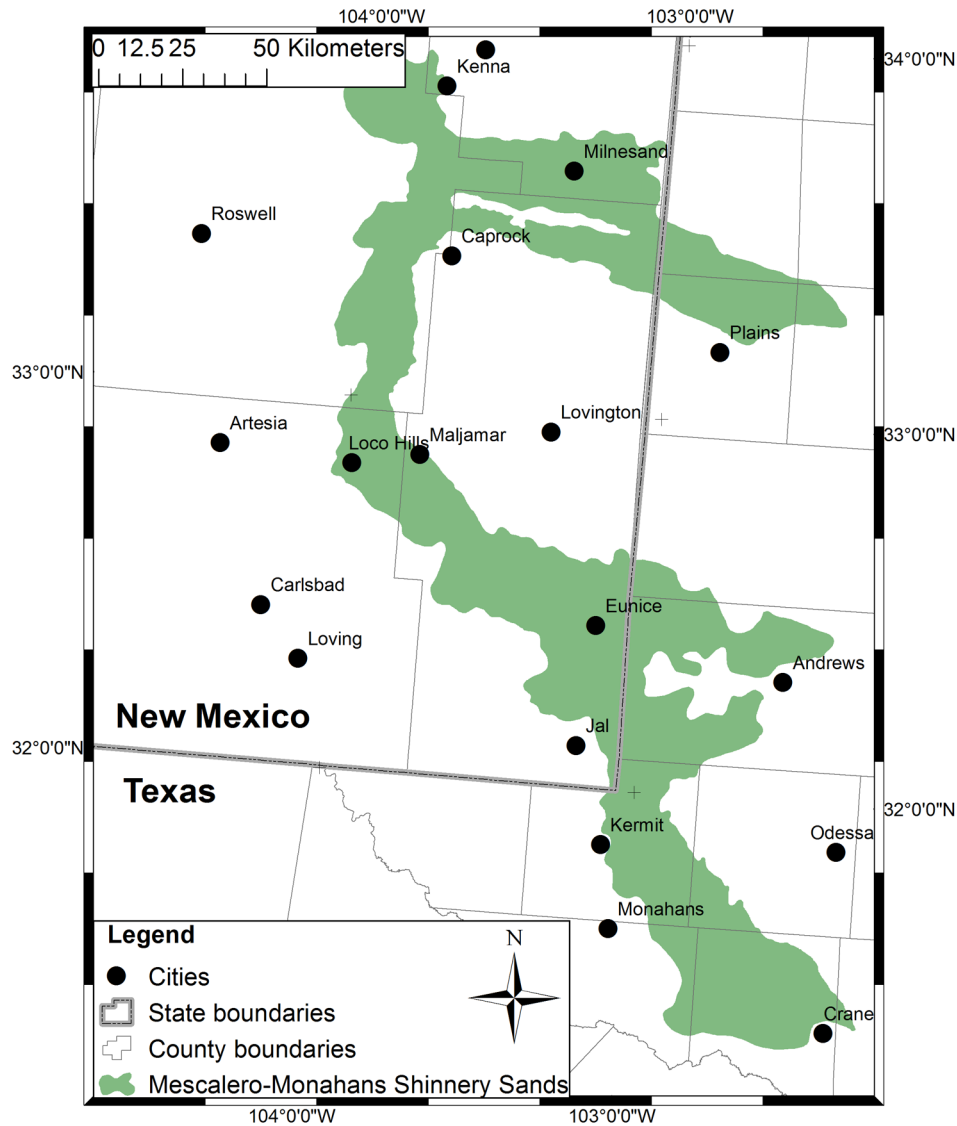


Fig. 1. The Mescalero-Monahans shinnery sands ecosystem of southeastern New Mexico and west Texas. This interpretation of the extent of the ecosystem was shown in Griffith et al. (2004) and Griffith et al. (2006) in broader mapping of ecoregions in New Mexico and Texas.

(Neville et al. 2007) plant associations found within the Mescalero-Monahans shinnery sands. 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*), 3 teiids (*Aspidozelis gularis*, *A. 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

We sampled the lizard communities in trapping grids at nine fragmented and eighteen non-fragmented sites ($n = 27$) from April–September of 2009, 2010, and 2011. Sites were categorized as fragmented if they occurred in a landscape with more than 13 oil well pads per section (2.59 km^2) interconnected with networks of roads. 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>). Each of the 27 sites had a 5 by 6 grid of 30 pit traps (20-L plastic buckets) spaced 20 m apart, making a total of 810 traps. Each trapping grid sampled an area of 1.2 ha. Sampling periods lasted 4 trap-days; 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, we clipped a 1.2 ha area corresponding to the location of each trapping grid from a landcover layer in ArcGIS 9.3 (ESRI 2008; Environmental Systems Research Institute, Redlands, CA). The landcover layer was derived from satellite imagery (Neville et al. 2007), and classification of sand-dune blowouts and areas of open sand was derived from 1m digitally rectified ortho-quarterquads. We used the program FRAG-STATS (McGarigal et al. 2002) to calculate five class metrics (percent land cover, number of patches, total area, aggregation index, and perimeter area ratio) for “Sand” (open sand, including shinnery dune blowouts) and “Shinnery Oak Duneland” (shinnery oak dominated vegetation) landcover classes and one landscape metric (total edge) for each trapping location.

Statistical analyses

We calculated species richness, total captures,

and diversity ($\Delta 1$: Hurlbert 1971, Olszewski 2004) at each site for comparisons between non-fragmented and fragmented groups. We conducted analysis of similarity (ANOSIM: Clarke 1993) on log-transformed lizard abundance at each site 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 in low abundance at two trapping grids). For this analysis, we selected the Bray-Curtis dissimilarity metric because it ignores shared absences between sites (Field et al. 1982). We applied non-metric multidimensional scaling (NMDS) to log-transformed lizard abundance data to visualize differences between non-fragmented and fragmented groups. We 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 abundances from 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. We 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 our data because it was

Table 1. Abundance and diversity measures for lizards in non-fragmented and fragmented groups in the Mescalero-Monahans shinnery sands ecosystem, New Mexico. Significant ($P \leq 0.05$) results from Wilcoxon tests are shown in bold.

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

clear that after three years of intensive trapping, all species present at each site were known. We ran 1000 iterations to make comparisons between null and observed community matrices. We 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).

We conducted a multivariate analysis of variance (MANOVA) to test the null hypothesis of no difference in environmental variables between non-fragmented and fragmented groups. We 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. We 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. We 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 as a whole (Table 1), but there were fewer species present on trapping grids in fragmented areas. Species diversity (Δ_1) was higher in the non-fragmented group compared to the fragmented group due to higher average captures per site for two species in the non-fragmented group, *S. arenicolus* and *H. maculata* (Table 1). Nearly all species were captured in lower numbers in the fragmented group with the exception of *U. stansburiana*, which was slightly more abundant at fragmented locations (Table 1).

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 in the non-fragmented and fragmented landscapes (Fig. 2). 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 this axis was correlated with captures of *H. maculata*, *S. arenicolus*, total captures, and Δ_1 . Species richness, Δ_1 , captures of *S. arenicolus*, and *S. consobrinus* were negatively correlated with NMDS axis 1 (Table 2). Total captures and *U. stansburiana* captures were positively correlated

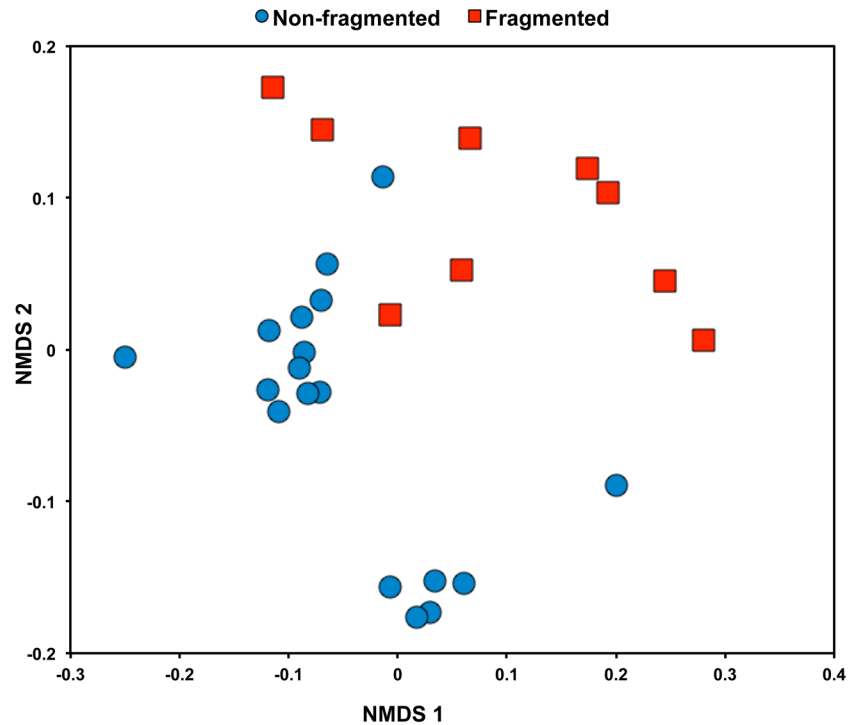


Fig. 2. Two-dimensional ordination of 27 lizard communities from a non-metric multidimensional scaling (NMDS) of Bray-Curtis dissimilarity values of species relative abundances by trapping grid in the Mescalero-Monahans shinnery sands ecosystem, New Mexico. Stress = 0.12.

with NMDS axis 1 (Table 2). Total captures, Δ_1 , *A. marmorata*, *H. maculata*, and *S. arenicolus* were negatively correlated with NMDS axis 2 (Table 2). The NMDS axis 2 showed the greatest spread between the non-fragmented and fragmented groups and this pattern was driven by Δ_1 and *S. arenicolus* captures (Fig. 2, Table 2).

Because lizard communities in 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,

Table 2. Spearman's 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.

Measure	NMDS Axis 1		NMDS Axis 2	
	r	P	r	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***
Abundance				
<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

Table 3. Assessments of coherence, species turnover, and boundary clumping for the non-fragmented and fragmented groups and the idealized pattern of metacommunity structure suggested from analysis of Elements of Metacommunity Structure. Significant ($P \leq 0.05$) results are in bold.

Axis	Coherence			Species turnover			Boundary clumping		Idealized pattern
	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
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
2	4	0.06	6.6 \pm 1.4	8	0.36	16.2 \pm 8.9	1.11	0.29	random

both axes for the fragmented landscape were classified as random due to the lack of coherence (Table 3). 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). In EMS, nestedness or nested subsets refers to sets of species that occupy portions of environmental gradients that are occupied by larger sets of species. 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 suggestive of a quasi-nested subsets model (Table 3) (*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 at all 18 non-fragmented sites but was absent from four of the nine fragmented trapping grids (44%). Other species absent from fragmented areas that contributed to the lack of coherence were *S. consobrinus*, *H. maculata*, and *P. cornutum*.

Non-fragmented and fragmented landscapes differed in a number of environmental variables as demonstrated by MANOVA (Wilks' $\lambda = 0.14$, $F_{17,9} = 3.34$, $P = 0.03$). The number of patches,

patch density, and perimeter area ratio of the Sand cover class were all significantly higher for the non-fragmented landscapes (Table 4). Total area and aggregation index (a measure of the number and compactness of patches) for Sand class were significantly higher for the fragmented areas (Table 4). Differences between trapping grids on the fragmented and non-fragmented areas with regard to general shape and patch counts for the Sand cover class were congruent with the results from the DA. Two of the 18 non-fragmented and two of the 9 fragmented sites were not correctly classified by the DA (Fig. 3). Visual inspection of selected sites demonstrated how total area and aggregation index differed between trapping grids in non-fragmented and fragmented areas (Fig. 3A). The Sand class identified sparsely vegetated open areas in the far left (fragmented) landscape that are connected, creating a configuration of relatively few large patches of relatively open sand compared to the far right (non-fragmented) landscape where natural formations of dune blowouts are numerous and compact (Fig. 3A). The large patch at the bottom center of the fragmented trapping grid is an open area of sparsely vegetated sand that was pushed aside when shinnery dunes were bulldozed during creation of a nearby oil well pad. The far right landscape depicts a relatively undisturbed shinnery dune landscape in a non-fragmented trapping location. Importantly, patch density of Sand class and perimeter area ratio for Sand class loaded high for non-fragmented areas (0.001 and 0.0004, respectively) and total Edge and patch density for Shinnery oak class loaded highest for fragmented grids (-0.003 and -0.002 , respectively). To examine observed patterns in lizard community structure and environmental structure, we compared the

Table 4. Wilcoxon rank sum tests for difference in values (mean \pm SD) 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 in bold.

Environmental variable	Non-fragmented ($n = 18$)	Fragmented ($n = 9$)	W	P
Patch density				
Sand†	3752 \pm 1039	2971 \pm 1083	32.5	0.01**
Shinnery oak†	905 \pm 458	1558 \pm 666	116	0.08
Percent land cover				
Sand†	24.2 \pm 6.7	28.6 \pm 11.1	64	0.40
Shinnery oak†	68.5 \pm 10.4	49.3 \pm 15.7	64	0.40
No. patches				
Sand†	84.1 \pm 23.3	66.6 \pm 24.3	139	0.002**
Shinnery oak†	20.3 \pm 10.3	34.9 \pm 14.9	116	0.08
Total area				
Sand†	0.5 \pm 0.2	0.6 \pm 0.3	33	0.01**
Shinnery oak†	1.5 \pm 0.2	1.1 \pm 0.4	64	0.40
Aggregation index				
Shinnery oak†	95.4 \pm 0.9	93.2 \pm 1.8	63	0.38
Perimeter area ratio				
Sand†	23629 \pm 3294	23245 \pm 2493	143	<0.001***
Shinnery oak†	24863 \pm 3294	23698 \pm 4276	90	0.67
Total edge†	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

† Calculated with FRAGSTATS.

‡ Measured on site using centered point quarter method.

Δ_1 values with the DA scores (Fig. 4). Lizard species diversity was positively correlated with landscape DA scores ($r = 0.47$; $p = 0.02$). Also, none of the fragmented sites had Δ_1 values greater than 0.30, making a clear distinction between these sites and their non-fragmented equivalents.

DISCUSSION

Several lines of evidence in this study reveal how landscape configuration drives lizard community structure in a patchy environment, and how that structure is disrupted when a heterogeneous landscape is fragmented. Species diversity (Δ_1), community membership, and landscape pattern differed between non-fragmented and fragmented areas, demonstrating that community disassembly is occurring where the Mescalero-Monahans shinnery sands landscape has become fragmented. We also identified a consistent, predictable pattern of species losses responsible for the pattern of community disassembly. Although impacts of landscape fragmentation on ecological communities can be 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), our

study is among the first to provide strong insights as to how community structure is disrupted when the landscape is fragmented. Specifically, two species (*H. maculata* and *S. arenicolus*) consistently were captured at fewer sites in fragmented landscapes and occurred in lower abundances on fragmented sites where they were present. Nested community structure in non-fragmented areas was largely due to patterns of occurrence and abundance of *H. maculata*, *P. cornutum*, and *S. consobrinus*. Stochastic losses of these three species also explained random community structure in fragmented areas. We also described significant differences in small-scale habitat features between non-fragmented and fragmented areas, all of which related to size, shape and configuration of patches in the sand cover class (Fig. 3). An important conclusion from our study is that differences in landscape pattern observed at the small scale resulted from large-scale landscape fragmentation (building caliche well pads and roads), and this was associated with the loss of species diversity. Specifically, fragmented sites had fewer large dune blowouts compared to non-fragmented trapping grids. In this region, networks of roads in oil fields, and infrastructure such as pipelines and power-line roads, fragment

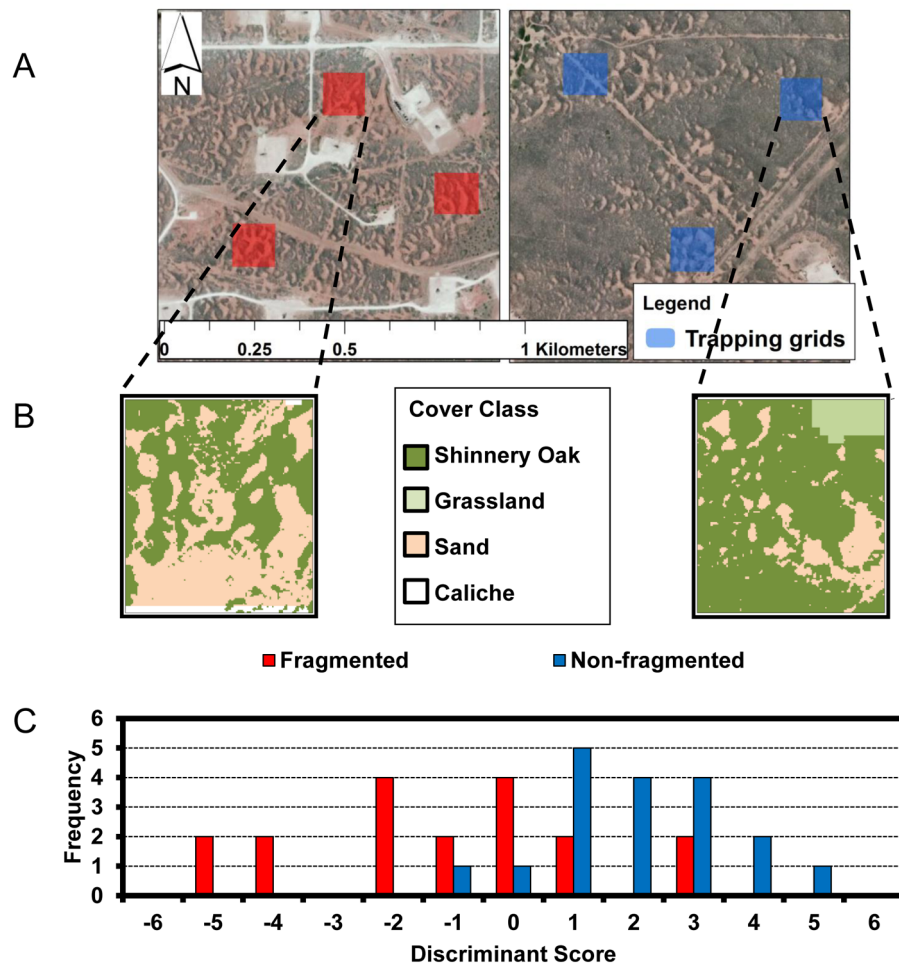


Fig. 3. Examples of fragmented and non-fragmented landscapes, cover classes, and a frequency histogram of discriminant analysis (DA) scores of environmental variation between fragmented and non-fragmented areas. (A) Satellite imagery of fragmented (left) and non-fragmented sites (right). (B) Landscape models representing the trapping grids (1.2 ha) at the extreme end for each grouping in the DA with a legend of cover classes. (C) Frequency histogram of discriminant scores for environmental variables from an analysis of 27 trapping grids classified into non-fragmented and fragmented groups.

large patches of shinnery dunes and increase areas of flat open sand and barren land. *Sceloporus arenicolus*, a habitat specialist on shinnery dune blowouts, and *H. maculata* were apparently sensitive to these kinds of landscape alteration, which helps explain their lower numbers or absence from fragmented trapping sites (Leavitt 2012).

Our results complement findings of prior studies of fragmentation and community structure, and enhance our understanding of regional and local scale impacts of fragmentation (Fischer

et al. 2005, Bell and Donnelly 2006, Hamer et al. 2006). In our case, regional species richness was unchanged by fragmentation, in that all species were present when added up among all fragmented sites. However, richness was consistently lower at individual fragmented sites compared to non-fragmented sites (Table 2). This paradox of intact regional richness and predictable local species loss can be explained by regional variation in local, small-scale community structure. At the regional scale, there is a mix of sites with nested community structure and other sites

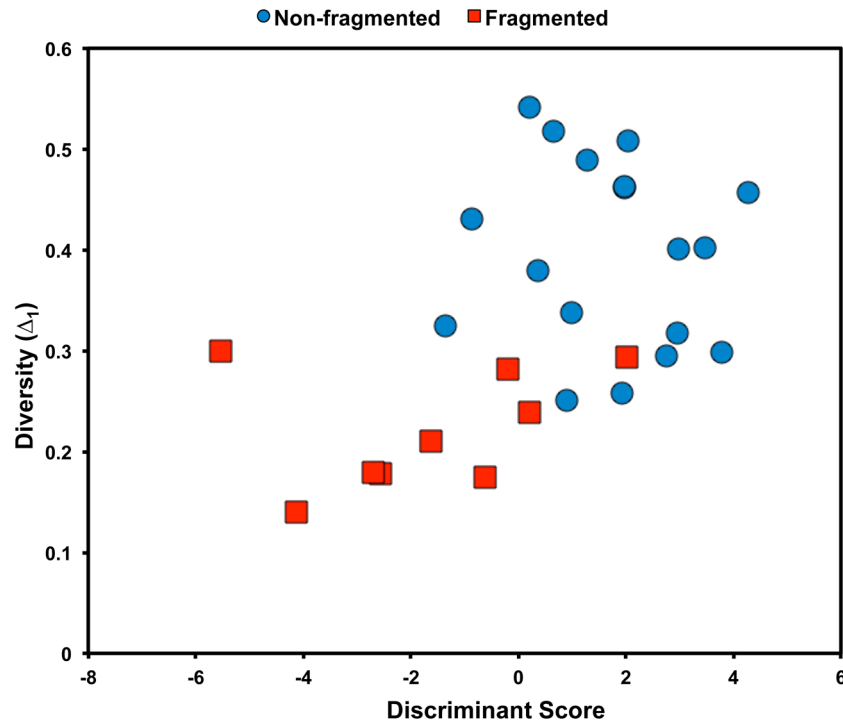


Fig. 4. Correlation between discriminant scores and species diversity (Δ_1) for fragmented and non-fragmented trapping grids in the Mescalero-Monahans shinnery sands, New Mexico.

exhibiting varying degrees of community disassembly. Similar patterns of disassembly have been documented in forest remnants for amphibians and reptiles (Fischer et al. 2005, Bell and Donnelly 2006), in grasslands bird communities (Hamer et al. 2006), and in island mammal communities (Okie and Brown 2009). In the Mescalero-Monahans shinnery sands, four species (*A. marmorata*, *A. sexlineata*, *S. arenicolus*, and *U. stansburiana*) were present at every site located in non-fragmented landscapes. A striking result was *S. arenicolus* was all but lost from all fragmented sites. Lower Δ_1 on fragmented trapping grids was driven by lower numbers and absences of *S. arenicolus* and *H. maculata*, suggesting a deterministic processes congruent with predictions of extinction debt (Tilman et al. 1994) and community disassembly (Zavaleta et al. 2009). In this system, these two species represent the early losers in the process of disassembly following fragmentation. 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) including the sort of predictable localized extinctions we observed (Zavaleta et al. 2009). We determined that patch configuration, patch counts, and aggregation metrics of the Sand cover class explained reduced diversity at fragmented sites. Shinnery dune blowouts are geomorphological features of dune systems however, flat open sand and barren land are not common naturally occurring features of this landscape nor are they habitat for *S. arenicolus*. In fragmented areas, flat open land generally was a result of disturbance and is not used by *S. arenicolus* (Leavitt 2012, this study). The disturbed sand shown in Fig. 3A is an example of open area in the Sand class measure that is not a shinnery dune blowout formation. The spatial classification of the Sand cover class included some open and barren areas in fragmented sites. As such, fragmented landscapes contributed more overall area to the Sand class, but the area was more due to flat open areas and barren areas resulting from anthropogenic dis-

turbance; these areas in the Sand class are not true sand dune blowouts. Fragmented sites also had fewer patches of Sand cover class than non-fragmented trapping grids, because fragmented sites had larger areas of open sand and barren ground and relatively fewer patches of intact shinnery dunes with blowouts.

The end result of fragmentation in our study system was an altered landscape configuration generally consisting of smaller, fewer, and more dispersed sand dune blowouts, resulting in a landscape that is less suitable for persistence of *S. arenicolus*. The ecological specialist *S. arenicolus* was sensitive to fragmentation and occurred in much lower abundance at fragmented sites. *Sceloporus arenicolus* is dependent on landscapes with many shinnery dune blowouts densely arranged in a matrix of shinnery oak (Chan et al. 2009, Fitzgerald and Painter 2009, Smolensky and Fitzgerald 2011, Leavitt 2012, Ryberg et al. 2013). It appears landscape fragmentation of the magnitude tested in this study is associated with less presence and abundance of *S. arenicolus*. In contrast, more patches of the Sand cover class were consistently present in the shinnery oak duneland cover class in non-fragmented grids, where *S. arenicolus* was strikingly more abundant. This conclusion is consistent with other detailed population studies of *S. arenicolus*. Ryberg et al. (2013) found population dynamics of *S. arenicolus* was tightly linked to the landscape configuration of shinnery dunes, specifically area of shinnery dune blowouts, shinnery dune blowout contiguity, and east and west aspects of dune blowouts were correlated with size of lizard neighborhoods.

Occupancy and abundance of *H. maculata* was also reduced at fragmented sites. *Holbrookia maculata* occurs in various habitats throughout a broad geographic range (Degenhardt et al. 1996), and tends to occur in relatively flat areas. In our study sites *H. maculata* is observed using caliche roads and well pads, thus we did not predict its sensitivity to landscape fragmentation. We did not find a clear association between landscape metrics and numbers of *H. maculata*, presumably because its populations may be responding to landscape features, biotic, or abiotic resources that have yet to be identified. The observation that *H. maculata* was sensitive to fragmentation, but not in the same ways as *S. arenicolus* drives

home the point that fragmentation triggers distinct mechanisms of population decline for different species and these may operate at different scales.

This work presents novel findings that demonstrate how fragmentation at the landscape scale can influence smaller-scale community dynamics in a heterogeneous environment. We found a predictable pattern of community disassembly at local scales that we attribute to fragmentation, while species richness at the regional scale was not affected. Species responded differently to fragmentation, and future research in this system could identify thresholds of community change in response to fragmentation and fine-scale behavioral and demographic responses of species. In this study, networks of roads interconnecting between 3 and 15 well pads per section encompass thresholds of sensitivity of several species to landscape fragmentation. An overarching implication for conservation is that increased knowledge about sensitivity of species to fragmentation will inform land use practices aimed at ensuring persistence of species.

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