



Linking irreplaceable landforms in a self-organizing landscape to sensitivity of population vital rates for an ecological specialist

Wade A. Ryberg,*†§ Michael T. Hill,* Charles W. Painter,‡ and Lee A. Fitzgerald*

*Department of Wildlife and Fisheries Sciences, Biodiversity Research and Teaching Collections, Texas A&M University, College Station, TX 77843, U.S.A.

†Texas A&M Institute of Renewable Natural Resources, 1500 Research Parkway, College Station, TX 77843, U.S.A.

‡Endangered Species Program, New Mexico Department of Game and Fish, Santa Fe, NM 87507, U.S.A.

Abstract: Irreplaceable, self-organizing landforms and the endemic and ecologically specialized biodiversity they support are threatened globally by anthropogenic disturbances. Although the outcome of disrupting landforms is somewhat understood, little information exists that documents population consequences of landform disturbance on endemic biodiversity. Conservation strategies for species dependent upon landforms have been difficult to devise because they require understanding complex feedbacks that create and maintain landforms and the consequences of landform configuration on demography of species. We characterized and quantified links between landform configuration and demography of an ecological specialist, the dunes sagebrush lizard (*Sceloporus arenicolus*), which occurs only in blowouts (i.e., wind-blown sandy depressions) of Shinnery oak (*Quercus havardii*) sand-dune landforms. We used matrix models to estimate vital rates from a multisite mark-recapture study of 6 populations occupying landforms with different spatial configurations. Sensitivity and elasticity analyses demonstrated demographic rates among populations varied in sensitivity to different landform configurations. Specifically, significant relationships between blowout shape complexity and vital rate elasticities suggested direct links between *S. arenicolus* demography and amount of edge in Shinnery oak sand-dune landforms. These landforms are irreplaceable, based on permanent transition of disturbed areas to alternative grassland ecosystem states. Additionally, complex feedbacks between wind, sand, and Shinnery oak maintain this landform, indicating restoration through land management practices is unlikely. Our findings that *S. arenicolus* population dynamics depended on landform configuration suggest that failure to consider processes of landform organization and their effects on species' population dynamics may lead to incorrect inferences about threats to endemic species and ineffective habitat management for threatened or endangered species. As such, successful conservation of these systems and the biodiversity they support must be informed by research linking process-oriented studies of self-organized landforms with studies of movement, behavior, and demography of species that dwell in them.

Keywords: arid ecosystems, demography, dunes sagebrush lizard, elasticity, inland sand dunes, *Sceloporus arenicolus*

Conexión de Formaciones Terrestres Irreemplazables en un Terreno Auto-organizado con la Sensibilidad de las Tasas Vitales de la Población de un Especialista Ecológico

Resumen: Los accidentes geográficos auto-organizados e irremplazables y la biodiversidad endémica y ecológicamente especializada que éstos mantienen están amenazados globalmente por perturbaciones antropogénicas. Aunque el resultado de perturbar los accidentes geográficos es conocido de cierta forma, existe poca información que documente las consecuencias poblacionales de la perturbación de éstos sobre la biodiversidad endémica. Las estrategias de conservación para especies que dependen de los accidentes geográficos han sido difíciles de concebir ya que requieren del entendimiento de las retroalimentaciones complejas las crean y

§Address for correspondence: Texas A&M Institute of Renewable Natural Resources, 1500 Research Parkway, College Station, TX 77843, U.S.A., email waryberg@tamu.edu

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*mantienen y a las consecuencias de su configuración sobre la demografía de las especies. Caracterizamos y cuantificamos las conexiones entre la configuración de las formaciones terrestres y la demografía de un especialista ecológico, la lagartija de artemisa de las dunas (*Sceloporus arenicolus*), que sólo ocurre en accidentes geográficos de dunas de arena con depresiones arenosas causadas por el viento y la presencia del roble *Quercus havardii*. Usamos modelos matriciales para estimar las tasas vitales a partir de un estudio multi-sitio y multi-marca de seis poblaciones que ocupaban accidentes geográficos con diferentes configuraciones espaciales. Los análisis de sensibilidad y elasticidad demostraron que las tasas demográficas dentro de las poblaciones variaron en sensibilidad a las diferentes configuraciones de accidentes geográficos. En específico, las relaciones significativas entre la complejidad de formas de las depresiones arenosas y la elasticidad de las tasas vitales sugieren una conexión directa entre la demografía de *S. arenicolus* y la cantidad de bordes en los accidentes geográficos de dunas arenosas y robles. Estos accidentes geográficos son irremplazables, con base en la transición permanente de áreas perturbadas a estados alternativos de ecosistemas de pastizales. Además, la retroalimentación compleja entre el viento, la arena y los robles mantiene a este accidente geográfico, lo que indica que la restauración por medio del manejo de suelos no es probable. Nuestro hallazgo de que las dinámicas poblacionales de *S. arenicolus* dependen de la configuración de los accidentes geográficos sugiere que el fracaso en la consideración de los procesos de organización de los accidentes geográficos y sus efectos sobre las dinámicas poblacionales de las especies puede llevar a suposiciones incorrectas sobre las amenazas para las especies endémicas y el manejo inefectivo de hábitat para especies amenazadas o en peligro. Por esto, la conservación exitosa de estos sistemas y la biodiversidad que mantienen debe informarse con investigaciones que conecten estudios orientados a procesos sobre los accidentes geográficos auto-organizados con estudios de movimiento, comportamiento y demografía de especies que habiten en ellos.*

Palabras Clave: demografía, dunas de arena tierra adentro, ecosistemas áridos, elasticidad, lagartija de artemisa de las dunas, *Sceloporus arenicolus*

Introduction

Self-organized landforms support endemic and ecologically specialized biodiversity in ecosystems worldwide (e.g., Scheffer et al. 2001; Rietkerk et al. 2004; Le Saout et al. 2013). In polar, alpine, arid, savannah, coastal, and marine ecosystems, self-organized landforms consist of patterned ground and seabed, complex vegetation structure, and various arrangements of dune and reef types (Werner & Fink 1993; Werner 1995, 1999; Kessler & Werner 2003; Puig et al. 2012). Although it is implicitly understood that endemic biodiversity share a common fate with landforms in which they evolved (Vega et al. 2000), there is little understanding of the mechanisms by which landform structures influence population dynamics and persistence of species over time.

Traditionally, distribution and demographic stability of populations across structured landscapes has been evaluated in terms of size and degree of separation of distinct habitat patches (e.g., Wiens 1989; Levin 1992; Hanski 1999). Landscapes with self-organized landforms merit different consideration, however, because landscape structure frequently emerges within individual habitat patches (Rietkerk et al. 2004). Recent studies suggest that spatial heterogeneity within habitat patches can also drive regional population dynamics by shaping the movement, behavior, and habitat selection of organisms (Ryberg et al. 2013; Ye et al. 2013). Thus, we predicted different landform configurations should influence species' demographic vital rates and therefore

persistence. Dependencies between ecological specialists and the configuration of landforms they occupy have not been quantified in any systems we are aware of, and understanding them will help prioritize conservation of landscape features necessary for persistence of specialist species.

In general, landform configurations emerge from self-reinforcing, biogeomorphic processes linked across spatial and temporal scales (e.g., Werner & Fink 1993; Werner 1999; Puig et al. 2012). Self-reinforcing processes are typically fragile and exhibit weak resilience to disturbance (Folke et al. 2004). Even slow and gradual disturbances can lead to catastrophic shifts in structure and function of landforms and have consequences for endemic biodiversity they support (Vega et al. 2000; Scheffer et al. 2001). Restoration of landforms, such as the configuration of coastal and inland dunes, structure of reefs, or complex patterns of vegetation, has proven difficult or impossible, making such landforms irreplaceable (Goudie & Seely 2011; DeAngelis 2012). Although disruption of irreplaceable landforms is somewhat understood (reviewed in DeAngelis 2012), surprisingly little information is available to document consequences of landform disturbance on endemic biodiversity. Failure to understand complex feedbacks that create and maintain landforms and the consequences of resulting landscape structure for demography of endemic, threatened, or endangered species may lead to incorrect inferences about threats to populations and causes of their decline (Rietkerk et al. 2004).

Arid ecosystems cover nearly 30% of Earth's land surface and many have been identified as irreplaceable areas for both landforms and biodiversity due to their geomorphological richness and high levels of endemism and ecological specialization (ranked second in species, family, and endemic richness [MEA 2005; Goudie & Seely 2011; Le Saout et al. 2013]). Landforms in arid systems and the endemic biodiversity they sustain are threatened globally by desertification, climate change, habitat conversion, and fragmentation (MEA 2005; Kefi et al. 2007; Goudie & Seely 2011). Well-recognized examples of degraded landforms are found in dune systems worldwide and in patterned vegetative formations such as tiger bush in sub-Saharan Africa (DeAngelis 2012). Once disturbed, these systems shift to alternative stable states with unique sets of biotic and abiotic conditions, which makes them very difficult to restore (DeAngelis 2012). Indeed, while deteriorating processes act swiftly at broad scales, natural reclamation processes occur slowly or not at all for these irreplaceable landforms (Tsoar 1990).

Endemism and ecological specialization are pervasive wherever arid landforms exist, because organisms evolve extreme morphological, physiological, and behavioral adaptations to exploit unique and isolated microhabitats created by landforms (e.g., Arnold 1995). In particular, coastal and inland dune systems on every continent but Antarctica host a variety of endemic, sand-dwelling (psammophilic) biodiversity (e.g., Morton et al. 1995; Rodrigues 1996; Simmons et al. 1998). Conservation and management strategies for biodiversity occupying such systems have been difficult to devise because they require an understanding of complex feedbacks that create and maintain irreplaceable landforms and the consequences of landscape structure on demography of species (Rietkerk et al. 2004).

We quantified how variation in dune landform configuration influences demography of Dunes Sagebrush Lizards (*Sceloporus arenicolus*). The Dunes Sagebrush Lizard is endemic to the Mescalero-Monahans Sandhills ecosystem of southeastern New Mexico and adjacent west Texas (Degenhardt et al. 1996). This psammophilic habitat specialist resides in parabolic sand-dune landforms created from an interaction between wind, sand, and growing Shinnery Oak (*Quercus havardii*) that stabilizes the parabolic dunes (Fitzgerald & Painter 2009; Laurencio & Fitzgerald 2010). As seen in other parabolic dune systems, strong winds erode a section of vegetated sand creating a depression called a blowout. The sand from blowouts is deposited on the leeward slope of a parabolic-shaped dune with "arms" held in place by vegetation (Wasson & Hyde 1983; Rietkerk et al. 2004). Self-organized patterns evident in parabolic dune fields are an emergent property of a complex system (Werner 1995) and can be characterized by landform configurations that vary from irregular mosaics to linear chains or bands of vegetated dunes mixed with blowouts (Fig. 1) (HilleRisLambers et al. 2001).

Within Shinnery Oak sand-dune landforms, *S. arenicolus* prefers large blowouts with steep slopes and coarse sand-grain size (e.g., Fitzgerald & Painter 2009; Ryberg et al. 2012; Hibbitts et al. 2013), and it moves among interconnected blowouts of varying size and shape. The spatial configuration of blowouts across dune landforms either constrains or facilitates *S. arenicolus* movement, leading to local aggregations of lizards or neighborhoods of different sizes (Ryberg et al. 2013). Larger neighborhoods exhibit higher recruitment and population diffusion rates, presumably acting as sources for smaller neighborhood sinks with negligible recruitment. This diffusion mechanism of population connectivity is very different from the classic source-sink metapopulation dynamic, where individuals emigrate among distinct patches. Instead, population connectivity appears to be driven by spatially variable recruitment, which is correlated with specific metrics of landform configuration (Ryberg et al. 2013). To test our prediction that landform configuration determines variation in vital rates, we designed a study to characterize variation in Shinnery oak sand-dune landform configuration and to assess its influence on vital rates and population dynamics of Dunes Sagebrush Lizards.

Methods

Data Collection

To estimate vital rates of *S. arenicolus*, we sampled lizards at 6 sites within an undisturbed Shinnery oak sand-dune landform that varied in landform configuration (Fig. 1). In a multisite mark-recapture study, we used pitfall trapping grids consisting of 36 (20 L) buckets in a 6 × 6 pattern spaced 15 m apart. Each site was 5625 m², large enough to contain dozens of dune blowouts. Pairwise distance between sites ranged from 0.6 to 3.6 km. We observed no lizard immigration among sites over 5 years, so we treated sites as independent demographic units (Ryberg et al. 2013).

We sampled lizards during peak activity season (Fitzgerald & Painter 2009) in June 2005, June–July 2006, May–September 2007–2008, and April–September 2009. We opened traps 1 week each month, which resulted in 16–19 trapping occasions over the 5 years. We measured snout-vent length (SVL) and mass for all lizards captured, noted sex, and determined reproductive status of females by palpation. Each lizard was marked permanently by toe clipping, and capture location was noted. We estimated vital rates from multiple recaptures of 21, 29, 10, 41, 17, and 12 individuals from sites 1 to 6, respectively.

Model Development and Sensitivity Analysis

From the mark-recapture data set, we estimated individual *S. arenicolus* growth rates for each site (Supporting

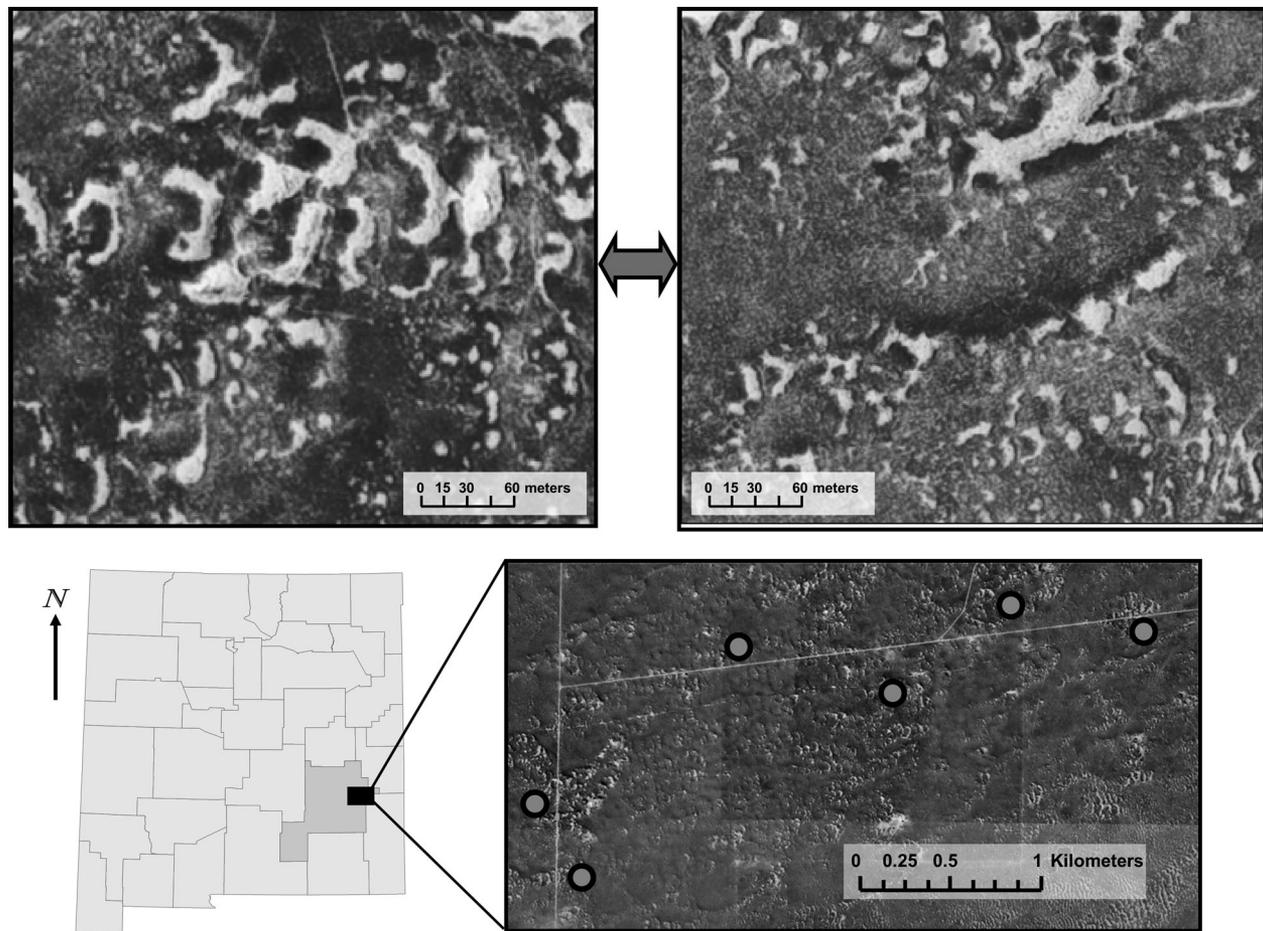


Figure 1. Locations of 6 *S. arenicolus* demographic study sites in Chaves County, New Mexico (U.S.A.) (bottom). Shinnery oak sand-dune landform configuration across sites varied from linear chains of dunes with blowouts (top left) to irregular mosaics (top right).

Information) and size at sexual maturity for females. Juvenile growth rates were higher than adult growth rates ($F_{1,213} = 378.1$, $P < 0.001$); male and female growth rates were indistinguishable ($F_{1,160} = 0.1$, $P = 0.730$). Size at sexual maturity for females was 47 mm (SVL), determined by identifying the smallest gravid individual. Based on growth rates and size at maturity, we determined a 2-stage model structure with juveniles and adults would most accurately reflect demography of natural populations (Supporting Information) because most individual lizards reach sexual maturity within their first year (Fitzgerald & Painter 2009). There was no evidence of variation in fertility rate with female size ($r^2 = 0.008$, $F_{1,107} = 0.828$, $P = 0.365$).

In this model, female fertility (f_a) represents the number of new individuals produced by an adult female during the reproductive season. Juvenile survival (s_j) represents the expected proportion of individuals in the juvenile class during their first season that reached the adult class in their second season, and adult survival (s_a) represents the expected proportion of adults during one season that survived to the next season. Female

fertility (f_a) was estimated as the mean number of eggs per female for each study site over the 5-year sample period, which assumes no egg mortality. Sensitivity analysis allowed evaluation of this assumption. There were too few juvenile recaptures in the mark-recapture data set to estimate juvenile survival reliably. Thus, juvenile survival (s_j) was estimated for each study site with the methods of Pike et al. (2008), which illustrate how the probability of juvenile survival can be quantified from known population parameters under the simplifying assumption that overall population sizes remain stable through time. When the duration of a female's reproductive life and the number of offspring she is likely to produce annually are known, then her lifetime reproductive output can be calculated. If the age of maturity and adult survival rate are also known, then the juvenile survival rate necessary to maintain the population in a stable numerical equilibrium can be calculated using the following equation:

$$s_j = \sqrt{\frac{2(1 - s_a)}{nc}}, \quad (1)$$

Table 1. Estimated population growth rate (λ) and current values, sensitivities, and elasticities for vital rates of *S. arenicolus* across all study sites.

Site	λ	Vital rate*	Value	Sensitivity	Elasticity
1	1.08	s_j	0.19	1.62	0.29
		s_a	0.65	0.71	0.43
		f_a	2.46	0.13	0.29
2	1.14	s_j	0.20	1.50	0.26
		s_a	0.74	0.74	0.48
		f_a	2.32	0.13	0.26
3	1.26	s_j	0.29	1.54	0.35
		s_a	0.57	0.65	0.29
		f_a	3.00	0.15	0.35
4	1.16	s_j	0.23	1.44	0.29
		s_a	0.69	0.71	0.42
		f_a	2.36	0.14	0.29
5	1.22	s_j	0.35	1.11	0.32
		s_a	0.65	0.68	0.36
		f_a	2.00	0.20	0.32
6	1.21	s_j	0.27	1.36	0.30
		s_a	0.69	0.70	0.40
		f_a	2.33	0.16	0.30
Mean (SD)	1.18 (0.06)	s_j	0.26 (0.06)	1.42 (0.18)	0.30 (0.03)
		s_a	0.67 (0.06)	0.70 (0.03)	0.40 (0.07)
		f_a	2.41 (0.33)	0.15 (0.03)	0.30 (0.03)

*Definitions: s_j , juvenile survival; s_a , adult survival; f_a , female fertility.

where s_j is the annual juvenile survival rate, a is the age at first reproduction, n is the number of clutches per year, c is the number in a clutch, and s_a is the annual adult survival rate (Supporting Information). Age at first reproduction (a) was calculated as the time from initial hatchling capture to gravid adult recapture. Annual adult survival (s_a) was calculated as the product of estimated monthly adult survival rates reported in Ryberg et al. (2013). Incorporating these vital rates into the model structure yields population projection matrices for each of the 6 study sites (Table 1 & Supporting Information).

Using these projection matrices, we integrated each set of vital rates to yield an estimate of population growth (λ) for each study site (Table 1). Next, we conducted a sensitivity analysis on each vital rate to determine which contributed most to population growth in each of the 6 demographic units. Specifically, we calculated sensitivity (S_{ij}) of λ_{site} to changes in matrix elements x_{ij} from the eigenvectors of the projection matrix using the following formula (Caswell 2001):

$$S_{ij} = \frac{\partial \lambda_{\text{site}}}{\partial x_{ij}} = \frac{v_i w_j}{\sum_{i=1}^y v_i w_i}, \quad (2)$$

where y is the number of classes in the matrix, w_j is the j th element of the dominant right eigenvector, v_i is the i th element of the dominant left eigenvector of the projection matrix, and the denominator is the scalar product of the 2 eigenvectors.

Elasticity analyses are often conducted when comparing sensitivity values among vital rates whose absolute values exhibit different magnitudes or scales of variance. By rescaling values of vital rates to reflect proportional rather than absolute differences, we used elasticity analyses to

measure proportional changes in population growth (λ) that resulted from proportional changes in each vital rate. We calculated elasticity (E_{xi}) of λ_{site} to changes in matrix elements x_i as

$$E_{xi} = \frac{\partial \lambda_{\text{site}} / \lambda_{\text{site}}}{\partial x_i / x_i}, \quad (3)$$

where the numerator is the proportional change in λ_{site} and the denominator is the proportional change in x_i (Morris & Doak 2002). Population analyses were conducted in MATLAB version 7.9.

Landscape Metrics

We characterized variation in landform configuration for the 6 sites by mapping their locations on 2 digitized land-cover layers in a geographic information system (GIS). One layer was a classification of vegetation types for sites at a 1-m resolution derived from Landsat Enhanced Thematic Mapper satellite imagery and aerial photos (Neville et al. 2005). The other layer was a classification of dune blowouts derived directly from 1-m digitally rectified orthoquarterquads taken in 2004 using ArcInfo (Environmental Systems Research Institute). The spatial extent of our landscape analysis was selected to match the scale of demographic data. Specifically, we measured landform configuration from 100×100 m plots framing each sampling grid (75 m/side) with an additional 12.5 m buffer per side. We clipped these plots from the land-cover layers and calculated landscape metrics with Program FRAGSTATS (McGarigal et al. 2002). Only blowout and Shinnery oak land-cover types occurred in plots. Because lizards occur in Shinnery oak sand-dune blowouts

(Fitzgerald & Painter 2009), we focused landform configuration calculations on the blowout land-cover type.

We quantified blowout area (area), radius of gyration (gyrate), fractal dimension (FRAC), landscape shape index (LSI), and Euclidean nearest neighbor (ENN) distance for each site (defined in Supporting Information). None of these variables were significantly correlated (Pearson's r , $P > 0.05$). Blowout area measured the amount of habitat. Larger blowouts were thought to permit higher quality home ranges for *S. arenicolus* and thus higher survival and fecundity. Radius of gyration and fractal dimension measured blowout spatial extent and shape complexity, respectively. Controlling for area, more extensive, irregularly shaped blowouts with a lot of edge were thought to constrain home range size and quality and reduce survival and fecundity. Landscape shape index and ENN distance were used to measure blowout aggregation and isolation, respectively. Shinnery oak sand-dune landforms composed of disaggregated or isolated blowouts were thought to be more difficult to traverse for *S. arenicolus*, leading to lower survival and fecundity in those areas.

Results

Juvenile survival (s_j) estimates were 27–54% lower than adult survival (s_a) estimates (Table 1). Comparing across sites, variation in juvenile (s_j) and adult survival (s_a) and female fertility (f_a) was low (Table 1). Vital rates were not significantly correlated across sites (Pearson's r , $P > 0.05$). Variation in vital rates across sites was not explained by any of the landscape metrics calculated (Supporting Information), although there was a moderately significant negative relationship between adult survival and radius of gyration ($y = -0.30x + 1.04$, $r^2 = 0.52$, $F_{1,4} = 6.30$, $P = 0.070$).

Population growth rates were most sensitive to juvenile survival (s_j) and least sensitive to female fertility (f_a) in all 6 study sites (Table 1 & Figs. 2a–c). Comparing across sites, variation in sensitivity to juvenile (s_j) and adult survival (s_a) and female fertility (f_a) was low (Table 1). Variation in vital rate sensitivity across sites was not explained by the landscape metrics calculated (Supporting Information), except for a moderately significant negative relationship between adult survival sensitivity and radius of gyration ($y = -0.058x + 0.82$, $r^2 = 0.50$, $F_{1,4} = 5.97$, $P = 0.070$).

Subtle differences observed among elasticity values suggested that population growth rate was slightly more sensitive to adult survival (s_a) in sites 1–2 and 4–6 and slightly more sensitive to juvenile survival (s_j) and female fertility (f_a) in site 3 (Table 1 & Figs. 2d–f). Linear regressions between landscape metrics and elasticities indicated the fractal dimension index, which measures blowout shape complexity, explained significant

variance in elasticity values at all 6 sites. Specifically, we found a significant positive relationship between blowout shape complexity and elasticity of juvenile survival (s_j) and fertility (f_a) (Fig. 3a, $y = 0.36x - 0.16$, $r^2 = 0.72$, $F_{1,4} = 14.10$, $P = 0.020$; Fig. 3c, $y = 0.36x - 0.16$, $r^2 = 0.72$, $F_{1,4} = 14.10$, $P = 0.020$) and a significant negative relationship between blowout shape complexity and elasticity of adult survival (s_a) (Fig. 3b, $y = -0.79x + 1.4$, $r^2 = 0.78$, $F_{1,4} = 18.89$, $P = 0.012$). Radius of gyration, which measures blowout extent, exhibited a weaker relationship with elasticities for each vital rate and explained less variation than fractal dimension index (Supporting Information). Specifically, we found a moderately significant positive relationship between blowout extent and elasticity of juvenile survival (s_j) and fertility (f_a) ($y = 0.06x + 0.18$, $r^2 = 0.50$, $F_{1,4} = 5.97$, $P = 0.070$; $y = 0.05x + 0.17$, $r^2 = 0.50$, $F_{1,4} = 5.97$, $P = 0.070$, respectively) and a moderately significant negative relationship between blowout extent and elasticity of adult survival (s_a) ($y = -0.13x + 0.67$, $r^2 = 0.55$, $F_{1,4} = 7.11$, $P = 0.060$). None of the other landscape metrics explained variation in elasticities (Supporting Information).

Discussion

Our results demonstrated how spatially variable vital rates of population growth were sensitive to specific features of a self-organizing landform. Specifically, where Shinnery oak sand-dune landforms were dominated by extensive, irregularly shaped blowouts with a lot of edge, female fertility, and juvenile survival contributed most to *S. arenicolus* population growth rates. Alternatively, within landforms dominated by more compact, regularly shaped blowouts with comparatively less edge, adult survival had the greatest contribution. Ours is the first study to provide an explicit basis for how variation in landform configuration can influence population dynamics and persistence of an endemic species specialized on a unique, irreplaceable landform.

Blowout shape complexity, and to a lesser degree blowout extent, suggested a direct relationship between *S. arenicolus* demography and amount of edge in Shinnery oak sand-dune landforms. Skewed demographic structure among sites is a likely mechanism determining this relationship. Previous research shows local sites with larger, more compactly shaped blowouts (i.e., with less edge) contain higher densities of adult lizards than sites with smaller, less compactly shaped blowouts (Ryberg et al. 2013). Given that *S. arenicolus* is territorial (Fitzgerald & Painter 2009), adult lizards occupying regularly shaped blowouts with less edge leads to dispersal of juveniles into unoccupied territories with irregularly shaped blowouts with lots of edge. Additionally, adult females make nesting migrations out of their home range, which can also contribute to skewed demographic

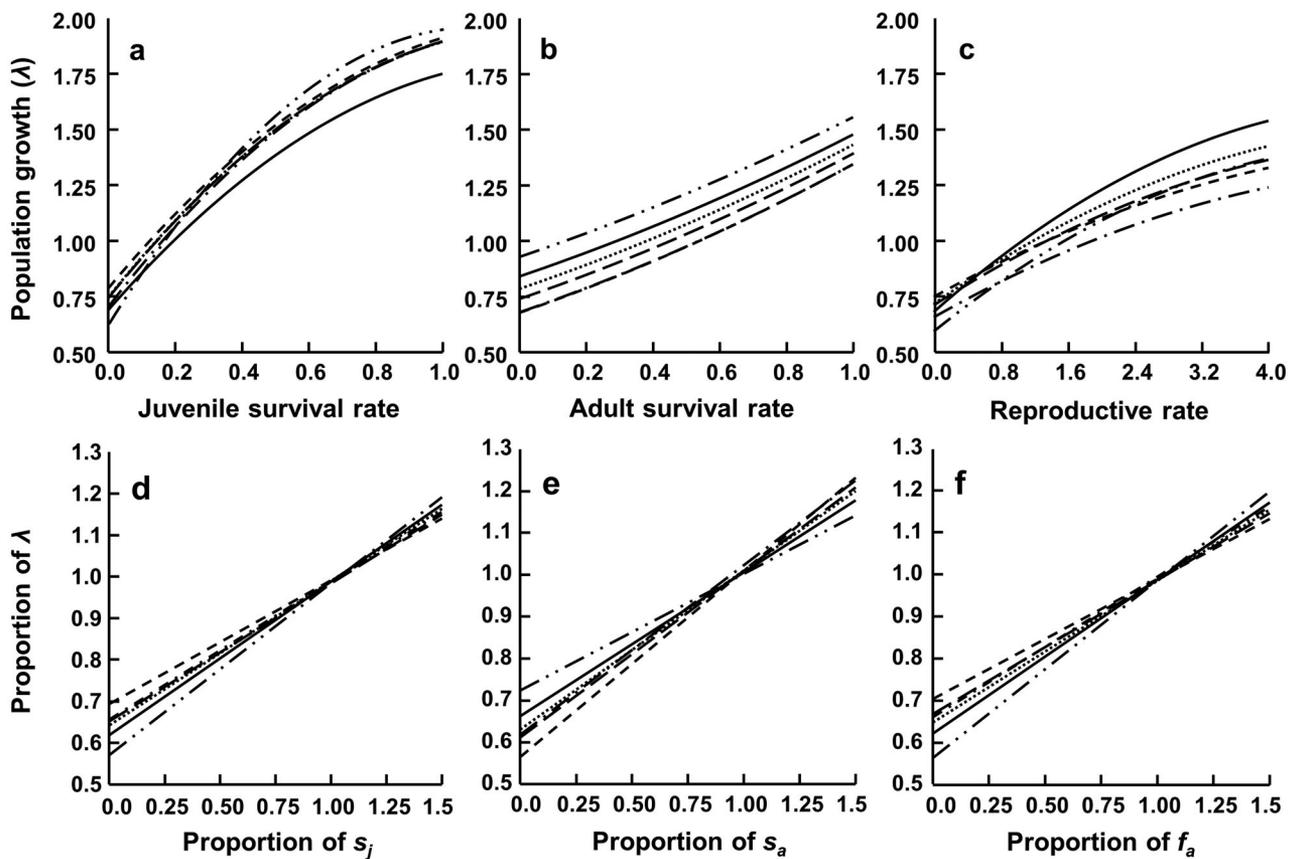


Figure 2. Sensitivity (slope) of population growth rate (λ) to changes in annual *S. arenicolus* (a) juvenile survival (s_j), (b) adult survival (s_a), and (c) reproductive rate (f_a) for each demographic unit and elasticity (slope) of proportional change in λ to proportional changes in annual (d) juvenile survival, (e) adult survival, and (f) reproductive rate for each study site (lines: site 1, dash-dot; site 2, dashed; site 3, dash-dot-dot; site 4, long dash; site 5, solid; and site 6, dotted).

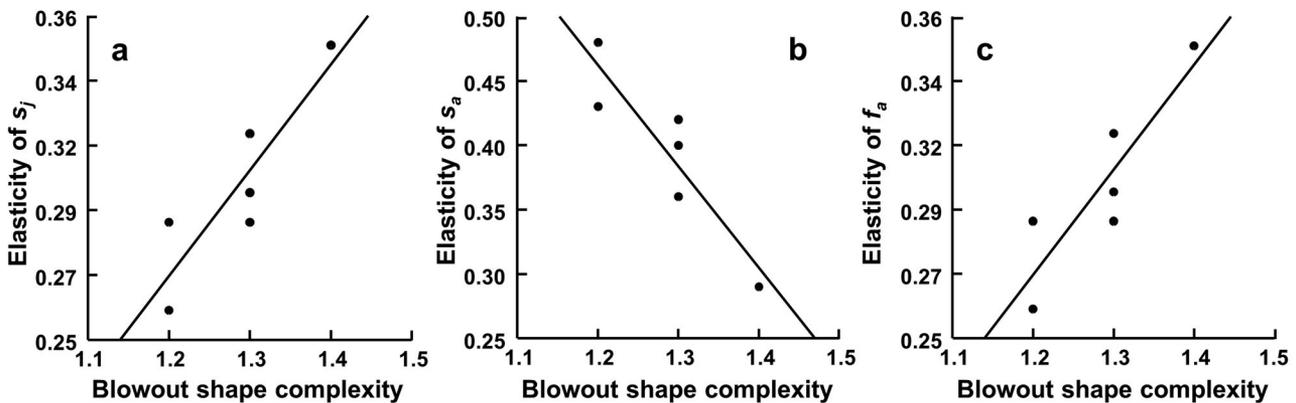


Figure 3. Relationship between blowout shape complexity (fractal dimension index) at each site and elasticity of *S. arenicolus* (a) juvenile survival (s_j), (b) adult survival (s_a), and (c) fertility (f_a). Blowout shape complexity ranges from 1 (perfect square) to infinity as shapes become highly irregular.

structure (Fitzgerald & Painter 2009). For these reasons, we suggest adult bias in demographic structure at sites with less edge helps explain why population growth was most sensitive to adult survival in those areas. In contrast,

juvenile bias in demographic structure at sites with more edge and female nesting in sites with more edge, could explain why population growth was most sensitive to juvenile survival and female fecundity in those areas.

Fractal dimension index and radius of gyration exhibited identical relationships with vital rate elasticities (Fig. 3 & Supporting Information), although relationships involving radius of gyration were much weaker. Both of these metrics of patch extent and shape measure aspects of habitat edge. Radius of gyration also exhibited moderately significant negative relationships with raw adult survival and adult survival sensitivity that were consistent with the adult survival elasticity relationship. Failure to observe statistically significant relationships for other landscape variables could be due to the small amount of variation across sites for vital rates and their sensitivities (Table 1 & Fig. 2), scale effects, or possibly low sample size (Supporting Information). Metrics other than fractal dimension index are sensitive to scale of measurement, whereas fractal dimension index is a scaleless measure (Mandelbrot 1982). Thus, it is possible that area, extent, aggregation, and isolation of blowouts within the landform could be important to *S. arenicolus* population dynamics at scales we did not consider. Despite a relatively small number of demographic units, fractal dimension index explained more than 70% of the variation in *S. arenicolus* vital rate elasticities, which we interpret as a robust biological linkage between populations and landscape complexity, with meaningful conservation and management implications.

In our case, fractal dimension index might be used to identify and prioritize particular sites where conservation strategies can be tailored to each demographic stage to achieve the greatest contribution to population growth for species. For example, at sites under threat of development with irregularly shaped blowouts, the needs of juveniles and reproductive females could be targeted because those life-history stages have the greatest contribution to population growth rate in those areas. Alternatively, in sites under threat with regularly shaped blowouts, the needs of adults could be targeted for the same reason. Thus, a critical lesson from our study is that an understanding of the population–landform interaction can help identify what kinds of land management may be most beneficial to biodiversity in different landscape contexts.

Although we identified tight linkages between landform configuration and variation in *S. arenicolus* population dynamics, all 6 populations were increasing. With populations growing across all sites, why stress conservation and management implications of differences in sensitivity and elasticity among different landform configurations? *Sceloporus arenicolus* populations decline with only minor disturbances to the landform, and populations disappear from fragmented areas where degraded dune blowouts remain (Leavitt & Fitzgerald 2013). Even in contiguous habitat, recruitment does not balance mortality at degraded sites, and persistence depends on diffusion dispersal through interconnected dune blowouts (Ryberg et al. 2013). It would be extremely

difficult to obtain precise vital rates as we have done in this study, where landforms are degraded because lizard abundance is too low to estimate them reliably. Finally, we may have sampled during a period when populations at this intact study site were growing above a long-term mean growth rate. It is well known that populations of lizard species exhibit large stochastic fluctuations, and in a given period regional populations may be well above or below the long-run mean growth rate (Fitzgerald 1994). Regardless of whether populations were growing or declining, the overarching result that vital rates were sensitive to landform characteristics should apply to all scenarios of population growth and decline, and, because of the sensitivity of *S. arenicolus* to landform condition, the pattern would likely be more intense in a small and declining population.

Our results refine the current understanding of extreme specialization of *S. arenicolus* on the Shinnery oak sand-dune landform at multiple scales. At the finest scale within this landform, individual *S. arenicolus* prefer the steepest slopes of relatively large blowouts (Fitzgerald & Painter 2009; Hibbitts et al. 2013). Females prefer open sand with high moisture content and large sand grain size composition for nesting (Ryberg et al. 2012; Ryberg & Fitzgerald 2014). At the scale of localized populations, the spatial configuration of blowouts (i.e., landscape pattern) determines size and structure of *S. arenicolus* neighborhoods, which drives a regional population dynamic through diffusion dispersal (Ryberg et al. 2013). Our results show that elasticity in vital rates also depended on landform configuration and help explain the function of low- and high-quality neighborhoods. At the largest landscape scales, quantity and quality of the landform are positively correlated, and presence is associated with large contiguous patches of sand-dune landforms (Smolensky & Fitzgerald 2011). Population genetic differentiation is structured south to north by configuration of dunes, and immigration rates are very low (Chan et al. 2009). Thus, across a hierarchy of scales, the microtopography, edaphic features, shape and configuration of blowouts, and spatial extent of the irreplaceable dune blowout landform are all tightly linked with population dynamics of this species.

Like many other irreplaceable landforms globally (Goudie & Seely 2011; Le Saout et al. 2013), the Shinnery oak sand-dune landform is threatened by habitat loss and fragmentation. Of considerable importance here is that this landform is particularly susceptible to disturbance and difficult to restore due to the presence of alternative stable states (DeAngelis 2012). This claim is substantiated by direct long-term observations. In the Mescalero-Monahans Sandhills ecosystem, 42 areas (approximately 51,903 hectares) were sprayed with Tebuthiuron herbicide to kill Shinnery oak and promote growth of grasses between 1982 and 1993. The Shinnery oak sand-dune landform was lost in all of them, and *S. arenicolus*

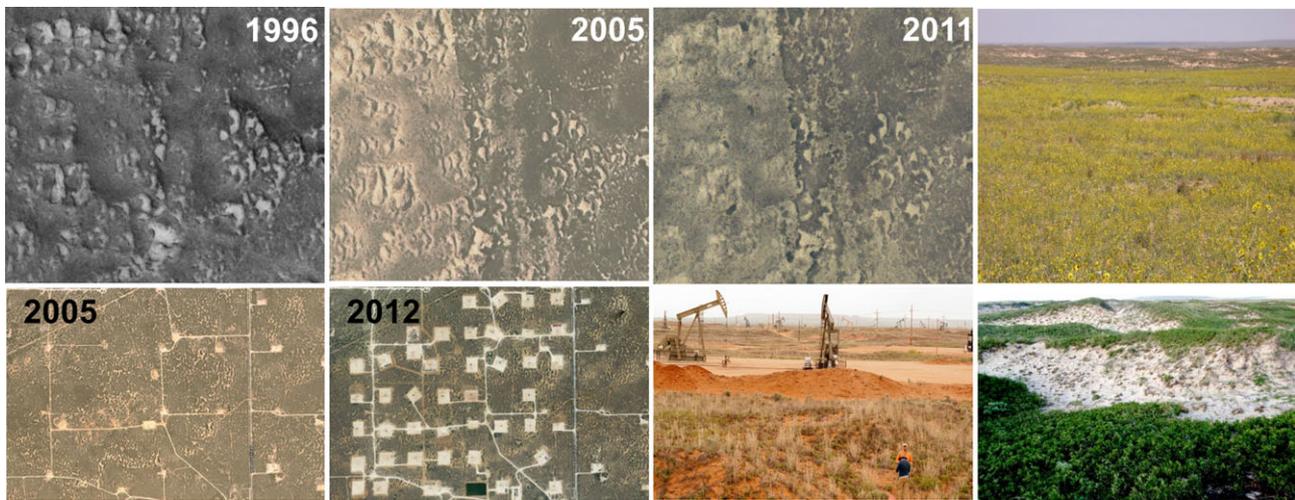


Figure 4. (Top) Flat grasslands that emerged after herbicide application to a Shinnery oak sand-dune landform in 1993. A fence line marking sprayed and intact landscape bisects the images. In 1996, dead Shinnery oak was still present, but by 2005, dead oaks had decomposed and the landform had eroded and was replaced with a flat grassland. By 2011, the dune blowout landform was still absent from the sprayed site. The view from this sprayed area looking east (far right) was of a flat landscape with remains of sand-dune blowouts surrounded by sunflowers (Shinnery oak is absent). Intact Shinnery oak sand-dune landforms with blowouts are in the background. (Bottom) Effect of habitat fragmentation from oil and gas development within the Shinnery oak sand-dune landform. Left 2 pictures show the increase in well-pad (squares) and road density from 2005 to 2012. Right 2 pictures show disturbed (left) and intact (right) landforms.

was never observed at those sites again (Laurencio & Fitzgerald 2010). Areas sprayed more than 20 years ago are now flat grasslands, some with mesquite encroachment, and still *S. arenicolus* is not present (Fig. 4). Additionally, habitat loss and fragmentation due to oil and gas development in this ecosystem disrupts the structural integrity of Shinnery oak sand-dune landforms, leading to changes in lizard community composition and a decrease in *S. arenicolus* abundance (Fig. 4) (Hibbitts et al. 2013; Leavitt & Fitzgerald 2013). There is no evidence that Shinnery oak sand-dune landforms are self-regenerating in disturbed areas.

There are some general lessons from this study that can be applied to global conservation of irreplaceable landforms and endemic biodiversity they support. The relationships we discovered in this system probably occur in many systems where species have evolved in concert with formation of self-organizing landforms. Endemic species are found in dune systems worldwide (Morton et al. 1995; Rodrigues 1996; Simmons et al. 1998), and it stands to reason their population dynamics are linked to identifiable landform features. Future work should focus on identifying and conserving those features that comprise the population-landform linkages in those systems.

By understanding population-landform linkages, conservationists and land managers can set priorities and recognize limitations in the protection and restoration of irreplaceable landforms (Goudie & Seely 2011; Le Saout et al. 2013). Our findings highlight significant obstacles

that impede restoration of self-organizing landforms to the extent necessary to sustain populations of specialized species. Self-organizing landforms are derived from complex systems that can shift to new stable states, which means that traditional land use practices relying on ecological succession will not work as a restoration strategy (DeAngelis 2012). Instead, restoration would likely entail engineering mimics of natural landforms (e.g., dunes, reefs, seabeds) that may or may not fulfill the habitat requirements for target species. In cases like the one we considered here, where demographic processes are tightly linked to landscape features at different scales, it is far from certain that artificial dune blowouts could support populations of the species. Given current limitations to restoration of landscapes characterized by landforms that are irreplaceable and nonrenewing, the logical priority for conservation would be to avoid disturbance and disruption of biogeomorphic feedbacks that create and maintain landforms (Goudie & Seely 2011; Le Saout et al. 2013).

We illustrated how population dynamics of an ecological specialist are tightly linked to landscape configuration in an ecosystem characterized by an irreplaceable, self-organized landform. This research bears important implications for conservation of biodiversity in ecosystems containing self-organized landforms world-wide. The dual challenges to conservation in systems characterized by self-organizing landforms are both the preservation of the landforms themselves and

conservation of the endemic, specialized biodiversity they sustain. Indeed, conservation strategies in such ecosystems are difficult to devise because they require an understanding of the complex feedbacks that create and maintain landforms and the consequences of resulting landscape structure for demography of species. Failure to consider the processes of landform organization and their effects on species population dynamics may lead to incorrect inferences about threats to populations and causes of their decline. In addition, failure to recognize the irreplaceability of self-organized landforms on which biodiversity depends may lead to uninformed or ineffective habitat management practices with correspondingly poor outcomes for threatened or endangered species. Successful conservation of irreplaceable landforms and the biodiversity they support must focus on explicitly linking process-oriented studies of landforms with studies of movement, behavior, and demography of species that dwell in them.

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Supporting Information

Information on *S. arenicolus* growth rates, age at first reproduction, offspring per clutch, and clutches per year (Appendices S1 and S3), figures depicting matrix model structure (Appendix S2) and site-specific model elements (Appendix S4), definitions of landform configuration metrics (Appendix S5), and results of statistical analyses (Appendices 6–8) are available online. The authors are solely responsible for the content and functionality of these materials. Queries should be directed to the corresponding author.

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