



Effects of habitat alteration on lizard community and food web structure in a desert steppe ecosystem



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ABSTRACT

Habitat alteration has major impacts on biodiversity, but we do not fully understand how changes in vegetation structure alter community interactions among vertebrate predators and their prey. Desertification is a major threat to degraded steppe habitats, prompting re-vegetation efforts to slow wind erosion. These processes alter both the structure and composition of the vegetation, and thus could influence predator and prey abundances, and their interactions. We investigated how habitat structure (degraded [sparse], natural [intermediate], or re-vegetated [dense]) influences lizard species richness, abundance, and diversity, and the interactions between these predators and invertebrate prey in the arid desert steppe. Structurally sparse and dense vegetation supported higher lizard abundances than natural habitats, with *Phrynocephalus frontalis* and *Eremias argus* dominating sparse and dense habitats respectively, and *P. frontalis* and *E. multiocellata* co-dominating natural habitats. Habitats that were structurally dense also supported the most complex trophic interactions among predators and prey, whereas structurally sparse habitats had low interaction diversity and interaction evenness, with most energy flowing along few trophic pathways. Steppe degradation therefore simplifies community trophic interactions, and restoration through enhanced protection of natural steppe habitat structure may play an important role in the conservation of healthy predator–prey communities. Desertification is a pressing issue throughout most of the arid steppe; revegetation efforts resulted in robust communities, in addition to promoting persistence of *E. argus*, which is endemic and threatened. Maintaining a heterogeneous structural landscape thus may be the most promising way to combat desertification while at the same time restoring predator–prey community composition.

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1. Introduction

Habitat alteration is a major threat to biodiversity and the continued survival of many species worldwide (Chapin et al., 2000; Brooks et al., 2002; Dirzo and Raven, 2003) because it can alter species diversity and community composition (Tilman et al., 2001; Pike et al., 2011b). Habitat alteration resulting in habitat loss, degradation, and fragmentation has profound, and often irreversible, negative effects on animal species richness, abundance and diversity (Vallan, 2002; Watson et al., 2004; Scott et al., 2006; Todd and Andrews, 2008; D'Cruze and Kumar, 2011). We can sometimes restore degraded habitats to maintain or increase biodiversity through the recovery of individual species and communities (Huxel and Hastings, 1999; Leynaud and Bucher, 2005; Pike et al., 2011a; Steen et al., 2013). The effects of habitat alteration

and subsequent restoration are not uniform across species, however, and habitat preferences of individual species and their ability to exploit or tolerate modified conditions will determine future persistence and survival (Watson et al., 2004; Pike et al., 2011b; Pelegrin and Bucher, 2012). For conservation and land management purposes, it is essential to understand how animal species and communities respond to anthropogenic habitat alteration (Scott et al., 2006).

Habitat alteration is likely to have cascading effects within ecological networks due to its simultaneous impacts on multiple species across different trophic levels (Tylianakis et al., 2008). Resource quality and availability not only alters the structure and assemblage of complex communities, but also affects species interactions by limiting energy transfer to consumers and their predators (Bukovinszky et al., 2008; Poisot et al., 2011). Food webs describe the community structure through trophic interactions among species, and can reconcile the structure and function of biodiversity (Polis et al., 1997; Thompson et al., 2012). Understanding

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food web structure can contribute to predicting biodiversity loss and ecosystem function (Dunne et al., 2002; Matthews et al., 2002; Whiles et al., 2006). To date, however, our understanding of how habitat alteration affects the structure of food webs is still in its infancy, especially with regards to interactions between vertebrate predators and their prey. Most studies focus on community responses to habitat change, but ignore the important trophic links within and between community members (Attum et al., 2006; Scott et al., 2006; Lindenmayer et al., 2008; Todd et al., 2008; Pike et al., 2011b; Steen et al., 2013). This has limited our ability to understand how habitat alteration impacts ecological networks, especially whether habitat alters functional relationships between predators and prey, and thus nutrient flow and ecosystem functioning.

Grasslands are dominant ecosystems worldwide, but are ecologically very fragile. Grasslands cover 40% of the national land area of China (Kang et al., 2007), and anthropogenic activities have caused large-scale degradation and desertification across vast regions (Wang et al., 2006). The most severely degraded habitat is the arid desert steppe located throughout the Inner Mongolian Plateau (Kang et al., 2007). Wind erosion and conversion of natural habitat to agriculture have contributed to widespread desertification (Yang et al., 2005; Su et al., 2007). These ecosystems are often rehabilitated by planting drought-tolerant vegetation to slow the effects of wind erosion (Kuchelmeister and Meyer, 2007; Su et al., 2007; Heshmati, 2013). These activities are slowing the desertification process, but also change the structure and composition of the habitat. We do not yet understand whether this leads to changes in biodiversity and community interactions between predators and their prey (Yang et al., 2005). Determining how changes in habitat structure (e.g., vegetation loss or thickening) alter these interactions will help us to understand the impacts of habitat change on animal community composition and energy flow between predators and prey.

Lizards are dominant terrestrial predators in desert ecosystems worldwide, and mainly consume a wide range of invertebrates (Pianka, 1986). Lizard communities are particularly sensitive to changes in habitat structure that alter thermoregulatory opportunities (Attum et al., 2006; D'Cruze and Kumar, 2011; Pike et al., 2011a,b; Cosentino et al., 2013). In this study, we used field experiments to elucidate how lizard community structure varied among different habitats in the desert steppe ecosystem of Inner Mongolia, China. We hypothesized that anthropogenic alteration of steppe vegetation has impacted habitat structure, and the richness, abundance, diversity, and community structure of lizard predators. Changes in lizard community composition should parallel the habitat preferences of individual species, where open habitat specialists are replaced as vegetation becomes denser, and shade tolerant species are replaced as vegetation becomes sparser. Predator composition likely determines community interactions among invertebrate prey, and shifts in predator abundance or diversity could alter functional aspects of the ecosystem. To test these hypotheses, we quantified the food web interactions among lizard predators and invertebrate prey across three replicated desert steppe habitats differing in structure (natural habitat of intermediate structure, and human-modified habitats that were sparser or denser). Our aim was to provide insight into how habitat changes alter the structure of lizard community and predator–prey food webs, and thus the flow of energy through fragile steppe ecosystems.

2. Materials and methods

2.1. Study system

Our study was conducted at Ordos Key Research Station for Field Observation of Ecological Environments on Sandy Grasslands,

managed by the Ministry of Agriculture, People's Republic of China. The Station is located in Jungar Banner, a cold semi-arid region of Inner Mongolia (40°12'17"N, 111°07'43"E; elevation 1036 m). The mean annual temperature is 6–7 °C with an average maximum of 39.1 °C in July and an average minimum of –32.8 °C in January. Annual precipitation ranges from 300 to 380 mm, with most rain falling between July and September.

The study area is predominately sandy grassland with low to moderate levels of sparse vegetation dominated by *Artemisia ordosica*, with scattered *A. sphaerocephala*, *Agriophyllum pungens*, *Bassia dasyphylla*, *Corispermum declinatum*, *Inula salsoloides*, and *Poa sphondylodes*. Much of the natural habitat in this region has been altered for agricultural purposes (cash crops, such as herba ephedra [*Ephedra sinica*], alfalfa [*Medicago sativa*], and millet) and to combat desertification (e.g., by planting introduced drought-enduring species including sweetvetch [*Hedysarum leave*, *H. scoparium*], korshinsk peashrub [*Caragana korshinskii*], and erect milkvetch [*Astragalus adsurgens*]). These vegetation changes have increased habitat heterogeneity since the early 2000s, and are designed to combat desertification by slowing wind erosion (Yang et al., 2005; Kuchelmeister and Meyer, 2007; Su et al., 2007). Compared to the natural (undisturbed) habitat, the altered habitat is generally either vegetatively: (1) sparser and dominated by *E. sinica* and *A. frigida*, or (2) more dense and dominated by *H. leave* and *M. sativa*. This provided three distinctive habitat types for study (sparse [degraded], natural [intermediate structure], and dense [actively re-vegetated]). We surveyed habitat characteristics and community composition of lizard predators and invertebrate prey at 10 sites in each of these three habitat types ($n = 30$ sites total; see [Online Supplementary Material, Fig. A1](#)). Sites were separated by at least 500 m, and each contained two drift fence arrays with pitfall traps for lizards and two pitfall traps for invertebrates.

2.2. Habitat characteristics

We quantified habitat structure and vegetation cover at each drift fence array using three 1×1 m quadrats placed two meters away from each array. In each quadrat we recorded maximum vegetation height (to 0.1 cm), basal vegetation cover (%), and bare ground (%). These metrics provide information on the amount of vegetation available to a lizard in terms of the vertical structure, the relative patchiness of sun and shade, and microhabitat availability for invertebrate prey. We used separate one-way ANOVAs to determine whether these variables differed among habitat type (sparse, natural, or dense). For these analyses we treated all quadrats within the same habitat type as replicates ($n = 60$ quadrats/habitat type; 6 quadrats per site \times 10 sites).

We recorded environmental temperatures available to lizards and invertebrates on the ground (sand), 15 cm below the surface of the soil, and 30 cm below the surface (i.e., at depths available to lizards within their burrows). The recorded temperatures enabled us to quantify the thermal characteristics of these microhabitats in each habitat type. Temperatures were recorded every 30 min during the active season (June to September 2012) and every 4 h during the inactive season (October 2012 to May 2013). We placed four iButton temperature loggers (Dallas Semiconductor, Dallas, Texas, USA; diameter, 15 mm; height, 6 mm) randomly at each of the three soil layers in each habitat (sparse, natural, dense). We used these data to calculate weekly mean temperatures over the course of a year for each datalogger, and averaged these data for each microhabitat/habitat structure combination. We compared broad differences in temperatures among habitats using Friedman's ANOVA.

2.3. Animal community diversity

The lizard community is composed of three insectivores that vary in their habitat preferences: *Eremias argus*, *E. multiocellata*, and *Phrynocephalus frontalis*. These lizards inhabit self-excavated burrows during periods of inactivity (e.g., at night and during winter). The Mongolian racerunner (*E. argus*) is an oviparous lacertid lizard that generally occupies grassy sand dunes and thickets where it is relatively warm, dry, and exposed to sunshine. The multiocellated racerunner (*E. multiocellata*) is a viviparous lacertid lizard that generally occupies arid or semi-arid regions covered by sparse vegetation. The steppe toad-headed agama (*P. frontalis*) generally inhabits desert, semi-desert or grassland habitats with low and sparse vegetation (Zhao et al., 1999). Potential avian predators of these lizards include the grey shrike (*Lanius excubitor*), magpie (*Pica pica*), red-footed falcon (*Falco amurensis*), kestrel (*Falco tinnunculus*), and cuckoo (*Cuculus canorus*). It is possible that these visual predators differentially affect survival of the lizard species in this community or interact with habitat structure, such that lizards are more susceptible to predation in more open habitats.

We sampled for lizards in two drift fence arrays (spaced 30 m apart) per site. Each array consisted of four buckets (25 cm diameter \times 35 cm deep) arranged in a “Y” shape with the central bucket connected to the three ends by 4 m long \times 0.3 m high steel drift fencing (see Nogueira et al., 2005). We trapped lizards for seven consecutive days and nights during each of June, July, and September 2012 ($n = 21$ trapping days/site). Buckets were checked hourly during peak lizard activity times, from 07:00 to 19:00 h. Captured lizards were identified, given an individual mark by toe clipping, and then released at the capture site. Recaptures were excluded from our analyses because community structure metrics provide abundance estimates.

We surveyed invertebrate species richness and abundance near each pitfall trap array during monthly lizard sampling. Invertebrate pitfall traps consisted of 25-mm diameter plastic buckets half-filled with a solution of water and detergent and buried flush with the ground, placed near each drift fence array. Invertebrate samples were collected daily during the trapping period and transferred to 70% ethanol for storage and later identification based on morphology.

We used the lizard and invertebrate capture data to calculate the following community indices for each of our 30 sites: species richness (R ; sum of the total number of species, S), Shannon's diversity (H' ; number of species and their relative abundance; Shannon and Weaver, 1949), Pielou's evenness (J' ; similarity of the abundances of different species; Pielou, 1975), and Simpson's dominance (D ; the probability that two randomly selected individuals from a community will belong to the same species; Magurran, 1988). Shannon's index (H') was calculated as $H' = -\sum P_i \ln P_i$ (Shannon and Weaver, 1949), where P_i is the proportion of individuals of the species i for both lizard predators and invertebrate prey. Pielou's index was calculated as $J' = H' / \ln S$ (Pielou, 1975). Simpson's dominance (D) was calculated as $D = \sum (P_i)^2$ (Magurran, 1988). We used separate one-way ANOVAs to determine whether these community indices differed significantly among habitat type (sparse, natural, dense) using individual sites within habitats as replicates.

2.4. Food web structure

We examined lizard stomach contents to determine the invertebrate prey these predators consumed. We collected stomach samples from adult lizards in all three habitats in June, July and September 2012. We set up a single 50 \times 50 m plot located 50 m away from each of our thirty sites (see Online Supplementary Material, Fig. A1). Lizards were captured by hand or noose from 11:00 to 16:00 h on sunny days, so that individuals had the

opportunity to consume prey before being captured. Lizards were euthanized shortly after capture by injection of sodium pentobarbitone (60 mg ml⁻¹) into the abdominal cavity, and immediately preserved in 70% ethanol. In the laboratory, we removed the stomachs from preserved lizards, separated the contents, and identified the prey remains under a dissecting microscope. Prey items were identified to the lowest taxon possible, usually to the order or family level, based upon entire items or estimates of residues. We scored the frequencies of different invertebrate prey types from 124 stomach samples for *E. argus*, 70 for *E. multiocellata*, and 154 for *P. frontalis*.

We quantified food web relationships among lizard predators and invertebrate prey by pooling data for each of the 10 sites in each habitat type. To do this we calculated the quantitative, weighted measures of the ratio of prey taxa to lizard taxa ($N:P_q$), linkage density (LD_q , the mean number of trophic links per taxon), connectance (C_q , the fraction of all possible links that are realized, and a standard measure of food web complexity), interaction diversity (ID_q , the quantitative diversity of trophic links), interaction evenness (IE_q , the dominance structure of trophic links, and a measure of the uniformity of energy flows along different pathways), generality (G_q , the mean number of prey species per lizard species) and vulnerability (V_q , the mean number of lizard species per prey species). Calculations follow Bersier et al. (2002), Albrecht et al. (2007), and Tylianakis et al. (2007) (see Online Supplementary Material, Appendix A).

Exploratory data analysis of these food-web metrics revealed intercorrelations among many of the variables (see Online Supplementary Material, Table A2). We thus tested the effects of habitat on these metrics using a general linear model (GLM) with multivariate responses, and then made subsequent individual analyses of each metric to reduce the probability of making a type I statistical error. To account for any effects of among-habitat variation in the species richness of lizard predators and invertebrate prey, we fitted GLMs with habitat type as a fixed factor and lizard and invertebrate richness as covariates. By introducing habitat type into the model before or after lizard and invertebrate diversity, it was possible to quantify the overall variance in food web metrics across habitat types, as well as the variance after controlling for differences in lizard and invertebrate diversity among habitats (using type III sums of squares). We used the software package SPSS 19.0 for data analysis and report summary statistics as means \pm 1 SE.

3. Results

3.1. Habitat characteristics

Habitat change profoundly influenced fundamental characteristics of the natural vegetation structure, in terms of height, basal cover, and bare ground (Fig. 1). The sparse and natural habitats were significantly shorter ($F_{2,177} = 309.14$, $P < 0.0001$) and had less basal cover ($F_{2,177} = 38.58$, $P < 0.0001$) than the dense habitats (Fig. 1). By contrast, the sparse and natural habitats had greater proportions of bare ground than the dense habitat ($F_{2,177} = 10.77$, $P < 0.0001$; Fig. 1). These structural differences significantly influenced the thermal environment; weekly mean temperatures on the surface were highest in the sparse habitat, lowest in the natural habitat, and intermediate in the dense habitat ($\chi^2 = 41.654$, $df = 2$, $P < 0.0001$; see Online Supplementary Material, Fig. A2). Weekly mean temperatures were significantly higher in the sparse and natural habitats than in the dense habitat at both 15 cm ($\chi^2 = 39.846$, $df = 2$, $P < 0.0001$) and 30 cm soil depths ($\chi^2 = 38.115$, $df = 2$, $P < 0.0001$) (see Online Supplementary Material, Fig. A2).

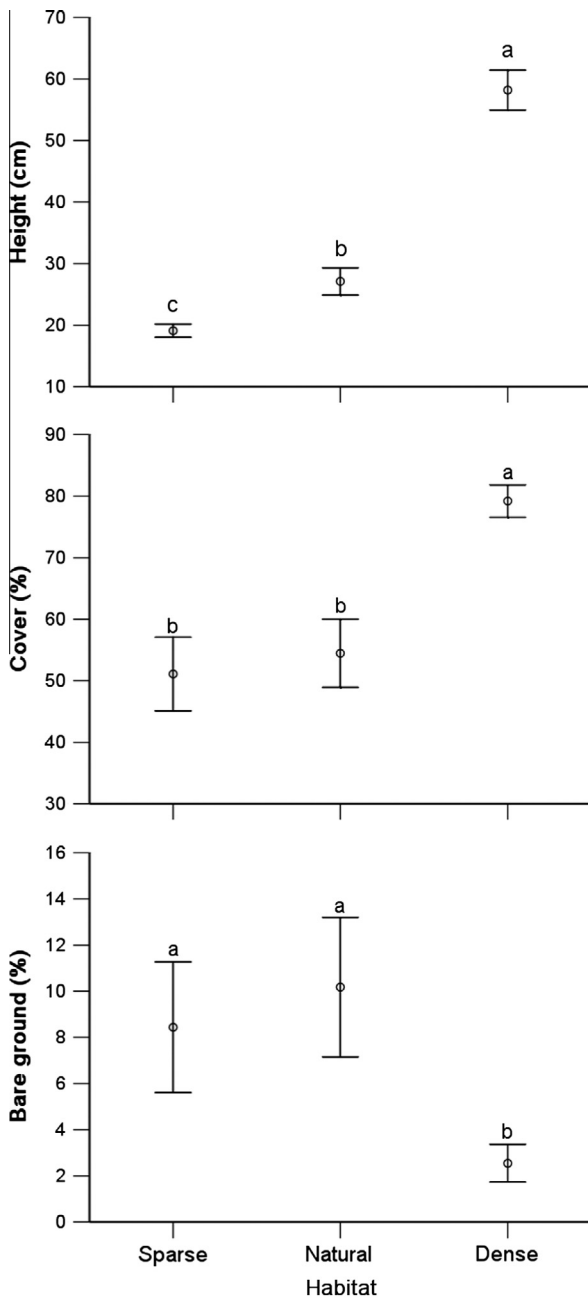


Fig. 1. Vegetation characteristics (height, basal cover and bare ground) of three different habitats with sparse, natural or dense vegetation in the desert steppe of Inner Mongolia, China in 2012. Graphs show mean \pm 1 SE. Means with different letters above the error bars are statistically different (Tukey's HSD tests).

3.2. Animal community diversity

Habitat type did not alter the species richness of lizard predators ($F_{2,27} = 0.60$, $P = 0.556$), but did significantly affect the diversity of lizard predator and invertebrate prey communities (Table 1). Compared to natural habitat, the sparse and dense habitats supported significantly lower lizard species diversity ($F_{2,27} = 6.80$, $P = 0.004$) and evenness ($F_{2,27} = 8.79$, $P = 0.001$), but higher dominance ($F_{2,27} = 9.84$, $P < 0.001$) and abundance ($F_{2,27} = 14.73$, $P < 0.0001$; Table 1). In the natural habitat, *P. frontalis* (51.6%) and *E. multocellata* (38.2%) dominated the lizard community, whereas *E. argus* (10.2%) was rare; in the dense habitat, *E. argus* became dominant (78.1%), whereas *P. frontalis* dominated the sparse habitat (82.7%).

Habitat type did not alter the species richness of invertebrate prey ($F_{2,27} = 2.84$, $P = 0.076$), but did significantly alter invertebrate species diversity ($F_{2,27} = 22.65$, $P < 0.0001$), evenness ($F_{2,27} = 22.41$, $P < 0.0001$), dominance ($F_{2,27} = 9.77$, $P < 0.001$) and abundance ($F_{2,27} = 33.49$, $P < 0.0001$). As compared to the natural habitat, the dense habitat had lower invertebrate species diversity and evenness, but higher dominance (Table 1). By contrast, the three diversity character parameters were similar between the sparse and natural habitats. Invertebrate abundance was significantly reduced in the sparse habitat and enhanced in the dense habitat as compared to the natural habitat. Araneae species dominated the natural habitat (13.8%), Tenebrionidae dominated the sparse habitat (14.6%), and Coccinellidae dominated the dense habitat (18.4%).

3.3. Food web structure

We found striking and highly significant differences in quantitative food-web structure among habitat types (multivariate general linear model (GLM): Wilks' lambda = 0.072, $F_{12,44} = 10.016$, $P < 0.0001$; Table 2, Fig. 2). These differences were still highly significant after controlling for the effects of predator and prey species richness (multivariate GLM: Wilks' lambda for effect of habitat = 0.066, $F_{12,42} = 10.175$, $P < 0.0001$), which did not differ significantly across habitats (ANOVA: $F_{2,27} = 1.058$, $P = 0.361$).

Quantitative food webs differed significantly among habitats in terms of the ratio of prey taxa to lizard taxa ($N:P_q$), generality, vulnerability, link density, connectance, and interaction evenness (Table 2, Fig. 3). Habitat conversion from natural to either sparse or dense habitats increased the mean number of effective prey species per lizard species, according to the changes of quantitative weighted generality and $N:P_q$ (Table 2, Fig. 3). Compared to natural habitats, the dense habitats had significantly higher quantitative weighted link density and connectance. Compared to natural or dense habitats, the sparse habitats had significantly lower quantitative weighted vulnerability and interaction evenness (Table 2, Fig. 3). We found no significant differences in quantitative weighted interaction diversity across habitats ($P = 0.095$). Interaction diversity differed significantly among habitats after controlling for the effects of lizard and invertebrate richness ($P < 0.001$; Table 2), with sparse habitats having lower interaction diversity than dense habitats (Fig. 3).

4. Discussion

We studied the effects of habitat structure on the network of community interactions between lizard predators and invertebrate prey in a Mongolian desert steppe ecosystem. Habitat structure had little effect on overall species richness of either predators or prey, but had striking effects on abundance and diversity, and strongly altered the pathways of species interactions within the ecosystem. In dense habitats modified to combat desertification, the structure of predator–prey food webs became more complex and robust, with high connectance among community members. The diversity and evenness of the interaction frequencies declined along the gradient from dense to sparsely vegetated habitats. Desert steppe lizard and invertebrate biodiversity are both sensitive to habitat modification, leading to changes in community dynamics that likely alter ecosystem functioning and affect monitoring for community recovery.

The impacts of changes in habitat structure on species richness can vary across studies and be complex. In some cases, severe habitat modification has little impact on biodiversity; for example, host and parasitoid species richness did not vary across a severe modification gradient spanning from intact forest to rice paddies (Tylianakis et al., 2007). Despite some exceptions, however, most

Table 1
Diversity character parameters (mean \pm 1 SE) of invertebrate and lizard communities in habitats differing in vegetation structure in 2012 ($n = 10$ sites per habitat type). Means with different letters after the error data are statistically different (Tukey's test).

Community	Habitat type	Richness index (R)	Shannon's diversity index (H')	Pielou's evenness index (J')	Simpson's dominance index (D)	Abundance
Lizard	Sparse	2.8 \pm 0.2	0.537 \pm 0.083b	0.489 \pm 0.075b	0.707 \pm 0.049a	42.2 \pm 4.5b
	Natural	2.9 \pm 0.1	0.862 \pm 0.052a	0.820 \pm 0.046a	0.469 \pm 0.032b	28.3 \pm 2.8c
	Dense	3.0 \pm 0.0	0.656 \pm 0.049b	0.597 \pm 0.045b	0.637 \pm 0.034a	57.9 \pm 4.1a
Invertebrate	Sparse	34.3 \pm 0.9	2.907 \pm 0.027a	0.823 \pm 0.008a	0.089 \pm 0.005b	344.3 \pm 21.8c
	Natural	35.4 \pm 1.0	2.726 \pm 0.084a	0.765 \pm 0.022a	0.113 \pm 0.017b	565.6 \pm 45.3b
	Dense	32.3 \pm 0.8	2.302 \pm 0.071b	0.663 \pm 0.019b	0.172 \pm 0.016a	1020.1 \pm 90.1a

Table 2
Effects of habitat type on individual food web metrics. $N:P_q$ is the ratio of prey taxa to lizard taxa. Results derived from independent GLMs. Model 1 has habitat type entering the model first, before lizard and prey diversity. Model 2 has habitat type entering last, with lizard and prey diversity as covariates.

Variable	Model 1			Model 2		
	$F_{2,27}$	P	r^2	$F_{3,26}$	P	r^2
$N:P_q$	10.930	<0.001	0.406	12.289	<0.0001	0.539
Generality	5.670	0.009	0.244	9.353	<0.001	0.464
Vulnerability	20.082	<0.00001	0.568	15.357	<0.00001	0.598
Link density	6.239	0.006	0.265	8.113	<0.001	0.424
Connectance	14.307	<0.0001	0.479	15.963	<0.00001	0.608
Interaction diversity	2.571	0.095	0.098	10.132	<0.001	0.486
Interaction evenness	4.113	0.028	0.177	7.168	0.001	0.390

studies report higher species richness in primary habitats than in anthropogenically disturbed or degraded habitats (Kruess and Tscharntke, 2002; Attum et al., 2006; D'Cruze and Kumar, 2011; Pelegrin and Bucher, 2012). Although we found that species richness was broadly similar among habitat types, habitat alteration significantly reduced species diversity. In dense habitats we found reduced species diversity and evenness of invertebrates, and reduced lizard species diversity. Such losses of species diversity are common consequences of anthropogenic disturbance in many ecosystems (Kruess and Tscharntke, 2002; D'Cruze and Kumar, 2011; Pelegrin and Bucher, 2012). Changes in diversity are much harder to detect than changes in richness; in our study all three lizard predator species were present in all habitat types, but their abundances and relationships to invertebrate prey differed markedly (Fig. 2). Thus, simply using broad surveys for the major predators may have revealed erroneous conclusions about the effects of habitat structure on predator populations.

Lizard species did not respond to habitat alteration in the same manner. As a result of vegetation loss, primary habitats supported increased lizard abundances over sparse habitats that have experienced anthropogenic disturbance or degradation (Attum et al., 2006; D'Cruze and Kumar, 2011; Pelegrin and Bucher, 2012). In our study, however, the sparse habitats had higher abundance and dominance of lizards than the natural habitats. In the natural habitats, *P. frontalis* and *E. multiocellata* co-dominated the lizard community (Fig. 2). *P. frontalis* and *E. argus* became the dominant species in the sparse and dense habitats, respectively, indicating that the effect of habitat alteration was not uniform across species. Predation risk and interspecific competition may affect lizard community assemblage across habitat types (Daly et al., 2008; Lisičić et al., 2012). Nevertheless, responses to changes in habitat structure are often dependent upon the microhabitat preferences of individual species (Attum et al., 2006; Scott et al., 2006; Pike et al., 2011b). For example, some sand specialist lizard species are ubiquitous in desert lizard communities, whereas other generalist lizard species are found primarily in natural (undegraded) habitats (Attum et al., 2006). Removing forest canopy cover can increase relative abundances of reptile species preferring sun-exposed habitats and decrease the abundances of shade-tolerant species (Pike et al., 2011b). In our study, *P. frontalis* dominated

sparse habitats, which had higher ground temperatures, less vegetation cover, and more bare ground than the dense habitats in which *E. argus* dominated. Microhabitat temperature is a primary determinant of reptile habitat selection, and often differs among community members (Shine et al., 2002; Pike et al., 2011b). We hypothesize that *P. frontalis* prefers the warm thermal environments provided by sparse habitats, *E. multiocellata* has an intermediate thermal preference appropriate for natural habitats, and *E. argus* prefers the cooler thermal environments provided by dense habitats. If these lizard species differ in their microhabitat and thermal preferences, their dominance across the arid steppe may depend on the heterogeneous network of vegetation structure across the landscape. This has important implications for the recovery of natural communities through habitat restoration, and how habitat connectivity may shape population and community dynamics. A heterogeneous vegetation structure, consisting of more natural habitats interspersed with re-vegetated dense habitats, is important for restoring the natural predator–prey dynamics and combating desertification in steppe ecosystems.

Habitat alteration markedly altered the structure and composition of invertebrate–lizard food webs. The dense habitats had higher link density, connectance and interaction diversity than both sparse and natural habitats (Fig. 3). Food web robustness generally increases with connectance (Dunne et al., 2002), and we found that food web structure was richer or more complex in the dense habitats than the other two habitats. The sparse habitats had significantly lower diversity and evenness of the interaction frequencies than either natural or dense habitats, indicating that in sparse habitats most energy flows along very few predator–prey pathways. Evidently, food web structure in the degraded sparse habitats became more fragile and unstable, so that the sparse habitats potentially lose the maintenance function played by healthy ecosystems, even though they are still able to support the same lizard predator richness.

Reptiles are threatened by habitat loss and over-exploitation; 26–37% of reptile species globally are assessed as threatened or near threatened (Böhm et al., 2013; IUCN, 2013). In our study, *P. frontalis* and *E. multiocellata* co-dominated the lizard community in the natural habitat, whereas *E. argus* became dominant species in the dense habitat. *E. argus* is endemic to eastern Asia, and is

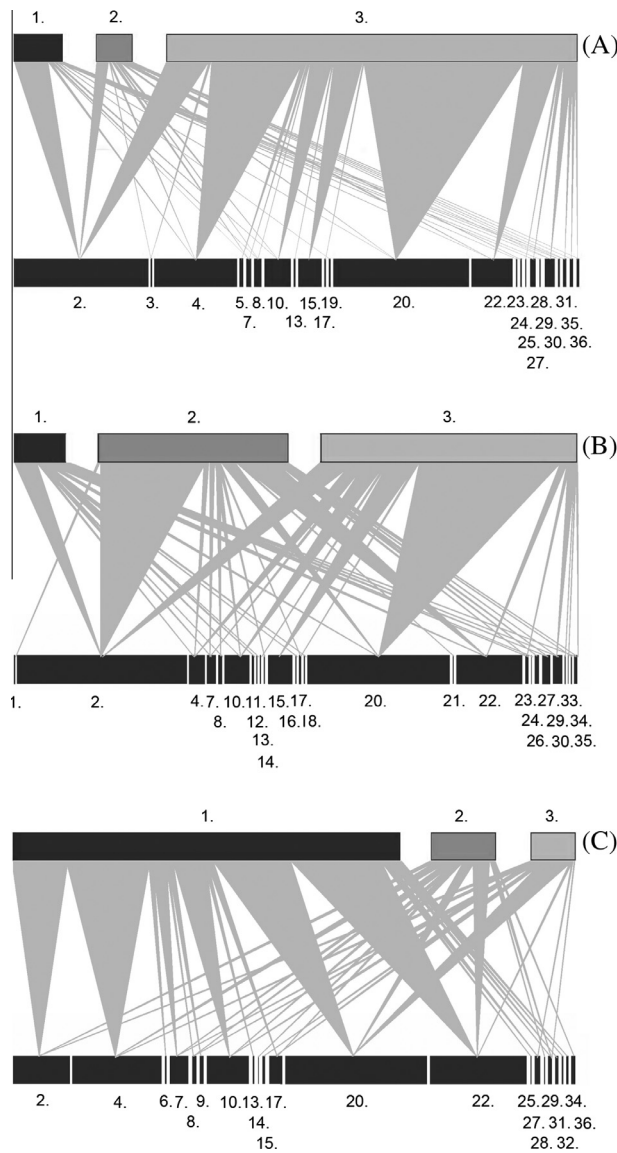


Fig. 2. Quantitative lizard predator-invertebrate prey food webs within the desert steppe of Inner Mongolia, China, shown for sparse (A), natural (B), and dense (C) habitats. For each web, the upper bars represent lizard abundance in each habitat (*Eremias argus* = darker grey, *E. multiocellata* = lighter grey, and *Phrynocephalus frontalis* = lightest grey; pooled number of individual lizards). Lower bars depict the abundance of invertebrate prey (taxon codes are provided in Table A1). The width of the base of each “wedge” represents the frequency of each predator–prey trophic interaction, in terms of the relative contribution of resource flows (prey, energy) to the production of each consumer (lizard), summing to the total inflows. Webs show interaction data pooled across ten replicates within each habitat type, although analyses were conducted on a per-site basis.

listed as endangered in South Korea due to its limited distribution and declining population sizes (Kim et al., 2012). The geographic distribution of *E. argus* has also shrunk rapidly in China because of anthropogenic disturbance. The structurally dense habitats that have been used to combat desertification supported increased abundance of *E. argus* that had a more robust food web structure. The re-vegetated dense habitats are effective for *E. argus* conservation, despite the overall decreased lizard diversity in these habitats. It is also clear that in degraded sparse habitats the proportions of the two *Eremias* species in the lizard community decreased. In desert steppe environments, management for the threatened lizard species likely benefits from re-vegetating eroded habitats to help combat desertification; in addition, the more

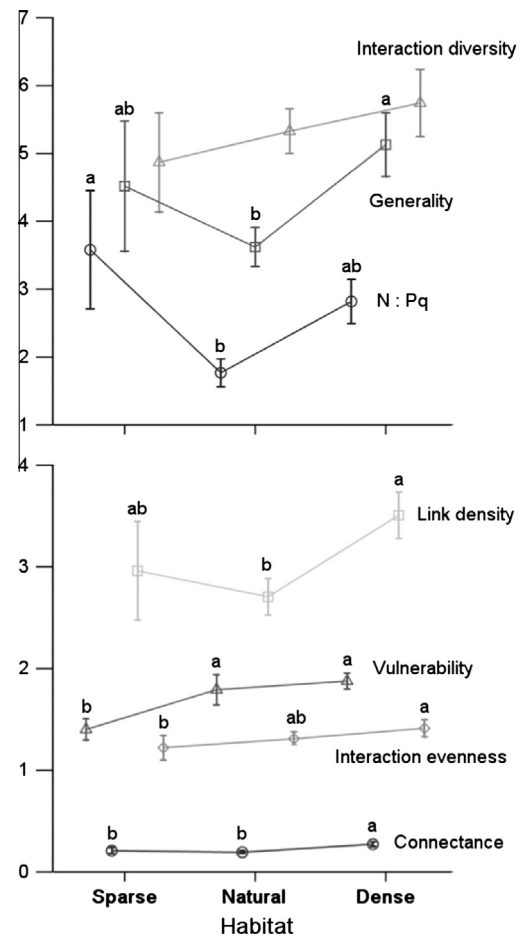


Fig. 3. The effects of habitat type (sparse, natural, dense) on seven quantitative food web community indices relating lizard predators to their invertebrate prey. Indices are presented as means ± 1 SE, and include: ratio of invertebrate prey taxa to lizard predator taxa ($N:Pq$), generality (mean number of prey species per lizard species), vulnerability (mean number of lizard predator species per prey species), link density, connectance, interaction diversity, and interaction evenness. Letters above individual means indicate statistically significant differences among habitat types for that particular index (Tukey's test, $P < 0.05$); letters in common or no letter indicates no significant difference ($P > 0.05$).

natural habitat structure enhances overall community diversity of lizard predators and invertebrate prey. Enhanced protection of structurally natural steppe habitats may play an important role in the process of species conservation for lizards, whether or not natural structural regimes are maintained or exceeded, or coexist together in a heterogeneous landscape.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.09.011>.

References

- Albrecht, M., Duelli, P., Schmid, B., Müller, C.B., 2007. Interaction diversity within quantified insect food webs in restored and adjacent intensively managed meadows. *J. Anim. Ecol.* 76, 1015–1025.
- Attum, O., Eason, P., Cobbs, G., Baha El Din, S.M., 2006. Response of a desert lizard community to habitat degradation: do ideas about habitat specialists/generalists hold? *Biol. Conserv.* 133, 52–62.
- Bersier, L.F., Banasek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. *Ecology* 83, 2394–2407.
- Böhme, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., et al., 2013. The conservation status of the world's reptiles. *Biol. Conserv.* 157, 372–385.
- Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G., Hilton-Taylor, C., 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16, 909–923.
- Bukovinsky, T., van Veen, F.J.F., Jongema, Y., Dicke, M., 2008. Direct and indirect effects of resource quality on food web structure. *Science* 319, 804–807.
- Chapin III, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Diaz, S., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Cosentino, B.J., Schooley, R.L., Bestelmeyer, B.T., Coffman, J.M., 2013. Response of lizard community structure to desert grassland restoration mediated by a keystone rodent. *Biodivers. Conserv.* 22, 921–935.
- Daly, B.G., Dickman, C.R., Crowther, M.S., 2008. Causes of habitat divergence in two species of agamid lizards in arid central Australia. *Ecology* 89, 65–76.
- D'Cruze, N., Kumar, S., 2011. Effects of anthropogenic activities on lizard communities in northern Madagascar. *Anim. Conserv.* 14, 542–552.
- Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.* 28, 137–167.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* 5, 558–567.
- Heshmati, G.A., 2013. Successful biological methods for combating desertification at degraded areas of China. In: Heshmati, G.A., Squires, V.R. (Eds.), *Combating Desertification in Asia, Africa and the Middle East: Proven Practices*. Springer, Dordrecht, Heidelberg, New York, London, pp. 49–71.
- Huxel, G.R., Hastings, A., 1999. Habitat loss, fragmentation and restoration. *Restor. Ecol.* 7, 309–315.
- IUCN, 2013. IUCN Red List of Threatened Species. Version 2013.2. <<http://www.iucnredlist.org>>.
- Kang, L., Han, X., Zhang, Z., Sun, O.J., 2007. Grassland ecosystems in China: review of current knowledge and research advancement. *Philosoph. Transact. Roy. Soc. B: Biol. Sci.* 362, 997–1008.
- Kim, I.-H., Ra, N.-Y., Park, D., 2012. Habitat use, home range, and hibernaculum of the Mongolian racerunner, *Eremias argus* (Lacertidae, Reptilia) in a coastal sand dune in South Korea. *Asian Herpetol. Res.* 3, 133–140.
- Kruess, A., Tschamntke, T., 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1570–1580.
- Kuchelmeister, G., Meyer, N., 2007. Desertification control in China – a formula for success? *Agric. Rural Develop.* 14, 16–18.
- Leynaud, G.C., Bucher, E.H., 2005. Restoration of degraded Chaco woodlands: effects on reptile assemblages. *Forest Ecol. Manag.* 213, 384–390.
- Lindenmayer, D.B., Wood, J.T., MacGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R., Driscoll, D.A., 2008. How predictable are reptile responses to wildfire? *Oikos* 117, 1086–1097.
- Lisičić, D., Drakulić, S., Herrel, A., Đikić, D., Benković, V., Tadić, Z., 2012. Effect of competition on habitat utilization in two temperate climate gecko species. *Ecol. Res.* 27, 551–560.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, New Jersey, USA.
- Matthews, K.R., Knapp, R.A., Pope, K.L., 2002. Garter snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and nonnative trout introductions? *J. Herpetol.* 36, 16–22.
- Nogueira, C., Valdujo, P.H., França, F.G.R., 2005. Habitat variation and lizard diversity in a Cerrado area of Central Brazil. *Stud. Neotrop. Fauna E.* 40, 105–112.
- Pelegrin, N., Bucher, E.H., 2012. Effects of habitat degradation on the lizard assemblage in the Arid Chaco, central Argentina. *J. Arid Environ.* 79, 13–19.
- Pianka, E.R., 1986. *Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton, New Jersey, USA.
- Pielou, E.C., 1975. *Ecological Diversity*. Wiley, New York, USA.
- Pike, D.A., Webb, J.K., Shine, R., 2011a. Chainsawing for conservation: ecologically informed tree removal for habitat management. *Ecol. Manage. Restor.* 12, 110–118.
- Pike, D.A., Webb, J.K., Shine, R., 2011b. Removing forest canopy cover restores a reptile assemblage. *Ecol. Appl.* 21, 274–280.
- Poisot, T., Lepennetier, G., Martinez, E., Ramsayer, J., Hochberg, M.E., 2011. Resource availability affects the structure of a natural bacteria–bacteriophage community. *Biol. Lett.* 7, 201–204.
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Scott, D.M., Brown, D., Mahood, S., Denton, B., Silburn, A., Rakotondraparany, F., 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. *Biol. Conserv.* 127, 72–87.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana, Illinois, USA.
- Shine, R., Barrott, E.G., Elphik, M.J., 2002. Some like it hot: effects of forest clearing on nest temperatures of montane reptiles. *Ecology* 83, 2808–2815.
- Steen, D.A., Smith, L.L., Conner, L.M., Litt, A.R., Provencher, L., Hiers, J.K., Pokswinski, S., Guyer, C., 2013. Reptile assemblage response to restoration of fire-suppressed longleaf pine sandhills. *Ecol. Appl.* 23, 148–158.
- Su, Y.Z., Zhao, W.Z., Su, P.X., Zhang, Z.H., Wang, T., Ram, R., 2007. Ecological effects of desertification control and desertified land reclamation in an oasis-desert ecotone in an arid region: a case study in Hexi Corridor, northwest China. *Ecol. Eng.* 29, 117–124.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr., R.O., Hladysz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: reconciling the structure and function of biodiversity. *Trends Ecol. Evol.* 27, 689–697.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281–284.
- Todd, B.D., Andrews, K.M., 2008. Response of a reptile guild to forest harvesting. *Conserv. Biol.* 22, 753–761.
- Todd, B.D., Rothermel, B.B., Reed, R.N., Luhring, T.M., Schlatter, K., Trenkamp, L., Gibbons, J.W., 2008. Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles. *Biol. Invasions* 10, 539–546.
- Tylianakis, J.M., Tschamntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445, 202–205.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* 11, 1351–1363.
- Vallan, D., 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. *J. Trop. Ecol.* 18, 725–742.
- Wang, X., Chen, F., Dong, Z., 2006. The relative role of climatic and human factors in desertification in semiarid China. *Global Environ. Chang.* 16, 48–57.
- Watson, J.E.M., Whittaker, R.J., Dawson, T.P., 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *J. Biogeogr.* 31, 1791–1807.
- Whiles, M.R., Lips, K.R., Pringle, C.M., Kilham, S.S., Bixby, R.J., Brenes, R., Connelly, S., Colon-Gaud, J.C., Hunte-Brown, M., Huryn, A.D., Montgomery, C., Peterson, S., 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Front. Ecol. Environ.* 4, 27–34.
- Yang, X., Zhang, K., Jia, B., Ci, L., 2005. Desertification assessment in China: an overview. *J. Arid Environ.* 63, 517–531.
- Zhao, E.M., Zhao, K.T., Zhou, K.Y., 1999. *Fauna Sinica, Reptilia, vol. 2, Squamata*, Chinese Science Press, Beijing, China.