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 heterogenous 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

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 × 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.