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Nematodes as an indicator of plant–soil interactions associated with desertification

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ABSTRACT

Conversion of perennial grasslands to shrublands is a desertification process that is important globally. Changes in aboveground ecosystem properties with this conversion have been well-documented, but little is known about how belowground communities are affected, yet these communities may be important drivers of desertification as well as constraints on the reversal of this state change. We examined nematode community structure and feeding as a proxy for soil biotic change across a desertification gradient in southern NM, USA. We had two objectives: (1) to compare nematode trophic structure and species diversity within vegetation states representing different stages of desertification, and (2) to compare nematode community structure between bare and vegetated patches that may be connected via a matrix of endophytic fungi and soil biotic crusts. The gradient included a perennial grassland dominated by *Bouteloua eriopoda*, the historic dominant in the Chihuahuan Desert, a duneland dominated by the shrub, *Prosopis glandulosa*, and the ecotone between them. We also sampled a relatively undisturbed, ungrazed *B. eriopoda* grassland at a nearby site to serve as an end member of our gradient. Nematode communities were sampled using soil cores to depth of 50 cm at each location in 2009 and 2010. Results showed that grasslands and mesquite dunelands had different trophic groupings and herbivorous nematode communities with lower species diversity and evenness compared with the ecotone. Nematode trophic structure and herbivore communities were significantly different in all vegetation states with the highest observed diversity in the undisturbed, ungrazed *B. eriopoda* grassland in 2010. Vegetated and bare ground patches within the two grassland sites had similar herbivore communities, especially species from the family Tylenchinae. However, the mesquite duneland showed the lowest sampled diversity of all sites, but had significantly larger nematode abundances in vegetated dunes than interdune areas that are void of vegetation and soil biotic crusts where bacteriovores dominated. Decreased nematode trophic structure and species diversity in the Jornada black grama grassland samples compared with the undisturbed grassland illustrate the effect of desertification on the soil biotic community. Our results show that nematodes can be used to identify changes in belowground community structure based on trophic interactions. Large-scale disturbances like desertification can have consequences on the diversity and soil biotic functioning at finer spatial scales.

1. Introduction

Desertification of arid lands is a global problem, with nearly 40% of the world's land area either already converted or susceptible to a state change from productive grasslands to degraded shrublands or woodlands (Reynolds and Stafford Smith, 2002). These 'state' changes are difficult to restore because of the loss of herbaceous productivity, grass propagules, and modifications in soil surface properties that result in increases in runoff and erosion and losses in soil nutrients that favor woody plants (Schlesinger et al., 1990; Archer, 1994; Abrahams et al., 1995; Parsons et al., 1997; Whisenant, 1999; Wainwright et al., 2000; Peters, 2002a,b). Examining effects of drivers (e.g., multi-year drought, livestock overgrazing) of state changes on landscape-scale patterns often focus on vegetation responses; much less is known about changes in belowground communities that can influence vegetation dynamics. However, shifts in belowground community structure associated with desertification may provide a constraint on the ability of grasses to recover if soil biota critical to grass success are missing from the shrubland. Because arid ecosystems consist of a mosaic of grass or shrub plants and bare soil interspaces (i.e., gaps), differences in soil biota between these two microhabitats may

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have important consequences for grass recovery. Our goal was to determine how soil biota differs across a grassland-to-shrubland gradient of increasing woody plant abundance.

The composition of soil organisms (e.g., nematodes, bacteria, fungi, etc.) determines the influence of the soil microbial community on plant assemblages, in general (Ogle and Reynolds, 2004; Reynolds et al., 2004; Collins et al., 2008). Soil biota can affect the establishment and abundance of individual plant species with consequences for functional group and species diversity (van der Putten et al., 1993; Molofsky, 1994; Bever et al., 1997; Mills and Bever, 1998; Klironomos et al., 2000; Molofsky et al., 2001; O'Hanlon-Manners and Kotanen, 2004; Reinhart et al., 2003, 2005). A disruption or disturbance to soil biotic consortia can play an integral role in the dynamics of a system, and may be responsible for either promoting shrub invasion or limiting grass recovery (Wardle et al., 2004). In some cases, interactions between soil biota and plants can generate feedback mechanisms among soil biotic crusts, fungi, and plants (Belnap, 1996; Collins et al., 2008; Green et al., 2008; Lucero et al., 2008; Porras-Alfaro et al., 2007, 2011; Porra-Alfaro et al., 2008). Soil biotic crusts serve as an interface between the soil and atmosphere capable of fixing N and C while affecting the abundance, diversity, and successional maturity of other soil biota (Evans and Belnap, 1999; Belnap, 2003; Garcia-Pichel et al., 2003; Darby et al., 2006). Dark septate fungi (DSF) are the dominant colonizers of many native plants as well as *B. eriopoda* in the arid southwest that have the ability to manage and regulate carbon in plant communities, aid in nutrient acquisition and allocation, and provide increased drought tolerance to hosts (Barrow, 1997; Barrow et al., 2004; Lucero et al., 2006; Porra-Alfaro et al., 2008) The extension of fungal symbionts of *B. eriopoda* leads us to expect that increased connectivity of vegetated patches in grasslands harbor soil biotic communities linking vegetation and soils biotic crusts that occupy bare ground patches. Shrub encroachment and increases in bare ground gaps that perpetuate erosion/deposition processes causes vegetative production and decomposition of organic matter to be much more heterogeneous that can have long term effects on nutrient availability and relegate soil biotic communities to isolated vegetated patches (Schlesinger et al., 1990; Kéfi et al., 2007; Ravi et al., 2007; Scanlon et al., 2007).

The Chihuahuan Desert of North America provides an opportunity to evaluate these processes and feedbacks. The vegetation on sandy soils consists of perennial grasses, primarily black grama (*Bouteloua eriopoda*) and the shrub, honey mesquite (*Prosopis glandulosa*) that occur at variable proportions of cover across a landscape, yet total vegetation cover is similar. A key system property that differentiates grasslands from shrublands is the spatial distribution and density of plants and their associated bare soil interspaces (gaps) (Herrick et al., 2005; Okin et al., 2006). The low diversity of soil organisms compared with mesic systems is most likely due to species operating close to their physiological tolerance limits in the hot and dry abiotic environment (Whitford, 1996). Therefore, the limited functional redundancy of soil biota in arid systems increases the susceptibility of soil biotic communities to disturbances that can lead to profound impacts upon ecosystem processes (Wall and Virginia, 1999). A study of plant parasitic nematodes revealed less herbivory within a duneland site compared with grassland sites that was suggested to aid in establishment of mesquite (Wall and Virginia, 1999).

Because of the ubiquity and abundance of nematodes and the trophic specificity they exhibit, nematode community structure offers an efficient tool to assess soil biological function and food web quality (Bongers and Ferris, 1999). Specific nematode genera are active within each heterotrophic food web level and can be grouped by functional guilds whose members respond similarly to food web enrichment and to environmental perturbation and recovery (Yeates et al., 1993; Bongers and Bongers, 1998; Bongers, 1999; Ritz and Trudgill, 1999; Bongers and Ferris, 1999; Ferris et al., 2001; Neher, 2010).

This study relies on the quantification of nematodes with specific, morphologically distinguishable feeding behaviors as a proxy for characterizing changes in soil biota. We addressed the questions to represent two spatial scales across a desertification gradient: (1) how do nematode communities, and presumably the soil biotic consortia of vegetation states (black grama grasslands vs. mesquite shrublands), change? and (2) how do nematode communities differ between bare soil gaps and vegetated patches within each dominant vegetation type?

2. Methods

2.1. Study site

The study was conducted at the USDA-ARS Jornada Experimental Range (JER) and Jornada Basin Long-Term Ecological Research Site in southern New Mexico, USA (32°37′N, 106°40′W, and 1260 m a.s.l.). The JER is a 100,000 ha research site located within the northern extent of the Chihuahuan Desert. Long-term (1915–2009) mean annual rainfall is 246 mm that is highly variable from year to year with more than half of the precipitation occurring between July and October. Mean monthly average temperatures peak in June (26 °C) and are lowest in January (4 °C). Upland grasslands on sandy soils with a petrocalcic horizon at the JER are dominated by black grama (*B. eriopoda*) with mesa dropseed (*Sporobolus flexuosus*) and various three-awn species (*Aristida* spp.) as sub-dominate species. Over the past century, large areas of the upland grasslands have converted to shrublands dominated by honey mesquite (*P. glandulosa*) (Fig. 1).

Sample locations were selected to represent both remnant black grama patches and historic areas that were previously grasslands and are currently dominated by mesquite. The black grama and mesquite sites are the two end members of a desertification gradient, with a mixture of grasses and shrubs in the ecotone (Bestelmeyer et al., 2006). The ecotone sampling area represents the transition zone between the two end members as part of the desertification gradient. These transition zones, or ecotones, present optimal conditions because they are areas that have a high probability of response and are likely to experience threshold behavior, possess key processes that must be manipulated or maintained in order to uphold current conditions or to reverse a current undesirable trend, and provide early warning indicators that can be used to monitor and evaluate changes in critical processes (Peters et al., 2006). Because ecotones are defined by specific characteristics, they allow for the evaluation of the impact of desertification on a landscape scale interacting with fine-scale soil biotic communities specific to *B. eriopoda* and *P. glandulosa*.

Soils on the Jornada vary in texture from sandy loams to loamy sands with an indurated calcium carbonate layer at 15 to >50 cm depths (Hochstrasser et al., 2002). All geomorphic descriptions for the Jornada Basin follow Monger et al. (2006). Sample locations all occur on the same ancestral Rio Grande alluvium parent material of the Camp Rice Formation, Fluvial Facies. These strongly developed soils with thick petrocalcic horizons are components of the La Mesa surface where wind erosion has been the main source of quartzose sand accumulated on down-wind piedmont slopes and bedrock areas.

Nematode samples were also collected from Otero Mesa on June 11, 2010 to be used as a complement to the desertification gradient on the JER. Otero Mesa represents a reference site of intact, relatively undisturbed *B. eriopoda* grasslands. This Chihuahuan Desert site (32°30′N, 105°47′W) has the largest intact, public desert grassland in America (485,622 ha). Roughly half of