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Scale-dependent effects of *Gypsophila paniculata* invasion and management on plant and soil nematode community diversity and heterogeneity

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ABSTRACT

Invasion by exotic plant species has led to concerns of homogenization of biotic communities. Where plant invasion occurs, heterogeneity in plant community composition can decrease, even when other diversity responses are minimal. Homogenization of soil communities may also result from exotic plant invasion, though responses of soil communities to plant invasion are relatively understudied. In a long-term study underway since 2007, we examined effects of invasion and subsequent management of *Gypsophila paniculata*, a large invasive forb on Lake Michigan sand dunes, on aboveground plant community diversity and heterogeneity and belowground nematode community diversity and heterogeneity using Bray-Curtis and Jaccard dissimilarity measures. While invasion and management had only minor effects on plant and nematode richness and Shannon diversity, we found that invasion reduced plant and nematode community heterogeneity while management of the invasive species increased heterogeneity at smaller spatial scales. However, at larger spatial scales, neither invasion nor management had any effect on plant or nematode community heterogeneity. Overall this indicates that this invasion had the effect of homogenizing local communities, while landscape-level heterogeneity was unaffected. Reduced heterogeneity, particularly belowground, could have effects on plant community dynamics, since plant-soil interactions can contribute to continued invasion. Including the study of the soil community will enhance our understanding of community responses during exotic plant invasion and management.

1. Introduction

Exotic plant invasions are one aspect of global change (Mack et al., 2000) that pose a serious threat to biodiversity (Hejda et al., 2009; Vilà et al., 2011), among other negative impacts. Since plants form the basis for terrestrial food webs, effects of invasive plants are not limited to the plant community but can cascade through the food web, and management goals should consider impacts on multiple trophic levels. For example, many studies have documented that aboveground invertebrate communities are altered following plant invasion (reviewed in Bezemer et al., 2014; Simao et al., 2010). Some invasive species management goals now include restoration of pollinators or other important invertebrates (Baskett et al., 2011; Kaiser-Bunbury et al., 2017). Belowground communities have also been shown to change during exotic plant invasion (Belnap and Phillips, 2001; Chen et al., 2007; Ricciardi et al., 2017; Xiao et al., 2013), but effects of invasive plant management on soil communities have received less focus. Any changes in belowground communities in response to plant invasion or management could have consequences for ecosystem functioning such as nutrient cycling or soil formation (Ehrenfeld, 2003, 2010; Hawkes et al., 2005). In particular, responses of soil nematodes are important to study since nematodes occupy nearly every trophic level in the soil food web (plant-parasite, bacterivore, fungivore, predator), and their abundance and diversity can reflect overall soil ecosystem health (Liu et al., 2016; Yeates, 2003).

In addition to altering alpha diversity (e.g., species richness), plant invasions and subsequent management can alter beta diversity as well – defined within this study as the variation or heterogeneity in community composition (Anderson et al., 2011). Invasive plants may contribute to reduced heterogeneity by becoming locally dominant. High local dominance by invasive plants can alter heterogeneity in both community and habitat structure above and belowground. Aboveground, Lindsay and Cunningham (2012) found decreased ground-level spatial heterogeneity, based on plant basal area and gap size, associated with invasion by exotic grasses. Belowground, Vaness et al. (2014) found that invasion of *Agropyron cristatum* resulted in decreased heterogeneity in root distributions in grassland systems. Since plant roots and litter from aboveground plant tissues are the primary inputs of

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organic matter into soil communities (Sylvain and Wall, 2011), changes in aboveground heterogeneity are likely to cascade to affect belowground communities as well.

When evaluating diversity and heterogeneity responses to plant invasion and management, it is important to consider how the relationships could vary at different spatial scales (Sax and Gaines, 2003). A recent meta-analysis found an inverse relationship between spatial scale and effect size of invasion (Powell et al., 2011). Invasive plants tended to have stronger effects on species richness at smaller spatial scales, typically by achieving high local dominance. However at larger scales, their impacts on species richness were generally weaker (Powell et al., 2011), as invasive plants were less likely to eliminate species across larger areas.

Given the amount of resources that land managers use to manage invasive species, it is important to understand responses of organisms at multiple trophic levels and at multiple spatial scales when evaluating invasive species impacts and restoration effectiveness from a biodiversity perspective. In this study, we focused on the invasion and management of *Gypsophila paniculata* (baby's breath) in the Great Lakes' sand dunes. *Gypsophila paniculata* is a shrub-like tumbleweed native to Eurasia. It was likely introduced in the late 1800s as an ornamental (Darwent and Coupland, 1966), and has spread throughout sand dune habitats on the northwestern coast of the Lower Peninsula of Michigan, where it can achieve 80% cover in some places (Karamanski, 2000). Invasion by *G. paniculata* is associated with over-stabilization of sand dunes which can make the habitat unsuitable for native species (Emery et al., 2013). Additionally, *G. paniculata*, which has a deep root system, may outcompete native dune plant species for resources (Darwent and Coupland, 1966; Karamanski, 2000).

To combat this invasion, the National Park Service at Sleeping Bear Dunes National Lakeshore (SBDNL) and The Nature Conservancy (TNC) in Michigan, USA developed a collaboration to remove *G. paniculata* from their properties (Emery and Doran, 2013; Emery et al., 2013). For this study, we evaluated the effects of *G. paniculata* invasion and management on diversity and heterogeneity of plant and soil nematode communities. Specifically, we ask (1) Do invasion and management alter plant community diversity and heterogeneity? (2) Do invasion and management alter soil nematode community diversity and heterogeneity? (3) Do any effects on community heterogeneity differ based on spatial scale? To answer these questions, we utilized an ongoing long-term experiment containing invaded, uninvaded, and managed sites.

2. Methods

2.1. Sampling design

Details of the experimental design can be found in Emery et al. (2013). Briefly, fifteen 1000 m^2 (20 m × 50 m) plots across two sites were established in 2007. Nine of the 15 plots were located within Sleeping Bear Dunes National Lakeshore (SBDNL; 44.80°N, 86.06° W) and six were located within TNC's Zetterberg Preserve at Pt. Betsie (TNC; 44.68°N, 86.25° W). Six plots were invaded by *Gypsophila paniculata* which was subsequently managed each year 2008–2015 (‘managed’). Four plots were invaded by *G. paniculata*, but no management occurred during the study (‘invaded’). Five plots had no *G. paniculata* present or only in very low abundances, and therefore served as reference plots for restoration (‘reference’). These designations were consistent from the start of the experiment in 2007 through 2015, with the exception of two plots located on TNC property. One plot (Pt. Betsie D) was spot managed from 2008 to 2010, but management ceased by 2011 and so is considered an “invaded” plot for our analyses here, as *G. paniculata* cover quickly rebounded. One “invaded” plot (Pt. Betsie E) did not receive management from 2008 to 2010, but after 2010, regular management of *G. paniculata* began and so is considered a ‘managed’ plot for analyses here. We used park site as a block factor in analyses, due to differences in latitude and management history of the two parks (Emery et al., 2013). All three plot types occurred at both sites.

2.2. Management methods

From 2008 to 2010, management of *G. paniculata* involved mechanical removal by cutting the taproot of the plant as deeply as possible with a spade to minimize resprouting (Emery et al., 2013; McGowan-Stinski and Gostomski, 2006). After 2010, management of larger populations switched to a glyphosate herbicide treatment (RoundUp ProMAX, Monsanto, 2.3% concentration) with surfactant and blue indicator dye. Mechanical management was still applied for smaller populations and when weather conditions did not permit herbicide application. Dead plants were left on plots following management (S. Howard, *pers. comm*; J. Christian, *pers. comm.*).

2.3. Vegetation and nematode sampling

In 2007 (pre-management) and 2015, we measured plant diversity in each plot by estimating cover of individual species, as well as the percent bare ground, in ten 1 m × 1 m quadrats using a modified Daubenmire scale (Daubenmire, 1959). Quadrats were spaced approximately 10 m apart along the perimeter of plots. Species cover and plant species richness values from the quadrats were averaged to give cover values for each species in each of the 15 plots. We calculated Shannon diversity (H′) per plot based on the average species cover values for the whole plot. Pre-management (2007) differences in plant diversity are reported elsewhere (Emery et al., 2013), and these early data are used here only to calculate pre-treatment heterogeneity (see below).

In 2015 only, we sampled the soil nematode community by collecting five 2 cm diameter × 20 cm depth soil cores from each of five haphazard locations within each plot. At each of the five haphazard locations, we collected five soil cores which were combined and stored on ice or refrigerated at 4 °C until nematode extraction. This produced five separate soil samples per plot. From each sample, we extracted nematodes from a 100 ml subsample of soil using the centrifugal flotation method (Jenkins, 1964). Nematodes were fixed in hot 3% formalin, mounted on microscope slides, counted, and identified to genus using a compound microscope (Nikon Optophot-2) at 100–1000× magnification. Plot-level nematode genera richness and Shannon diversity were calculated by consolidating the 5 replicate samples into one group for each plot.

2.4. Data analyses

To evaluate effects of invasion and management on above and belowground diversity, we used mixed linear models with treatment as the fixed effect and park site as a random block effect. Response variables included average *G. paniculata* cover, % bare ground, % native plant cover, plant species richness, plant Shannon diversity, nematode genera richness, nematode Shannon diversity, nematode abundance, nematode Maturity Index, and nematode Plant-Parasitic Index at the plot level. We compared absolute abundances of each nematode functional group across treatments using MANOVA. Nematode abundance data were ln-transformed to better meet model assumptions. We assessed the average relative abundance of the various nematode feeding groups among treatments, and calculated treatment nematode maturity and plant-parasitic indices using the Nematode Indicator Joint Analysis program (Sieriebriennikov et al., 2014), which assigns feeding groups based on Yeates et al. (1993). The Maturity Index classifies nematodes into groups of colonizers and persisters, based on life history strategies and responses to disturbance (Bongers, 1990). The Plant-Parasitic Index is similar, except that it includes only the plant-parasitic nematodes. Finally, we used an Indicator Species Analysis (ISA; McCune et al., 2002) to evaluate whether individual nematode genera were associated with the different plot treatments, with Monte-Carlo randomizations to