The spatial influence of aboveground diversity on belowground communities

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Abstract. Little is known about the effect of diversity surrounding a focal plant species on the belowground community under that species. At least two alternative hypotheses exist. First, studies involving a range of ecosystems and taxonomic groups have shown that changes in diversity in one group of species can promote diversity in other groups. Alternatively, many studies in soil ecology have shown that belowground communities are strongly determined by the dominant aboveground species. To better understand the role of aboveground diversity on belowground communities, we examined soil nematode communities directly under *Panicum virgatum* (switchgrass) in areas of high and low surrounding plant diversity. We found that soil nematode diversity under switchgrass in areas of high plant diversity (native prairies) was not significantly different from soil nematode diversity under switchgrass in areas of extremely low plant diversity (switchgrass monocultures), indicating that an agricultural monoculture can maintain high levels of belowground diversity on a plant scale. However, reduced plant diversity surrounding focal switchgrass plants resulted in a compositional shift in the belowground community toward fewer herbivorous nematodes. This evidence for the influence of surrounding diversity on belowground communities under a focal plant species is a major shift in perspective from the conventional view on belowground community ecology. Furthermore, the work has broad implications for ecological perspectives on agricultural systems.

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INTRODUCTION

Many studies in community ecology involving a broad range of ecosystems and taxonomic groups have revealed a general pattern showing that diversity in one trophic group often influences and promotes diversity in other trophic groups within a community (Wills et al. 1997). For example, insect diversity is positively correlated with prairie plant diversity in a temperate grassland (Haddad et al. 2001). Alternatively, communities may be structured by the dominant species as opposed to diversity per se (Gilbert et al. 2009). For example, the identity of the dominant plant species in an experimental grassland system strongly influenced the invasibilty of the entire community (Emery and Gross 2007). Our understanding of intertrophic diversity interactions has largely been informed by studies in aboveground communities (De Deyn and Van der Putten 2005). Studies on aboveground and belowground community interac-

tions, however, have found weak support for a general intertrophic diversity relationship, with greater support for the importance of dominance. Some have found weak positive correlations between plant and soil biodiversity (Stephan et al. 2000), while others have revealed only idiosyncratic relationships (Hedlund et al. 2003). Most studies, however, cite the identity of the dominant plant species above a given location as the most important aboveground factor influencing the structure and composition of belowground communities (De Deyn et al. 2004, Viketoft et al. 2009, Bezemer et al. 2010).

We examined the relative importance of aboveground diversity on belowground communities while controlling for the effect of the aboveground dominant species. To accomplish this, we looked at the influence of aboveground plant diversity in the immediate vicinity of a dominant plant species on the soil community directly under the dominant species. We chose to address this question in a terrestrial plant system because many soil organisms interact intimately with plants. Wardle (2002) points out that "given that diversity of soil organisms can be determined by factors known to be influenced by plants [e.g., organic matter content, nitrogen concentration, and disturbance regime], it seems reasonable that plant species effects should serve as important drivers of soil biodiversity." For example, plant exudates are known to influence and structure the soil microbial community (Bais et al. 2006). Plant-mediated changes in the microbial community, in turn, have the potential to alter the diversity and community structure of the entire soil-based food web.

Our study focused on soil nematode communities directly under *Panicum virgatum* (switchgrass, Poaceae) in native prairies (areas of high plant diversity) and in switchgrass monocultures (areas of low plant diversity). Nematodes are exceedingly abundant in most soils and play important roles in vital ecosystem functions, including nutrient cycling, plant productivity, and decomposition (Ingham et al. 1985). Soil nematode communities are also composed of many feeding types, ranging from herbivores to carnivores. This trophic complexity makes nematode communities a good proxy for the rest of the soil community. We chose a switchgrass-centered system because this plant species occurs

naturally in native prairies and is also grown in monoculture for biofuel studies, seed production, and cattle feed. A study of nematode communities under switchgrass in native prairies and in nearby monocultures is a "quasi-natural" experiment that can help elucidate the effect of aboveground diversity on soil communities over a substantial period of time. Some switchgrass monocultures are over 40 years old and some native prairies have never been plowed. Thus, we are able to look at nematode communities over a much longer time span than can be done with an experimental approach (Viketoft et al. 2009).

Understanding more about nematode communities under switchgrass in natural and agricultural habitats is also important because switchgrass is currently being studied as a potential biofuel crop (Keshwani and Cheng 2009), and the negative impact of nematodes on monoculture crops is well documented (Mai 1985, Williamson and Hussey 1996). Little, however, is known about nematode communities under switchgrass, with only a few surveys of plant parasitic nematode species having been performed (Cassida et al. 2005, Mekete et al. 2009). Moreover, switchgrass has only recently been domesticated. Since most crops were domesticated hundreds or thousands of years ago, in many cases we are not able to compare nematode communities under cultivated populations to nematode communities under wild populations. We have a very limited understanding of how cultivation has affected nematode communities under major crops like potato, corn, and soybean. Work on switchgrass can provide insights into how plant domestication affects nematode communities early in the domestication process.

Methods

Sampling design

Nematode and plant communities were sampled at 40 sites across two habitat types: diverse prairies and switchgrass monocultures. Twenty sites in four native prairies (five sites/prairie) and 20 sites in four switchgrass monocultures (five sites/monoculture) were sampled in Lancaster, Otoe, and Saline Counties in southeast Nebraska. Prairies ranged in size from 7 to 223 acres and monocultures ranged from 3 to 27 acres. One

prairie has never been plowed or grazed, one has never been plowed but was overgrazed until in the early 1990s, and two have been restored from soybean/corn rotation (one in the 1970s and one in 1989). All four prairies are managed by annual or periodic burning. All switchgrass monocultures were converted from corn/soybean rotations (except one which was planted in Illinois bundle flower and then in soybean) in 1975, 1987, 2000, and 2006, respectively and planted with "Nebraska 28" seed cultivars ⟨http://www. nativeseednetwork.org/viewrelease?release_id= 9333⟩. All monocultures are managed by annual haying. The 2000 and 2006 monocultures were also enriched with 50–80 lbs N/acre/year and given infrequent aboveground herbicide treatments (atrizide). No monocultures have been treated with nematicides.

In prairies, sampling sites were selected within discrete stands of switchgrass. A stand of switchgrass was considered discrete if no other switchgrass stands were located within a 20-meter radius. In monocultures, samples were taken at 40–50 m toward the center from each monoculture corner, with a 5th sampling site near the center of each monoculture. All sites within monocultures were at least 20 meters from the next nearest sampling site. Plant communities at all sites in prairies and monocultures were sampled to morphospecies at two scales to account for differences between spatial scales on the effect of plant diversity on nematode communities: percent cover inside a 20-cm diameter circle (314 cm^2) centered on each site, and linear abundance along a 10-m line transect centered on each 20-cm circle. Linear abundances were estimated by calculating percentage cover of each plant species overlapping the line transects. Nematodes were sorted from an aggregate of 8 soil cores (~490 cm^3 each) evenly spaced around the perimeter of a 20-cm ring centered on each site in both prairies and monocultures.

Nematode extraction and identification

Nematodes were extracted from 100 ml subsamples of each aggregated soil sample using rapid sugar centrifugal-flotation. Total nematode abundances in the 100 ml subsamples were estimated by direct counting. Up to 200 nematodes were randomly selected from each extrac-

tion and heat killed and preserved in 4% formalin/2% glycerin solution. If a subsample contained less than 200 nematodes, all nematodes in that subsample were heat killed and preserved. In all cases, some nematodes were destroyed or lost in the preservation process. On average, 116 nematodes per subsample were preserved and identified to genus (Andrassy 1984, Siddiqi 1986) and trophic group (bacterivore, fungivore, herbivore, omnivore, and carnivore) (Yeates et al. 1993) based on morphological characters. Between 60–80% of nematodes in each of the 40 samples were identified. Unidentified nematodes were either ambiguous juveniles or poorly preserved.

Nematode diversity and richness

To examine whether nematode diversity under switchgrass in prairies is different from nematode diversity under switchgrass in monocultures, nematode Shannon diversity between all 20 prairie and 20 monoculture sites was compared using nested mixed-effect Analysis of Variance (ANOVA) (*nlme* in R). Nested mixed-effect ANOVA accounted for field as a random effect and for possible non-independence of sites within fields (five sites were sampled from each field and fields are nested within field type: prairie and monoculture). Habitat type (prairie vs. monoculture) was included as a fixed effect. In addition, nematode genus richness was analyzed alone because the Shannon diversity index combines taxonomic richness and evenness into a single number for each site. Richness was rarefied at n = 50 (*vegan* in R) because the number of nematodes in each sample varied from 50–162.

Categorizing sites as prairie or monoculture ignores the continuous variation that exists among these sites in terms of plant diversity. To examine nematode diversity across a continuous range of plant diversity in prairie and monoculture sites, nematode Shannon diversity was linearly regressed on plant Shannon diversity across all 40 sites at both plant-sampling scales (20-cm and 10-m) in R. Because many monoculture sites consisted of a single species, a regression that excluded monoculture sites was also performed.

Nematode community composition and trophic diversity

To examine nematode community composition between prairie and monoculture sites, the abundance of each genus at each site was analyzed using Detrended Correspondence Analysis (DCA) (Hill and Gauche 1980) (*vegan* in R). DCA was used because it is more interpretable than other approaches used to analyze community similarity (Jackson and Somers 1991). Most importantly, the distance between points on DCA are actual representations of similarity between those points. The distance between points in other ordination approaches (e.g., non-metric multidimensional scaling, or NMDS) is less informative. Relationships between site history (land-use and age) and nematode community composition were also analyzed by coding for site history on the Detrended Correspondence Analysis described above. Prairies ranged from "virgin pristine" to "recently restored," while monocultures ranged in age from 5–40 years old. Following confirmed differences in overall community composition, specific differences in average generic nematode abundances across habitats were examined by Indicator Species Analysis (Dufrene and Legendre 1997) (*labdsv* in R).

Nematode trophic diversity was also examined across sites by grouping genera into functional groups classified by feeding habit and then calculating a trophic diversity index for each site ($TDI = 1/\Sigma pi^2$, where *pi* is the proportion of individuals of the *ith* functional group in the total population). Mean trophic diversity, as well as mean total abundance, across prairie sites was compared to mean trophic diversity across monoculture sites via nested mixed-effect ANOVA (*nlme* in R). Following a confirmed difference in mean trophic diversity, differences in relative abundances of trophic groups between field types were analyzed by Indicator Species Analysis (Dufrene and Legendre 1997).

While the primary purpose of this design was to understand biotic differences among sites, abiotic soil factors may also affect nematode community composition (Veen et al. 2010). Soil type and soil fertility were selected, from a suite of possible abiotic factors which may affect nematode abundance, so as to provide some contrast with the biotic factors. Correlation between soil type and field type (prairie vs. monoculture) across all sites was examined via contingency table analysis. Soil types for each sampling site in both prairies and monocultures were determined using soil surveys prepared by the United States Department of Agriculture and University of Nebraska (Brown et al. 1980, Sautter et al. 1982, DaMoude et al. 1990). To account for a relationship between soil fertility and nematode community composition, C/N ratios for each site were linearly regressed against the first axis of the Detrended Correspondence Analysis described above. C/N ratios were determined from subsamples of each soil core aggregate by dry combustion GC in a Costech ECS 4010 in the Ecosystem Analysis Laboratory at the University of Nebraska-Lincoln.

RESULTS

On average, total estimated abundance of nematodes was greater in prairies than in monocultures (883.1 and 454.9 nematodes/100 cc soil, respectively; p = 0.043), with a significant random effect of field (p < 0.0001).

Nematode diversity and richness

Mean nematode Shannon diversity under switchgrass in prairies was not significantly different from mean nematode Shannon diversity in monocultures of switchgrass (1.58 and 1.63, respectively; p = 0.55; Fig. 1A). Mean rarefied nematode richness under switchgrass in prairies was not significantly different from mean rarefied nematode richness in monocultures (8.79 and 8.35, respectively; p = 0.45; Fig. 1B). There was no significant random effect of field on Shannon diversity or richness (p = 0.9 in both cases), indicating independence among all 40 sites.

Across all sites in prairies and monocultures there was no significant relationship between nematode Shannon diversity and plant Shannon diversity when examined across a continuous range of plant diversity at either small or large spatial scales of plant sampling (20-cm: p = 0.90; 10-m: p = 0.45). These results are robust to the exclusion of sites from monoculture fields (20-cm: p = 0.53; 10-m: p = 0.58; Fig. 2).
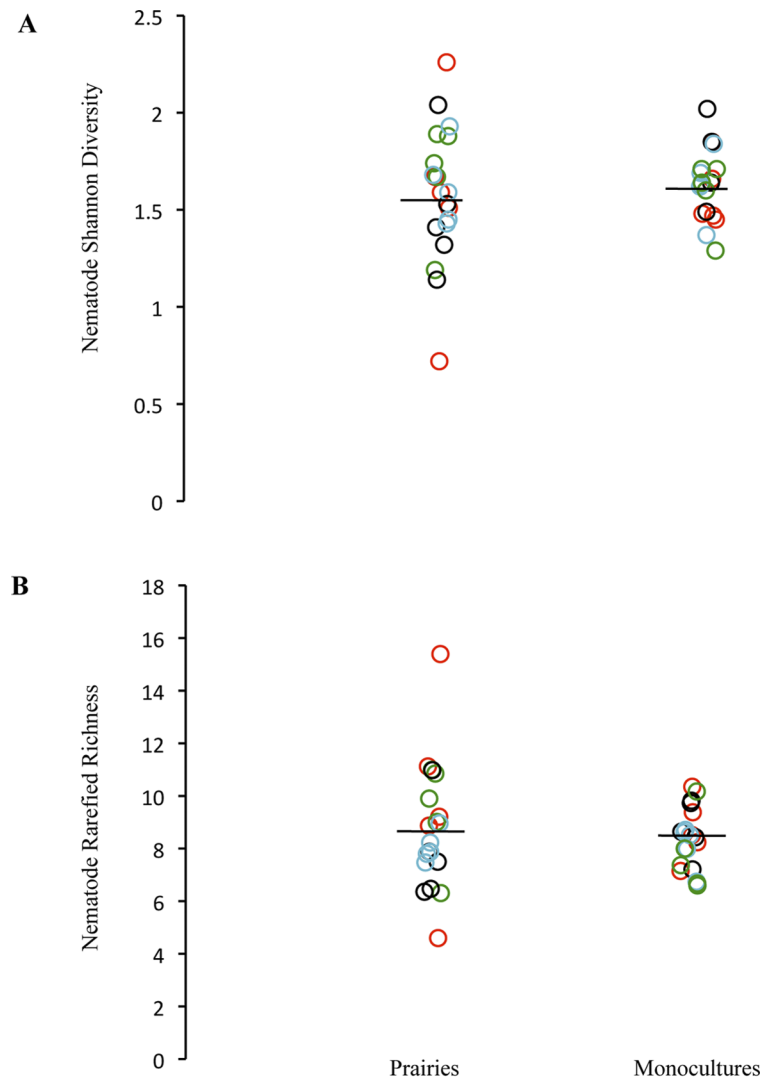
Fig. 1. The average diversity of soil nematodes under switchgrass in prairies is not significantly different from the average diversity of soil nematodes in monocultures of switchgrass as measured by (A) the Shannon Diversity Index and (B) rarefied richness. Black horizontal lines indicate means of each diversity measure. Sampling sites within individual prairies and monocultures are similarly colored.

Nematode community composition and trophic diversity

A clear separation of prairie and monoculture sites in the Detrended Correspondence Analysis on the abundance of each nematode genus showed that nematode communities under switchgrass in prairie sites were compositionally different from nematode communities under switchgrass in monoculture sites (Fig. 3). This difference was statistically confirmed by Indicator Species Analysis showing significant differ-

ences between average abundances of nematode genera from different trophic groups and different abundance classes across prairie and monoculture sites (Fig. 4 and Table 1). While not tested statistically, coding for field history on the Detrended Correspondence Analysis indicates a trend in that pristine virgin prairie sites were most divergent from monoculture sites, but also exhibited the most variability among themselves. The oldest monoculture sites were most similar to prairie fields (Fig. 5).
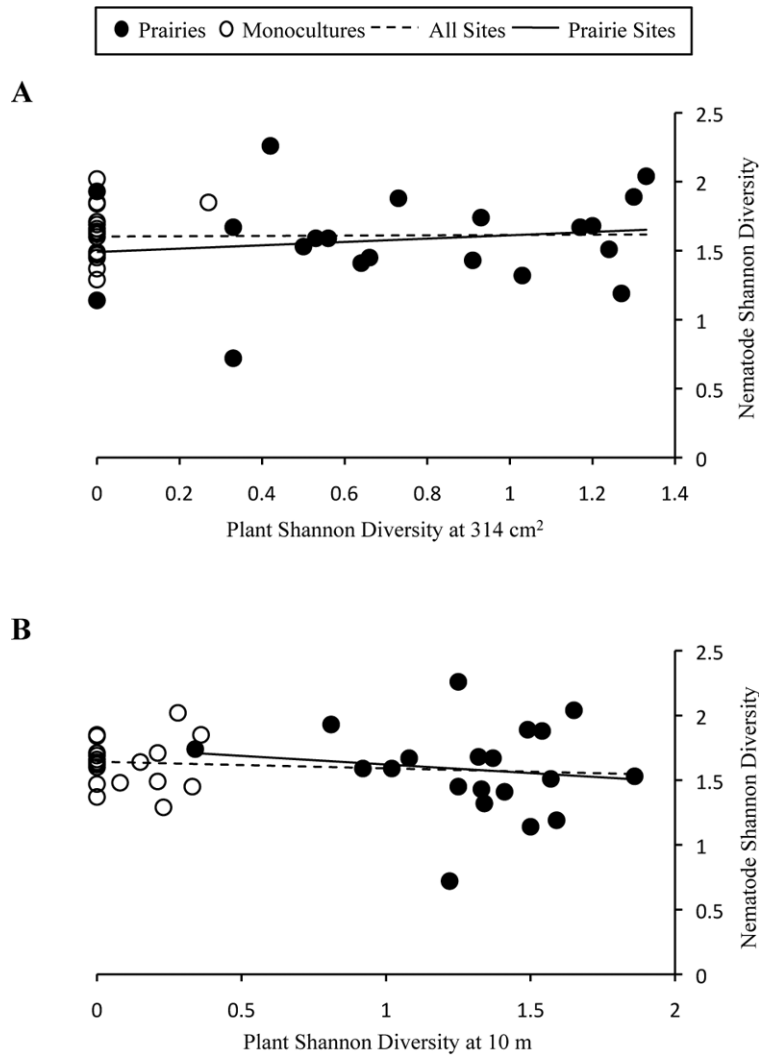
Fig. 2. There is no significant correlation between plant diversity and nematode diversity under switchgrass across prairie and monoculture sites (dashed line, closed + open circles) or in prairie sites alone (solid line, closed circles). Plant diversity was measured at 2 scales: (A) percent cover within 20 cm rings (314 cm^2) and (B) along 10 m line transects.

Mean trophic diversity of prairie sites was statistically different from mean trophic diversity of monoculture sites ($p = 0.040$), even after accounting for a significant random effect of field ($p = 0.049$). On average, individuals from plant-feeding genera were more abundant in prairie sites ($p = 0.005$), while individuals from bacterial feeding genera were more abundant in monoculture sites ($p = 0.005$). Average abundances of individuals from carnivorous, fungivorous, and omnivorous genera were not statistically different between prairie and mono-culture sites ($p = 0.54$, $p = 0.47$, and $p = 0.54$, respectively).

Nematode community composition was not significantly related to soil C/N ratio ($p = 0.17$). However, there was a significant association between field type and soil type ($p < 0.0001$). Prairie sites usually consisted of clay loam soils, while cultivated field sites generally consisted of silty clay loam soils.
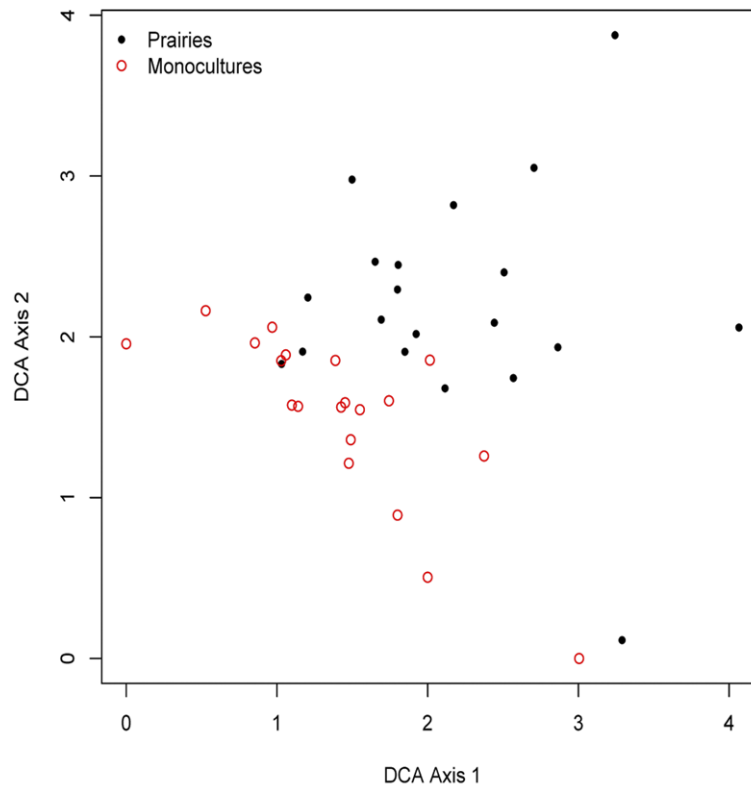
Fig. 3. Detrended Correspondence Analysis examining the relationships between prairie sites (closed black circles) and monoculture sites (open red circles) in terms of nematode community composition. Distinctive clustering of prairie sites in the upper right side and of monoculture sites in the lower left side indicates that prairie sites are more similar to each other than they are to monoculture sites and vice versa.

Discussion

We found that soil nematode diversity under switchgrass in remnant prairies is not significantly different from soil nematode diversity under switchgrass in monoculture, despite the fact that plant diversity in monocultures is very low. Soil fertility is not driving this relationship, consistent with recent findings (Veen et al. 2010). Our results indicate that plant diversity surrounding switchgrass does not influence nematode diversity directly under switchgrass. However, we found that the diversity of plants surrounding switchgrass does have a significant influence on the composition of nematode communities under this species, a result consistent with Bezemer et al. (2010). These contrasting results are surprising from both a general ecology and a soil ecology perspective. In general ecology, intertrophic diversity relationships are common; whereas, in soil ecology, the aboveground dominant species is considered to be the most important factor influencing belowground communities. Presumably this is because aboveground species, such as insect herbivores, move much more readily among plants while belowground species, such as nematodes and microbes, are far more restricted in their movement patterns. Previous studies have found positive diversity relationships between plant and nematode communities (De Deyn et al. 2004, Viketoft et al. 2009, Bezemer et al. 2010, Veen et al. 2010), due at least in part due to increased sampling of nematode communities under a diversity of plant species. In contrast, we sampled exclusively under a single plant species. Given the presumed restricted movement of belowground fauna, the influence of surrounding plant diversity is likely due to an indirect spatial cascade via biotic interactions. Alterna-
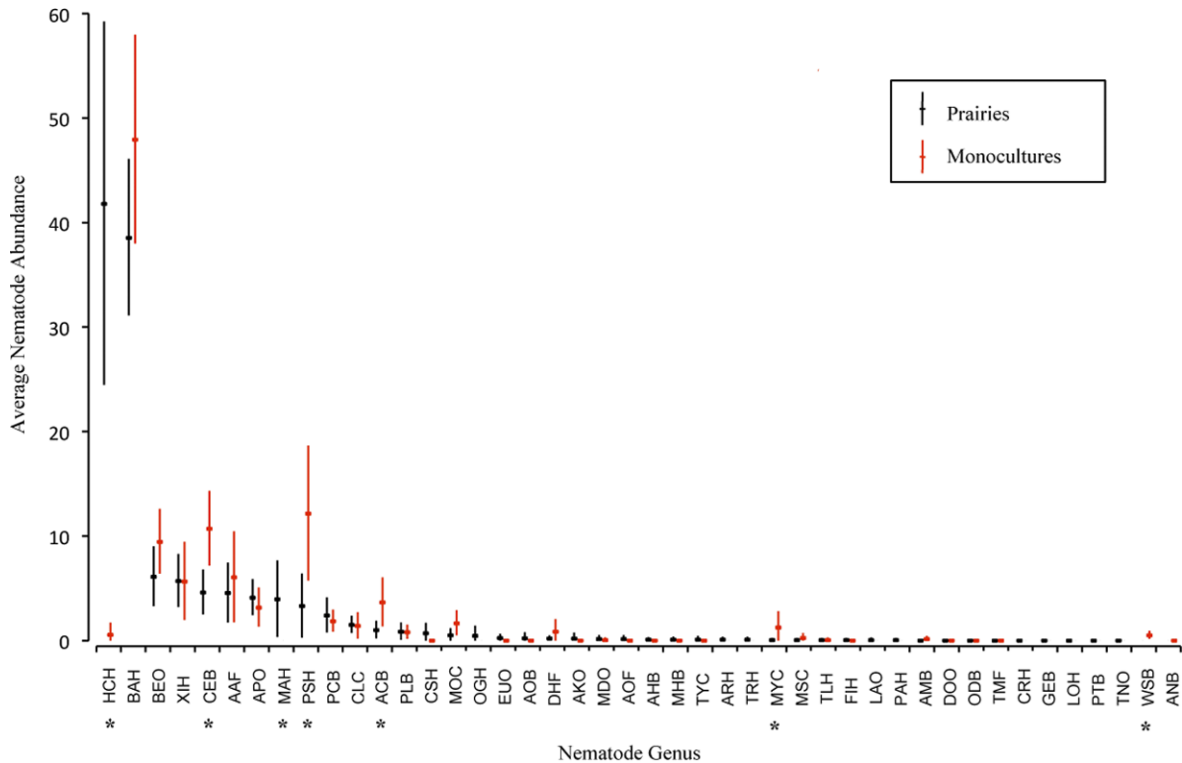
Fig. 4. Average abundance of nematode genera in prairies (black) and monocultures (red) across all sites. Error bars show ± 1 standard error of the mean. The first two letters of each code indicate genus (see Table 1). The third letter of each code indicates trophic group: B – Bacterivore, C – Carnivore, F – Fungivore, H – Herbivore, O – Omnivore. An asterisk indicates significant differences in average abundances between prairies and monocultures at the p = 0.05 level.

tively, individuals are moving among the surrounding plant communities to a great enough degree that community structure is altered. Our study shows that while aboveground diversity does not affect diversity below a dominant species, aboveground diversity surrounding the dominant species does influence belowground community composition.

Because we controlled for the effect of the dominant plant species, our results indicate that switchgrass is able maintain nematode diversity on its own. Switchgrass has a deep, highly fibrous root system that may ameliorate the effect of reduced plant diversity in monoculture. This extensive root structure may allow for a high level of niche specialization by herbivorous and microbivorous nematode species, leading to increased nematode diversity at higher trophic levels within nematode communities. Recent work has shown that increasing nematode diversity can decrease levels of herbivory by nematodes in crop systems (Brinkman et al. 2005). The maintenance of nematode diversity under switchgrass in monoculture may be good news for future switchgrass production. At the same time, we are unable to make any statements about overall nematode diversity in prairie systems because our samples in prairies were constrained to nematode diversity directly under clustered stands of switchgrass. For example, if we were to randomly sample nematode diversity *across* a given prairie, we would be very likely to find a higher diversity of nematodes than what we would see from a sample across a similarly sized switchgrass monoculture.

Belowground herbivory has been shown to influence soil microbial function and abundance (Gange 2001), promote rhizodeposition (Bardgett and Chan 1999), and both positively and negatively affect plant growth (Belovsky and Slade

Table 1. Nematode genus codes used in Fig. 4.

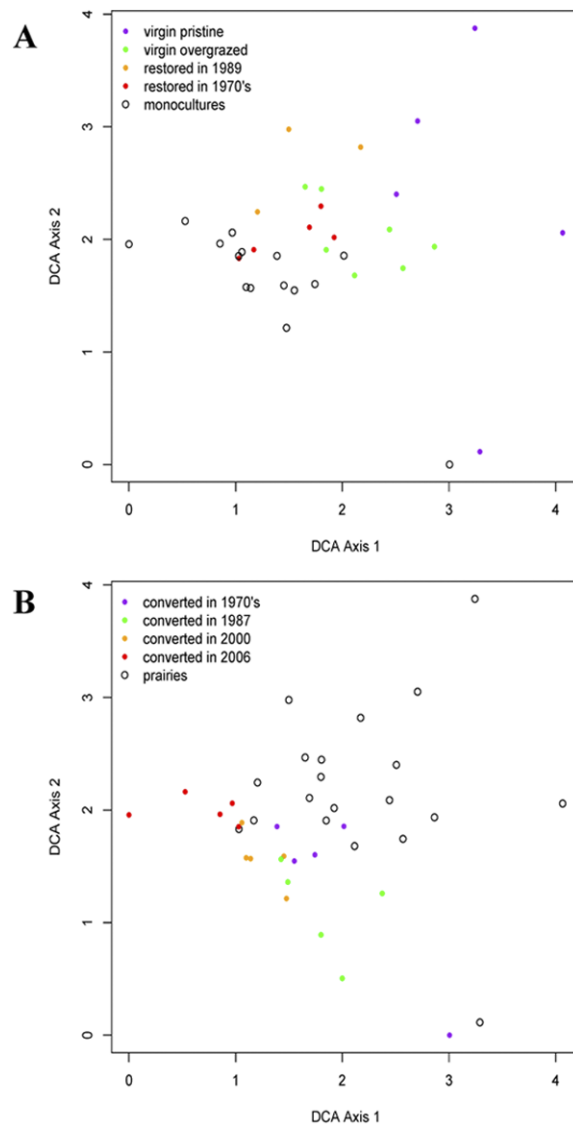| Genus name	Code
Aphelenchus	AAF
Acrobeles	ACB
Achromodora	AHB
Akrotonus	AKO
Alaimus	AMB
Anaplectus	ANB
Acrobeloides	AOB
Aphelenchoides	AOF
Aporcelaimellus	APO
Aorolaimus	ARH
Basiria	BAH
Belondira	BEO
Cephablobus	CEB
Clarkus	CLC
Criconema	CRH
Coslenchus	CSH
Diphtherophora	DHF
Dorylaimus	DOO
Eudorylaimus	EUO
Filenchus	FIH
Geomonhystera	GEB
Helicotylenchus	HCH
Laimydorus	LAO
Longidorus	LOH
Macroposthonia	MAH
Microdorylaimus	MDO
Monhystera	MHB
Mononchus	MOC
Michonchus	MSC
Mylonchulus	MYC
Odontolaimus	ODB
Ogma	OGH
Paratylenchus	PAH
Plectus	PCB
Prismatolaimus	PLB
Psilenchus	PSH
Pristionchus	PTB
Tylenchus	TLH
Tylencholaimellus	TMF
Thonus	TNO
Tylenchorhynchus	TRH
Tripyla	TYC
Wilsonema	WSB
Xiphinema	XIH
Xiphinema	XIH

Fig. 5. The Detrended Correspondence Analysis in Fig. 3, coded for history of each prairie site (panel A) and year of conversion to switchgrass of each monoculture site (panel B). Open circles represent monoculture sites in (A) and prairie sites in (B). Closed circles are color-coded by prairie in (A) and by monoculture in (B).

2000, De Deyn and Van der Putten 2005). The often devastatingly negative effects of plant parasitic nematodes on crop production have been well documented (Mai 1985). Species of the most abundant nematode genus in our study, Helicotylenchus, are classified as a ecto- or semiendoparasites on roots. Typically, the host ranges of species in this group are extremely broad including monocots and dicots, annuals, and perennials. Helicotylenchus life-cycles are generally completed within 4 weeks, depending on temperature, and many species can survive months in the soil without a host (Fortuner 1991). The hardiness implied by these life-history traits

are especially interesting in light of our results because Helicotylenchus is almost completely absent from monoculture sites, suggesting that switchgrass in monoculture may be suppressing certain herbivores. While we did not measure herbivory levels empirically, the implication our

results provide for a potential reduction in belowground herbivory from natural to cultivated sites would contrast with conventional wisdom that nematode herbivory levels are generally quite high in agricultural systems (Mai 1985).

Our results also lead to a number of contrasting hypotheses about the early effects of plant domestication on nematode diversity in general. First, nematode diversity in crops (even tilled crops) may not be reduced at the plant scale compared to nematode diversity under native plantings of those crop species. This hypothesis would be difficult to test, given the time that has elapsed since domestication of most crops. Second, nematode diversity under other crops may have decreased gradually over time as communities have evolved in response to reduced plant diversity. This hypothesis leads to the prediction that nematode diversity under switchgrass may be following a similar trajectory, with the possibility that an economically important nematode pest of switchgrass will yet appear through evolutionary time. Even if this second idea is true, our results indicate that 40 years is not sufficient time for nematode communities to experience a reduction in diversity under switchgrass in monoculture. Third, nematode diversity in other crops may be reduced compared to nematode diversity under native plantings, but switchgrass is able to maintain nematode diversity despite a reduction in plant diversity in monoculture. The mechanism by which switchgrass is able to maintain nematode diversity should be investigated more closely.

Land-use history should also be considered when comparing soil communities. Switchgrass is a no-till perennial crop. Most crops that experience high levels of nematode herbivory are plowed, severely disturbing nematode communities on an annual basis (Stetina et al. 2008). These high levels of disturbance may decrease nematode diversity and shift nematode community composition and trophic diversity toward r-strategists, many of which are known to be important herbivores of crop plants (Bongers 1990). Annual soil disturbance may thus maintain high levels of herbivorous nematodes, leading to decreased plant productivity over time. Our results show that this may not always be the case, however. Many of the switchgrass

monoculture sites were recently tilled (half within the last 10 years and all within the last 40 years) and all but one have fewer herbivorous nematodes (by fraction and by total abundance) than prairie sites that have never been disturbed. This may indicate that nematode communities in general are able to recover relatively quickly from structural habitat disturbances of conventional tilling when traditional crop fields are converted to no-till crops. In addition, our results show that nematode community composition and soil C/N ratio (one measure of soil organic matter) are not correlated. This is true despite annual nitrogen enrichment in monoculture fields. Soil type, on the other hand, is significantly correlated with field type. Nearly all prairie sites (17) consist of clay loam soil, while all monoculture sites (20) consist of silty clay loam soils. The effect of this correlation on differences in nematode community composition is likely small, as others have shown that many nematode genera present in our study have been found across a large range of soil types (De Goede and Bongers 1998). For example, species in the most abundant genus in our results, Helicotylenchus, are known to have a extremely broad host ranges across a wide array of soil types (Fortuner 1991).

Our study shows that in nematode communities under switchgrass, changes in plant diversity do not necessarily translate into changes in nematode diversity. But, differences in plant diversity can lead to changes in nematode community composition and trophic structure. These community differences may, in turn, influence shifts in the ecosystem functioning of nematode communities under switchgrass in areas of high and low plant diversity. These results highlight a major shift in perspective from the conventional view on belowground community ecology. The spatial influence of aboveground diversity on belowground communities is more diffuse than previously thought. Furthermore, from an environmental and economic standpoint, the ability of switchgrass to maintain nematode diversity and possibly lower nematode herbivory in monoculture is a finding that warrants further investigation in both the fundamental and applied fields of ecology.

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