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If we build it, will they colonize? A test of the field of dreams paradigm with soil macroinvertebrate communities

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ABSTRACT

Soil invertebrates transfer energy and material between belowground and aboveground systems, but a clear understanding of their recovery following long-term disturbance to soil is lacking. We quantified trophic, taxonomic, and compositional change of soil macroinvertebrates in cultivated fields, prairies restored for 1–21 years, and prairies that had never been cultivated. Taxonomic diversity (H′; based on morphospecies), richness, and evenness did not change across the chronosequence. Average taxonomic richness across all restorations was intermediate to cultivated fields and remnant prairie. Detritivores increased linearly across the chronosequence, while omnivores peaked at 5–8 years following restoration, coinciding with high plant richness. Spiders were the only predators that increased across the chronosequence. Proportional similarity of the macroinvertebrate communities to the average structure of remnant prairies increased across the chronosequence, but this relationship was not upheld when individual remnant prairies with different community structures were used. This study demonstrates that remnants can vary widely in macroinvertebrate trophic structure, diversity, and taxonomic composition and include exotic macroinvertebrate species, indicating a real dilemma for assessing recovery of restorations to a "target" community.

1. Introduction

Soil invertebrates contribute to decomposition, nutrient cycling, water infiltration, trophic transfer of energy and material in ecosystems (Lavelle et al., 1997; Riggins et al., 2009), and can influence the successional trajectory of vegetation (Brown and Gange, 1989, 1992; De Deyn et al., 2003; Schadler et al., 2004). Despite their critical role in terrestrial ecosystem functioning and composition (Lavelle et al., 1997), soil invertebrates are frequently overlooked in ecological restorations (Snyder and Hendrix, 2008). Knowledge of how their communities change in response to restoration is needed for a more holistic assessment of ecosystem recovery from disturbance.

The extensive conversion of the grassland biome to row crop agriculture (Ellis and Ramankutty, 2008), including >90% of the tallgrass prairie in North America (Samson and Knopf, 1994), has negatively impacted soil invertebrates (Giller et al., 1997; Postma-Blaauw et al., 2012). Ecological restoration is the only means to increase the extent and quality of grassland, and this practice often involves reintroduction (sowing) of historic plant species (Hobbs and Harris, 2001). Invertebrate propagules, however, are rarely introduced into restorations (Lawrence et al., 2013). Thus, colonization of soil biota is generally dependent on natural dispersal from the regional species pool from the surrounding landscape, which is highly fragmented and agricultural. Hilderbrand et al. (2005) refer to this mechanism of community assembly as the "field of dreams myth," in reference to the 1989 American film starring Kevin Costner. Hilderbrand et al. (2005) suggest physical template and process driven restoration are important, but self assembly of pre-disturbance communities may not occur.

Soil invertebrate communities are influenced by the quantity and quality of organic matter input from the plant community (Scheu and Schaefer, 1998; Callaham et al., 2003; Evans et al., 2005a) and interactions with higher trophic levels (Siemann, 1998). The density and biomass of soil invertebrates varies with fire frequency, mowing, and nutrients in tallgrass prairie (Callaham et al., 2003). Burning and mowing reduced the quantity and quality (higher C:N ratio) of root inputs, corresponding with a reduction in invertebrate density, whereas nutrient addition tended to increase invertebrate density or biomass. Berg and Hemerik (2004) found

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that soil macroinvertebrates (isopods, millipedes, and centipedes) in four European grasslands recovering from long term fertilization responded to changes in soil nutrient status that were driven by successional changes in the plant community. Recovery of specific groups may occur in the absence of whole community recovery. For example, Brand and Dunn (1998) found restoration time to be important for recovery of Collembola species richness.

A clear understanding of belowground macroinvertebrate community recovery from disturbance and in response to restoration is lacking for most systems. We quantified soil macroinvertebrates across a chronosequence of restored tallgrass prairies to better understand the rate and compositional change in response to time since cessation of cultivation coinciding with restoration. We hypothesized that taxonomic richness, evenness and diversity of macroinvertebrates would increase across the chronosequence in response to developing root systems and soil organic matter inputs (Matamala et al., 2008; Baer et al., 2010). Additionally, we hypothesized that different trophic groups would respond to the chronosequence idiosyncratically because detritivores and herbivores are likely more dependent on developing root systems than omnivores and predators. We predicted omnivores would be more responsive to plant richness because previous study has shown the dominant taxa in this group, ants, were correlated with plant richness (Wodika et al., 2014). Predator density was not expected to change across the chronosequenec since prey resources can be abundant early in restorations. Finally, because recovery of roots and perennial plant cover can occur within two decades of grassland restoration (Baer et al., 2002, 2010), but plant diversity can fail to represent that of remnant prairie (Sluis, 2002; Hansen and Gibson, 2014), we predicted that macroinvertebrate community structure would become similar to but not representative of remnant prairie following two decades of restoration.

2. Materials and methods

2.1. Site description and study design

Soil invertebrates were sampled at Nachusa Grasslands, owned by The Nature Conservancy and located in Ogle and Lee (41°53′27.36″ N, 89°20′36.56″ W) counties of northern Illinois. Nachusa Grasslands contains >1100 ha of small prairie remnants and independently restored prairies embedded in a matrix of active agricultural fields. The soils of the study site are sandy loams formed by alluvial and Aeolian processes (Argiudoll, Haplodoll, and Hapludalf great groups). Temperatures during this study were comparable to long term averages at 8.6 °C and 8.7 °C in 2008 and 2009. Precipitation exceeded the thirty year average (975 mm) in the years of this study, totaling 1230 mm in 2008, and 1488 in 2009 (NOAA, 2013).

We used a chronosequence (space for time substitution) approach to quantify changes in the soil invertebrate community across prairies restored for different periods of time. Our study design contained two active agriculture fields (age = 0), 18 restorations (restored for 1–21 years), and two remnant prairies that have never been plowed (Table 1). We used remnant prairies to assess the trajectory of change and compare the recovery of macroinvertebrate community structure in the restorations.

Restoration followed cessation of conventional tillage agriculture for corn (*Zea mays* L.) and soybean (*Glycine max* (L.) merrn) production. Each field was independently restored by broadcasting a locally collected seed mixture containing up to 200 species of native forbs and graminoids. Restorations were often over-seeded before the second growing season and occasionally in the third year (Bill Kleiman, personal communication). Non-native plants were controlled through mechanical removal and spot-spraying with herbicides. All sites were burned regularly. Prescribed fire is applied to the preserve in the spring and in fall such that study sites experienced a fire return interval of approximately every 18 months (Bill Kleiman and Cody Considine, personal communication).

Table 1
Prairie restoration chronosequence including field identifications, age of the restoration, and soil properties.

Site name	Years restored	Soil texture	Soil classification
Cultivated	0	Loam	Mesic Typic Hapludoll
Cultivated	0	Loam	Mesic Typic Arguidoll
TNC 74	1	Loam	Mesic Typic Argiudoll
TNC 69	1	Loam	Mesic Typic Hapludoll
TNC 68	1	Loam	Mesic Typic Hapludoll
TNC 66	1	Loam	Mesic Typic Argiudolls
TNC 58	5	Silt loam	Mesic Typic Hapludalf
TNC 57	5	Loam	Mesic Typic Argiudoll
TNC 56	5	Loam	Mesic Typic Argiudoll
TNC 55	5	Loam	Mesic Typic Hapludoll
TNC 53	8	Silt loam	Mesic Typic Hapludalf
TNC 52	8	Loam	Mesic Typic Hapludoll
TNC 25	9	Loam	Mesic Typic Hapludoll
TNC 15	13	Loam	Mesic Typic Argiudoll
TNC 37	16	Loam	Mesic Typic Argiudoll
TNC 31	16	Loam	Mesic Typic Argiudoll
TNC 13	21	Loam	Mesic Typic Argiudoll
TNC 12	20	Loam	Mesic Typic Argiudoll
TNC 9	16	Loam	Mesic Aquic Argiudoll
TNC 7	21	Loam	Mesic Typic Argiudoll
Remnant 1	Prairie	Loam	Mesic Typic Argiudoll
Remnant 2	Prairie	Loam	Mesic Lithic Hapludolls

Prior to purchase by The Nature Conservancy, the remnant prairies in this study were degraded by overgrazing cattle and encroachment by woody vegetation. Management has consisted of cattle removal, tree/shrub removal, and a frequent fire regime. Plant surveys of these prairies in 2008 demonstrated that Remnant 1 had a plant community of greater diversity than Remnant 2 (Klopf, 2013).

2.2. Soil invertebrate sampling and processing procedures

Soil macroinvertebrates (≥0.5 mm in length) were sampled from soil monoliths extracted along a transect established to measure plant community. Each field was sampled twice to capture seasonal variation in the belowground macroinvertebrate communities: once in the spring and once in the fall. Most fields were sampled in October 2008 and June 2009. We were able to add more fields to the chronosequence in the spring, so these fields were sampled in June 2009 and October 2009. On each sampling occasion, five monoliths (25 cm length × 25 cm width × 25 cm deep) were removed from each field at 5 m intervals along a transect. Soil monoliths were sampled 2 m away from the vegetation transect in a cardinal direction.

Soil monoliths were broken apart by hand and visually searched for macroinvertebrates in the lab. Specimens were preserved in ~8% formaldehyde. To assess recovery of the entire community, we assigned individuals to morphospecies. The morphospecies method is useful when examining an entire invertebrate assemblage (Oliver and Beattie, 1996; Litt and Steidl, 2010), and especially useful in this study as the soil environment contains numerous immature invertebrates that lack genus and species keys. Dindal (1990) was used to identify many of the soil invertebrates encountered (Oligochaeta, Diplopoda, Chilopoda, Isopoda, Opiliones). Adult insects were sorted and identified to order and then family based on characteristics in Triplehorn et al. (2005). Ants (Hymenoptera: Formicidae) were identified to genus or species