



Effects of woodland restoration and management on the community of surface-active arthropods in the metropolitan Chicago region



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ABSTRACT

Restoration of woodlands that have been invaded by exotic plants has primarily focused on restoring vegetation structure by removing invaders and planting native species that have declined in abundance. Management practices to date continue to focus on plant communities, but if restoring ecosystem integrity is the goal of restoration, knowledge of how the fauna has recovered is essential. We examined the impact of vegetation restoration and management on the surface-active arthropod community across a spectrum of 22 woodland sites in the greater metropolitan Chicago region. Sites were grouped into three categories based on existing condition. Invaded sites had never been restored or managed (“Control”, $n = 5$); had been undergoing restoration for 3–21 years (“Managed-int”, $n = 12$) but were not yet near the management goal; or were restored plots (11–21 years of management) that land managers identified as representative of their restoration target based upon the vegetation present (“Managed-REF”, $n = 5$). Each site was a one-ha plot containing four pitfall traps used to assess activity-densities of 35 taxa of epigeic arthropods. Permutational analysis of variance (PERMANOVA) and subsequent canonical analysis of principal coordinates (CAP) revealed that arthropod community structure varied between *Control* and *Managed-REF* sites, with the *Managed-int* sites demonstrating convergence toward the *Managed-REF*. The activity-densities of non-native isopods (detritivores) were nearly twice as high in *Control* sites compared to *Managed-REF* sites, whereas traps in *Managed-REF* sites had four times the number of Collembola (fungivores). Distance-based redundancy analysis (dbRDA) revealed that invasive woody plant cover and rates of uptake of soil P and NO_3^- by root simulators explained over 40% of the variation in arthropod community structure. Our findings suggest that restoration management targeted at the vegetation also restores the arthropod community in woodlands to a composition that has fewer non-native arthropods.

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1. Introduction

Invasive plants have been a major cause of habitat degradation worldwide (Vitousek et al., 1997; Powell et al., 2011). Invasive plants can impact communities by altering nutrient cycling and availability (Ehrenfeld, 2003; Weidenhamer and Callaway, 2010), changing disturbance regimes (Mack and D’Antonio, 1998; Brooks et al., 2004), or by outcompeting the native plant community (Callaway and Aschehoug, 2000; Brown et al., 2002). As a consequence, the impact of invasive plants has been regarded as one of the most important global-scale factors threatening natural communities (MacDougall and Turkington, 2005; Moser et al., 2009).

In response to habitat degradation by invasive plants in the Chicago region, the Chicago Wilderness conservation alliance created its Biodiversity Recovery Plan as a guide “to sustain, restore, and expand the remnant natural communities of the Chicago region” (Chicago Wilderness Biodiversity Council, 1999). Restoration strategies utilized by agencies that are part of Chicago Wilderness usually include invasive plant removal, native replanting, and the implementation of prescribed burning, with the primary goal being to restore the composition and diversity of native trees, shrubs, and herbaceous vegetation (Wallis De Vries et al., 2002; Wagner et al., 2004; Knapp, 2010). Such management strategies, while comprising a vital step toward the restoration and preservation of natural communities in urbanized areas, must be reinforced by fundamental understandings of how the entire

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ecosystem responds to management (Morris, 2000; Wallis De Vries et al., 2002; Woodcock et al., 2005).

Epigeic (i.e. surface-active) arthropods are major components of the belowground food web (Coleman and Hendrix, 2000), and because they are active on the soil surface, also provide a link to aboveground food webs (Bardgett and Wardle, 2010). Surface-active arthropods are important players in litter decomposition, with implications for nutrient cycling (Swift et al., 1979; Petersen and Luxton, 1982; Seastedt, 1984; Lawrence and Wise, 2004). For example, Chamberlain et al. (2006) illustrated that springtail (Collembola) activity caused greater availability of carbon to the soil microbial community. Pieper and Weigmann (2008) demonstrated higher mobilization of several nutrients, such as litter-derived organic carbon, in the presence of isopods. A number of other studies have also demonstrated that soil fauna break down complex litter substrate and further release nutrients into the soil (Ayres et al., 2009; Carrillo et al., 2011; Bokhorst and Wardle, 2013), thus influencing rates of nutrient cycling in terrestrial ecosystems.

Recent studies have documented changes to epigeic arthropod diversity and community composition following the implementation of restoration techniques, but the pattern of results is mixed. For instance, Coleman and Rieske (2006) demonstrated that repeated prescription burns in an oak-pine forest in southeastern USA decreased the overall abundance of leaf-litter arthropods. Longcore (2003) found that replanting native vegetation in a sage scrub in southern California resulted in lower arthropod abundance and diversity compared to invaded plots – an unexpected result. Other studies have found that arthropod diversity and community composition are affected by particular restoration/management procedures, including prescribed burning (Morris, 1975; Hanula and Wade, 2003), invasive-plant removal (Gratton and Denno, 2005; Emery and Doran, 2013), and replanting native vegetation (Samways et al., 1996; Magoba and Samways, 2012).

Studies to date have examined the impact of a single management activity on epigeic arthropods, rather than examining the effects of a suite of restoration and management techniques – hereafter termed “comprehensive vegetation management”. Land managers and restoration practitioners often practice a combination of techniques concurrently and rarely employ just one technique as a part of their management regime (Chicago Wilderness Biodiversity Council, 1999; Lindenmayer and Franklin, 2002; Knapp, 2010). Thus, in order to understand how restoration management directed at the plant community affects the entire ecosystem, it is important to have an understanding of the cumulative effects of comprehensive vegetation management on major ecosystem components such as the epigeic arthropod community.

Changes in both biotic and abiotic environmental factors will drive the response of epigeic arthropods to comprehensive vegetation management. Epigeic arthropod densities and community structure are affected, directly or indirectly, by soil characteristics, microclimate, depth and quality of leaf litter, and plant diversity and structure (e.g. Uetz, 1979; Bultman and Uetz, 1982; Samways et al., 1996; Haddad et al., 2001). Kappes et al. (2007) demonstrated that species richness of snails and woodlice decreased with decreasing soil pH. Average activity-densities of ground beetles (Carabidae), rove beetles (Staphylinidae), and spiders (Araneae) can be twice as high in soils richer in several nutrients (N, Ca, K, S, Mg, and P) (Mäder et al., 2002). Several studies have reported a positive relationship between epigeic arthropod diversity and floral species richness (Siemann, 1998; Knops et al., 1999; Haddad et al., 2001), or structural complexity of the vegetation (Schwab et al., 2002; Diehl et al., 2013).

The consequences of comprehensive vegetation management cannot readily be investigated through replicated, controlled experiments due to the large number of sites needed, the need to

assign treatments at random, and the number of years required before conclusions could be drawn. We took advantage of one-ha sites that are part of a “natural experiment,” the Chicago Wilderness Land Management Research Program (Heneghan et al., 2012) to investigate the degree to which comprehensive vegetation management has led to the restoration of the epigeic arthropod community in metropolitan woodland ecosystems. Our study compared communities of epigeic arthropods across a gradient of restoration and management efforts and outcomes. We asked two questions: (1) How does comprehensive vegetation management affect the community structure of epigeic arthropods? (2) Which biotic and abiotic environmental variables correlated with restoration and management activities potentially explain observed changes in the epigeic arthropod community?

2. Methods

2.1. Overview of sites and management categories

Sites were located in northeastern Illinois in the Chicago metropolitan region (Fig. 1), and represent a subset of plots that are part of the Chicago Wilderness Land Management Research Program (CWLMRP), a collaborative project between land managers and research ecologists. The CWLMRP has established over 100 one-ha long-term study plots that include remnant prairie, abandoned agricultural lands being restored to prairie vegetation, woodlands and savanna habitats. Sites were selected to represent a gradient of management efforts and success. Initial phases of the CWLMRP involved collection of baseline vegetation and soil-nutrient data; baseline data relevant to this study are reported here.

We sampled the epigeic arthropod community on 22 one-ha oak-dominated sites (*Quercus alba*, *Quercus macrocarpa*, or *Quercus rubra*) on which vegetation structure and composition are highly variable, ranging from dense understories of invasive shrubs to open savannas with scattered herbaceous vegetation (Table 1). A major restoration activity on these sites has been the removal of invasive shrubs such as *Rhamnus cathartica* (European buckthorn), *Lonicera* spp. (honeysuckle), *Berberis thunbergii* (Japanese barberry), and *Rosa multiflora*; and herbaceous species such as *Alliaria petiolata* (garlic mustard). These invasive plants present many challenges, most notably because high numbers of seeds are produced that can remain viable for many years.

At the inception of the CWLMRP, plots were selected by local land managers that could be placed into one of three categories reflecting management history and the managers' perceptions of site quality: *Control*, *Managed-int*, and *Managed-REF*. We selected a subset of CWLMRP sites to reflect these categories. *Control* sites ($n = 5$) were unmanaged, never restored, and considered by the managers to be degraded. These were generally dominated by invasive plants such as *R. cathartica*, *Lonicera* spp., *A. petiolata*, and *B. thunbergii*. Understories were usually homogenous, mainly composed of dense thickets of buckthorn and other invasive shrubs. *Managed-int* sites ($n = 12$) had been undergoing restoration and management for 3–21 years, and were currently being managed. The understory for these sites was highly variable, ranging from little or no herbaceous layer to dense layers of herbaceous vegetation (both non-native and native species). The *Managed-REF* category consisted of restored sites ($n = 5$) that land managers identified as representing high-quality woodlands for the region, with each site having <10% cover of invasive plants on average. These sites had been under active, long-term management for 11–21 years, and serve as examples of a target for restoration – hence their designation as “reference” sites. *Managed-REF* sites were characterized by an open understory with few or no

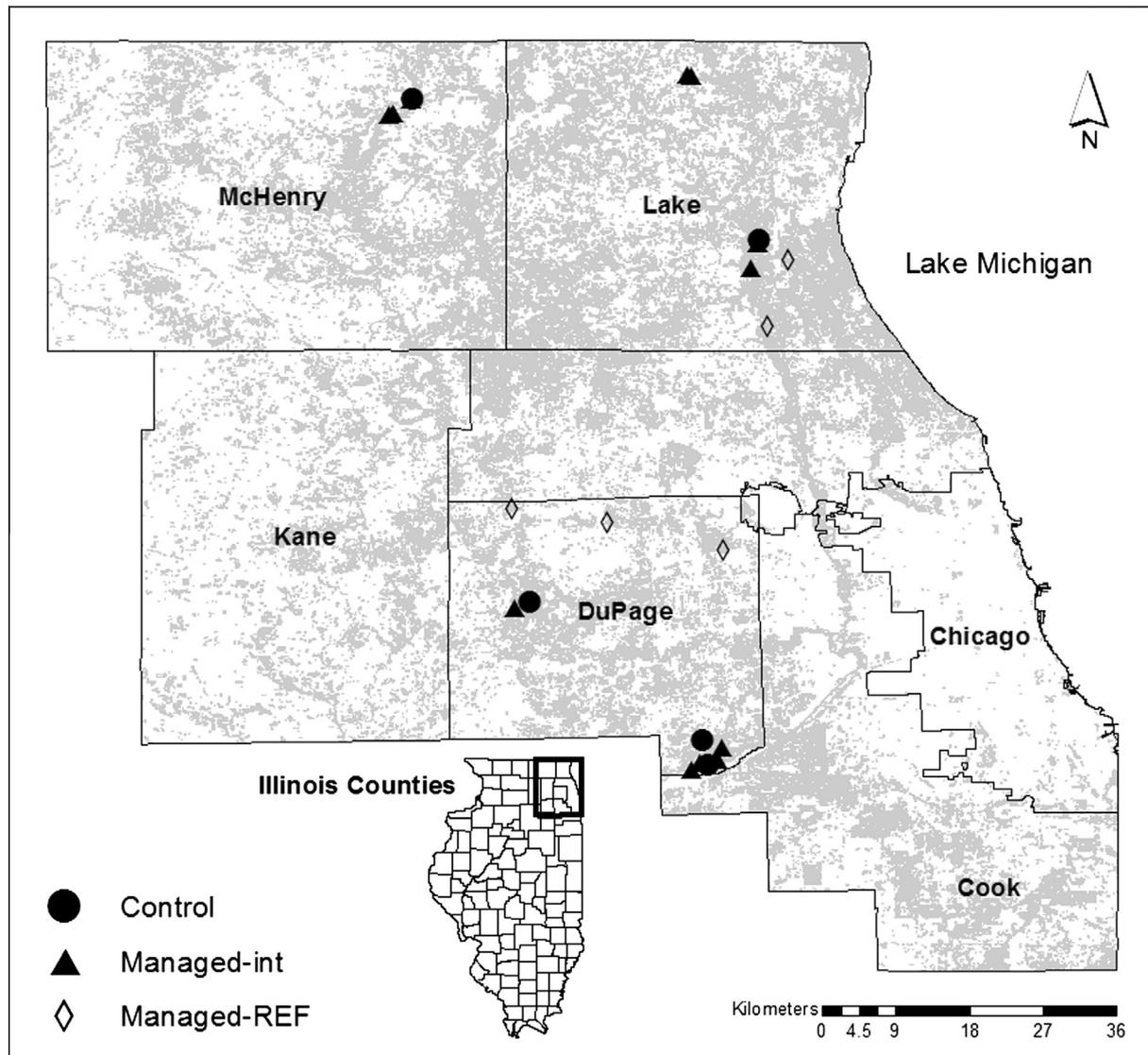


Fig. 1. The distribution of sites by management category across the Chicago metropolitan region. Dark shading represents forested regions and the names represent Illinois counties.

invasive plant species. The Chicago Wilderness region contains no pristine woodlands unaffected by invasive species or intense land development; therefore, it was not possible to incorporate non-managed target sites into CWLMRP. The *Managed-int* and *Managed-REF* sites had not been managed identically, but all sites were representative of restoration management consisting of the removal of invasive/non-native plants, the reintroduction of native seeds, and reintroduction of periodic fire as a natural disturbance (Chicago Wilderness Biodiversity Council, 1999). Refer to Appendix A for additional details on site management.

2.2. Sampling of surface-active arthropods

Epigeic arthropods were sampled with pitfall traps (Ausden, 1996). The number trapped reflects both the mobility of individuals and population density, producing a composite index termed 'activity-density' (Southwood, 1978). Four traps were opened at each site for two 10 day intervals (early June and mid-August 2011). The traps were located using a combination of systematic and random placement. A random number from 1 to 360 indicated

the compass direction to walk approximately 20 m from the center of the site (identified by GPS coordinates). The first pitfall trap was then installed in the nearest (i.e. within ~1 m) patch of bare ground or the thickest patch of leaf litter. The second trap was positioned by adding 90° to the first direction, pacing 20 m from the center of the site, and so forth, through the cardinal directions. At each site two traps were installed in bare ground and two within the thickest layer of leaf litter. This arrangement was chosen because litter amount can affect the mobility and density of epigeic arthropods (Bultman and Uetz, 1982; Melbourne, 1999; Morris, 2000).

The pitfall trap was a white plastic Solo™ cup (9 cm diameter, 12 cm deep) placed within an outer sleeve (an identical cup buried in the ground) in order to minimize trap disturbance during servicing (Lenski, 1982). The removable inner cup was placed flush with the soil surface and contained 150 mL of a 50:50 mixture of propylene glycol (Prestone™ anti-freeze) and water to serve as both killing agent and preservative (Hall, 1991). Traps were installed with a closed lid at least one week prior to sampling to eliminate 'digging effects' (Digweed, 1995). When a trap was opened for sampling, a

Table 1
Characteristics of Control, Managed-int, and Managed-REF sites.

Site	Coordinates	Years managed	Avg. annual temp (C)	Summer rain (cm)	Soil texture	Vegetation summary
<i>Control</i>						
Old School 1	42°16'33"N, 87°55'9"W	0	14.4	26.6	Clay Loam	Mature <i>Quercus rubra</i> (red oak) and <i>Quercus alba</i> (white oak) canopy. <i>Rhamnus cathartica</i> (buckthorn) is present but not dense. Other shrubs include <i>Crataegus</i> spp. (hawthorn), <i>Carya</i> spp. (hickory), and <i>Ulmus americana</i> (elm). Herbaceous layer of mostly buckthorn seedlings, hickory, and <i>Lonicera</i> spp. (honeysuckle). Minimal detritus present
WFG Northgate Woods	41°43'19"N, 87°58'55"W	0	15.4	15.1	Silty Clay Loam	Canopy of some mature hickory, red and white oak. Shrub layer is very dense, which is dominated by buckthorn and honeysuckle. There appears to also be an early invasion of <i>Fraxinus</i> spp. (ash). There is very little leaf litter present
WFG South Central	41°41'47"N, 87°58'31"W	0	15.4	15.1	Clay Loam	Red oak-dominated canopy. Some buckthorn and elm – not too heavily invaded though. Herbaceous layer of ash seedlings, buckthorn seedlings, <i>Polygonum</i> spp. (knotweed) and sparse weeds. Detritus and fallen oak branches present
WM Highlake Savanna	41°52'33"N, 88°10'18"W	0	13.8	14.7	Clay Loam	White oak, <i>Prunus</i> spp. (cherry), and some red oak canopy. Very heavy buckthorn invasion, with <i>Rosa</i> spp. (multiflora rose) and honeysuckle also present in the shrub layer. Some weedy species in the herbaceous level. There is a fair amount of detritus present
GP Sladkey East	42°25'52"N, 88°18'6"W	0	14.1	7.8	Clay Loam	Invaded by honeysuckle and buckthorn. Mature <i>Quercus macrocarpa</i> (burr oak) canopy. Old walkway with herbaceous layer. No herbs in invaded area. Little leaf litter present
<i>Managed-int</i>						
Ethel Woods 1	42°27'28"N, 87°59'55"W	3	13.7	9.2	Silty Clay Loam	White oak and <i>Carya ovata</i> (sharpbark hickory) canopy. Shrub layer mostly ovate saplings. Herbaceous layer covered with rose, <i>Solidago</i> spp. (goldenrod), <i>Ageratina altissima</i> , <i>Aster</i> spp., and <i>Rudbeckia</i> spp. A good amount of detritus present
Ethel Woods 2	42°27'23"N, 87°59'35"W	6	13.7	9.2	Silty Clay Loam	White oak and sharpbark hickory canopy. Shrub layer is mostly hickory saplings. Herbaceous layer covered with goldenrod, rose, <i>Ageratina altissima</i> , <i>Aster</i> spp., and <i>Rudbeckia</i> spp. Detritus present
GP DeCarlo	42°24'49"N, 88°19'40"W	4	14.1	7.8	Clay Loam	Mature burr oak canopy with a lot of invasive shrubs. Rose, buckthorn, <i>Populus</i> spp. (cottonwood), honeysuckle all abundant. Small amount of detritus is present
West DuPage Woods	41°52'13"N, 88°11'21"W	12	20.1	13.7	Silty Clay Loam	White oak canopy with some cherry. Shrub layer also includes buckthorn and a lot of rose. Buckthorn seedlings, goldenrod, and <i>Aster</i> spp. make up the herbaceous layer. Not much detritus
WFG Cemetery Ridge	41°41'58"N, 87°59'5"W	6	15.4	15.1	Silty Clay Loam	Canopy of burr oak, younger red and white oak, and ash. Minimal amount of shrubs. Solid herbaceous layer: goldenrod, <i>Carex</i> spp., and <i>Aster</i> spp. A good amount of litter cover
MacArthur Woods	42°14'42"N, 87°55'40"W	12	14.4	27.3	Silty Clay Loam	Mature white oak canopy. <i>Tilia</i> spp. and <i>Acer</i> spp. (maple) shrub layer. Good herbaceous layer with lots of young knotweed. Minimal detritus, some dead buckthorn stems
Old School 2	42°16'16"N, 87°55'14"W	13	14.4	26.6	Silty Clay	Mature red and white oak canopy. Buckthorn is present but is not dense. Other shrubs include hawthorn, hickory, and elm. No herbaceous layer but numerous buckthorn, hickory, and honeysuckle seedlings. Not much detritus
GP Sladkey West	42°25'51"N, 88°18'12"W	13	14.1	7.8	Clay Loam	Mature burr oak canopy. Invaded by honeysuckle and buckthorn. Old walkway with herbaceous layer. No herbs in invaded area. Some remaining dead tree stumps left behind from management activities
GP Weidrich	42°24'57"N, 88°19'22"W	13	14.1	7.8	Loam	This site has a lot of topography with a burr oak, white oak, and some hickory canopy. <i>Cornus</i> spp. (dogwood) shrubs. Some early invasion by buckthorn. Thick herbaceous layer and a fair amount of detritus
WFG Old Glen Woods	41°42'60"N, 87°57'36"W	19	15.4	15.1	Silty Clay Loam	Canopy of burr, white, and red oak. Good mature tree cover. Shrubs of hickory, cherry, buckthorn (sparse but mature.) A lot of rose and grasses make up the herbaceous layer. Good amount of detritus present

(continued on next page)

Table 1 (continued)

Site	Coordinates	Years managed	Avg. annual temp (C)	Summer rain (cm)	Soil texture	Vegetation summary
WFG Poverty Savanna	41°41'28"N, 87°59'39"W	21	15.4	15.1	Silty Clay Loam	Red and white oak, hickory, <i>Juglans nigra</i> (walnut) canopy. Minimal amount of shrubs. Thick herbaceous layer of goldenrod, rose, and <i>Aster</i> spp. A fair amount of leaf litter
WFG Rocky Glen	41°42'6"N, 87°57'56"W	20	15.4	15.1	Clay Loam	Hickory, maple, and elm-dominated canopy. Honeysuckle and some buckthorn make up a dense shrubby layer. Herbaceous layer is barely present
Managed-REF Fischer Woods	41°56'4"N, 87°57'34"W	18	10.6	8.9	Silty Clay Loam	Dominated by a <i>Quercus velutina</i> (black oak) canopy (a full and mature canopy), with rose, hickory, elm, <i>Ostrya virginiana</i> , and <i>Tilia Americana</i> present. The understory is open, with many herbaceous plants. A fair amount of oak litter present
Housier's Grove	41°58'43"N, 88°11'33"W	15	10.4	10.1	Silty Clay Loam	Dominated by white oak, rose, and <i>Prunus serotina</i> . Diverse understory with many herbaceous species. Mature canopy and a dense leaf-litter layer
Meacham Grove	41°57'50"N, 88°5'10"W	21	10.6	8.9	Silty Clay Loam	Canopy, which is full and mature, is dominated by <i>Acer saccharum</i> (sugar maple), <i>Tilia americana</i> , and <i>Ostrya virginiana</i> . No shrub layer, understory very open. Moderate amount of leaf litter present
Middlefork	42°15'11"N, 87°53'11"W	16	18.9	10	Clay Loam	Very open canopy with mature oaks (namely white oak) with a lot of high-quality herbaceous species in understory. No or very little leaf litter
Ryerson	42°10'51"N, 87°54'35"W	11	13.1	16.1	Silty Clay Loam	Mature and full white oak canopy. Shrub layer of sugar maple and cherry. Herbaceous layer is almost non-existent –only some seedlings of sugar maple, cherry, and ash. Extremely dense leaf-litter layer (most dense layer of all sites), mainly consisting of white oak litter

plastic hardboard lid (18 × 18 cm) painted dark brown was placed over the trap with a ~2 cm gap to exclude rain, leaves and other plant debris. Samples were collected after 10 days in the field, filtered, and then preserved in 70% ethanol. Samples were blind-sorted to eliminate unintentional biases in sorting effort between management categories (Melbourne et al., 1997).

Arthropods were sorted into 35 taxonomic units, from family to class depending upon the organism (Table 2). Each taxonomic unit (family, order, or class) was then assigned to a functional group based on feeding characteristics. Taxonomic groups whose primary method of locomotion is flight, i.e. Diptera, Hymenoptera (excluding Formicidae), Lepidoptera, Odonata, and Neuroptera, were excluded from analysis because pitfall trapping is not appropriate for sampling these groups (Ausden, 1996).

2.3. Environmental variables

The CWLMRP research team sampled the plant community and measured soil characteristics on the sites before pitfall trapping was initiated. We explain the methods below; the detailed data set, which was used to explore correlations of changes in arthropod community structure with biotic and abiotic factors, appears in Appendix B.

2.3.1. Vegetation measurements

We modified the Whittaker-plot sampling design to sample the vegetation at each one-ha site in 2010 or 2011. All trees within nine 100 m² circles were identified to genus, or species when possible, and diameters were measured at breast height (1.3 m). The nine 100 m² circles were arranged in a 3 × 3-grid to cover each one-ha site, with each circle being spaced 25 m from the nearest circle. In the center of each 100 m² circle we identified and counted, within 2 × 2 m quadrats, all shrubs by height class (0.5–1 m, 1–1.3 m, and >1.3 m). Within each 2 × 2 m quadrat we also used the Braun-Blanquet cover classification system to categorize

plant cover by functional group: bare ground, litter layer, moss, woody debris, herbaceous, shrub, trees, invasive herbs, and invasive woody. Functional groups were classified into a cover-class range of 0–6: 0 (not present), 1 (<1%), 2 (1–4%), 3 (5–24%), 4 (25–49%), 5 (50–74%), and 6 (>75%). These values were then converted to mid-points for each functional-group cover, and then averages of the mid-points were generated at each site according to the functional group.

2.3.2. Soil-nutrient measurements

Plant Root Simulator probes (PRSTM, Western Ag Innovations Inc., Saskatoon, SK, Canada) were used to measure potential soil-nutrient uptake rates. These probes report rates of nutrient uptake, which differ from measured values usually reported in conventional soil-nutrient studies (Western Ag Innovations Inc., 2009). PRS probes were inserted in replicate pairs (anion and cation probes) at two locations within each study site ($n = 8$) for 28–31 days during the summer of 2010 or 2011. Probes were retrieved, cleaned with deionized water and a brush, cooled on ice, and sent to Western Ag Innovations Inc. for analysis. The data for each site was based on the pooled values for the four probes. The anion probes measured iron (Fe), lead (Pb), manganese (Mn), nitrate (NO₃), phosphorous (P), and sulfur (S). Cation probes measured aluminum (Al), ammonium (NH₄), boron (B), calcium (Ca), copper (Cu), magnesium (Mg), potassium (K), and zinc (Zn). Total nitrogen (N) was determined by combining the values for ammonium and nitrate. Uptake rates are reported as µg nutrient/10 cm²/month (~30 days) (the standard units reported by Western Ag Innovations Inc. for PRS probes).

2.4. Statistical analyses

2.4.1. Management and arthropod community structure

To test for differences between management categories in functional group and arthropod composition, permutational

Table 2

Mean activity–density (with standard error) of arthropod taxa by management category, and total number trapped during the study. Taxa are listed in alphabetical order.

Class/Order	Family	Functional Group	Control Mean (SE), n = 5	Managed-int Mean (SE), n = 12	Managed-REF Mean (SE), n = 5	Total
Araneae	Agelenidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	6
	Amaurobiidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1
	Corinnidae	Predator	0.1 (0.1)	0.7 (0.2)	0.2 (0.1)	78
	Dictynidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1
	Dysderidae	Predator	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	2
	Gnaphosidae	Predator	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	9
	Hahniidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	3
	Linyphiidae	Predator	4.8 (1.2)	4.0 (0.8)	10.5 (2.8)	993
	Liocranidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	3
	Lycosidae	Predator	1.8 (0.8)	3.8 (0.6)	3.8 (1.3)	594
	Mimetidae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1
	Pisauridae	Predator	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1
	Salticidae	Predator	0.1 (0.0)	0.1 (0.0)	0.1 (0.1)	21
	Theridiidae	Predator	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	2
	Thomisidae	Predator	0.3 (0.1)	0.5 (0.1)	0.5 (0.2)	76
Chilopoda	Not Disting	Predator	0.2 (0.1)	0.2 (0.1)	0.2 (0.1)	40
Coleoptera	Carabidae	Predator	6.8 (1.5)	5.8 (0.7)	12.4 (2.2)	1320
	Curculionidae	Herbivore	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)	34
	Nitidulidae	Herbivore	0.2 (0.1)	0.5 (0.1)	0.3 (0.1)	72
	Staphylinidae	Omnivore	6.6 (1.8)	9.9 (2.3)	10.4 (3.8)	1632
Collembola	Entomobryidae	Fungivore	29.5 (7.7)	109.6 (18.6)	134.6 (36.8)	18,279
	Hypogastruridae	Fungivore	0.1 (0.1)	11.1 (4.2)	0.8 (0.3)	1100
	Isotomidae	Fungivore	0.6 (0.2)	3.4 (0.8)	2.9 (0.7)	463
	Sminthuridae	Fungivore	4.0 (0.9)	5.7 (1.2)	7.3 (2.9)	1003
	Tomoceridae	Fungivore	5.9 (1.1)	34.6 (8.0)	7.3 (1.5)	3850
Diplopoda	Abacionidae	Detritivore	0.1 (0.0)	0.1 (0.0)	0.0 (0.0)	7
	Caseyidae	Detritivore	1.4 (0.8)	0.1 (0.1)	0.0 (0.0)	68
	Julidae	Detritivore	1.2 (0.3)	1.9 (0.4)	1.6 (0.4)	296
	Paradoxosomatidae	Detritivore	20.9 (5.2)	14.1 (4.2)	10.9 (4.3)	2620
	Polydesmidae	Detritivore	3.1 (1.9)	0.3 (0.2)	0.3 (0.1)	158
	Spirobolidae	Detritivore	0.0 (0.0)	0.3 (0.1)	0.0 (0.0)	28
	Xystodesmidae	Detritivore	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	7
	Hymenoptera	Formicidae	Omnivore	8.9 (1.8)	19.9 (6.0)	8.6 (1.1)
Isopoda	Oniscidea	Detritivore	98.7 (19.4)	106.8 (14.8)	59.3 (9.3)	16,570
Opiliones	Opiliones	Predator	11.1 (2.0)	20.8 (2.5)	10.8 (2.1)	2872

multivariate analysis of variance (PERMANOVA: 10,000 permutations of the entire data set; Type III SS) using management category as a fixed factor was performed on a Bray–Curtis dissimilarity matrix based upon activity–densities (Anderson et al., 2008). To account for habitat variation among sites, which could influence the number of arthropods trapped, the raw data were standardized by samples to represent proportions of total numbers of taxa trapped for a site (Clarke and Warwick, 2001). We also performed parallel permutational analyses of multivariate dispersions (PERMDISP; Clarke and Warwick, 2001; Anderson et al., 2008) in order to examine whether, in addition to differences in compositional location, there were any differences in community dispersion (i.e. group variability) among treatments. To visualize which taxa were likely causing changes in our multivariate measure of community structure, we used vector overlays on Canonical Analysis of Principle Coordinates (CAP) ordinations constrained by management category. A vector reflects the multiple (partial) correlation coefficient of an arthropod taxon with the two axes; vectors with $r > 0.5$ are shown. We performed follow-up univariate analyses (e.g. ANOVAs and simple linear regressions) on taxa with displayed vectors to further interpret the multivariate patterns.

2.4.2. Arthropod community structure and environmental variables

Distance-based redundancy analysis (dbRDA) (Anderson et al., 2008) was used to model linear relationships between environmental variables and axes of the ordination of sites based upon Bray–Curtis dissimilarities. The most parsimonious distance-based linear model was selected by stepwise selection (adjusted- R^2 criterion, 10,000 permutations). Before performing dbRDA, highly correlated independent variables (Pearson's $r > 0.95$) were removed, and remaining variables that were right-skewed were fourth-root transformed. No transformations were performed on vegetation data because it consisted of cover classes. Simple linear regressions were then used to further examine relationships between taxa and individual environmental variables as revealed by CAP (taxa) and dbRDA (environmental variables).

We also examined if the number of years under restoration management progressively influenced the community of epigeic arthropods. We first conducted an unpaired Student's t -test to examine if there was a difference in years under management between the *Managed-int* and *Managed-REF* sites. We then performed a separate dbRDA analysis using time under management

as the environmental/predictor variable for epigeic arthropod community structure for both *Managed-int* and *Managed-REF* sites. This dbRDA analysis was based on a square-root transformed Bray–Curtis dissimilarity matrix and was executed with the same criterion as above.

PERMANOVA, PERMDISP, CAP, and dbRDA analyses were performed using PRIMER-E/PERMANOVA + software (Anderson et al., 2008). ANOVAs, simple linear regressions and the unpaired *t*-test were conducted with the R Statistical Computing language (R Development Core Team, 2013).

3. Results

In total, 54,820 arthropods were collected (Table 2). Fungivores comprised 45% of the collection; the second most abundant group, comprising 36%, was detritivores. When individual taxa were considered, springtails (Collembola) of the family Entomobryidae had the highest overall activity–density, representing 33% of all arthropods trapped. Woodlice (suborder Oniscidea of Isopoda) were the second most abundant group, comprising 30% of the collection. Entomobryids and isopods represented high proportions of the fungivores (74%) and detritivores (84%), respectively.

3.1. Effects of comprehensive vegetation management on arthropod functional groups

Three-factor PERMANOVA indicated no significant interactions among management category and either season (spring and summer), or trap placement (open ground or litter) ($P = 0.99$). Therefore, arthropod activity–densities were averaged across season and trap location for each site before calculating the distance matrix for the next set of analyses.

Functional arthropod composition differed between the three management categories (PERMANOVA, $Pseudo-F_{2, 19} = 4.95$, $P = 0.01$). Pairwise comparisons revealed strong differences in community structure between the *Control* and *Managed-REF* ($P < 0.01$). Functional community structure diverged from degraded, unmanaged sites to the restoration target, with the centroids of *Control* and *Managed-REF* sites clearly different in

ordination space, and *Managed-int* sites overlapping the two clusters (CAP plot, Fig. 2). Differences in dispersion (group variability) also contributed to the divergence in ordination space (PERMDISP, $t_{2, 19} = 6.27$, $P = 0.01$), with the *Managed-REF* sites being the most tightly clustered and the *Managed-int* sites the most dispersed (Fig. 2).

The divergence in arthropod functional composition between *Control* and *Managed-REF* sites is correlated with opposite trends for detritivores and fungivores, with fungivores tending to have higher activity–densities in the reference sites, and detritivores having higher values in the degraded, unmanaged *Control* sites (Fig. 2). These vectors represent partial correlation coefficients, and therefore represent trends more accurately than separate univariate analyses. Nevertheless, univariate patterns exhibit parallel trends: activity–densities of fungivores were four times higher in *Managed-REF* than *Control* sites (Fig. 3; ANOVA, $F_{2, 19} = 3.74$, $P = 0.044$), and detritivores showed an opposite but weaker pattern (Fig. 3; ANOVA, $F_{2, 19} = 0.90$, $P = 0.42$). Abundances of fungivores and detritivores in the *Managed-int* sites were intermediate to *Control* and *Managed-REF* values (Fig. 3).

3.2. Effects on community structure defined by taxa

Analyses of community structure based upon taxonomic composition reveal broadly similar patterns to analyses of functional groups, showing a progressive trend from unmanaged sites to the restoration target (Fig. 4; PERMANOVA, $Pseudo-F_{2, 19} = 2.96$, $P = 0.02$). Clusters of *Control* and *Managed-REF* sites are clearly separated in ordination space, with *Managed-int* sites broadly overlapping clusters of *Control* and *Managed-REF* sites. Another similarity between analyses based upon functional and taxonomic structure is the tight clustering in ordination space of the *Managed-REF* sites compared to other management categories in ordination space (Fig. 4; PERMDISP, $t_{2, 19} = 5.9$, $P = 0.02$).

Vector analysis reveals that activity–densities of entomobryids and isopods are most strongly related to separation of the *Control* and *Managed-REF* centroids (Fig. 4). Entomobryid activity–densities were four times higher in *Managed-REF* than *Control* sites, with *Managed-int* values in between (Fig. 5; ANOVA,

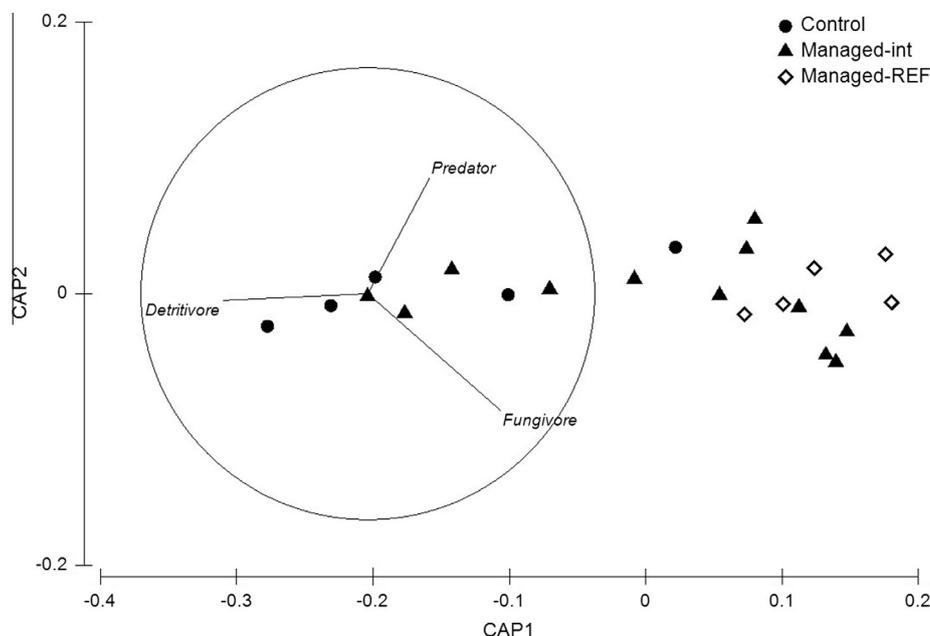


Fig. 2. Canonical Analysis of Principal Coordinates (CAP) on functional grouping constrained by management category (partial correlation $r > 0.5$ for vector overlays; circle represents $r = 1$) on standardized data. Each symbol of the ordination plot represents one of the 22 sites. The length and direction of each vector indicates the strength of relationship (partial correlation) between the ordination axes and the associated variable.

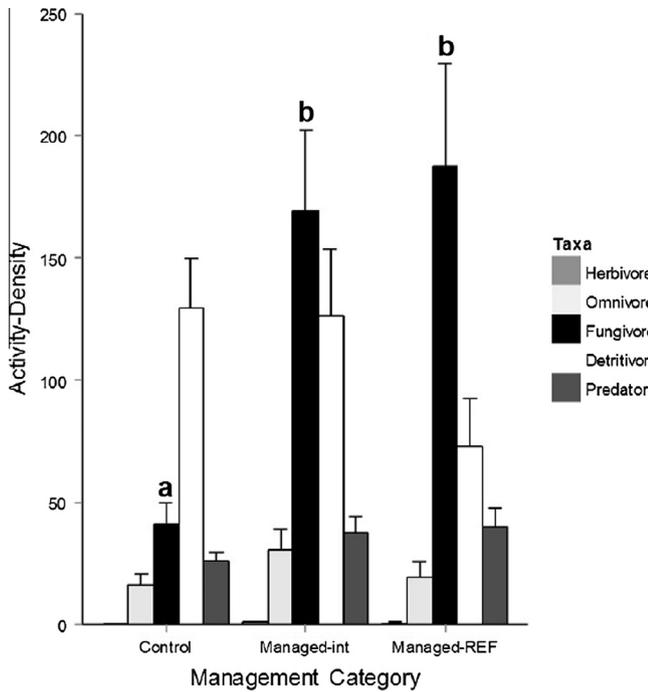


Fig. 3. Effects of comprehensive vegetation management on functional groups. Different letters denote $P < 0.05$ using post hoc Tukey's HSD comparisons. Values are means + SE.

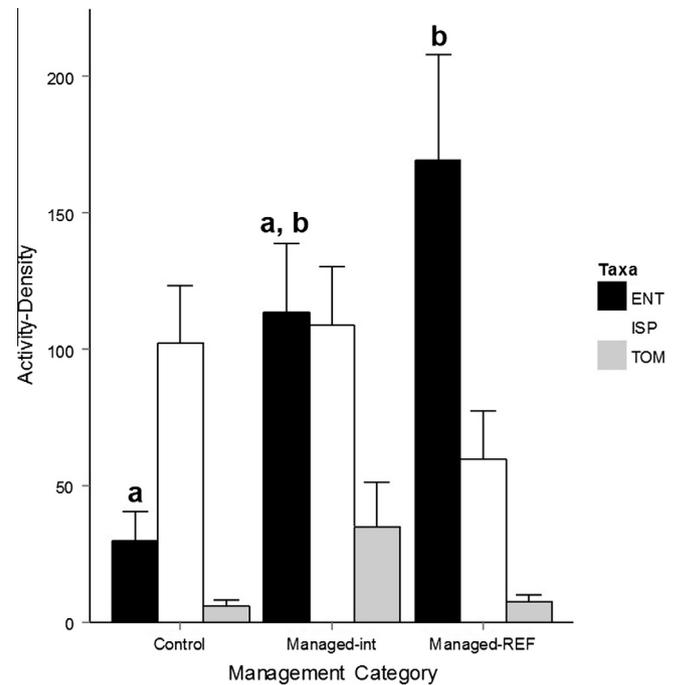


Fig. 5. Effects of management on Entomobryidae (ENT), Isopoda (ISP), and Tomoceridae (TOM), the three most abundant taxa. Different letters denote $P < 0.05$ using post hoc Tukey's HSD comparisons. Values are means + SE.

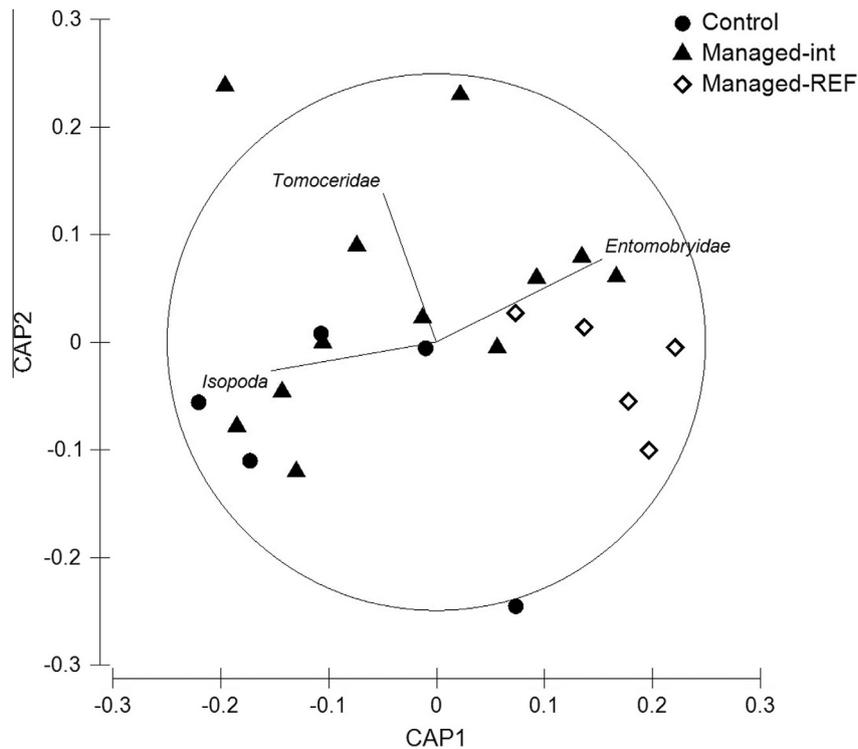


Fig. 4. Canonical Analysis of Principal Coordinates (CAP) on arthropod taxa constrained by management category (partial correlation $r > 0.5$ for vector overlays) on standardized data.

$F_{2, 19} = 4.03, P = 0.035$). Isopods tended to be less abundant in the reference sites, but the relationship is weaker than the pattern shown by the vector representing the partial correlation with the CAP axes (Fig. 5 versus Fig. 4). Additionally, tomocerid Collembola may have had slightly higher activity-densities in *Managed-int* than *Control* and *Managed-REF* sites (Figs. 4 and 5).

3.3. Environmental variables correlated with structure of the epigeic arthropod community

Variation in two environmental variables – invasive woody plant cover and phosphorous uptake – explained over 50% of the variation in arthropod community structure based upon functional

Table 3

Results of distanced-based redundancy analyses (dbRDA), giving the relative influence of selected environmental variables on epigeic arthropod community structure (ordination of distance matrices calculated on standardized data) for communities defined by (A) functional groups and (B) arthropod taxa.

Variables	Sequential tests (Best Model)		
	% Variation	F	P
<i>(A) Functional group</i>			
Invasive woody	39.4	14.65	0.003
P	14.6	7.34	0.002
Moss	1.8	1.78	0.15
Total	55.8		
<i>(B) Arthropod taxa</i>			
Invasive woody	26.2	8.47	0.001
P	9.6	3.99	0.006
NO ₃	6.0	2.94	0.009
K	3.5	2.15	0.065
Herbaceous	1.2	1.37	0.25
Moss	0.4	1.13	0.32
Total	46.9		

groups (Table 3A). Invasive plant cover was the most important, accounting for over half (70%) of the explained variation. The comparable dbRDA for community structure based upon arthropod taxa revealed that the same two variables, along with nitrate uptake, accounted for just over 40% of the variation in community structure (Table 3B).

A critical question is the extent to which these dbRDA results are correlated with the impact of management on arthropod community structure. An overlay of environmental-variable vectors on the dbRDA-constrained ordination reveals that invasive woody-plant cover and the uptake of phosphorus are correlated with the separation of the *Control*, *Managed-int*, and *Managed-REF* sites when the community is defined by functional groups, with unmanaged *Control* sites having more invasive shrubs and higher rates of phosphorus uptake (Fig. 6A). Moss cover is also correlated with the separation of the *Control* and *Managed-REF* sites (Fig. 6A). Invasive woody cover is the most strongly correlated variable with the *Control* – *Managed-REF* separation for the community defined by arthropod taxa (Fig. 6B). Uptake of nitrate is correlated strongly with the second axis of the ordination, which only explains a small

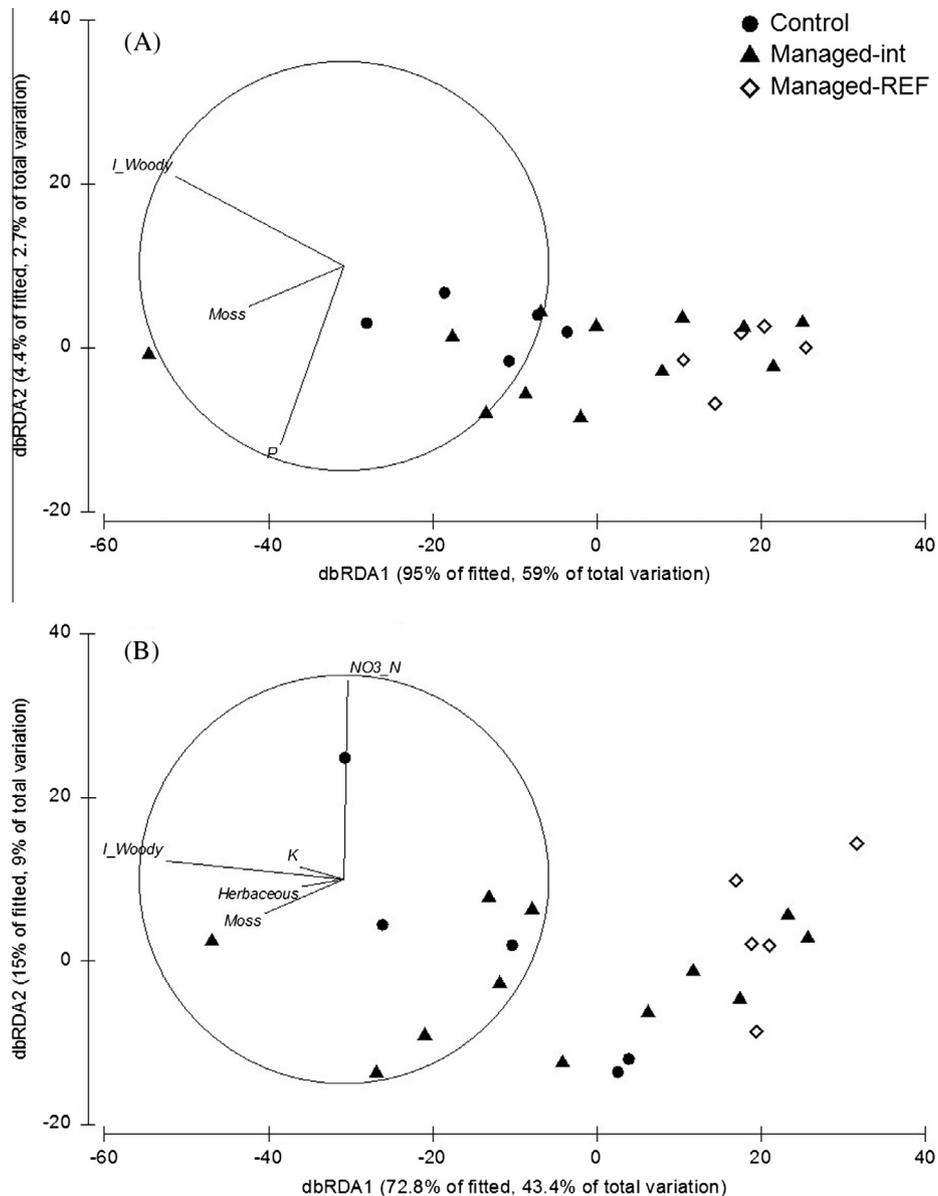


Fig. 6. Ordination plots of Distance-based Redundancy Analysis (dbRDA) of (A) functional group and (B) arthropod taxa using Bray–Curtis similarity for standardized data. Each symbol on the ordination represents one of the 22 sites.

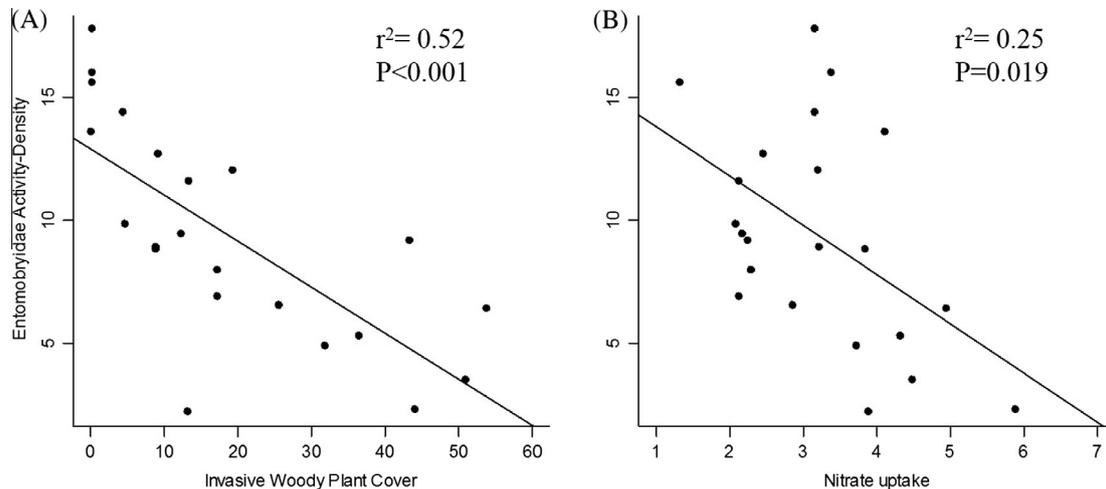


Fig. 7. Relationship between activity–density of Entomobryidae and (A) invasive woody plant cover; (B) nitrate uptake. Entomobryid activity–density was square-root transformed, and nitrate uptake was $\log(X+1)$ transformed.

amount of the fitted variation and is not related to management history.

Entomobryid activity–density was negatively correlated with invasive plant cover (Fig. 7A; $r = -0.72$, $F_{1, 20}$ (coefficient of linear model) = 22.06, $P < 0.001$, adj $r^2 = 0.50$). Entomobryid Collembola were also negatively correlated, but not as strongly, with the rate of NO_3^- uptake (Fig. 7B; $r = -0.50$, $F_{1, 20} = 6.57$, $P = 0.019$, adj $r^2 = 0.21$). Activity-densities of isopods, the second most numerous taxon, were not clearly correlated with either invasive woody plants ($r = 0.39$, $P(F_{1, 20}) = 0.076$, adj $r^2 = 0.11$) or NO_3^- uptake ($r = -0.14$, $P(F_{1, 20}) = 0.43$, adj $r^2 = 0.02$).

The *Managed-REF* sites tended to have been managed longer than the *Managed-int* sites, but the difference was not pronounced (mean_{*Managed-int*} = 12 yrs, SE = 1.8, mean_{*Managed-REF*} = 16 yrs, SE = 1.7; unpaired *t*-test, $P = 0.097$). Given this similarity, it is not surprising that time under management and epigeic arthropod community structure were not correlated (dbRDA; $r = 0.25$, $P = 0.21$, adj $r^2 = 0.017$).

4. Discussion

4.1. The impact of comprehensive vegetation management on the epigeic arthropod community

Comprehensive vegetation management altered the relative activity-densities of surface-active arthropods, resulting in a clear shift in epigeic arthropod community structure. There was a positive correlation between comprehensive vegetation management and two functional feeding guilds: fungivores and detritivores. These two groups play major roles in the detrital food web through direct and indirect effects on stocks of detritus and rates of primary decomposition (Heneghan and Bolger, 1998; Pieper and Weigmann, 2008; Crowther et al., 2011), and they are high-quality prey for major arthropod predators such as spiders and ground beetles (Kajak, 1995; Chen and Wise, 1999; Řezáč and Pekár, 2007). Thus, this change in functional structure of the epigeic arthropod community has implications for food-web structure and dynamics.

The above pattern can be explained by a shift in epigeic arthropod community structure defined by taxa that is driven primarily by changes in the two most-frequently captured groups: springtails of the family Entomobryidae, which are primarily fungal grazers (Vegter, 1983; Lavy and Verhoef, 1996); and

non-native isopod crustaceans (Jass and Klausmeier, 2000; Maerz et al., 2005), which largely consume detritus directly (Hassall et al., 1987; Lavy et al., 2001; Zimmer et al., 2002). Entomobryids were more prevalent in the *Managed-REF* sites, which represent land managers' restoration goals of pre-disturbance conditions, whereas introduced isopods occurred in higher proportions in the degraded *Control* sites. Another group of fungivores, the Tomoceridae, may have responded weakly to comprehensive vegetation management; they tended to have higher abundances in the *Managed-int* sites, though the pattern is only suggestive, and is not clear why they were not more abundant in the *Managed-REF* samples. Given that tomocerids are also large-bodied and active springtails, one might speculate that they were not captured more frequently in the reference sites – where conditions are favorable for fungivores – because of increased competition with entomobryids.

Despite clear responses by entomobryid and isopods to management, no other groups showed consistent differences between management categories. This result is surprising given the studies demonstrating the negative impacts of invasive plants on soil arthropod communities (e.g. Samways et al., 1996; Mgobozi et al., 2008; McGrath and Binkley, 2009). Entomobryids and isopods accounted for two-thirds of the arthropods collected; thus, other groups, some of which may have responded either directly or indirectly to management protocols, may not have been sampled intensively enough for effects to be detected. In addition, some of the non-responding groups may be dependent on restoration of a component of the vegetation that has not occurred yet. Furthermore, the index of activity–density determined by pitfall trapping may not accurately reflect effects of management on densities of taxa that are less mobile and/or less susceptible to trapping. Groups less susceptible to trapping would be expected not to show an effect of management on activity–density even though their population densities may have been, in fact, affected.

We found no evidence that time under management had a progressive effect on the community composition of surface-active arthropods. One might predict that over time the arthropod communities would show signs of converging on a structure comparable to that of the reference (*Managed-REF*) sites. We found no such trend, possibly due to initial differences in vegetation composition among the *Managed-int* sites, or to variation in restoration effort. Densities of invasive plants were likely dissimilar across management categories because managers typically use the level of

invasive plant cover as a metric for prioritizing on which areas to focus restoration efforts, i.e. sites with less invasive plant cover are more likely to be restored first. Because CWLMRP is a large-scale “natural experiment”, we could not control for differences between sites in vegetation structure when restoration commenced, or the management effort involved. Thus, the absence of a clear trajectory over time could be due to the large variation in arthropod composition as a result of initial variation in vegetation structure or restoration effort both within, and across, management categories.

4.2. Likely mechanism for response of epigeic arthropod community to restoration and management of the plant community

The effects of restoration activities on epigeic arthropods were likely due to differences in inputs of plant litter between degraded (*Control*) and managed sites. The degraded sites were generally dominated by invasive shrubs such as *R. cathartica* (European buckthorn) and *Lonicera* spp. (honeysuckle); thus, *Control* sites were covered with high-quality, nitrogen-rich leaf-litter (i.e. low C: N ratio) (Heneghan et al., 2002; Arthur et al., 2012). Terrestrial isopods, which feed on plant litter, are attracted to higher-quality litter (Rushton and Hassall, 1983; Loranger-Merciris et al., 2008), which may explain the higher activity–density of isopods in the *Control* sites. Abelho and Molles (2009) demonstrated that differences in leaf-litter total N and C: N ratios could consistently explain patterns of consumption and performance of terrestrials isopods in a study conducted in central New Mexico. They attributed the increased consumption to the higher nitrogen content and increased palatability of the preferred litter. Their finding parallels the higher activity-densities of isopods in the *Control* sites, which were generally dominated by invasive shrubs with highly nutritious leaf-litter.

Because comprehensive vegetation management in woodlands targets the elimination of invasive shrubs and invasive herbaceous plants (Lindenmayer and Franklin, 2002), the managed sites of our study supported plant communities with fewer invasives and understory vegetation more representative of an oak-dominated system. The leaf litter within these sites would consist of lower-quality, high C: N-ratio oak tissue – a recalcitrant litter substrate (Melillo et al., 1982; McClaugherty et al., 1985; Piatek et al., 2010). The increase in lower quality, high-lignin litter would favor conditions for populations of fungivorous arthropods (e.g. entomobryids), where basidiomycete saprophytic fungi are the most prevalent primary decomposers (Dix and Webster, 1995; Bardgett and Wardle, 2010). Our findings agree with previous studies that discovered higher abundances of fungivorous arthropods in recalcitrant litters compared to litters of higher N content and greater palatability (Coleman et al., 1983; Ilieva-Makulec et al., 2006; Szanser et al., 2011). Both a possible decrease in saprophytic fungi in the *Control* sites and an increase in invasive woody plants that produce rapidly consumed leaf litter could explain the lower activity-densities of fungivores in the unmanaged *Control* sites of our study.

4.3. Consequences of changes in populations of Collembola and Isopoda for higher trophic levels

Collembola are frequent prey in the diets of many arthropod predators in leaf litter, e.g. pseudoscorpions, centipedes, and spiders (Weygoldt, 1969; Foelix, 1996; Lewis, 2007). Chen and Wise (1999) demonstrated that increased detrital input produced higher abundances of fungivorous arthropods (Collembola and Diptera), with resulting higher densities of pseudoscorpions, centipedes, and some families of spiders, including wolf spiders (Lycosidae). We found that lycosid captures were positively correlated with activity-densities of entomobryid springtails across our sites (Fig. 8; $r = 0.52$, $F_{1, 20} = 7.58$, $P = 0.012$, adj $r^2 = 0.24$), providing

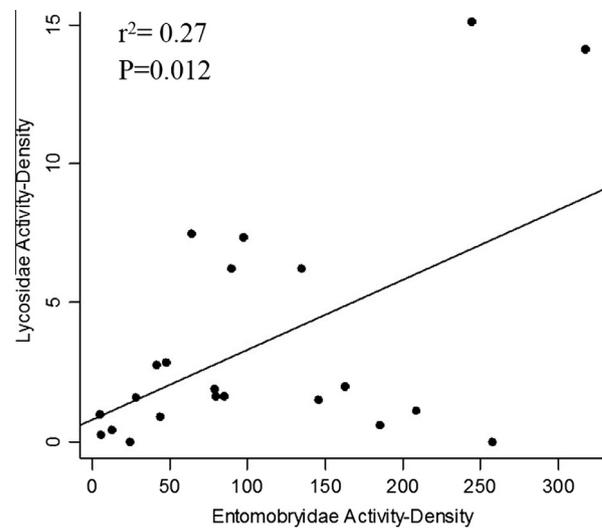


Fig. 8. Relationship between activity–density of Lycosidae (wolf spiders) and Entomobryidae activity–density.

indirect evidence that restoration of the vegetation in woodlands affects higher trophic levels of the detritus-based food web. Because of their high mobility and inability to climb smooth surfaces, lycosids are captured frequently in pitfall traps and therefore were collected frequently enough for us to observe a positive response to increased numbers of entomobryids. We found no such correlation with linyphid spiders ($r = 0.02$, $P(F_{1, 20}) = 0.93$, adj $r^2 = 0.05$), likely because they are more sedentary and less mobile than wolf spiders (Wise, 1993). We also found no correlations between spiders and tomocerid activity-densities, but the variation in captures across sites was much less for tomocerids than entomobryids.

In the degraded sites not only were springtails less common, but isopods were more frequently trapped. These differences have implications for higher trophic levels. Most spiders avoid terrestrial isopods, except for the non-native isopod specialist *Dysdera crocata* (Bristowe, 1958; Hopkin and Martin, 1985; Řezáč and Pekár, 2007). Thus, it is reasonable to hypothesize that *D. crocata* will be more abundant in the *Control* sites; and spiders more dependent upon Collembola, less abundant. Because *D. crocata* usually nests under stones and/or woody debris and is an ambush predator (Cooke, 1965), our sampling technique was not appropriate to detect a positive correlation between *D. crocata* and isopod numbers. It is also possible that *D. crocata* is not abundant in woodlands, which would explain why isopod numbers were so high in the degraded sites. This hypothesis deserves testing. It is clear, however, that increased abundance of introduced isopods and reduced springtail abundance in degraded sites will likely alter the dynamics of predators compared with *Managed-REF* woodlands. Because trophic-level omnivory and intraguild predation (IGP) are common interactions among leaf-litter predators (Wise, 1993; Chen and Wise, 1999; Wise and Chen, 1999; Lensing and Wise, 2004), a higher proportion of non-palatable prey in non-restored sites will likely increase rates of cannibalism and IGP among spiders and other generalist predators (Polis et al., 1989), leading to a different food-web structure compared with the *Managed-REF* woodlands.

4.4. Implications for ecological restoration and management of woodlands

In order to fully assess the extent to which restoration and management of the vegetation restores ecosystem functioning and

patterns of biodiversity – the overall goal of restoration management – a fundamental understanding of how current restoration management regimes impact all components of the system is required. Our results suggest that woodland restoration and management aimed primarily at increasing native-plant diversity and altering abundances of plant functional groups also restructures the surface-active arthropod community to favor small fungivores, such as springtails, while simultaneously generating undesirable conditions for non-native terrestrial isopods. This shift to increased availability of nutritious prey items (springtails) from high numbers of less-preferred prey (isopods) will likely have important implications for arthropod predators, thus impacting food-web structure and dynamics.

Other studies have also shown that vegetation management can have an impact on arthropod community composition (Samways et al., 1996; Gratton and Denno, 2005; Gratton, 2006; Magoba and Samways, 2012). For example, Hanula and Horn (2011a, 2011b), discovered that opening up the sub-canopy by removing the invasive Chinese shrub (*Ligustrum sinense*) from a riparian woodland in southeastern United States resulted in a twofold increase in the abundance and diversity of butterflies and bees compared to unmanaged plots. Mgobozi et al. (2008) demonstrated that management of the invasive *Chromolaena odorata* restored spider community composition to a state similar to uninvaded sites in a savanna of South Africa.

Given the increasing number of studies demonstrating the effects of comprehensive vegetation management on arthropod communities, we recommend that restoration programs be expanded to incorporate monitoring of arthropod diversity and community structure. This will allow us to gauge the extent to which comprehensive vegetation management also restores the arthropod food web to a structure similar to a less-impacted system. This in turn will lead to a more robust evaluation of restoration success.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.06.005>.

References

- Abelho, M., Molles, M.C., 2009. Effect of introduced exotic tree litter on consumption patterns of the introduced exotic isopod *Armadillidium vulgare*. *Eur. J. Soil Biol.* 45, 306–311.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods, PRIMER-E edn, Plymouth, UK.
- Arthur, M.A., Bray, S.R., Kuchle, C.R., McEwan, R.W., 2012. The influence of the invasive shrub, *Lonicera maackii*, on leaf decomposition and microbial community dynamics. *Plant Ecol.* 213, 1571–1582.
- Ausden, M., 1996. Arthropods. In: Sutherland, W.J. (Ed.), *Ecological census techniques: a handbook*. Cambridge University Press, Cambridge, UK, pp. 139–177.
- Ayres, E., Steltzer, H., Berg, S., Wall, D.H., 2009. Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. *J. Ecol.* 97, 901–912.
- Bardgett, R.D., Wardle, D.A., 2010. *Aboveground–Belowground Linkages: Biotic Interactions, Ecosystem Processes, and Global Change*. Oxford University Press, Oxford, UK.
- Bokhorst, S., Wardle, D.A., 2013. Microclimate within litter bags of different mesh size: implications for the ‘arthropod effect’ on litter decomposition. *Soil Biol. Biochem.* 58, 147–152.
- Bristowe, W.S., 1958. *The World of Spiders*. Collins New Naturalist, London, UK.
- Brooks, M.L., D’antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Ditomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.
- Brown, B.J., Mitchell, R.J., Graham, S.A., 2002. Competition for pollination between an invasive species (purple loosestrife) and a native congener. *Ecology* 83, 2328–2336.
- Bultman, T.L., Uetz, G.W., 1982. Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia* 55, 34–41.
- Callaway, R.M., Aschehoug, E.T., 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523.
- Carrillo, Y., Ball, B.A., Bradford, M.A., Jordan, C.F., Molina, M., 2011. Soil fauna alter the effects of litter composition on nitrogen cycling in a mineral soil. *Soil Biol. Biochem.* 43, 1440–1449.
- Chamberlain, P.M., McNamara, N.P., Chaplow, J., Stott, A.W., Black, H.I., 2006. Translocation of surface litter carbon into soil by Collembola. *Soil Biol. Biochem.* 38, 2655–2664.
- Chen, B., Wise, D.H., 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80, 761–772.
- Chicago Wilderness Biodiversity Council, 1999. *Chicago Wilderness Biodiversity Recovery Plan*. Chicago Region Biodiversity Council, Chicago, IL.
- Clarke, K., Warwick, R., 2001. *Changes in Marine Communities: an Approach to Statistical Analysis and Interpretation*, second ed. Primer-E, Plymouth, UK.
- Coleman, D.C., Hendrix, P.F., 2000. *Invertebrates as Webmasters in Ecosystems*. Cabi Publishing, England, UK.
- Coleman, T.W., Rieske, L.K., 2006. Arthropod response to prescription burning at the soil–litter interface in oak–pine forests. *For. Ecol. Manage.* 233, 52–60.
- Coleman, D.C., Reid, C., Cole, C., 1983. Biological strategies of nutrient cycling in soil systems. *Adv. Ecol. Res.* 13, 1–55.
- Cooke, J., 1965. Spider genus *Dysdera* (Araneae, Dysderidae). *Nature* 205, 1027–1028.
- Crowther, T.W., Boddy, L., Jones, T.H., 2011. Species-specific effects of soil fauna on fungal foraging and decomposition. *Oecologia* 167, 535–545.
- Diehl, E., Mader, V.L., Wolters, V., Birkhofer, K., 2013. Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia* 173, 579–589.
- Digweed, S., 1995. Digging out the “digging-in effect” of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39, 561–576.
- Dix, N.J., Webster, J.W., 1995. *Fungal Ecology*. Chapman and Hall, London, UK.
- Ehrenfeld, J.G., 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6, 503–523.
- Emery, S.M., Doran, P.J., 2013. Presence and management of the invasive plant *Gypsophila paniculata* (baby’s breath) on sand dunes alters arthropod abundance and community structure. *Biol. Conserv.* 161, 174–181.
- Foelix, R., 1996. *Biology of Spiders*. Oxford University Press, New York, USA.
- Gratton, C., 2006. Interactions between a native silkworm *Hemileuca* sp and an invasive wetland plant, *Lythrum salicaria*. *Ann. Entomol. Soc. Am.* 99, 1182–1190.
- Gratton, C., Denno, R.F., 2005. Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restor. Ecol.* 13, 358–372.
- Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M., Knops, J.M., 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *Am. Nat.* 158, 17–35.
- Hall, D.W., 1991. The environmental-hazard of ethylene-glycol in insect pit-fall traps. *Coleopt. Bull.* 45, 193–194.
- Hanula, J.L., Horn, S., 2011a. Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. *For. Ecol. Manage.* 262, 674–680.
- Hanula, J.L., Horn, S., 2011b. Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States. *Insect Conserv. Divers.* 4, 275–283.
- Hanula, J.L., Wade, D.D., 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. *For. Ecol. Manage.* 175, 163–184.
- Hassall, M., Turner, J., Rands, M., 1987. Effects of terrestrial isopods on the decomposition of woodland leaf litter. *Oecologia* 72, 597–604.
- Heneghan, L., Bolger, T., 1998. Soil microarthropod contribution to forest ecosystem processes: the importance of observational scale. *Plant Soil* 205, 113–124.
- Heneghan, L., Clay, C., Brundage, C., 2002. Rapid decomposition of buckthorn litter may change soil nutrient levels. *Ecol. Restoration* 20, 108–111.
- Heneghan, L., Mulvaney, C., Ross, K., Umek, L., Watkins, C., Westphal, L.M., Wise, D.H., 2012. Lessons learned from Chicago wilderness – implementing and sustaining conservation management in an urban setting. *Diversity* 4, 74–93.

- Hopkin, S., Martin, M., 1985. Assimilation of zinc, cadmium, lead, copper, and iron by the spider *Dysdera crocata*, a predator of woodlice. *Bull. Environ. Contam. Toxicol.* 34, 183–187.
- Ilieva-Makulec, K., Olejniczak, I., Szanser, M., 2006. Response of soil micro- and mesofauna to diversity and quality of plant litter. *Eur. J. Soil Biol.* 42, S244–S249.
- Jass, J., Klauemper, B., 2000. Endemics and immigrants: North American terrestrial isopods (Isopoda, Oniscidea) north of Mexico. *Crustaceana* 73, 771–799.
- Kajak, A., 1995. The role of soil predators in decomposition processes. *Eur. J. Entomol.* 92, 573–580.
- Kappes, H., Catalano, C., Topp, W., 2007. Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. *Appl. Soil Ecol.* 36, 190–198.
- Knapp, E.E., 2010. *Ecological Effects of Prescribed Fire Season: a Literature Review and Synthesis for Managers*. Diane Publishing, Pennsylvania, USA.
- Knops, J.M., Tilman, D., Haddad, D.N., Naeem, S., Mitchell, C., Haarstad, J., Ritchie, M., Howe, K., Reich, P., Siemann, E., 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* 2, 286–293.
- Lavy, D., Verhoef, H., 1996. Effects of food quality on growth and body composition of the collembolan *Orchesella cincta*. *Physiol. Entomol.* 21, 64–70.
- Lavy, D., Van Rijn, M., Zoomer, H., Verhoef, H., 2001. Dietary effects on growth, reproduction, body composition and stress resistance in the terrestrial isopods *Oniscus asellus* and *Porcellio scaber*. *Physiol. Entomol.* 26, 18–25.
- Lawrence, K.L., Wise, D.H., 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48, 149–157.
- Lensing, J.R., Wise, D.H., 2004. A test of the hypothesis that a pathway of intraguild predation limits densities of a wolf spider. *Ecol. Entomol.* 29, 294–299.
- Lenski, R.E., 1982. The impact of forest cutting on the diversity of ground beetles (Coleoptera: Carabidae) in the southern Appalachians. *Ecol. Entomol.* 7, 385–390.
- Lewis, J.G.E., 2007. *The Biology of Centipedes*. Cambridge University Press, Cambridge, UK.
- Lindenmayer, D.B., Franklin, J.F., 2002. *Conserving Forest Biodiversity: a Comprehensive Multiscaled Approach*. Island Press, District of Columbia, USA.
- Longcore, T., 2003. Terrestrial arthropods as indicators of ecological restoration success in coastal sage scrub (California, USA). *Restor. Ecol.* 11, 397–409.
- Loranger-Merciris, G., Laossi, K.R., Bernhard-Reversat, F., 2008. Soil aggregation in a laboratory experiment: Interactions between earthworms, woodlice and litter palatability. *Pedobiologia* 51, 439–443.
- MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86, 42–55.
- Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. *Trends Ecol. Evol.* 13, 195–198.
- Mäder, P., Fließbach, A., Dubois, D., Gunst, L., Fried, P., Niggli, U., 2002. Soil fertility and biodiversity in organic farming. *Science* 296, 1694–1697.
- Maerz, J.C., Karuzas, J.M., Madison, D.M., Blossey, B., 2005. Introduced invertebrates are important prey for a generalist predator. *Divers. Distrib.* 11, 83–90.
- Magoba, R.N., Samways, M.J., 2012. Comparative footprint of alien, agricultural and restored vegetation on surface-active arthropods. *Biol. Invasions* 14, 165–177.
- McClagherty, C.A., Pastor, J., Aber, J.D., Melillo, J.M., 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology*, 266–275.
- McGrath, D.A., Binkley, M.A., 2009. *Microstegium vimineum* invasion changes soil chemistry and microarthropod communities in Cumberland Plateau forests. *Southeast. Nat.* 8, 141–156.
- Melbourne, B.A., 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Aust. J. Ecol.* 24, 228–239.
- Melbourne, B.A., Gullan, P.J., Su, Y.N., 1997. Interpreting data from pitfall-trap surveys: crickets and slugs in exotic and native grasslands of the Australian Capital Territory. *Memoirs Museum Victoria* 56, 361–367.
- Melillo, J.M., Aber, J.D., Murator, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.
- Mgobozi, M.P., Somers, M.J., Dippenaar-Schoeman, A.S., 2008. Spider responses to alien plant invasion: the effect of short- and long-term *Chromolaena odorata* invasion and management. *J. Appl. Ecol.* 45, 1189–1197.
- Morris, M.G., 1975. Preliminary observations on the effects of burning on the hemiptera (Heteroptera and Auchenorrhyncha) of limestone grassland. *Biol. Conserv.* 7, 311–319.
- Morris, M., 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biol. Conserv.* 95, 129–142.
- Moser, W.K., Barnard, E.L., Billings, R.F., Crocker, S.J., Dix, M.E., Gray, A.N., Ice, G.G., Kim, M.S., Reid, R., Rodman, S.U., 2009. Impacts of nonnative invasive species on US forests and recommendations for policy and management. *J. Forest.* 107, 320–327.
- Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. *Oikos*, 288–388.
- Piatek, K.B., Munasinghe, P., Peterjohn, W.T., Adams, M.B., Cumming, J.R., 2010. A decrease in oak litter mass changes nutrient dynamics in the litter layer of a central hardwood forest. *North. J. Appl. For.* 27, 97–104.
- Pieper, S., Weigmann, G., 2008. Interactions between isopods and collembolans modulate the mobilization and transport of nutrients from urban soils. *Appl. Soil Ecol.* 39, 109–126.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.*, 297–330.
- Powell, K.L., Chase, J.M., Knight, T.M., 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *Am. J. Bot.* 98, 539–548.
- R Development Core Team, 2013. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Řezáč, M., Pekár, S., 2007. Evidence for woodlice-specialization in *Dysdera* spiders: behavioural versus developmental approaches. *Physiol. Entomol.* 32, 367–371.
- Rushton, S.P., Hassall, M., 1983. The effects of food quality on the life history parameters of the terrestrial isopod (*Armadillidium vulgare* (Latreille)). *Oecologia* 57, 257–261.
- Samways, M.J., Caldwell, P.M., Osborn, R., 1996. Ground-living invertebrate assemblages in native, planted and invasive vegetation in South Africa. *Agric. Ecosyst. Environ.* 59, 19–32.
- Schwab, A., Dubois, D., Fried, P.M., Edwards, P.J., 2002. Estimating the biodiversity of hay meadows in north-eastern Switzerland on the basis of vegetation structure. *Agric. Ecosyst. Environ.* 93, 197–209.
- Seastedt, T., 1984. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29, 25–46.
- Siemann, E., 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79, 2057–2070.
- Southwood, T.R.E., 1978. *Ecological Methods*. Chapman and Hall, London, UK.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. *Decomposition in Terrestrial Ecosystems*. University of California Press, California, USA.
- Szanser, M., Ilieva-Makulec, K., Kajak, A., Gorska, E., Kusińska, A., Kisiel, M., Olejniczak, I., Russel, S., Sieminiak, D., Wojewoda, D., 2011. Impact of litter species diversity on decomposition processes and communities of soil organisms. *Soil Biol. Biochem.* 43, 9–19.
- Uetz, G.W., 1979. The influence of variation in litter habitats on spider communities. *Oecologia* 40, 29–42.
- Vegter, J., 1983. Food and habitat specialization in coexisting springtails (Collembola, Entomobryidae). *Pedobiologia* 25, 253–262.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. *N. Z. J. Ecol.* 21, 1–16.
- Wagner, R.G., Newton, M., Cole, E.C., Miller, J.H., Shiver, B.D., 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. *Wildl. Soc. Bull.* 32, 1028–1041.
- Wallis De Vries, M.F., Poschod, P., Willems, J.H., 2002. Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biol. Conserv.* 104, 265–273.
- Weidenhamer, J.D., Callaway, R.M., 2010. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. *J. Chem. Ecol.* 36, 59–69.
- Western Ag Innovations Inc., 2009. *Plant root simulator (PRS) TM operations manual*. 411 Downey Road, Suite 3, Canada.
- Weygoldt, P., 1969. *The Biology of Pseudoscorpions*. Harvard University Press, Massachusetts, USA.
- Wise, D.H., 1993. *Spiders in Ecological Webs*. Cambridge University Press.
- Wise, D.H., Chen, B., 1999. Impact of intraguild predators on survival of a forest-floor wolf spider. *Oecologia* 121, 129–137.
- Woodcock, B., Pywell, R., Roy, D., Rose, R., Bell, D., 2005. Grazing management of calcareous grasslands and its implications for the conservation of beetle communities. *Biol. Conserv.* 125, 193–202.
- Zimmer, M., Pennings, S., Buck, T., Carefoot, T., 2002. Species-specific patterns of litter processing by terrestrial isopods (Isopoda: Oniscidea) in high intertidal salt marshes and coastal forests. *Funct. Ecol.* 16, 596–607.