Biol Invasions
DOI 10.1007/s10530-008-9347-6

ORIGINAL PAPER

Dominance of an invasive earthworm in native and non-native grassland ecosystems

Yaniria Sánchez-de León · Jodi Johnson-Maynard

Received: 9 May 2008 / Accepted: 15 August 2008

Abstract More attention is currently being focused on earthworm invasions; however, in many ecosystems the relative abundance of native and invasive earthworm species is unknown. We characterized earthworm populations of two grassland types within the Palouse region: native prairie remnants and Conservation Reserve Program (CRP) set asides planted with exotic grasses. The earthworm community in both grassland types was completely dominated by the exotic-invasive *Aporrectodea trapezoides*. Only one individual of a native species, *Driloleirus americanus* (the giant Palouse earthworm), was found in a prairie remnant. No differences were found between prairie remnants and CRP sites for mean earthworm density (24–106 individuals m^{-2}) or fresh weight (12–45 g m^{-2}). Our results suggest that the combined effects of land-use change, habitat fragmentation and competitive interactions have resulted in the decimation of native earthworm populations and dominance of invasive earthworms in native and non-native grasslands of the Palouse region.

Y. Sánchez-de León · J. Johnson-Maynard
Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83844-2339, USA

Y. Sánchez-de León (✉)
Department of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 West Taylor Street, Chicago, IL 60607-7060, USA
e-mail: ysl@uic.edu

Keywords Invasive earthworms · Grasslands · Palouse prairie · Conservation Reserve Program

Introduction

Earthworms are considered to be one of the most important groups of soil organisms in grassland ecosystems (Curry 1994, 1988) and under favorable environmental conditions earthworms can dominate grassland soil invertebrate biomass (Curry 1994). In European calcareous grasslands, for example, earthworms compose 70–80% of the soil animal biomass (Zaller and Arnone 1999a). Earthworms can significantly influence grassland ecosystems through their effects on soil nutrient and carbon (C) cycling, soil aggregation and porosity, decomposition and plant productivity (Lee 1985; Curry 1994, 1988; Zaller and Arnone 1999b).

Although the activity of introduced exotic earthworms may have beneficial effects in agricultural systems (Lee 1985; Edwards and Bohlen 1996; Baker et al. 2006), there is increasing concern over exotic earthworm invasions in native habitats (Hendrix and Bohlen 2002; Hendrix 2006; Frelich et al. 2006). The negative effects of earthworm invasions on ecosystem processes have been more obvious and dramatic in temperate and cold-temperate deciduous and mixed deciduous-conifer forests in areas of North America where native earthworms are absent due to

Quartenary glaciations (Bohlen et al. 2004; Frelich et al. 2006). Introduction of invasive earthworms into these previously earthworm-free habitats has been related to increased soil compaction and significant changes in C and nitrogen (N) cycling, plant community composition, microbial and microarthropod communities and the soil food web (e.g. Hendrix and Bohlen 2002; Bohlen et al. 2004; Bohlen 2006; Frelich et al. 2006; Eisenhauer et al. 2007; Holdsworth et al. 2007). In non-glaciated regions where native earthworms are present, there is additional concern over competitive interactions among native and invasive earthworms (Kalisz and Wood 1995; Hendrix et al. 2006).

Native habitat disturbance (e.g. grazing, vegetation conversion for agricultural production or pasture land, suppression of fire, fertilization) usually decreases the abundance of native earthworms and increases the abundance of exotic earthworms (James 1991; Callaham et al. 2003; Hendrix et al. 2006; Winsome et al. 2006). Results of these previous studies of earthworm community composition in undisturbed and disturbed grassland ecosystems suggest that native earthworms may be present in native undisturbed grasslands but are less abundant or absent in disturbed grasslands. However, the ability of an exotic earthworm to successfully invade any ecosystem is related to factors such as the degree of disturbance, competition with native species, and adaptability to site climatic and edaphic conditions (Hendrix et al. 2006).

The Palouse region of southeastern Washington and northern Idaho provides an excellent opportunity to study earthworm populations in native prairie and non-native grassland vegetation that was reestablished after agricultural disturbance. The Palouse region is characterized by a Mediterranean type climate, deep loess soils and native steppe vegetation (Lichthardt and Moseley 1997; Black et al. 1998). The Palouse grassland ecosystems are composed principally of native prairie remnants and CRP set asides. After European settlement, most of the land was converted to agricultural use and currently less than 1% of the original Palouse prairie remains (Noss et al. 1995; Lichthardt and Moseley 1997; Black et al. 1998). Most of the Palouse prairie remnants are located on steep slopes and rocky areas that were difficult to plow (Lichthardt and Moseley 1997).

The CRP was originally established in 1985 as a way to improve water quality, reduce soil erosion and enhance wildlife habitat (Farm Service Agency 2007). Conservation Reserve Program set asides were established by removing lands of low productivity and high susceptibility to erosion from agriculture production (Uri and Bloodworth 2000; Farm Service Agency 2007). In the Palouse region, most of these set asides were planted with exotic perennial grasses (Black et al. 1998).

Little is known about native earthworms of the Palouse region. One native earthworm reported for the region is *Driloleirus americanus*, commonly known as the giant Palouse earthworm. This earthworm was once described as being "abundant" in the Palouse region close to Pullman, Washington (Smith 1897); however, information on its abundance and distribution is limited to taxonomic studies and ecological survey-type descriptions (Fender and McKey-Fender 1990; Fender 1995; James 2000). Previous to this study, the last unofficial sighting of this species was reported 18 years ago in a forested area close to the town of Moscow, Idaho (James D. Johnson, personal communication). Results of previous earthworm population studies in the Palouse region indicate that exotic earthworm species are dominant in urban areas (Smetak et al. 2007) and in agricultural fields (James 2000; Fauci and Bezdicek 2002). Among exotic earthworm species reported, *Aporrectodea trapezoides*, *A. tuberculata* and *Lumbricus terrestris* were the most common in urban and agricultural areas within the Palouse (James 2000; Fauci and Bezdicek 2002; Smetak et al. 2007). Earthworm populations in native and non-native grassland ecosystems of the region have not been studied. The main purpose of this study was to characterize and compare native and exotic earthworm populations in two important grassland ecosystems of the Palouse region, native prairie remnants and CRP set asides. In addition, we wanted to describe the relationship between earthworm populations and select soil characteristics within each grassland type. We asked the following research questions: Does earthworm species composition differ in native and non-native grasslands of the Palouse? What is the potential of these grassland ecosystems to provide adequate habitat for native and exotic invasive earthworms? Based on the differences in disturbance, we hypothesized that native earthworms would be dominant in prairie remnants and exotic earthworms would be dominant in CRP set asides.

Methods

We conducted this study on private lands in the eastern Palouse region located within Latah County, Idaho and Whitman County, Washington. We selected study sites that contained a large prairie remnant (>10 ha) and an adjacent CRP set aside, for a total of four sites (Table 1). The study sites were selected following a randomized block design where factors such as aspect, slope and soil type were kept as constant as possible. The vegetation type in each prairie remnant was the *Festuca-Symphorocarpos* association as described in Daubenmire (1970). Conservation Reserve Program sites were dominated by hard fescue (*Festuca brevipila* Tracey), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth and D. R. Dewey) and smooth brome (*Bromus inermis* Leyss.). All CRP sites have been under perennial grassland vegetation for 20–25 years. Soils were mostly Ultic Argixerolls and Ultic Haploxerolls, and prairie soils had 35% or more rock fragments by volume as specified by the loamy-skeletal taxonomic classification (Table 1). Annual precipitation in this area ranges from 460 to 610 mm year^{-1} and mean annual temperature between 8 and 11°C (NRCS 2007a, b).

We sampled earthworms at the study sites during the months of May and June for three consecutive years (2003–2005), except for 2003, when only three prairie remnants and corresponding CRP sites were sampled. Five pits (25 cm by 25 cm and 30 cm deep) were randomly located at each prairie and CRP site and earthworms were sampled by hand sorting. All the earthworms found were collected, taken to the laboratory, and classified to species using the taxonomic key developed by Schwert (1990). Earthworms were counted and fresh weight was measured by weighing the earthworms on the same day of collection.

Soil samples were collected during earthworm sampling in 2003 and 2004. Samples were collected in 10-cm thick increments down to the 30-cm depth. Soil total C and N percentages were measured by dry combustion using a CNS analyzer (Vario Max CNS from Elementar Analysensysteme, Germany). Soil pH was measured using the 1:1 (soil:water) method as described in Thomas (1996). Bulk density was measured by the core method using a 4.7-cm diameter soil core sampler as described by Grossman and Reinsch (2002). Bulk density values were used to calculate C and N on a mass per area unit (kg m^{-2}) to a depth of 30 cm.

Data analysis

We performed repeated measures analysis of variance (ANOVA) using the general linear model to compare earthworm density and fresh weight between land

Table 1 General site and soil characteristics of Palouse prairie remnants and Conservation Reserve Program (CRP) study sites

Study site	Land use	Aspect	Slope (%)	Dominant soil type[a]
Paradise Ridge	Prairie	E	40	Loamy-skeletal, mixed, mesic Lithic Ultic Argixeroll
	CRP	E	27	Fine-silty, mixed, mesic Boralfic Argixeroll
Tomer Butte	Prairie	S	18	Loamy-skeletal, mixed, mesic Lithic Ultic Argixeroll
	CRP	S	15	Fine-silty, mixed, mesic Ultic Argixeroll
Smoot Hill	Prairie	NW	25	Loamy-skeletal, mixed, mesic Ultic Argixeroll
	CRP	NW	33	Fine-silty, mixed, mesic Boralfic Argixeroll
Bald Butte	Prairie	SW	31	Loamy-skeletal, mixed, mesic Ultic Argixeroll
	CRP	SW	12	Fine-silty, mixed, mesic Boralfic Argixeroll

[a] Dominant soil types as specified in Latah County, ID and Whitman County, WA Soil Survey (NRCS 2007a, b)

uses (i.e. prairie remnants and CRP set asides) across years. For statistical analysis, we followed the analysis for a randomized block split-plot in time design, where data was blocked by study site. To test the effect of land use, the interaction between study site and land use (site × land use) was used as the error term. We used the same analysis to compare soil characteristics across soil depths, and used the interaction between study site and land use (site × land use) as the error term to test the effect of land use on soil properties.

Linear correlations were performed between measured soil characteristics and earthworm data. Soil data (i.e. C, N, C:N, and pH) were averaged across depths and earthworm data (i.e. density and fresh weight) were averaged across years for Paradise Ridge, Tomer Butte and Smoot Hill study sites. All the statistical analyses were performed using the software SAS® version 9.1 (SAS Institute, Cary, NC) and the significance level was set at $\alpha = 0.05$.

Results

Earthworm populations

We found four species at the study sites. The exotic species, *Aporrectodea trapezoides* was present in both prairie and CRP, but *A. longa* and *Lumbricus terrestris* were only found at CRP sites (Table 2). *Apporectodea longa* was only found in Bald Butte CRP and *L. terrestris* was found only at Tomer Butte CRP. Only one native earthworm individual of the species *Driloleirus americanus*, the giant Palouse earthworm, was found at the Smoot Hill prairie remnant. The exotic-invasive *Aporrectodea trapezoides* was dominant and represented over 90% of the total earthworm density and fresh weight across sites and years (Table 2). Most of the earthworms found were within the top 10 cm of soil.

Mean earthworm density and fresh weight did not significantly differ between prairie remnants and CRP sites (Table 3). Earthworm density and fresh weight showed high variability across years for both land uses (Fig. 1a–h). Overall mean earthworm density in prairie remnants was 37.0 ± 7.1 individuals m^{-2} and 87.5 ± 18.4 individuals m^{-2} in CRP sites. Mean earthworm fresh weight was 19.0 ± 5.6 g m^{-2} in prairies and 38.8 ± 4.8 g m^{-2} in CRP sites.

Soil characteristics

Few differences were found between prairie and CRP sites for soil characteristics. Total soil C and N, bulk density and pH were not statistically different between grassland types (Table 4). Soil C:N ratio within the 0- to 30-cm depth tended to be higher in CRP sites than in prairies ($P = 0.09$).

Table 3 Statistics of repeated measures ANOVA ($n = 4$) for total earthworm density and biomass at prairie and CRP sites (i.e. land use)

Source	df	*F*	*P*
Density			
Land use	1	4.22	0.13
Site	3	1.44	0.29
Year	2	2.93	0.10
Land use × year	2	2.04	0.18
Fresh weight			
Land use	1	5.22	0.11
Site	3	0.46	0.71
Year	2	2.18	0.16
Land use × year	2	1.36	0.30

Table 2 Mean earthworm density and fresh weight (±SE) by species in prairie and CRP sites of the Palouse region

Species	Origin	Density (individuals m^{-2})		Fresh weight (g m^{-2})	
		Prairie	CRP	Prairie	CRP
A. trapezoides	European	38.0 (7.2)	82.8 (20.2)	18.4 (5.1)	35.2 (6.3)
A. longa	European	0.0 (0.0)	6.7 (6.7)	0.0 (0.0)	5.0 (5.0)
L. terrestris	European	0.0 (0.0)	5.6 (5.6)	0.0 (0.0)	4.2 (4.2)
D. americanus	Native	0.8 (0.8)	0.0 (0.0)	3.7 (3.7)	0.0 (0.0)

Earthworm species *A. longa*, *L. terrestris* and *D. americanus* were only found at one study site

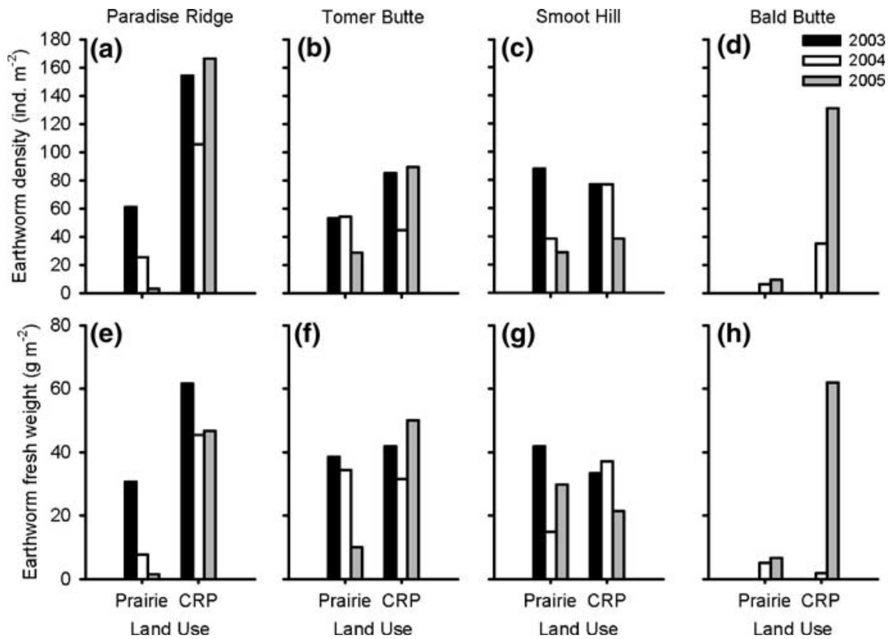

Fig. 1 Earthworm density (**a**–**d**) and fresh weight (**e**–**h**) in prairie remnants and CRP sites across years. No significant differences were detected according to repeated measures ANOVA ($n = 4$). Bald Butte study site was included in year 2004

Table 4 Means (±SE) of soil bulk density, pH, C, N and C:N ratio in prairie remnants and CRP study sites

Soil depth (cm)	Bulk density (g cm^{-3})		pH		C (kg m^{-2})		N (kg m^{-2})		C:N ratio	
	Prairie	CRP	Prairie	CRP	Prairie	CRP	Prairie	CRP	Prairie	CRP
0–10	1.0 (0.09)	1.4 (0.03)	6.6 (0.1)	5.9 (0.3)	2.8 (0.2)	2.5 (0.6)	0.2 (0.02)	0.2 (0.04)	13.1 (0.4)	14.3 (0.4)
10–20	1.1 (0.08)	1.4 (0.03)	6.5 (0.1)	6.0 (0.2)	3.0 (0.2)	1.8 (0.6)	0.2 (0.01)	0.1 (0.04)	12.8 (0.3)	14.9 (0.1)
20–30	1.2 (0.06)	1.5 (0.01)	6.3 (0.04)	6.2 (0.2)	2.1 (0.2)	1.8 (0.6)	0.2 (0.01)	0.1 (0.04)	13.1 (0.4)	14.5 (0.3)

No significant effect of land use was found according to repeated measures ANOVA ($n = 3$)

Significant negative interactions were found between soil pH and earthworm density and fresh weight. Soil pH was negatively correlated with mean earthworm density ($y = -116.72x + 797.3$, $r = 0.97$, $P = 0.002$) and with mean earthworm fresh weight ($y = -33.432x + 241.14$, $r = 0.84$, $P = 0.034$) across sites. Earthworm density and fresh weight were not significantly correlated with the other measured soil characteristics.

Discussion

Earthworm populations

Our hypothesis, that native earthworms would be dominant in prairie remnants and exotic earthworms dominant in CRP set asides, was not supported by the data. We found a clear dominance of the exotic-invasive earthworm *A. trapezoides* in both grassland types. Our results are consistent with those of previous earthworm population studies conducted in disturbed grasslands and CRP lands in the United States. European lumbricid earthworms dominated in a managed and disturbed (fertilized, after vegetation conversion) grassland in California (Winsome et al. 2006) and in CRP lands in North Dakota (Deibert and Utter 2003). In Kansas tall grass prairie soils, Callaham et al. (2003) found that earthworm populations were composed of three earthworm genera and that two of these were European earthworms. In addition, Callaham et al. (2003) found that introduced European species, including *A. trapezoides*, were dominant in treatments excluded from historical disturbance (fire and grazing). Deibert and Utter (2003) found only exotic earthworm species (*A. trapezoides*, *A. caliginosa*, *A. tuberculata*, *Dendrobaena octaedra* and *L. rubellus*) in 12 CRP sites in North

Dakota. At these sites *A. tuberculata* and *A. trapezoides* were the dominant species.

Contrary to our hypothesis, we did not find dominance of native earthworms in prairie remnants. In fact, we found only one native earthworm, the rare (at least rarely encountered in recent times) giant Palouse earthworm, *D. americanus*. Only one individual was collected, in the prairie remnant located at the Smoot Hill Biological Preserve, WA (Smoot Hill site); no other native species were found. It should be noted that exotic earthworm abundance at Smoot Hill prairie was not different from those measured at other prairie sites (Fig. 1). This finding is not consistent with the results of other studies showing that native earthworms predominate in undisturbed or minimally disturbed grasslands (James 1991; Callaham et al. 2003; Winsome et al. 2006). The rarity of native earthworms in our prairie sites provides support for the replacement of native earthworms by exotic earthworms in visibly intact remnants of fragmented habitats as proposed by Kalisz and Wood (1995). Kalisz and Wood (1995) proposed two mechanisms for earthworm species substitution in fragmented habitats: (1) exotic species out compete native species; or (2) undetected, ecologically significant changes (e.g. gradual changes in plant and animal diversity, changes in microclimate, edge effects) occur as a consequence of habitat fragmentation. From our data, however, we cannot exclude the possibility that *D. americanus* did not historically occur in high densities within these prairie remnants due to steep slope and/or high rock content—the very factors that have prevented these areas from being plowed, preserving them as remnant prairie.

The fact that native earthworm species are found in fragmented native habitats along with exotic earthworms (Kalisz and Wood 1995) suggests that coexistence of *D. americanus* with exotic species in Palouse prairie remnants is possible. Resilient earthworm species include deep-burrowing species, that do not depend on fresh litter input of a particular vegetation type as a principal component of their diet; and species that are adapted to local conditions that are unfavorable to exotic earthworms (e.g. low resource availability, seasonal low soil moisture or seasonal high temperatures) (James 1991; Kalisz and Wood 1995; Callaham et al. 2001; Hendrix et al. 2006; Winsome et al. 2006). Whether *D. americanus* is a resilient species based on its deep burrowing behavior [*Driloleirus* genus have burrows up to 4.5 m deep (Smith 1897; Fender and McKey-Fender 1990)], or whether our results are showing a species replacement process, remains unknown and certainly deserves further study.

We propose that a combination of extensive habitat fragmentation in the Palouse region, low habitat quality of remaining prairie remnants, and possibly competitive interactions with exotic earthworms, decimated *D. americanus* populations at our study sites. No information is available on pre-agricultural density or distribution of *D. americanus*; however, the description of the species as being abundant by Smith (1897) contrasts to the rarity of finding the earthworm today, suggesting a significant reduction in its population size. As mentioned previously, land use change from native vegetation to agriculture and habitat fragmentation in the Palouse region was extensive, resulting in a reduction of more than 99% of the Palouse prairie ecosystem (Noss et al. 1995; Lichthardt and Moseley 1997; Black et al. 1998). Extensive land use conversion to agriculture in the Palouse must have severely reduced available habitat for *D. americanus* and promoted undetected disturbance in the remaining prairie patches. In addition, the remaining prairie remnants could represent a low quality habitat for native earthworms. Remaining prairie remnants tend to have shallow and rocky soils in contrast to the deep, silt-loam textured soil that characterizes the area (Lichthardt and Moseley 1997). Lower quality of the remaining habitat for native earthworms could represent an undetected, but ecologically significant change produced by habitat fragmentation in the Palouse region.

Competition among native and invasive earthworms has been suggested as a mechanism that may lead to the dominance of exotic species at a site (e.g. Kalisz and Wood 1995; Hendrix et al. 2006). Biological traits of *A. trapezoides* such as tolerance to varying environmental conditions, rapid growth, parthenogenetic reproduction and ability to live under a wide range of land uses and soils (Fender 1985; Winsome et al. 2006), could give *A. trapezoides* a competitive advantage to successfully establish and dominate grassland ecosystems of the Palouse region. In addition, the ecological categories of each species suggests that *A. trapezoides* and *D. americanus* may compete for food resources within prairie remnants.

Driloleirus americanus is suggested to be an anecic earthworm (James 2000). Anecic earthworms are species that live in the soil and feed from surface litter and soil (Brown 1995; Lavelle 2002; Coleman et al. 2004). *Aporrectodea trapezoides* is classified as a polyhumic endogeic earthworm in James (2000) and as an epi-endogeic earthworm in Winsome et al. (2006). Polyhumic endogeic earthworms are species that inhabit soil close to the surface (within top 15 cm), and feed from soils high in organic matter content. Epi-endogeic earthworms also live close to the soil surface, but their diet is composed primarily of leaf litter and microbial biomass (Brown 1995; Lavelle 2002; Coleman et al. 2004). If *A. trapezoides* is an epi-endogeic earthworm, then there is the possibility of direct competition for food resources with *D. americanus.* Although describing competitive interactions among earthworm species was beyond the scope of our study, it is possible that *A. trapezoides* is out-competing other earthworms at our prairie and CRP sites based on its biological and ecological characteristics.

Earthworm sampling methodology could have influenced our results. The hand sorting sampling method is regarded as the best method to estimate abundance of most earthworm species, but is also known to underestimate the abundance of deep-burrowing species (Lee 1985; Schwert 1990; Edwards and Bohlen 1996) such as *D. americanus* or *L. terrestris*. For future studies, we suggest use of a combination of methods, including non-destructive alternatives such as electrical methods (Schmidt 2001; Weyers et al. 2008) and/or extraction methods with chemicals of low toxicity [e.g. Allyl isothiocyanate (Zaborski 2003)], that are more suited for deep-burrowing earthworm species.

Influence of soil characteristics on earthworm populations

Our results do not support the hypothesis that soil bulk density, total C and N content, or C:N ratio influence earthworm populations in Palouse prairie remnants and CRP study sites. This absence of a pattern contrasts somewhat with previous studies in CRP sites or urban areas of the Palouse. Deibert and Utter (2003) found that earthworms were not present in North Dakota CRP sites where organic matter was less than 2.6%, and also found a positive correlation between earthworm densities and soil nitrate content. In urban areas of the Palouse, Smetak et al. (2007) found that earthworms were positively correlated with soil C and N, and earthworms were negatively correlated with bulk density.

Of the soil characteristics measured in our study, only soil pH showed a significant negative correlation with earthworm density across sites. Earthworm species and their spatial distribution are sensitive to differences in pH (Edwards and Bohlen 1996; Chan and Mead 2003). Certain species can tolerate a wide range of pH values, but in general most earthworms prefer soils with a neutral pH, and earthworms are rare under a pH of 4 and absent at pH values lower than 3.5 (Lee 1985; Edwards and Bohlen 1996). The earthworm *A. trapezoides* was more abundant in CRP sites which tended to have lower pH values (pH from 5.9 to 6.2) than prairie soils (pH from 6.3 to 6.6). These results are contrary to studies that show positive relationships between lumbricid earthworm densities, including *A. trapezoides*, and soil pH (up to pH $\sim$7.0) (Edwards and Bohlen 1996; Chan and Mead 2003). It is possible that soil pH was influenced by another factor not measured in this study that was also affecting earthworm density and fresh weight in the prairie remnants and CRP sites. For example, CRP sites were likely fertilized in the past when utilized as agricultural soils. The application of inorganic nitrogenous fertilizer is known to promote soil acidification but may also indirectly increase earthworm density through increasing the quality and quantity of organic inputs into the soil (Edwards and Bohlen 1996), as well as promote soil acidification. Thus, the negative relationship between earthworm density and soil pH could be a reflection of a past land use effect rather than a direct effect of soil pH on earthworms.

Conclusions

Earthworm populations are dominated by the exotic-invasive *A. trapezoides* in both native prairie remnants and CRP grasslands of the Palouse region. No differences were found in total earthworm density and fresh weight between prairie remnants and CRP sites, but increasing pH had a negative relationship with earthworm abundance. A single individual of the native earthworm species *D. americanus*, the giant

Palouse earthworm, was found in a prairie remnant. We propose that changes in land use, effects of habitat fragmentation on ecological interactions within prairie remnants and competitive interactions have led to the almost complete dominance of exotic-invasive earthworms in grasslands of the Palouse region. Other ecological effects of *A. trapezoides* within prairie remnants and CRP sites are currently unknown; possible impacts include reduction in microbial biomass and alteration of soil physical structure.

Acknowledgements We are grateful to private landowners and Washington State University for letting us work on their lands. This work was funded by National Science Foundation-Integrative Graduate Education and Research Traineeship grant No. 0114304, the Inland Northwest Research Alliance, the University of Idaho's Center for Research on Invasive Species and Small Populations and the Department of Plant, Soil and Entomological Sciences. We are extremely grateful to Michael Westwind-Fender for identification of the native earthworm species. We thank K. Smetak, J. Villa-Romero, P. Wanjugi, N. Whitaker, J. Lugo-Perez and K. Umiker for their help in the field. We are also grateful to N. Bosque-Perez, P. McDaniel, J. Marshall and D. H. Wise for useful comments on previous versions of this manuscript.

References

Baker GH, Brown G, Butt K et al (2006) Introduced earthworms in agricultural and reclaimed land: their ecology and influences on soil properties, plant production and other soil biota. Biol Invasions 8:1301–1316. doi:10.1007/s10530-006-9024-6

Black AE, Strand E, Wright RG et al (1998) Land use history at multiple scales: implications for conservation planning. Landsc Urban Plan 43:49–63. doi:10.1016/S0169-2046(98)00096-6

Bohlen PJ (2006) Biological invasions: linking the aboveground and belowground consequences. Appl Soil Ecol 32:1–5. doi:10.1016/j.apsoil.2005.10.001

Bohlen PJ, Groffman PM, Fahey TJ et al (2004) Ecosystem consequences of exotic earthworm invasion of north temperate forests. Ecosystems (NY, Print) 7:1–12. doi:10.1007/s10021-003-0126-z

Brown GG (1995) How do earthworms affect microfloral and faunal community diversity? Plant Soil 170:209–231. doi:10.1007/BF02183068

Callaham MA, Blair JM, Hendrix PF (2001) Different behavioral patterns of the earthworms *Octolasion tyrtaeum* and *Diplocardia* spp. in tallgrass prairie soils: potential influences on plant growth. Soil Biol Biochem 35:1079–1093. doi:10.1016/S0038-0717(03)00153-6

Callaham MA, Blair JM, Todd TC et al (2003) Macroinvertebrates in North American tallgrass prairie soils: effects of fire, mowing, and fertilization on density and biomass. Soil Biol Biochem 35:1079–1093. doi:10.1016/S0038-0717(03)00153-6

Chan K, Mead JA (2003) Soil acidity limits colonization by *Aporrectodea trapezoides*, an exotic earthworm. Pedobiologia (Jena) 47:225–229. doi:10.1078/0031-4056-00186

Coleman DC, Crossley DA Jr, Hendrix PF (2004) Fundamentals of soil ecology. Elsevier Academic Press, New York

Curry JP (1988) Factors affecting earthworm abundance in soils. In: Edwards A (ed) Earthworm ecology, 2nd edn. St. Lucie Press, Boca Raton, pp 37–64

Curry JP (1994) Grassland invertebrates: ecology influence on soil fertility and plant growth. Chapman and Hall, New York

Daubenmire RF (1970) Steppe vegetation of Washington. Technical Bulletin 62 Washington agricultural experiment station. Washington State University, Washington

Deibert EJ, Utter RA (2003) Earthworm (Lumbricidae) survey of North Dakota fields placed in the US conservation reserve program. J Soil Water Conserv 58:39–45

Edwards CA, Bohlen PJ (1996) Biology and ecology of earthworms. Champman and Hall, New York

Eisenhauer N, Partsch S, Parkinson D et al (2007) Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. Soil Biol Biochem 39:1099–1110. doi:10.1016/j.soilbio.2006.12.019

Farm Service Agency (2007) Fact sheet, conservation reserve program. Available via http://www.fsa.usda.gov/Internet/FSA_File/crp07.pdf. Accessed 20 Oct 2007

Fender WM (1985) Earthworms of the western United States. Part I. Lumbricidae. Megadrilogica 4:93–129

Fender WM (1995) Native earthworms of the Pacific Northwest: an ecological overview. In: Hendrix PF (ed) Earthworm ecology and biogeography in North America. Lewis Publisher, Boca Raton, pp 53–64

Fender WM, McKey-Fender D (1990) Oligochaeta: Megascolecidae and other earthworms from western North America. In: Dindal DL (ed) Soil biology guide. Wiley, New York, pp 357–378

Fauci MF, Bezdicek DF (2002) Lumbricid earthworms in the Palouse region. NW Sci 76:257–260

Frelich LE, Hale CM, Scheu S et al (2006) Earthworm invasion into previously earthworm-free temperate and boreal forests. Biol Invasions 8:1235–1245. doi:10.1007/s10530-006-9019-3

Grossman RB, Reinsch TG (2002) Bulk density and linear extensibility. In: Dane JH, Topp C (eds) Methods for soil analysis, part 4. Physical methods. SSSA book series, no. 5. Soil Science Society of America, Inc, Wisconsin, pp 201–228

Hendrix PF (2006) Biological invasions belowground - earthworms as invasive species. Biol Invasions 8:1201–1204. doi:10.1007/s10530-006-9048-y

Hendrix PF, Bohlen PJ (2002) Exotic earthworm invasions in North America: ecological implications. Bioscience 52:801–811. doi:10.1641/0006-3568(2002)052[0801:EEIINA]2.0.CO;2

Hendrix PF, Baker GH, Callaham MA et al (2006) Invasion of exotic earthworms into ecosystems inhabited by native earthworms. Biol Invasions 8:1287–1300. doi:10.1007/s10530-006-9022-8

Holdsworth AR, Frelich LE, Reich PB (2007) Effects of earthworm invasion on plant species richness in northern hardwood forests. Conserv Biol 21:997–1008. doi:10.1111/j.1523-1739.2007.00740.x

James SW (1991) Soil, nitrogen, phosphorus and organic matter processing by earthworms in tallgrass prairie. Ecology 72:2101–2109. doi:10.2307/1941562

James S (2000) Earthworms (Annelida: Oligochaeta) of the Columbia River basin assessment area. General technical report PNW-GTR-491. USD A Forest Service, Pacific Northwest Research Station, Portland

Kalisz PJ, Wood HB (1995) Native and exotic earthworms in wildland ecosystems. In: Hendrix PF (ed) Earthworm ecology and biogeography in North America. Lewis Publisher, Boca Raton, pp 117–126

Lavelle P (2002) Functional domains in soils. Ecol Res 17:441–450. doi:10.1046/j.1440-1703.2002.00509.x

Lee KE (1985) Earthworms—their ecology and relationships with soils and land use. Academic Press, Sydney

Lichthardt J, Moseley RK (1997) Status and conservation of the Palouse Grassland in Idaho. Department of Fish and Game. Available via http://fishandgame.idaho.gov/cms/tech/CDC/cdc_pdf/PALOUS97.PDF. Accessed 20 Oct 2007

Noss RF, Laroe ET III, Scott JM (1995) Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. US Geological Survey, Biological Resources. Biological Report 28. Available via http://biology.usgs.gov/pubs/ecosys.htm. Accessed 20 Oct 2007

NRCS Natural Resources Conservation Service (2007a) Soil data mart of Latah County, Idaho. Available via http://soildatamart.nrcs.usda.gov/Survey.aspx?County=ID057. Accessed 20 Oct 2007

NRCS Natural Resources Conservation Service (2007b) Soil data mart of Whitman County, Washington. Available via http://soildatamart.nrcs.usda.gov/Survey.aspx?County=WA075. Accessed 20 Oct 2007

Schmidt O (2001) Appraisal of the electrical octet method for estimating earthworm populations in arable land. Ann Appl Biol 138:231–241. doi:10.1111/j.1744-7348.2001.tb00107.x

Schwert DP (1990) Oligochaeta: Lumbricidae. In: Dindal DL (ed) Soil biology guide. Wiley, New York, pp 341–356

Smetak KJ, Johnson-Maynard J, Lloyd JE (2007) Earthworm population density and diversity in different-aged urban systems. Appl Soil Ecol 37:161–168. doi:10.1016/j.apsoil.2007.06.004

Smith F (1897) Upon an undescribed species of Megascolides from the United States. Am Nat 31:202–204. doi:10.1086/276573

Thomas GW (1996) Soil pH and soil acidity. In: Sparks DL (ed) Methods for soil analysis, part 3. Chemical methods. SSSA book series, no. 5. Soil Science Society of America, Inc, Wisconsin, pp 475–490

Uri ND, Bloodworth H (2000) Global climate change and the effect of conservation practices in US agriculture. Glob Environ Change 10:197–209. doi:10.1016/S0959-3780(00)00023-6

Weyers SL, Schomberg HH, Hendrix PF et al (2008) Construction of an electrical device for sampling earthworm populations in the field. Appl Eng Agr 24:391–397

Winsome T, Epstein L, Hendrix PF et al (2006) Competitive interactions between native and exotic earthworm species as influenced by habitat quality in a California grassland. Appl Soil Ecol 32:38–53. doi:10.1016/j.apsoil.2005.01.008

Zaborski ER (2003) Allyl isothiocyanate: an alternative chemical expellant for sampling earthworms. Appl Soil Ecol 22:87–95. doi:10.1016/S0929-1393(02)00106-3

Zaller JG, Arnone JAIII (1999a) Earthworm responses to plant species loss and elevated CO_2 in calcareous grassland. Plant Soil 208:1–8. doi:10.1023/A:1004424720523

Zaller JG, Arnone JAIII (1999b) Interactions between plant species and earthworm casts in a calcareous grassland under elevated CO_2. Ecology 88:873–881