Applied Soil Ecology 83 (2014) 133–139

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Removal of an invasive shrub (Chinese privet: *Ligustrum sinense* Lour) reduces exotic earthworm abundance and promotes recovery of native North American earthworms

Joshua W. Lobe[a], Mac A. Callaham Jr.[b,*], Paul F. Hendrix[a], James L. Hanula[b]

[a] *University of Georgia, Odum School of Ecology, Athens, GA, USA*
[b] *Southern Research Station, USDA Forest Service, Athens, GA, USA*

ARTICLE INFO

Article history:
Received 31 January 2013
Received in revised form 30 October 2013
Accepted 31 March 2014
Available online 29 April 2014

Keywords:
Earthworms
Invasive plants
Native earthworms
Chinese privet
Exotic earthworms
Facilitation

ABSTRACT

This study investigated the possibility of a facilitative relationship between Chinese privet (*Ligustrum sinense*) and exotic earthworms, in the southeastern region of the USA. Earthworms and selected soil properties were sampled five years after experimental removal of privet from flood plain forests of the Georgia Piedmont region. The earthworm communities and soil properties were compared between sites with privet, privet removal sites, and reference sites where privet had never established. Results showed that introduced European earthworms (*Aporrectodea caliginosa*, *Lumbricus rubellus*, and *Octolasion tyrtaeum)* were more prevalent under privet cover, and privet removal reduced their relative abundance (from >90% to ~70%) in the community. Conversely, the relative abundance of native species (*Diplocardia michaelsenii*) increased fourfold with privet removal and was highest in reference sites. Soils under privet were characterized by significantly higher pH relative to reference plots and privet removal facilitated a significant reduction in pH. These results suggest that privet-mediated effects on soil pH may confer a competitive advantage to European lumbricid earthworms. Furthermore, removal of the invasive shrub appears to reverse the changes in soil pH, and may allow for recovery of native earthworm fauna.

1. Introduction

As the second greatest cause of modern extinctions, invasive species are a major threat to biodiversity (Soule, 1990). Early studies of invasive species showed that they can have large effects on ecosystems (Vitousek et al., 1987) and have spurred further research in this area. Unsurprisingly, most of this work has involved species that can be easily seen such as plants, vertebrates, and insects (Hendrix, 2006). This has unfortunately resulted in less attention to some of the more obscure invertebrates, such as earthworms despite their being recognized as very important creatures in the history of the world (Darwin, 1881).

Earthworms have been described as ecosystem engineers due to their proclivity to create long-lasting ecosystem level impacts on the soil environment (Jones et al., 1994). They greatly influence nutrient cycling, soil formation, soil properties, seed germination, microbial communities, soil invertebrate communities, and even aboveground communities (Edwards and Bohlen, 1996; Lavelle, 2001; Lee, 1985). With the ability to produce such broad and fundamental changes, it is likely that invasive earthworms would significantly impact the ecosystems they invade. Indeed, striking alterations to ecosystems have been observed when European earthworms invade regions where there are no native earthworms (Bohlen et al., 2004; Eisenhauer et al., 2007). In North America, areas north of the Wisconsinan glaciation have been free of earthworms for about 12,000 years (Callaham et al., 2006; James, 1995) and introductions of earthworms in this region completely alter conditions within the forest floor, with potential drastic changes to forest species composition over the long term (Bohlen et al., 2004; Eisenhauer et al., 2009; Hale et al., 2006).

Potentially aiding the invasion of exotic earthworms are positive and facilitative relationships with other non-native invasive species. 'Invasional meltdown' is a hypothesis suggesting that one invasive species creates an environment favorable to another, leading to increased or simultaneous invasions (Simberloff and Von Holle, 1999). Many invasive plants are known to change soil properties, often increasing N levels in the soil or altering pH (Asner

---

* Corresponding author at: Center for Forest Disturbance Science, Southern Research Station, USDA Forest Service, 320 Green Street, Athens, GA 30602, USA. Tel.: +1 706 559 4321; fax: +1 706 559 4317.
E-mail addresses: mcallaham@fs.fed.us, mac.callaham@gmail.com (M.A. Callaham Jr.).

http://dx.doi.org/10.1016/j.apsoil.2014.03.020
0929-1393/Published by Elsevier B.V.

and Beatty, 1996; Ehrenfeld et al., 2001; Vitousek et al., 1987) and increased exotic earthworm densities have been observed under many of these plants, especially those with high quality leaf litter (Aplet, 1990; Heneghan et al., 2007; Kourtev et al., 1999). Furthermore, European buckthorn (*Rhamnus cathartica* L.) and honeysuckle (*Lonicera* × *bella* Zabel) are common invasive plants of the Midwestern United States with high quality leaf litter and their removal led to a decreased abundance of invasive earthworms (Madritch and Lindroth, 2009).

The southeastern United States was not glaciated during the Wisconsinan glaciation and therefore has a native earthworm fauna (Hendrix et al., 2008), but soils are also occupied by exotic European lumbricid earthworms as well as the Asian genus *Amynthas* (Callaham et al., 2003). The region is also host to Chinese privet (*Ligustrum sinense* Lour.), a highly invasive semi-evergreen shrub that was brought to the southeast in 1852 for ornamental purposes (Dirr 1983). Privet escaped cultivation and is now well established in the southeastern U.S. and can be found from Texas to Massachusetts (Miller, 2003). Similar to European buckthorn and honeysuckle, privet is known to have leaf litter of high quality, with lower lignin, cellulose, and C:N ratios relative to native leaf litter. Also, privet litter has been shown to have faster decomposition rates relative to native litters in floodplains of western Georgia, as well as a fivefold increase in soil N mineralization rates (Mitchell et al., 2011). Privet does especially well in floodplains and riparian areas of the Southern Appalachian Piedmont region, where it often creates monotypic stands that crowd out native plants (Brantley, 2008; Hanula et al., 2009). This includes the Upper Oconee River basin in northeast Georgia, where privet now covers at least 59% of the entire floodplain (Ward, 2002). This drastic change of plant species composition in southeastern floodplains would be expected to have significant impacts on these important ecosystems. Land managers are developing methods of privet control to conserve the biodiversity of southeastern floodplains. Although these strategies have proven successful at conserving aboveground biodiversity (Hanula and Horn, 2011a,b; Hanula et al., 2009), our study is the first to investigate the effects of privet and its removal on belowground diversity.

Other than the studies by Brantley (root biomass estimates [2008]) and Mitchell et al. (N mineralization assays and decomposition studies [2011]), there have been no studies of the effects of privet on belowground biotic communities or processes. This leads to the question of how privet invasion and its management via removal may affect soils and influence the earthworm communities in southeastern floodplain habitats. To address these questions, we quantified soil properties as well as earthworm abundance and community composition in sites with privet, sites where privet has been experimentally removed, as well as in sites that have not yet been invaded by privet. Objectives for this study were to evaluate the impact of privet invasion and privet removal on a suite of soil characteristics, and to determine the effects of privet management on the structure of the earthworm community in these riparian forests. We expect these results to provide further insight on the role of facilitation in invasion by specifically addressing the relationships between privet and soil properties and their interactions with native and exotic earthworms.

2. Methods

2.1. Site description

We utilized experimental privet-removal plots established by the U.S. Forest Service in 2005. These plots have been used to study the effects of privet removal on biodiversity in numerous studies. The site and the privet removal process are described in detail in Hanula et al. (2009). Briefly, the study design was a completely randomized block design with four blocks consisting of three experimental treatments. Each block consisted of two privet removal treatments and a control plot where existing privet was not treated in any way. The first privet removal treatment involved mechanical mastication of all vegetation <10 cm dbh with a tractor-mounted Gyrotrac® head (= "mulched" treatment hereafter). The second privet removal treatment involved hand-felling of all privet stems using power saws (= "felled" treatment hereafter), and the resulting slash was brush sawed to achieve a height above soil surface of <1 m. Both removal treatments involved herbicide application (glyphosate) following re-sprouting of privet stumps. The sites were located within the Oconee River watershed in northeast Georgia (Fig. 1). Plots were approximately 2 ha in size and contained similar levels of privet in the shrub and herbaceous plant layers prior to treatment. Three additional plots with minimal privet invasion were used as reference sites, considered to be representative of conditions prior to privet infestation, as well as reflective of the management objective for floodplains without privet. These reference sites were located on the Oconee National Forest near the Scull Shoals and Watson Springs treatment sites. Because of the difficulty associated with finding floodplain forest that has not been invaded by Chinese privet, reference sites were located some distance away from the blocks of treatment plots. As such, these sites may not be directly comparable to the treatment blocks, but we nevertheless included them in our analysis in order to have some form of "reference" to the desired condition for these floodplain forests. Importantly, the plots where privet removal treatments were applied were immediately adjacent to the untreated privet "control" plots, and thus are more comparable due to their proximity, and because they are situated on similar soils, with similar overstory vegetation and similar privet invasion history. Soils at the sites were variously classified as Fluvaquentic Dystrudepts, Fluvaquentic Endoaquepts, and Typic Udifluvents (series names Chewacla, Wehadkee, and Toccoa).

2.2. Earthworm sampling

Sample points were randomly placed in each quadrant of all plots. Earthworm sampling was performed every three months at each sample point beginning September 2010 with the final collection date in July 2011. Earthworms were collected by hand sorting 30 cm × 30 cm × 30 cm soil monoliths and were placed in a 70% ethanol solution to preserve them for later identification. At each sample date, the exact location of sampling pits was moved less than two meters from the original point to avoid sampling soil disturbed by previous digging.

Adult earthworms were identified to species using the keys of Schwert (1990), James (1990), and Reynolds (1978). Aclitellate worms were identified to genus or species based on key characteristics: namely the prostomium type, pigmentation, and setal arrangement. Aclitellate *Amynthas* and *Sparganophilus* could only be identified to genus, whereas aclitellate *Octolasion tyrtaeum*, *Diplocardia michaelsenii*, *Aporrectodea caliginosa*, *Eisenoides lonnbergi*, and *Lumbricus rubellus* could be identified to species.

2.3. Soil sampling

Soil samples were collected in September 2010 at all earthworm sample points to determine pH, mineral N, potential N-mineralization, and soil texture (% sand, silt, and clay). Samples were collected by taking multiple (6 or 8) 10 cm deep and 2 cm diameter soil cores around the earthworm sample points and compositing the cores for each point. Samples were kept in a cooler for transportation and were processed for potential N-mineralization

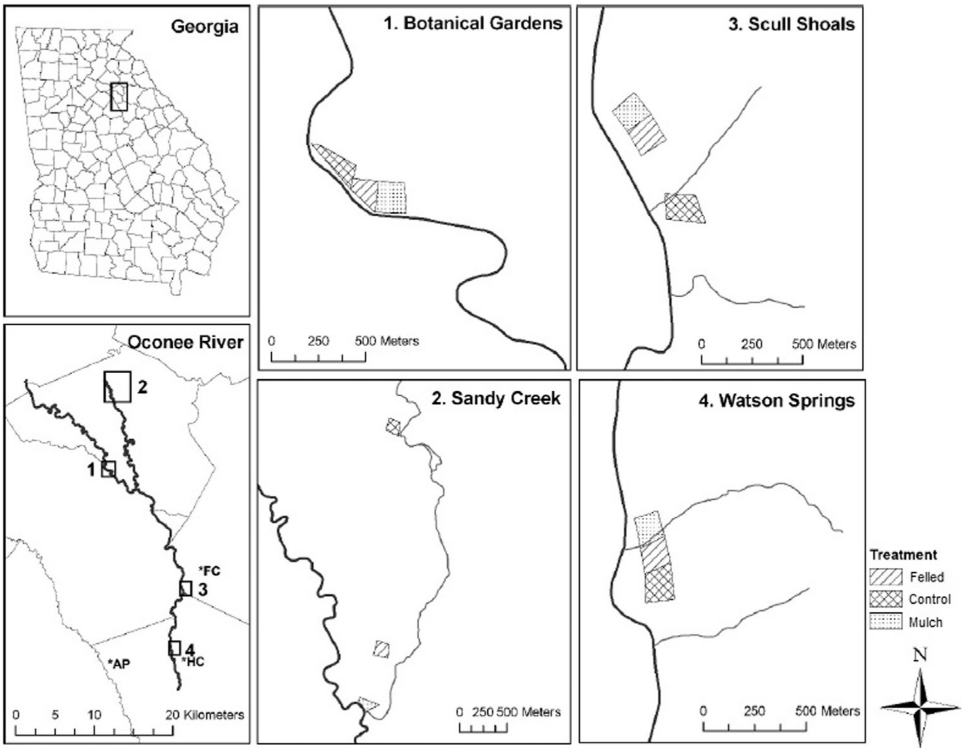

Fig. 1. Position of treatment plots within the upper Oconee river watershed in the State of Georgia in southeastern USA. The panel at bottom left shows the four treatment areas (smaller rectangles with numbers corresponding to the panels to the right), as well as the location of the three "reference" plots where no privet invasion had occurred (indicated by asterisks and AP, HC, and FC).

within 7 days. Soils collected in September were subsequently air-dried and analyzed within one year for pH and texture.

Each sample was passed through a 5 mm screen to break up large aggregates, after which sub-samples were taken. For the first site sampled in September, Watson Springs Forest, the sub-samples were 10 g of field moist soil each, but the sub-sample weight was increased to 20 g for all other samples to improve the homogeneity of samples. Four sub-samples of field moist soil from each sample were placed in 125 mL Erlenmeyer flasks. One of these four was extracted immediately by adding 50 mL of 2 M KCl and shaking for 1 h. The resulting suspension was then filtered (Watman 40) and stored frozen. The other three samples from each site were incubated for 21 days at 23 °C ± 3 °C in the dark before being extracted, filtered, and stored. Moisture contents varied among soils and were maintained at original levels if above 15%. Moisture loss was measured weekly during the incubation period and distilled water was added as necessary. For samples with moisture content below 15%, distilled water was added to reach and maintain this level. For soil samples collected in December, only one sample was incubated and soil-moisture content was maintained via automated humidity control in a growth chamber. Sub-samples were extracted and processed after 21 days of incubation as described above for initial extractions. The filtered extracts were measured colorimetrically for exchangeable NH_4^+ and NO_3^- using an autoanalyzer.

The pH of soil samples from all sampling sites was measured using a 1:1 soil to water solution with a pH meter. Sand, silt, and clay percentages were measured using the pipette method (Soil Conservation Service, 1984).

2.4. Statistical analysis

Abundances of adult and aclitellate earthworms for each species were grouped for analyses, except earthworms of the genus *Amynthas*, which were grouped together considering the dominance of *Amynthas corticis* and the low abundances of *A. agrestis* and *A. hilgendorfi*. Grouping the three species of this genus allowed the use of aclitellate *Amynthas* earthworms in analyses of total abundances. Although the original experimental design for this study was a completely randomized block design, we were unable to analyze data using this design structure due to failure to meet assumptions of parametric data analysis, despite several attempts at data transformation. Instead, a non-parametric Kruskall–Wallis ANOVA was used to analyze earthworm densities, as these were not normally distributed. Pairwise comparisons were accomplished using a Mann–Whitney test with sequential Bonferroni correction. Data for the N variables were log transformed and analyzed using the GLM procedure in SAS (Cary, NC). Multiple comparisons were performed with the PDIFF procedure. Polynomial regression was used for significant correlations of pH and earthworm species. All values are reported as means ± 1 standard error.

3. Results

3.1. Earthworm communities

Fourteen earthworm species were found over the course of the study (Table 1). The species originated from three continents: five species were native to North America, six were European lumbricids, and three were of the Asian genus *Amynthas*. Some species were found at very low densities, and two species were represented by a single specimen.

The average total earthworm abundances with standard errors ranged from 97.22 ± 23.35 to 154.51 ± 16.63 earthworms per m^2. Total earthworm abundances were similar between privet plots and the removal treatments, with abundances at reference plots being significantly lower. Overall, greater abundances of native earthworms were found in the reference and felled plots, and the lowest abundances of native earthworms were found in the privet

Table 1
Species of earthworms found over the course of the study. Density estimates are calculated as the total number of individuals of each species divided by the total number of pits excavated over the study period (240).

Species	Origin	Average density/m^2
Aporrectodea caliginosa	Europe	18.70
Diplocardia michaelsenii	North America	10.97
Octolasion tyrtaeum	Europe	8.70
Lumbricus rubellus	Europe	2.36
Amynthas cortisis	Asia	1.02
Eiseniella tetraedra	Europe	0.42
Bimastos longicinctus	North America	0.37
Amynthas agrestis	Asia	0.32
Sparganophilus sp.	North America	0.23[a]
Amynthas hilgendorfi	Asia	0.19[a]
Dendrobaena rubida	Europe	0.19[b]
Eisenoides lonnbergi	North America	0.09
Diplocardia singularis	North America	0.05[c]
Lumbricus terrestris	Europe	0.05[c]

[a] Found in only one pit.
[b] Found in a single treatment plot.
[c] One single earthworm.

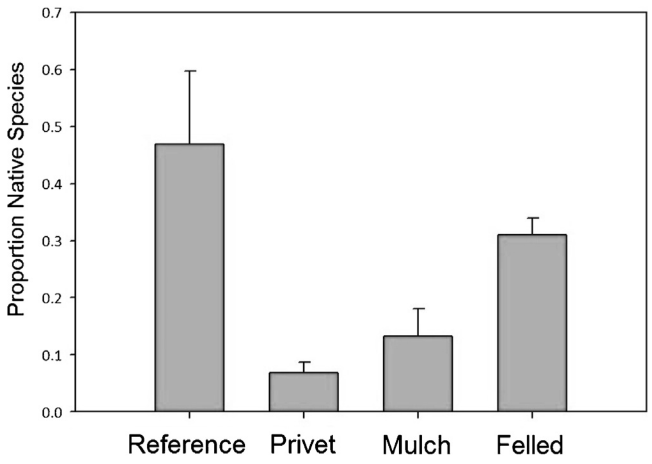

Fig. 2. Relative abundances of native earthworms, represented as the proportion of total earthworms found which are native. Bars are means and error bars are standard error.

plots. Conversely, higher abundances of exotic earthworms were found in the privet and mulched plots, with the lowest abundances in reference plots (Table 2). This was also reflected in the relative abundances of native and exotic species (Fig. 2) and the pattern was especially true for the two most common species, *A. caliginosa* and *D. michaelsenii*. In reference sites, the native *D. michaelsenii* dominated the community, but in privet sites its relative abundance was much lower. The European *A. caliginosa* was the most common species at privet sites, but was rare in reference sites (Fig. 3).

L. rubellus was another European species that was significantly less abundant in reference sites and was most abundant in the privet and mulch sites (Tables 2 and 3). *O. tyrtaeum*, another European lumbricid, had its greatest abundance in the felled sites. It is also notable that the epigeic Asian genus *Amynthas* significantly favored the reference sites, the opposite pattern of the most common epigeic species, *L. rubellus* (Tables 2 and 3). The native species *Bimastos longicinctus* and *Diplocardia singularis* were only found at the reference sites.

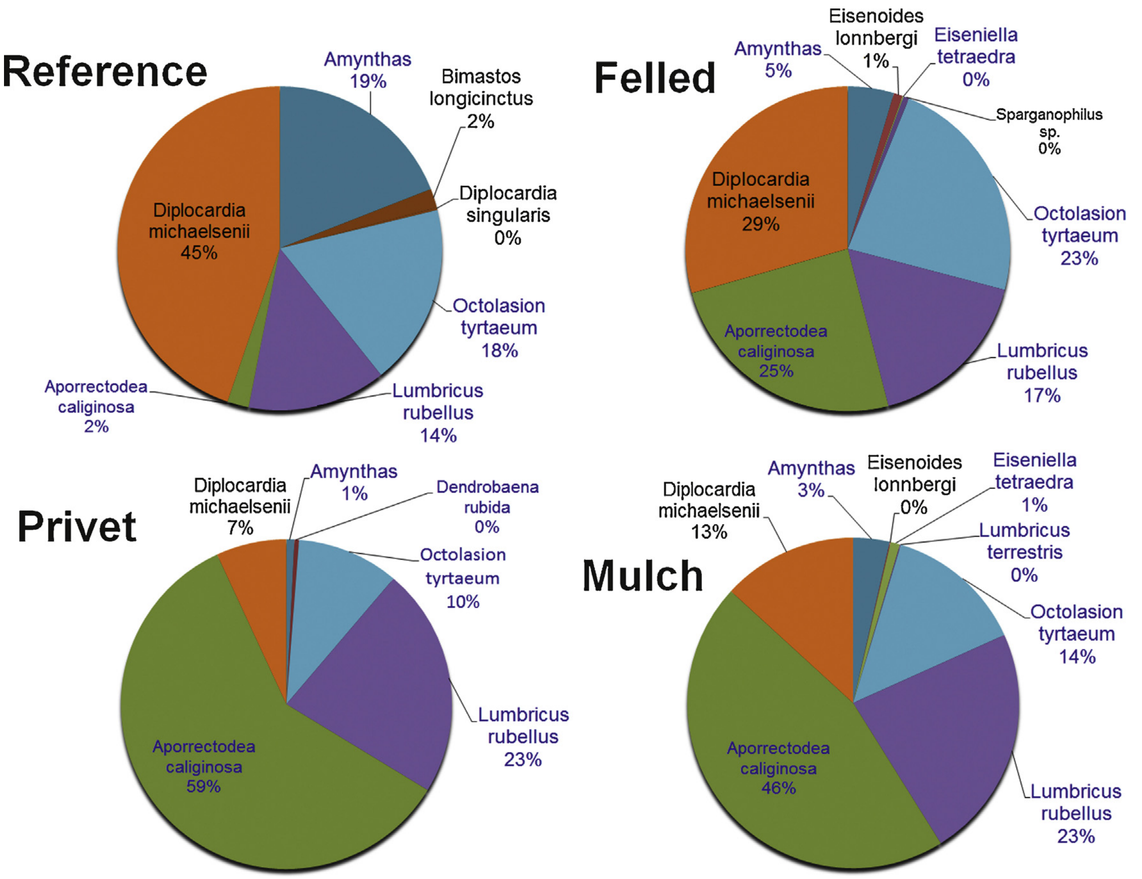

Fig. 3. Relative abundances of earthworm species for each treatment. Species denoted in black are native to North America, and species in blue are introduced from Europe or Asia.

Table 2
Earthworm species abundance (per m^2) by treatment. Different letters along rows represent significant differences of Kruskall–Wallis ANOVA ranked score means with Bonferroni corrections.

	Reference	Privet	Mulch	Felled
Total earthworms	97.22 ± 23.35 a	156.08 ± 14.48 b	171.18 ± 22.03 b	154.51 ± 16.63 b
Native earthworms	45.6 ± 12.4 a	10.76 ± 2.9 b	22.74 ± 4.97 ab	47.92 ± 7.31 a
Exotic earthworms	51.62 ± 12.33 a	145.31 ± 13.81 b	148.44 ± 20.77 b	107.81 ± 13.36 b
Aporrectodea caliginosa	2.08 ± 0.71 a	92.71 ± 10.51 c	78.13 ± 12.17 bc	38.19 ± 7.56 b
Diplocardia michaelsenii	43.52 ± 12.4 ab	10.76 ± 2.91 a	22.57 ± 4.98 ab	45.66 ± 7.2 b
Octolasion tyrtaeum	17.59 ± 6.56 ab	15.63 ± 5.22 b	23.26 ± 6.03 ab	35.59 ± 8.09 a
Lumbricus rubellus	13.43 ± 4.86 a	35.07 ± 7.27 b	39.06 ± 7.43 ab	26.22 ± 5.63 ab
Amynthas group	18.52 ± 5.1 a	1.22 ± 0.43 b	6.08 ± 2.05 b	6.25 ± 3.25 b

Table 3
Effects of treatment on earthworm species abundance.

	H	df	*p*
Total earthworms	16.81	3	0.0008
Native earthworms	19.86	3	0.0002
Exotic earthworms	25.73	3	<.0001
Aporrectodea caliginosa	65.84	3	<.0001
Diplocardia michaelsenii	18.33	3	0.0004
Octolasion tyrtaeum	8.71	3	0.0334
Lumbricus rubellus	9.90	3	0.0194
Amynthas group	22.78	3	<.0001

Table 4
Effects of treatment on the measured soil variables.

	F	df	*p*
Nitrogen mineralization (μg N/kg soil/28 days)	4.20	3	0.0095
Total available mineral nitrogen (μg N/g soil)	17.39	3	<.0001
Available NH_4^+ (μg N/g soil)	3.82	3	0.0147
Available NO_3^- (μg N/g soil)	6.44	3	0.0008
pH	2.60	3	0.0611

3.2. Soil properties

Measured variables for nitrogen were significantly different between treatments, while differences observed for pH were marginally significant ($p = 0.061$, Table 4). Available ammonium (NH_4^+) and nitrate (NO_3^-) concentrations were significantly lower at the reference sites than at the privet and privet removal sites (Fig. 4). Additionally, NO_3^--N concentrations were significantly higher at the mulch sites relative to the untreated privet sites, with felled sites having intermediate concentrations of NO_3^-. Potential N mineralization was also lowest at the reference sites (Fig. 5). The differences in pH, while marginally significant statistically ($p = 0.061$), did show relatively high pH at the privet sites (Fig. 6).

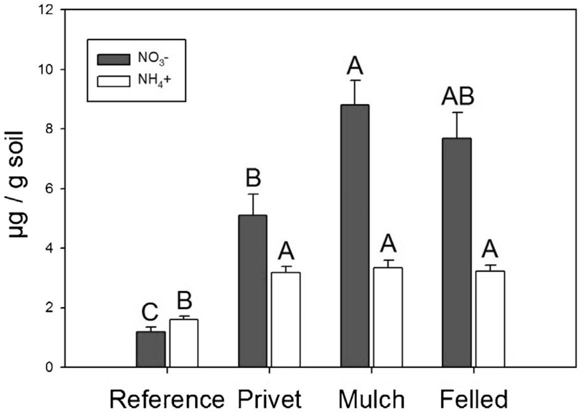

Fig. 4. Available mineral nitrogen (NH_4^+ and NO_3^-) of soils collected in the fall of 2010. Different letters represent significant differences of means at $p = 0.05$. Bars are means and error bars are standard error.

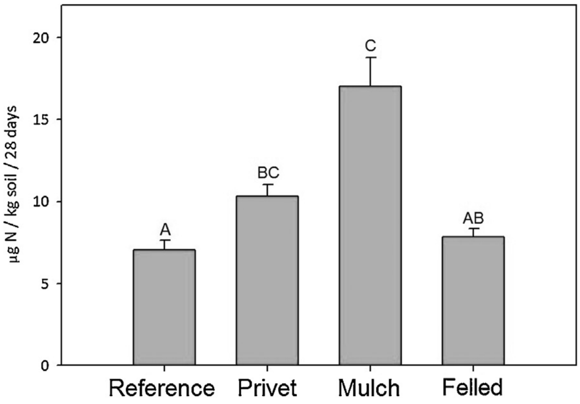

Fig. 5. Potential N-mineralization of soils collected in the fall of 2010. Different letters represent significant differences of means at $p = 0.05$. Bars are means and error bars are standard error.

A. caliginosa and *D. michaelsenii* had significant quadratic relationships with pH (Fig. 7). The soil texture varied across sites, but only reference sites had significantly sandier soils (data not shown).

4. Discussion

Results from our study confirm the pattern of greater earthworm densities observed by other researchers in systems invaded by non-native shrubs. Increased earthworm densities have been observed under other invasive plants known to increase soil N and pH and also to produce highly labile leaf litter with low C:N ratios (Aplet, 1990; Heneghan et al., 2007; Kourtev et al., 1999). Chinese privet has important similarities to these invasive plants as its leaf litter is of high quality, with a low C:N ratio relative to native leaf litter, and N-mineralization is stimulated in areas heavily infested with privet (Mitchell et al., 2011). We know of only

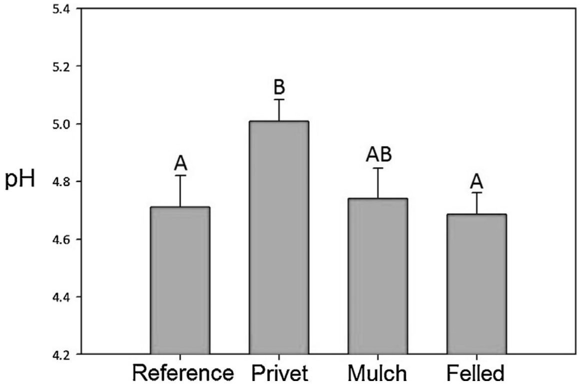

Fig. 6. Measured pH of soils collected in the fall of 2010. Different letters represent significant differences of means at $p = 0.061$. Bars are means and error bars are standard error.

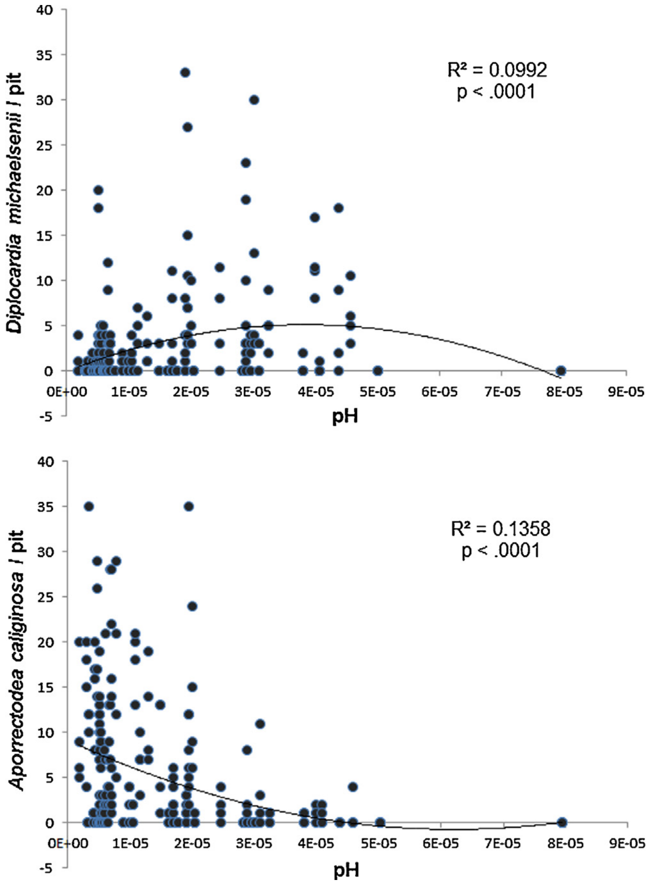

Fig. 7. Correlations between pH and *A. caliginosa* and *D. michaelsenii*. Note: with pH in this plot is expressed as H+ ion activity.

one other study where earthworm densities were evaluated following removal of invasive shrubs (Madritch and Lindroth, 2009). Madritch and Lindroth (2009) observed that exotic earthworm populations decreased following removal of buckthorn and honeysuckle, and this contrasts somewhat with results from our study, which showed that total earthworm densities remain elevated even five years after the removal of privet.

One potential explanation for the maintenance of earthworm numbers in our study could lie in the fact that the aboveground biomass of the invasive plants was removed in the Wisconsin study (Madritch and Lindroth, 2009), and there was no reestablishment of native vegetation. We suggest that this removal of organic matter from the system rapidly reduced the resources available for earthworms at those sites, and that this partly explains the subsequent decrease in earthworm abundance three years later. In our study, the privet biomass was left on site, and the way in which privet was treated seemed to have an effect on N dynamics. Among the four treatments, the mulch sites had the highest N-mineralization rates and inorganic NO_3^--N concentrations while the felled sites had N-mineralization rates comparable to reference sites. This difference between treatments probably existed because the privet mulch was much more readily decomposed (due to smaller particle size) and was incorporated into soil organic matter more quickly than the cut branches of the felled sites. It is also likely that most of the coarse fraction (e.g. >1 cm diameter branches) of material on the felled sites was washed downstream during floods in 2007 before they had a chance to decompose on site, although most of the leaves would have become available to decomposers in the first year following felling. The fact that the N dynamics in the removal treatment sites are different from the reference and privet sites shows a probable effect of the privet biomass that was reincorporated into the soil and represents a potential source of nutrients for the soil food web. The significantly higher earthworm abundances in the privet removal treatment plots, relative to the reference plots, provide evidence that the earthworms are able to use these resources, even five years after the privet removal.

The southeastern U.S. was not glaciated during the Wisconsinan Glaciation, and maintained a native earthworm fauna. It is also now home to European *Lumbricidae* as well as the Asian genus *Amynthas* (Callaham et al., 2003). This allows some insights into the relationships not only between exotic earthworms and invasive plants, but also native earthworms. Reference sites were found to have the greatest proportion of native earthworms while privet sites had the lowest. Here again it is worthwhile to note that our reference sites were somewhat removed from the sites where privet was treated, and that direct comparisons of these plots may be problematical due to differences in soil texture and perhaps in original nutrient status. Nevertheless, the comparisons of treated plots and untreated privet plots are more robust, given their proximity, and probably similarity at the outset of the experiment, and focusing on these treated and untreated sites reveals that many of the responses in our study are interesting regardless of comparisons to "reference" sites. For example, mulch and felled removal sites had greater proportions of native earthworms than privet sites, and since the total number of earthworms remained elevated after privet removal, this suggests a replacement of exotic species by natives following privet removal. Some of the measured soil variables could help to explain these results. Soil pH was significantly higher in privet sites than in the felled and reference sites. This is one important factor that could partially explain the species distributions, especially of the endogeics *A. caliginosa* and *D. michaelsenii*. Both of these endogeic species had significant quadratic relationships with the soil pH, displaying apparently different pH preferences. The range of pH of these soils is at the low end of *A. caliginosa's* preferred pH range, as soils with pH lower than 4.5 rarely contain *A. caliginosa* as a major component of the earthworm community in the species' native range in Germany (Römbke et al., 2005, 2012). Furthermore, the work of Lowe and Butt (2005) suggests that pH tolerances of *A. caliginosa* are in the same range as those reported by Römbke et al. (2005, 2012), and this lends support our hypothesis that pH lowering due to privet removal may partly explain the diminished importance of *A. caliginosa* in the removal plots. In contrast to *A. caliginosa*, the data collected in our study suggest that optimal pH for *D. michaelsenii* is well represented within the measured range of pH for the soils at our sites (e.g., Fig. 6, top panel). Similarly, *L. rubellus* and *O. tyrtaeum* are known to have broad niches with a tolerance for a wide range of conditions, including a wide range of soil pH (Jaenicke et al., 1980; Römbke et al., 2005). It is thus unsurprising that the abundances of these species did not show a relationship to pH and had similar relative abundances at all sites.

Some studies investigating the effect of increased nutrients on native and exotic earthworms have suggested that competition may play a role in reducing native earthworm abundance. In these studies, native species could successfully utilize additional nutrients, but they were competitively displaced by exotic earthworms in environments with increased nutrients (Huang et al., 2006; Winsome et al., 2006). Given the results of our study, we speculate that the privet-mediated changes to the pH favor some exotic earthworm species, but that at lower pH some native species may be able to successfully utilize the additional resources available from the privet biomass in the removal sites, even in the presence of exotic earthworms. Although more experimental work is clearly needed, we further speculate that these native species are not only able to use the additional resources, but they may even be able to competitively displace some exotic species at lower pH, as evidenced by decreased total and relative abundance of *A. caliginosa* at the felled and mulch sites. Alternatively, native species may simply be replacing the exotic species in these plots as soil conditions (specifically pH) return to conditions similar to those in soils not affected by privet. We recommend that these questions be addressed in future studies of the interactions between Chinese privet and earthworm communities in infested forests.

At the same sites used for this study, butterfly and bee diversity was found to increase after the removal of privet, with diversity and abundance returning to reference levels within one or two years (Hanula and Horn, 2011a,b). Similarly, this study showed that while earthworm abundances remained elevated even five years after privet removal, diversity was similar between treatment sites and reference sites. Not only did diversity increase after the removal of privet, but it was largely attributable to the recovery of native species. Felled sites actually had the highest total abundance of native earthworms, although reference plots still had the highest proportion of natives. Our results provide evidence that some native earthworm species can recover following the removal of an invasive plant. This result also supports the idea of a facilitative relationship between exotic earthworms and an invasive plant as some exotic earthworm species thrived under the conditions created by the privet, and seemed to lose their competitive advantage when it was removed. As suggested by Madritch and Lindroth (2009), targeting a key invasive species, such as privet, could benefit land managers by decreasing positive interactions between this key species and other exotics, and thus potentially short-circuiting the invasional meltdown process. Furthermore, as this study shows, native earthworm species have the potential to recover after the removal of an invasive plant despite the presence of exotic earthworm species.

Acknowledgements

The authors wish to acknowledge the land managers at Oconee National Forest, The State Botanical Garden of Georgia, and The Sandy Creek Nature Center for their cooperation in the establishment of the research plots. Scott Horn of the USDA Forest Service in Athens, Georgia, was instrumental in the planning and establishment of plots and in orienting personnel associated with this project. Becca Risser contributed substantially to the N-mineralization portion of the study. This work was supported by a cooperative agreement (SRS 09-CA-11330136-146) between the University of Georgia and the USDA Forest Service, Southern Research Station.

References

Aplet, G.H., 1990. Alteration of Earthworm Community Biomass by the Alien *Myrica faya* in Hawai'i. Oecologia 82, 414–416.

Asner, G.P., Beatty, S.W., 1996. Effects of an African grass invasion on Hawaiian shrubland nitrogen biogeochemistry. Plant Soil 186, 205–211.

Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M.A., Migge, S., Groffman, P.M., Parkinson, D., 2004. Non-native invasive earthworms as agents of change in northern temperate forests. Front. Ecol. Environ. 2, 427–435.

Brantley, E.F., 2008. Influence of Chinese privet (*Ligustrum sinense* Lour.) on Riparian Forests of the Southern Piedmont: Net Primary Productivity, Carbon Sequestration, and Native Plant Regeneration. Auburn University, Auburn, Alabama, USA.

Callaham, M.A., Gonzalez, G., Hale, C.M., Heneghan, L., Lachnicht, S.L., Zou, X.M., 2006. Policy and management responses to earthworm invasions in North America. Biol. Invasions 8, 1317–1329.

Callaham, M.A., Hendrix, P.F., Phillips, R.J., 2003. Occurrence of an exotic earthworm (*Amynthas agrestis*) in undisturbed soils of the southern Appalachian Mountains, USA. Pedobiologia 47, 466–470.

Darwin, C., 1881. The Formation of Vegetable Mould Through the Action of Worms: With Observations on Their Habits. Charles Darwin. J. Murray, London.

Edwards, C.A., Bohlen, P.J., 1996. Biology and Ecology of Earthworms. Chapman & Hall, London, UK.

Ehrenfeld, J.G., Kourtev, P., Huang, W.Z., 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecol. Appl. 11, 1287–1300.

Eisenhauer, N., Partsch, S., Parkinson, D., Scheu, S., 2007. Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. Soil Biol. Biochem. 39, 1099–1110.

Eisenhauer, N., Straube, D., Johnson, E.A., Parkinson, D., Scheu, S., 2009. Exotic ecosystem engineers change the emergence of plants from the seed bank of a deciduous forest. Ecosystems 12, 1008–1016.

Hale, C.M., Frelich, L.E., Reich, P.B., 2006. Changes in hardwood forest understory plant communities in response to European earthworm invasions. Ecology 87, 1637–1649.

Hanula, J.L., Horn, S., 2011a. Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. Forest 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., Horn, S., Taylor, J.W., 2009. Chinese privet (*Ligustrum sinense*) removal and its effect on native plant communities of riparian forests. Invasive Plant Sci. Manage. 2, 292–300.

Hendrix, P.F., 2006. Biological invasions belowground—earthworms as invasive species. Biol. Invasions 8, 1201–1204.

Hendrix, P.F., Callaham Jr., M.A., Drake, J.M., Huang, C.-Y., James, S.W., Snyder, B.A., Zhang, W.X., 2008. Pandora's box contained bait: the global problem of introduced earthworms. Ann. Rev. Ecol. Evol. Syst. 39, 593–613.

Heneghan, L., Steffen, J., Fagen, K., 2007. Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: Impact on leaf litter decomposition. Pedobiologia 50, 543–551.

Huang, C.Y., Gonzalez, G., Hendrix, P.F., 2006. The re-colonization ability of a native earthworm, *Estherella* spp., in forests and pastures in Puerto Rico. Caribb. J. Sci 42, 386–396.

James, S.W., 1990. Oligochaeta: Megascolecidae and other earthworms from southern and midwestern North America. In: Dindal, D.L. (Ed.), Soil Biology Guide. John Wiley & Sons, New York, pp. 379–386.

James, S.W., 1995. Systematics, biogeography, and ecology of neartic earthworms from eastern, Central, Southern, and Southwestern United States. In: Hendrix, P.F. (Ed.), Earthworm Ecology and Biogeography. CRC Press Inc., Boca Raton.

Jaenicke, J., Parker Jr., E.D., Selander, R.K., 1980. Clonal niche structure in the parthenogenetic earthworm *Octolasion tyrtaeum*. Am. Nat. 116, 196–205.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Kourtev, P.S., Huang, W.Z., Ehrenfeld, J.G., 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. Biol. Invasions 1, 237–245.

Lavelle, P., 2001. Soil Ecology/by Patrick Lavelle and Alister Spain. Kluwer Academic Publishers, Dordrecht; Boston.

Lee, K.E., 1985. Earthworms, their Ecology and Relationships with Soils and Land Use. Academic Press, Sydney.

Lowe, C.N., Butt, K.R., 2005. Culture techniques for soil dwelling earthworms: a review. Pedobiologia 49, 401–413.

Madritch, M.D., Lindroth, R.L., 2009. Removal of invasive shrubs reduces exotic earthworm populations. Biol. Invasions 11, 663–671.

Miller, J.H., 2003. Nonnative Invasive Plants of Southern Forests [Electronic Resource]: A Field Guide for Identification and Control/by James H. Miller. U.S. Dept. of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Mitchell, J.D., Lockaby, B.G., Brantley, E.F., 2011. Influence of Chinese privet (*Ligustrum sinense*) on decomposition and nutrient availability in riparian forests. Invasive Plant Sci. Manage. 4, 437–447.

Reynolds, J.W., 1978. The earthworms of Tennessee (Oligochaeta) IV. Megascolecidae, with notes on distribution, biology and a key to the species in the state. Megadrilogica 3, 117–129.

Römbke, J.J., Jänsch, S., Didden, W., 2005. The use of earthworms in ecological soil classification and assessment concepts. Ecotox. Env. Safe. 62, 249–265.

Römbke, J.J.S/, Roß-Nickoll, M., Toschki, A., Höfer, H., Horak, F., Russell, D., Burkhardt, U., Schmitt, H., 2012. Determination and Analysis of the Soil Quality in the Context of the Implementation and Further Development of the National Strategy on Biodiversity. ECT Oekotoxikologie GmbH, Dessau-Roßlau.

Schwert, D.P., 1990. Oligochaeta: *Lumbricidae*. In: Dindal, D.L. (Ed.), Soil Biology Guide. John Wiley & Sons, New York, pp. 341–356.

Simberloff, D., Von Holle, B., 1999. Positive interactions of nonindigenous species: invasional meltdown? Biol. Invasions 1, 21–32.

Soil Conservation Service, 1984. Soil Survey Laboratory Methods and Procedure for Collecting Soil Samples. Soil Survey Investigations, U.S. Department of Agriculture, Washington, DC.

Soule, M.E., 1990. The onslaught of alien species, and other challenges in the coming decades. Conserv. Biol. 4, 233–239.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Muellerdombois, D., Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238, 802–804.

Ward, R.W., 2002. Extent and dispersal rates of Chinese privet (*Ligustrum sinense*) invasion on the upper Oconee River floodplain, North Georgia. Southeastern Geographer. 42, 29–48.

Winsome, T., Epstein, L., Hendrix, P.F., Horwath, W.R., 2006. Competitive interactions between native and exotic earthworm species as influenced by habitat quality in a California grassland. Appl. Soil Ecol. 32, 38–53.