EFFECTS OF THE REMOVAL OF THE INVASIVE SHRUB, CHINESE PRIVET (*Ligustrum sinense*), ON SOIL PROPERTIES AND EARTHWORM COMMUNITIES

by

JOSHUA WAECHTER LOBE

(Under the Direction of Mac Callaham)

ABSTRACT

This study investigated the possibility of a facilitative relationship between Chinese privet (*Ligustrum* sinense) and exotic earthworms. Earthworms and some soil properties were sampled five years after the removal of privet, and were compared between sites with privet, privet removal sites, and reference sites where privet had never established. Introduced European earthworms were more prevalent under privet, and privet removal reduced their relative abundance in the community. Conversely, the relative abundance of native species was highest in reference sites. Soils under privet were characterized by significantly higher pH relative to reference plots. Privet removal facilitated a 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.

INDEX WORDS: Earthworms, Invasive plants, Native earthworms, Chinese privet, Mineral N, Exotic earthworms

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Invasive species are identified as being the second greatest cause of modern extinctions, trailing only habitat loss in that distinction (Soule 1990). As a major threat to biodiversity, it is important to understand the ecology of species invasions. 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 left earthworms less studied, despite being known as one of the most important creatures in the history of the world (Darwin 1881).

Earthworms have been called ecosystem engineers for their proclivity to create long-lasting ecosystem level impacts on the environment (Jones et al. 1994). They greatly influence nutrient cycling, soil formation, soil properties, germination of seeds, microbial communities, soil communities, and even aboveground communities (Lee 1985, Edwards and Bohlen 1996, Lavelle 2001). The most striking ecosystem effects due to exotic earthworms have been observed in regions where there are no native earthworms. In North America, areas north of the Wisconsin glaciation have been free of earthworms for about 12,000 years (Callaham et al. 2006). This includes Minnesota, where the introduction of earthworms has completely altered some forests. The arrival of earthworms in these forests obliterates the litter layer, incorporating it into the upper mineral soil. In forests without earthworms, the litter layer plays a crucial role in the ecosystem by serving as a protective bed for plants and theirs seeds and seedlings. With increased earthworm abundance, and especially *Lumbricus rubellus*, there is a corresponding drop in understory plant species richness (Hale et al. 2006). Earthworms are known to affect which plants emerge from the seedbank, and earthworm invasion could lead to a change in forest composition in other forests previously free of earthworms (Eisenhauer et al. 2009), as is being seen in Minnesota.

Not only do earthworms affect seedbank emergence, but their presence in formerly earthworm free areas can stress established trees. In New York, depletion of the litter layer and mixing of the soil by exotic earthworms has been shown to negatively affect arbuscular mycorrhizal colonization of sugar maples. This is a potential cause of the recently noted nutrient deficiencies of northeastern sugar maples (Lawrence et al. 2003). Earthworms can also reduce the drought tolerance of trees. Tree cores were used to accurately detect when a forest was invaded by earthworms based on the differential growth of the trees after earthworms invaded. These cores also showed that sugar maples were more sensitive to moisture after earthworm invasions. This was probably due to the earthworms' alteration of the soil hydrology and effects on the fine roots of the trees (Larson et al. 2010). Earthworms have been observed to increase the bulk density of the soil in formerly glaciated regions of North America as they mix the litter layer with the upper mineral soil, which likely causes the changes to water infiltration and runoff (Bohlen et al. 2004, Hale et al. 2005) leading to greater drought stress of the mature trees.

In New York, also north of the Wisconsin glaciation, the invasion of *Amynthas gracilis* and *Aporrectodea caliginosa* has altered soil properties in patches where the earthworms are found. Again, the earthworms mixed the upper layers of the soil, resulting in the disappearance of the litter layer. The quality of the soil organic matter, the pH, and the NO_3^- : NH_4^+ ratio increased in the presence of earthworms, creating favorable conditions for bacteria. This led to an increase in denitrification and a loss of soil C (Burtelow et al. 1998). These effects are consistent with those found in other studies (McLean and Parkinson 1997, Ozawa et al. 2005) (Kourtev et al. 1999).

Some of the best examples of the change that exotic earthworms can create in ecosystems do not just come from unintentional introductions. Exotic earthworms have been introduced intentionally in some places with the goal of harnessing the earthworms' system-altering abilities. Native earthworms did not fare well in pastures of exotic plants in New Zealand, so the pastures were successfully inoculated with the exotic *Aporrectodea caliginosa*. The earthworms broke up the accumulated thatch mats that had formed, increasing aeration and water infiltration. The result was a 25% increase in the long term carrying capacity of the pastures (Stockdill 1982). The same effects were realized in Dutch polder grasslands after the introduction of earthworms, with a 10% increase in the carrying capacity (Hoogerkamp et al. 1983).

Some ecosystems may be more immune to earthworm invasions than others. Disturbance is not necessary for earthworm invasions in the Great Lakes region (Tiunov et al. 2006), yet human activity is usually the main cause (Hale 2008, Seidl and Klepeis 2011). One example of this was in the mountains of Kentucky. Exotic earthworms were found at disturbed sites, while less disturbed habitats had more native earthworms. At the less disturbed sites, two native worms of the genus *Diplocardia* were much less affected by previous disturbance and were able to exist with exotic earthworms, unlike the other native species found (Kalisz and Dotson 1989). Similarly, in Brazil and Colombia, the common tropical exotic earthworm *Pontoscolex corethrurus* was found to coexist with native earthworms. The native earthworm populations were unaffected by the presence of *P. corethrurus* in forests, but there were less native species found in pastures. Statistical analyses showed that *P. corethrurus* responded to different soil factors than the native fauna. Conversion of land from forest to pasture elevated pH and soil N, and these conditions favored *P. corethrurus* and caused a decline in the native species (Marichal et al. 2010).

The elevated soil N could be the key to explaining the pattern of disturbed habitats favoring exotic species. Elevated N levels are a common result of human disturbance (Vitousek et al. 1997). An increase in resources could favor nonnative species and lead to competitive exclusion of native species. Evidence for this possibility was found in California grasslands, where the exotic species *Aporrectodea trapezoides* was found to thrive in nutrient rich pastures, while the native earthworm *A. marmoratus* was well established in nutrient poor native grassland, where *A. trapezoides* was not found. In the laboratory, both earthworms responded equally well to nutrient enrichment, suggesting that *A.trapezoides* was competitively displacing *A. marmoratus* in the nutrient rich pastures, and that possibly the reverse relationship existed in the nutrient poor grassland (Winsome et al. 2006). A similar distribution gradient was found in Puerto Rico where the exotic *P. corethrurus* was found in high numbers in pastures, but at low numbers in mature forests. No native earthworms were found in the pastures, but low numbers of multiple native species were found in the mature forests (Leon et al. 2003). Also in Puerto Rico, the native earthworm *Estherella spp.* was shown to survive equally well in mature forests and pastures in a field mesocosm experiment, suggesting that re-colonization of disturbed habitats by native species may be impeded by competition rather than changed soil properties (Huang et al. 2006).

Potentially aiding the invasion of exotic earthworms are positive and facilitative relationships with other nonnative invasive species. 'Invasional meltdown' is a hypothesis that one invasive species creates an environment favorable to another (Simberloff and Von Holle

1999). If increased resources promote the prevalence of exotic earthworms, then invasive plants could very well be the promoters of invasions. Many invasive plants are known to change soil properties, often increasing N levels in the soil (Vitousek et al. 1987, Asner and Beatty 1996). Increased earthworm densities have been found under diverse groups of invasive plants. *Myrica faya* is a nitrogen fixing tree introduced to Hawaii, where it thrives on the islands' nitrogen poor soils. Increased earthworm abundances were noted directly under individual trees, probably due to the increased nitrogen in the soil (Aplet 1990). *Microstegium vimineum*, an annual grass, and *Berberis thunbergii*, a shrub, are two nonnative invasive plants that are known to increase the pH of the soil (Kourtev et al. 1998). Increased earthworm densities were observed under both of these plants in conjunction with increased available nitrate and net potential nitrification in the soil. The plants did have relatively higher nitrate reductase activities in their leaves than native flora, showing they were better able to utilize the available nitrate than the native plants (Kourtev et al. 1999). Similar observations were made in Illinois with the invasive shrub European buckthorn (*Rhamnus cathartica*). This shrub is associated with higher total soil N and increased pH (Heneghan et al. 2006). Higher earthworm densities were also found in stands of *R. cathartica*. The leaf litter of *R. cathartica* was shown to have a higher relative N content than native litter, providing excellent food for the earthworms (Heneghan et al. 2007).

If the invasive plants and nonnative earthworms do have a facilitative relationship, it would be expected that the removal of one would lead to a decline of the other. This occurred after the removal of the common invasive plants of the Midwest, *R. cathartica* and *Lonicera x bella* (honeysuckle). Both of these plants produce high quality leaf litter and support greater earthworm densities relative to sites with native vegetation. After the aboveground biomass of the invasive plants was removed, earthworm densities declined by 50% and remained depressed for three years. However, the decline in earthworm abundance could be due to the removal of the understory and not the removal of the invasive plants (Madritch and Lindroth 2009).

The southeastern United States was not glaciated during the Wisconsin glaciation and therefore has a native earthworm fauna. It has also been invaded by European lumbricids as well as the Asian genus *Amynthas* (Callaham et al. 2003). The southeast 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). It escaped cultivation and is now well established in the southeastern U.S. and can be found from Texas to Maryland (Miller 2003). Like the invasive plants highlighted above, privet is known to have leaf litter of high quality, with lower lignin, cellulose, and C:N ratios relative to native leaf litter. This led to quicker decomposition of privet litter in floodplains of western Georgia (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 (Hanula et al. 2009). In the Upper Oconee River basin in northeast Georgia, privet now covers 59% of the floodplain (Ward 2002). This drastic change in plant species composition in southeastern floodplains would be expected to have significant impacts on these important ecosystems. In fact, the removal of privet has been shown to increase the diversity of understory vegetation (Hanula et al. 2009) as well as that of butterflies and bees found in the floodplain forest (Hanula and Horn 2011b, a).

Other than the studies by Brantley (2008) and Mitchell et al. (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 removal affect earthworm abundance, diversity, and the associated ecosystem processes in southeastern floodplain habitats. To address these questions, we quantified earthworm abundance and community composition in sites with privet, sites where privet has been removed, and sites that have not yet been invaded by privet. This allowed us to determine (1) if earthworm abundances increase following privet invasion, (2) if the expected increase in earthworm abundance is primarily due to an increase in exotic earthworm species, and (3) whether native earthworm species abundances recover following privet removal and (4) if differing earthworm abundances affect decomposition of privet litter. We expect these results to provide further insight on the theory of invasional meltdown as well as the relationships between invasive plants and their interactions with native and exotic earthworms.

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CHAPTER 2

DIFFERING RESPONSES OF NATIVE AND EXOTIC EARTHWORMS TO THE REMOVAL OF THE INVASIVE SHRUB, CHINESE PRIVET (*Ligustrum sinense*)

Invasive species are a major threat to biodiversity and the second greatest cause of modern extinctions (Soule 1990). Thus, it is important to understand how species invasions affect ecosystems. 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 left earthworms less studied, despite being recognized as one of the most important creatures in the history of the world (Darwin 1881).

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Some ecosystems may be more likely to host an earthworm invasion than others. Disturbance is not necessary for earthworm invasions in the Great Lakes region (Tiunov et al. 2006), yet human activity is usually the driving force of an earthworm invasion (Hale 2008, Seidl and Klepeis 2011). One example of this human influence of invasions was observed in the mountains of Kentucky where exotic earthworms were found at heavily disturbed sites while less disturbed habitats supported more native earthworms. At the less disturbed sites, two native worms of the genus *Diplocardia* were much less affected by previous disturbance than other native species and were able to coexist with exotic earthworms. Other native species in the study only inhabited sites with no previous disturbance and no exotic species present (Kalisz and Dotson 1989). Similarly, in Brazil and Colombia, the common tropical exotic earthworm *Pontoscolex corethrurus* was found to coexist with native earthworms. The native earthworm populations were unaffected by the presence of *P. corethrurus* in forests, but there were less native species found in pastures. Statistical analyses suggested that *P. corethrurus* responded to different soil factors than the native fauna. Conversion of land from forest to pasture elevated pH and soil N, and these conditions favored *P. corethrurus* and caused a decline in the native species (Marichal et al. 2010).

The elevated soil N could be the key to explaining the pattern of disturbed habitats favoring exotic species. Elevated N levels are a common result of human disturbance (Vitousek et al. 1997). An increase in resources could favor nonnative species and lead to competitive exclusion of native species. Evidence for this possibility was found in California grasslands, where the exotic species *Aporrectodea trapezoides* was found to thrive in nutrient rich pastures, while the native earthworm *Argilophilus marmoratus* was well established in nutrient poor native grassland, where *Ap. trapezoides* was not found. In the laboratory, both earthworms responded equally well to nutrient enrichment, suggesting that *Ap. trapezoides* was competitively displacing *Ar. marmoratus* in the nutrient rich pastures, and that possibly the reverse relationship existed in the nutrient poor grassland (Winsome et al. 2006). A similar distribution gradient was found in Puerto Rico where the exotic *P. corethrurus* was found in high numbers in pastures, but at low numbers in mature forests. No native earthworms were found in the pastures, but low numbers of multiple native species were found in the mature forests (Leon et al. 2003). Also in Puerto Rico, the native earthworm *Estherella spp.* was shown to survive equally well in mature forests and pastures in a field mesocosm experiment, suggesting that re-colonization of disturbed habitats by native species may be impeded by competition rather than changed soil properties (Huang et al. 2006).

Potentially aiding the invasion of exotic earthworms are positive and facilitative relationships with other nonnative invasive species. 'Invasional meltdown' is a hypothesis that one invasive species creates an environment favorable to another (Simberloff and Von Holle 1999). If increased resources promote the prevalence of exotic earthworms, then invasive plants could very well be the promoters of invasions. Many invasive plants are known to change soil properties, often increasing N levels in the soil (Vitousek et al. 1987, Asner and Beatty 1996) and increased exotic earthworm densities have been observed under many of these plants (Aplet 1990, Kourtev et al. 1999, Heneghan et al. 2007).

If the invasive plants and nonnative earthworms do have a facilitative relationship, it would be expected that the removal of one would lead to a decline of the other. This occurred after the removal of the common invasive plants of the Midwest, *Rhamnus cathartica* and *Lonicera x bella* (honeysuckle). Both of these plants produce high quality leaf litter and support greater earthworm densities relative to sites with native vegetation. After the removal of the aboveground biomass of these invasive plants, earthworm densities declined by 50% and remained depressed for three years. However, the decline in earthworm abundance could have been due to the removal of the understory and not the removal of the invasive plants (Madritch and Lindroth 2009).

The southeastern United States was not glaciated during the Wisconsin glaciation and therefore has a native earthworm fauna. It is also occupied by exotic European lumbricid earthworms as well as the Asian genus *Amynthas* (Callaham et al. 2003). The southeast 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). It escaped cultivation and is now well established in the southeastern U.S. and can be found from Texas to Massachusetts (Miller 2003). Like the invasive plants highlighted above, privet is known to have leaf litter of high quality, with lower lignin, cellulose, and C:N ratios relative to native leaf litter. This led to quicker decomposition of privet litter in floodplains of western Georgia as well as a fivefold increase of soil N mineralization (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 has occurred in the Upper Oconee River basin in northeast Georgia, where privet now covers 59% of the floodplain (Ward 2002). This drastic change of plant species composition in southeastern floodplains would be expected to have significant impacts on these important ecosystems.

Other than the studies by Brantley (2008) and Mitchell et al. (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 removal affect earthworm abundance, diversity, and the associated ecosystem processes in southeastern floodplain habitats. To address these questions, we quantified earthworm abundance and community composition in sites with privet, sites where privet has been removed, and sites that have not yet been invaded by privet. This allowed us to determine (1) if earthworm abundances increase following privet invasion, (2) if the expected increase in earthworm abundance is primarily due to an increase in exotic earthworm species, and (3) whether native earthworm species abundances recover following privet removal. We expect these results to provide further insight on the theory of invasional meltdown as well as the relationships between invasive plants and their interactions with native and exotic earthworms.

METHODS

Site description

We utilized experimental privet-removal plots set up 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 and the privet removal process is described in detail in past publications (Hanula et al. 2009). There are four study sites within the Oconee River watershed in northeast Georgia (Figure 1). These were selected based on their extensive privet infestations, access for machinery, and potential for public visitation and use in education and outreach programs. The sites were the Sandy Creek Nature Center (N33″ 59.167′ W083″ 22.865′) on the North Oconee River north of Athens; the Georgia State Botanical Gardens (N33″ 54.046′, W083″ 23.435′) on the Middle Oconee River south of Athens; the Scull Shoals Experimental Forest (N33″ 46.132′, W083″ 16.897′) on the Oconee River in the Oconee National Forest; and the University of Georgia's, Warnell School of Forest Resources' Watson Springs Forest (N33″ 41.908′, W083″ 17.695′) that is also along the Oconee River. Common overstory tree species in the treatment areas were ash (*Fraxinus* spp.), willow oak (*Quercus phellos* L.), sugarberry (*Celtis laevigata* Willd.), sycamore (*Platanus occidentalis* L.) and loblolly pine (*Pinus taeda* L.). Within each site, three homogeneous plots were located in areas with the heaviest privet infestation. Plots were approximately 2 ha in size and contained similar levels of privet in the shrub and herbaceous plant layers prior to treatment. All plots were located to provide at least a 10-m buffer of untreated area between the plot boundary and the stream bank to reduce stream edge effects and to minimize potential soil movement into the streams resulting from soil disturbance by heavy machinery.

Three additional plots with minimal privet were used as representatives of the forest type without privet as well as references for desired future conditions after privet removal. These were located on the Oconee National Forest near the Scull Shoals and Watson Springs treatment sites. These plots had similar overstory tree species as removal plots, but the shrub layer and herbaceous plant community were distinctly different. All plots were located at least 10 m from rivers or streams. One plot was located along Harris Creek (N33″ 41.503′, W083″ 16.714′) in Greene County, a second was adjacent to the Apalachee River (N33″ 39.463′, W083″ 22.363′) in Greene County and the third was next to Falling Creek (N33″ 46.977′, W083″ 14.668′) in Oglethorpe County, Georgia. Only the Falling Creek plot had detectable levels of privet with 1.4% privet shrub cover and 0.35% privet cover in the herbaceous layer (Hanula et al. 2009).

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. Sampling consisted of removing the litter layer from a 30 cm x 30 cm square to a flattened plastic garbage bag and searching the litter for earthworms. The cleared area was then dug to a depth of 30 cm and the $0.027m^3$ soil monolith was hand sorted in an attempt to find all earthworms in the pit. Earthworms 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, pigmentation, and setal arrangement. Aclitellate *Amynthas* and *Sparganophilus* could only be identified to genus, whilst aclitellate *Octolasion tyrtaeum*, *Diplocardia michaelsenii*, *Aporrectodea caliginosa*, *Eisenoides loennbergi*, and *Lumbricus rubellus* could be identified to species.

Soil Sampling

Soil samples were collected in September 2010 at all earthworm sample points to determine pH, total C and N, texture, and potential N-mineralization. Samples were collected by taking multiple 10 cm deep soil cores around the points and compositing the cores at each point, resulting in four samples per plot and 12 samples per site as well as four samples for each desired-future condition plot. Samples were kept in a cooler for transportation and were processed for potential N-mineralization within 7 days. Soils were subsequently air-dried and analyzed within one year for pH, texture, and C and N content.

Each sample was pressed through a 5mm screen to break up large clumps, after which sub-samples of each sample were removed. For the first site sampled in September, Watson Springs Forest, the sub-samples were 10g of field moist soil each, but the sub-sample weight was increased to 20g for all other samples to increase the homogeneity of the samples. Four sub-samples of field moist soil from each sample were placed in four 125mL Erlenmeyer flasks. One of these four was extracted immediately by adding 50mL of 2M KCl and shaking for 1 hour. The resulting suspension was then filtered through Whatman 40 filter paper and stored frozen. The suspension was measured for exchangeable NH_4^+ and NO_3^- colorimetrically with an AlpChem autoanalyzer**.** The other three samples from each site were incubated for 21 days at 23°C ±3ºC in the dark. 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. Sub-samples were extracted and processed after 21 days of incubation as described above for initial extractions. For soil samples collected in December, soil-moisture content was maintained in a growth chamber.

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). Total C and N were measured using a Carlos Erba model 1500 C/N analyzer (Milan, Italy).

Statistical Analysis

Abundances of adult and aclitellate earthworms for each species were grouped for analyses excepting earthworms of the genus *Amynthas*, which were grouped together considering the low abundances of *A. agrestis* and *A. hilgendorfi*. Grouping these three species allowed the use of aclitellate *Amynthas* earthworms in analyses of total abundances. A 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. Multiple comparisons were performed with the PDIFF procedure. Simple linear regression was used to for significant correlations. All values and plots are reported as means ± 1 standard error.

RESULTS

Earthworm Communities

Fourteen earthworm species were found over the course of the study. The species originate from three continents: five species were native to North America, six were European lumbricids, and three were of the Asian genus *Amynthas* (Table 1). Some species were found at very low densities, and two of the species were represented by a single earthworm. The average total abundances of the treatments 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. Felled sites had the highest calculated Shannon diversity index ($e^{H'}$), evenness (J'), and species richness while privet sites had the lowest values for these indices (Table 2).

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 plots. Conversely, higher abundances of exotic earthworms were found in the privet and mulched plots, with the lowest abundances in reference plots (Table 3). This was reflected by the relative abundances of native and exotic species between treatments (Fig. 1).   This pattern was especially true for the two most common species, *Aporrectodea caliginosa* and *Diplocardia michaelsenii*. In reference sites, the native *D. michaelsenii* was the most abundant species, comprising 45% of the earthworms found, but in privet sites it only made up 7% of the community (Figures 1&2). The European *A. caliginosa* was the most common species at privet sites, comprising 59% of earthworms found at these sites, while it was only 2% of the community in reference sites. The mulch and felled sites had intermediate relative abundances of these two species. In the mulch plots, *A. caliginosa* made up 46% of the community while *D. michaelsenii* made up 13% of the community. In the felled plots, the relative abundances were 25% for *A. caliginosa* and 29% for *D. michaelsenii* (Figures 3&4).

These percentages are based on total abundances of each species shown in Table 3. *D. michaelsenii* was similarly abundant in the felled and reference sites, while less abundant in the privet sites, although only privet and felled site abundances were significantly different (Table 4). Conversely, *A. caliginosa* was most abundant in the privet sites, and was least abundant in the reference sites. Felled sites also had significantly lower abundances of *A. caliginosa*. *Lumbricus rubellus* was another European species that was significantly less abundant in reference sites. This species had its highest abundances in the privet and mulch sites, where it made up 23% of the earthworm communities. *Octolasion tyrtaeum*, also a European lumbricid, was found to be most abundant in the felled site, and made up 23% of the community there. It is also worth noting that the epigeic Asian genus *Amynthas* significantly favored the reference sites. While making up 5% or less of the earthworm communities at the felled, mulch, and privet sites, the genus composed 19% of the community at the reference sites. This was the opposite pattern of the most common epigeic species, *L. rubellus*, which had its highest densities in the mulch and privet sites.

Significant differences in seasonal abundances of the populations were observed also (Table 5). Highest total abundances were observed during winter and spring with lowest abundances during the fall sampling (Table 6). Both native and exotic worms had significantly higher abundances in winter and spring than in summer and fall. This pattern was reflected by the commonly found European lumbricid, *A. caliginosa*, although differences of abundances between seasons for this species were not significant. For the most common native earthworm, *D. michaelsenii*, abundances for the winter and spring seasons were significantly higher than fall and summer. This was also true for *L. rubellus*, while *O. tyrtaeum* had similar abundances across all seasons. The *Amynthas* grouping had significantly lower abundances in winter than in the spring.

Soil Properties

Measured variables for nitrogen were significantly different between treatments, while differences observed for pH were nearly significant (Tables 7 & 8). Available and total mineral N concentrations were lowest at the reference sites. Although total mineral N concentrations were not significantly different between the privet sites and the removal treatments, the mulch site did have the highest concentrations (Table 8, Figure 6)). This difference was primarily due to differences in NO_3^--N concentrations as NH_4^+ -N concentrations were very similar between the privet and removal treatments, and twice as high as concentrations at the reference sites (Table 8, Figure 7). On the other hand, NO_3^--N concentrations were highest at the mulch and felled sites, and these concentrations, as well as those at the privet sites were significantly higher than at the reference sites. Potential N mineralization was also lowest at the reference sites, although only significantly lower than potential mineralization of the mulch sites (Figure 8). The differences in pH, while not significant (P=0.061), did show relatively high pH at the privet sites (Table 8, Figure 9).

Some soil properties were found to significantly correlate with earthworm species, although the correlations with the N related variables were limited to the fall season as this was when the soils were collected. *A. caliginosa* was found to have a positive relationship with N mineralization (Figure 10) as well as NO_3^- (Figure 11). *A. caliginosa* also had a negative relationship with H+ ion activity, or soil acidity (Figure 12). It was found at greater abundances with higher pH. *O. tyrtaeum* was found to have the strongest relationship with potential N mineralization of all the earthworm species, and it was positively associated with higher N mineralization rates (Figure 13).

DISCUSSION

It is not surprising that greater earthworm densities were found in sites where privet has invaded. Increased earthworm densities have been observed under other invasive plants known to increase soil N and produce highly labile leaf litter with low C:N ratios (Aplet 1990, Kourtev et al. 1999, Heneghan et al. 2007). Privet has similar qualities 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). This study showed that total earthworm densities remain elevated even five years after the removal of privet, however the species composition changes. This may seem to be in direct contrast to a similar study in Wisconsin, where the removal of invasive shrubs led to a decrease of exotic earthworms (Madritch and Lindroth 2009), but there are two important differences between the studies which highlight the key points of this study.

First, the aboveground biomass of the invasive plants was removed in the Wisconsin study. This rapidly reduced the resources available for earthworms at those sites and subsequently the earthworm abundance decreased 50% in three years. In this 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 and reincorporated into the soil than the cut branches of the felled sites. It is also likely that most of the branches were washed downstream during floods before they had a chance to decompose on site, although it would be expected that most of the leaves would have become available to decomposers. 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 treatment sites after privet removal provides evidence that the earthworms are able to use these resources, even five years after the privet removal.

The second difference of note between the studies is that Wisconsin does not have a native earthworm fauna, and all the earthworms in the study were exotics. The southeastern U.S. was not glaciated during the Wisconsin 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 and felled and mulch sites had intermediate proportions of native earthworms. Some of the measured soil variables could help to explain these results. The pH was significantly higher in privet sites than in the felled and reference sites. This is one important factor that could partially explain the higher relative abundance of European lumbricids, and especially the endogeic *A. caliginosa*, in the privet and mulch sites. The distribution of this species correlated negatively with increasing H^+ ion activity ($p<0.0001$, $R^2=0.1191$), showing a preference for higher pH. *Lumbricus rubellus* was also found at higher abundances in the mulch and privet sites (23% of total earthworms found at both), and while this species showed no significant correlation with pH in this study, it has previously shown a preference for higher pH (Irmler 2010). The increased soil N in the privet and removal treatment sites could also be an important factor favoring exotic earthworms. While correlations could only be made for earthworms found in the fall season when the N-mineralization was measured, the exotic species *A. caliginosa* ($p=0.0549$, $R^2=0.0621$) and *O. tyrtaeum* ($p=0.0062$, $R^2=0.1220$) showed weak correlations with N-mineralization.

Some studies investigating the effect of increased nutrients on native and exotic earthworms have suggested that exotic earthworms competitively displace natives in environments with increased nutrients (Huang et al. 2006, Winsome et al. 2006). This is a possible explanation for the earthworm distributions in this study. In reference sites, where N-mineralization and inorganic soil N content is lowest, native earthworms dominate the community. Where privet becomes established, N-mineralization, inorganic soil N, and the pH increase. These environmental conditions favor the European lumbricids, and especially the species with demonstrated preferences for the elevated pH, *A. caliginosa* and *L. rubellus*. When privet is removed, the pH seems to recover to pre-invasion levels more quickly than the N variables. While in the mulch site, N-mineralization and NO_3^--N concentrations are both higher than in privet sites, only the NO_3^--N concentrations are higher in the felled sites. Interestingly, native earthworms are twice as abundant in the felled sites than in the mulch sites and are equally abundant in the felled sites as in reference sites. This suggests that the increased soil N does not negatively affect the native species, and they are able to compete with the exotic earthworms when privet is removed from a site.

Seasonal distributions of earthworm species also showed some interesting results. Functional groupings seemed to play an important part in seasonal distribution for some earthworms. *L.rubellus* is an epigeic earthworm and was found to be most prevalent in the winter and spring. The endogeic lumbricids *A. caliginosa* and *O. tyrtaeum* showed no seasonal preferences. These could be related to moisture content of the soil, although that was not measured in this study. *Amynthas* had extremely low densities in the winter, exhibiting a different seasonal pattern than the other earthworms present in the study. It would seem it is less limited by moisture and heat than other species, and more limited by cold. A similar seasonal abundance pattern for *Amynthas agrestis* was also observed in north Georgia, where no earthworms were found in winter and the highest numbers of mature earthworms were found in September (Callaham et al. 2003).

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 2011b, a). While earthworm abundance remained elevated even five years after privet removal treatments, diversity indices were similar between treatment sites and reference sites. Not only does diversity increase after the removal of privet, but it is largely due to the recovery of native species. Felled sites actually have the highest average abundance of native earthworms, although reference plots still have the highest proportion of natives. This study provides evidence that the native earthworm species community can recover following the removal of an invasive plant. This result also supports the idea of 'invasional meltdown' as some exotic earthworm species thrived under the conditions created by the privet, and seemed to suffer 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. Furthermore, as this study shows, native earthworm species can potentially recover after the removal of an invasive plant despite the residual effects of privet on soil properties.

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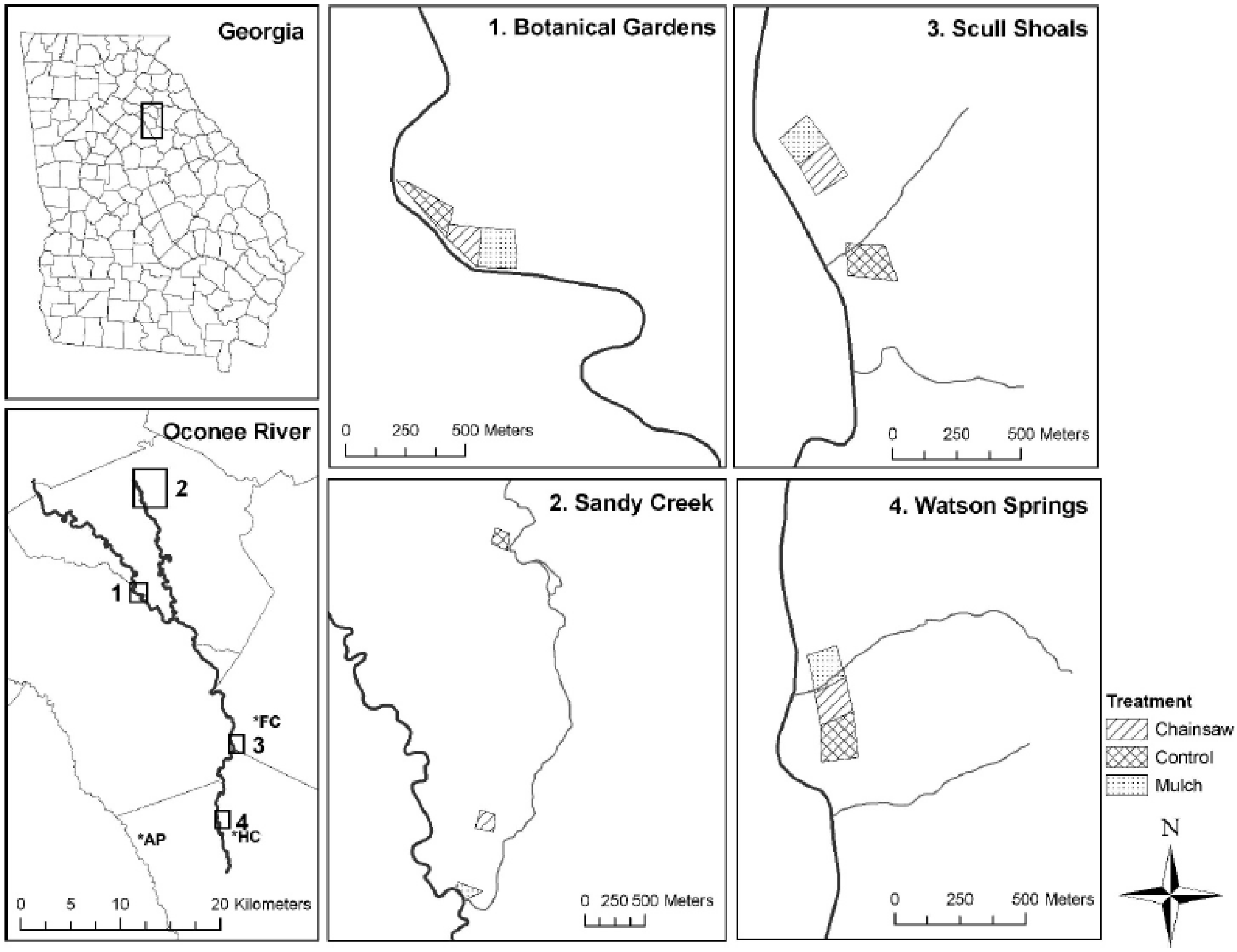

Figure 2.1 Maps showing the location of the study area in Georgia and the distribution of plots within each location. Desired-future condition plots on Harris Creek (HC), Falling Creek (FC), and Apalachee River (AR) are marked with asterisks.

Table 2.1 Species of earthworms found over the course of the study.

Species	Origin	Average Density / m²
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**
Amynthas hilgendorfi	Asia	0.19**
Dendrobaena rubida	Europe	0.19***
Eisenoides lonnbergi	North America	0.09
Diplocardia singularis	North America	0.05*
Lumbricus terrestris	Europe	0.05*

*One single earthworm
**Found in only one pit
***Found in a single treatment plot

Table 2.2 Total abundance and diversity of earthworms across all study sites. Different letters represent significant differences of Kruskall-Wallis ANOVA ranked score means with Bonferroni corrections.

	Total Earthworm Abundance / m²	Species Richness	Shannon Index $e^{H'}$	Evenness J'
Reference	97.22±23.35 a	7	4.181	0.6880
Privet	156.08±14.48 b	6	3.070	0.5394
Mulch	171.18±22.03 b	8	4.093	0.6777
Felled	154.51±16.63 b	8	4.774	0.7518

Mean total earthworm abundances for treatments with standard errors. Different letters represent significant differences of Kruskall-Wallis ANOVA ranked score means with Bonferroni corrections.

Figure 2.2 Relative abundances of native earthworms, represented as the proportion of total earthworms found which are native.

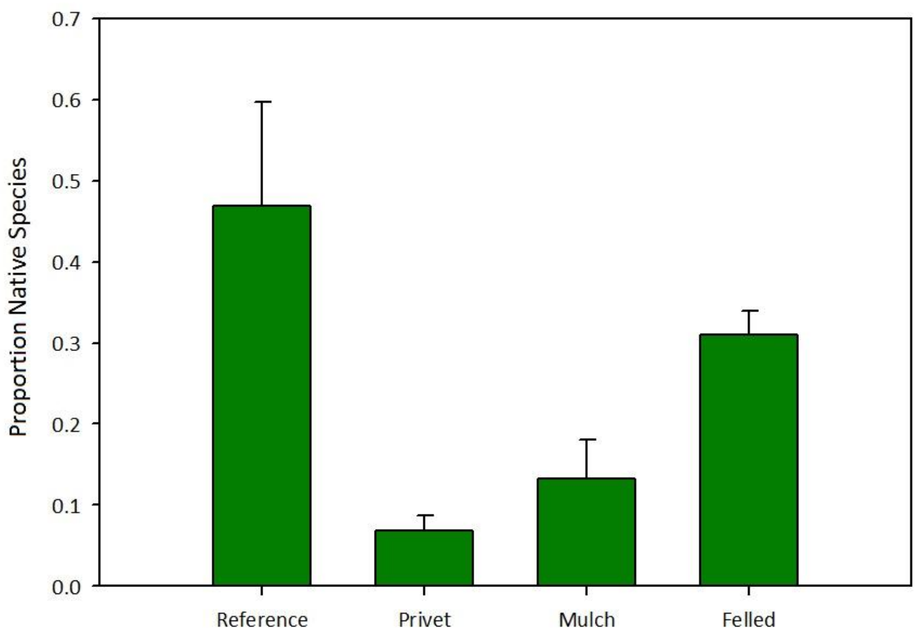

Table 2.3 Earthworm species abundance (per m²) by treatment. Different letters along rows represent significant differences of Kruskall-Wallis ANOVA ranked score means with Bonferroni corrections.

	Reference	Privet	Mulch	Felled
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 2.4 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

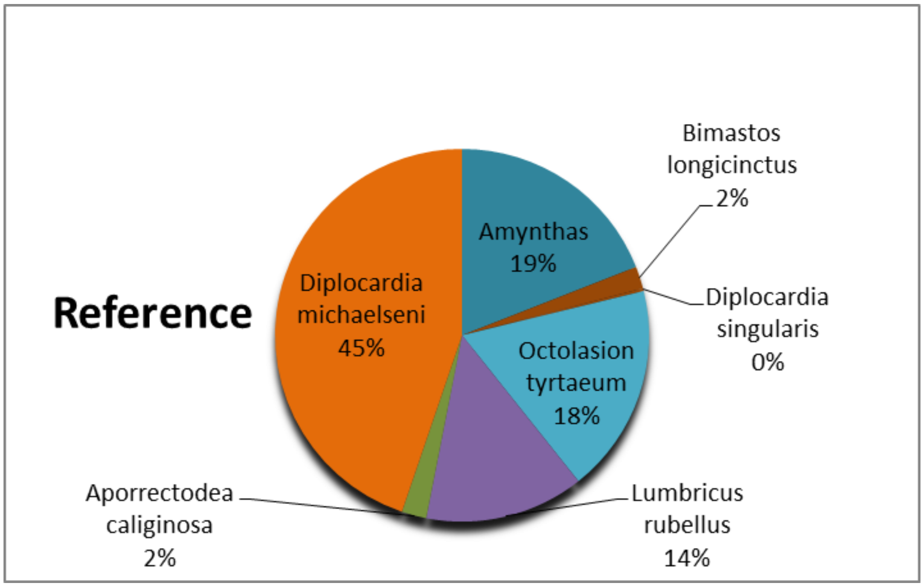

Figure 2.3 Relative abundance of earthworm species at reference sites.

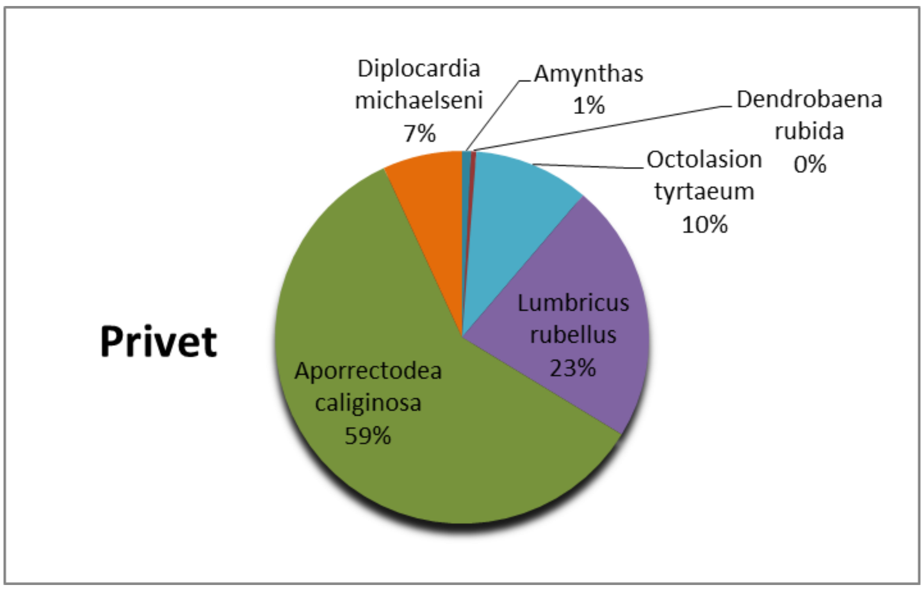

Figure 2.4 Relative abundance of earthworm species at privet sites.

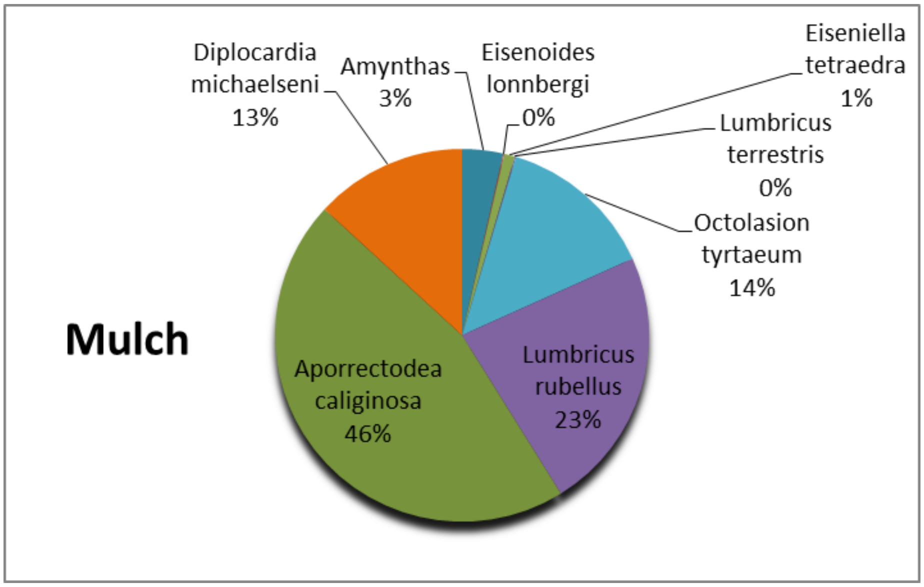

Figure 2.5 Relative abundance of earthworm species at mulch sites

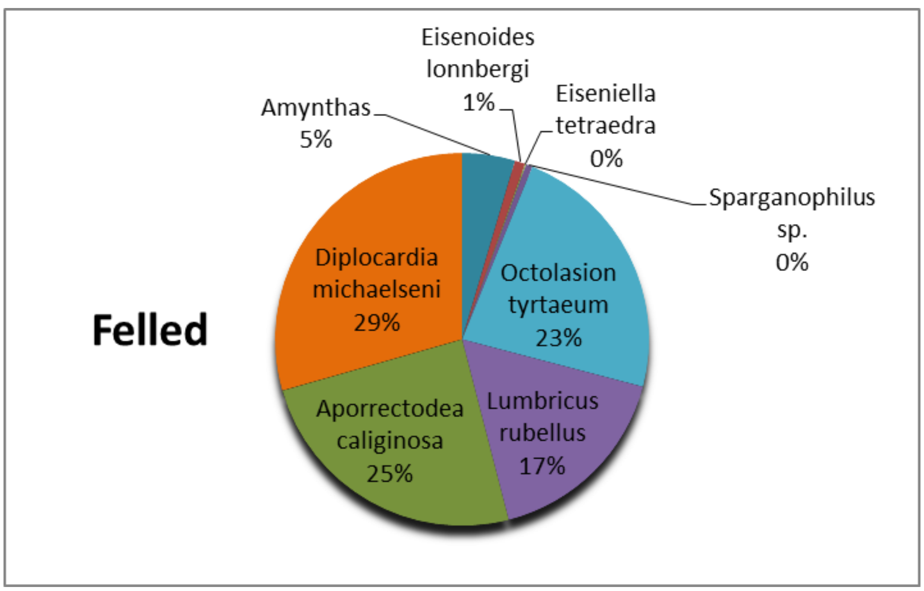

Figure 2.6 Relative abundance of earthworm species at felled sites

Table 2.5 Effects of season on earthworm species abundance.

	H	df	*P*
Total Earthworms	18.24	3	0.0004
Native Earthworms	13.64	3	0.0034
Exotic Earthworms	12.91	3	0.0048
Aporrectodea caliginosa	1.75	3	0.6263
Diplocardia michaelsenii	12.19	3	0.0068
Octolasion tyrtaeum	1.63	3	0.6532
Lumbricus rubellus	46.90	3	<.0001
Amynthas group	17.63	3	0.0005

Table 2.6 Earthworm species abundance (per m²) by season across all study sites. Different letters along rows represent significant differences of Kruskall-Wallis ANOVA ranked score means with Bonferroni corrections.

	Fall	Winter	Spring	Summer
Total Earthworms	99.44±14.63 a	171.85±20.40 ab	210.56±23.22 b	109.81±13.85 a
Native Earthworms	17.22±4.16 a	44.63±8.29 b	45.56±10.20 ab	15.93±3.15 a
Exotic Earthworms	82.22±13.60 a	127.22±17.51 ab	165.93±19.10 b	94.26±13.11 a
Aporrectodea caliginosa	50.93±10.23	66.30±12.09	63.70±10.91	43.70±7.82
Diplocardia michaelsenii	17.22±4.17 a	42.78±8.22 b	43.70±10.16 ab	15.37±3.10 a
Octolasion tyrtaeum	23.33±7.65	18.15±4.52	31.67±8.16	20.37±5.59
Lumbricus rubellus	1.67±0.58 a	41.85±7.04 bc	51.30±8.83 c	22.96±5.29 b
Amynthas group	6.30±2.45 ab	0.93±0.48 a	15.93±4.92 b	6.11±1.91 ab

Table 2.7 Effects of treatment on the measured soil variables.

	F	df	*P*
Nitrogen Mineralization (mg N / kg soil / 28 days)	4.20	3	0.0095
Total Available Mineral Nitrogen (mg / g soil)	17.39	3	<.0001
Available NH_4^+ (mg / g soil)	3.82	3	0.0147
Available NO_3^- (mg / g soil)	6.44	3	0.0008
pH	2.60	3	0.0611

Table 2.8 Measured soil variables by treatment, of soils collected in the Fall of 2010. Different letters represent significant differences of means of transformed data. Differences in pH were marginally significant (P=0.061).

	Nitrogen Mineralization (mg N / kg soil / 28 days)	Total Mineral Nitrogen (µg / g soil)	Available NH_4^+ (µg / g soil)	Available NO_3^- (µg / g soil)	pH
Reference	7.06±0.573 a	2.78±0.207 a	1.60±0.122 a	1.18±0.166 a	4.71 a
Privet	10.3±0.728 ab	8.28±0.655 b	3.17±0.221 b	5.11±0.714 b	5.01 b
Mulch	17.05±1.74 b	12.1±0.814 b	3.34±0.263 b	8.80±0.842 c	4.74 ab
Felled	7.86±0.509 a	10.9±0.865 b	3.24±0.204 b	7.69±0.859 bc	4.69 a

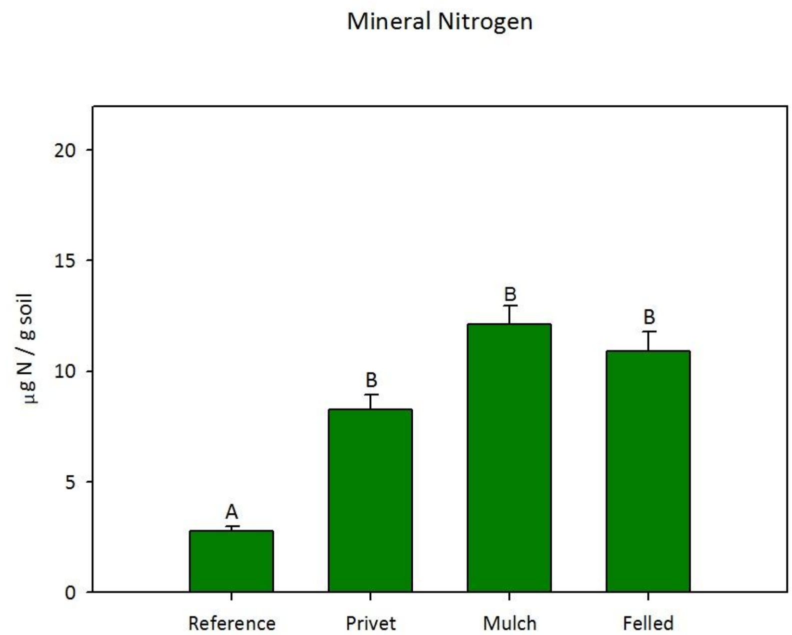

Figure 2.7 Total available mineral nitrogen of soils collected in the fall of 2010. Different letters represent significant differences of means at p=0.05.

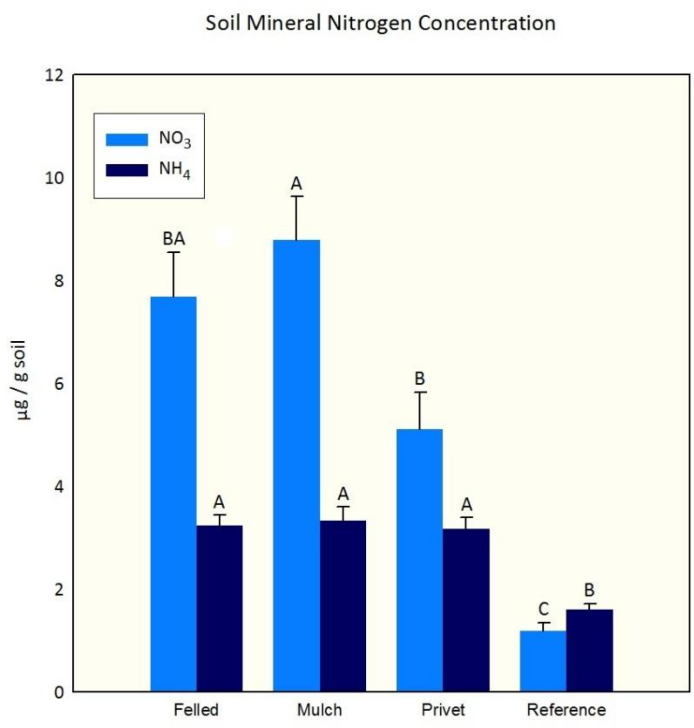

Figure 2.8 Available mineral nitrogen (NH_4^+ and NO_3^-) of soils collected in the fall of 2010. Different letters represent significant differences of means at p=0.05.

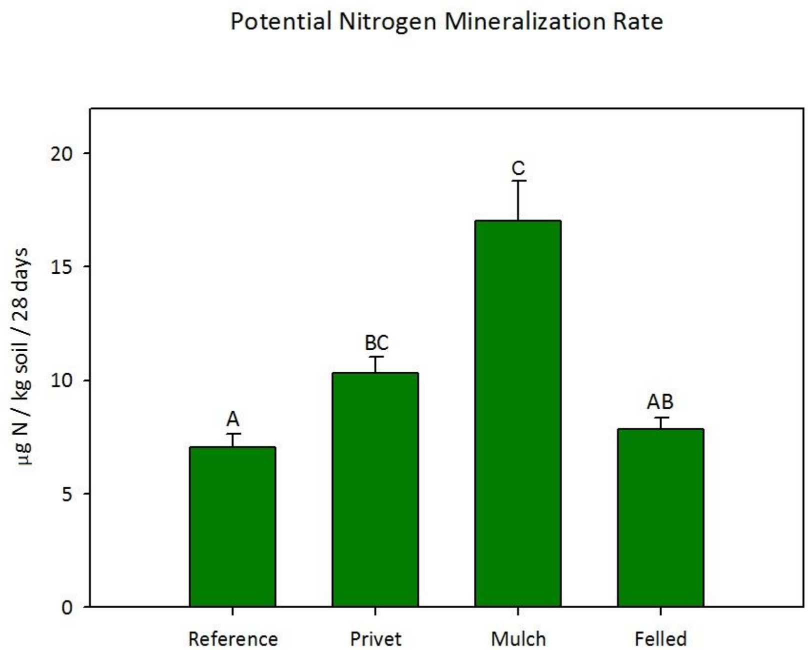

Figure 2.9 Potential N-mineralization of soils collected in the fall of 2010. Different letters represent significant differences of means at p=0.05.

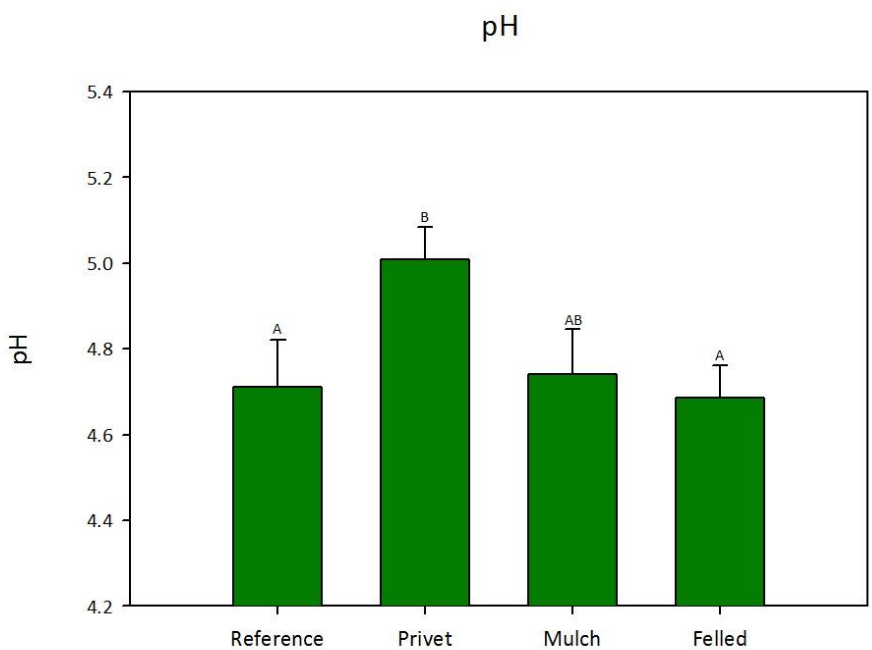

Figure 2.10 Measured pH of soils collected in the fall of 2010. Different letters represent significant differences of means at p=0.061.

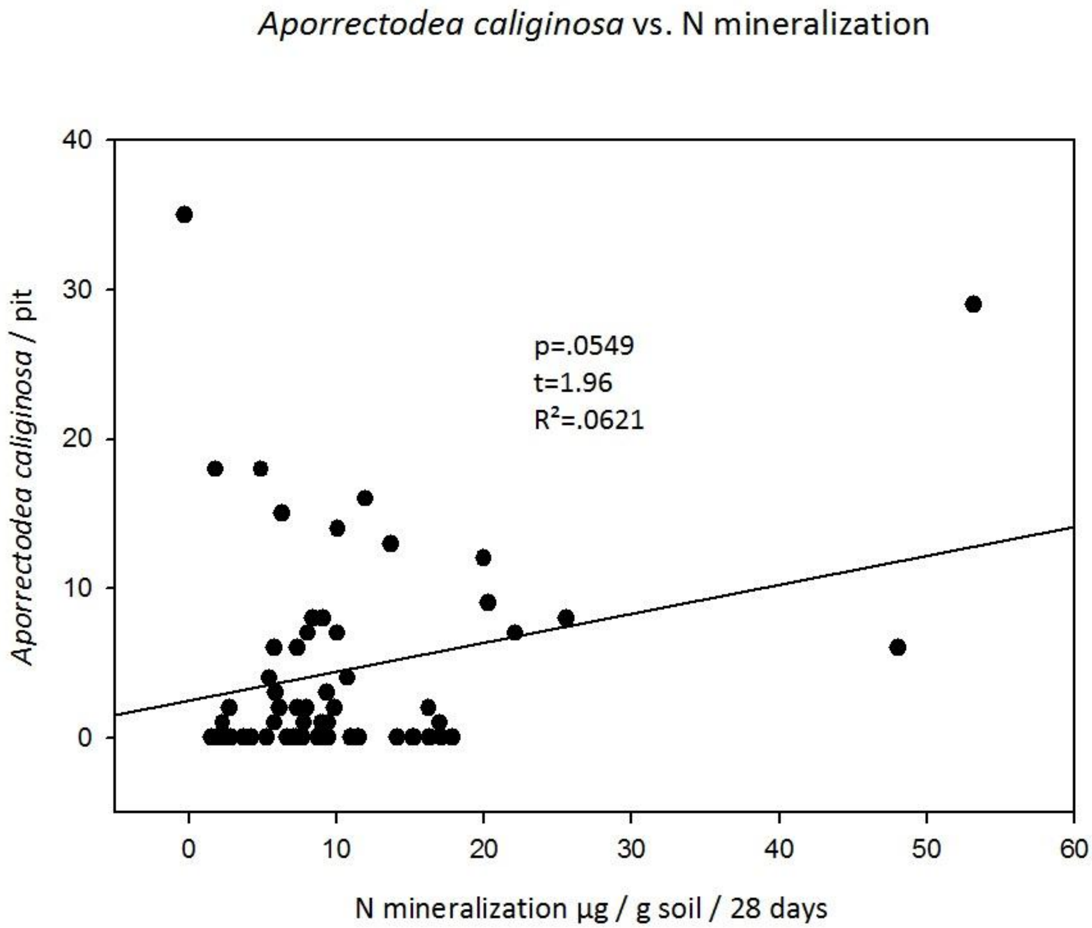

Figure 2.11 Correlation of *A. caliginosa* and potential N-mineralization in the fall of 2010.

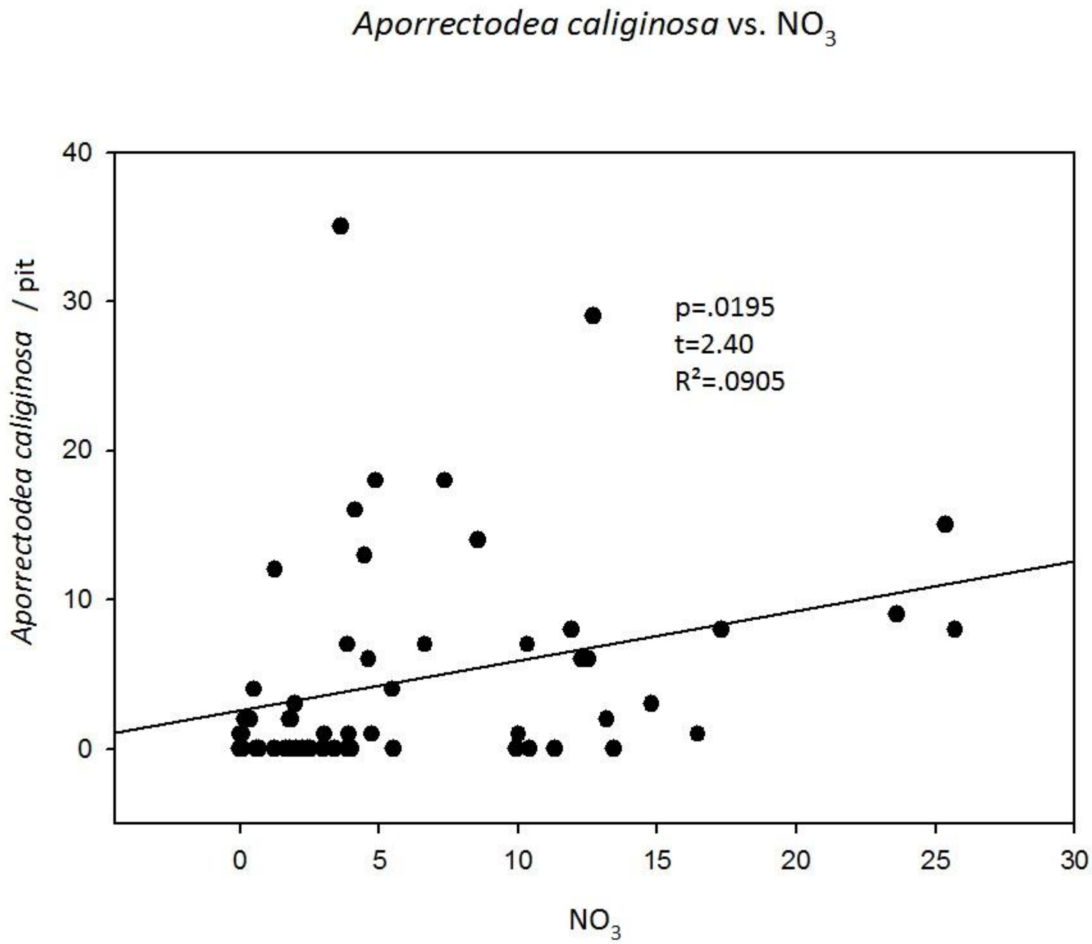

Figure 2.12 Correlation of *A. caliginosa* and NO_3^- in the fall of 2010.

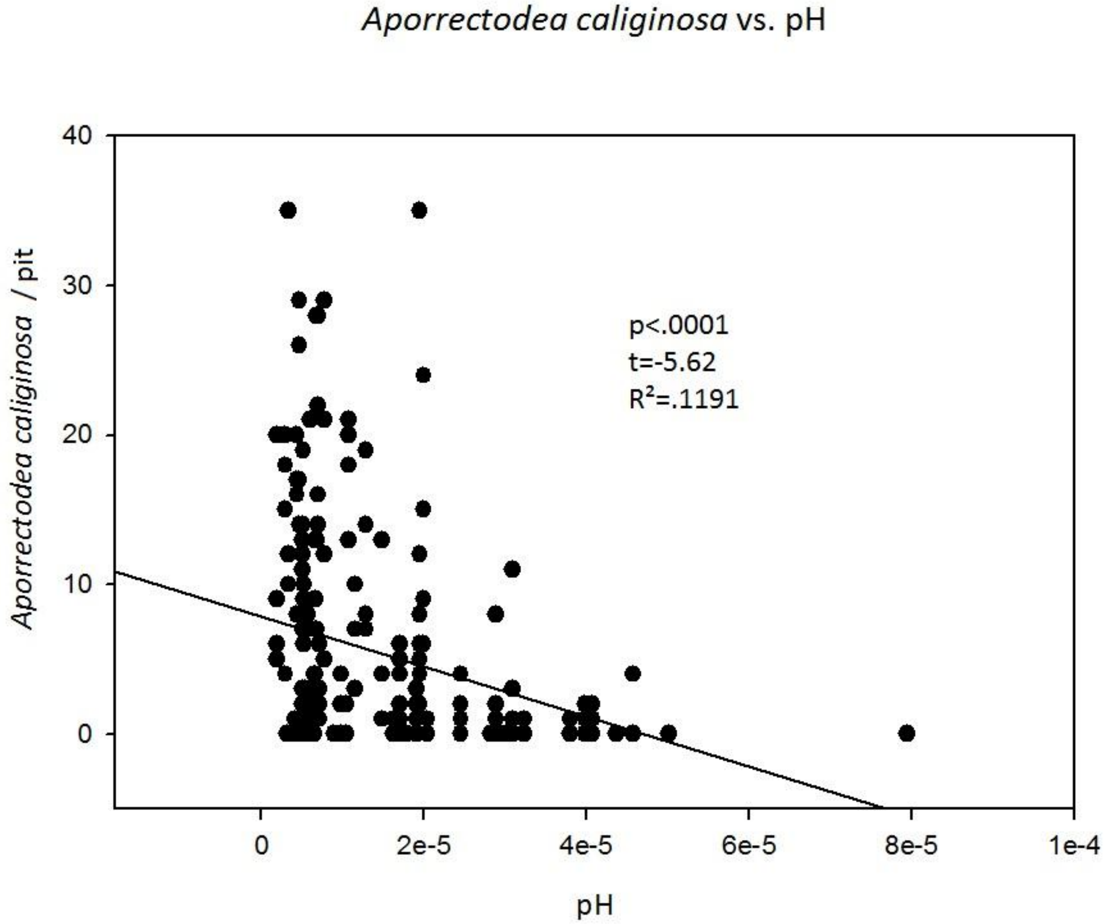

Figure 2.13 Correlation between *A. caliginosa* and pH, as H+ ion activity.

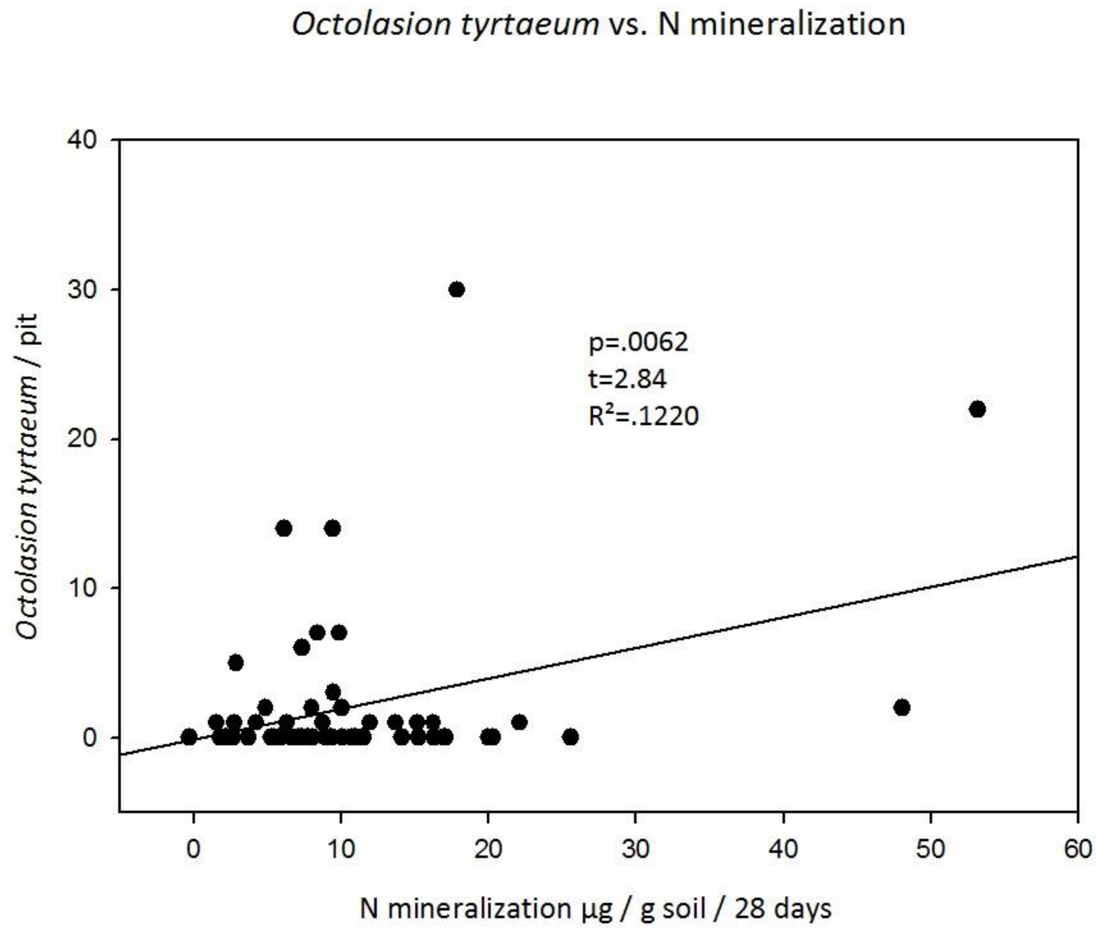

Figure 2.14 Correlation of *O. tyrtaeum* and potential N-mineralization in the fall of 2010.

CHAPTER 3

MACROINVERTEBRATE EFFECTS ON THE DECOMPOSITION OF PRIVET LITTER

Invasive species are identified as being the second greatest cause of modern extinctions, trailing only habitat loss in that distinction (Soule 1990). As a major threat to biodiversity, it is important to understand the processes involved in specific species invasions, especially since invasive species can cause major changes to ecosystems (Vitousek et al. 1987). Changes to soil properties and nutrient cycling caused by invasive species are especially important as these effects can last for a long time due to the long periods of time soil properties take to develop (Kourtev et al. 1999).

Many invasive plants are known to alter soil properties, often increasing N levels in the soil (Vitousek et al. 1987, Asner and Beatty 1996). Some common traits have been identified among invasive plants that alter nutrient stocks and fluxes. Among these traits is fast growth relative to native species, high litter N content, and a capacity to form a dominating ground cover (Ehrenfeld 2004). While these traits are often found in exotic invasives, this is not always the case. *Microstegium vimineum*, an annual grass, and *Berberis thunbergii*, a shrub, are examples of two nonnative invasive plants that have been shown to increase the pH of the soil, and *B. thunbergii* also increases soil NO_3^-. *M. vimineum* is unlike the shrub *B. thunbergii* in that its litter has low N content while *B. thunbergii* litter has high relative N content (Kourtev et al. 1998). Both of these plants were found to have relatively higher nitrate reductase activity in their leaves compared to native flora, showing they were better able to utilize the available nitrate than the native plants (Kourtev et al. 1999). Similar observations were made in Illinois with the invasive shrub European buckthorn (*Rhamnus cathartica*) where this plant is associated with higher total soil N and increased pH (Heneghan et al. 2006).

The changes to soil properties and plant communities that invasive plants effect are likely to alter nutrient cycling (Hooper and Vitousek 1998, Hector et al. 1999) , and for some invasive plants nutrient cycling seems to speed up. This is at least partially due to the plants' relatively labile leaf litter compared to native species. The leaf litter of *R. cathartica* was shown to have a higher relative N content than native litter, and it decomposed much more quickly than native leaf litter (Heneghan et al. 2007). Under *M. vimineum* and *B. thunbergii*, there was less leaf litter found on the soil than under native vegetation, providing evidence that the litter of these plants decomposes much more quickly than native plant litter. Interestingly, higher earthworm densities were found under the invasive plants as well (Kourtev et al. 1999). This increase of earthworms could be a result of higher quality litter being available from the invasive plants, while the earthworms could also be contributing to a feedback causing the litter to decay more quickly, providing more nutrients to the fast growing invasive plants. This potential feedback loop was also observed under *R. cathartica*, where increased earthworm densities were also observed (Heneghan et al. 2007).

The southeastern U.S. is host to Chinese privet (*Ligustrum sinense* Lour.), a highly invasive semi-evergreen shrub that was introduced in 1852 for ornamental purposes (Dirr 1983). It escaped cultivation and is now well established in the southeastern U.S. and can be found from Texas to Maryland (Miller 2003). 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 (Hanula et al. 2009). In the Upper Oconee River basin in northeast Georgia, privet now covers 59% of the floodplain (Ward 2002). As has occurred with similar invasive shrubs, the invasion of privet in southeastern floodplains would be expected to have significant impacts on nutrient cycling and soil processes in these important ecosystems. Like the invasive plants highlighted above, privet has leaf litter of high quality; with lower lignin, cellulose, and C:N ratios relative to native leaf litter. This led to quicker decomposition of privet litter in floodplains of western Georgia. In the same study, N-mineralization was found to be five times greater in heavily invaded sites than in non-invaded sites during the growing season (Mitchell et al. 2011).

The large-scale removal of privet in certain areas is one potential option to increase biodiversity, potentially restore ecosystem processes that may have been altered by privet, and even to improve recreational opportunities. The removal of privet has been shown to quickly restore understory plant, bee, and butterfly diversity to pre-invasion levels (Hanula et al. 2009, Hanula and Horn 2011b, a). The question remains as to how the removal of privet affects soil properties and processes.

This study aims to use litterbags to determine (1) if decomposition is affected by the removal of privet, and by using two different mesh sizes, (2) if macroinvertebrate access to litter affects privet decomposition differentially among treatments. The results will show the effects of large-scale removal of an invasive plant on N cycling and decomposition five years following the removal of the plant.

METHODS

Litterbag Study

Chinese privet litter was collected in late summer of 2010 by pulling fresh leaves off live branches. The litter was dried at 33˚C initially and then stored in a dry room. Approximately 3 grams of dried Chinese privet leaves were placed into two styles of litterbags. The smaller-mesh bags were made using a soldering iron to mold 1 mm mesh fiberglass screen into 15 cm x 15 cm pockets, while the larger-mesh bags, had 4 mm mesh to allow larger fauna to enter. One of the four sampling points used to sample earthworms was randomly selected to host the litterbags for each plot. The Sandy Creek site was not used for the litterbag study for logistical reasons. At least 15 of each style of litterbag were placed at the sampling points. Three litterbags of each type were collected after 1, 3, 7, 15, and 31 weeks. The contents were dried and weighed to determine mass loss. Litter was then ground in a Spex ball mill (Metuchen, NJ) and subsamples of the ground litter were ashed at 450°C for 4 h to determine percent ash-free dry mass. Corrections for soil contamination were required. Total percent carbon and nitrogen were determined on subsamples of the ground litter on a Carlos Erba model 1500 total C/N analyzer (Milan, Italy).

Statistical analysis

The GLM procedure of SAS was used to analyze differences between treatments for percent mass remaining and the k values for instantaneous decay rates, both overall and by each date. All values and plots are reported as means ± 1 standard error.

RESULTS

There were no significant differences between treatments for percent mass remaining or k values of the decay rates of privet leaves for either mesh size. While differences among treatments were not significant, the average k values for reference sites and mulch were very similar, as were the k values of the privet and felled sites. This pattern was true for both mesh sizes (Table 1). Litter decay rates did show a general pattern similar for both mesh sizes, although only small mesh litterbags at the reference sites had smaller decay rates at the first collection than at the second (Figs 1 and 2). Litterbags collected on day 21 generally had lower k values than other collection dates, while litterbags collected on day 49 had higher k values, although these differences were not significant. Large mesh litterbags did lose more litter over the course of the study (Figs 3 and 4). The proportion of litter remaining (± SE) at day 217 ranged from 0.27±0.05 to 0.34±0.04 in large mesh litterbags and 0.40±0.07 to 0.45±0.08 in small mesh litterbags (Table 2).

DISCUSSION

Chinese privet has been shown to decompose faster than native riparian vegetation in Georgia (Mitchell et al. 2011). Mass loss in this study was comparable to the study performed by Mitchell et al (2011) even though only privet litter was used for this study. Privet litter is similar to other invasive shrubs which are favorable to higher earthworm densities (Kourtev et al. 1999, Heneghan et al. 2007), containing higher levels of N than native litter, and it decomposes quickly. Earthworms are known to play a major role in decomposition, and are suspected of increasing decomposition rates of low quality litter (McDonnell et al. 1997, Pouyat and Carreiro 2003). Thus differences in earthworm densities could have significant impacts on the rate of decomposition.

This study showed no differences for either decomposition rates or percent mass remaining between treatments for either large or small mesh litterbags. This was unexpected, as a similar litterbag study showed increased decomposition under buckthorn where higher densities of earthworms were present. The differences were especially pronounced in the large mesh litterbags designed to allow earthworms access to the leaf litter (Heneghan et al. 2007). In this study, differences were expected as earthworm densities and soil N-mineralization differed among treatments (Chapter 2). Earthworm densities were significantly lower in reference sites, but decomposition rates and percent mass remaining were not different between reference and the other study sites.

One potential explanation for this lack of observed difference is that the soil differences between these sites are not important to the decomposition process that occurs at the soil surface, and therefore do not affect the decomposition rates of the litterbags. This is supported by a litterbag study in which litter decomposition was correlated with soil organic matter and moisture, but not biological or chemical characteristics of the soil (Pavao-Zuckerman and Coleman 2005). Additionally, differences among the treatment sites may have been minimized as the litterbag study was conducted five years following privet removal, providing enough time for the privet biomass to be incorporated into the soil or removed from the site during a flood. However, this would not explain the lack of differences of decomposition rates between privet sites and the privet removal sites. Given the uniformly high resource quality of the privet litter used across all sites, it is likely that the dominant variables driving decomposition were micro-climatic conditions (i.e., temperature and soil moisture; (Swift et al. 1979) which were not measured in this study but which may have been similar in these forested, bottomland habitats. Future studies should include the use of data loggers to make continuous measurements of these variables.

To conclude, the decomposition process of high quality litter at the soil surface does not seem to be affected by soil characteristics that are affected by the removal of privet. The high quality privet litter decomposes at equal rates at all sites, even with differing earthworm densities.

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Table 3.1 Average k values (± SE) of litter decay by treatment and mesh size, calculated for weeks in the field.

	Reference	Privet	Mulch	Felled
Large	0.0553±0.0088	0.0668±0.0119	0.0549±0.0111	0.0659±0.0112
Small	0.0329±0.0068	0.0434±0.0056	0.0394±0.0042	0.0429±0.0064

Table 3.2 Average proportion (± SE) of litter remaining at day 217.

	Reference	Privet	Mulch	Felled
Large	0.3367±0.0385	0.2789±0.0803	0.3273±0.1112	0.2700±0.0465
Small	0.4297±0.0145	0.3960±0.0709	0.4344±0.1058	0.4541±0.0772

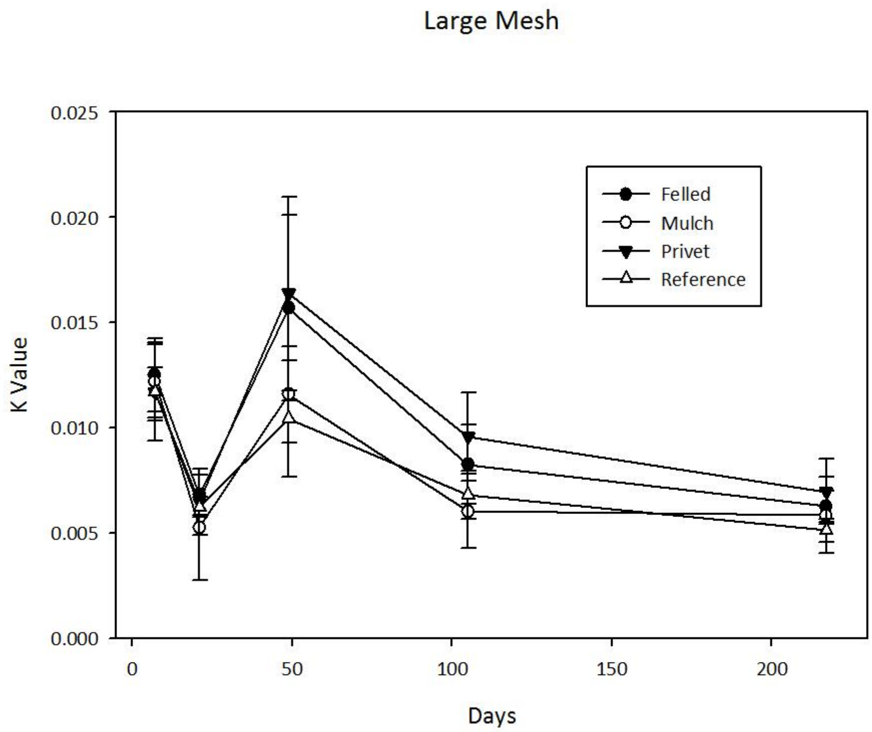

Figure 3.1 K values of large mesh litterbags.

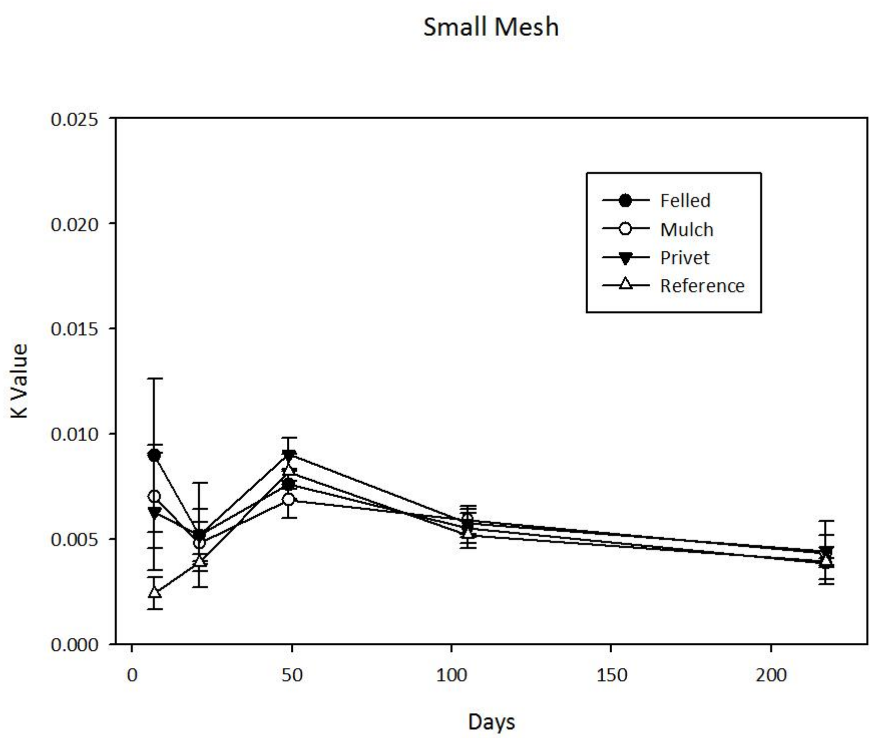

Figure 3.2 K values of small mesh litterbags.

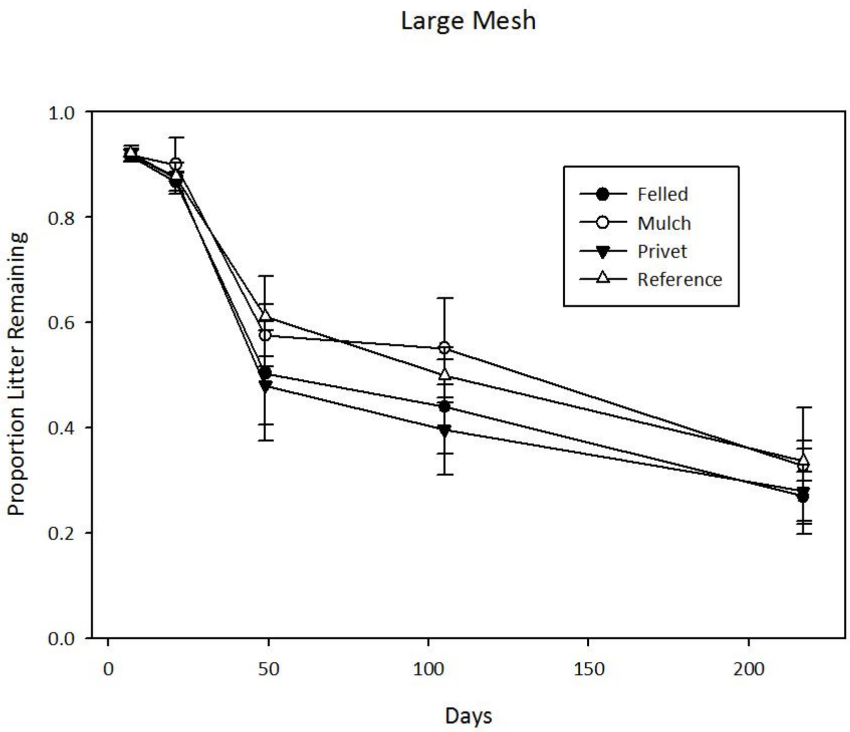

Figure 3.3 Proportion of mass remaining for large mesh litterbags.

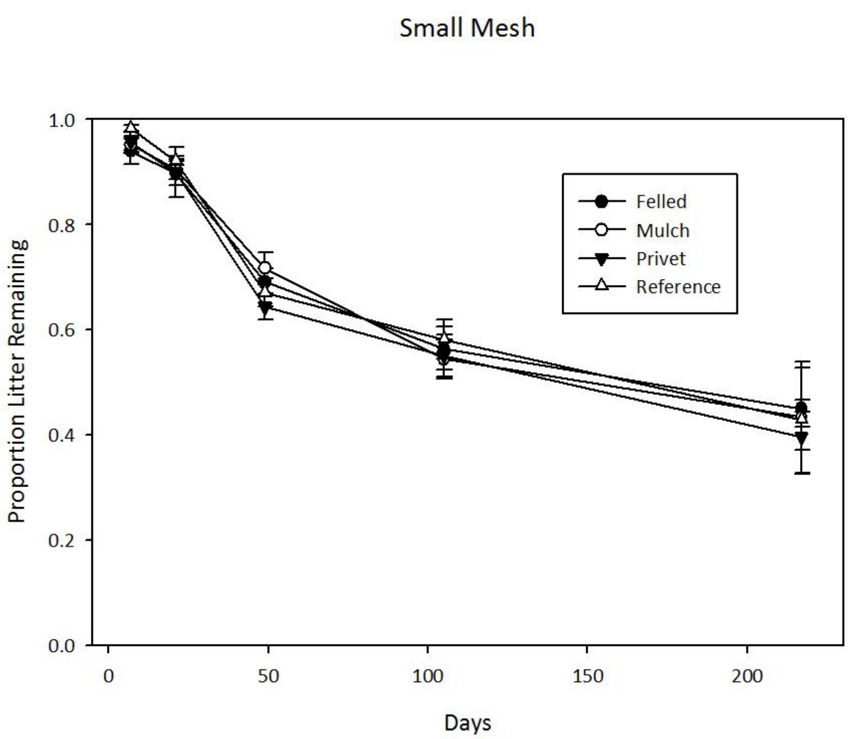

Figure 3.4 Proportion of mass remaining of small mesh litterbags.

CHAPTER 4

CONCLUSIONS

Chinese privet is an invasive species of great concern in the southeast where it frequently becomes the dominant vegetation cover in riparian zones(Ward 2002). Privet shares traits with other invasive plants (Aplet 1990, Kourtev et al. 1999, Heneghan et al. 2007) which could greatly alter ecosystem processes in riparian zones where it invades (Vitousek et al. 1987). Very few studies (Brantley 2008, Mitchell et al. 2011) have investigated the effects of privet on belowground biotic communities or processes. This study aimed to answer the questions of how privet invasion and its removal affect earthworm abundance, diversity, and the associated ecosystem processes in southeastern floodplain habitats. To address these questions, we quantified earthworm abundance and community composition in sites with privet, sites where privet has been removed, and sites that have not yet been invaded by privet. This allowed us to determine (1) if earthworm abundances increase following privet invasion, (2) if the expected increase in earthworm abundance is primarily due to an increase in exotic earthworm species, and (3) whether native earthworm species abundances recover following privet removal and (4) if differing earthworm abundances affect decomposition of privet litter.

Chapter two focuses on the effects of privet, and the large scale removal of privet, on soil properties and the earthworm communities in floodplains of northeast Georgia. Reference sites, where privet had not established, supported lower total abundances of earthworms. However, these sites had the highest total and relative abundances of native earthworms. Sites with well-established privet had higher earthworm abundances, and most of the earthworms were exotic European lumbricids. Privet sites also had the lowest diversity of all the sites. Removal of privet led to an increase in the relative abundances of native earthworms, especially in the felled sites where the privet biomass was probably removed from the site by flooding.

The different abundances and community structures of earthworms at these sites can be partially explained by the soil variables measured in this study. Reference sites had low soil pH, lowest levels of mineral nitrogen in the soil, and the lowest N-mineralization rates. Privet sites had the highest soil pH, with elevated mineral N and N-mineralization. The mulch sites had intermediate pH and the highest N-mineralization and mineral N levels of all sites. Felled sites had the lowest soil pH, but similar N-min and mineral N levels to levels at privet sites. It would seem that the privet invasion increases the amount of N cycling in the soil, and this is enhanced when privet is removed. This is evidenced by the larger increases in N-mineralization and mineral N that were found in the mulch sites, where the privet biomass was more easily incorporated into the soil. It is remarkable that these differences in soil mineral N and N-mineralization remain five years after the removal of privet, while the pH recovers to reference levels.

The higher total earthworm abundances in the privet and removal treatment sites seem to indicate that the earthworms are able to use the additional resources of the privet, even after its removal, although the amount of resources available after removal depends on the specific removal treatment. While native earthworms were most abundant in the felled and reference sites, they were least abundant in privet sites. Since felled sites had even higher soil mineral N levels than privet sites, the pH is the most likely explanatory variable measured to explain the difference in abundances between these sites. It is possible that the higher pH found in the privet sites is more favorable to the common European lumbricids found at these sites, whereas at felled sites, the native earthworms are able to utilize the increased available resources and coexist with the exotic species. This seems plausible, as it is known that native earthworms can be competitively displaced by exotic earthworms at high resource sites, even when they are able to coexist or outcompete the same exotic earthworms at low nutrient levels(Leon et al. 2003, Huang et al. 2006, Winsome et al. 2006).

Chapter three attempts to determine if the observed differences in earthworm abundances between treatments affect privet litter decomposition. Using privet litter to evaluate decay rates, no significant differences were found between treatments.   A potential explanation for this lack of observed difference is that the soil differences between these sites are not important to the decomposition process that occurs at the soil surface, and therefore do not affect the decomposition rates of the litterbags. This is supported by a litterbag study in which litter decomposition was correlated with soil organic matter and moisture, but not biological or chemical characteristics of the soil (Pavao-Zuckerman and Coleman 2005). Given the uniformly high resource quality of the privet litter used across all sites, it is likely that the dominant variables driving decomposition were micro-climatic conditions (i.e., temperature and soil moisture; (Swift et al. 1979)) which were not measured in this study but which may have been similar in these forested, bottomland habitats.   The decomposition process of high quality litter at the soil surface does not seem to be affected by soil characteristics that are affected by the removal of privet and decomposes at equal rates at all sites, even with differing earthworm densities.

The results of these experiments show that privet invasion and removal strongly affect earthworm communities and soil properties, and are likely to affect other soil communities. The invasion of privet led to a decrease in earthworm diversity, similar to decreases in diversity of bees, butterflies, and plants observed at the same sites (Hanula et al. 2009, Hanula and Horn 2011b, a). Also similar to the responses of these taxa, the removal of privet promoted a subsequent increase in diversity of earthworms. Not only is the diversity of sites without privet higher, but the relative abundance of native species is higher. This suggests that privet removal is an effective way to preserve native species and promote diversity.

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