IMPACT OF INVASIVE EARTHWORMS ON IXODES SCAPULARIS AND OTHER LITTER-DWELLING ARTHROPODS IN HARDWOOD FORESTS, CENTRAL NEW YORK STATE.

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by

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ABSTRACT

Invasive earthworms alter the structure of soils in northern hardwood forests, but the quantitative impacts on litter-dwelling invertebrates are unclear. Litter loss should reduce the habitat space, but nutrient-rich earthworm burrows might provide food resources. We investigated the impact of invasive earthworms on populations of *Ixodes scapularis* (Black-legged Ticks), the small mammal community, and other litter-dwelling arthropods to determine the impact of a reduced litter environment. We used five pairs of one-hectare sites (earthworm invaded versus reference) within four contiguous forests in New York State. The presence of earthworms decreased the density of nymphal *I. scapularis* by 46.1% and larval *I. scapluaris* by 29.3%. We also observed a dramatic decline in the total abundance of litter-dwelling arthropods with 69.9% of the arthropod population disappearing in the presence of earthworms. Earthworm invasion did not impact small mammal populations. Implications regarding the position *Ixodes scapularis* within the litter ecosystem are explored.

BIOGRAPHICAL SKETCH

James Burtis was born in New York City on July 3rd 1986. He spent the first 18 years of his life moving in and out of New York City. When he was in his final year of high school he joined a program that allowed James to spend much of his time hiking in the Adirondack and Catskill Mountains, which as a city-dweller he found both fascinating and a bit terrifying. These outdoor experiences are what inspired James to go to college at Bennington College in rural Vermont. Originally he intended to major in Japanese, but he began to take an interest in Biology during his first semester. Thanks to the efforts of the incredibly patient professors at Bennington College James' interest continued to grow throughout his freshman year. Ultimately he declared his major to be biology concentrating on ecology. His time at Bennington College was well spent, not only academically, but also socially. He made many lifelong friends, but most importantly he met his closest friend Jessie Miglus (his wife).

After he graduated from Bennington College James was employed as a research technician on various ecological projects. It was during this time that he began to focus his research interests and consider possible projects of his own. In 2009 James worked at Cornell University on a research project under Joseph Yavitt and Timothy Fahey, who encouraged him to apply to graduate school. In 2010 he applied and the next year James and Jessie moved to Ithaca NY. Over the following three years James has spent most of his time reading, writing, teaching and learning more than he had ever expected to, all while he and Jessie explored this beautiful portion of Central New York together.

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1. Introduction

Hardwood forests in Canada and the northern United States lack earthworms, which were eliminated during the most recent glacial period and have not colonized from further south (James, 2004). As a result, this area is highly susceptible to invasion by non-native European earthworm species. These northern forests have a well-developed forest floor (Gates, 1982; Reynolds, 1994) and reduction of the organic horizon by earthworm feeding activity and mixing has profound effects on forest ecosystem dynamics (Bohlen et al., 2004a), including major changes in nutrient cycling (Bohlen et al., 2004b; Hale et al., 2005), and decreases in the biodiversity of plant and animal communities (Frelich et al., 2006; Maerz et al., 2009). Loss of the forest floor has a direct influence on the community of litter-dwelling arthropods that rely on leaf litter for food and shelter (Burke et al., 2011; McLean and Parkinson, 2000; Migge-Kleian et al., 2006). Population density of *Ixodes scapularis* (Black-legged Tick), is of particular interest, given their role in the transmission of many tick-borne diseases; including Lyme disease, Babesiosis, and Anaplasmosis (Estrada-Peña and Jongejan, 1999; Keirans et al., 1996; Spielman et al., 1985).

The effect of earthworms on soil and litter-dwelling microarthropods, particularly Oribatid mites (Burke et al., 2011; McLean and Parkinson, 2000) and Collembola (Eisenhauer et al., 2007; Salmon et al., 2005) has varied. For example, earthworms can create nutrient-rich microhabitats near their middens, increasing the density and richness of microarthropods (McLean and Parkinson, 1998; Salmon, 2001), a pattern which appears to be particularly common in European forests where earthworms are native (Loranger et al., 1998; Maraun et al., 1999; Migge-Kleian et al., 2006; Wickenbrock and Heisler, 1997). In contrast, Burke et al. (2011) showed that invasive earthworms decreased the diversity and abundance of Oribatid mites

in a hardwood forest in New York State. The same pattern was observed for soil arthropod communities in aspen forests in the Canadian Rocky Mountains (Cameron, 2013; Eisenhauer et al., 2007). The alteration of microarthropod communities is probably caused by changes in the structure and chemical composition of the forest floor following earthworm invasion (Eisenhauer, 2010).

Competition between native millipedes (Diplopoda) and invasive earthworms may have a negative effect on both groups (Snyder et al., 2013), but the effects of earthworm invasion on native macroarthropod saprophages (isopods and diplopods) and predators (Araneae and Chilopoda) have not been reported. Although invasive earthworms should reduce prey availability, the interactions with populations of arthropod predators could be fairly complex. For instance some larger spiders (Nyffeler et al., 2001), and centipedes (Migge-Kleian et al., 2006) are known to feed on earthworms. Moreover some arthropod predators are known to feed on *I. scapularis* in laboratory settings (Samish and Alekseev, 2001), although the frequency of these predation events in nature remains unknown.

The survival and activity of *Ixodes scapularis* are sensitive to variation in temperature and relative humidity (Bertrand and Wilson, 1996; Stafford, 1994; Vail and Smith, 1998). Therefore, earthworms should influence the population density of *I. scapularis* because, like other litter-dwelling mites, they are dependent upon the microhabitat provided by the forest floor (Lindsay et al., 1999). The manual removal of leaf litter has been shown to be an effective management method for reducing populations of *I. scapularis* (Schulze et al., 1995). Similar effects have been demonstrated using controlled burns to remove the leaf litter (Stafford et al., 1998), but the long-term effects of litter reduction or removal on tick populations is unknown.

The potential effect of earthworm invasion on the community composition of the mammalian hosts for *I. scapularis* is important because it may affect the infection rate of *I. scapularis* by *Borrelia burgdorferi*, the agent of Lyme disease (LoGiudice et al., 2003; Brunner et al., 2011). Of particular importance is the relative abundance of *Peromyscus leucopus* (White-footed mouse) in the small mammal community. *P. leucopus* is one of the primary hosts for larval (first instar) *I. scapularis* (Brunner et al., 2011) and the most competent reservoir for *B. burgdorferi* (LoGiudice et al., 2003); therefore, their density and relative abundance is likely to have a strong impact on the infection rate of nymphal (second instar) *I. scapularis*. *P. leucopus* is a highly adaptable generalist (Yahner, 1992) and may not be affected by earthworm invasion as strongly as other potential hosts.

We hypothesized that the density of *I. scapularis* is lower in forests with invasive earthworms as populations of other litter dwelling microarthropods have exhibited a strong decrease in the presence of earthworms. We also expected an increase in the proportion of nymphal *I. scapularis* infected with *B. burgdorferi* if the relative abundance of *P. leucopus* is higher on the earthworm sites.

2. Methods

2.1 Site Descriptions

This project took place in four separate contiguous forests in New York State. Three were in the Finger Lakes region, and one was in the Adirondacks. At each site we located adjacent pairs of forest plots with and without invasive earthworms. The three sites located in the Finger Lakes region were; 1) Ringwood preserve (Cornell University), 2) Arnot Teaching and Research Forest (Cornell University), and 3) Hammond Hill State Forest (New York State Department of Environmental Conservation, NYSDEC). The site in the Adirondacks was in the Moose River Plains Wild Forest (NYSDEC). See appendix 1 for the relative locations of the sites within New York State.

Arnot Teaching and Research Forest is a 1649 hectare forest owned and maintained by Cornell University. We established two pairs of sites in Arnot Forest, which will hereafter be referred to as Arnot 1 (42°16'59" N, 76°38'18" W) and Arnot 2 (42°16'45" N, 76°38'14" W). Arnot Forest is located in the Allegheny Plateau in New York State. The mean temperature ranges from 22° C in the summer to -4° C in the winter, with annual precipitation of approximately 1000 mm. There is significant snow cover in the winter. The soils are derived from bedrock till containing shales from the Upper Devonian Period. In areas devoid of earthworms the forest floor is well developed (~ 4 cm thick). The soils are primarily shallow, acidic (pH 4.5-5.0) Dystrochrepts and Fragiochrepts of the Lordstown-Volusia-Mardin series. The elevation on our sites ranges from 500 to 570 m. Historically, Arnot forest was logged intensively in the late 19th century and our sites were never farmed (Fain et al., 1994). The dominant overstory tree species were sugar maple (*Acer saccharum*), red maple (*A. rubrum*),

American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), red oak (*Quercus rubra*), bigtooth aspen (Populus grandidentata), and eastern hemlock (*Tsuga canadensis*).

Hammond Hill State Forest is a 1503 hectare forest owned by New York State and maintained by the NYSDEC. We had a single pair of sites in Hammond hill (42°26'33" N, 76°18'09" W). Hammond Hill is also in the Allegheny Plateau and has similar geology, soil type, and climate to Arnot Forest. Unlike Arnot forest most of the land in Hammond Hill was intensively farmed in between the mid-19th century through the early-20th century. Many of these farms were poorly managed and were abandoned during the great depression. Trees were planted in some areas in the mid-20th century (NYSDEC, 2013) and our sites consisted of a mixture of naturally regeneration and planted trees. The elevation on our sites ranged from 480 to 550 m. The dominant overstory tree species were eastern hemlock (*T. canadensis)*, planted red pine (*Pinus resinosa*), American beech (*F. grandifolia*), sugar maple (*A. saccharum*), and red oak (*Q. rubra*).

Ringwood Preserve is a 140 hectare forest owned and maintained by Cornell University. We had a single pair of sites in Ringwood Preserve (42°26'58" N, 76°22'09" W). Ringwood Preserve has similar geology, land use history, and climate to Arnot Forest. The soils at Ringwood are acidic (pH 4.2-5.0), deep, well-drained glacial outwash soils (Welbourne, 1979). The dominant soil series are Howard and Palmyra (Soil Survey Staff, 2013). The elevation at Ringwood ranges from 450 to 500 m. Our sites were extensively logged in the late 19th century, but not farmed. The dominant overstory tree species were sugar maple (*A. saccharum*), American beech (*F. grandifolia)*, bigtooth aspen (*Populus grandidentata*), American basswood (*Tilia Americana*), and red oak (*Q. rubra*).

Moose River Plains Wild Forest is a 33,321 hectare forest owned and maintained by the NYSDEC within the Adirondack State Park. We had a single pair of sites within Moose River Plains (43°46'00" N, 74°42'00" W). The climate is colder and slightly wetter in this region than it is in the Finger Lakes. The mean temperature ranges from 18° C in the summer to -15° C in the winter. Annual precipitation is approximately 1300 mm. There is significant snow cover throughout the winter. Our sites were located in a Maple-basswood rich mesic forest (NYSDEC, 2011). The area was intensively logged from the mid-19th century through the mid-20th century, when it was sold to New York State. The soils are derived primarily from glacial till, they are slightly acidic (pH 5.0-5.5) owing to the presence of metasedimentary rocks in the underlying glacial till. The dominant soil series are Becket - Adams (Soil Survey Staff, 2013). The elevation on our sites ranges from 550 to 600 m. The dominant tree species were eastern hemlock (*T. canadensis),* American basswood (*T. americana*), American beech (*F. grandifolia*), sugar maple (*A. saccharum*), and red oak (*Q. rubra*).

2.2 Experimental Design

There were five pairs of one-hectare sites established within the four separate contiguous forests described above. A 64-plot sampling grid was laid out in each site. Each point on the grid was separated by 15 m. The distance between each pair of sites was between 50 and 200 m; this distance varied depending on the availability of suitable earthworm invaded areas adjacent to suitable reference sites. Paired sites were kept at least 50 m apart to limit the movement of ticks hosted on small mammals between sites.

2.3 Earthworm Sampling

Earthworms were collected in October 2012 using the hot mustard extraction method (Lawrence and Bowers, 2002) at eight points on each grid. 80 g of powdered mustard seed was

placed in 8 L of water and mixed. The mixture was poured into a 50 x 50 cm area. Earthworms were collected with tweezers as they came out of the soil attempting to escape the irritating effect of the mustard. They were then brought back to the laboratory and stored in a 10% formalin solution until they were sorted by species or genus (juveniles) using the available guides (Reynolds, 1977, Dindal and Schwert, 1990). The earthworms were dried at 65° C for 48 hours and a dry weight was recorded. One sample of each species for each site (38 samples total) were burned in a muffle furnace at 550° C to correct the earthworm biomass for any differences in mineral gut content between the different sites and species.

2.4 Tick Sampling

Black-legged Ticks were collected in May/June and August/September in 2012 and May/June in 2013 using a drag sampling method (Schulze et al., 1997). A 1 m^2 white corduroy cloth was dragged over the leaf litter, and every 30 meters the cloth was examined for ticks. The cloth was examined for a minimum of 10 minutes every 30 m. Sampling transects were randomly selected and no transect was sampled more than once every two weeks. Paired sites were sampled on the same day between 9:00 AM and 4:00 PM, as tick activity is known to show temporal variation (Schulze et al., 2001). In 2012 each pair of sites was sampled a total of eight times (450 m^2 per sample), four times in May/June and four times in August/September; three pairs of sites were re-sampled three times in May/June of 2013 (40,050 m^2 total). The spring and late summer dragging periods allowed us to capture the peak activity of the nymphal and larval life stages, respectively. In 2013 nymphs were collected from the two Arnot sites and Hammond Hill (Ringwood was unavailable for sampling).

Nymphs and larvae were placed in a vial partially filled with moistened plaster and returned to the laboratory where they were identified to species (Keirans and Litwak, 1989;

Keirans et al., 1996). After identification nymphs collected in 2012 were tested for infection by the Lyme disease spirochete, *B. burgdorferi*, using a direct fluorescent antibody method (Ostfeld et al., 2001). Larvae from 2012 and nymphs from 2013 were placed in 70% ethanol for long-term storage.

2.5 Small mammals

White-footed Mice were trapped on two pairs of sites, one in Arnot forest in July and one in Ringwood preserve in August. Mice were trapped for 6 days split between 2 weeks (Tuesday through Thursday) on each site. 64 Sherman traps (22.9 x 8.9 x 7.6 cm) with cover boards were set out on each site. The traps were locked open and pre-baited with sunflower seeds for 7 days prior to trapping, they also contained raw cotton for bedding. During the trapping periods traps were set in the evening between 4:30 PM and 5:30 PM, and then checked the following morning between 8:00 AM and 11:00 AM. Mice were marked by clipping a small square patch of fur from their chest. The heads and ears of mice were examined for the presence of larval *I. scapularis*. These areas are where the majority of ticks feed on mice, and this method has been determined to provide an accurate measure of the comparative larval body burden for White-footed Mice in the wild (Schmidt, 1999). All small mammal handling methods and practices were approved by the Cornell University Institutional Animal Care and Use Committee.

2.6 Litter and arthropod sampling

Litter-dwelling arthropods were collected twice per site in 2012, first in early July, and again after leaf fall in late October. Eight collection points on each site were spread out evenly throughout the one ha area. At each point a 50 x 50 cm sample of the Oi and Oe horizon (hereafter referred to as forest floor) was collected and a wet weight was recorded. The Oa horizon was absent on earthworm sites and was not collected on reference sites to avoid

sampling a different arthropod community. Litter samples were placed under a 40 W light source in Berlese funnels which were connected to a vial containing 70% ethanol (Coleman et al., 2004). Arthropods were preserved in ethanol until they could be sorted to order. Once the arthropods were extracted leaf material from each funnel was separated from the woody biomass and dried at 65° C for an additional 48 hours. A dry weight was recorded for the woody biomass and the leaf material from each sample. These numbers were combined to give the dry weight of the forest floor which was subtracted from the wet weight yielding the water content for each sample.

The arthropod samples were sorted into 25 orders using the available guides (Gibb and Oseto, 2006; Krantz, 2009; Thyssen, 2010), and the number of individuals in each order was recorded. Larvae for the orders Coleoptera, Diptera, and Lepidoptera were counted separately from their adult form. We did not classify arthropods into ecological functional groups because many litter arthropods are known to be generalists (Maraun et al., 2003; Halaj et al., 2005), which combined with an incomplete knowledge of their dietary habits makes identifying their functional roles extremely difficult and unreliable (Krantz, 2009; Setala, 2002; Setala and Aarnio, 2002). The data from the eight samples on each site were combined to estimate the number of individuals per m^2. We also divided the number of individuals per sample by the dry mass of the litter sample to estimate the number of individuals per gram of litter.

2.7 Statistical Methods

All analyses for this study were performed using packages in the R statistical software. Normality and homoscedasticity were tested using Shapiro-Wilk tests and Bartlett tests, respectively. All arthropod count and litter data were square root transformed. No transformations were applied to the earthworm or *I. scapularis* density data. Earthworm density

and biomass was analyzed across the 5 sites with a one-way ANOVA. Litter data were analyzed using multifactor ANOVAs including sites (1-5), season (summer/fall), and earthworm presence (earthworm/reference) as factors. The relationship between litter mass and total arthropod count was determined using a linear regression model with site, season and earthworm presence included as factors. The effects of season and earthworm presence on the individual arthropod orders were analyzed using two-way ANOVAs; site was not included as a factor because these data were analyzed at the site level. The data from each tick drag sample on each site were combined to represent a tick density per 450 meters squared. The density of larval *I. scapularis* was analyzed using a multifactor ANOVA to examine the effect of earthworm presence and site; for nymphal density we included year (2012 / 2013) as a factor. The rate of *Borrelia burgdorferi* infection of *I. scapularis* nymphs was compared across groups using a chi-squared test. The body burden of mice found with larvae feeding on them was compared between earthworm and reference sites using a Wilcoxon-Mann-Whitney test because the data did not meet the assumption of normality. The percentage of mice with larvae feeding on them was analyzed using a chi-squared test between groups. Total *P. leucopus* populations and 95% confidence intervals were estimated using the Schnabel method (Krebs, 1989).

To explore the impact of season, site and earthworm presence on arthropod communities we used NMDS ordinations constructed with the "Vegan" package in R. NMDS is a robust ordination technique, which is effective for biological community data (McCune and Grace, 2002). We created a dissimilarity matrix with the Bray-Curtis distance measure and chose 3-dimensional solutions as the best representation of the dissimilarities based on the stress values of the ordinations. We constructed one ordination to explore whether the average community composition of each site was clustered by group and season. We determined whether the

arthropod communities were clustered significantly by earthworm presence and season using a permutational MANOVA, with 1000 permutations of the distance matrix. We built four additional ordinations to determine the effect of litter variables on the arthropod communities of each of the 180 collections. We split the collection data into four groups: 1) “Summer Earthworms”, 2) “Summer Reference, 3) “Fall Earthworms”, and 4) “Fall Reference”. Environmental vectors were fit to these ordinations. P-values were determined using 1000 permutations of the data. This allowed us to determine whether the non-woody litter mass, woody biomass, or percent moisture of the litter collections affected the community composition of each of the 4 groups differently.

3. Results

3.1 Earthworm Density

Earthworm Taxon	*Units*	*Arnot 1*	*Arnot 2*	*Ringwood*	*Hammond Hill*	*Adirondacks*
Aporrectodea tuberculata	Count	0	0	2.00 (±) 0.76	0	0
	Mass	0	0	0.07 (±) 0.05	0	0
	Percent	(0%)	(0%)	(*3.6%*)	(*0%*)	(*0%*)
Aporrectodea trapezoids	Count	1.00 (±) 0.65	0.50 (±) 0.50	7.00 (±) 3.44	8.00 (±) 2.00	1.00 (±) 0.65
	Mass	0.13 (±) 0.08	0.03 (±) 0.03	0.30 (±) 0.11	0.32 (±) 0.06	0.06 (±) 0.04
	Percent	(*2.5%*)	(*0.7%*)	(*8.6%*)	(*12.8%*)	(*3.2%*)
Dendrodrilus rubidus	Count	0.50 (±) 0.50	0	0	0	1.00 (±) 0.65
	Mass	0.005 (±) 0.005	0	0	0	0.006 (±) 0.004
	Percent	(*0.1%*)	(*0%*)	(*0%*)	(*0%*)	(*0.4%*)
Octolasion tyrtaeum	Count	12.0 (±) 2.39	8.50 (±) 2.20	7.00 (±) 1.25	6.50 (±) 2.61	2.50 (±) 1.05
	Mass	0.36 (±) 0.08	0.29 (±) 0.08	0.28 (±) 0.05	0.15 (±) 0.06	0.12 (±) 0.07
	Percent	(*14.7%*)	(*9.7%*)	(*7.5%*)	(*8.8%*)	(*3.6%*)
Lumbricus terrestris	Count	5.50 (±) 1.05	2.50 (±) 0.73	7.50 (±) 1.76	2.50 (±) 1.05	5.00 (±) 1.96
	Mass	1.93 (±) 0.43	1.04 (±) 0.41	2.99 (±) 0.74	1.03 (±) 0.44	1.48 (±) 0.61
	Percent	(*46.9%*)	(*21.6%*)	(*51.8%*)	(*25.6%*)	(*30.6%*)
Lumbricus rubellus	Count	1.00 (±) 0.65	10.5 (±) 2.26	3.50 (±) 1.92	5.00 (±) 1.25	1.50 (±) 0.73
	Mass	0.35 (±) 0.28	1.16 (±) 0.19	0.31 (±) 0.19	0.36 (±) 0.10	0.08 (±) 0.04
	Percent	(*7.5%*)	(*38.2%*)	(*6.6%*)	(*12.9%*)	(*3.9%*)
Juvenile Lumbricus	Count	21.5 (±) 3.77	24.0 (±) 4.47	26.0 (±) 5.76	38.0 (±) 7.96	16.0 (±) 2.27
	Mass	0.65 (±) 0.20	0.79 (±) 0.18	0.83 (±) 0.23	0.81 (±) 0.15	0.62 (±) 0.20
	Percent	(*17%*)	(*26.3%*)	(*15.6%*)	(*31.4%*)	(*18.9%*)
Juvenile Aporrectodea	Count	5.50 (±) 3.54	3.00 (±) 1.65	14.5 (±) 3.29	17.0 (±) 4.39	13.5 (±) 3.85
	Mass	0.08 (±) 0.06	0.04 (±) 0.02	0.19 (±) 0.07	0.22 (±) 0.07	0.47 (±) 0.13
	Percent	(*3.4%*)	(*1.2%*)	(*4.1%*)	(*7.0%*)	(*20.1%*)
Juvenile Octolasion	Count	29.0 (±) 10.0	11.0 (±) 3.44	4.00 (±) 2.00	3.50 (±) 1.92	22.5 (±) 5.75
	Mass	0.26 (±) 0.07	0.07 (±) 0.02	0.07 (±) 0.06	0.04 (±) 0.02	0.35 (±) 0.10
	Percent	(*7.8%*)	(*2.2%*)	(*2.1%*)	(*1.5%*)	(*19.3%*)
Total:	Count	**76.0 (±) 12.4**	**60.0 (±) 10.9**	**71.5 (±) 9.75**	**80.5 (±) 9.60**	**63.0 (±) 8.20**
	Mass	**3.76 (±) 0.51**	**3.43 (±) 0.64**	**5.05 (±) 0.78**	**2.92 (±) 0.44**	**3.18 (±) 0.77**
	Percent	**(*100%*)**	**(*100%*)**	**(*100%*)**	**(*100%*)**	**(*100%*)**

Table 1: All values shown in the table above represent means values per m^2 from the 8 earthworm collection points on the 5 earthworm plots ± 1 SE (n = 8). In the unit column, "count" represents the mean number of earthworms collected, "mass" represents the mean earthworm mass in grams collected, and "percent" represents the relative density of each earthworm taxon as a percentage of total earthworm mass on each site.

The mean density of earthworms per m^2 across all earthworm sites was 70.2 (± 0.72). Six species were identified in our collections. There was no significant difference in the total number of earthworms ($F_{4,35} = 0.703$, $P = 0.595$), or total earthworm biomass ($F_{4,35} = 1.676$, $P = 0.177$) across all the earthworm sites. The dominant adult species by biomass on all five sites were *Lumbricus terrestris*, *L. rubellus*, *Apporectodea trapezoids*, and *Octolasion tyrtaeum*, and juvenile *Lumbricus* were very abundant. All points sampled on the reference sites were earthworm free, with the exception of one point at Hammond Hill with an average earthworm density of 2.5 (± 2.5) earthworms per m^2.

3.2 Forest floor collections

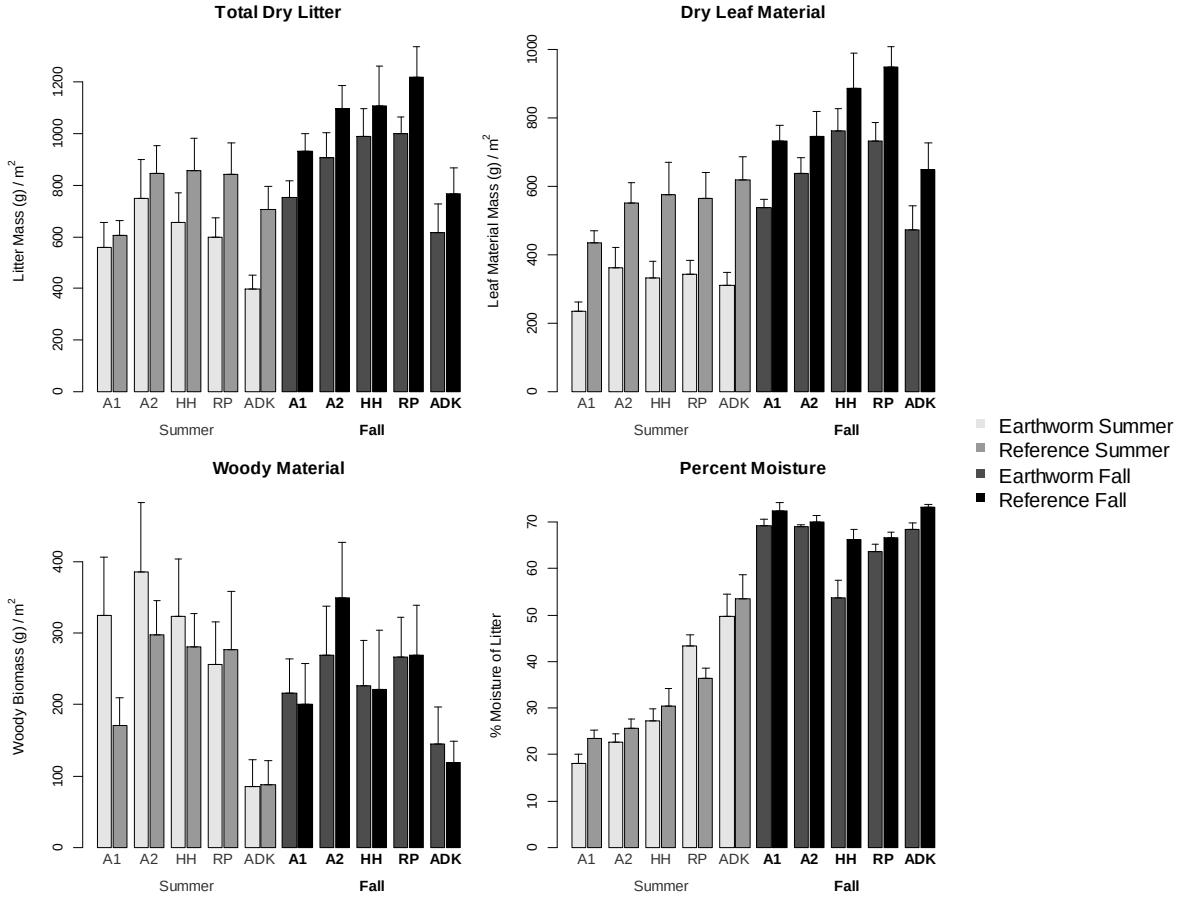

Figure 1: Bars represent the mean + 1 SE (n = 8) of the litter collections per m^2 between the 5 sites split by season and earthworm presence. A1 = Arnot 1, A2 = Arnot 2, HH = Hammond Hill, RP = Ringwood Preserve, and ADK = Adirondacks.

The forest floor mass was significantly greater in reference sites than in sites with earthworms ($F_{1,153}$ = 17.07, P = <0.001), it also differed between sites ($F_{4,153}$ = 7.37, P = <0.001), and season ($F_{1,153}$ = 35.62, P = <0.001). The differences between earthworm and reference sites were associated with non-woody litter material ($F_{1,153}$ = 48.47, P < 0.001) as we observed no effect of earthworm presence on woody litter biomass. Litter moisture content was slightly, but significantly higher in the reference than the earthworm sites ($F_{1,153}$ = 3.95, P = 0.049) (*Fig. 1*).

3.3 Arthropod community

Arthropod Taxon	Earthworms	Reference	F-value$_{1, 17}$	Pr
Araneae	33.15 (±) 6.44	78.80 (±) 7.70	**22.8**	**< 0.001**
Entomobryomorpha	274.3 (±) 82.34	527.4 (±) 86.17	**5.90**	**0.027**
Geophilomorpha	1.90 (±) 0.46	3.9 (±) 0.83	**5.76**	**0.028**
Lithobiomorpha	1.60 (±) 0.82	5.85 (±) 1.86	**10.1**	**0.006**
Mesostigmata	95.60 (±) 12.35	402.3 (±) 49.98	**46.8**	**< 0.001**
Poduromorpha	85.05 (±) 28.83	378.9 (±) 107.43	**7.39**	**0.015**
Pseudoscorpionida	14.90 (±) 4.98	34.05 (±) 8.23	**3.32**	**0.086**
Sarcoptiformes	580.5 (±) 121.7	2458.8 (±) 358.8	**61.7**	**< 0.001**
Symphypleona	72.00 (±) 22.03	98.45 (±) 43.61	**0.10**	**0.757**
Trombidiformes	14.2 (±) 3.70	68.9 (±) 13.12	**25.1**	**< 0.001**
Total density	**1288.0 (±) 232.7**	**4277.05 (±) 495.9**	**71.4**	**< 0.001**

Table 2: Mean arthropod density m^2 (±) 1 SE (N = 10) for the major microarthropod orders and the most strongly impacted macroarthropods orders in our collections. Total density includes all 25 orders that were collected. Data on other common orders is in appendices.

In total we counted 113,031 arthropods across all orders from our Berlese sample extractions. There were 25 orders present, and 20 were found in at least 15% of our samples. We term these the "common" categories; they were analyzed for differences between group and season (*Tables 2 and 4*). There were 8 "uncommon" orders which were not present in high numbers including: Isopoda (6.9% of samples), Lepidoptera (adult) (11.9%), Mantodea (0.63%),

Opiliones (13.1%), Orthoptera (4.4%), Polydesmida (8.8%), Protura (7.5%), and Trichoptera (Larvae) (9.4%). These data were included in the ordinations and total arthropod counts, but not independently in ANOVAs.

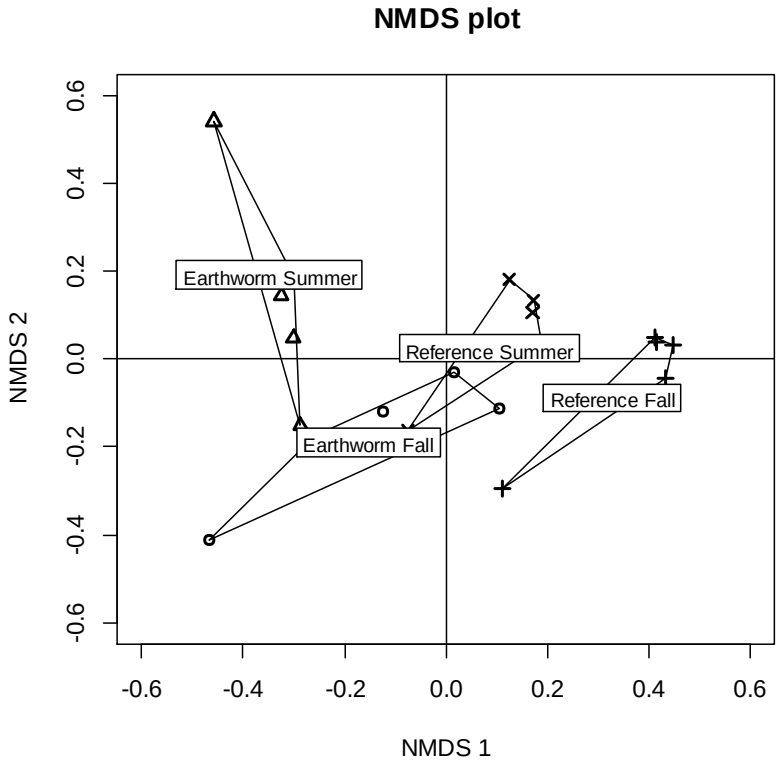

Figure 2: A 2 dimensional representation of the 3 dimensional NMDS ordination showing how the arthropod communities of the five sites cluster by group (earthworm/reference) and season (summer/fall). The stress value of the ordination is 5.56, and $R^2 = 0.982$.

The overall effects of earthworms on arthropod density were fairly consistent (*Table 2*) across all orders: many common arthropod orders were significantly less abundant in the presence of earthworms. The mean total arthropod density was 4336 per m^2 in the reference plots and 1326 per m^2 in the earthworm plots. There were no orders that increased in the presence of earthworms. Of the 20 most common arthropods there were six that were not significantly affected by the presence of earthworms: Diptera (larvae), Hemiptera, Psocoptera, Spirobolida, Symphypleona, and Thysanoptera. The other 14 common categories showed a significantly

lower abundance in the presence of earthworms. The abundance of arthropods in the fall was generally greater than in the summer (*Appendix 3*).

NMDS ordination was used to evaluate the effects of earthworms and season on the composition of the litter arthropod community. The ordination was based on all 25 arthropod orders that were identified (*Fig. 2*). The ordination reached a stable solution after 50 runs and had a stress value of 5.56. This indicates a strong relationship as an ordination with a stress value below 10 is considered to be a good representation (McCune and Grace, 2002). The R^2 value was 0.982. The similarity among the arthropod communities on each site by season and group are shown in an ordination plot in figure 2. Using a permutational MANOVA with 1000 permutations we observed that arthropod community composition was significantly clustered both by season and depending on earthworm presence (R statistic = 0.5367, P value = 0.001).

3.4 Density of Ixodes scapularis

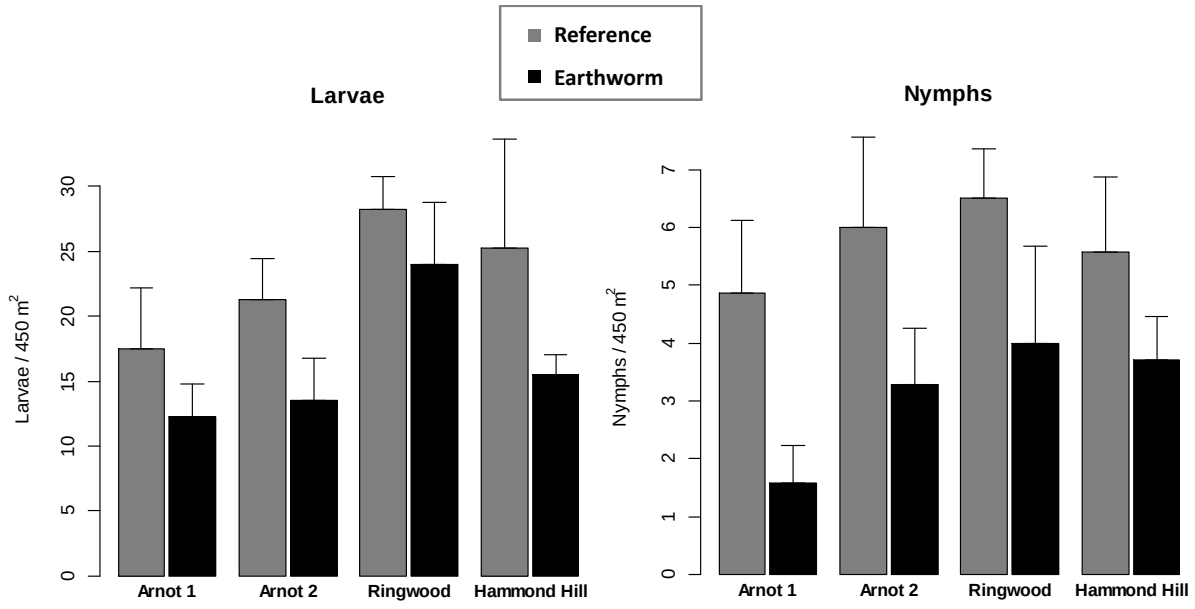

Figure 3: The bars represent the mean + 1 SE for the density of questing larvae and nymphs on the earthworm and reference sites per 450 square meter collection. The density of questing nymphs and larvae show a significant ($P < 0.05$) decrease in the presence of earthworms.

In 2012 a total of 129 *I. scapularis* nymphs were collected; 114 in May and June, and an additional 15 nymphs in August and September. In 2013, 104 nymphs were collected in May and June. The density data from the May and June collections in 2012 and 2013, during the peak of nymphal activity, were used to compare the density of nymphs between the earthworm and reference sites. In 2012 we collected a total of 654 *I. scapularis* larvae, 24 in May and June, and 630 in August and September. The density data from the 2012 August and September collections were used to examine differences in the larval densities between earthworm and reference sites. There were no *I. scapularis* detected on the Adirondack sites, so that pair of sites was excluded from the analyses of tick density. The density of questing nymphs was significantly higher on the reference sites than the earthworm sites ($F_{1,41} = 12.03$, $P = 0.001$). The mean density of nymphs was higher in the 2013 collections than in the 2012 collections ($F_{1,41} = 7.65$, $P = 0.008$). The mean 2012 larval density was also significantly lower in the earthworm sites than in the reference sites ($F_{1,24} = 4.86$, $P = 0.037$) (*Fig. 3*). Site was not a significant factor in any of our analyses of tick density when the Adirondack sites were excluded.

	Infected	***Uninfected***	**chi-square value**	0.0833
Earthworm	9	34	**df**	1
Reference	12	59	**p-value**	0.773

Table 3: The number of nymphs infected with *B. burgdorferi* in the earthworm and reference plots and the results of a chi-squared test comparing infection rate between earthworm and reference groups.

A total of 114 *I. scapularis* nymphs from 2012 were tested for the presence of the Lyme disease spirochete, *B. burgdorferi*. Overall 18.4% of the nymphs tested positive for *B. burgdorferi*, 16.9% on the reference sites and 20.9% on the earthworm sites. There was no significant difference between the two groups (*table 3*).

3.5 Litter Environment and Arthropod community

We constructed four separate ordinations (one for each cluster shown in figure 2) allowing us to fit environmental variables to arthropod communities (*Fig. 4*). The final ordination for the summer earthworm plots had a stress value of 11.3 ($R^2 = 0.987$), for summer reference a stress value of 6.00 ($R^2 = 0.996$), for fall earthworms a stress value of 9.09 ($R^2 = 0.992$), and for fall reference a stress value of 9.98 ($R^2 = 0.99$).

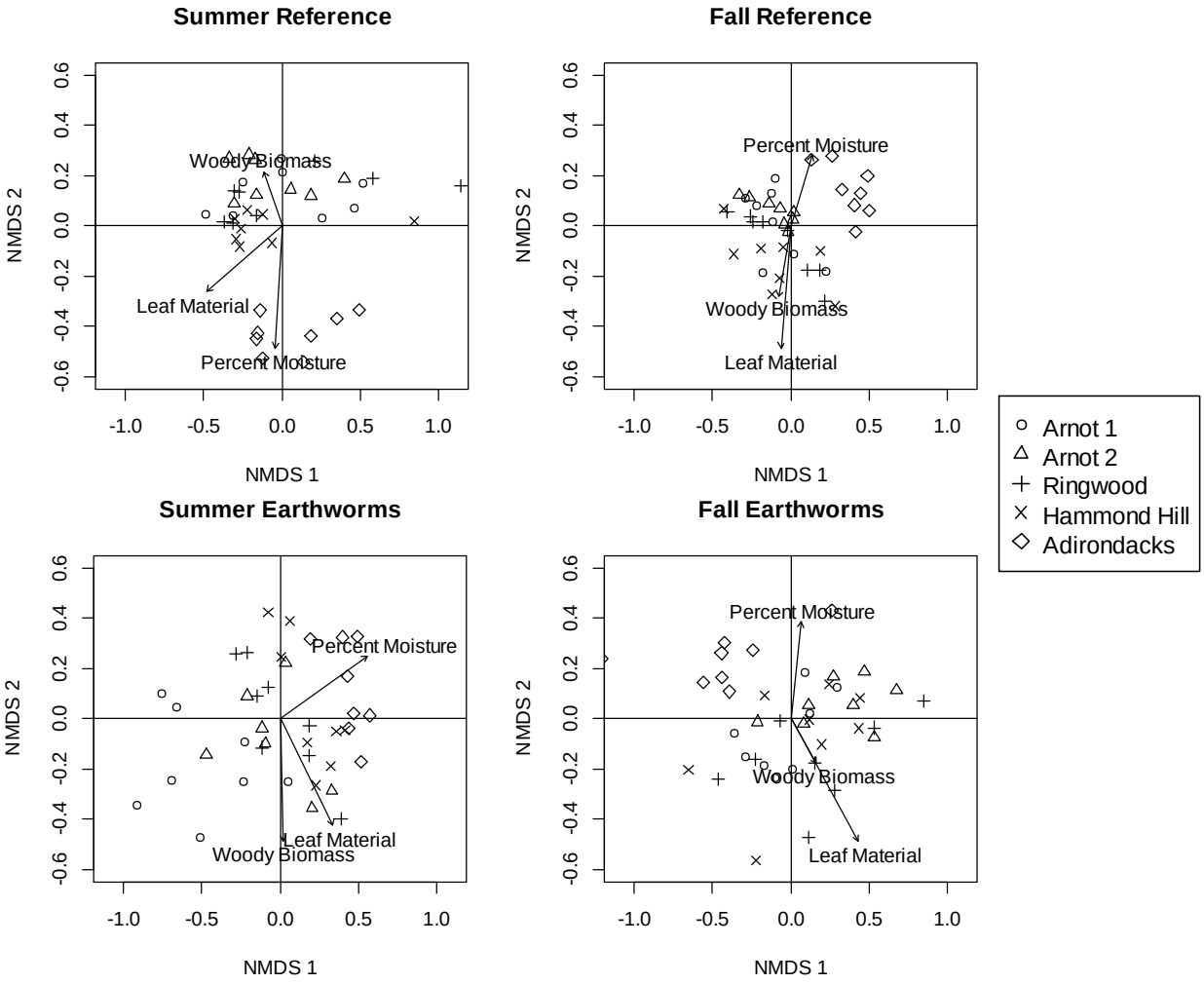

Figure 4: 2 dimensional representations of the ordinations for the arthropod collections by group and season fitted with vectors which show the effect of percent moisture, woody biomass and leaf material mass on the arthropod community composition. Longer lines indicate stronger relationships.

In all cases both site and the mass of non-woody litter had a strong impact on the community composition of arthropods. We also found that the amount of woody biomass had a significant impact on the summer arthropod community in the earthworm site that was not present in the fall. In the summer percent moisture ($r^2 = 0.54$, $P = 0.001$), non-woody litter mass ($r^2 = 0.412$, $P = 0.001$), and woody litter biomass ($r^2 = 0.347$, $P = 0.003$) all had a significant effect on the arthropod community composition on the earthworm sites. In the summer on reference sites, only non-woody litter mass ($r^2 = 0.631$, $P = 0.001$) had a significant impact. Again, only non-woody litter mass had a significant impact ($r^2 = 0.388$, $P = 0.001$) on the earthworm sites in the fall. In the fall on the reference sites the percent moisture ($r^2 = 0.409$, $P = 0.001$) and non-woody litter mass ($r^2 = 0.312$, $P = 0.005$) had a significant effect on community composition.

The total arthropod density was positively correlated with litter mass in our samples ($F_{1,155} = 88.76$, $P = <0.001$), and to further evaluate the effect of earthworms on litter habitat quality we calculated arthropod abundance per 100 g of litter. The total abundance of arthropods was significantly lower in the earthworm sites than in the reference sites, with means of 183.5 per 100 g of litter and 495.9 per 100 g of litter, respectively. The abundance of 13 of orders was significantly lower in the presence of earthworms (*Table 4*), indicating that the changes in abundance exhibited in the density data are not due to litter mass reduction alone, but to also to changes in the quality of the remaining litter habitat.

Arthropod Taxon	Earthworms	Reference	F-value$_{1, 17}$	Pr
Araneae	5.01 (±) 1.18	8.84 (±) 0.70	**9.14**	**0.008**
Entomobryomorpha	37.29 (±) 11.44	60.16 (±) 9.83	**3.35**	**0.085**
Geophilomorpha	0.29 (±) 0.09	0.48 (±) 0.09	**2.45**	**0.136**
Lithobiomorpha	0.29 (±) 0.21	0.71 (±) 0.27	**5.44**	**0.032**
Mesostigmata	13.70 (±) 2.18	45.63 (±) 3.94	**53.64**	**< 0.001**
Poduromorpha	10.32 (±) 3.32	38.48 (±) 10.55	**6.42**	**0.021**
Pseudoscorpionida	1.99 (±) 0.65	3.86 (±) 1.01	**2.51**	**0.132**
Sarcoptiformes	76.78 (±) 10.78	280.92 (±) 34.76	**59.5**	**< 0.001**
Symphypleona	11.00 (±) 3.75	13.65 (±) 6.60	**0.01**	**0.928**
Trombidiformes	2.12 (±) 0.52	8.51 (±) 1.78	**15.1**	**0.001**
Total abundance	**177.54 (±) 23.54**	**488.38 (±) 40.34**	**68.2**	**< 0.001**

Table 4: Mean arthropod order abundance per 100 g of litter collected (±) 1 SE (N = 10) for the major microarthropod orders and the most strongly impacted macroarthropods orders in our collections. Total abundance includes all 25 orders that were collected. Data on other common orders is in appendices.

3.6 Small Mammals

P. leucopus made up the majority of the trapped small mammals. 87% of animals caught on the reference sites and 92% of animals caught on the earthworm sites. A total of 134 *P. leucopus* were caught over 1536 trap nights (384 trap nights per site). Larval ticks were detected on 33 mice (24.6% of those caught), 16 on the reference sites and 17 on the earthworm sites. The body burden on these 33 mice averaged 1.30 (±0.12) larvae per mouse and did not differ significantly between earthworm and reference sites (ns, p = 0.921). Summer population estimates for *P. leucopus* did not differ significantly between the earthworm and reference sites. The estimated mouse population on both of the reference sites was slightly higher than that of the earthworm sites, but not significantly so (*appendix 2*).

4. Discussion

We observed significantly lower densities of litter-dwelling arthropods and *I. scapularis* on earthworm-invaded compared to reference forests in central New York State. We also found that arthropod abundance, as measured per gram of litter, was lower in earthworm sites than reference sites. This suggests that the remaining litter in the earthworm invaded sites was not of equal quality to that in the reference sites and could not support the equivalent arthropod population. Although we cannot conclusively ascribe cause and effect, we explore several possible mechanisms to explain these density decreases below.

4.1 Earthworms and small mammal populations

It appears unlikely that differences in the small mammal host community affected populations of *I. scapularis* because estimated densities of *P. leucopus* were similar between earthworm and reference sites (*appendix 2*). *P. leucopus* comprised the majority of the small mammal community on all sites (87% in the reference sites, 92% in the earthworm sites). It is not unusual for small mammal communities in the forests of the northeastern United States to be dominated (< 70%) by a single species (Kirkland, 1985), and these communities are known to have a large degree of temporal variation (Kirkland, 1990). Furthermore, we found no significant difference in the rate of *B. burgdorferi* infection in nymphal *I. scapularis* (20.9% in earthworm sites, 16.9% in reference sites). If the mammalian host communities were driving differences in tick populations we would expect to see a difference in nymphal infection rate as well (Ostfeld et al., 2001). A more diverse population of small mammals would be likely to lower the Lyme disease infection rate by presenting alternative hosts which are less competent reservoirs than *P. leucopus* (LoGiudice et al., 2003). Given the abundance of *P. leucopus* on both the reference and

earthworm sites, and the even infection rates it is unlikely that the difference in *I. scapularis* density between earthworm and reference sites is due to host community composition.

4.2 Earthworms and microarthropods

The reduction of the abundance of litter-dwelling microarthropods in the presence of earthworms suggests that earthworms are altering the litter in ways that impact many trophic levels within the litter arthropod community. Abundances of the Collembolan orders, Poduromorpha and Entomobryomorpha, were significantly less in the presence of earthworms (*Table 2*), possibly because of the reduced availability of fungi in these sites (Dempsey et al., 2011), which may decrease this preferred food source of Collembola (Jorgensen et al., 2005). The impact of earthworms was particularly strong on litter-dwelling mites. Mite populations declined both in the number of individuals per m^2, and the number of individuals per 100 grams of leaf litter (*Tables 2 and 4*). This decrease indicates that earthworms not only reduce habitat availability for mites, but also appear to decrease the quality of the remaining habitat. This change in habitat quality is probably explained by alterations of litter structure associated with earthworm feeding activity (Eisenhauer, 2010), as well as the selective feeding habits exhibited by many species of epigeic and anecic earthworms that feed preferentially on leaf material with a low C:N ratio (Belote and Jones, 2008); earthworm taxa (*Lumbricus rubellus and L. terrestris*) from these feeding groups dominated the earthworm community on all the sites (*Table 1*). In general microarthropod density is strongly dependent on leaf litter availability (Hasegawa et al., 2013; Sayer et al., 2010; Takeda, 1987) and quality (Yang et al., 2007) because many taxa rely on litter as their primary source of food (Saitoh et al., 2011; Sayer, 2006).

4.3 Earthworms and macroarthropods

The effect of earthworm invasion on macroarthropods was less consistent than for microarthropods. The four orders of macroarthropods that were most strongly impacted were Araneae, Coleoptera, Geophilomorpha, and Lithobiomorpha. With the exception of Coleoptera, which is a very diverse order with a wide variety of feeding habits (White, 1983), these orders are comprised of non-flying, obligate predators. The trophic interactions of litter communities are complex and variable (Ponsard, 2000), but altering the food sources of detritivores is known to have a cascading effect on arthropod predators (Chen and Wise, 1999), and that effect may have caused the lower abundance of arthropod predators that we observed in the presence of earthworms.

The effect of earthworms on the macroarthropod community could have affected tick populations, which are significantly lower on earthworm than reference plots. The incidence of predation of *I. scapularis* by arthropod predators is unknown, although there are species of arthropod predators that are known to prey on *I. scapularis* in a laboratory setting (Samish and Alekseev, 2001). Although arthropod predators (Araneae and Chilopoda) exhibited a significant decrease in the presence of earthworms, it is possible that those remaining predators increased feeding on *I. scapularis* as an alternative food source, thereby reducing their population. Additionally, it has been observed that in a system with a simple litter structure arthropod predators exert a stronger top-down force than they do in a system with a complex litter structure (Kalinkat et al., 2013). Experimental manipulations of the arthropod food web would be needed to evaluate these possible explanations.

Populations of the most common order of macroarthropod detritivores, Spirobolida (millipedes; Class: Diplopoda), were comparable in the earthworm and reference sites. Other

studies have found significant impacts of earthworm invasion on millipede populations both in the lab and in the field, and these impacts have been attributed to direct competition (Snyder et al., 2009; Snyder et al., 2011; Snyder et al., 2013). The different responses between mites and millipedes may have arisen because mites are more reliant on the presence of finely shredded leaf material (Eisenhauer, 2010), whereas millipedes are large enough to shred larger fragments (Snyder et al., 2013).

4.4 Earthworms and the litter environment

Another mechanism that may contribute to decreased density of ticks and other arthropods is the impact of earthworms on litter microhabitat availability. Earthworms are known to reduce and alter the microhabitat availability for many microarthropods, including mites (Eisenhauer, 2010). This is a likely mechanism by-which earthworms are affecting the density of *I. scapularis*. There is evidence that populations of *I. scapularis* are immediately reduced by the manual removal or reduction of leaf litter (Schultz et al., 1995; Stafford et al., 1998). It is unclear whether there are long-term effects of litter removal on the survival of *I. scapularis*, but its survival is strongly correlated with microclimate suitability (Williams and Ward, 2010; Bertrand and Wilson, 1996). Specifically, *I. scapularis* survival is negatively impacted by several conditions, including increased summer temperature, variations in humidity and higher vapor pressure deficits. Leaf litter mass was significantly reduced by the presence of earthworms, matching observations in other studies in northern hardwood forests (Hale et al., 2005). We also observed that both litter mass and moisture had a strong effect on the litter arthropod community as a whole, particularly in the summer (*Fig. 4*). It seems likely that the decrease in litter mass would reduce the availability of humid microclimates, but further work on this mechanism is needed.

In conclusion we observed a decrease in the density of nymphal and larval *I. scapularis* in the presence of earthworms, as well as a decrease in the density of many other litter-dwelling arthropods. Considering the strong impact earthworms had on both the litter environment and the arthropod community the decrease in the density of *I. scapularis* is likely due to a combination of changes in the litter food web, possibly causing an increased rate of predation, and a reduction in microhabitat availability in the leaf litter caused by earthworms. This study highlights our limited understanding of the mechanisms by which the litter environment may affect litter-dwelling arthropods including the population density of an important disease vector. Further experimental manipulations of macroarthropod predator populations and the litter environment in a natural setting will be important steps towards improving our understanding of the position of *I. scapularis* in litter ecosystems.

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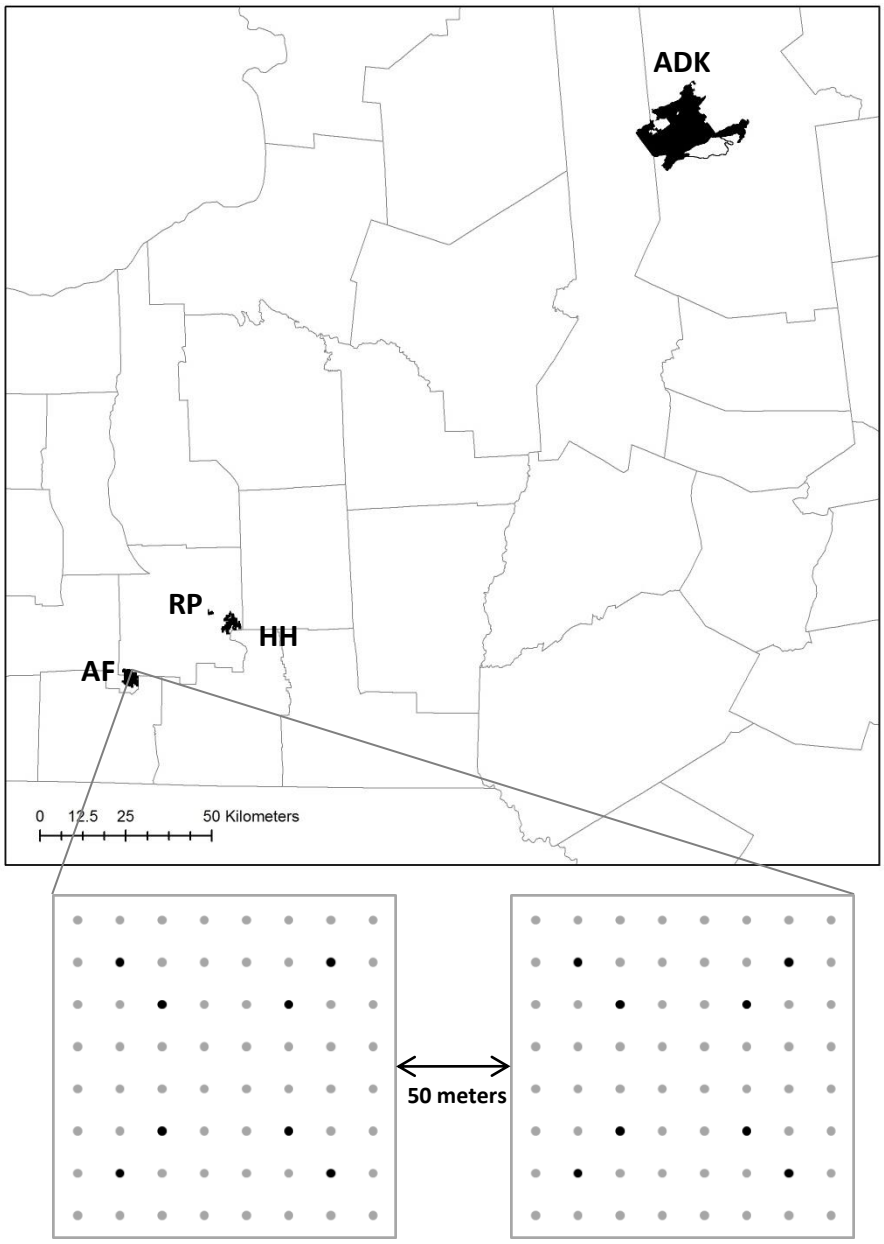
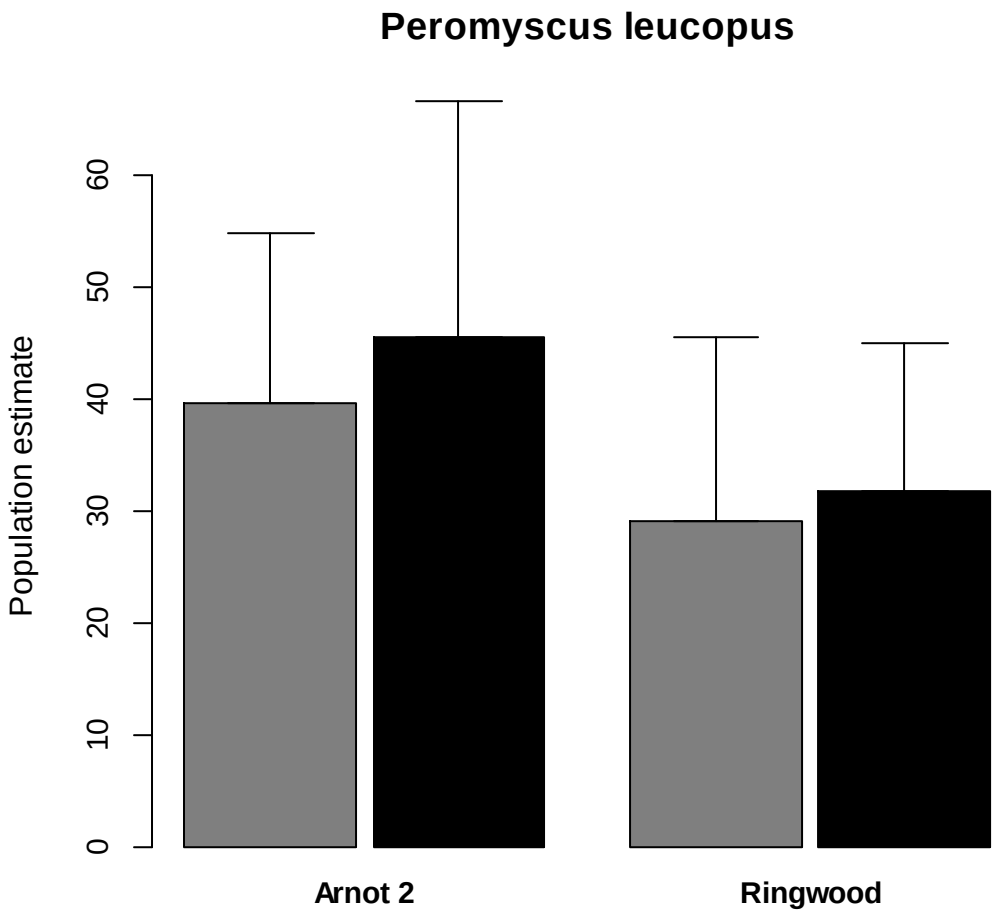
APPENDICES

Appendix 1: This figure shows the setup of the paired sampling grid on the sites and the locations of the forest fragments within New York State. The black spots on the grids are collection points for arthropods and earthworms.



Appendix 2: Schnabel estimates for summer populations of *P. leucopus* on each site on which small mammals were sampled. The error bars represent the 95% confidence intervals. Black bars are reference sites, gray bars are earthworm sites.



Appendix 3: Mean arthropod density m^2 (±) 1 SE (N = 10) for each order. The results from two-way ANOVAs are in the p-value column. "G" stands for group (Reference / Earthworm), and "S" stands collection season (Summer / Fall).

Arthropod Taxon	**Earthworms**	**Reference**	**Fall**	**Summer**	***P-values***	
					G	**S**
Araneae	33.15 (±) 6.44	78.80 (±) 7.70	63.80 (±) 11.94	48.15 (±) 7.78	***<0.001***	***0.194***
Coleoptera (adult)	6.55 (±) 2.20	19.75 (±) 2.50	15.95 (±) 3.31	10.35 (±) 2.83	***<0.001***	***0.089***
Coleoptera (larvae)	11.25 (±) 4.78	27.25 (±) 6.85	29.45 (±) 7.33	9.05 (±) 2.67	***0.026***	***0.011***
Diptera (adult)	5.75 (±) 1.82	12.50 (±) 4.74	1.20 (±) 0.48	17.05 (±) 3.75	***0.096***	***<0.001***
Diptera (larvae)	10.30 (±) 6.43	25.95 (±) 13.02	34.10 (±) 12.94	2.15 (±) 0.68	***0.101***	***0.001***
Entomobryomorpha	274.3 (±) 82.34	527.4 (±) 86.17	454.3 (±) 102.38	347.5 (±) 81.53	***0.027***	***0.351***
Geophilomorpha	1.90 (±) 0.46	3.9 (±) 0.83	3.75 (±) 0.79	2.05 (±) 0.58	***0.028***	***0.033***
Hemiptera	12.95 (±) 6.53	13.00 (±) 3.55	18.90 (±) 6.67	7.05 (±) 1.74	***0.686***	***0.084***
Hymenoptera	13.55 (±) 4.90	29.70 (±) 8.54	13.45 (±) 6.22	29.80 (±) 7.61	***0.074***	***0.047***
Lepidoptera (larvae)	11.90 (±) 3.19	20.40 (±) 5.59	6.35 (±) 1.73	25.95 (±) 4.59	***0.038***	***<0.001***
Lithobiomorpha	1.60 (±) 0.82	5.85 (±) 1.86	2.65 (±) 0.70	4.80 (±) 2.09	***0.006***	***0.462***
Mesostigmata	95.60 (±) 12.35	402.3 (±) 49.98	269.9 (±) 70.77	228 (±) 52.61	***<0.001***	***0.495***
Poduromorpha	85.05 (±) 28.83	378.9 (±) 107.43	363 (±) 107.6	101.0 (±) 42.27	***0.015***	***0.022***
Pseudoscorpionida	14.90 (±) 4.98	34.05 (±) 8.23	15.00 (±) 4.72	33.95 (±) 8.40	***0.086***	***0.115***
Psocoptera	15.05 (±) 7.01	24.55 (±) 9.50	2.7 (±) 0.54	36.90 (±) 8.89	***0.344***	***<0.001***
Sarcoptiformes	580.5 (±) 121.7	2458.8 (±) 358.8	2082.5 (±) 457.6	956.8 (±) 244.6	***<0.001***	***<0.001***
Spirobolida	8.80 (±) 2.76	12.7 (±) 3.37	9.50 (±) 2.41	12.00 (±) 3.70	***0.298***	***0.679***
Symphypleona	72.00 (±) 22.03	98.45 (±) 43.61	107.5 (±) 28.38	63.00 (±) 38.87	***0.757***	***0.116***
Thysanoptera	16.25 (±) 4.71	27.05 (±) 5.64	18.90 (±) 6.21	24.40 (±) 4.50	***0.184***	***0.242***
Trombidiformes	14.2 (±) 3.70	68.9 (±) 13.12	58.90 (±) 15.27	23.90 (±) 7.01	***<0.001***	***<0.001***
Total	**1288.0 (±) 232.7**	**4277.05 (±) 495.9**	**3574.7 (±) 714.5**	**1990.4 (±) 382.6**	***<0.001***	***<0.001***

Appendix 4: Mean arthropod order abundance per 100 g of litter collected (±) 1 SE (N = 10). The results from two-way ANOVAs are in the p-value column. "G" stands for group (Reference / Earthworm), and "S" stands collection season (Summer / Fall).

Arthropod Taxon	**Earthworms**	**Reference**	**Fall**	**Summer**	***P-values***	
					G	**S**
Araneae	5.01 (±) 1.18	8.84 (±) 0.70	6.8 (±) 1.09	7.04 (±) 1.22	**0.008**	**0.889**
Coleoptera (adult)	0.86 (±) 0.28	2.27 (±) 0.30	1.63 (±) 0.36	1.51 (±) 0.39	**0.003**	**0.582**
Coleoptera (larvae)	1.10 (±) 0.30	3.04 (±) 0.76	2.98 (±) 0.77	1.15 (±) 0.30	**0.013**	**0.022**
Diptera (adult)	1.06 (±) 0.40	1.79 (±) 0.78	0.13 (±) 0.04	2.72 (±) 0.64	**0.310**	**<0.001**
Diptera (larvae)	0.88 (±) 0.35	2.94 (±) 1.55	3.50 (±) 1.48	0.32 (±) 0.11	**0.076**	**0.002**
Entomobryomorpha	37.29 (±) 11.44	60.16 (±) 9.83	46.55 (±) 8.95	50.89 (±) 13.24	**0.085**	**0.964**
Geophilomorpha	0.29 (±) 0.09	0.48 (±) 0.09	0.44 (±) 0.08	0.33 (±) 0.11	**0.136**	**0.183**
Hemiptera	3.14 (±) 2.02	1.51 (±) 0.45	3.46 (±) 2.02	1.18 (±) 0.29	**0.586**	**0.284**
Hymenoptera	2.46 (±) 0.96	3.29 (±) 0.87	1.44 (±) 0.64	4.31 (±) 0.92	**0.316**	**0.006**
Lepidoptera (larvae)	2.12 (±) 0.77	2.61 (±) 0.78	0.70 (±) 0.18	4.02 (±) 0.75	**0.265**	**<0.001**
Lithobiomorpha	0.29 (±) 0.21	0.71 (±) 0.27	0.30 (±) 0.08	0.70 (±) 0.33	**0.032**	**0.412**
Mesostigmata	13.70 (±) 2.18	45.63 (±) 3.94	29.22 (±) 6.56	30.11 (±) 5.81	**<0.001**	**0.766**
Poduromorpha	10.32 (±) 3.32	38.48 (±) 10.55	36.61 (±) 10.57	12.19 (±) 4.64	**0.021**	**0.036**
Pseudoscorpionida	1.99 (±) 0.65	3.86 (±) 1.01	1.46 (±) 0.42	4.38 (±) 0.99	**0.131**	**0.038**
Psocoptera	2.65 (±) 1.33	3.52 (±) 1.51	0.36 (±) 0.07	5.81 (±) 1.56	**0.635**	**<0.001**
Sarcoptiformes	76.78 (±) 10.78	280.92 (±) 34.76	227.89 (±) 45.83	129.84 (±) 31.69	**<0.001**	**0.002**
Spirobolida	1.18 (±) 0.38	1.69 (±) 0.58	1.21 (±) 0.42	1.65 (±) 0.55	**0.423**	**0.572**
Symphypleona	11.00 (±) 3.75	13.65 (±) 6.60	15.26 (±) 5.06	9.40 (±) 5.52	**0.928**	**0.195**
Thysanoptera	2.75 (±) 0.89	3.59 (±) 0.86	2.41 (±) 0.92	3.92 (±) 0.78	**0.495**	**0.095**
Trombidiformes	2.12 (±) 0.52	8.51 (±) 1.78	7.11 (±) 2.04	3.52 (±) 0.91	**0.001**	**0.070**
Total	**177.54 (±) 23.54**	**488.38 (±) 40.34**	**389.84 (±) 68.45**	**276.07 (±) 46.30**	**<0.001**	**0.014**