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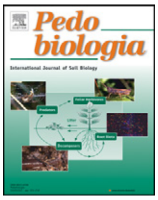

Impacts of emerald ash borer-induced tree mortality on leaf litter arthropods and exotic earthworms

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ABSTRACT

Because leaf litter occurs at the interface between the soil and atmosphere, the invertebrates inhabiting it represent important linkages between above- and below-ground food webs. The responses of these organisms to forest disturbance brought about by invasive species should therefore have far-reaching ecological effects. The purpose of this study was to explore how canopy gap formation (gap fraction 1–10%) and fallen ash trees ("logs") resulting from extensive (>99%) ash tree mortality caused by the invasive emerald ash borer (EAB) affect the distributions of litter-dwelling arthropods and earthworms. These organisms did not vary in abundance across the gap fraction range studied but, as predicted from the literature, many taxa (e.g., Aranea, Coleoptera, Collembola, Diplopoda, Isopoda, Opiliones and exotic earthworms) were more abundant next to logs than away from them. Contrary to expectations, arthropods did not become more concentrated next to logs as canopy openness increased, with isopods exhibiting the opposite response. These results suggest litter-dwelling arthropods in EAB-infested forests are favored by inputs of ash wood to the forest floor but are largely unaffected by increases in canopy openness, at least across the gap fraction range studied.

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Introduction

The first reports of emerald ash borer (EAB) (*Agrilus planipennis* Fairmaire), a phloem-feeding buprestid beetle endemic to Asia, infesting ash trees (*Fraxinus* spp.) in North America were made near Detroit, Michigan and Windsor, Ontario in 2002 (Haack et al. 2002). Since then, nearly all mature ash trees have been killed in forests closest to the point of introduction (Herms et al. 2009) and all North American ash species tested have been found to be susceptible to attack (Poland and McCullough 2006). With EAB continuing to spread rapidly into new areas, extensive extirpation of ash throughout North America appears increasingly probable (Herms et al. 2004). The severe decline or elimination of an entire genus of tree, especially one as historically widespread and abundant as *Fraxinus*, will profoundly alter forest communities (Gandhi and Herms 2010a). At least 43 North American arthropod species, for example, are strictly dependent on ash whereas many others utilize ash resources to some extent (Gandhi and Herms 2010b).

Extensive ash mortality is likely to affect many species not directly associated with ash as well, including the diverse community of predators, mycophages, and detritivores found within the litter layer on the forest floor. These organisms tend to be small and highly sensitive to fluctuations in moisture availability (Levings and Windsor 1984; Chikoski et al. 2006; Entling et al. 2007). Canopy thinning brought about by EAB infestation should reduce leaf litter moisture by increasing the amount of light reaching the forest floor and these changes are likely to negatively affect litter-dwelling arthropod communities (Yi and Moldenke 2008). On the other hand, inputs of dead ash wood are likely to favor litter-dwelling arthropods by providing food (Wallwork 1976), nutrients (Kappes et al. 2007) and refuge (Banerjee 1967; Penney 1967; Higgins and Lindgren 2006).

While some litter-dwelling invertebrate taxa are truly saproxylic, meaning they require resources or conditions provided by dead wood (Speight 1989), many others colonize dead wood opportunistically (Lloyd 1963; Seastedt et al. 1989; Setälä and Marshall 1994; Caldwell 1996; Johnston and Crossley 1996; Snider 1996) or are more abundant in leaf litter near dead wood than away from it (Table 1). One of the most important functions of dead wood for many non-saproxylic taxa may be to provide a relatively stable source of moisture (Maser and Trappe 1984; Amaranthus et al. 1989; Marra and Edmonds 1998) and this may be especially true near canopy openings. For example, Jabin et al. (2004) found the positive influence of dead wood on litter-dwelling arthropods in a German deciduous forest to be more pronounced near the

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Table 1
Summary of findings from previous studies comparing invertebrate communities from leaf litter near and far from dead wood (findings from the current project are included).

Taxon	Variable	Higher near	Higher far	No difference
Acari	Abundance	Evans et al. (2003)[b] (several morphospecies)		Ulyshen and Hanula (2009a)[f], Déchêne and Buddle (2010)[g], current study[i]
	Richness			Déchêne and Buddle (2010)[g]
Araneae	Abundance	Evans et al. (2003)[b] (Amphinectidae), Jabin et al. (2004)[c], Ulyshen and Hanula (2009a)[f], Castro and Wise (2010)[h], current study[i]		
	Richness	Castro and Wise (2010)[h]		
Chilopoda	Abundance	Jabin et al. (2004)[c], Jabin et al. (2007)[d]		Ulyshen and Hanula (2009a)[f], current study[i]
	Richness	Jabin et al. (2007)[d]		
Coleoptera	Abundance	Jabin et al. (2004)[c], Topp et al. (2006a)[d], Ulyshen and Hanula (2009a)[f], current study[i]	Evans et al. (2003)[b] (Elateridae)	
	Richness	Topp et al. (2006a)[d], current study[i]		
Collembola	Abundance	Current study[i]		Ulyshen and Hanula (2009a)[f]
Diplopoda	Abundance	Evans et al. (2003)[b] (Dalodesmidae), Topp et al. (2006b)[d], current study[i], Kappes et al. (2007)[e]		Ulyshen and Hanula (2009a)[f]
	Richness	Kappes et al. (2007)[e]		
Diptera	Abundance		Evans et al. (2003)[b] (Therevidae)	Ulyshen and Hanula (2009a)[f], current study[i]
Formicidae	Abundance			Andrew et al. (2000)[a], Ulyshen and Hanula (2009a)[f], current study[i]
	Richness	Andrew et al. (2000)[a]		
Gastropoda	Abundance	Kappes (2005)[e], Kappes et al. (2006)[d], Kappes (2006)[e], Kappes et al. (2007)[e]		
	Richness	Kappes (2005)[e], Kappes et al. (2006)[d], Kappes (2006)[e], Kappes et al. (2007)[e]		
Hemiptera	Abundance			Ulyshen and Hanula (2009a)[f], current study[i]
Hymenoptera (excl. Formicidae)	Abundance			Current study[i]
Isopoda	Abundance	Jabin et al. (2004)[c], Topp et al. (2006b)[d], current study[i], Kappes et al. (2007)[e]		
	Richness	Kappes et al. (2007)[e]		
Isoptera	Abundance			Ulyshen and Hanula (2009a)[f]
Opiliones	Abundance	Current study[i]		
Pseudoscorpiones	Abundance	Evans et al. (2003)[b] (Neobisiidae), Jabin et al. (2004)[c,j]		Ulyshen and Hanula (2009a)[f], current study[i]
Psocoptera	Abundance	Ulyshen and Hanula (2009a)[f]		Current study[i]
Thysanoptera	Abundance		Evans et al. 2003[b] (Phlaeothripidae)	Ulyshen and Hanula (2009a)[f]
Holometabolous insect larvae	Abundance	Ulyshen and Hanula (2009a)[f]		Current study[i]
Annelida	Abundance	Current study[i]		

[a] *Eucalyptus* logs in a secondary forest, Australia.
[b] *Nothofagus* logs (decay class III) in a primary forest, New Zealand.
[c] Moderately decayed logs (decay class II) in a mature hardwood forest, Germany.
[d] decayed logs (decay classes II–IV) in a primary hardwood forest, Slovakia.
[e] Secondary mixed hardwood forests, Germany.
[f] *Pinus* logs (∼2, 6 and 10-years-old) in a secondary forest, USA.
[g] *Populus* logs (decay classes III–IV) in a secondary forest, Canada.
[h] Decayed logs (decay classes II–III) in a secondary mixed hardwood forest, USA.
[i] *Fraxinus* logs (decay class I) in secondary forests, USA.
[j] Difference was observed only near the forest edge.

forest edge than in the interior. The authors attributed their findings to leaf litter near the forest edge being drier as a consequence of sunnier and windier conditions.

Because canopy thinning significantly reduces leaf litter moisture content (Shure and Phillips 1991; Yi and Moldenke 2008) and dead wood represents a relatively stable source of moisture (Amaranthus et al. 1989; Marra and Edmonds 1998; Remsburg and Turner 2006), gap formation and inputs of woody debris to the forest floor resulting from EAB-induced ash mortality may have interacting effects on litter-dwelling arthropods. The current study was designed to explore this possibility as part of a long-term multidisciplinary project investigating the ecological impacts of EAB. We hypothesized that (1) the abundances of some arthropod and earthworm taxa would decrease with increasing canopy openness, (2) the densities of some taxa would be higher near dead ash logs than away from them and (3) the extent to which these taxa were concentrated near logs would increase with increasing canopy openness.

Methods

Study area

This research took place in 36 transects previously established in mature second-growth forests throughout the Upper Huron River watershed within Oakland and Washtenaw counties, Michigan (Smith 2006). Transects were located in Huron-Clinton Metroparks (Hudson Mills, Indian Springs, and Kensington) and Michigan Department of Natural Resources Recreation Areas (Highland, Pontiac, and Proud Lake). Hydric sites prone to flooding were intentionally avoided in this study. The seedling, understory, and overstory woody vegetation have been characterized in detail for all transects (Smith 2006). Tree genera typical of the region, including *Acer*, *Betula*, *Carya*, *Liriodendron*, *Populus*, *Prunus*, *Quercus*, *Tilia*, *Ulmus*, etc., dominated the overstory throughout the study area. Although *Fraxinus* spp. (i.e., *F. americana* L., *F. nigra* Marsh. and *F. pennsylvanica* Marsh.) were formerly common in the overstory (Smith 2006), more than 99% of ash trees with stem diameters greater than 4 cm have since been killed by EAB, and many had fallen to the ground by the time of sampling (Herms et al. 2009).

Leaf litter sampling

One *Fraxinus* "log" (i.e., fallen tree) was selected within or near each of the 36 transects. On average (±SE), the logs were 85 ± 4% covered by bark (range: 10–100%), 19 ± 1 m long (range: 9–35 m) and 30 ± 2 cm in basal diameter (range 11–54 cm). To be selected, each log had to belong to decay class 1 (Woodall and Williams 2005), be in contact with the ground along much of its length and be surrounded by leaf litter. All logs were killed by EAB as evidenced by galleries etched into the sapwood and the presence of characteristic D-shaped adult emergence holes. At two times in 2010 (May and June) leaf litter was sampled immediately next to ("near") and 1–3 m away from ("far") each log. The variable distance of the "far" samples resulted from the presence of other dead wood nearby as these samples were not taken within 1 m of any dead wood in contact with the forest floor. Collections were made using a 10 cm-wide hand-held garden rake. Samples were sifted through chicken wire (hexagonal mesh openings approximately 3.5 long × 3 cm wide) into 473 ml plastic cups until full. While the volume of litter sampled was held constant at all locations, the area of the forest floor sampled varied noticeably among plots due to differences in leaf litter depth (e.g., in some cases the humus layer was nearly absent).

Arthropod and earthworm extraction and processing

After each collection, the 72 samples were simultaneously placed in Berlese funnels for 1 week to extract arthropods and earthworms. The Berlese funnels consisted of 473 ml plastic cups lined with wire mesh (3 mm square openings). The samples were situated approximately 13 cm below 15 W light bulbs, the light and heat from which gradually forced the arthropods and earthworms out of the sample and into vials of ethanol attached to a funnel below. Abundance data were collected for all taxa and beetles were assigned to morphospecies.

Canopy gaps

After full leaf expansion, a hemispherical photograph was taken above each log using a digital camera (Nikon Coolpix, 8400) with a fisheye lens (Nikon FC-E9). The WinSCANOPY program (Regent Instruments, Quebec, Canada) was then used to calculate canopy gap fraction, the percentage of pixels per image classified as sky as opposed to vegetation.

Data analysis

Data from the two sampling periods were combined before analysis. Simple linear regression analyses were performed to test whether the abundances (log(x) or square-root transformed, when necessary, to better satisfy normality assumptions) of major arthropod taxa and earthworms decreased with increasing gap fraction (i.e., hypothesis 1). The nonparametric Wilcoxon signed rank test (Wilcoxon 1945) was used to compare arthropod and earthworm abundances (and species richness, for Coleoptera) between locations (i.e., hypothesis 2). When necessary, the data were log(x + 1)-transformed to satisfy symmetry assumptions. Finally, simple linear regression analyses were carried out for taxa found to differ in abundance (or species richness, for Coleoptera) between the two locations. The response variables in these analyses were the ratios (near + 1)/(far + 1) (i.e., using abundance or richness data), representing how concentrated arthropods were next to the logs (i.e., hypothesis 3). The independent variable was gap fraction. Again, when necessary, the data were log(x) or square-root transformed to achieve normality.

Results

A total of 70,548 arthropods were collected (mostly Acari and Collembola) including 86 beetle morphospecies. Canopy gap fraction was normally distributed, ranging from about 1 to 10%. Based on regression analyses, none of the major arthropod taxa nor earthworms varied in abundance across this gap fraction range (results not shown). Abundances of Aranea, Coleoptera, Collembola, Diplopoda, Isopoda, Opiliones and Annelida, however, were significantly higher near logs than away from them (Table 2). Coleoptera morphospecies richness was also significantly higher near logs (Table 2). Of these taxa, only isopods were affected by canopy gap fraction, being significantly (p = 0.008) less concentrated next to logs as canopy gap fraction increased. This relationship strengthened when three outliers were excluded (Fig. 1).

Discussion

Our first hypothesis, that some arthropod and earthworm taxa would become less abundant with increasing canopy openness, was not supported, perhaps due to the relatively narrow gap fraction range. Support was found, however, for our second hypothesis, that the densities of some taxa would be higher near dead ash logs

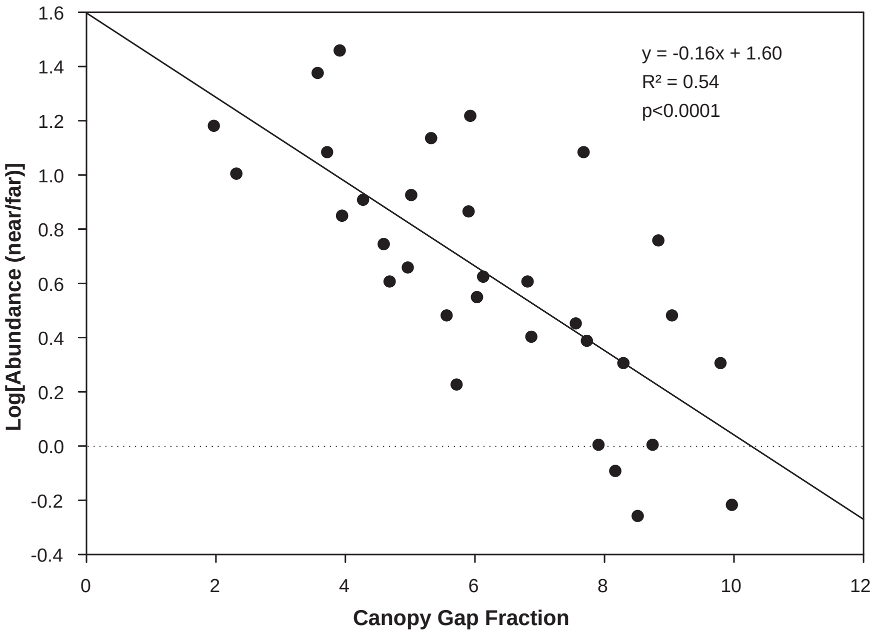

Fig. 1. Relationship between the concentration of isopods near ash logs and canopy gap fraction. The ratio near/far represents the extent to which isopods were more abundant near (0–10 cm) logs than far (1–3 m) from them (i.e., isopods were more abundant near the logs above the dotted line).

Table 2
Mean ± SE (n = 36) abundance (and richness, for Coleoptera) of common (>50 individuals) invertebrate taxa collected from leaf litter taken near (0–10 cm) and far (1–3 m) from *Fraxinus* logs in Michigan, USA. p-Values are given for the Wilcoxon signed rank test.

	Near	Far	p
Acari	522.5 ± 63.4	564.4 ± 77.9	0.20
Araneae	5.2 ± 0.5	2.6 ± 0.4	<0.01
Chilopoda	1.3 ± 0.2	0.9 ± 0.2	0.14[a]
Coleoptera	25.6 ± 3.2	18.0 ± 2.1	0.01[a]
Coleoptera-richness	6.5 ± 0.3	4.9 ± 0.3	<0.01
Collembola	397.4 ± 42.1	226.0 ± 31.1	<0.01
Diplopoda	8.9 ± 1.3	4.8 ± 1.0	<0.01
Diptera	1.4 ± 0.2	1.4 ± 0.2	0.70[a]
Formicidae	19.4 ± 2.7	17.9 ± 2.9	0.72[a]
Hemiptera	1.1 ± 0.2	0.8 ± 0.2	0.33[a]
Hymenoptera	2.5 ± 0.4	2.4 ± 0.3	0.85
Isopoda	15.2 ± 2.6	3.9 ± 1.2	<0.01[a]
Opiliones	1.2 ± 0.2	0.6 ± 0.2	<0.01[a]
Pseudoscorpiones	6.8 ± 1.2	6.2 ± 1.1	0.34[a]
Psocoptera	4.3 ± 1.0	3.6 ± 0.8	0.27[a]
Holometabolous insect larvae	44.1 ± 4.3	45.9 ± 4.5	0.86
Annelida	6.6 ± 1.2	5.1 ± 1.1	0.01

[a] Data log(x + 1)-transformed to satisfy symmetry assumptions.

than away from them. While these findings are consistent with those from studies carried out in other regions (Table 1), this is the first in which recently fallen logs belonging to decay class I were used. Because logs at early stages of decay represent nutrient sinks (as opposed to sources, see Evans et al. 2003) and are too intact to be readily colonized by litter-dwelling arthropods (see Irmler et al. 1996), they probably benefit these organisms the most by maintaining favorable conditions (e.g., moisture) in adjacent litter (Amaranthus et al. 1989; Marra and Edmonds 1998; Remsburg and Turner 2006).

Although gap formation is known to decrease leaf litter moisture (Yi and Moldenke 2008), we found no support for our third hypothesis, that arthropods would be more concentrated near logs as canopy gap fraction increased. It is possible that canopy gap fraction did not vary over a wide enough range in this project to appreciably affect the distributions of litter-dwelling arthropods with respect to dead wood. Isopods, however, were significantly less concentrated near logs as canopy gap fraction increased, a surprising result considering these organisms are among the most desiccation-prone of all litter-dwelling arthropods. Because hydric sites prone to flooding were intentionally avoided in this study, the possibility that canopy thinning increased leaf litter moisture by raising the water table seems unlikely. Other cues (e.g., temperature, sunlight, etc.) may have governed the patterns observed for this taxon.

Because leaf litter occurs at the interface between the soil and atmosphere, the invertebrates inhabiting it represent important linkages between above- and below-ground food webs. The responses of these organisms to forest disturbance brought about by invasive species should therefore have far-reaching ecological effects. It can be concluded from the current study that litter-dwelling arthropods in EAB-infested forests are favored by inputs of ash wood to the forest floor but are largely unaffected by increases in canopy openness, at least across the gap fraction range studied. It remains unclear whether coarse woody debris increases the abundance of litter-dwelling arthropods and earthworms or just affects how they are distributed (Ulyshen and Hanula 2009b).

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