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5 **Title: Response of the forest floor invertebrate community to canopy gap formation caused**
6 **by early stages of emerald ash borer-induced ash mortality**

8 Running Title: Perry and Herms: Emerald ash borer and forest floor invertebrates

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Abstract

Emerald ash borer (EAB; *Agrilus planipennis*) is an invasive wood-boring beetle that causes rapid ash tree mortality, widespread formation of canopy gaps, and accumulation of coarse woody debris (CWD) in forests. The objective was to quantify the effects of canopy gaps, ash CWD and their interaction caused by EAB-induced ash mortality on the forest floor invertebrate community. A two-year manipulative experiment was conducted in forests at NASA Plum Brook Research Station in Ohio, USA. Canopy gaps caused by ash mortality decreased the activity-abundance of some taxa, such as Opiliones, Carabidae and several families of Collembola, as well as invertebrate richness and diversity, but had minor effects on community composition. CWD had minimal effects on the forest floor invertebrate community overall, but altered the activity-abundance of several invertebrate groups, and marginally increased taxonomic evenness in closed canopy treatments. The results of this study suggest that the effects of ash mortality on forest floor invertebrate communities change over time due to an inverse temporal relationship in magnitude effects of canopy gaps, which diminish over time, and accumulation of CWD, which increases over time. These findings contribute to our understanding of the effects of disturbance on ecosystems and the cascading ecological impacts of emerald ash borer invasions in forests.

Keywords: biological invasions, community structure, disturbance, ecological impacts, forests, ground-dwelling invertebrates

1.1 Introduction

The establishment and spread of non-native species has had unprecedented economic and ecological impacts worldwide (Vitousek *et al.*, 1996; Hulme, 2009), because biological invasions pose a severe threat to native habitat, biodiversity and ecosystem services (Allen and Humble, 2002; Holmes *et al.*, 2009; Aukema *et al.*, 2011). In North American forests, non-native species often cause irreversible and cascading direct and indirect impacts on community dynamics and ecosystem processes (Liebhold *et al.*, 1995; Lovett *et al.*, 2006; Gandhi and Herms, 2010a). As the frequency of biological invasions continues to increase globally (Levine and D'Antonio, 2003; Aukema *et al.*, 2010), understanding the effects of exotic species has become essential for biodiversity conservation and ecosystem management (Byers *et al.*, 2002; Moser *et al.*, 2009).

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) is an invasive wood-boring buprestid beetle native to SE Asia that has killed hundreds of millions of ash trees (*Fraxinus* spp.) since its accidental introduction into North America (Herms and McCullough, 2014). Ash mortality was reported to exceed 99% in forests in southeast Michigan, USA (Klooster *et al.*, 2014), where EAB first established in North America (Siegert *et al.*, 2014). Widespread EAB-induced ash mortality is having direct and indirect ecological impacts on forest structure, function and successional trajectories (Gandhi and Herms, 2010a, b; Smith *et al.*, 2015).

Ash mortality caused by EAB is increasing the frequency of gaps in the forest canopy and ash logs and branches (CWD; coarse woody debris) on the forest floor, as trees are dying rapidly and relatively simultaneously (Gandhi and Herms, 2010a; Knight *et al.*, 2013; Klooster *et al.*, 2014). When canopy gaps are formed, environmental conditions and resources on the forest floor are altered, such as light availability, temperature, moisture and understory vegetation (Collins and Pickett, 1987; Gray *et al.*, 2002). As ash trees die and fall, CWD accumulates on the forest floor, increasing overall habitat heterogeneity in forest ecosystems. Although changes

in microclimate and habitat structure on the forest floor have the potential to impact forest communities, such as populations of forest floor invertebrates (Levings and Windsor, 1984; Shure and Phillips, 1991), CWD may act as refugia and reduce the variability in environmental conditions, such as temperature and moisture, induced by increased light (Evans *et al.*, 2003; Remsburg and Turner, 2006).

Canopy gaps and CWD from EAB-induced ash mortality may interact to impact the forest floor invertebrate community. Accumulation of CWD in canopy gaps may stabilize changing environmental conditions on the forest floor by reducing the variability caused by increased light. Forest floor invertebrates living throughout the leaf litter and soil layers are highly diverse and respond to changes in habitat structure and microclimate factors on the forest floor, such as soil moisture (Levings and Windsor, 1984), coarse woody debris (Ulyshen and Hanula, 2009a), leaf litter (Koivula *et al.*, 1999), and vegetation cover (Shure and Phillips, 1991).

Ulyshen *et al.* (2011) found that many invertebrate taxa, including earthworms, spiders, harvestmen, isopods, millipedes, beetles and springtails, were more abundant in leaf litter near ash logs than in leaf litter away from logs, but there was no effect of canopy gaps in these forests invaded by EAB. These results suggest EAB can have indirect impacts on ground-dwelling invertebrates through the accumulation of ash CWD (Ulyshen *et al.*, 2011). We propose that there is a temporal pattern to the magnitude effects of canopy gaps and accumulation of CWD as a result of EAB-induced ash mortality. At early stages of ash mortality, large canopy gaps created by the recent death of ash trees have the greatest magnitude effect on the ground flora and fauna, while downed CWD has yet to accumulate in large amounts on the forest floor. As time progresses, there is a large pulse of ash branches and logs that fall to the ground, as growth

from understory and surrounding canopy trees close the gaps. How canopy gaps and CWD interact over time to affect ground-dwelling invertebrates needs further investigation.

A previous companion study utilizing the same experimental design investigated the effects of EAB-induced ash mortality on ground beetle abundance, species diversity and assemblage composition (Perry and Herms, in press). We documented initial decreases in ground beetle activity-abundance and changes in species composition in response to canopy gaps created by EAB, but these were ephemeral, suggesting assemblages may be resilient to this level of canopy disturbance (Perry and Herms, in press). The current study expands upon this by investigating the indirect impacts of EAB-induced ash mortality on forest floor invertebrates to understand community responses. The objective of this study was to test the effects of early stages of EAB-induced ash mortality to understand how canopy gaps and ash CWD interact to impact the ground-dwelling invertebrate community. Based on the proposed inverse temporal relationship between canopy gap size and accumulation of CWD, we predicted that (1) canopy gaps created by EAB-induced ash mortality would decrease forest floor invertebrate abundance and diversity, resulting in a change in community composition; and (2) in canopy gaps, ash CWD would increase invertebrate abundance and diversity by buffering environmental changes on the forest floor induced by increased light.

1.2 Materials and Methods

1.2.1 Study Site

Research was conducted at National Aeronautics and Space Administration (NASA) Plum Brook Research Station (N41°23.619; W82°40.955) in Ohio, USA. Plum Brook's 2,600 hectares (Harrington, 1999) consists of patches of open field and deciduous forest dominated by

ash, (*Fraxinus* spp.), maple (*Acer* spp.), elm (*Ulmus* spp.) and oak (*Quercus* spp.) species. Average tree importance values ($\pm$ SE) for these dominant species at Plum Brook were 77.5 ($\pm$ 0.3), 65.1 ($\pm$ 10.1), 36.7 ($\pm$ 2.4) and 15.2 ($\pm$ 1.1), for ash, maple, elm and oak trees, respectively (Long, 2013). These values are calculated for each tree by summing the relative density, relative frequency and relative dominance (McCormick and Platt, 1980). Average ash density (stems/ha) in over 100 forest plots in southeastern Michigan, where EAB first established, was 171 ($\pm$ 112) with a corresponding average ash importance value of 62 ($\pm$ 23) (Smith *et al.*, 2015). An average importance value of 77.5 suggests ash trees were common at Plum Brook. The percentage cover of CWD was low in the forests at Plum Brook where the study plots are located, with a reported average of 2.2% (Long, 2013). This suggests the ash trees killed by EAB had not fallen to the forest floor at the time of this study. Mesic forest soils supported vernal pools in the spring. Common understory plants included spicebush (*Lindera benzoin* (L.) Blume), multiflora rose (*Rosa multiflora* Thunb.) and Japanese barberry (*Berberis thunbergii* DC).

1.2.2 Experimental Design

To test the effects of canopy gaps, ash CWD, and their interaction on the forest floor invertebrate community, a manipulative experiment was implemented with a factorial combination of two treatments: presence/absence of canopy gaps and presence/absence of ash CWD, resulting in four treatment combinations: 1) canopy gaps present, CWD present; 2) gaps present, CWD absent; 3) gaps absent, CWD present; 4) gaps absent, CWD absent (control and no disturbance). The experiment contained eight blocks, and each block contained all four treatment combinations represented once. A previous paper reported the effects of these

treatments on ground beetle species activity-abundance and diversity (Perry and Herms, in press).

Blocks consisted of two existing canopy gaps (20-30 meters apart) ranging in size from one to four dead dominant or codominant ash trees. Closed canopy treatments were established in a random direction ≥ 20 m away from the canopy gaps. To confirm differences in light availability on the forest floor, canopy openness was measured on 28 June 2011 and 21 June 2012 using spherical crown densiometer calculations (Perry and Herms, in press). When these treatments were implemented, canopy gaps were at their maximum size because the ash trees had died recently. The dead trees were still standing, and the growth of understory and surrounding canopy trees had not yet begun to close the gaps. Therefore, the magnitude of the treatment corresponds with the maximum size of canopy gaps caused by EAB-induced ash mortality at the study site.

Standing dead ash trees that had been killed by EAB were harvested for the CWD treatment in the surrounding forest away from the experimental blocks. Trunks were cut into one meter bolts (15-20 cm in diameter) so that all sections of ash CWD used in the experiment were of the same size and decay stage (i.e., stage I: intact bark, sound structural integrity) (Harmon and Sexton, 1996; Pyle and Brown, 1999; Woodall and Williams, 2005). In 2011, four bolts were placed at each treatment location in pairs. Within the treatment, pairs of bolts were approximately 5 m apart, and each pair was placed parallel with approximately 0.5 m of space between them. Ash bolts were left in the field for the duration of the two-year experiment.

At the study site, the majority of ash trees greater than 2.5 cm in diameter had been killed by EAB, but the trees were still standing, suggesting they had died recently. A significant amount of CWD can accumulate on the forest floor as ash trees begin to uproot or snap at the

base. However, the amount of CWD on the forest floor was limited because this pulse had not yet occurred at the study site, suggesting the magnitude of our CWD treatment was comparable to background levels at the time the experiment was initiated. Therefore, the size of the canopy gaps and the intensity of the CWD treatment in this study were biologically relevant, reflecting the early stages of EAB-induced ash mortality when gaps in the canopy are large, but the amount of downed ash CWD is still low.

1.2.3 Invertebrate Collection

Forest floor invertebrates were quantified using pitfall traps (Yi *et al.*, 2012). Although pitfall traps are a common tool for collecting ground-dwelling arthropods, this passive sampling method tends to collect more active invertebrates. Therefore, the abundance of invertebrates is presented as activity-abundance (individuals per treatment) (Spence and Niemelä, 1994; Yi *et al.*, 2012). Each treatment had two pitfall traps (5 m apart) either between two CWD bolts (i.e., CWD present) or ≥ 5 meters away from any CWD (i.e., CWD absent). Pitfall traps were placed in the center of the gap for the canopy treatment. Traps consisted of an outer (1 L) and an inner (500 mL) plastic cup dug into the ground flush with the soil surface (Spence and Niemelä, 1994). Approximately 4 cm of propylene glycol (recreational vehicle and marine antifreeze, Peak Company[®]) and 2-3 drops of detergent were added to the inner cup for invertebrate collection and preservation. A piece of Masonite board (100 cm²) was positioned approximately 3 cm above each cup to exclude rain. Hardware cloth (500 cm²) was secured over the entire trap with 30 cm stakes to limit animal disturbance.

Sampling was conducted for two-week intervals once per month during the growing season of 2011 and 2012. Forest floor invertebrates were collected from June through October in

2011 and June through September in 2012, resulting in four collection periods each year. Sampling intervals included June 28-July 11, July 25-August 8, August 22-September 5 and September 19-October 3, 2011 and June 5-21, July 3-17, July 31-August 14 and August 28-September 10, 2012. During both years, all traps were emptied on the same day for each sampling interval. Non-insect invertebrates were identified to order and insects were identified to family based on taxonomy presented in Triplehorn and Johnson (2005).

1.2.4 Data Analysis

The effects of canopy gaps, ash CWD and their interaction on the forest floor invertebrate community were analyzed using repeated measures analysis of variance (ANOVA) with univariate analyses for each date in SAS (SAS Institute, 2013). Mean separation tests (LSD, $\alpha = 0.05$) were used if there was a significant *F*-test. Community response variables were total invertebrate activity-abundance, richness, evenness and diversity. Predictor variables were canopy gaps (presence/absence) and CWD (presence/absence) as fixed factors, sampling interval as a repeated factor, and block as a random factor. Pitfall catches for each forest floor invertebrate group were averaged for replicate traps in each treatment. Activity-abundance data were rank transformed to meet statistical assumptions of normality and homogeneity of variance. Rank transformations can be applied to parametric tests to correct these issues as an alternative to the use of non-parametric tests (Quinn and Keough, 2002). Data from the 11 July 2011 collection were removed from all analyses due to high disruption of pitfall traps by animals. Years were analyzed separately. Forest floor invertebrate taxonomic richness (number of taxa per treatment), Pielou's *J* evenness index (Pielou, 1966) and Shannon diversity index (Peet, 1974) were calculated using PC-ORD software (McCune and Mefford, 2006).

Activity-abundance of each invertebrate taxon was individually assessed for the effects of canopy gap and CWD treatments using ANOVA tests. Activity-abundance was pooled over the sampling intervals for each year separately, resulting in the total summer activity-abundance for each group in 2011 and 2012 as the response variables. Model predictor variables included canopy gaps (presence/absence), CWD (presence/absence) and block. Abundance data were rank transformed to improve normality. For each year, invertebrate activity-abundance was evaluated for groups that had ≥ 50 total individuals collected throughout the season. Invertebrate taxonomic groups excluded due to low activity-abundance include Chilopoda: Geophilomorpha and Lithobiomorpha, Pseudoscorpiones, Diplura, Elateridae, Curculionidae, Forficulidae, and Blattidae.

Changes in forest floor invertebrate community composition between canopy treatments and between CWD treatments was assessed using multi-response permutation procedures (MRPP), and these differences were visualized using non-metric multidimensional scaling (NMDS). Criteria used in the NMDS ordination included Sørensen's distance measure with two dimensions, 500 iterations, 50 runs of real data, and 20 runs for the Monte Carlo test. Invertebrate activity-abundances were pooled per treatment and ordinations were conducted separately for each year. MRPP analyses and NMDS ordinations were conducted using PC-ORD software (McCune and Mefford, 2006).

Indicator species analyses (ISA) were performed to determine if any forest floor invertebrate taxa were associated with either canopy gap or CWD treatments in 2011 and 2012. ISA identifies species that are indicative of a particular environmental characteristic or habitat. To be considered a good indicator, the taxa must be present in high abundance and high frequency at most treatments possessing the characteristic of interest (Dufrêne and Legendre,

1997; McCune and Grace, 2002). Forest floor invertebrate taxa were included in the analyses if present in at least 15% of observations and ≥ 50 individuals were collected. Indicator values were calculated and tested for significance using a Monte Carlo permutation procedure. ISA analyses were conducted using PC-ORD software (McCune and Mefford, 2006).

1.3 Results

A total of 60,835 individuals were collected in pitfall traps in 2011 and 2012, representing 10 non-insect invertebrate taxa and 19 insect families (Table 1). Of these 29 taxa, 13 taxonomic groups were uncommon ($< 1\%$ of total individuals collected; Silphidae, Scarabaeidae, Elateridae, Curculionidae (excl. Scolytinae), Forficulidae, Blattidae, Diplura, Pseudoscorpiones, Geophilomorpha, Lithobiomorpha, Spirobolida, and Gastropoda: snails and slugs), 13 groups were common (1-10% of total individuals collected; Isotomidae, Sminthuridae, Hypogastruridae, Carabidae, Staphylinidae, Nitidulidae, Scolytinae, Formicidae, Rhaphidophoridae, Gryllidae, Araneae, Opiliones, and Polydesmida), and three were abundant ($> 10\%$ of total individuals; Tomoceridae, Entomobryidae, and Isopoda). The most abundant invertebrates by far were Collembola, comprising over 50% of the total trap catch each year, totaling 30,781 individuals. Five different families of Collembola were collected, including Isotomidae, Entomobryidae, Sminthuridae, Tomoceridae and Hypogastruridae.

Activity-abundance of several forest floor invertebrate taxa decreased in canopy gaps, but total invertebrate activity-abundance was not significantly lower in canopy gaps in 2011 ($F_{1,21} = 3.09$, $P = 0.093$) and unaffected in 2012 ($F_{1,18} = 0.00$, $P = 0.980$) (Table 2). In 2011, the activity-abundance of Carabidae ($F_{1,83} = 24.2$, $P < 0.001$), Scarabaeidae ($F_{1,83} = 6.56$, $P = 0.012$), Rhaphidophoridae ($F_{1,83} = 5.81$, $P = 0.018$), Sminthuridae ($F_{1,78} = 11.80$, $P = 0.001$) and

Opiliones ($F_{1,83} = 8.07$, $P = 0.005$) decreased in canopy gaps. For Carabidae, an average of 2.6 ± 0.4 beetles were collected in canopy gaps compared to 5.2 ± 0.6 in closed canopy treatments. In 2012, Opiliones ($F_{1,109} = 22.9$, $P < 0.001$), Rhaphidophoridae ($F_{1,109} = 9.74$, $P = 0.002$), Isotomidae ($F_{1,108} = 8.63$, $P = 0.004$) and Hypogastruridae ($F_{1,108} = 16.5$, $P < 0.001$) had lower activity-abundances in canopy gaps compared to closed canopy treatments. Opiliones had an average of 1.5 ± 0.2 individuals in canopy gaps compared to 3.0 ± 0.3 in closed canopies. Polydesmida, an order of millipedes, was the only invertebrate group that increased in canopy gaps (2012: $F_{1,109} = 12.3$, $P < 0.001$). Activity-abundance of most forest floor invertebrates was not affected by CWD treatments in 2011 ($P = 0.156$ to 0.946) or 2012 ($P = 0.186$ to 0.957). Isopoda was the only invertebrate taxa affected by the CWD treatment, with increased activity-abundance in the presence of CWD (2012: $F_{1,109} = 3.96$, $P = 0.049$).

Forest floor invertebrate richness was lower in canopy gaps compared to closed canopy treatments in 2011 ($F_{1,16} = 7.69$, $P = 0.013$) and 2012 ($F_{1,16} = 4.55$, $P = 0.048$) (Table 2). Similarly, invertebrate diversity decreased in canopy gaps compared to closed canopy treatments in 2011 ($F_{1,16} = 6.87$, $P = 0.018$) and 2012 ($F_{1,16} = 5.71$, $P = 0.029$) (Fig.1, Table 2). Forest floor invertebrate evenness was not affected by canopy gaps. CWD did not affect forest floor invertebrate richness, evenness or diversity in either year (P ranged 0.086 to 0.981) (Table 2).

Forest floor invertebrate community composition was similar between canopy gap and closed canopy treatments overall in 2011 (MRPP: $P = 0.395$) and 2012 (MRPP: $P = 0.436$), but composition changed over the growing season each year (MRPP: 2011 $P < 0.001$ for all month combinations; 2012 $P = 0.03$ to < 0.001). Therefore, separate analyses were conducted for each sampling interval in 2011 and 2012. In 2011, forest floor invertebrate community composition differed between canopy gap and closed canopy treatments during the fourth sampling interval

(September 19-October 3; 2 dimensions, final stress = 11.48, axis 1 R^2 = 50.5%, axis 2 R^2 = 37.6%; MRPP: P = 0.050), but was similar for all other intervals (MRPP: P = 0.088 to 0.485). In 2012, community composition differed between canopy treatments during the third interval (July 31-August 14; 2 dimensions, final stress = 13.95; axis 1 R^2 = 44.0%, axis 2 R^2 = 39.3%; MRPP: P = 0.002), but was similar for all other intervals (MRPP: P = 0.366 to 0.481). The CWD treatment did not affect invertebrate community composition in 2011 (MRPP: P = 0.265 to 0.900) or 2012 (MRPP: P = 0.444 to 0.962).

Several invertebrate taxa were identified as indicators (Table 3). Seven taxonomic groups were found to be good indicators of the closed canopy treatment, and three groups were considered indicators of CWD. Polydesmida was the only taxonomic group considered an indicator of canopy gaps.

Interactive effects of canopy gap and CWD treatments on the forest floor invertebrate community were largely taxa-specific and only observed in 2012. CWD mediated the activity-abundance of Carabidae, Tomoceridae and Gastropoda, and forest floor invertebrate taxonomic evenness. The activity-abundance of Carabidae decreased in canopy gaps with CWD, and in closed canopies without CWD ($F_{1,109} = 15.3$, $P = 0.0002$). Tomoceridae activity-abundance was marginally lower in canopy gaps, but the presence of CWD decreased numbers further ($F_{1,108} = 3.15$, $P = 0.078$). In the closed canopy treatment, activity-abundance of Gastropoda, specifically slugs, was highest when CWD was present and lowest when it was absent ($F_{1,109} = 5.56$, $P = 0.031$). Invertebrate taxonomic evenness was marginally higher in closed canopy treatments with CWD ($F_{1,16} = 3.97$, $P = 0.063$) (Fig. 3).

1.4 Discussion

Ash mortality caused by emerald ash borer had variable effects on the forest floor invertebrate community, but overall these impacts were modest to minimal. Canopy gaps decreased the activity-abundance of several invertebrate groups, taxonomic richness and diversity in both years, which is consistent with our first prediction that ash mortality would reduce the abundance and diversity of the forest floor invertebrate community. However, we did not observe a significant change in community composition. Total invertebrate activity-abundance was not affected by canopy gaps, but when taxa were analyzed individually, there were several group-specific responses. Activity-abundance of Opiliones, Carabidae, Scarabaeidae, Rhaphidophoridae, Sminthuridae, Hypogastruridae and Isotomidae decreased in canopy gaps compared to closed canopy treatments. Sminthuridae, Hypogastruridae and Isotomidae are all families of Collembola. Members of Sminthuridae, Hypogastruridae and Isotomidae were generally the smallest individuals collected, and may have been more susceptible to high light levels and desiccation in canopy gaps (Verhoef, 1977; Verhoef and van Selm, 1983). The CWD treatment had minimal effects on the forest floor invertebrate community overall. However, CWD altered the activity-abundance of some invertebrate taxa in canopy gap and closed canopy treatments with the direction of change being group-specific.

Canopy gaps caused by natural and anthropogenic disturbances alter the environment on the forest floor through increased light availability, higher temperatures and soil moisture levels, reduced leaf litter moisture and depth, and increased downed CWD (Gray *et al.*, 2002; Greenberg and Forrest, 2003; Richardson *et al.*, 2010; Perry and Herms, in press). These changes to the forest floor environment have the potential to impact ground-dwelling invertebrate species differently depending on their life history strategies and habitat requirements. For example, the abundance of small ground-dwelling invertebrates, such as

Collembola, is often related to litter and soil moisture content with degree of drought tolerance likely driving species-specific responses (Verhoef, 1977; Verhoef and van Selm, 1983; Levings and Windsor, 1984). Responses of ground-dwelling invertebrates may also be dependent on the extent of environmental differences on the forest floor between the surrounding forest and the open patch created by canopy disturbance. Shure and Phillips (1991) reported higher densities of ground-dwelling invertebrates in small (0.016 ha) and large (2.0 – 10 ha) canopy openings, but lower densities in mid-sized (0.08-0.4 ha) gaps. The authors suggest that differences in environmental conditions between forest openings and the surrounding forest is minimal for small gaps, and buffered by increased understory vegetation cover in large gaps (Shure and Phillips, 1991). The existing canopy gaps created by EAB-induced ash mortality utilized in this study ranged in size from one to four dead ash trees. Because the trees had died recently, the understory vegetation had just begun responding to increased light levels and growing space in these gaps, and did not minimize environmental conditions on the forest floor (Perry and Herms, in press).

There were more invertebrate taxa found to be indicators of the closed canopy treatment compared to only one group (Polydesmida) identified as an indicator of canopy gaps. Opiliones, Carabidae, Scarabaeidae, Rhaphidophoridae, Sminthuridae, Isotomidae and Hypogastruridae were indicative of closed canopy treatments. These invertebrate groups represent several functional guilds (Coleman *et al.*, 2004), which suggests undisturbed forest may be more indicative of a functionally diverse invertebrate community than patches with canopy disturbance. Not surprisingly, these indicator taxa are the same invertebrates that decreased in activity-abundance in canopy gap treatments, and are likely the groups driving community patterns. Both Opiliones and Carabidae are mobile predators that feed on a variety of

invertebrate prey (Bristowe, 1949; Thiele, 1977; Adams, 1984; Lövei and Sunderland, 1996), providing top-down regulation of the detritivore community on the forest floor, as well as mediating ecosystem processes such as decomposition. Scarabaeidae is a diverse family of beetles containing many species that are coprophagous, feeding on animal dung and contributing to nutrient cycling (Nichols *et al.*, 2008). Three families of Collembola, including Sminthuridae, Isotomidae and Hypogastruridae, were also considered indicators of closed canopy treatments. Collembola are abundant in forest litter and soil, and provide important ecosystem services, as they can be categorized as fungivores, detritivores or predators depending on the species (Hopkin, 1997). Other studies investigating the impacts of canopy gaps on forest floor invertebrates have reported adverse effects of gaps overall with strong responses from select taxa and functional guilds. Greenberg and Forrest (2003) observed reduced total ground-dwelling macroarthropod activity-abundance and biomass in canopy gaps created by wind disturbance compared to undisturbed forest. Total macroarthropod responses were driven by changes in a few dominant taxa representing multiple functional groups, such as Carabidae, Araneae, Julida, Spirobolidae and Scolopendromorpha (Greenberg and Forrest, 2003). Similarly, Richardson *et al.* (2010) found reduced diversity and biomass in canopy gaps with predators and large detritivores driving these patterns, while fungivores, such as Acari, Collembola and Psocoptera, increased in gaps.

CWD did not increase the abundance and diversity of the forest floor invertebrate community in canopy gaps during either year of the study, but instead decreased the activity-abundance of invertebrates such as Carabidae and Tomoceridae in canopy gaps. Therefore, we found no evidence to support our second prediction that ash CWD would increase forest floor invertebrate abundance and diversity in canopy gaps. Perhaps this was because the magnitude of

our CWD treatment, which corresponds with the amount of ash CWD in early stages following tree mortality, was too low. However, other studies that have investigated the effects of CWD have found minimal effects on most ground-dwelling invertebrate taxa (Evans *et al.*, 2003; Ulyshen and Hanula, 2009b). Carabidae was the only taxa that increased in species diversity following dead wood manipulations that substantially increased CWD volume (Ulyshen and Hanula, 2009b). Perhaps reduction or removal of downed CWD in forests has a greater impact on ground-dwelling invertebrates than additions. Hanula *et al.* (2006) reported reduced catches of 10 invertebrates families, including Carabidae and three families of spiders, compared to increased catches of three invertebrate families following removal of all CWD. Additionally, CWD did not buffer changes in microclimate on the forest floor, such as soil temperature and moisture, in canopy gaps (Perry and Herms, in press). However, CWD increased the activity-abundance of some invertebrate taxa in the closed canopy treatment, such as slugs and isopods, and may be more important in this context, especially for taxa that are susceptible to desiccation (Getz, 1959; Dias *et al.*, 2012).

CWD played a marginal role in increasing invertebrate evenness in closed canopy treatments in 2012. Evenness is a community index that describes how evenly abundances are distributed between species or taxonomic groups (McCune and Grace, 2002). Uneven communities often have one or a few dominant species while the majority of the community is present at low abundances. In our study, CWD marginally increased invertebrate taxonomic evenness in closed canopy treatments, suggesting canopy gaps support more uneven forest floor invertebrate communities, which may reduce ecosystem functional stability and resilience (Wittebolle *et al.*, 2009).

Canopy gaps caused by EAB-induced ash mortality had the greatest impact on the forest floor invertebrate community, while the effects of CWD were minimal, as predicted by our model describing the inverse temporal relationship between canopy gaps and CWD. Perry and Herms (in press) also reported a greater impact of canopy gaps on carabid assemblages during the early stages of EAB-induced ash mortality. However, patterns of carabid and forest floor invertebrate community responses differed in that the effects of the gap treatment diminished during the second year of the study, and ground beetles showed resilience to canopy disturbance (Perry and Herms, in press). The family-level analyses reported in this study are consistent with this observation, as the activity-abundance of Carabidae was only affected by canopy gaps in 2011. Forest floor invertebrate taxonomic diversity was lower in canopy gaps during both years of the study, although the strength of gap effects varied over the growing season. In contrast, species diversity of Carabidae was not affected by gaps during either year (Perry and Herms, in press). Carabidae are widely considered biological indicators of environmental change (Rainio and Niemelä, 2003; Pearce and Venier, 2006), but they may not be suitable indicators of other taxa. These findings suggest that changes occurring at the community-level are not necessarily reflected in the species responses of individual taxa.

In forest ecosystems, the properties of natural and anthropogenic disturbances result in distinct temporal patterns of the magnitude effects of canopy gaps and CWD. We propose an inverse temporal relationship between the effect size of canopy gaps and accumulation of CWD caused by EAB-induced ash mortality on the forest floor invertebrate community (Fig. 4A). The effects of gaps diminish with canopy closure while the effects of CWD increase as trees fall over time. In contrast to tree mortality caused by insects, wind results in a different temporal pattern where the magnitude effects of canopy gaps and accumulation of CWD are greatest immediately

following the disturbance and decrease over time (Fig. 4B). Although estimates vary widely for both canopy recovery time and CWD decomposition owing to a suite of biotic and abiotic factors, the magnitude effects of CWD would likely persist for longer than canopy gaps (Harmon *et al.*, 1986; Everham and Brokaw, 1996), especially for forest floor invertebrates. Depending on the environmental conditions, decomposition of woody debris can take up to several decades or longer (Harmon *et al.*, 1986). Although size of the area impacted by wind disturbance may influence recovery time, we predict the effects of canopy gaps on forest floor invertebrates will likely dissipate faster than CWD, especially if the effects are mitigated by the growth of saplings and understory vegetation in large canopy gaps (Shure and Phillips, 1991). Canopy gaps consisting of one to four dead dominant or codominant ash trees killed by EAB would close more rapidly, within several years, from the growth of released understory trees and lateral growth of surrounding canopy trees.

During the early stages of ash mortality, canopy gaps have the greatest impact on the forest floor invertebrate community initially. The canopy gaps are at their maximum size, as the ash trees have died recently. Because the trees are still standing as snags, the amount of ash CWD on the forest floor is low during these early stages. The results from this study as well as those reported by Perry and Herms (in press) and Gandhi *et al.* (2014) align with the predicted effects of early stages of ash mortality. Ash CWD does not become abundant on the forest floor until the late stages of ash mortality, and this accumulation of woody debris coincides with canopy gap closure. Ulyshen *et al.* (2011) documented higher densities of ground-dwelling invertebrates near ash logs, but no effect of canopy gaps. These findings reflect the late stages of ash mortality when CWD is predicted to have a greater impact on the forest floor invertebrate community.

After investigating the interaction between canopy gaps and CWD during the early stages of EAB-induced ash mortality, we found the formation of gaps had a greater impact on the forest floor invertebrate community than CWD. Gandhi *et al.* (2014) documented decreased ground beetle activity-abundance and species diversity in canopy gaps caused by EAB-induced ash mortality. This study was conducted in the same forest plots as Ulyshen *et al.* (2011), but several years earlier when the canopy gaps had recently formed and were larger. Gandhi *et al.* (2014) reported $18.8 (\pm 1.8)$ in 2006 and $23.6 (\pm 2.1)$ average percentage canopy openness ($\pm$ SE), while Ulyshen *et al.* (2011) observed a range of canopy openness from 1 to 10%. In this study, canopy gaps ranged from 13-59% canopy openness with an average of $26.5\% (\pm 2.0)$ (Perry and Herms, in press), which is consistent with gaps sizes observed by Gandhi *et al.* (2014) and much larger than the gap fraction observed by Ulyshen *et al.* (2011). In large canopy gaps, CWD may not function as favorable habitat for forest floor invertebrates, especially for insects colonizing downed woody debris (Graham, 1925). Reduced activity-abundance was observed for several taxa, suggesting CWD may be more important in a closed canopy forest environment. Additionally, the amount of downed CWD during the early stages of EAB-induced ash mortality is limited, and therefore may have minimal impacts on forest floor invertebrates. Ulyshen *et al.* (2011) conducted their study after many of the ash trees had fallen to the ground, and gaps in the canopy had already begun to close. These results align with our model that predicts the effects of EAB-induced ash mortality change over time due to an inverse temporal relationship between canopy gap size and accumulation of CWD.

1.4.1 Conclusion

In eastern deciduous forests of North America, EAB is causing rapid and relatively simultaneous ash tree mortality, exceeding 99% in some areas (Klooster *et al.*, 2014). Cascading direct and indirect effects of EAB-induced ash mortality are likely in forests affected by this exotic species (Gandhi and Herms, 2010a, b). During the early stages of ash mortality, canopy gaps had a greater impact on the activity-abundance and diversity of forest floor invertebrates, while patterns reported by Ulyshen *et al.* (2011) suggest CWD had the greatest affect following the major pulse of downed ash woody debris that occurs during the later stages of ash mortality. These findings support the predicted inverse temporal effects of canopy gaps and CWD on forest floor invertebrates, as opposed to those patterns predicted for other disturbance types such as wind. This research contributes to our understanding of the cascading ecological impacts of emerald ash borer on native forest communities.

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Table 1. Forest floor invertebrates sampled with unbaited pitfall traps in canopy gap and closed canopy treatments in 2011 and 2012 at NASA Plum Brook Research Station, Sandusky, Ohio, U.S.A.

Invertebrate Taxa			2011		2012		Total
Class	Order	Family	Canopy Gap	Closed Canopy	Canopy Gap	Closed Canopy	
Gastropoda	Snails				44	27	1033
	Slugs		206	176	237	343	
Chilopoda	Geophilomorpha		12	10	10	13	63
	Lithobiomorpha				11	7	
Diplopoda	Polydesmida				3077	1142	5076
	Spirobolida		260	232	186	179	
Malacostraca	Isopoda		1551	1600	1918	1678	6747
Arachnida	Araneae		469	464	989	914	2836
	Opiliones		273	432	193	379	1277
	Pseudoscorpiones ^a		na	na	9	9	18
Insecta	Diplura	Campodeidae ^a	na	na	8	1	9
	Collembola	Entomobryidae	980	1120	2634	2660	7394
		Isotomidae	306	286	811	1498	2901
		Hypogastruridae	253	161	1798	3141	5353
		Sminthuridae	886	1478	1144	1526	5034
		Tomoceridae	2298	2509	2648	2644	10099
	Coleoptera	Carabidae	250	505	420	374	1549
		Curculionidae	6	11	7	39	63
		Scolytinae ^a	na	na	1220	1425	2645
		Elateridae	0	8	1	6	15
		Nitidulidae ^a	na	na	713	499	1212
		Scarabaeidae	39	111	31	78	259
		Silphidae	49	105	33	74	261
		Staphylinidae	357	497	1475	1695	4024
	Hymenoptera	Formicidae	258	112	317	279	993
	Dermoptera	Forficulidae	7	25	14	13	59

Table 1 (*Continued*)

Invertebrate Taxa			2011		2012		Total
Class	Order	Family	Canopy Gap	Closed Canopy	Canopy Gap	Closed Canopy	
	Orthoptera	Gryllidae	109	127	274	315	825
		Rhaphidophoridae	241	396	156	258	1051
	Blattodea	Blattidae	4	13	5	17	39
Total			8,841	10,378	20,383	21,233	60,835

^ana denotes taxa that were not counted in 2011

Table 2. Main effects of canopy gap and coarse woody debris (CWD) treatments on forest floor invertebrate activity-abundance, richness, evenness and diversity (mean $\pm$ SE) in 2011 and 2012 for forests at NASA Plum Brook Research Station, Sandusky, OH. Results are given for the repeated measures ANOVA. Significant ($\alpha \leq 0.05$) *P* values are shown in bold.

Invertebrate Index	Year	df	Light Availability				Coarse Woody Debris				Gap $\times$ CWD	
			Canopy Gap	Closed Canopy	F	<i>P</i>	CWD	No CWD	F	<i>P</i>	F	<i>P</i>
Activity-Abundance	2011	1,21	92.1 $\pm$ 10.1	108.1 $\pm$ 8.2	3.09	0.093	105.3 $\pm$ 9.6	94.8 $\pm$ 8.8	0.64	0.432	0.07	0.792
	2012	1,18	167.4 $\pm$ 12.7	173.6 $\pm$ 13.5	0.00	0.980	172.9 $\pm$ 11.4	168.1 $\pm$ 14.5	0.06	0.811	0.20	0.661
Richness	2011	1,16	12.7 $\pm$ 0.3	14.0 $\pm$ 0.3	7.69	0.013	13.4 $\pm$ 0.3	13.3 $\pm$ 0.3	0.00	0.981	2.16	0.981
	2012	1,16	16.7 $\pm$ 0.4	17.6 $\pm$ 0.4	4.55	0.048	17.0 $\pm$ 0.4	17.3 $\pm$ 0.4	3.33	0.086	0.15	0.705
Evenness	2011	1,16	0.775 $\pm$ 0.01	0.770 $\pm$ 0.01	0.26	0.619	0.762 $\pm$ 0.01	0.784 $\pm$ 0.01	2.02	0.174	0.36	0.559
	2012	1,16	0.739 $\pm$ 0.01	0.763 $\pm$ 0.00	2.78	0.114	0.754 $\pm$ 0.01	0.747 $\pm$ 0.01	1.04	0.322	3.97	0.063
Shannon Diversity	2011	1,16	1.94 $\pm$ 0.03	2.02 $\pm$ 0.03	6.87	0.018	1.96 $\pm$ 0.03	2.01 $\pm$ 0.03	3.08	0.098	0.60	0.448
	2012	1,16	2.06 $\pm$ 0.03	2.16 $\pm$ 0.03	5.71	0.029	2.12 $\pm$ 0.03	2.11 $\pm$ 0.03	0.00	0.948	2.28	0.150

Table 3. Forest floor invertebrate indicator taxa for canopy gap and coarse woody debris (CWD) treatments in 2011 and 2012 for forests at NASA Plum Brook Research Station, Sandusky, OH. *P* values were generated through Monte Carlo permutation tests.

Indicator Group	Year	Treatment	Observed Indicator Value (IV)	IV from Randomized Groups		
				Mean	Standard Deviation	<i>P</i>
Carabidae	2011	Closed Canopy	64.3	48.9	4.06	0.005
Scarabaeidae	2011	Closed Canopy	37.8	24.7	5.03	0.015
Sminthuridae	2011	Closed Canopy	62.0	54.2	3.68	0.024
Opiliones	2011	Closed Canopy	54.5	47.9	4.24	0.077
Formicidae	2011	CWD	50.4	40.6	5.80	0.046
Entomobryidae	2011	CWD	57.4	51.0	4.41	0.083
Polydesmida	2012	Canopy Gap	68.5	52.2	5.20	0.001
Opiliones	2012	Closed Canopy	58.6	42.6	3.45	0.001
Isotomidae	2012	Closed Canopy	60.6	48.9	4.07	0.004
Hypogastruridae	2012	Closed Canopy	50.0	41.8	4.93	0.068
Rhaphidophoridae	2012	Closed Canopy	48.9	39.3	4.02	0.026
Isopoda	2012	CWD	59.6	52.3	3.72	0.038

Figure Legends

Figure 1. Main effects of canopy gaps on forest floor invertebrate diversity (Shannon Diversity Index) (mean $\pm$ SE) in 2011(left) and 2012 (right) for forests at NASA Plum Brook Research Station, Sandusky, OH. In 2011, sampling intervals included (2) July 25-August 8, (3) August 22-September 5, and (4) September 19-October 3. Samples from the first interval in 2011, June 28-July 11, were removed from all analyses due to high disruption of pitfall traps in the field. In 2012, sampling intervals included (1) June 5-21, (2) July 3-17, (3) July 31-August 14, and (4) August 28-September 10. Results are given for the repeated measures ANOVA. Asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

Figure 2. Non-metric multidimensional scaling (NMDS) ordination of forest floor invertebrate communities for the canopy gap treatment using Sørensen's distance measure. In 2011(A), community composition differed during September 19-October 3, and the first two axes of the ordination explained 88.1% of the total variation, with R^2 values of 50.5% and 37.6% for axes 1 and 2, respectively. In 2012 (B), composition differed during July 31-August 14, and the first two axes explained 83.3% of the total variation, with R^2 values of 44% and 39.3% for axes 1 and 2, respectively. P values are given for the multi-response permutation procedure that uses Monte Carlo tests to determine significance.

Figure 3. Interaction plot for forest floor invertebrate taxonomic evenness for canopy gap and closed canopy treatments with (left) and without (right) ash coarse woody debris (CWD) in 2012 for forests at NASA Plum Brook Research Station, Sandusky, OH. Sampling intervals include (1) June 5-21, (2) July 3-17, (3) July 31-August 14, and (4) August 28-September 10. Results are given for the repeated measures ANOVA. Asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

Figure 4. Models depicting predicted temporal relationships between the effect size of canopy gaps and accumulation of coarse woody debris (CWD) caused by emerald ash borer-induced ash mortality (A) and wind disturbance (B).

Figure 1

Figure 2

Figure 3

Figure 4