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

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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.

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, 2010b; 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,

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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, 2016). 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, 2016). 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 canopy gaps and 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.

2. Materials and methods

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 2600 ha (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 (± SE) for these dominant species at Plum Brook were 77.5 (± 0.3), 65.1 (± 10.1), 36.7 (± 2.4) and 15.2 (± 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 (± 112) with a corresponding average ash importance value of 62 (± 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 were 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).

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, 2016).

Blocks consisted of two existing canopy gaps (20–30 m 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, 2016). 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