

Effects of Late Stages of Emerald Ash Borer (Coleoptera: Buprestidae)-Induced Ash Mortality on Forest Floor Invertebrate Communities

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Abstract

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) is an invasive wood-borer causing rapid, widespread ash tree mortality, formation of canopy gaps, and accumulation of coarse woody debris (CWD) in forest ecosystems. The objective of this study was to quantify the effects of canopy gaps and ash CWD on forest floor invertebrate communities during late stages of EAB-induced ash mortality, when the effects of gaps are predicted to be smallest and effects of CWD are predicted to be greatest, according to the model proposed by [Perry and Herms 2016a](#). A 2-year study was conducted in forest stands that had experienced nearly 100% ash mortality in southeastern Michigan, USA, near where EAB first established in North America. In contrast to patterns documented during early stages of the EAB invasion, effects of gaps were minimal during late stages of ash mortality, but invertebrate communities were affected by accumulation and decomposition of CWD. Invertebrate activity-abundance, evenness, and diversity were highest near minimally decayed logs (decay class 1), but diverse taxon-specific responses to CWD affected community composition. Soil moisture class emerged as an important factor structuring invertebrate communities, often mediating the strength and direction of their responses to CWD and stages of decomposition. The results of this study were consistent with the predictions that the effects of CWD on invertebrate communities would be greater than those of canopy gaps during late stages of EAB-induced ash mortality. This research contributes to understanding of the cascading and long-term ecological impacts of invasive species on native forest ecosystems.

Key words: biological invasion, disturbance, gap dynamics, ecological impacts, *Fraxinus*

Biological invasions continue to cause unprecedented economic and ecological impacts worldwide ([Vitousek et al. 1996](#), [Holmes et al. 2009](#), [Aukema et al. 2011](#)) as their frequency increases ([Levine and D'Antonio 2003](#), [Aukema et al. 2010](#)). The establishment and spread of invasive species threatens native habitat, biological diversity, and ecosystem services ([Allen and Humble 2002](#), [Aukema et al. 2011](#), [Boyd et al. 2013](#)). Therefore, understanding the effects of invasive species on native ecosystems has become a priority for the conservation and management of biodiversity ([Byers et al. 2002](#), [Moser et al. 2009](#), [Trumbore et al. 2015](#)). North American forests have faced many threats from invasive species, which often cause cascading direct and indirect effects on community dynamics and ecosystem processes ([Liebhold et al. 1995](#), [Lovett et al. 2006](#), [Gandhi and Herms 2010a](#)).

Emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) is an invasive wood-boring beetle (Coleoptera: Buprestidae) native to southeast Asia that was accidentally introduced to North America ([Herms and McCullough 2014](#)), and first established in southeastern

Michigan, USA at least by the early 1990s ([Siegert et al. 2014](#)). EAB has since killed hundreds of millions of ash trees (*Fraxinus* spp.) ([Herms and McCullough 2014](#)), with nearly 100% ash mortality documented in forests surrounding the epicenter of invasion ([Klooster et al. 2014](#)). Widespread ash mortality caused by EAB is having cascading direct and indirect ecological impacts on forest structure, function, and successional trajectories ([Gandhi and Herms 2010a,b](#), [Smith et al. 2015](#)).

EAB kills ash trees rapidly and most in a forest die relatively simultaneously ([Knight et al. 2013](#), [Klooster et al. 2014](#)). EAB-induced ash mortality increases the frequency of canopy gaps and ash coarse woody debris (CWD; logs and large branches >10 cm in diameter at the large end and >1 m in length; [Harmon and Sexton 1996](#)) on the forest floor ([Gandhi and Herms 2010a](#), [Ulyshen et al. 2011](#)). Canopy gaps created when trees die alter the forest floor environment by changing microclimate and resources such as light availability ([Canham et al. 1990](#), [Perry and Herms 2016b](#)), soil temperature and moisture ([Gray et al. 2002](#), [Perry and Herms 2016b](#)),

and ground-level vegetation (Collins et al. 1985). These changes have the potential to impact forest communities such as populations of forest floor invertebrates (Levings and Windsor 1984, Shure and Phillips 1991). The forest floor invertebrate community is highly diverse and many taxa respond to changes in habitat structure or microclimate, such as moisture regimes (Levings and Windsor 1984), leaf litter (Koivula et al. 1999), ground-level vegetation (Shure and Phillips 1991), and CWD (Ulyshen and Hanula 2009a,b).

The bole of dead ash trees often snaps at the base or uproots, which results in accumulation of large volumes of woody debris on the forest floor that varies with density of ash in the forest (Ulyshen et al. 2011). Downed CWD increases overall resource and habitat heterogeneity in forest ecosystems (Harmon et al. 1986, Tews et al. 2004). Forest floor invertebrates use downed CWD for food, refugia, and breeding sites, but the degree of log decay may influence how and when different taxa utilize this resource (Harmon et al. 1986, Seastedt et al. 1989, Stokland and Siitonen 2012). Therefore, non-xylophagous invertebrate fauna are predicted to change as decomposition of downed CWD progresses, with habitat or resource specificity becoming more important than the identity of the tree species (Harmon et al. 1986, Stokland and Siitonen 2012).

Perry and Herms (2016a) proposed a model describing the effects of EAB-induced ash mortality on forest floor invertebrates that predicts an inverse temporal relationship in the effects of canopy gaps and accumulation of ash CWD. During the early stages of ash mortality when ash trees have recently died, large canopy gaps, which have not yet begun to close, are predicted to have their greatest effect on forest floor invertebrates. Because the dead ash trees are still standing as snags, large quantities of downed CWD have yet to accumulate on the forest floor (Perry and Herms 2016a). Conversely, CWD is predicted to accumulate and have its greatest effect on invertebrates during late stages of ash mortality as ash snags uproot or snap. Concurrently, growth from previously suppressed understory trees, as well as surrounding dominant and codominant canopy trees, steadily close the gaps (Perry and Herms 2016a).

Gandhi et al. (2014) and Perry and Herms (2016a,b) observed the effects of canopy gaps, but not ash CWD, on forest floor invertebrate communities during the early stages of EAB-induced ash mortality. Forest floor invertebrate richness and diversity, as well as the activity-abundance of several invertebrate taxa, were lower in canopy gaps caused by EAB than under closed canopy, with minimal effects of ash CWD (Perry and Herms 2016a). Activity-abundance and species diversity of ground beetle assemblages also were lower in canopy gaps, but there was some evidence that these effects were ephemeral, and that ground beetles may be resilient to this degree of canopy disturbance (Gandhi et al. 2014, Perry and Herms 2016b).

Conversely, Ulyshen et al. (2011) detected the effects of ash CWD, but not canopy gaps, on forest floor invertebrate communities during late stages of EAB-induced ash mortality. Densities of many forest floor invertebrate taxa were higher in leaf litter near ash CWD than in leaf litter away from ash CWD (Ulyshen et al. 2011). Ulyshen et al. (2011) detected minimal effects of canopy gaps that had decreased in size to 1–10% canopy openness. These gaps were smaller than those (18–26% canopy openness) observed by Gandhi et al. (2014) and Perry and Herms (2016b) during early stages of ash mortality.

This study expands upon the work of Ulyshen et al. (2011) by investigating the effects of CWD decomposition on the forest floor invertebrate community during late stages of EAB-induced ash mortality when the effects of CWD are predicted to be greatest. The objective was to test the effects of proximity to CWD, CWD decomposition, canopy gap size, and their interaction on forest

floor invertebrates. On the basis of the proposed inverse temporal relationship in the effect sizes of canopy gaps and accumulation of CWD (Perry and Herms 2016a), we predicted that (1) canopy gaps would have minimal effects on the structure of forest floor invertebrate communities because canopy closure had already begun, (2) forest floor invertebrate community activity-abundance and diversity would be higher near CWD, and (3) forest floor invertebrate community composition would change as ash CWD decomposed.

Materials and Methods

Study Site

The study was conducted in transects previously established in forests stands in the Upper Huron River Watershed in southeastern Michigan, USA near the epicenter of the EAB invasion (Klooster et al. 2014, Smith et al. 2015). Stands consisted of mature second-growth deciduous forests dominated by tree species in the genera *Quercus*, *Acer*, *Tilia*, *Prunus*, *Ulmus*, *Larix*, *Carya*, *Juglans*, and *Populus* (Smith et al. 2015). Ash trees (*Fraxinus* spp.) were once abundant in these stands (Smith et al. 2015), but all mature ash had been killed by EAB with tree mortality exceeding 99% by 2010 (Klooster et al. 2014), and many trees had fallen. Average percentage (\pm SE) of ground covered by downed CWD was 19.3% (\pm 0.8) (range: 7–31%). Transects were composed of three replicate circular plots, each with an 18-m radius (Klooster et al. 2014, Smith et al. 2015). In 22 transects, one plot was randomly selected for this study. Forest transects were classified previously according to edaphic conditions as mesic ($n = 11$) or xeric ($n = 11$) (Klooster et al. 2014) in which green ash (*Fraxinus pennsylvanica* Marsh.) or white ash (*Fraxinus americana* L.) were the most common ash species, respectively (Smith et al. 2015).

Study Design and Invertebrate Collection

Two logs on the forest floor were randomly selected ~10 m from the center of each circular plot in opposing cardinal directions. Logs had to be considered downed CWD, which was determined by the diameter at the large end (≥ 10 cm), length (≥ 1.0 m) (Harmon and Hua 1991, Harmon and Sexton 1996), and distance above the forest floor (≤ 10 cm; leaning snags and suspended woody debris were excluded), and the logs were not attached to stumps or supported by a root system (Woodall and Williams 2005). Average length (contiguous) (m) (\pm SE) of CWD selected for the study was 11.3 m (\pm 0.8) (range: 1.9–20.1 m) in 2011 and 12.1 m (\pm 0.9) (range: 1.7–23.0 m) in 2012. Average width (cm) (\pm SE) was 17.6 cm \pm 1.3 (range: 8.0–57.0 cm) in 2011 and 22.2 cm \pm 1.4 (range: 9.3–56.0 cm) in 2012. Downed CWD was categorized according to decay class using a 1–5 decay stage scale adapted from Pyle and Brown (1999) and Woodall and Williams (2005). In each plot, replicate logs were of the same decay class, and therefore, plot was the unit of replication. Downed logs were only selected if they belonged to decay classes 1 ($n = 7$), 2 ($n = 8$), or 3 ($n = 7$) and evidence of EAB infestation was identified by D-shaped emergence holes from adults or the presence of serpentine galleries. Selection of downed logs belonging to decay classes 1–3 created an ash woody debris decomposition chronosequence.

Forest floor invertebrates were sampled using pitfall traps during the summers of 2011 and 2012. Because this method tends to collect more active invertebrates, results are reported as activity-abundance (invertebrates per trap) (Spence and Niemelä 1994, Yi et al. 2012). Pitfall traps were installed adjacent to (≤ 10 cm) and toward the center of each downed ash log, resulting in two traps per plot. Traps consisted of a 1-liter outer cup and a 500-ml inner cup (~11 cm in

diameter) filled with ~4 cm of propylene glycol (recreational vehicle and marine antifreeze, Peak Company Old World Industries, Clear Lake, TX) and a few drops of detergent. Masonite board (100 cm²) covered each cup to exclude rain and 30 cm stakes secured hardware cloth (500 cm²) over the entire trap as a barrier to animals.

In a subset of the plots ($n = 10$) in 2012, two additional pitfall traps were installed in the remaining two cardinal directions 8–15 m from the center of the plot and ≥ 5 m away from any woody debris to investigate the effects of proximity to downed CWD on the forest floor invertebrate community. In these plots, the other two pitfall traps were adjacent to CWD belonging to one of the three decay classes; 1 ($n = 3$), 2 ($n = 4$), or 3 ($n = 3$).

Percentage canopy openness was measured above each pitfall trap using spherical crown densiometer calculations on 14–17 June 2011 and 12–14 June 2012. Canopy openness was calculated above each trap and then averaged to yield a final plot measurement.

Sampling was conducted for 2-week intervals once per month during the summers of 2011 and 2012, resulting in four collection periods each year. In 2011, sampling intervals were 15–29 June, 12–26 July, 9–23 August, and 8–22 September. In 2012, intervals were 12–26 June, 10–24 July, 7–21 August, and 4–18 September. In the field, trap catch was separated from the propylene glycol with a 10-cm fine mesh strainer, emptied into specimen cups, and preserved with 70% ethanol. Insects were identified to family using Triplehorn and Johnson (2005) and other invertebrates were identified to order.

Statistical Analyses

Replicate trap catches of each forest floor invertebrate taxon were averaged to yield a mean for each plot. To account for variation in sampling interval length and trap disruption, invertebrate counts were standardized to 14 trap days ([trap catch/total number of days trap was operational] \times 14) for each interval (Spence et al. 1996, Gandhi et al. 2008). Data from the 15–29 June 2011 sampling interval were removed from all analyses due to high disruption of the pitfall traps by animals. Data were checked for statistical assumptions of normality and variance, and activity-abundance data were rank transformed to improve normality (Quinn and Keough 2002). Forest floor invertebrate taxonomic richness (number of taxa per plot), Pielou's J evenness index (Pielou 1966), and Shannon diversity index (Peet 1974) were calculated using PC-ORD software (McCune and Mefford 2006).

Effects of canopy gaps and CWD on the forest floor invertebrate community were analyzed using repeated-measures analysis of covariance (ANCOVA) tests with univariate analyses for each date in SAS (SAS Institute 2016). Following a significant F -test, mean separation tests (least significant difference [LSD], $\alpha = 0.05$) were used. Community response variables were total invertebrate activity-abundance, taxonomic richness, evenness, and diversity. The predictor variables CWD decay class (1, 2, 3) and soil moisture class (mesic, xeric) were fixed factors, sampling interval a repeated factor, and percentage canopy openness a covariate. Each year was analyzed separately. A similar ANCOVA test with the presence/absence of CWD (0, 1) as a predictor variable rather than CWD decay class was conducted separately for 2012 data.

Activity-abundances of each forest floor invertebrate taxon for which ≥ 30 individuals were collected during a year was analyzed individually to compare CWD decay classes, proximity to CWD, and soil moisture classes using similar repeated-measures ANCOVA tests with percentage canopy openness as the covariate. Each year was analyzed separately. Invertebrate taxa excluded due to low activity-abundance were Gastropoda (snails), Geophilomorpha,

Lithobiomorpha, Pseudoscorpiones, Campodeidae, Curculionidae, Elateridae, Forficulidae, and Blattidae.

Changes in forest floor invertebrate community composition were assessed using multi-response permutation procedures (MRPP), and these differences were visualized using non-metric multidimensional scaling (NMDS). Community composition was compared between the presence and absence of CWD, between CWD decay classes, and between soil moisture classes. Criteria used in the NMDS ordination included the Sørensen distance measure with two dimensions, 500 iterations, 50 runs of real data, and 20 runs for the Monte Carlo test. MRPP analyses and NMDS ordinations were conducted separately for each year using PC-ORD software (McCune and Mefford 2006).

Effects of time on the size of canopy gaps (percentage canopy openness) were analyzed using an ANOVA test with the documented year of 100% mortality of ash trees (≥ 2.5 cm dbh) in the plot as the fixed factor and year (2011 and 2012) as a random factor.

Results

In 2011 and 2012, a total of 40,176 individuals were collected in pitfall traps representing 12 non-insect invertebrate taxa, 12 insect families, and 1 insect subfamily (Table 1). Of these 25 taxa, 10 taxonomic groups were collected in low numbers (<1% of total individuals collected; Scarabaeidae, Elateridae, Curculionidae [excluding Scolytinae], Forficulidae, Blattidae, Diplura, Pseudoscorpiones, Geophilomorpha, Lithobiomorpha, and Gastropoda [snails]), 12 groups were common (1–10% of total individuals collected; Gastropoda [slugs], Carabidae, Nitidulidae, Silphidae, Scolytinae, Formicidae, Rhaphidophoridae, Gryllidae, Araneae, Opiliones, Spirobolida, and Polydesmida), and 3 were collected in high numbers (>10% of total individuals; Collembola, Isopoda, and Staphylinidae). Collembola were the most commonly captured invertebrates with 15,922 individuals sampled, which comprised over 40% of the total trap catch each year.

Canopy Gaps

Canopy openness did not affect forest floor invertebrate activity-abundance, taxonomic richness, evenness, or diversity in either year ($P = 0.078$ – 0.813) (Table 2), and had minimal effects on the activity-abundances of individual taxa (Table 3). In 2011, activity-abundance of Araneae increased in mesic and decreased in xeric plots with increasing percentage canopy openness ($F_{1,10} = 13.7$, $P = 0.004$). Activity-abundance of Gryllidae increased near logs of decay classes 1 and 3 with increasing percentage canopy openness, but decreased near logs of decay class 2 ($F_{1,10} = 8.38$, $P = 0.016$). In 2012, activity-abundance of Scolytinae decreased away from CWD as percentage canopy openness increased ($F_{1,9} = 5.39$, $P = 0.024$).

Proximity to CWD

Proximity to CWD interacted with soil moisture classes to affect forest floor invertebrate richness and the activity-abundances of several taxa in 2012, but did not affect total invertebrate activity-abundance, taxonomic evenness, or diversity ($P = 0.370$ – 0.913). Taxonomic richness was generally lower away from CWD in mesic plots, but was lower near CWD in xeric soils in September (Fig. 1; $F_{2,9} = 5.42$, $P = 0.023$). Isopoda were more abundant near CWD in mesic plots from July through September, but there was no difference in xeric plots where activity-abundance was highly variable ($F_{2,9} = 5.62$, $P = 0.021$). Formicidae were less abundant away from CWD in mesic plots throughout the entire summer, but more abundant away from CWD in xeric plots in June ($F_{2,9} = 18.0$, $P < 0.001$). Staphylinidae tended to be more abundant away from CWD during

Table 1. Forest floor invertebrates sampled with unbaited pitfall traps near coarse woody debris (CWD) of different decay classes in 2011 and 2012, and ≥ 5 m away from CWD (No CWD), in the Upper Huron River Watershed in southeastern Michigan, USA

Invertebrate taxa			CWD decay class						Total		
Class	Order	Family	2011			2012					
			I	II	III	No CWD	I	II		III	
Gastropoda	Snails		633	131	117	2	7	8	6	3,118	
	Slugs					778	535	449	452		
Chilopoda	Geophilomorpha		2	0	4	4	1	3	1	19	
	Lithobiomorpha					0	1	3	0		
Diplopoda	Polydesmida		78	102	53	12	201	115	171	1,182	
	Spirobolida					95	92	125	138		
Malacostraca	Isopoda		1,111	965	929	720	454	961	742	5,882	
Arachnida	Araneae		104	96	184	271	209	254	190	1,308	
	Opiliones		89	98	116	164	71	111	133	782	
	Pseudoscorpiones ^d		na	na	na	0	0	2	1	3	
Diplura	Rhabdura	Campodeidae ^d	na	na	na	1	0	0	0	1	
Collembola			1,657	2,030	3,015	2,956	1,444	2,181	2,639	15,922	
Insecta	Coleoptera	Carabidae	40	39	92	157	148	82	84	642	
		Curculionidae	7	3	14	7	20	8	9	68	
		Scolytinae ^d	na	na	na	129	122	48	86	385	
		Elateridae	0	0	2	2	3	1	5	13	
		Nitidulidae ^d	na	na	na	327	718	316	223	1,584	
		Scarabaeidae	7	2	14	49	43	28	46	189	
		Silphidae	15	19	79	123	85	62	57	440	
		Staphylinidae	130	211	241	1322	1664	1228	905	5,701	
	Hymenoptera	Formicidae	210	166	221	488	272	301	292	1,950	
	Dermaptera	Forficulidae	9	0	6	0	0	3	0	18	
	Orthoptera	Gryllidae	27	34	48	135	96	94	52	486	
		Rhaphidophoridae	8	18	17	99	128	67	126	463	
	Blattodea	Blattidae	3	2	6	2	1	4	2	20	
	Total			4,130	3,916	5,158	7,843	6,315	6,454	6,360	40,176

^dna denotes taxa that were not counted in 2011.

Table 2. Main effects of CWD decay classes, soil moisture classes, and canopy gaps on total ground-dwelling invertebrate activity-abundance, taxonomic richness, evenness, and diversity (mean \pm SE) in 2011 and 2012 in the Upper Huron River Watershed in southeastern Michigan, USA

Invertebrate index	Year	CWD decay classes			Decay \times time			Soil moisture class			Decay \times moisture			Canopy openness		
		d.f.	F	P-value	d.f.	F	P-value	d.f.	F	P-value	d.f.	F	P-value	d.f.	F	P-value
Activity-abundance	2011	2,10	0.00	0.999	4,20	0.34	0.847	1,10	0.64	0.442	2,10	6.86	0.013	1,10	2.57	0.139
	2012	2,7	0.85	0.460	6,21	2.03	0.096	1,7	2.58	0.142	2,7	0.52	0.616	1,7	0.81	0.391
Richness	2011	2,10	0.66	0.538	4,20	0.95	0.455	1,10	0.01	0.918	2,10	1.20	0.339	1,10	2.09	0.178
	2012	2,7	1.22	0.338	6,21	0.53	0.781	1,7	3.22	0.106	2,7	0.31	0.746	1,7	3.93	0.078
Evenness	2011	2,10	2.00	0.185	4,20	6.07	0.002	1,10	0.44	0.523	2,10	0.04	0.959	1,10	0.62	0.451
	2012	2,7	0.45	0.651	6,21	0.34	0.908	1,7	0.35	0.571	2,7	0.18	0.840	1,7	0.38	0.550
Shannon Diversity	2011	2,10	1.03	0.391	4,20	7.70	<0.001	1,10	0.31	0.589	2,10	0.20	0.824	1,10	2.18	0.171
	2012	2,7	0.58	0.581	6,21	0.38	0.883	1,7	0.52	0.490	2,7	0.18	0.841	1,7	3.32	0.101

Repeated-measures ANOVA with significant ($\alpha \leq 0.05$) *P* values shown in bold. Treatment \times time interaction indicates significance of sampling intervals within a year.

August in xeric plots and more abundant near CWD during June and July in mesic plots ($F_{2,9} = 3.89$, $P = 0.053$).

Spirobolida, Collembola, and Opiliones were the only taxa affected by proximity to CWD alone. Spirobolida ($F_{1,9} = 5.72$, $P = 0.020$) and Collembola ($F_{1,9} = 4.30$, $P = 0.042$) were more abundant near CWD early in the summer; otherwise their numbers were highly variable. Activity-abundance of Opiliones was

higher away from CWD during August and September ($F_{1,9} = 5.24$, $P = 0.026$).

CWD Decay Classes

Effects of CWD decay classes on forest floor invertebrates communities changed over the sampling season in 2011 (Table 2). Evenness ($F_{2,10} = 6.07$, $P = 0.002$) and diversity ($F_{2,10} = 7.70$, $P < 0.001$)

Table 3. Main effects of CWD decay classes, soil moisture classes, and canopy gaps on the activity-abundance (mean \pm SE) of ground-dwelling invertebrate taxa in 2011 and 2012 in the Upper Huron River Watershed in southeastern Michigan, USA

Invertebrate taxa			Year	CWD decay class			Soil moisture class			Decay \times moisture			Canopy openness			
Class	Order	Family		d.f.	F	P-value	d.f.	F	P-value	d.f.	F	P-value	d.f.	F	P-value	
Gastropoda	Slugs		2011	2,10	13.2	0.001^a	1,10	0.76	0.404	2,10	6.79	0.013^a	1,10	0.03	0.862	
			2012	2,7	3.22	0.101	1,7	4.38	0.074	2,7	6.22	0.028	1,7	5.12	0.056	
Diplopoda	Polydesmida		2011 ^b	2,10	2.11	0.172 ^a	1,10	0.00	0.976	2,10	7.44	0.010^a	1,10	0.00	0.947	
			2012	2,7	4.08	0.067	1,7	8.23	0.024	2,7	1.49	0.289	1,7	4.82	0.064	
	Spirobolida		2011 ^b													
			2012	2,7	4.36	0.058 ^a	1,7	8.82	0.020^a	2,7	1.55	0.277	1,7	4.29	0.077	
Malacostraca	Isopoda		2011	2,10	3.93	0.055	1,10	0.14	0.712	2,10	10.30	0.003^a	1,10	1.70	0.221	
			2012	2,7	1.75	0.227	1,7	2.63	0.139	2,7	0.49	0.640	1,7	0.39	0.548	
Arachnida	Araneae		2011	2,10	0.57	0.583	1,10	0.04	0.845	2,10	0.52	0.612	1,10	13.7	0.004	
			2012	2,7	0.42	0.670	1,7	0.281	0.128	2,7	1.41	0.327	1,7	0.48	0.507	
	Opiliones		2011	2,10	0.79	0.481 ^a	1,10	1.53	0.244	2,10	0.24	0.793 ^a	1,10	3.58	0.087	
			2012	2,7	2.99	0.101 ^a	1,7	4.36	0.066	2,7	4.81	0.048	1,7	1.88	0.203	
Collembola			2011	2,10	0.15	0.860	1,10	0.03	0.855	2,10	4.68	0.050	1,10	1.33	0.275	
			2012	2,7	2.99	0.101	1,7	4.36	0.660	2,7	5.80	0.049	1,7	1.88	0.203	
			2011													
Insecta	Coleoptera	Carabidae	2011	2,10	0.28	0.761	1,10	0.23	0.640	2,10	2.95	0.098	1,10	0.30	0.597	
			2012	2,7	1.45	0.297	1,7	1.88	0.212	2,7	2.57	0.145	1,7	4.30	0.076	
			Scolytinae ^c	2011												
				2012	2,7	1.34	0.309	1,7	0.48	0.506	2,7	0.10	0.905	1,7	1.02	0.339
		Nitidulidae ^c	2011													
				2012	2,7	0.66	0.538	1,10	0.64	0.445	2,7	0.39	0.693	1,10	1.84	0.207
		Scarabaeidae ^d	2011													
				2012	2,7	3.05	0.097 ^a	1,7	5.63	0.041	2,7	2.90	0.145	1,7	3.80	0.083
		Silphidae	2011	2,10	6.41	0.016^a	1,10	2.44	0.149 ^a	2,10	2.40	0.141 ^a	1,10	0.51	0.492	
			2012	2,7	0.33	0.727 ^a	1,7	0.13	0.730 ^a	2,7	0.32	0.739	1,7	0.33	0.583 ^a	
		Staphylinidae	2011	2,10	0.01	0.993	1,10	0.47	0.510	2,10	4.73	0.035	1,10	0.17	0.691	
			2012	2,7	1.59	0.256	1,7	3.44	0.096	2,7	0.43	0.669	1,7	4.40	0.065	
		Hymenoptera	Formicidae	2011	2,10	0.31	0.742	1,10	0.07	0.797	2,10	0.47	0.640 ^a	1,10	4.07	0.071
				2012	2,7	0.28	0.762	1,7	0.83	0.386	2,7	0.02	0.982	1,7	2.70	0.144
		Orthoptera	Gryllidae	2011	2,10	2.98	0.096	1,10	3.71	0.082	2,10	2.42	0.139	1,10	8.38	0.016
			2012	2,7	0.52	0.613	1,7	0.04	0.845	2,7	0.18	0.842 ^a	1,7	0.01	0.926	
		Rhaphidophoridae ^d	2011													
			2012	2,7	0.42	0.670	1,7	0.27	0.617	2,7	1.39	0.310	1,7	1.87	0.205	

Repeated-measures ANOVA with significant ($\alpha \leq 0.05$) *P* values shown in bold. Treatment \times time interaction indicates significance of sampling intervals within a year. Analyses were conducted for invertebrate taxa with ≥ 30 individuals collected each year. Taxa that did not meet these criteria for either year of the study included Gastropoda (snails), Geophilomorpha, Lithobiomorpha, Pseudoscorpiones, Campodeidae, Curculionidae, Elateridae, Forficulidae, and Blattidae.

^aSignificant treatment \times time interaction at $\alpha \leq 0.05$.

^bTaxa that were identified to class in 2011.

^cTaxa that were not counted in 2011.

^dAnalyses were not performed because < 30 individuals were collected.

decreased over time near CWD of decay classes 2 and 3, but not near decay class 1 (Fig. 2). CWD decay class had minimal effects on the activity-abundance of forest floor invertebrate taxa (Table 3). The only taxon affected was Silphidae in 2011, which had higher activity-abundance near logs of decay class 3 than near decay classes 1 and 2 ($F_{2,10} = 6.41$, $P = 0.016$). Invertebrates were also affected by the interaction between CWD decay classes and soil moisture classes. Total activity-abundance of forest floor invertebrates was higher near CWD of decay class 1 in xeric plots than near CWD of other decay classes. In mesic plots, however, activity-abundance was higher near CWD of decay class 2 (Fig. 3; $F_{2,10} = 6.86$, $P = 0.013$).

Gastropods, specifically slugs, and Collembola were the only two invertebrate taxa affected by the interaction between CWD decay classes and soil moisture classes during both years of the study. In 2011, slugs were more abundant near logs of decay class 1 in August regardless of soil moisture class, but their activity-abundance was higher overall and more variable in xeric plots ($F_{2,10} = 6.79$, $P = 0.013$). In 2012, slugs were more abundant near logs of decay

class 1 in xeric plots, but more abundant near logs of decay classes 2 and 3 in mesic plots ($F_{2,7} = 6.22$, $P = 0.028$). Collembola were more abundant near logs of decay class 1 and least abundant near decay class 2 in xeric plots, while in mesic plots, the opposite pattern was observed, and activity-abundance was higher near logs of decay class 2 in 2011 ($F_{2,10} = 4.68$, $P = 0.050$). In 2012, Collembola were least abundant near logs of decay class 2 in xeric plots, and least abundant near decay class 1 in mesic plots ($F_{2,7} = 5.80$, $P = 0.049$).

The interacting effects of CWD decay classes and soil moisture classes on other invertebrate taxa were not consistent between years (Table 3). In 2011, Staphylinidae were more abundant near CWD of decay class 2 in mesic plots, but activity-abundance in xeric plots was greater near decay class 1 in July and August, and near decay class 3 in September ($F_{2,10} = 4.73$, $P = 0.035$). During August and September, millipedes were more abundant in mesic plots near logs of decay class 2 but activity-abundance was similar in xeric plots ($F_{2,10} = 7.44$, $P = 0.010$). Activity-abundance of Isopoda was also highest in mesic plots near CWD of decay class 2 in August and

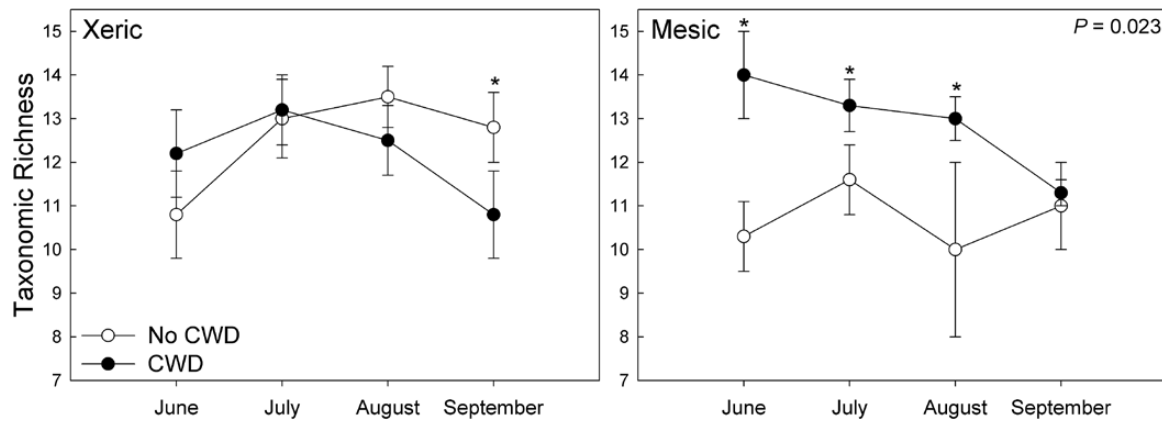


Fig. 1. Interaction plots of forest floor invertebrate taxonomic richness (\pm SE) near and away from CWD in xeric (left) and mesic (right) plots in 2012 in the Upper Huron River Watershed in southeastern Michigan, USA. Repeated-measures ANOVA followed by Tukey's pairwise comparisons, asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

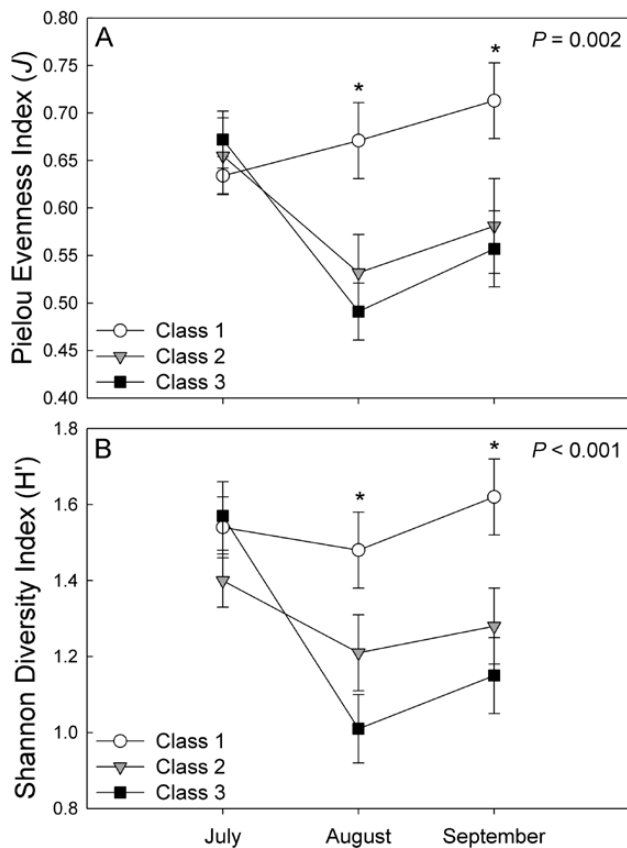


Fig. 2. Main effects of CWD decay class on forest floor invertebrate taxonomic evenness (Pielou's J Index) (A) and diversity (Shannon Diversity Index, H') (B) (\pm SE) in 2011 in the Upper Huron River Watershed in southeastern Michigan, USA. Samples from the first interval in 15–29 June 2011 were removed from all analyses due to high disruption of pitfall traps in the field. Repeated-measures ANOVA followed by Tukey's pairwise comparisons, asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

September, followed by decay class 1, and lowest near decay class 3 ($F_{2,10} = 10.30$, $P = 0.003$). However, in xeric plots, there was no difference between decay classes. In 2012, activity-abundance of Opiliones was higher near logs of decay class 1 in xeric plots, but highest near decay class 3 and lowest near decay class 1 in mesic plots ($F_{2,7} = 4.81$, $P = 0.048$).

Invertebrate Community Composition

Forest floor invertebrate community composition was similar near all CWD decay classes in 2011 ($P = 0.123$), although composition was more variable near logs of decay classes 1 and 2 than decay class 3. In 2012, community composition differed between CWD decay classes 1 and 2 ($P = 0.009$), and between decay classes 1 and 3 ($P < 0.001$), but not between decay classes 2 and 3 ($P = 0.074$) (Fig. 4; NMDS: two dimensions, final stress = 10.3, axis 1 $R^2 = 38.2\%$, axis 2 $R^2 = 48.9\%$; MRPP: $A = 0.022$, $P < 0.001$). Invertebrate communities were highly variable in the absence of CWD (Fig. 4), and no difference in composition was detected when compared with communities near CWD (all decay stages pooled; MRPP: $A = 0.0003$, $P = 0.386$). Community composition away from CWD differed from communities near CWD of decay class 2 ($P = 0.050$) and decay class 3 ($P = 0.039$), but was similar for decay class 1 ($P = 0.240$).

Invertebrate community composition differed between xeric and mesic soil moisture classes in 2011 (MRPP: $A = 0.018$, $P = 0.012$) and 2012 (MRPP: $A = 0.013$, $P < 0.001$), and was affected in both years by interactions between soil moisture class and decay stage of CWD (MRPP: $A = 0.156$, $P = 0.005$ in 2011; MRPP: $A = 0.129$, $P = 0.007$ in 2012). In 2011, invertebrate community composition differed between xeric and mesic plots for CWD decay classes 1 ($P = 0.023$), 2 ($P < 0.001$), and 3 ($P = 0.025$) (NMDS: two dimensions, final stress = 9.48, axis 1 $R^2 = 7.0\%$, axis 2 $R^2 = 85.5\%$). In 2012, a similar pattern was observed, and community composition differed between xeric and mesic plots for CWD decay classes 1 ($P = 0.011$) and 3 ($P = 0.023$) (NMDS: two dimensions, final stress = 9.30, axis 1 $R^2 = 43.2\%$, axis 2 $R^2 = 43.9\%$). There was a marginal difference in invertebrate community composition between xeric and mesic plots near CWD decay class 2 ($P = 0.061$).

Canopy gaps created by EAB-induced ash mortality decreased in size during the 2-year study ($F_{1,42} = 9.29$, $P = 0.004$), suggesting that canopy closure was still occurring in these plots. Average canopy openness (\pm SE) was $10.0 \pm 1.0\%$ (range: 5.4–21.8%) in 2011, and $8.1 \pm 0.7\%$ (range: 3.7–17.6%) in 2012. Canopy gaps were larger in forest plots where 100% mortality of trees ≥ 2.5 cm dbh occurred in 2010, with smaller gaps observed in plots that reached 100% ash mortality sooner (2006–2009) ($F_{4,42} = 3.31$, $P = 0.019$).

Discussion

The model proposed by Perry and Herms (2016a) describes an inverse temporal relationship in the effect sizes of canopy gaps and

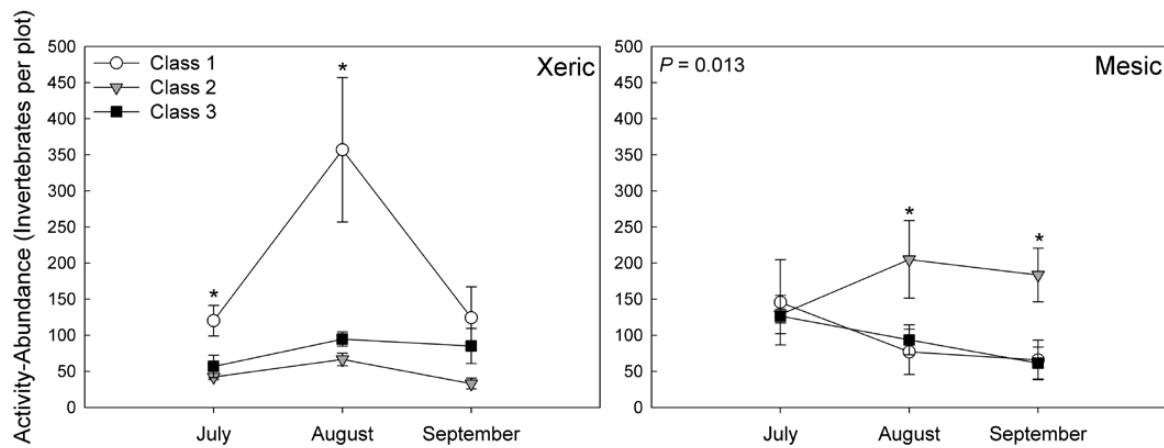


Fig. 3. Interaction plots of total forest floor invertebrate activity-abundance (\pm SE) by CWD decay class in xeric (left) and mesic (right) plots in 2011 in the Upper Huron River Watershed in southeastern Michigan, USA. Samples from the first interval in 15–29 June 2011 were removed from all analyses due to high disruption of pitfall traps in the field. Repeated-measures ANOVA followed by Tukey's pairwise comparisons, asterisk denotes intervals where treatments are significantly different ($\alpha < 0.05$).

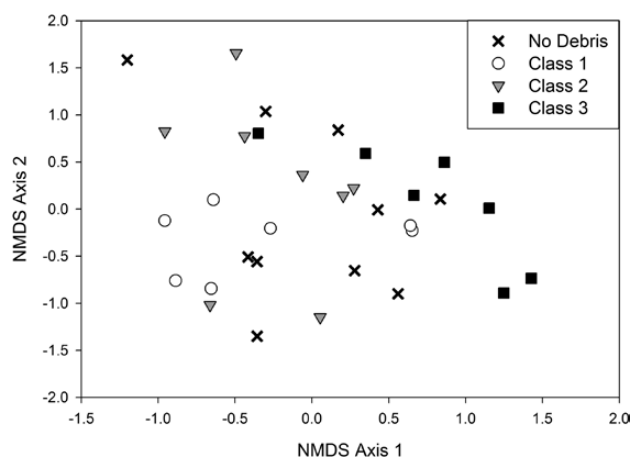


Fig. 4. NMDS ordination of forest floor invertebrate communities in 2012 near CWD of different decay classes and away from CWD. The first two axes of the ordination explained 87.1% of the total variation, with R^2 values of 38.2 and 48.9% for axes 1 and 2, respectively. Ordination analyses used the Sørensen distance measure.

accumulation of CWD caused by EAB-induced ash mortality on the forest floor invertebrate community. The effects of CWD are predicted to increase following the major pulse of woody debris accumulation that occurs during the late stages of EAB-induced ash mortality, while the effects of gaps are predicted to simultaneously decrease over time as the growth of understory and surrounding trees result in canopy closure. The objective of the current study was to test predictions of this model that relate to the late stages of EAB-induced ash mortality in forests stands that have experienced nearly 100% ash mortality for several years (Klooster et al. 2014). In these forests, downed ash CWD was abundant and canopy gaps were in the process of closing, as opposed to forests experiencing early stages of EAB-induced ash mortality (Gandhi et al. 2014, Perry and Herms 2016b).

Overall, the results of this study support the inverse temporal relationship between the effects of gaps and CWD. As predicted, the forest floor invertebrate community was affected during the late stages of EAB-induced ash mortality by the accumulation and decomposition of ash CWD, while the effects of canopy gaps were minimal. Soil moisture class emerged as an important factor

structuring forest floor invertebrate communities, the effects of which were often mediated by CWD.

Over time, as ash snags uproot or snap, and depending on the density of ash in the forest, significant amounts of woody debris may accumulate on the forest floor. CWD decomposes slowly, so its effects on ground-dwelling invertebrates are likely to persist for many years. The rate of woody debris decomposition is determined by complex interactions between the biotic and abiotic environment, and therefore, estimates vary widely spanning several decades or longer (Harmon et al. 1986, Freschet et al. 2012, Stokland and Siitonen 2012, Stokland 2012). In this study, cover of downed woody debris was higher (19.3%) than reports in forest stands in northwestern Ohio (2.2%) experiencing early stages of EAB-induced ash mortality (Long 2013). Effects of CWD are predicted to be greatest following this pulse of woody debris accumulation on the forest floor during the late stages of ash mortality (Perry and Herms 2016a).

The range in canopy sizes observed in this study during the late stages of ash mortality were much smaller than previously observed during early stages of EAB-induced ash mortality (Gandhi et al. 2014, Perry and Herms 2016b), because of gap closure by other tree species, and more comparable to those reported by Ulyshen et al. (2011), who also studied late stages of mortality. During the early stages of ash mortality, Perry and Herms (2016b) documented an average of 26.5% (\pm 2.0) canopy openness (range: 13–59%) in forest stands in northwestern Ohio. Gandhi et al. (2014) observed average canopy gap sizes of 18.8% (\pm 1.8) and 23.6% (\pm 2.1) in 2006 and 2007, respectively, measured in the same forest stands in southeastern Michigan several years before the study conducted by Ulyshen et al. (2011) and the current study. Ulyshen et al. (2011) reported gap sizes ranging from 1 to 10% in 2010. This study observed average canopy gap sizes of 10.0% (\pm 1.0) in 2011 and 8.1% (\pm 0.7) in 2012, which were slightly larger than the average canopy openness reported by Perry and Herms (2016b) for closed canopy forest (7.1% \pm 0.3). In addition, gap size decreased over our 2-year study, suggesting canopy closure was still occurring.

The size of canopy gaps observed in this study had no effect on the activity-abundance, taxonomic richness, or diversity of the forest floor invertebrate community, and only minor effects on individual taxa. This is consistent with the first prediction of this study that canopy gaps would have minimal effects on the structure of forest floor invertebrate communities during the late stages of EAB-induced

ash mortality because of canopy closure (Perry and Herms 2016a). The responses of Araneae, Gryllidae, and Scolytinae to soil moisture classes, CWD decay classes, and proximity to CWD, respectively, changed as canopy gap size increased.

Proximity to CWD had variable effects on the structure of forest floor invertebrate communities, perhaps due to high variation in community composition observed in the absence of CWD. When effects were detected, soil moisture classes often mediated the direction of these responses and seem to be a major contributing factor to invertebrate community structure in these forest stands. Invertebrate taxonomic richness was generally higher near CWD in mesic soils characterized by moderate moisture availability. Moisture content in soils is an important regulating factor of decomposition and nutrient cycling, and woody debris in moist environments contribute to a more stable habitat for forest floor invertebrates that are prone to desiccation (Swift et al. 1979, Harmon et al. 1986, Jonsson and Stokland 2012). In late summer, however, taxonomic richness was lower near CWD in xeric soils, perhaps because low soil moisture affected forest floor invertebrate habitat selection.

Activity-abundances of several invertebrate taxa were higher closer to CWD, providing some support for the second prediction that forest floor invertebrate activity-abundance and diversity would be higher near CWD following its major pulse of accumulation during the late stages of EAB-induced ash mortality. However, these patterns were more apparent as taxon-specific responses rather than general community trends. Isopods, ants (Formicidae), and rove beetles (Staphylinidae) were more abundant near CWD in mesic plots. Spirobolida, an order of millipedes, and springtails (Collembola) were more abundant near than far from CWD regardless of soil moisture class. Millipedes are vulnerable to desiccation and often utilize vegetation, leaf litter, or woody debris for cover and feeding sites (Coleman et al. 2004). Springtails are small, soft-bodied invertebrates that are also prone to desiccation. Their vertical and horizontal distributions on the forest floor have been linked to soil moisture levels in the leaf litter and soil layers (Verhoef 1977, Verhoef and van Selm 1983, Hassall et al. 1986, Hopkin 1997).

Many studies have reported positive effects of downed CWD on forest floor invertebrate taxa, such as Gastropoda (Kappes 2005, Perry and Herms 2016a), Araneae (Hanula et al. 2006, Ulyshen and Hanula 2009a, Castro and Wise 2010), Diplopoda (Hanula et al. 2006, Topp et al. 2006), Chilopoda (Jabin et al. 2004), Isopoda (Jabin et al. 2004, Topp et al. 2006, Perry and Herms 2016a), Collembola (Marra and Edmonds 1998), and Coleoptera (Pearce et al. 2003, Jabin et al. 2004, Hanula et al. 2006, Ulyshen and Hanula 2009a, b). Ulyshen et al. (2011) also reported increased activity-abundances near CWD during late stages of EAB-induced ash mortality for many of the same forest floor invertebrate taxa, including Collembola, Diplopoda, Isopoda, and Opiliones but also Araneae, Coleoptera, and Annelida. Moreover, Evans et al. (2003) reported increased activity-abundances of invertebrate taxa, including Diplopoda, Pseudoscorpions, Acari, and Araneae near red beech logs (*Nothofagus fusca* [Hook.f.]). Kappes et al. (2007) documented increased densities of detritivores such as Diplopoda, Isopoda, and Gastropoda near (within 10 cm) compared to away (> 200 cm) from woody debris. Woody debris undoubtedly contributes to the patchy distribution of invertebrates in forest ecosystems.

Forest floor invertebrate community composition varied by CWD decay class over time within a single season and between years, but was generally less variable near CWD, especially within each decay class. Invertebrate community composition was highly variable in the absence of CWD. These findings suggest that invertebrate utilization of woody debris may be specialized as decay progresses

(Harmon et al. 1986, Stokland and Siitonen 2012), providing support for the third prediction that forest floor invertebrate community composition changes with CWD decomposition. Newly fallen ash logs (decay class 1) supported more diverse invertebrate communities with more even distributions of taxa than did more decomposed CWD (decay classes 2 and 3). CWD belonging to decay class 1 is characterized by sound structural integrity, intact bark, and the general absence of decay (Pyle and Brown 1999, Woodall and Williams 2005, Stokland and Siitonen 2012), and is thought to maintain a more stable environment on the forest floor by buffering variability in temperature and moisture (Marra and Edmonds 1998, Remsburg and Turner 2006, Jonsson and Stokland 2012). However, this buffering effect was not observed for CWD in canopy gaps (Perry and Herms 2016b). CWD belonging to decay classes 2 and 3 maintain some degree of structural integrity as the heartwood is still sound, but enough decay has occurred to loosen the bark and allow for the colonization of fungal mycelium (Woodall and Williams 2005, Stokland and Siitonen 2012). Altered habitat and resources as CWD decomposes may explain why invertebrate community composition changed near CWD along the decomposition chronosequence.

CWD decay classes interacted strongly with site-specific edaphic conditions, and together these factors contributed significantly to patterns of forest floor invertebrate activity-abundance and community composition, more than either factor individually. Invertebrate communities near CWD of the same decay class were distinctly different in xeric versus mesic plots during both years of the study. Total forest floor invertebrate activity-abundance was higher near CWD of decay class 1 in xeric plots, especially in August, with this pattern driven predominantly by the activity-abundance of slugs, but also rove beetles, harvestmen, and springtails. In mesic plots, invertebrate activity-abundance was higher near CWD of decay class 2, and this pattern was driven by the activity-abundances of slugs, harvestmen, rove beetles, springtails, isopods, and millipedes. Slugs and springtails were the only invertebrate taxa consistently affected by these factors, and their responses were generally consistent during both years of the study. Similar to springtails, slugs tend to require cool and moist conditions on the forest floor (Coleman et al. 2004), and may utilize woody debris for refugia (Getz 1959). Perhaps these results can be explained by different patterns of CWD decomposition and loss of wood mass, moisture and nutrient content, and colonization by fungi in mesic and xeric stands (Harmon et al. 1986, Stokland et al. 2012). The moisture holding capacity of logs tends to increase as decay progress (Harmon et al. 1986, Jonsson and Stokland 2012), which may provide a favorable environment for many forest floor invertebrate taxa.

Establishment and spread of EAB is causing widespread and rapid ash mortality, exceeding 99% in some eastern deciduous forests of North America (Klooster et al. 2014). Nearly simultaneous ash mortality is resulting in cascading direct and indirect effects in forests affected by EAB (Gandhi and Herms 2010a,b). The results of this study were consistent with predictions that EAB-induced ash mortality will affect forest floor invertebrates via an inverse temporal relationship in the effect sizes of canopy gaps and accumulation of ash CWD (Perry and Herms 2016a). Consistent with patterns reported by Ulyshen et al. (2011), ash CWD affected forest floor invertebrate communities, primarily through taxon-specific responses, but canopy gaps had minor effects during the late stages of EAB-induced ash mortality. Soil characteristics emerged as an important factor contributing to the structure of forest floor invertebrate communities. After ash trees fall to the forest floor, the effects of woody debris accumulation and decomposition over time interacted with site-specific edaphic conditions, mediating the strength

and direction of invertebrate responses, and thus affecting community composition. These results highlight the importance of CWD in forest ecosystems, and suggest that management strategies should consider the volume and diversity of woody debris decay stages to maintain forest floor invertebrate biodiversity. Moreover, this study contributes to understanding the ecological impacts of invasive species on native forest communities.

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