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Forest disturbance and arthropods: Small-scale canopy gaps drive invertebrate community structure and composition

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Abstract. In forest ecosystems, disturbances that cause tree mortality create canopy gaps, increase growth of understory vegetation, and alter the abiotic environment. These impacts may have interacting effects on populations of ground-dwelling invertebrates that regulate ecological processes such as decomposition and nutrient cycling. A manipulative experiment was designed to decouple effects of simultaneous disturbances to the forest canopy and ground-level vegetation to understand their individual and combined impacts on ground-dwelling invertebrate communities. We quantified invertebrate abundance, richness, diversity, and community composition via pitfall traps in response to a factorial combination of two disturbance treatments: canopy gap formation via girdling and understory vegetation removal. Formation of gaps was the primary driver of changes in invertebrate community structure, increasing activity-abundance and taxonomic richness, while understory removal had smaller effects. Families of Collembola and Diplopoda, as well as some families of Coleoptera, increased in combined canopy and understory disturbance treatments, whereas Curculionidae and Nitidulidae were more abundant in undisturbed forest. Gaps increased light availability, height and cover of understory vegetation, and soil moisture levels, and decreased depth and cover of leaf litter compared to undisturbed forest. Decoupling of canopy and understory vegetation disturbances revealed gap formation as an important short-term driver of ground-dwelling invertebrate community structure and composition. Our findings increase understanding of how ground-dwelling invertebrate communities respond to disturbance and inform sustainable management of forest ecosystems to foster biodiversity and resilience.

Key words: arthropods; canopy gaps; community structure; disturbance; ground beetles; ground-dwelling invertebrates; insects; springtails; understory.

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Introduction

Disturbances alter energy and nutrient flow, habitat structure, and species composition in ecosystems (White and Pickett 1985), which increases spatial and temporal heterogeneity at multiple spatial scales (Oliver and Larson 1996, Frelich 2002). These events shape fluctuations in community dynamics and ecosystem processes over time (Runkle 1985, Schowalter 1985, Pickett et al. 1989). In forest ecosystems, disturbances can cause tree mortality and formation of canopy gaps. Gaps alter the forest floor environment by increasing light availability, altering soil temperature and

moisture regimes, reducing leaf litter moisture and depth, and changing understory vegetation composition and structure (Collins et al. 1985, Gray et al. 2002, Ishizuka et al. 2002, Fahey and Puettmann 2007, Perry and Herms 2016*b*). However, increased light availability on the forest floor stimulates growth of understory vegetation, seedlings, saplings, and advanced regeneration (Oliver and Larson 1996, Nelson et al. 2008), which then can mediate the initial abiotic conditions induced by canopy gaps (Shure and Phillips 1991). Therefore, it is probable that changes to the canopy and understory following disturbance interact to impact the abundance and diversity of ground-dwelling invertebrates (Shure and Phillips 1991, Bouget and Duelli 2004, Gandhi et al. 2008, Perry and Herms 2016*a*, *b*).

Ground-dwelling invertebrate communities are useful for detecting and characterizing the effects of multiple, interacting disturbances on forest ecosystems (Moldenke et al. 2000) because they respond quickly to changes in habitat complexity and microclimate conditions such as soil moisture (Levings and Windsor 1984), coarse woody debris (CWD; Ulyshen and Hanula 2009), leaf litter depth (Koivula et al. 1999), and vegetation cover and structure (Shure and Phillips 1991, Pakeman and Stockan 2014). Spiders (Araneae), springtails (Collembola), ground beetles (Carabidae), and ants (Formicidae) are common taxa that have been used as biological indicators to detect and monitor changes in the abiotic environment in response to disturbance (Folgarait 1998, Rainio and Niemelä 2003, Pearce and Venier 2006, Greenslade 2007). Effects of perturbations on ground-dwelling invertebrates have implications for ecosystem services such as decomposition, nutrient cycling, and maintenance of soil structure (Brussaard 1997, Ruiter et al. 2002, Lavelle et al. 2006).

Experiments that decouple impacts of interacting disturbances are often unfeasible, but necessary to evaluate the effect size of each factor individually. Studies that decoupled the effects of canopy gaps and accumulation of woody debris (Richardson et al. 2010, Perry and Herms 2016*a*, Seibold et al. 2016) and microhabitats created by tip-up mounds from fallen trees (Thorn et al. 2016) have identified canopy gaps as a major driver of ground-dwelling invertebrate community structure and composition. Because increased light availability from the formation of canopy gaps stimulates understory growth and alters vegetation composition (Collins et al. 1985, Oliver and Larson 1996), abiotic conditions on the forest floor may change following the response of the understory (Royo and Carson 2006).

The objective of this study was to investigate the individual and interacting effects of disturbance to the forest canopy and ground-level understory vegetation on ground-dwelling invertebrate communities by decoupling these two factors via a manipulative experiment. We predicted that (1) formation of canopy gaps would be the dominant environmental factor structuring ground-dwelling invertebrate communities; (2) invertebrate activity-abundance and diversity would decrease in response to combined canopy gap formation and ground-level understory vegetation removal; and (3) presence of ground-level understory vegetation in canopy gaps would increase invertebrate activity-abundance and diversity by buffering variability in environmental changes on the forest floor.

Materials and Methods

Study site

Research was conducted at Powdermill Nature Reserve (PNR; 40°09′ S, 79°16′ W) in Rector, Westmoreland County, Pennsylvania, in the Laurel Highlands. Powdermill Nature Reserve has approximately 900 ha of natural habitat across an elevation range of 392–647 m that is largely temperate deciduous forest composed of mesophytic species. Powdermill Nature Reserve was established as a nature reserve and the field research station for the Carnegie Museum of Natural History in 1956 and has been largely unmanaged since. Prior to this, the region experienced several major anthropogenic disturbances, including logging in the 19th century, agricultural production until the early- to mid-20th century, and then some areas of the reserve were surface mined for coal in the 1940s.

Dominant tree taxa (m^2/ha) were maple (*Acer* spp.), oak (*Quercus* spp.), beech (*Fagus* spp.), tulip poplar (*Liriodendron tulipifera* L.), and hickory (*Carya* spp.) (Murphy et al. 2015). Basal area (calculated from dbh measurements of trees greater than 8 cm in diameter) averaged 58.5 m^2/ha (ranged from 55.0 to 64.2) for all trees and

19.3, 19.2, 4.6, 4.4, and 3.6 m^2/ha for poplar, maple, oak, hickory, and beech, respectively. Stand height averaged 19.7 m (ranged from 11.2 to 24.5 m). The understory was dominated by spicebush (*Lindera benzoin* (L.) Blume), but the invasive shrubs multiflora rose (*Rosa multiflora* Thunb.) and Japanese barberry (*Berberis thunbergii* DC) were also present (Calinger et al. 2015). However, PNR has a diverse understory of herbaceous plants and woody shrub species. Some of the most abundant species were violet (*Viola* spp.), blackberry (*Rubus allegheniensis* Porter), round-lobed hepatica (*Hepatica Americana* (DC)), common cinquefoil (*Potentilla* spp.), dewberry (*Rubus hispidus* L.), partridgeberry (*Mitchella repens* L.), bedstraw (*Galium* spp.), sedges (Cyperaceae spp.), nettle (*Urtica* spp.), greenbrier (*Smilax* spp.), and several species of ferns (*Polystichum acrostichoides* (Michx.), *Dennstaedtia punctilobula* (Michx.), *Thelypteris noveboracensis* L., and *Dryopteris* spp.).

Experimental design

A manipulative experiment was established in the forests of PNR with two disturbance treatments: the presence/absence of canopy gaps and the presence/absence of ground-level understory vegetation removal, resulting in four treatment combinations including (1) closed canopy/understory present (undisturbed control); (2) closed canopy/understory removed; (3) canopy gap/understory present; and (4) canopy gap/understory removed. The four treatment combinations were distributed randomly among 24 quadrats 30 × 30 m in size (the experimental unit of replication) such that each treatment combination was replicated six times. Quadrats were identified in 2013 and treatments were implemented once in June 2014, such that disturbance intensity was manipulated rather than frequency. Eight undisturbed reference quadrats (30 × 30 m) were included for additional undisturbed controls (closed canopy/understory present).

To implement the canopy gap treatment, 8–12 dominant or codominant trees were girdled on 5–6 June 2014 to create gaps in the forest canopy (Appendix S1: Fig. S1). To girdle the trees, a chainsaw was used to cut a 2 cm wide ring (6–12 cm deep) around the entire circumference of the trunk about 1.5 m above the ground. A second ring was cut approximately 20–30 cm below the first. Across all canopy gap treatments, 117 trees were girdled, of which the most common were the diffuse-porous species red maple (*Acer rebrum* L.), sugar maple (*Acer saccharum* Marsh.), and tulip poplar (*L. tulipifera* L.). All girdled tree species listed in Appendix S1: Fig. S3).

The number of trees girdled in each canopy gap treatment varied depending on the density and size of trees in the quadrat and was determined by visually estimating the amount of cumulative canopy removal required to achieve the targeted gap size. Canopy gap size and the health of girdled trees were evaluated to assess changes in the canopy gap treatment during the study. Percentage canopy openness was quantified in all treatments once in July 2013 before treatments were implemented and monthly during the summers of 2014 and 2015. Degree of canopy dieback was visually assessed for each girdled tree biweekly and monthly during the summers of 2014 and 2015, respectively, using a 1–5 health rating scale (Smith et al. 2015), where one corresponded to a healthy tree with a full canopy, five corresponded to a dead tree, and 2–4 represented stages of increasing canopy thinning. All girdled trees were categorized as either diffuse- or ring-porous, as ring-porous trees were expected to decline faster due to their thinner functional xylem.

To implement the understory removal treatment, mechanical weed trimmers (KM 110 R KombiMotor, Stihl; Virginia Beach, Virginia, USA) and loppers were used to remove all understory herbaceous plants, woody shrubs, seedling, and saplings (≤2 cm stem diameter) within the 30 × 30 m experimental quadrats (Appendix S1: Fig. S2). Herbaceous vegetation residue remained on the forest floor in the quadrats, while all woody shrubs and saplings were removed and deposited in the surrounding forest away from the treatments. Understory vegetation was removed on 5–7 June 2014. Height and percentage cover of understory vegetation were quantified in two randomly selected 1 m^2 areas in all treatments once in 2013 before treatments were implemented and monthly during the summers of 2014 and 2015 to assess changes in the understory during the study.

Invertebrate sampling

Ground-dwelling invertebrates were sampled using unbaited barrier pitfall traps (Spence and Niemelä 1994, Latty et al. 2006). Pitfall traps are a

passive method commonly used to collect ground-dwelling invertebrates (Spence and Niemelä 1994, Yi et al. 2012). Because this method tends to collect more active invertebrates, abundance of invertebrates is presented as activity-abundance (individuals per trap) and results should be interpreted accordingly. One trap was installed 5 m from the center of each experimental quadrat in a randomly selected cardinal direction. Barrier pitfall traps consisted of two pairs of plastic cups (each pair consisted of an inner 500-mL and outer 1-L plastic cup) dug into the ground such that the rim of cups was flush with the soil surface and connected by garden edging (Eco Edge, Suncast, Batavia, Illinois, USA) 1 m in length. The garden edging was used as a barrier to increase trap catch (Durkis and Reeves 1982). The inner cup contained 4 cm of propylene glycol (recreational vehicle and marine antifreeze, Peak Company Old World Industries, Clear Lake, Texas, USA) along with a few drops of detergent to facilitate collection. Masonite board (100 cm^2) was placed 3 cm above each pair of cups to prevent flooding from rainwater, and steel hardware cloth was secured over each pair with 30-cm stakes to limit animal disturbance.

Pitfall trap sampling was conducted continuously over the summers of 2013–2015. Trap catch was collected every two weeks, and cups were refilled with propylene glycol for the next sampling interval. In 2013, traps were installed on 3–5 June, and samples were collected on 18–19 June, 1–2 July, 16–17 July, 30–31 July, 13–14 August, 27–28 August, and 10–11 September. In 2014, traps were installed on 3–4 June, and samples were collected on 17–18 June, 1–2 July, 15–17 July, 29–31 July, 12–13 August, 26–27 August, and 9–10 September. In 2015, pitfall traps were installed on 25–27 May, and samples were collected on 9–10 June, 23–25 June, 7–8 July, 21–22 July, 5–6 August, and 17–18 August. Trap catches were separated from the propylene glycol in the field using a 10-cm fine mesh strainer and placed into a specimen cup containing 70% ethanol for storage until sorting and identification.

Ground-dwelling invertebrates were first identified to family using Triplehorn and Johnson (2005), Shear (1999), Weaver (1982), Dindal (1990), Borror and White (1970), and White (1983). Ground beetles were identified to species using keys in Lindroth (1961–1969), Freitag (1969), Arnett and Thomas (2001), and Bousquet (2010) with nomenclature following Bousquet (2012). Ants were identified to species using keys in Coovert (2005), Fisher and Cover (2007), and Ellison et al. (2012). Scarab beetles were identified to species using keys in Ratcliffe (1991), Arnett et al. (2002), and Harpootlian (2001). Carrion and burying beetles were identified to species using Arnett and Thomas (2001) and Ratcliffe (1996). Sap beetles were identified to species using Price (2003) and Arnett et al. (2002). Species vouchers were deposited at the Museum of Biological Diversity, The Ohio State University, Columbus, Ohio, USA, where each specimen was given a unique identifier label (Appendix S1: Table S1).

Forest floor environment

Environmental conditions were quantified to assess the effects of the disturbance treatments on the forest floor microclimate. Percentage cover of leaf litter, bare ground, fine woody debris (FWD; <10 cm in diameter at the large end), CWD (≥10 cm in diameter at the large end), and rocks were assessed in two randomly selected 1 m^2 areas surrounding each pitfall trap once in 2013 and monthly during the summers of 2014 and 2015. Environmental conditions were quantified on 30–31 July in 2013; on 17–19 June, 29–31 July, and 26–27 August in 2014; and on 9–10 June, 7–8 July, and 5–6 August in 2015. Leaf litter depth was measured on 29–31 July 2014. Volume of downed CWD was estimated along 30-m transects within each treatment in 2014 using the line intercept method described by Harmon and Sexton (1996). Downed CWD along the transects was categorized according to decay class using a 1–5 decay stage scale adapted from Pyle and Brown (1999) and Woodall and Williams (2005). Soil temperature and moisture were measured adjacent to pitfall traps with a Durac Bi-Metallic Dial Thermometer and Dynamax TH_2O Portable Soil Moisture Meter and Theta Probe ML2x Sensor, respectively. Measurements were collected biweekly when trap samples were collected. Three readings were averaged together for the final quadrat measurement.

Statistical analyses

Data were evaluated for statistical assumptions of normality and homogeneity of variance.

Rank transformations were applied as necessary to achieve these assumptions, and the activity-abundances of taxa and species were rank transformed to improve normality (Quinn and Keough 2002). For each sampling interval, trap catches were standardized to 14 trap days to account for disruption and the number of operational days [(trap catch/total number of days trap was operational) × 14] (Spence et al. 1996, Gandhi et al. 2008). Taxonomic richness (number of invertebrate taxa per treatment), Pielou *J* evenness index (Pielou 1966), and Shannon diversity index (Peet 1974) were calculated using PC-ORD software (McCune and Mefford 2006).

Repeated measures analysis of variance (ANOVA) tests coupled with univariate analyses for each date and Tukey's pairwise comparisons for mean separation following a significant *F* test were used to compare ground-dwelling invertebrate communities in canopy gap and understory vegetation disturbance treatments using SAS software (SAS 2014–2016). Response variables were total ground-dwelling invertebrate activity-abundance, taxonomic richness, evenness, and diversity. Predictor variables for the models were canopy gaps (presence/absence) and understory vegetation (presence/absence) as fixed factors and sampling interval as a repeated factor. Each year was analyzed separately. If no pre-treatment differences were detected between experimental quadrats, total ground-dwelling invertebrate activity-abundance, taxonomic richness, evenness, and diversity were pooled over the summer in 2013 and used as covariates in the corresponding repeated measures ANCOVA tests for 2014 and 2015.

Similar repeated measures ANOVA tests were used to assess the change in canopy and understory disturbance treatments over the three-year study, as well as compare the forest floor environment between these treatments. Response variables were percentage canopy openness; percentage cover of understory vegetation, leaf litter, bare ground, FWD, CWD, and rocks; height of understory vegetation; leaf litter depth; soil temperature; and soil moisture. Each year was analyzed separately. Logistic regression analyses with maximum likelihood estimates were conducted to compare canopy decline of girdled trees over time using the 1–5 rating scale. Separate analyses were conducted to compare differences between tree species and between ring- and diffuse-porous trees.

Activity-abundances of ground-dwelling invertebrate taxa were analyzed to understand taxon-specific responses to the disturbance treatments. The activity-abundance of a taxon was analyzed if ≥20 individuals were collected during the year, and each year was analyzed separately. Activity-abundances of common species (≥150 total individuals collected) in the families Formicidae, Carabidae, Nitidulidae, Geotrupidae, Scarabaeidae, Trogidae, and Silphidae also were analyzed. Responses were assessed only for common species to ensure these were not transient, but have established populations at the study site. Similar repeated measures ANOVA tests as described above were used to analyze the activity-abundances of ground-dwelling invertebrate taxa and common species using SAS software (SAS 2014–2016).

Multivariate regression tree (MRT) analyses were used to investigate the relationship between ground-dwelling invertebrate community composition and the continuous ground-level environmental factors measured in the treatments. Multivariate regression tree is a constrained clustering method that is robust to complex ecological data that may contain missing values, nonlinear relationships between response and predictor variables, and interactions between predictor variables (Borcard et al. 2011). This technique repeatedly partitions the data into groups defined by thresholds in environmental variables (De'ath 2002, McCune and Grace 2002). Distance-based MRT (db-MRT) analyses were conducted separately for communities in 2014 and 2015 using the Bray-Curtis dissimilarity index. The size of each tree was selected by cross-validation using the ANOVA method to minimize the relative error and cross-validated relative error (De'ath 2002). Indicator species analyses (ISA) were conducted to identify invertebrate taxa that characterized each terminal group in the tree (De'ath 2002, Borcard et al. 2011). This technique is based on the relative abundance and relative frequency of taxa present in each quadrat (Dufrêne and Legendre 1997). Multivariate regression tree analyses were conducted using mvpart (De'ath 2014) and MVPARTwrap (Ouellette 2013) packages, and

ISA were conducted using labdsv (Roberts 2016) in R version 3.3.1 (R Development Core Team 2017).

Results

Changes caused by disturbance treatments

All trees had a canopy rating of 1 (healthy, full canopy) before girdling. After trees were girdled, the canopies of oaks and other species declined more rapidly than the canopies of maples and poplars (Appendix S1: Fig. S3A; $\chi^2 = 62.6$, $P < 0.001$; Time $\chi^2 = 451.4$, $P < 0.001$). The canopies of ring-porous species (oaks, ash, cherry, hickory, and elm) declined more rapidly than diffuse-porous species (maples, tulip poplar, basswood, beech and birch; Appendix S1: Fig. S3B; $\chi^2 = 175.2$, $P < 0.001$; Time $\chi^2 = 473.7$, $P < 0.001$).

Percentage canopy openness increased over time by nearly 10% ($F_{6,126} = 11.4$, $P < 0.001$) in the gap treatment as trees died following girdling compared to the closed canopy treatment (Fig. 1; $F_{1,21} = 48.5$, $P < 0.001$). Percentage cover of vegetation was nearly 30% lower in the understory removed treatment compared to the understory present treatment (Appendix S1: Fig. S4; $F_{1,27} = 6.67$, $P = 0.015$), but cover increased over time with vegetation regrowth (Fig. 2; $F_{1,162} = 8.49$, $P < 0.001$), and growth was greater in the canopy gap treatment ($F_{1,27} = 5.19$, $P = 0.030$). Percentage cover of understory vegetation was 2–17% higher overall in the canopy gap treatment ($F_{1,27} = 6.01$,

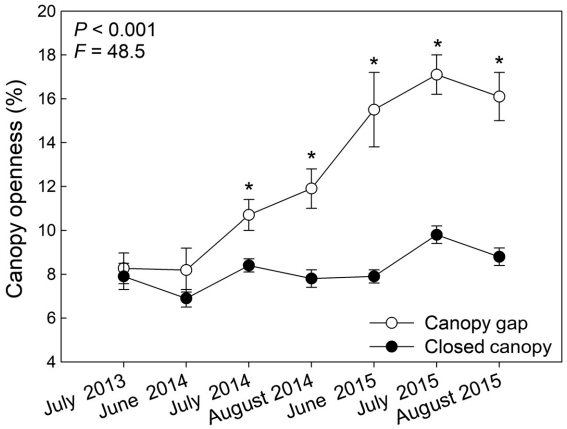

Fig. 1. Percentage canopy openness in canopy gap and closed canopy treatments at Powdermill Nature Reserve, Rector, Pennsylvania, USA. Measurements were collected once in July 2013 before the treatments were implemented. Trees were girdled on 5–6 June 2014, and measurements were collected once per month in 2014 and 2015. Repeated measures ANOVA with Tukey's pairwise comparisons; asterisks denote significant differences ($\alpha = 0.05$).

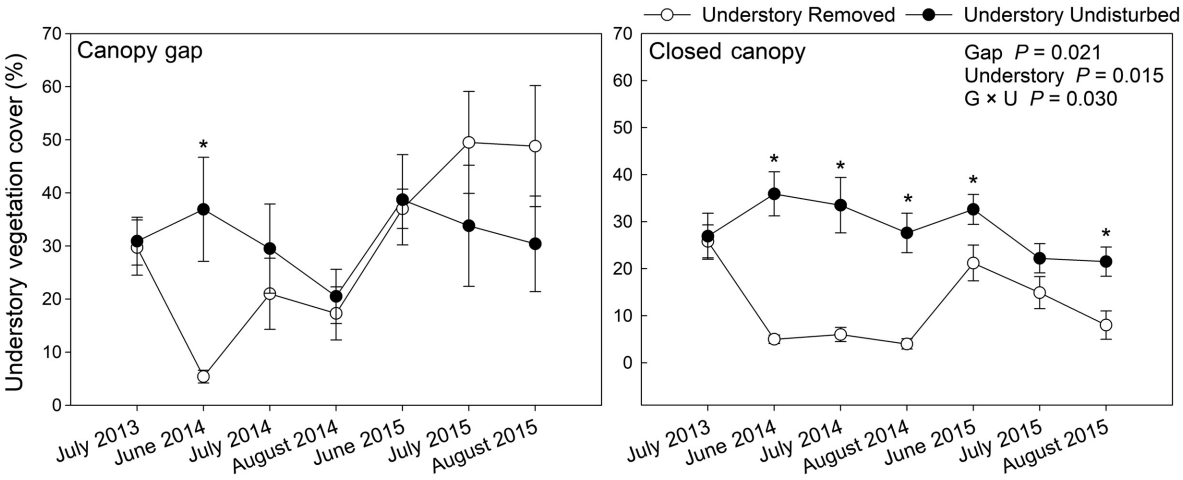

Fig. 2. Interaction plots for percentage understory vegetation cover in canopy gap (left) and closed canopy (right) treatments at Powdermill Nature Reserve, Rector, Pennsylvania, USA. Percentage cover of understory vegetation was measured once in July 2013 before treatments were implemented. Understory vegetation was removed on 5–7 June 2014, and vegetation cover was measured once per month in 2014 and 2015. Repeated measures ANOVA with Tukey's pairwise comparisons; asterisks denote significant differences ($\alpha = 0.05$).

$P = 0.021$), but less variable in the closed canopy treatment (Fig. 2). Understory vegetation was 0.05 m shorter in the understory removed treatment than in the understory present treatment ($F_{1,27} = 4.81$, $P = 0.037$) and increased over time in all treatments ($F_{6,126} = 13.9$, $P < 0.001$). Understory vegetation was 0.06–0.09 m taller in the canopy gap treatment than in the closed canopy treatment ($F_{1,27} = 5.26$, $P = 0.029$).

Forest floor environment

The forest floor environment was similar in all experimental quadrats in 2013 (Appendix S1: Table S2). After treatment implementation, soil temperature was consistently higher in the understory removed treatment (2014: $F_{1,24} = 8.01$, $P = 0.011$; 2015: $F_{1,24} = 5.19$, $P = 0.032$), while soil moisture was consistently higher in the canopy gap treatment (2014: $F_{1,24} = 11.3$, $P = 0.013$; 2015: $F_{1,24} = 5.16$, $P = 0.042$). Leaf litter depth (2014: $F_{1,27} = 4.82$, $P = 0.046$) and percentage cover (2014: $F_{1,21} = 7.30$, $P = 0.013$; 2015: $F_{1,21} = 12.2$, $P = 0.002$) were lower in canopy gaps than in the closed canopy treatment. Percentage cover of leaf litter ($F_{1,21} = 9.55$, $P = 0.005$) and bare ground ($F_{1,21} = 4.44$, $P = 0.047$) were higher in the understory removed treatment in 2014.

Invertebrate abundance and diversity

A total of 210,695 individuals were collected in unbaited pitfall traps representing 29 non-insect invertebrate taxa, 36 insect families, and five insect subfamilies during 2013–2015 (Table 1). Of the 70 ground-dwelling invertebrate taxa, 54 were uncommon (<1% of total individuals collected), 13 were common (1–10% of total individuals collected; Parajulidae, 1.1%; Scolytinae, 1.1%; Geotrupidae, 1.6%; Nitidulidae, 1.8%; Polydesmidae, 2.0%; Carabidae, 2.4%; Neanuridae, 2.7%; Entomobryidae, 2.8%; Araneae, 3.6%; Paradoxosomatidae, 3.9%; Formicidae, 5.5%; Staphylinidae, 6.2%; and Dicyrtomidae, 8.7%), and three taxa were abundant (Isotomidae, 11.8%; Tomoceridae, 18.1%; and Hypogastruridae, 20.0%). By far, the most abundant invertebrates were the 137,993 Collembola, comprising >65% of the total trap catch over the three-year study.

Coleoptera was the most abundant insect order, comprising 33 families and totaling 31,112 individuals. Beetles in the families Carabidae, Geotrupidae, Scarabaeidae, Trogidae, Silphidae, and Nitidulidae were identified to species (Appendix S1: Table S1). Carabidae was the most diverse family with 5166 individuals comprising 30 genera and 59 species, of which *Carabus goryi* Dejean and *Platynus angustatus* Dejean were the most abundant. In the family Geotrupidae, species in the genus *Geotrupes* were abundant (*Geotrupes semiopacus* Jekel, *Geotrupes splendidus* [Fabricius], and *Geotrupes balyi* Jekel). Nine genera and 15 species were identified in the family Scarabaeidae, with *Dialytellus striatulus* (Schmidt) and *Copris minutus* Drury being the most common. Only one species, *Trox variolatus* Melsheimer, was collected in the family Trogidae. *Nicrophorus orbicollis* Say was the dominant species of Silphidae. *Stelidota geminata* (Say) and *Glischrochilus sanguinolentus* Olivier were common species in the family Nitidulidae.

Formicidae also were common with 11,608 individuals in 12 genera and 24 species collected over the three-year study (Appendix S1: Table S1). *Aphaenogaster picea* Wheeler was numerically dominant throughout the study site, comprising 62.8% of the total number of ants. *Camponotus pennsylvanicus* (DeGeer), *Formica subsericea* Say, *Myrmecina americana* Emery, *Myrmica punctiventris* Roger, *Lasius alienus* (Foerster), *Lasius umbratus* (Nylander), and *Stenamma impar* Forel were common species.

Ground-dwelling invertebrate activity-abundance, taxonomic richness, evenness, and diversity were similar in all experimental quadrats in 2013 prior to treatment implementation ($P = 0.157$–0.995) (Table 2). In 2014, ground-dwelling invertebrate activity-abundance ($F_{1,20} = 4.44$, $P = 0.044$) and richness ($F_{1,20} = 4.96$, $P = 0.034$) were higher in canopy gaps than in the closed canopy treatment (Table 2). Taxonomic richness was higher in understory removed than in the understory present treatment (Fig. 3; $F_{1,20} = 6.33$, $P = 0.018$). In 2015, invertebrate activity-abundance (Fig. 4A; $F_{1,20} = 9.12$, $P = 0.006$) and richness (Fig. 4B; $F_{1,20} = 9.99$, $P = 0.004$) were higher in the canopy gap treatment. Taxonomic evenness was lower in gaps ($F_{1,20} = 8.29$, $P = 0.009$) than in the closed canopy treatment. Invertebrate Shannon diversity was unaffected, and no treatment interactions were detected (Table 2).

Responses to either canopy or understory disturbance treatments were detected for 20 ground-dwelling invertebrate taxa (Appendix S1: Table S3).

Table 1. Ground-dwelling invertebrate taxa sampled with unbaited barrier pitfall traps in disturbance treatments in 2013–2015 at Powdermill Nature Reserve in Rector, Westmoreland County, Pennsylvania, USA.

Class	Order	Family or subfamily	2013	2014	2015	Total
Clitellata	Haplotaxida		67	46	69	182
Gastropoda	Snails		332	255	562	1149
	Slugs		24	68	38	130
Chilopoda	Geophilomorpha		51	41	9	101
	Lithobiomorpha		131	75	106	312
	Scolopendromorpha		58	30	21	109
Diplopoda	Callipodida	Abacionidae	2	34	14	50
	Chordeumatida	Caseyidae	134	445	154	733
	Julida	Julidae	360	440	207	1007
		Parajulidae	273	1115	1027	2415
	Polydesmida	Paradoxosomatidae	2119	4606	1624	8349
		Polydesmidae	714	2083	1437	4234
		Xystodesmidae	23	5	18	46
	Polyzoniida	Polyzoniidae	8	4	18	30
	Spirobolida	Spirobolidae	819	84	122	1025
Malacostraca	Isopoda		182	307	149	638
Arachnida	Araneae		2750	2305	2606	7661
	Opiliones		89	223	480	792
	Pseudoscorpiones		22	8	120	150
Protura			2	0	0	2
Diplura		Campodeidae	1	0	0	1
Collembola	Poduromorpha	Onychiuridae	20	2	20	42
		Neanuridae	3103	1341	1417	5861
		Hypogastruridae	26,469	10,631	6339	43,439
	Entomobryomorpha	Isotomidae	5110	14,812	4994	24,916
		Tomoceridae	7998	12,102	18,249	38,349
		Entomobryidae	688	1514	3874	6076
	Symphypleona	Dicyrtomidae	5675	6640	6082	18,397
		Katiannidae	307	163	443	913
Insecta	Blattodea	Blattidae	2	3	7	12
	Hymenoptera	Formicidae	3742	4222	3644	11,608
	Orthoptera	Gryllidae	84	361	254	699
		Rhaphidophoridae	189	155	109	453
	Coleoptera	Carabidae	1682	2059	1425	5166
		Curculionidae	506	270	244	1020
		Scolytinae	1033	441	795	2269
		Cucujidae	0	2	12	14
		Elateridae	25	4	11	40
		Eucnemidae	1	1	0	2
		Histeridae	24	35	31	90
		Phalacridae	123	125	21	269
		Ptiliidae	28	278	55	361
		Nitidulidae	1136	781	1888	3805
		Geotrupidae	813	797	1954	3565
		Scarabaeidae	76	170	57	303
		Aphodiinae	40	61	13	114
		Dynastinae	1	0	0	1
		Melolonthinae	7	6	4	17
		Scarabaeinae	28	103	40	171
		Trogidae	30	49	44	123
		Silphidae	224	156	123	503
		Leptodiridae	0	8	1	9
		Staphylinidae	3966	5511	3719	13,196

(Table 1. Continued.)

Class	Order	Family or subfamily	2013	2014	2015	Total
		Anthribidae	1	0	0	1
		Pselaphidae	2	1	3	6
		Scydmaenidae	2	0	0	2
		Tenebrionidae	2	3	1	6
		Melandryidae	1	1	0	2
		Rhizophagidae	2	4	4	10
		Meloidae	3	0	0	3
		Leiodidae	4	0	3	7
		Mycetophagidae	0	9	4	13
		Cryptophagidae	0	0	5	5
		Erotylidae	0	0	1	1
		Anthicidae	1	0	0	1
		Throscidae	0	3	0	3
		Trogositidae	0	5	0	5
		Salpingidae	0	0	12	12
		Byrrhidae	0	1	0	1
		Cerylonidae	0	0	1	1
		Total	71,233	74,834	64,628	210,695

Table 2. Main effects of canopy gap formation and understory vegetation removal treatments on total ground-dwelling invertebrate activity-abundance, taxonomic richness, evenness, and diversity (mean ± SE) in 2013–2015 in forests at Powdermill Nature Reserve, Rector, Pennsylvania, USA.

			Canopy disturbance				Understory vegetation disturbance				Gap × veg		2013 covariate	
Taxonomic index	Year	df	Canopy gap	Closed canopy	*F*	*P*	Veg removed	Veg present	*F*	*P*	*F*	*P*	*F*	*P*
Activity-abundance	2013	1,18	634.9 ± 69.4	529.2 ± 34.6	1.07	0.314	551.1 ± 56.1	578.8 ± 42.4	0.14	0.708	1.82	0.194		
	2014	1,20	779.0 ± 98.1	516.9 ± 48.2	4.44	**0.044**	744.8 ± 86.9	537.4 ± 56.0	1.00	0.327	1.26	0.272	4.15	0.052
	2015	1,20	621.8 ± 49.1	428.1 ± 28.6	9.12	**0.006**	567.7 ± 53.4	455.3 ± 27.7	0.18	0.678	0.05	0.822	1.33	0.268
Richness	2013	1,18	28.3 ± 0.8	28.3 ± 1.1	0.06	0.802	29.5 ± 1.1	28.7 ± 0.8	1.15	0.297	0.00	0.995		
	2014	1,20	29.7 ± 0.9	25.9 ± 0.6	4.96	**0.034**	30.8 ± 1.0	25.3 ± 0.5	6.33	**0.018**	0.27	0.610	1.29	0.267
	2015	1,20	27.4 ± 0.9	23.9 ± 0.5	9.99	**0.004**	27.7 ± 0.8	23.8 ± 0.5	2.27	0.154	0.23	0.636	0.01	0.933
Evenness	2013	1,18	0.687 ± 0.02	0.704 ± 0.01	1.60	0.221	0.713 ± 0.01	0.688 ± 0.01	0.01	0.905	2.18	0.157		
	2014	1,20	0.676 ± 0.01	0.706 ± 0.01	2.65	0.137	0.682 ± 0.01	0.702 ± 0.01	0.00	0.950	1.58	0.223	0.00	0.961
	2015	1,20	0.680 ± 0.01	0.720 ± 0.01	8.29	**0.009**	0.716 ± 0.01	0.702 ± 0.01	0.12	0.736	1.11	0.310	3.68	0.069
Shannon diversity	2013	1,18	2.22 ± 0.06	2.33 ± 0.04	2.11	0.164	2.34 ± 0.05	2.25 ± 0.04	0.63	0.438	1.14	0.299		
	2014	1,20	2.26 ± 0.05	2.26 ± 0.03	0.04	0.846	2.30 ± 0.04	2.23 ± 0.03	1.06	0.316	0.19	0.669	0.02	0.880
	2015	1,20	2.21 ± 0.04	2.25 ± 0.03	0.66	0.429	2.34 ± 0.03	2.18 ± 0.03	3.71	0.068	0.54	0.474	0.79	0.390

Note: Repeated measures ANOVA, significant ($\alpha \leq 0.05$) *P* values in bold.

Activity-abundances of Caseyidae, Paradoxosomatidae, Isopoda, Araneae, Isotomidae, Tomoceridae, Dicyrtomidae, Katiannidae, Gryllidae, Carabidae, Scarabaeidae, and Staphylinidae were higher in canopy gaps than in the closed canopy treatment. Curculionidae and Nitidulidae were less abundant in canopy gaps. Activity-abundances of Lithobiomorpha, Hypogastruridae, Entomobryidae, Rhaphidophoridae, Geotrupidae, Scarabaeidae, and Staphylinidae were higher in understory removed than in the understory present treatment.

Canopy gap and understory vegetation removal treatments interacted to affect the activity-abundances of 11 ground-dwelling invertebrate taxa (Appendix S1: Table S3). In 2014, Caseyidae and Julidae were most abundant in the canopy gap/understory removed treatment compared to all other treatment combinations. Parajulidae was least abundant and Spirobolidae

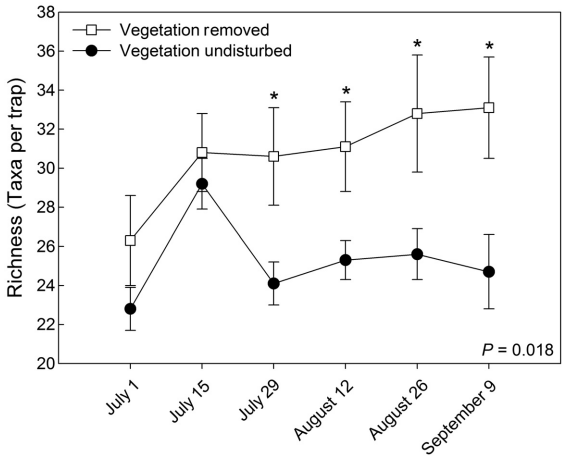

Fig. 3. Main effects of the understory vegetation removal treatment on ground-dwelling invertebrate taxonomic richness (± SE) in 2014 initially following treatment implementation at Powdermill Nature Reserve, Rector, Pennsylvania, USA. Results are given for the repeated measures ANOVA. Asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

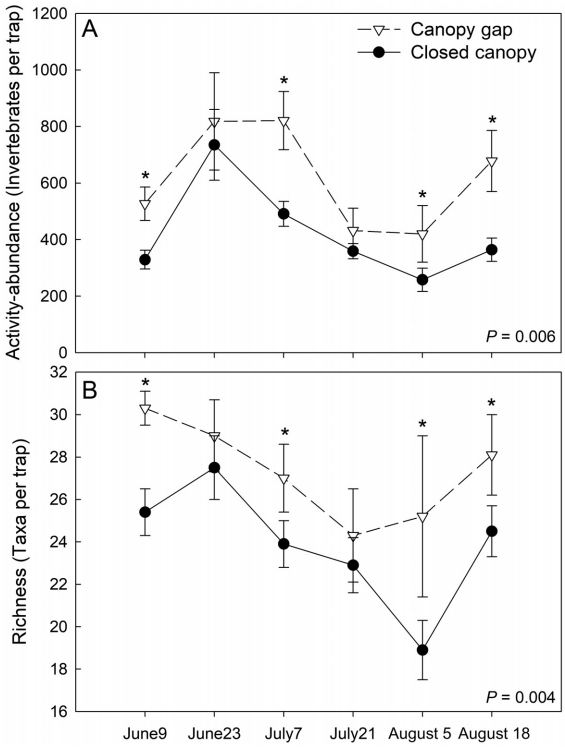

Fig. 4. Main effects of canopy gap formation on ground-dwelling invertebrate (A) activity-abundance (± SE) and (B) taxonomic richness (± SE) in 2015 in forests at Powdermill Nature Reserve, Rector, Pennsylvania, USA. Results are given for the repeated measures ANOVA. Asterisk denotes intervals where treatments are significantly different ($\alpha \leq 0.05$).

was most abundant in the canopy gap/understory present and the closed canopy/understory removed treatments. Polydesmidae, and to a lesser extent Paradoxosomatidae, were least abundant in the closed canopy/understory present treatment. Activity-abundance of Hypogastruridae was lowest in the closed canopy/understory present treatment, and a similar trend was observed for Isotomidae. In 2015, snails were most abundant in the canopy gap/understory present treatment, while slugs were least abundant in the closed canopy/understory removed treatment.

Two families of Coleoptera showed consistent patterns of activity-abundance across the two years following canopy and understory disturbance. Histeridae were least abundant in the closed canopy/understory present treatment compared to all other treatment combinations in 2014 ($F_{1,20} = 5.75$, $P = 0.023$) and 2015 ($F_{1,20} = 13.7$, $P = 0.001$). Scarabaeinae were most abundant in the canopy gap/understory removed treatment and least abundant in the closed canopy/understory removed treatment in 2014 ($F_{1,20} = 5.51$, $P = 0.028$) and 2015 ($F_{1,20} = 4.79$, $P = 0.042$).

Five ground beetle and one ant species were affected by canopy and understory disturbance treatments (Appendix S1: Table S4). Activity-abundances of *Chlaenius emarginatus* Say (2015: $F_{1,20} = 7.36$, $P = 0.013$), *Cyclotrachelus sigillatus* (Say) (2015: $F_{1,20} = 4.19$, $P = 0.050$), and *Pterostichus stygicus* (Say) (2014: $F_{1,20} = 8.84$, $P = 0.006$) were higher in canopy gaps than in the closed canopy treatment, while *Dicaelus teter* Bonelli (2015: $F_{1,20} = 5.38$, $P = 0.028$) was less abundant in canopy gaps. Activity-abundances of *C. goryi* (2014: $F_{1,20} = 4.39$, $P = 0.045$; 2015: $F_{1,20} = 7.33$, $P = 0.013$) and *D. teter* (2015: $F_{1,20} = 4.41$, $P = 0.048$) were higher in understory removed than in the understory present treatment. *Formica subsericea* (2015: $F_{1,28} = 4.79$, $P = 0.042$) was more abundant in canopy gaps.

Canopy gap and understory vegetation removal treatments interacted to affect the activity-abundances of four carabid species (Appendix S1: Table S4). In 2014, activity-abundances

of *C. sigillatus* ($F_{1,20}$ = 6.22, P = 0.019) and *Pterostichus lachrymosus* (Newman) ($F_{1,20}$ = 6.01, P = 0.021) were lowest in the closed canopy/understory removed and canopy gap/understory present treatments. In 2015, *P. stygicus* was more abundant in the canopy gap/understory present treatment than in other treatment combinations ($F_{1,20}$ = 7.96, P = 0.009). Activity-abundance of *P. angustatus* was lowest in the closed canopy/understory present treatment in 2014 ($F_{1,20}$ = 5.44, P = 0.029) and highest in the closed canopy/understory removed treatment and the canopy gap/understory present treatment in 2015 ($F_{1,20}$ = 11.9, P = 0.001).

Invertebrate community composition

In 2015, the invertebrate community was characterized by a three-branch db-MRT (Fig. 5) that was selected 98 of 100 times by cross-validation. The model explained 61.6% of the total variance, returning a relative error of 38.4% and a cross-validated error (±SE) of 1.3 (± 0.5). The first partition explained 36.5% of the variance and divided the tree based on a soil moisture threshold of 78.6%. Hypogastruridae (25.9%), Tomoceridae (16.4%), Staphylinidae (12.7%), and Dicyrtomidae (10.1%) contributed most to the variance explained by the first partition in the tree. Most treatment combinations were characterized by lower soil moisture levels (<78.6%; n = 30). Two quadrats were characterized by high soil moisture levels (≥78.6%), and Gastropoda (P = 0.001), specifically slugs, was identified as an indicator taxon. The second partition, explaining 25.1% of the variance, divided the branch characterized by soil moisture levels <78.6% further based on a 13% canopy openness threshold. Tomoceridae (36.7%) and Hypogastruridae (36.3%) contributed most to the variance explained by this split in the tree. Canopy gap (≥13% openness; n = 11) and closed canopy (<13% openness; n = 19) treatments clustered appropriately on the tree. Tomoceridae (P = 0.009), Hypogastruridae (P = 0.004), Staphylinidae (P = 0.001), Silphidae (P = 0.009), Geotrupidae (P = 0.028), Scarabaeidae (P = 0.016), Scolytinae (P = 0.015), Formicidae (P = 0.015), and Gryllidae (P = 0.001) were identified as indicator taxa for ≥13% canopy openness. No indicators were identified for the closed canopy treatment (<13% canopy openness).

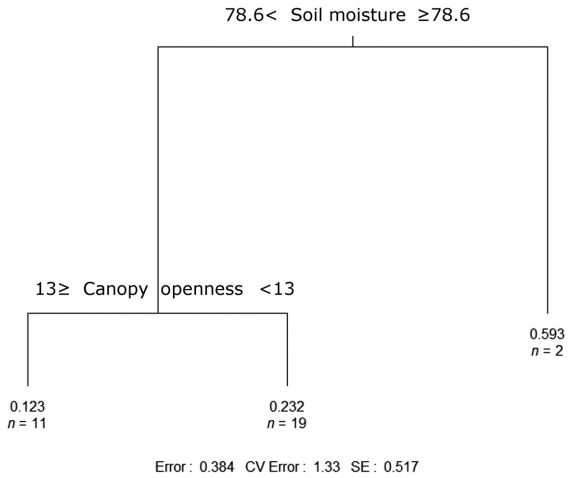

Fig. 5. Distance-based multivariate regression tree (db-MRT) comparing ground-dwelling invertebrate communities in canopy and ground-level understory vegetation disturbance treatments in 2015 at Powdermill Nature Reserve, Westmoreland County, Pennsylvania. The three-branch db-MRT partitioned the invertebrate community based on soil moisture levels (%) and canopy openness (%), explaining 61.6% of the total variance.

The ground-dwelling invertebrate community was characterized by a two-branch db-MRT in 2014 that was selected 96 of 100 times by cross-validation. The tree divided the community into two groups based on a threshold of 8.2% cover of FWD. Paradoxosomatidae (44.6%), Polydesmidae (20.2%), and Formicidae (15.0%) contributed most to the variance explained by the split, but model accounted for only 50% of the total variance, returning a high relative error of 50% and cross-validated relative error (± SE) of 1.6 (± 0.5), suggesting a poor fit overall. Percentage cover of FWD < 8.2% was observed for the majority (n = 26) of experimental quadrats, while fewer (n = 6; including the undisturbed control and canopy gap treatment) had ≥ 8.2% FWD cover.

Discussion

Formation of canopy gaps had a greater effect on the structure and composition of ground-dwelling invertebrate communities than did a pulse disturbance to the understory, which is consistent with our first prediction. This finding also is consistent with previous studies that found the formation of canopy gaps to be a

primary driver of invertebrate community structure (Richardson et al. 2010, Perry and Herms 2016*a*, Seibold et al. 2016, Thorn et al. 2016). Invertebrate activity-abundance and richness were consistently higher in canopy gaps. These patterns were primarily driven by increased activity-abundances of diverse functional guilds such as detritivores, fungivores, and predators that included families of Diplopoda, Collembola, and Coleoptera.

Although these findings corroborate the importance of canopy gap formation for structuring invertebrate communities following disturbance, the positive effects of gaps on invertebrate abundance and richness reported here are inconsistent with other studies (Greenberg and Forrest 2003, Gandhi et al. 2008, Richardson et al. 2010). For example, canopy gaps experimentally created to emulate hurricane disturbance had lower diversity and biomass of ground-dwelling invertebrates such as predators and large detritivores compared to undisturbed forest (Richardson et al. 2010). Greenberg and Forrest (2003) observed lower total ground-dwelling invertebrate activity-abundance and biomass in windthrow gaps created by Hurricane Opal than in nearby undisturbed forest, primarily due to lower activity-abundances of Carabidae, Araneae, Julida, Spirobolida, and Scolopendromorpha. Gandhi et al. (2008) documented lower activity-abundance and diversity of ground beetles in canopy gaps created by a windstorm than in undisturbed forest. In our study, families of Collembola were the most abundant taxa collected and were among the dominant taxa driving patterns in total ground-dwelling invertebrate responses. Greenberg and Forrest (2003) did not sample Collembola, and Richardson et al. (2010) pooled families for their analyses, which may have obscured family-specific responses and explain the divergent patterns in total ground-dwelling invertebrate activity-abundance. Alternatively, smaller size of the experimental quadrats compared to larger-scale windstorms may have facilitated use of the disturbed patch by forest and open-habitat invertebrates, thereby increasing total activity-abundance and richness.

Compared to undisturbed forest, light availability, height and cover of understory vegetation, and soil moisture levels were higher in gaps, and depth and cover of leaf litter were lower. These environmental changes on the forest floor induced by canopy gaps may have contributed to altered ground-dwelling invertebrate activity-abundance, richness, and community composition. The importance of canopy gaps as a driver of forest community structure and diversity is well documented (Runkle and Yetter 1987, Yamamoto 1992, McCarthy 2001, Schnitzer and Carson 2001, Perry and Herms 2017), as is the suite of environmental changes that occur on the forest floor following gap formation (Gray et al. 2002, Ishizuka et al. 2002, Ritter et al. 2005, Perry and Herms 2016*b*). Canopy gaps were the primary factor structuring ground-dwelling invertebrate community composition in 2015, although the MRT model had low predictive power, but were not identified as a significant factor in 2014. Ring-porous tree species declined quickly following girdling in 2014, but these gaps were not large enough to drive significant changes in ground-dwelling invertebrate community composition, as indicated by the poor fit of the MRT model overall. In 2015, the model partitioned the quadrats according to the presence or absence of canopy gaps, which were larger after more diffuse-porous species declined and died. In the canopy gap treatment, families of epedaphic Collembola were numerically dominant and contributed most to the construction of the model, suggesting they responded strongly to environmental changes on the forest floor. Collembola are susceptible to desiccation and responsive to changes in soil moisture regimes (Verhoef 1977, Verhoef and van Selm 1983, Hopkin 1997), especially those species that are active on the litter and soil layers. Soil moisture was consistently higher in canopy gaps than in the closed canopy treatment, which may have influenced surface-dwelling Collembola populations. Henneron et al. (2017) also documented increased abundance and richness of epedaphic Collembola following canopy tree removal, but found that euedaphic Collembola (soil-dwelling species) decreased in abundance and richness. Regardless of their small size, Collembola assemblages are responsive to perturbations in forests and may be useful as an indicator taxon for environmental change.

The pulse of resource availability that occurs initially after gap formation may provide more opportunities for diverse invertebrate taxa. Tree

death often increases soil moisture and nutrient levels (Minckler et al. 1973, Mladenoff 1987, Gray et al. 2002, Ishizuka et al. 2002). Increased soil temperatures and moisture levels create a conducive environment for decomposition, and increased mineralization and nitrification have been observed in forest openings (Likens et al. 1978, Runkle 1985). Detritivores and fungivores may have responded to this short-term resource pulse, and predators may have followed prey populations. Several epedaphic families of Collembola (Isotomidae, Tomoceridae, Dicyrtomidae, and Katiannidae), as well as common detritivores (Caseyidae, Paradoxosomatidae, Isopoda, and Scarabaeidae) and predators (Araneae, Carabidae, and Staphylinidae), were more abundant in canopy gap treatments. Soft-bodied arthropods such as Collembola are common prey for Araneae, Carabidae, and Staphylinidae, and their populations affect predator distributions (Chen and Wise 1999, Lawrence and Wise 2000, Birkhofer et al. 2010, Sereda et al. 2012). For example, the ground beetle species *Chlaenius emarginatus*, *Cyclotrachelus sigillatus*, and *Pterostichus stygicus* were more abundant in canopy gaps and may have recruited to these treatments due to abundant prey. All three species are predatory on soft-bodied invertebrates and are generalists in terms of their habitat requirements, as they are commonly collected in deciduous and mixed forest types as well as nearby fields (Larochelle and Larivière 2003). General habitat requirements may have primed these ground beetle species to take advantage of the abundant prey in canopy gap treatments, allowing them to remain in the disturbed patch. Patterns of movement of ground-dwelling invertebrates were mostly local in canopy gap treatments, as the majority of individuals dispersed only a short distance (<1–5 m) than those in undisturbed treatments (6–≥13 m; Perry 2016). This finding suggests that the majority of invertebrates remained within the disturbed patches (Perry 2016), perhaps due to the abundance of available resources in gaps.

This study investigated the impacts of disturbance intensity to the forest canopy and understory on ground-dwelling invertebrate communities. Therefore, treatments were implemented once and simulated a pulse rather than a press or chronic form of disturbance. Pulse disturbances that affect the canopy and understory such as windthrow are common in forest ecosystems (Oliver and Larson 1996, Bengtsson 2002, Frelich 2002), making this manipulative experiment a fairly good predictor for the impacts of natural disturbance events. However, because the disturbance treatments were only implemented once, temporal variability in canopy and understory conditions occurred during the course of the study. This variability may explain the poor fit of the MRT model characterizing ground-dwelling invertebrate community composition in 2014, as well as the dampened response of invertebrates to the understory removal treatment. The health of girdled trees declined over the summer in 2014, and the rate of tree decline was influenced by species-specific differences in vasculature structure (Wiant and Walker 1961), as ring-porous species (oak, ash, and hickory) declined faster than diffuse-porous species (maple and poplar). Hence, gap size increased over time in all quadrats, but more rapidly in quadrats that had a greater number of girdled ring-porous trees. Gaps were larger in 2015 once the majority of trees had died, suggesting the magnitude of the treatment effect was greater than in 2014. This temporal change in canopy gap size explains the importance of gaps in structuring ground-dwelling invertebrate communities in 2015, but not 2014. The understory removal treatment displayed the opposite pattern with vegetation regrowth occurring over time, which decreased the effect size of the treatment. Therefore, the magnitude of understory vegetation removal decreased with plant regrowth, while the effects of gaps increased as tree canopies declined over time. Temporal changes in the disturbance treatments added an additional complexity to this study, and the responses of invertebrate taxa should be interpreted in light of these patterns.

Removal of understory vegetation affected ground-dwelling invertebrate communities, but these effects appear to be in response to vegetation recovery rather than its removal. Although differences in understory cover and height were greatest between undisturbed and removal treatments following implementation in 2014, invertebrate richness initially was unaffected. However, regrowth of the understory in removal treatments maintained higher invertebrate richness, even though understory cover became more similar between treatments. Detritivores, fungivores, herbivores, and predators increased following understory

vegetation removal, similar to responses observed in canopy gaps, but these were largely different taxa. Neanuridae, Hypogastruridae, and Entomobryidae, all families of Collembola, increased following understory vegetation removal, even though movement of Collembola was lower (Perry 2016). Lithobiomorpha, a dominant predator on the forest floor, also was more abundant in the understory removal treatment. Woody plants were removed from the quadrats, but herbaceous plant residue remained on the forest floor to limit disturbance to the leaf litter layer. Additions of herbaceous organic material have been observed to stimulate microbial activity and soil nitrogen mineralization (Elliott et al. 2015), which may explain the increased richness of diverse invertebrate functional guilds in the understory removal treatment, as well as the rapid regrowth of vegetation.

The interaction between canopy and understory disturbances had less of an impact on ground-dwelling invertebrates than either treatment alone. Responses to treatment interactions were detected only at the family and species level. Moreover, there was no evidence that treatment interactions influenced community structure more than canopy gaps alone. These results are inconsistent with our second prediction that invertebrate activity-abundance and diversity would decrease in response to combined canopy gap formation and ground-level understory vegetation removal.

Depending on canopy gap size, a dense layer of vegetation may develop in the understory following disturbance (Royo and Carson 2006), potentially mitigating the effects of abiotic changes induced by increased light on ground-dwelling invertebrates (Shure and Phillips 1991). Although many taxa responded positively to the formation of canopy gaps, we were unable to detect an effect of the presence of ground-level vegetation due to the rapid growth response of the understory following removal in gap treatments. Therefore, our third prediction that the presence of understory vegetation in canopy gaps would increase invertebrate activity-abundance and diversity by buffering the variability in environmental changes on the forest floor could not be evaluated based on the current experimental design. Studies investigating responses of the understory herb layer following gap formation similar in size to this study found minimal differences in vegetation growth in canopy gaps compared to closed canopies (Collins and Pickett 1987, 1988*a*, *b*), but these studies did not manipulate the understory layer. Rapid growth of the forest understory to levels of cover higher than pre-treatment conditions may have been in response to increased light and resource availability from the creation of canopy gaps, removal of vegetation, and addition of herbaceous residue.

Responses of ground-dwelling invertebrates to disturbance will depend to some degree on their ability to disperse within and between habitat patches, which likely influences patterns of community reorganization (Petraitis et al. 1989, Bengtsson 2002, Chase 2003). Dispersal potential of ground-dwelling arthropods was generally limited for most taxa (Perry et al. 2017), and movement was further reduced following combined canopy and ground-level understory disturbances utilized in this study (Perry 2016). Diplopoda were consistently responsive to canopy and understory disturbance, as well as their interaction, with the direction of change being largely family-specific. Activity-abundances of Caseyidae and Julidae increased in the most disturbed treatments with canopy gaps and the understory removed, whereas Polydesmidae and Paradoxosomatidae increased in all of the disturbance treatments. Millipedes generally displayed high dispersal potential (Perry et al. 2017), but their movement, especially Paradoxosomatidae, was reduced in the most disturbed treatments with canopy gaps and understory vegetation removed (Perry 2016). Diplopods feed primarily on organic debris such as decaying plant material (Coleman et al. 2004, David 2009) that tends to have a patchy distribution on the forest floor. Therefore, they may be well adapted to exploit the pulse of resources in canopy gaps, affecting their patterns of movement.

A pulse disturbance event was emulated via a manipulative experiment, and responses of ground-dwelling invertebrates were comprehensively investigated before and after at the community, family, and species level, including those of key environmental indicator taxa. Decoupling of canopy and understory vegetation disturbances revealed canopy gap formation as an important short-term driver of ground-dwelling invertebrate community structure and composition, affecting the activity-abundance of diverse functional guilds, including predators, detritivores, and

fungivores. Not only were these taxa more abundant in canopy gaps, they also tended to stay in the gaps, but with increased local movement (<1–5 m), as evidenced from a companion mark–capture study conducted simultaneously in the same experimental quadrats (Perry 2016). Understanding how multiple components of natural and anthropogenic disturbances interact and impact forest communities can inform sustainable forest management practices, especially those that involve small- and large-scale canopy removal. As the frequency and intensity of strong storms are predicted to increase with climate change (Dale et al. 2000, 2001), disturbance to forest canopies likely will become more common and widespread. These findings will improve understanding of how invertebrate communities respond to natural and anthropogenic disturbances, and how disturbance impacts biodiversity and resilience in forest ecosystems.

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