

Forest disturbance and arthropods: small-scale canopy and understory disturbances alter movement of mobile arthropods

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Abstract. Dispersal of ground-dwelling arthropods is understudied in forest ecosystems, which hinders understanding of effects of disturbances on population dynamics. The objective of the study was to quantify movement of ground-dwelling arthropods in response to a factorial combination of canopy gap formation via girdling and understory vegetation removal, which was shown in a companion study to alter arthropod abundance and species richness. Arthropod movement was quantified using a self-mark–capture technique where arthropods were marked as they crossed three concentric bands of different colored fluorescent powders located 3, 8, and 15 m from the center of 30 × 30 m experimental quadrats. The number of colors found on an individual was considered representative of dispersal such that the more colors detected, the more an individual moved. The likelihood that arthropods were marked with fluorescent powder and the number of colors detected differed among taxonomic groups. Most taxa were marked with one color and a high proportion of those individuals were collected adjacent to the band in which they were marked, suggesting limited dispersal. Canopy gaps and understory vegetation removal influenced movement of three taxa of highly mobile arthropods: Parajulidae and Paradoxosomatidae (detritivores), and Opiliones (scavengers). Opiliones were less likely to be marked with fluorescent powder in canopy gaps than under closed canopy in July, but more likely to be marked in August. Paradoxosomatidae were less likely to be marked in canopy gaps than under closed canopy in August, but their movement was unaffected in July. Parajulidae were more likely to be marked with fluorescent powders when understory vegetation was removed in July and August. Limited dispersal of most other ground-dwelling arthropods suggests that these more sessile taxa may experience decreased survival and reproduction if they are unable to cope with environmental change in response to natural and anthropogenic disturbances. Understanding how disturbances mediate arthropod movement can inform biodiversity conservation strategies and sustainable forest management.

Key words: dispersal; disturbance; ground-dwelling; insects; invertebrates; mark–capture; sampling.

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INTRODUCTION

Dispersal is a fundamental biological process integral to understanding the propensity and ability of an organism to move within and between habitat patches (Clobert et al. 2001, Bonte and Doherty 2017). Dispersal capacity mediates the responses of species to environmental change including habitat fragmentation, altered disturbance regimes, and climate change, which can have long-term implications for population viability and persistence (Gadgil 1971, Driscoll et al. 2013, Jeltsch et al. 2013), as well as community assembly and metacommunity processes (Hanski 1998, Leibold et al. 2004, Schlögel et al. 2020). Therefore, knowledge of the dispersal capacity of species can inform management and policy directed at biodiversity conservation (Barton et al. 2015). Despite its ecological importance, dispersal has been challenging to study in the field and remains a significant knowledge gap (Driscoll et al. 2014), which hinders the understanding of species responses to natural and anthropogenic disturbances.

Disturbances shape patterns of environmental heterogeneity, community dynamics, and ecosystem processes on varying spatial and temporal scales and are integral to the maintenance of species diversity (White and Pickett 1985, Petraitis et al. 1989, Frelich 2002). In eastern temperate forests, small-scale, low-intensity disturbances that affect one or more canopy trees are caused by natural tree senescence, insect outbreaks, wind, and ice storms (Runkle 1985, Roberts and Gilliam 2014). These forms of natural disturbance are often described as pulses, which are abrupt events that alter ecosystem dynamics through changes in habitat and/or resource availability and are followed by a period of reorganization (Bengtsson 2002, Jentsch and White 2019). Small-scale, frequent pulse disturbances can generate canopy gaps and alter understory vegetation (Canham and Marks 1985, Collins et al. 1985, Runkle 1990, Oliver and Larson 1996). Canopy gaps increase light availability, alter temperature and moisture regimes, reduce leaf litter cover and depth, and change vegetation structure on the forest floor (Gray et al. 2002, Ishizuka et al. 2002, Fahey and Puettmann 2007, Perry and Herms 2016b, Perry et al. 2018). Changes in the forest canopy and understory also may have

interacting effects. For example, gap size may affect the magnitude of environmental variation between the canopy opening and surrounding undisturbed forest, as well as the growth response of the understory layer (Collins et al. 1985, Collins and Pickett 1987, Shure and Phillips 1991, Fahey and Puettmann 2007, Gilliam 2007).

Forest floor disturbances induced by canopy gaps can impact ground-dwelling arthropod abundance, as well as the structure and distribution of their communities (Shure and Phillips 1991, Greenberg and Forrest 2003, Richardson et al. 2010, Perry and Herms 2016a, Perry et al. 2018). For example, arthropods can respond to changes in soil moisture levels (Verhoef and van Selm 1983, Levings and Windsor 1984), amount and decay stage of downed woody debris (Ulyshen and Hanula 2009, Perry and Herms 2017), and leaf litter depth (Koivula et al. 1999). Arthropods also respond to vegetation cover and structure in the forest understory and shrub layers (Moir et al. 2005, Knuff et al. 2020), and structurally complex understories can facilitate dispersal and reduce predation risk for species moving between habitat patches (Cerdeña et al. 2015). For example, ground beetles (Coleoptera: Carabidae) experienced increased mortality from predators in pine plantations with a sparse understory layer than in plantations with a dense, undisturbed understory (Cerdeña et al. 2015). In a manipulative experiment, Perry et al. (2018) found that formation of canopy gaps had a greater impact on ground-dwelling arthropod community structure and composition than did understory disturbance, although the interaction between canopy and understory disturbances altered patterns of abundance of several taxa, including families of Diplopoda, Collembola, and Coleoptera. These responses to canopy and understory disturbances are likely influenced by the dispersal capacity of arthropods.

Dispersal of arthropods is understudied in forest ecosystems, especially for ground-dwelling species (Brouwers and Newton 2009), many of which are flightless, nocturnal, and/or live cryptic lifestyles in the soil and leaf litter layers (Coleman et al. 2004). Due to the challenges of studying dispersal in the field, previous studies of ground-dwelling arthropods in forests have disproportionately focused on the movement of well-studied insect groups such as Carabidae

(Brouwers and Newton 2009). A broader understanding of community-level responses and their implications for biodiversity conservation requires that dispersal be measured simultaneously for multiple taxa (Barton et al. 2015). Perry et al. (2017) investigated movement of ground-dwelling arthropods in a temperate deciduous forest using a novel self-mark–capture method that employed concentric bands of colored fluorescent powders applied to the forest floor. Dispersal of most taxa was limited, which has conservation implications for gene flow between populations and their resilience to anthropogenic disturbances such as habitat degradation and fragmentation, invasive species, and climate change (Wilcove et al. 1998, Tschamntke et al. 2002, Reigada et al. 2015). While limited dispersal of forest ground-dwelling arthropods was documented (Perry et al. 2017), it is unknown whether this will impact their responses to disturbance. Limited mobility of ground-dwelling arthropods may make them more vulnerable to disturbance than species capable of flight (den Boer et al. 1980, Niemelä 2001). The dispersal capacity of arthropods determines their ability to colonize nearby undisturbed forest patches as well as recolonize disturbed patches over time.

To understand the responses of ground-dwelling arthropods to forest disturbance, it is important to assess the effects of disturbance to the canopy and understory on the movement of arthropod taxa. Therefore, the objective of this study was to determine the main and interacting effects of the canopy and understory vegetation disturbances previously shown to affect arthropod community composition (Perry et al. 2018) on the movement of ground-dwelling arthropods using a mark–capture technique with fluorescent powders applied to the forest floor (Perry et al. 2017). We predicted that movement of ground-dwelling arthropods would be reduced in canopy gaps when ground-level understory vegetation was also removed, but the presence of understory vegetation would mitigate effects of gap formation on arthropod movement.

MATERIALS AND METHODS

Study area

This research was conducted at Powdermill Nature Reserve (PNR; 40°09'N, 79°16'W) in

Rector, Westmoreland County, Pennsylvania, USA. Powdermill Nature Reserve was established as a nature reserve and the field research station for the Carnegie Museum of Natural History in 1956. Prior to this, the region experienced several anthropogenic disturbances. Forests were logged in the 1800s followed by agricultural production until the early- to mid-1900s. Additionally, some locations were mined for coal in the 1940s.

Temperate deciduous forest at PNR was characterized by maple (*Acer* spp.), oak (*Quercus* spp.), beech (*Fagus* spp.), tulip poplar (*Liriodendron tulipifera* L.), and hickory (*Carya* spp.) (Murphy et al. 2015), and the understory contained diverse herbaceous and woody shrub species. A survey identified 851 species of vascular plants from PNR (Utech 1999). Tree basal area (calculated from diameter breast height measurements of trees >8 cm in diameter; Bonham 2013) averaged 58.5 m²/ha (ranged from 55.0 to 64.2) for all trees and 19.3 for poplar, 19.2 for maple, 4.6 for oak, 4.4 for hickory, and 3.6 for beech. Spicebush (*Lindera benzoin* (L.) Blume) dominated the understory, but the invasive shrubs multiflora rose (*Rosa multiflora* Thunb.) and Japanese barberry (*Berberis thunbergii* DC) were also present (Calinger et al. 2015). Other abundant understory species were violet (*Viola* spp.), blackberry (*Rubus allegheniensis*), round lobed hepatica (*Hepatica americana*), common cinquefoil (*Potentilla* spp.), dewberry (*Rubus hispidus*), partridgeberry (*Mitchella repens*), bedstraw (*Galium* spp.), sedges (*Cyperaceae* spp.), nettle (*Urtica* spp.), greenbrier (*Smilax* spp.), and several species of ferns (*Polystichum acrostichoides*, *Dennstaedtia punctilobula*, *Thelypteris noveboracensis*, and *Dryopteris* spp.).

Experimental design

As part of a larger study reported in Perry et al. (2018), a manipulative experiment was established in June 2014 with two disturbance treatments implemented in factorial combination: presence/absence of canopy gaps and presence/absence of ground-level understory vegetation removal, resulting in four treatment combinations: (1) closed canopy/understory present (undisturbed control); (2) closed canopy/understory removed; (3) canopy gap/understory present; and (4) canopy gap/understory removed. Treatments were implemented randomly among 30 × 30 m quadrats

(the experimental unit of replication), and four replicates of each treatment combination ($n = 16$) were used in this study.

The complete experimental design is described by Perry et al. (2018), and relevant details are summarized here. The canopy treatment was implemented by girdling 8–12 dominant and codominant trees to create gaps. Trees were girdled using a chainsaw. Two rings (2 cm wide, 6–12 cm deep) were cut around the entire circumference of the trunk approximately 1.5 m above the ground. Across all quadrats receiving the canopy gap treatment, 117 trees were girdled on June 5–6 2014. The number of trees girdled in each quadrat varied depending on size and density of trees present and was determined by visually estimating the amount of cumulative canopy removal required to achieve the targeted gap size. Before treatments were implemented, percentage canopy openness (\pm SE) was measured using a densiometer and averaged $8.0 \pm 0.4\%$ across all experimental quadrats. Percentage canopy openness averaged $10.2 \pm 0.5\%$ in canopy gaps and $7.7 \pm 0.2\%$ in closed canopy treatments following treatment implementation in 2014. When this study was conducted in 2015, average gap size had increased to $16.2 \pm 0.7\%$ (range: 5.7–28.3%) compared to $8.5 \pm 0.2\%$ (range: 5.2–14.5%) in closed canopy treatments (Perry et al. 2018).

The understory treatment was implemented by removing all understory herbaceous plants, woody shrubs, seedlings, and saplings (≤ 2 cm stem diameter) within the 30×30 m experimental quadrats using mechanical weed trimmers (KM 110 R KombiMotor, Stihl; Virginia Beach, Virginia, USA) and loppers on June 5–7 2014. Herbaceous vegetation residue remained on the forest floor in the quadrats. All woody shrubs and saplings were hauled out of the quadrat and deposited in the surrounding forest away from the treated quadrats. Before treatments were implemented, percentage cover of understory vegetation (\pm SE) was quantified in two randomly selected 1 m^2 areas and averaged $28.0 \pm 2.5\%$ across all experimental quadrats. Percentage cover of understory vegetation decreased from $31.3 \pm 2.4\%$ in the undisturbed treatment to $9.8 \pm 1.7\%$ in the understory removal treatment in 2014. In 2015, understory vegetation cover averaged $28.1 \pm 2.1\%$ (range:

3.5–85.0%) and $29.9 \pm 3.7\%$ (range: 1.5–90.0%) in the undisturbed and understory removal treatments, respectively, suggesting substantial regrowth of vegetation (Perry et al. 2018).

Arthropod movement

Arthropod movement was characterized using a self-mark–capture method as described in Perry et al. (2017) where colored fluorescent powders were applied in the field in three concentric circles. Concentric bands of fluorescent powder (Rocket Red Pigment A-13N, Horizon Blue A-19N, and Arch Yellow Pigment A-16N; DayGlo Color Corp., Cleveland, Ohio, USA) 0.4 m wide were applied directly to the forest floor 3, 8, and 15 m from the center of each 30×30 m experimental quadrat ($n = 16$), with each band consisting of a single color (pink, blue, or orange) (Fig. 1). Fluorescent powders were mixed with sand (1:8 fluorescent powder to Quikrete Play Sand; Quikrete Companies, Atlanta, Georgia) to improve adhesion (Reinecke 1990). Powder was applied to the forest floor using 18 cm mesh strainers held within 0.3 m to the ground (Perry et al. 2017). Efforts were made to reduce transfer of powder within and between quadrats. Fluorescent powders were transported to the field in ziplock bags secured in backpacks and protective suits and gloves were worn during powder application, removed immediately after, and placed in large garbage bags along with the strainers. All materials used for a specific colored powder were kept separate from those of other colors. Arthropods self-acquired fluorescent powders in the field directly during application or through subsequent contact as they crossed the bands (i.e., arthropods were not marked and released). Arthropods marked with more colors were assumed to have moved farther, crossing more bands than those marked with fewer colors (Perry et al. 2017). The experiment was repeated twice in 2015: July 13–17 and August 10–14, one year following the implementation of the disturbance treatments.

Arthropod sampling and processing

Arthropods were sampled via five-minute hand collections at 24 and 48 h following powder application in two adjacent 1×1 m sampling stations just inside each band of powder in

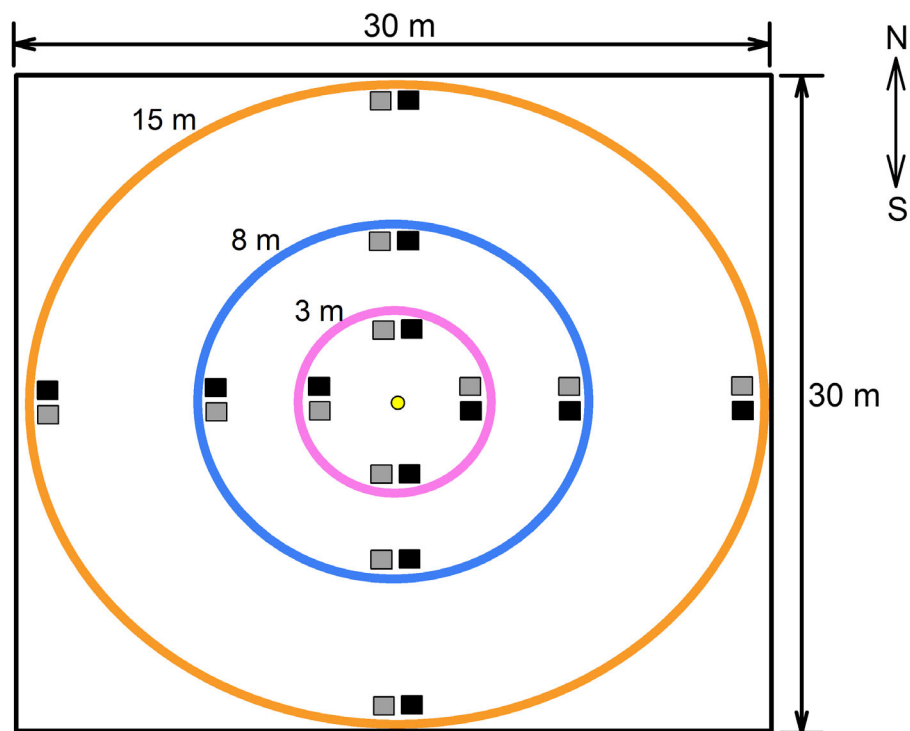


Fig. 1. Design schematic for the self-mark-capture experiment in forest experimental quadrats (30×30 m) at Powdermill Nature Reserve. Different colored circles represent different fluorescent powders [DayGlo; pink (Rocket Red Pigment A-13N), blue (Horizon Blue A-19N), and orange (Arch Yellow Pigment A-16N)], applied at 3 m (pink, inner band), 8 m (blue, middle band), and 15 m (orange, outer band) from the center of experimental quadrats (yellow filled circle). Arthropods were hand collected in 1×1 m sampling stations (colored squares) located in each cardinal direction just inside each band of fluorescent powder. Arthropods were collected in two adjacent 1×1 m sampling stations, one after 24 h (gray square) and the other after 48 h (black square) following fluorescent powder application.

each cardinal direction (Fig. 1) as described by Perry et al. (2017), resulting in 12 collections per quadrat per time period. Samples were collected in adjacent sampling stations after 24 h and after 48 h following powder application (Fig. 1) to avoid any effects of disturbance from the hand collections, which involved active searching for arthropods by moving leaf litter, rocks, and small pieces of woody debris without displacing the soil. After the five-minute sampling period, all debris was replaced to cover the soil. Individual arthropods were meticulously collected using toothpicks and stored singly in 1.5 mL microcentrifuge tubes. After each of the two sampling events, specimens collected at the four sampling stations in each cardinal direction were pooled to generate one sample per distance from the

quadrat center (3, 8, and 15 m) on each sampling date. Specimens were kept in a cooler in the field and then transferred to a -80°C freezer until further processing.

Fluorescent powder was detected on arthropods microscopically under ultra-violet black light. Occasionally, arthropods were coated in powder, but more often only a few flecks of powder were present on their bodies. To limit cross-contamination, arthropods were inspected for powders individually using fresh toothpicks to manipulate each specimen. Millipedes and insects were identified to family using Shear (1999) and Triplehorn and Johnson (2005), respectively. All other non-insect arthropods were identified to order. Ten of the arthropod taxa (Geophilomorpha, Scolopendromorpha,

Abacionidae, Xystodesmidae, Gryllidae, Curculionidae, Elateridae, Nitidulidae, Scarabaeidae, Silphidae, and Staphylinidae) were excluded from analyses because fewer than 20 individuals were collected.

Statistical analyses

Dispersal of ground-dwelling arthropods was described by analyzing the number of colors an individual was marked with as ordered categorical (hereafter “ordinal”) data. Individuals were classified as being marked with zero, one, two, or three colors, and dispersal was assessed based on the assumption that individuals marked with three different colors dispersed farther (i.e., crossed more colored bands) than individuals with zero colors. To test this assumption, chi-square tests were performed to determine whether those individuals marked with a single color were more likely to be collected adjacent to the band of that particular color. This approach provides a conservative measure of the probability of dispersal for each arthropod taxon.

To assess the impacts of canopy and understory disturbance on the dispersal of total arthropods, ordinal data were analyzed using cumulative link mixed models with the function `clmm2` in the package `ordinal` (Christensen 2019) in R version 3.6.0 (R Core Team 2019). The number of colors on an arthropod (i.e., the response variable) was modeled as explained by (1) the arthropod taxon that the individual belonged to, (2) the time of collection since powder application (either 24 or 48 h), (3) when the experiment was conducted (either July or August), (4) the presence or absence of canopy gaps, and (5) the presence or absence of ground-level understory vegetation removal. In addition to these fixed effects, the interaction between canopy gap and understory vegetation treatments was initially included, but subsequently removed from the model as likelihood ratio tests determined the term to be insignificant ($P = 0.96$). Likelihood ratio tests also showed that including `quadrat` as a random effect significantly improved the model. The `drop1` command was used to determine the optimal fixed effects structure for the model, which resulted in a final model that included arthropod taxa and experiment (July or August). Finally, the `Anova.clmm` function from the `RVAideMemoire` package (Hervé 2019) was

used to perform Wald type II chi-square tests to evaluate the influence of the fixed effects on the number of colored marks detected.

An important assumption of cumulative link mixed models is the proportional odds assumption, which implies that the effect of an independent variable on the odds of being in a certain category is consistent across all categories (O’Connell 2006). For example, if the proportional odds assumption is met, then if arthropods collected from the canopy gap treatment are three times more likely to cross one band than those collected from the closed canopy treatment, they also will be three times more likely to cross two bands or three bands. Using likelihood ratio tests, this assumption was evaluated for total ground-dwelling arthropods in the final model that included arthropod taxa and date of experiment (July or August), of which experiment violated the assumption ($P = 0.002$), but not arthropod taxa ($P = 0.053$). As a result, the final model treated date of experiment as a nominal effect, which allowed for a different set of thresholds (i.e., the cutoff values for inclusion in a particular number of colored marks category) to be used for the different experimental dates (i.e., July or August). This final model also had the fixed effect of arthropod taxa and the random effect of `quadrat`. The predicted probabilities of having zero, one, two, or three colors were calculated manually for each arthropod taxon (Appendix S1: Eq. S1) and confirmed using the `predict.clmm2` function in the `ordinal` package (Christensen 2019).

To examine taxon-specific responses to canopy and understory treatments, the number of colors was modeled separately for each arthropod taxon. Separate analyses were conducted for each arthropod taxon and each experimental date because date of experiment (July or August) violated the proportional odds assumption in the final model described above that assessed total arthropods. Once these data were separated by date of experiment, some of the taxa contained too few individuals ($n < 20$) to analyze (for July: Xystodesmidae, Spirobolidae, and Rhaphidophoridae; for August: Lithobiomorpha, Caseyidae, Xystodesmidae, Spirobolidae, Isopoda, and Rhaphidophoridae). As in the model above, the response variable, number of different colors, was analyzed using ordinal regression, with the

fixed effects of time of collection after powered bands were deployed (24 or 48 h), presence/absence of canopy gaps, presence/absence of ground-level understory vegetation, interaction between the canopy and understory vegetation treatments, and random effect of quadrat. Likelihood ratio tests assessed whether the random effect of quadrat and the interaction between canopy and understory vegetation treatments improved the model fit. Next, likelihood ratio tests were used to evaluate model significance by comparing it to a null (i.e., intercept) model using the *nagelkerke* function in the *rcompanion* package (Mangiafico 2019). When a model fit the data better than the null model, the *drop1* command was used to arrive at the best fit model for each arthropod taxon and experiment. When the final model did not contain a random effect, the function *nominal_test* from the *ordinal* package (Christensen 2019) was used to test whether any explanatory variables violated the proportional odds assumption. If the final model did include a random effect, this was done using a likelihood ratio test.

RESULTS

A total of 2447 ground-dwelling arthropods representing 15 orders and 11 families were collected, with the most abundant being Parajulidae, Paradoxosomatidae, Araneae, and Formicidae (Tables 1, 2). As reported in Perry et al. (2017), fluorescent powder was detected on 77.3% of individuals. Most arthropods (53.3%) were marked with one color, and a high proportion of those individuals were collected adjacent to the band of that color (Fig. 2; $\chi^2 = 1380.2$, $P < 0.001$).

When considering the ground-dwelling arthropod community, the number of colors detected on an individual was not influenced by the canopy gap treatment ($P = 0.66$), the understory removal treatment ($P = 0.47$), nor the time of collection since powdered bands were deployed ($P = 0.19$). However, the likelihood that arthropods were marked with fluorescent powder differed among taxa ($P < 0.001$). Because date of experiment (July or August) violated the proportional odds assumption, predicted probabilities of being marked with a certain number of colors were calculated separately for each arthropod

taxon for July (Fig. 3A) and August (Fig. 3B) (Appendix S1: Eq. S1, Table S1). In the July experiment, the majority of arthropod taxa (9 of 15; Lithobiomorpha, Caseyidae, Parajulidae, Polydesmidae, Isopoda, Araneae, Carabidae, Tenebrionidae, and Rhaphidophoridae) were most likely to have been marked with a single color. Three arthropod taxa (Julidae, Collembola, and Formicidae) were most likely to have been unmarked, three (Paradoxosomatidae, Spirobolidae, and Opiliones) were most likely to have been marked with two colors, and none were most likely to have been marked with all three colors of fluorescent powder. In August, all arthropod taxa were likely to have been marked. Eight of 15 taxa (Lithobiomorpha, Julidae, Parajulidae, Isopoda, Araneae, Collembola, Tenebrionidae, and Formicidae) were most likely to have been marked with a single color, three (Caseyidae, Polydesmidae, and Carabidae) with two colors, and four (Paradoxosomatidae, Spirobolidae, Opiliones, and Rhaphidophoridae) with all three colors.

The number of colors detected on three arthropod taxa (Parajulidae, Paradoxosomatidae, and Opiliones) were affected by the canopy gap and understory removal treatments (Table 3), while all other taxa were unaffected (i.e., model fit was not significantly better than the intercept model; Appendix S1: Table S2). Parajulidae were 1.6× more likely in July ($P = 0.03$) and 2× more likely in August ($P = 0.03$) to be marked with fluorescent colors where the understory was removed than where it was retained (Fig. 4). The likelihood that Opiliones were marked with fluorescent powder was affected by the canopy gap treatment, but the direction of this effect differed between July and August (Fig. 5). In July, Opiliones were 95% less likely to be marked in canopy gaps than in the closed canopy treatment ($P = 0.01$). In August, conversely, Opiliones were 6.5× more likely to be marked in canopy gaps than in the closed canopy treatment ($P = 0.01$). The number of colors detected on Paradoxosomatidae was unaffected by the canopy and understory disturbance treatments in July, but in August, individuals were 83% less likely to be marked in canopy gaps than in the closed canopy treatment (Fig. 6; $P = 0.03$). In July, Parajulidae were 1.7× ($P = 0.02$) and Opiliones were 7.5× ($P = 0.03$) more likely to be marked with

Table 1. Catches of ground-dwelling arthropod taxa that were marked with zero, one, two, or three colors of fluorescent powder in the canopy treatment in 2015 in forests at Powdermill Nature Reserve in Rector, Westmoreland County, Pennsylvania, USA.

Class	Order	Family	Canopy gap				Closed canopy				Total catches
			0	1	2	3	0	1	2	3	
Chilopoda	Geophilomorpha		0	0	0	0	0	0	0	1	1
	Lithobiomorpha		18	21	8	2	17	15	4	3	88
Diplopoda	Scolopendromorpha		1	0	1	0	1	0	0	1	4
	Callipodida	Abacionidae	0	0	1	0	0	0	0	0	1
	Chordeumatida	Caseyidae	5	20	17	5	0	14	8	3	72
	Julida	Julidae	7	19	4	0	22	12	8	2	74
		Parajulidae	46	64	41	5	67	107	52	15	397
	Polydesmida	Paradoxosomatidae	5	52	61	83	4	26	30	105	366
		Polydesmidae	6	21	14	9	7	20	8	4	89
		Xystodesmidae	0	1	2	3	2	3	1	1	13
Malacostraca	Spirobolida	Spirobolidae	0	2	5	2	2	5	6	3	25
	Isopoda		5	19	8	1	2	5	0	1	41
Arachnida	Araneae		33	134	42	16	43	95	47	21	431
	Opiliones		1	4	13	23	0	6	6	14	67
Collembola			74	76	23	8	38	37	22	1	279
Insecta	Coleoptera	Carabidae	6	21	10	7	6	26	10	6	92
		Curculionidae	0	0	0	0	0	0	0	1	1
		Elateridae	0	1	3	0	0	1	0	0	5
		Nitidulidae	1	0	0	0	0	1	0	0	2
		Scarabaeidae	0	0	0	1	0	1	0	0	2
		Silphidae	0	1	0	0	0	1	0	0	2
		Staphylinidae	1	3	0	1	0	0	0	0	5
		Tenebrionidae	11	22	9	1	4	11	7	2	67
	Hymenoptera	Formicidae	62	67	18	3	56	67	15	4	292
	Orthoptera	Gryllidae	1	1	3	1	0	0	0	1	7
		Rhaphidophoridae	0	3	5	6	1	3	4	2	24
	Total catches		283	552	288	177	272	456	228	191	2447

more colors after 48 h than 24 h. In contrast, Collembola were 66% less likely to be marked with more colors after 48 h than 24 h ($P = 0.01$).

DISCUSSION

Dispersal capacity is a key life-history trait that shapes the distribution of species and the dynamics of populations and communities across spatial and temporal scales (Clobert et al. 2001, Bonte and Dahiriel 2017). Knowledge of species' movement patterns is critical to inform biodiversity conservation management in light of environmental change (Driscoll et al. 2014), including altered disturbance regimes. Disturbances that affect forest ecosystems can cause the formation of canopy gaps and changes in ground-level understory vegetation (Oliver and Larson 1996), which alter the forest floor

environment (Gray et al. 2002, Fahey and Puettmann 2007). In this study, we investigated the effects of forest canopy and understory vegetation disturbances and their interaction on the movement of ground-dwelling arthropods. We predicted that canopy gap formation and removal of ground-level understory vegetation would reduce the movement of ground-dwelling arthropods. Our results revealed that small-scale canopy gap formation and understory vegetation removal treatments had context-dependent, seasonal impacts on the movement patterns of three taxa of highly mobile arthropods: Parajulidae and Paradoxosomatidae, which forage extensively as detritivores, and Opiliones which are primarily scavengers. Although movement patterns differed among taxa, most other arthropods were marked with one color of fluorescent powder, which indicates limited dispersal.

Table 2. Catches of ground-dwelling arthropod taxa that were marked with zero, one, two, or three colors of fluorescent powder in the understory treatment in 2015 in forests at Powdermill Nature Reserve in Rector, Westmoreland County, Pennsylvania, USA.

			Understory present				Understory removed					
Class	Order	Family	0	1	2	3	0	1	2	3	Total catches	
Chilopoda	Geophilomorpha		0	0	0	0	0	0	0	1	1	
	Lithobiomorpha		18	18	5	1	17	18	7	4	88	
Diplopoda	Scolopendromorpha		1	0	0	1	1	0	1	0	4	
	Callipodida	Abacionidae	0	0	1	0	0	0	0	0	1	
	Chordeumatida	Caseyidae	3	11	9	2	2	23	16	6	72	
	Julida	Julidae	22	18	7	1	7	13	5	1	74	
		Parajulidae	60	77	38	9	53	94	55	11	397	
	Polydesmida	Paradoxosomatidae	1	44	44	131	8	34	47	57	366	
		Polydesmidae	8	26	9	8	5	15	13	5	89	
Malacostraca		Xystodesmidae	0	2	3	2	2	2	0	2	13	
	Spirobolida	Spirobolidae	1	7	10	5	1	0	1	0	25	
	Isopoda		5	21	8	1	2	3	0	1	41	
	Arachnida	Araneae	45	125	43	17	31	104	46	20	431	
		Opiliones	0	5	9	14	1	5	10	23	67	
Collembola			51	58	26	9	61	55	19	0	279	
Insecta	Coleoptera	Carabidae	5	26	9	10	7	21	11	3	92	
		Curculionidae	0	0	0	1	0	0	0	0	1	
		Elateridae	0	1	1	0	0	1	2	0	5	
		Nitidulidae	0	0	0	0	1	1	0	0	2	
		Scarabaeidae	0	0	0	0	0	1	0	1	2	
		Silphidae	0	1	0	0	0	1	0	0	2	
		Staphylinidae	0	3	0	0	1	0	0	1	5	
		Tenebrionidae	9	17	8	2	6	16	8	1	67	
	Hymenoptera	Formicidae	68	63	14	2	50	71	19	5	292	
	Orthoptera	Gryllidae	1	0	0	1	0	1	3	1	7	
		Rhaphidophoridae	1	3	3	3	0	3	6	5	24	
	Total Catches			299	526	247	220	256	482	269	148	2447

Movement of Paradoxosomatidae and Opiliones was impacted by the canopy gap treatment, but the strength of these effects differed in the July and August experiments. Paradoxosomatidae, a family of millipedes that contains no native North American species (Nguyen and Sierwald 2013), displayed reduced movement in canopy gaps relative to the closed canopy treatment but only during August. In July, there were no differences. The opposite pattern was observed with Opiliones, which had reduced movement in canopy gaps in July relative to the closed canopy treatment, but increased movement in gaps in August. Formation of canopy gaps following disturbance has been consistently documented as a major driver of arthropod community structure in forest ecosystems (Shure and Phillips 1991, Greenberg and Forrest 2003, Bouget and Duelli 2004, Gandhi et al. 2008, Perry

and Herms 2016a, 2019), but studies typically assessed changes in arthropod abundance and diversity rather than movement. This study complements a companion study (Perry et al. 2018) that found that the formation of canopy gaps increased the abundance and taxonomic richness of ground-dwelling arthropods, including Caseyidae, Paradoxosomatidae, Isopoda, Araneae, Carabidae, and three families of Collembola (Tomoceridae, Dicyrtomidae, and Katiannidae) (Perry et al. 2018). Canopy gaps also increased height and cover of understory vegetation, soil moisture, and decreased depth and cover of leaf litter (Perry et al. 2018). In this study, we found that these previously reported impacts of gaps on the forest floor environment and arthropod community structure had minimal effects on movement of ground-dwelling arthropods except for Paradoxosomatidae and Opiliones,

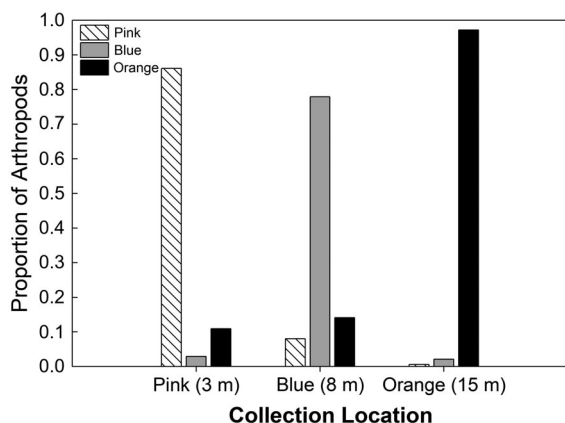


Fig. 2. Proportion of ground-dwelling arthropods marked with a single fluorescent powder, either pink (white striped bars), blue (gray bars), or orange (black bars), and collected at the 3 m (inner pink band), 8 m (middle blue band), or 15 m (outer orange band) sampling stations.

which were among the most mobile arthropod taxa. In summary, effects of these small-scale canopy gaps were taxon-specific, impacting movement of only highly mobile arthropods and likely mediated by seasonal changes such as temperature and moisture regimes and resource distributions. This also suggests that more sessile arthropod species may be more susceptible to environmental changes associated with these disturbances.

Parajulidae was the only arthropod taxon affected by the understory removal treatment, with individuals consistently more likely to be marked with fluorescent powder where understory vegetation was removed. By the time this study was initiated in 2015, substantial understory regrowth had occurred in response to the vegetation removal treatments implemented in 2014 (Perry et al. 2018), indicating that patterns of movement by arthropods may have been in response to recovery of the understory layer rather than removal. Rapid regrowth of vegetation likely increased habitat structure and heterogeneity in the understory, which can support high abundances of diverse insect taxa (Knuff et al. 2020). For example, early stages of plant regrowth following mining disturbance in *Eucalyptus* forests supported rich communities of Hemiptera, with highly mobile, generalist

species initially recolonizing disturbed forests (Moir et al. 2005). The flightless ground beetle species, *Ceroglossus chilensis* Eschscholtz, was more abundant, traveled shorter distances, and experienced lower mortality in pine plantations with a dense, undisturbed understory than when the understory was less dense or experimentally removed (Cerdeña et al. 2015). Compared to the overstory, the ground-level understory layer is often species-rich and contributes to the structure and function of forest ecosystems by depositing high-quality litter to the forest floor which influences nutrient cycling and availability (Gilliam 2007, Elliott et al. 2015) and provides shelter for ground- and soil-dwelling arthropods. Millipedes including species in the family Parajulidae are commonly found in the litter and soil layers of forests due to the high moisture content of these environments and their susceptibility to desiccation (Golovatch and Kime 2009). In forests, millipedes are ecologically important detritivores that primarily feed on organic decaying plant material (David 2009, Golovatch and Kime 2009), functionally contributing to the comminution of litter and increasing the surface area available to microbes for further decomposition (Coleman et al. 2004). Because herbaceous understory vegetation contains high nutrient concentrations, this litter decomposes rapidly on the forest floor (Gilliam 2007, Muller 2014). Highly mobile millipedes may be well adapted to locate and exploit patches of high-quality resources such as herbaceous litter following acute growth responses of the understory in response to disturbance.

Canopy gap and understory vegetation removal treatments did not strongly affect the movement of most ground-dwelling arthropods in this study. Small-scale, frequent pulse disturbances are typical of natural forest ecosystem dynamics (Spies and Turner 1999), and thus, it is predicted that most forest species including ground-dwelling arthropods are adapted to these disturbance regimes (Bengtsson 2002). Although movement was largely unaffected, abundance and richness of arthropods increased following implementation of canopy and understory disturbances (Perry et al. 2018). These findings suggest that arthropods have the capacity to respond to environmental changes to some extent, although for many taxa, their responses

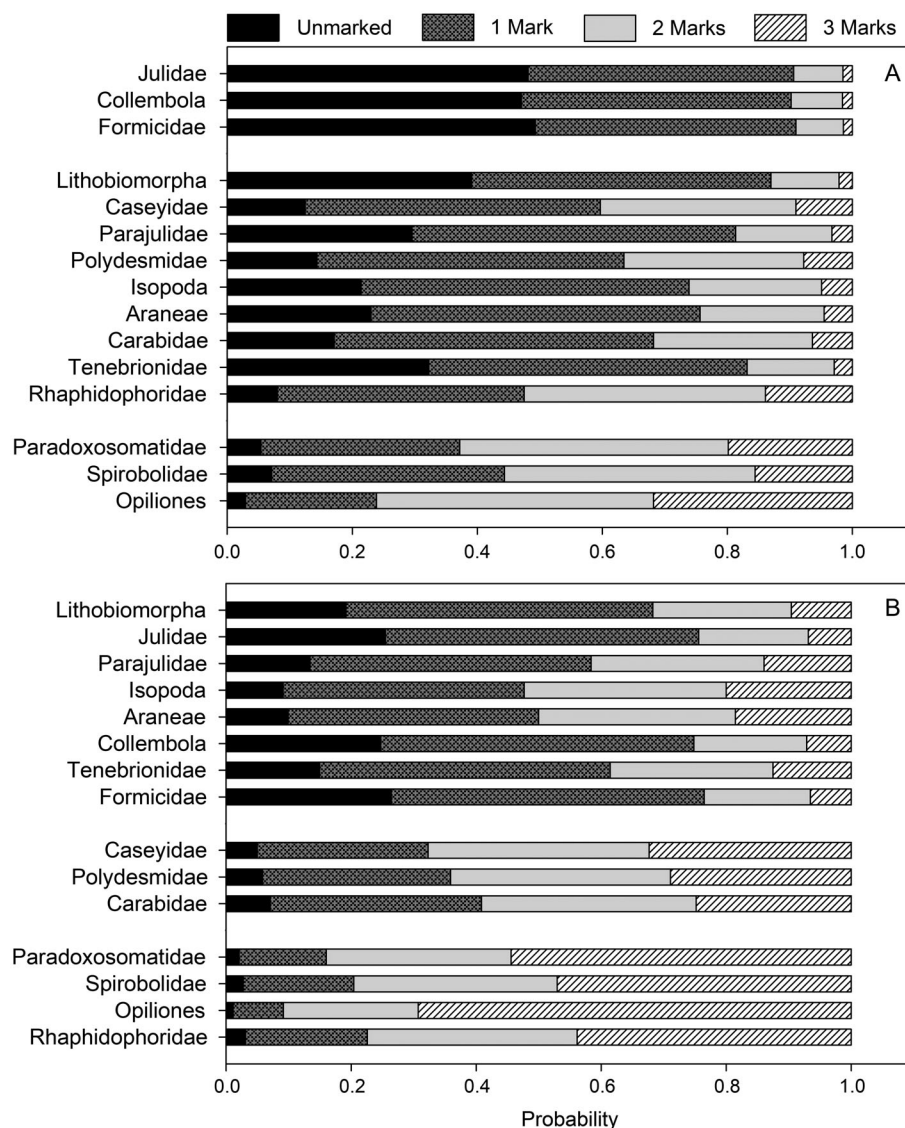


Fig. 3. Predicted probabilities for common ground-dwelling arthropod taxa to be unmarked (black) or marked with one (dark gray hatched), two (light gray), or three (white striped) fluorescent powders in the July (A) and August (B) experiments. Arthropod taxa are grouped by the marked category (unmarked, one, two, or three marks) for which they had the highest predicted probabilities. In July (A), three arthropod taxa were most likely to be unmarked (top), nine were most likely to be marked with one fluorescent powder (middle), and three were most likely to be marked with two powders (bottom). In August, eight arthropod taxa were most likely to be marked with one fluorescent powder (top), three were most likely to be marked with two powders (middle), and four taxa were most likely to be marked with all three fluorescent powders (bottom). No arthropod taxa were most likely to be marked by all three fluorescent powders in July and unmarked in August.

may be spatially constrained. For example, soil arthropods including mites, springtails, and beetles displayed strong spatial community structure at the genetic- and species-level among

forest stands at a 1 km scale, indicating highly constrained patterns of movement and dispersal limitations to community assembly (Arribas et al. 2021). In our study, most arthropods were

Table 3. Results from ordinal regression models for arthropod taxa in July (Experiment 1) and August (Experiment 2) where the model goodness of fit was significantly better than the null (intercept) model.

Class	Order	Family	Fixed effect	Estimate	SE	z	Pr(> z)	Odds ratio
Experiment 1: July								
Diplopoda	Julida	Parajulidae	Understory removed	0.51	0.24	2.15	0.03	1.66
			Collection time	0.53	0.23	2.30	0.02	1.70
Arachnida	Polydesmida	Paradoxosomatidae	—	—	—	—	—	—
	Opiliones		Canopy gap	−2.98	1.10	−2.72	0.01	0.05
			Collection time	2.02	0.94	2.15	0.03	7.52
Collembola			—	—	—	—	—	—
Experiment 2: August								
Diplopoda	Julida	Parajulidae	Understory removed	0.73	0.34	2.18	0.03	2.09
			Canopy gap	−1.77	0.83	−2.13	0.03	0.17
Arachnida	Opiliones		Canopy gap	1.87	0.72	2.62	0.01	6.51
Collembola			Collection time	−1.08	0.40	−2.71	0.01	0.34

Notes: Fixed effects included represent the best fit model after backward model selection. Collection time is 24 or 48 h since marker application.

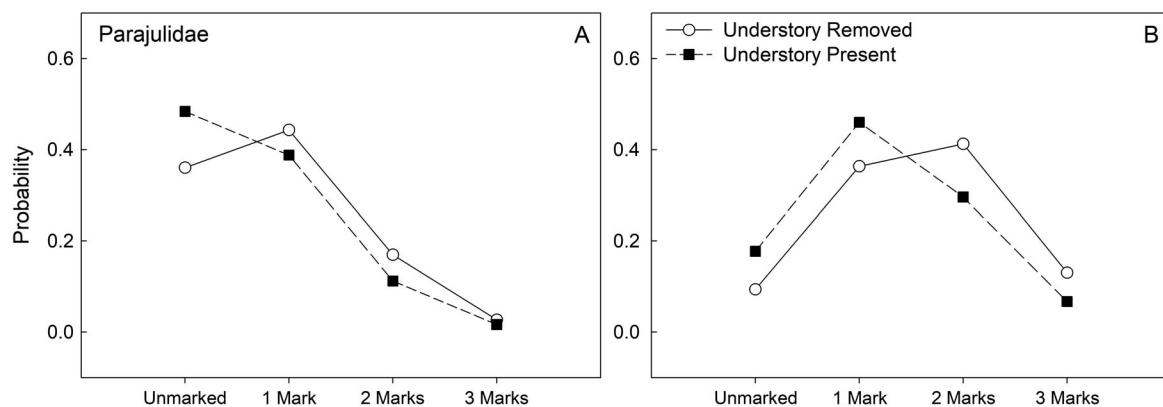


Fig. 4. Predicted probabilities for Parajulidae to be unmarked or marked with one, two, or three fluorescent powders in the understory vegetation removal (white circle) and undisturbed understory vegetation (black square) treatment in the July (A) and August (B) experiments. Statistical results from ordinal regression models provided in Table 3.

marked with only one color of fluorescent powder, indicating limited movement on the forest floor. Limited movement of most ground-dwelling arthropods was further supported by the finding that a high proportion of those arthropods marked with one fluorescent color were collected adjacent to the band in which they were marked, regardless of the specific marker color. Limited dispersal of most ground-dwelling arthropods, particularly flightless species, indicates that these taxa may have to cope with environmental changes that occur on the forest floor

rather than readily dispersing to more favorable habitats. This could lead to increased vulnerability of these arthropod taxa following novel, anthropogenic disturbances, especially those that occur at larger spatial scales, such as habitat fragmentation (Tscharrntke et al. 2002). Alternatively, these arthropods may be environmental generalists that find the altered resources or environmental conditions that occur following disturbances to remain suitable as habitat. Importantly, ground-dwelling arthropods primarily inhabit the soil and leaf litter layers in forests, which in

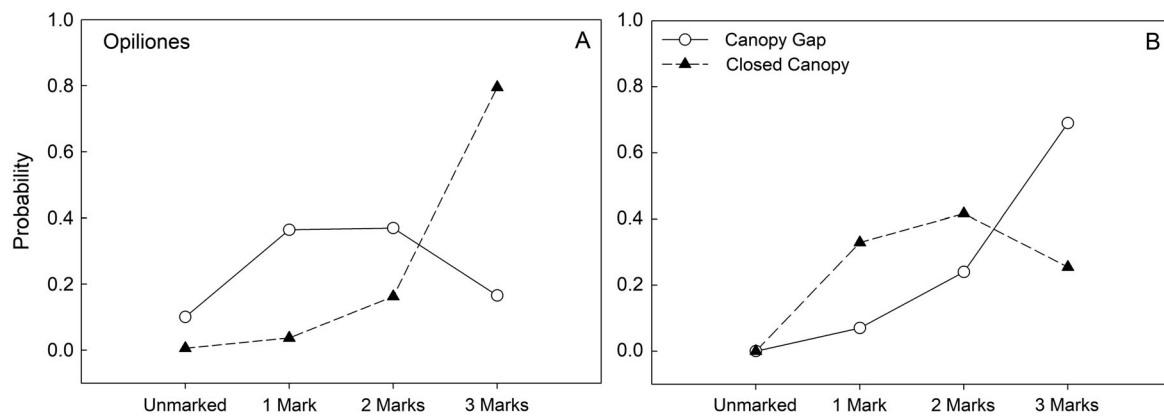


Fig. 5. Predicted probabilities for *Opiliones* to be unmarked or marked with one, two, or three fluorescent powders in the canopy gap (white circle) and closed canopy (black triangle) treatment in the July (A) and August (B) experiments. Statistical results from ordinal regression models provided in Table 3.

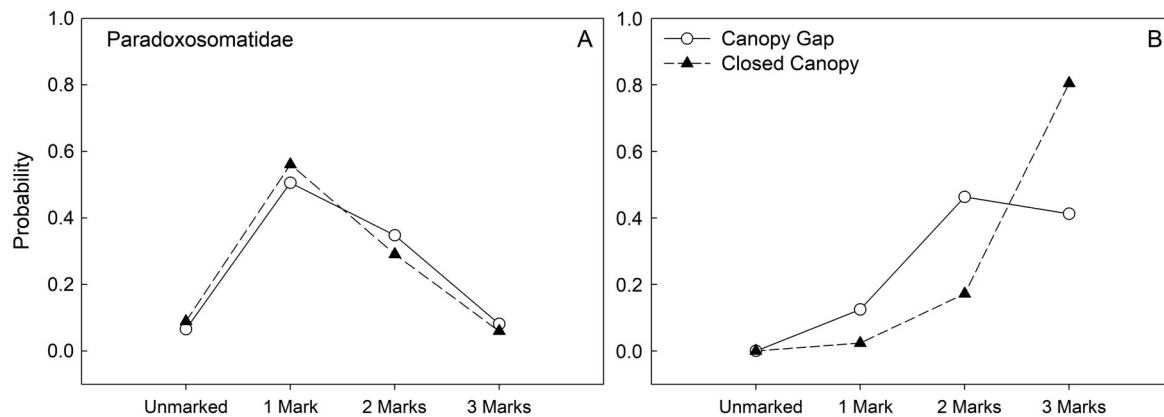


Fig. 6. Predicted probabilities for *Paradoxosomatidae* to be unmarked or marked with one, two, or three fluorescent powders in the canopy gap (white circle) and closed canopy (black triangle) treatment in the July (A) and August (B) experiments. Statistical results from ordinal regression models provided in Table 3.

our study, remained largely intact following implementation of the disturbance treatments, although leaf litter depth and cover decreased in the canopy gap treatment (Perry et al. 2018). Leaf litter is an important structural component of the forest floor that provides habitat and refugia for arthropods and helps to reduce microclimate variability at the soil surface (David et al. 1991, Ponge et al. 1993, Sayer 2006) and thus may help arthropods cope with disturbances that affect the forest canopy and understory.

The interaction between canopy and understory disturbances did not affect movement patterns of ground-dwelling arthropods. In this

study, canopy and understory disturbance intensity was manipulated rather than frequency, which resulted in temporal variability in the magnitude of canopy and understory conditions. For example, ring-porous tree species such as oak, ash, and hickory declined quickly following girdling, while diffuse-porous species such as maple and tulip poplar declined slowly (Perry et al. 2018). These species-specific differences in the rate of decline caused gap size to increase over time such that the magnitude of the canopy gap treatment effect was greatest in 2015 when this marking study was conducted. Conversely, the opposite temporal pattern was observed for

the understory removal treatment wherein vegetation regrowth occurred over time following mechanical removal in 2014. The magnitude of the understory removal treatment effect decreased as vegetation regrowth occurred, and by 2015, minimal differences in vegetation cover were observed between treatments (Perry et al. 2018). Due to these temporal changes following treatment implementation, the impacts of canopy and understory disturbance treatments on arthropod movement should be interpreted with this added ecological complexity in mind.

Dispersal capacity of species contributes to processes of community assembly at landscape and local scales, including patterns of probabilistic dispersal and recolonization following natural and anthropogenic disturbances. Studies of arthropod community assembly have often found that a combination of stochastic (neutral-based) and deterministic (niche-based) processes shape patterns of assembly (Thompson and Townsend 2006, Farnon Ellwood et al. 2009, Rominger et al. 2009, Ferrenberg et al. 2019, Perry et al. 2020), but disturbances can mediate the relative importance of these mechanisms. For example, following tree mortality caused by bark beetles, the relative importance of deterministic processes related to plant and soil habitat characteristics increased in strength for ground-dwelling arthropods, while stochastic processes related to dispersal limitations increased for soil-dwelling arthropods (Ferrenberg et al. 2016). Ground- and soil-dwelling arthropod communities increased in compositional similarity due to the lack of recolonization of key detritivores including isopods and millipedes nine months after a 100-yr flood that caused the area to remain submerged for four weeks (Roeder et al. 2018). This study documented limited dispersal potential of most ground-dwelling arthropods, the majority of which were flightless taxa that disperse primarily by walking and/or running, which suggests this community may be particularly vulnerable to dispersal limitations. Due to the small spatial and short temporal scales investigated, this study assessed station-keeping movements (also known as foraging movements, Jeltsch et al. 2013) which are local daily movements that occur frequently within an individual's home range (Schlägel et al. 2020). Although these daily station-keeping movements of

ground-dwelling arthropods were largely unaffected by small-scale canopy and understory disturbances, with the exception of three highly mobile taxa, limited dispersal may pose challenges for recolonization of fragmented forest patches at larger spatial scales. Therefore, future research avenues should address dispersal processes among arthropod taxa occurring over greater spatial and temporal scales in response to disturbances that affect multiple forest strata.

In conclusion, this study revealed that small-scale canopy and understory disturbances impacted movement of highly mobile ground-dwelling arthropod taxa that forage extensively as detritivores (Parajulidae and Paradoxosomatidae) and scavengers (Opiliones). The majority of ground-dwelling arthropod taxa studied exhibited limited movement, which suggests sessile arthropods may cope with the environmental changes they experience on the forest floor or become more susceptible to altered disturbance regimes for which they are not adapted. This study builds on a companion study (Perry et al. 2018) to collectively investigate the effects of canopy and understory disturbances on ground-dwelling arthropod community structure, composition, and dispersal, bridging biodiversity and movement ecology research. A focus on movement of multiple arthropod taxa simultaneously can inform observed patterns of species diversity following disturbances that affect multiple forest strata, as well as biodiversity conservation strategies and sustainable forest management.

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DATA AVAILABILITY

Data are available from Zenodo: <https://doi.org/10.5281/zenodo.5337015>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3771/full>