**Introduction:**

Natural disturbances, including fires, windstorms, floods, droughts, and insect outbreaks, have occurred in forests for millions of years (Lindenmayer et al. 2012). In forests of the eastern United States, wind disturbance from hurricanes, derechos (straight-line windstorms), and tornados is a dominant disturbance regime (Fischer et al. 2013). When windstorms knock down canopy trees, the increased sunlight reaching the understory and forest floor can induce environmental changes. Soil temperature extremes can increase, moisture can change depending on reduced evapotranspiration but increased summer temperature, leaf litter depth can decrease due to faster decomposition, and understory plants increase their growth rates (Greenberg and Forrest 2003, Urbanovi et al. 2014, Barber and Widick 2017). The growth of understory plants interacts with tree mortality and the creation of canopy gaps to alter microclimatic conditions (Perry et al. 2018). The fallen canopy trees cause an influx of woody debris, including both coarse and fine woody debris. Uprooted trees create tip-up mounds that alter topography of the forest floor (Perry and Herms 2019). These biological legacies that remain after the disturbance influence short- and long-term changes in forest structure and function (Lindenmayer et al. 2012). These legacies include the living and dead trees, understory shrubs and herbaceous plants, seeds, root systems, soils, and surviving animals.

Harvesting the fallen trees after a natural disturbance is a practice called salvage-logging, and this management practice is a common response to windstorms (Lindenmayer et al. 2012). Salvage logging can help landowners recover the economic value of the fallen trees, or it may be motivated towards reducing fire risk, insect outbreak risk, or safety hazard (Perry and Herms 2019). However, there is a growing interest in managing forests in ways that conserve biodiversity, including insect populations that are threatened globally due to environmental change (Wagner 2019). This includes understanding how management practices such as salvage-logging impact insect biodiversity (Thorn et al. 2018). For example, salvage-logging alters the biological legacies left by windstorms by reducing the amount and diversity of woody debris, as well as by disturbance of understory plants, potential for soil compaction from machinery, and modified tree species composition (McNabb et al. 2001, Curtze et al. 2018, Slyder et al. 2020).

To understand how insect biodiversity is affected by forest management, an indicator taxon can be used, which is a starting point for characterizing the response of the insect community (Langor and Spence 2006). Ground beetles (Coleoptera: Carabidae) are useful indicators because they are taxonomically well known, sensitive to abiotic and biotic conditions, and sensitive to forest disturbance (Koivula 2011). Ground beetles are diverse in multiple habitats, including both mature forests and early successional habitats such as tallgrass prairies, agricultural fields, urban areas, clearcuts, and floodplains (Silverman et al. 2008, Lambeets et al. 2008, Lundgren and McCravy 2011). Within mature forests, ground beetle communities can differ based on predominate tree species, managed vs. old-growth forest, and forests with dense vs open ground vegetation (Werner and Raffa 2000, Perry et al. 2018). Thus, the occurrence and species composition of ground beetles can indicate fine-scale differences in habitat.

Two processes occur to the ground beetle community after a forest disturbance: influx of new species and decline of resident species. After canopy gaps open and early successional plants begin to grow, a guild of open-habitat ground beetles typically disperses to the disturbed area. This group, including certain species of *Amara*, *Anisodactylus*, *Harpalus*, and *Chlaenius*, may immediately increase following disturbance, or may take a few years to locate the site, depending on landscape structure (Sklodowski and Garbalinska 2011, Lee et al. 2017, Barber and Widick 2017). While open-habitat species increase after disturbance, there is also a decline of forest-adapted ground beetles. For example, in Minnesota, jack pine stands that were wind-disturbed or salvaged 1-3 years prior had lower numbers of *Pterostichus pensylvanicus* LeConte, *Pterostichus coracinus* (Newman), and *Sphaeroderus lecontei* Dejean than undisturbed sites (Gandhi et al. 2008). In a scots pine forest in Poland, forest-specialists decreased in proportional abundance over a six-year period following a tornado (Sklodowski and Garbalinska 2011). These observed decreases in forest-adapted ground beetles after windstorms and salvage-logging could be caused by a variety of factors, including environmental changes such as increased sunlight, increased summer soil temperature, and decreased leaf litter (Greenberg and Forrest 2003). Although many microclimate variables stabilize after multiple years of tree regeneration following a disturbance, other variables, such as woody debris deposition or removal, remain for decades (Gore and Patterson III 1986, Perry and Herms 2019). Studies of clearcuts in Alberta indicate that differences in ground beetle communities between mature and clearcut forests remain even after 27 years (Pohl et al. 2007). Thus, it is unclear how long it could take for forest-adapted ground beetles to return to areas impacted by windstorms and salvage-logging, and this subject deserves further study to inform salvage-logging practices that may increase with climate change.

While much is known about how the taxonomic composition of ground beetle communities changes after forest disturbance, less is known about how these disturbances may impact the functional diversity of beetles via changes in traits. Studies have documented that ground beetle species common in tornado-disturbed forests were smaller in size, incorporated plant material or seeds into their diets, and were capable of flight, compared to those characteristic of undisturbed forest (Sklodowski and Garbalinska 2011, Perry and Herms 2019). However, ground beetle traits can vary even among, for example, equally-sized, carnivorous, flight-incapable species. For instance, ground beetles exhibit trait syndromes (Fountain-Jones et al. 2015) associated with locomotion strategy (Forsythe 1991), including surface-walking, pushing through leaf litter, burrowing, and climbing plants (Larochelle and Larivière 2003). Separately, ground beetle species also differ in their soil moisture preference, and this trait plays an important role in habitat selection (Thiele 1977). Because forest disturbance can affect leaf litter depth, ground vegetation height, soil density, woody debris cover, and soil moisture, these habitat changes could disproportionately increase the fitness of ground beetle species with certain locomotion strategies and moisture preferences. Research is required to determine whether the effect of forest disturbance on ground beetles is mediated by their species-specific traits.

Our objective is to use ground beetles to study the long-term impacts of salvage-logging after a tornado. To do this, we compared the taxonomic and functional diversity of ground beetle communities among undisturbed forest (hereafter “forest”), unsalvaged windthrow (hereafter: “windthrow”), and salvage-logged windthrow (hereafter: “salvaged”) treatments, at three and ten years after a tornado. We hypothesized that: (1) The taxonomic

**Methods**

Study site

Research was conducted at Powdermill Nature Preserve (PNR) in Rector, Westmoreland County, Pennsylvania (latitude: 40.159806558020556, longitude: -79.27176866978374). This preserve was established as the field research station for the Carnegie Museum of Natural History in 1956 and is largely temperate deciduous forest. The annual precipitation for the years 2012-2022 was between 45 and 70 in. with a mean of 53 in. (weather station: USC00362183) (“National Centers for Environmental Information: Past Weather” n.d.). In June 2012, a tornado uprooted or snapped many canopy trees in two large areas of the forest, each about 120 × 480 m (Figure 1). These two areas are on north- or northwest-facing slopes, which were dominated by maple (*Acer spp*.), tuliptree (*Liriodendron tulipifera*), and black cherry (*Prunus serotina*) (Murphy et al. 2015), with an understory of predominately spicebush (*Lindera benzoin*) (Calinger et al. 2015). The tornado created patchy areas of canopy openness: the impacted areas had canopy openness values of 25% up to 90% (Slyder et al. 2020). The elevation of the impacted area ranges from around 1650 ft. to 1750 ft. A waterway, Laurel Run, is found along the west side of the impacted areas.

A map of a mountain

AI-generated content may be incorrect.

Figure 1. Map of the pitfall trap locations (need to add shapefiles of impacted areas as well as a legend)

From mid-summer through winter of 2013, half of each wind-disturbed area was salvage-logged using heavy machinery to remove both fallen and residual standing trees. In 2015, three transects were established across each area of forest impacted by the tornado (total 6 transects) (Figure 1). Transects were established across the windthrow and salvaged disturbances that extended 50 m into the surrounding undisturbed forest on each side. Along each transect, four plots were established: one plot in windthrow, one in salvaged, and two in the surrounding undisturbed forest. This resulted in a sample size of 24 plots, wherein all data collection occurred.

Ground-dwelling invertebrate sampling

Ground-dwelling invertebrates were sampled using barrier pitfall traps in 2015 and 2022, representing three and ten years post-tornado (two and nine years post-salvage). Barrier pitfall traps consisted of two pairs of plastic cups (each pair having an inner 500 mL cup and an outer 1 L cup) which were placed into the ground so that the lip of the cup was flush with the ground surface. The two pairs of cups were placed 1 m from each other, and garden edging (Suncast® eco edge) was placed between them to create a barrier. Cups were filled 4 cm high with propylene glycol (recreational vehicle and marine antifreeze, Peak Company Old World Industries, Clear Lake, Texas) with a few drops of detergent. Masonite board (100 cm2) was placed at 3 cm above each cup to prevent flooding from rain. Steel hardware cloth was secured over cups using 30 cm stakes to limit mammal disturbance.

Pitfall trap sampling was conducted continuously over the growing seasons in 2015 and 2022. Trap catch was collected every two weeks, and cups were refilled with propylene glycol. In 2015, pitfall traps were installed on May 27-28, and samples were collected on 9-10 June, 24-25 June, 8 July, 22 July, 5 August, and 17 August. In 2022, traps were installed on 1-2 June, and samples were collected on 15 June, 29 June, 13 July, 27 July, 11 August, 23 August, and 9 September. Between 2015 and 2022, plot 63 had to be moved by 27 m because of fallen debris, but the new location was still within the windthrow treatment. Trap catch was collected by pouring the sample through a fine mesh strainer and storing the contents in a specimen cup with 70% ethanol until sorting and identification.

Ground beetles (Carabidae) were identified to species using taxonomic keys (Lindroth 1961, Freitag 1969, Bousquet 2010, Bousquet and Messer 2010, Hunting 2013, Harden and Guarnieri 2017). Nomenclature followed Bousquet (2012). Species vouchers were deposited at the C. A. Triplehorn Insect Collection (OSUC), Museum of Biological Diversity, The Ohio State University, Columbus, Ohio where each specimen was given a unique identifier label (Table 1).

Trait measurements

We selected eight morphological traits of beetles that have previously been shown to relate to habitat (Table 2) (Fountain-Jones, Baker, and Jordan 2015). These traits are body length, antenna length, eye protrusion, eye length, pronotum width, abdomen width, rear leg length, and rear trochanter length. Traits were measured under a dissecting microscope using an ocular micrometer to the nearest 0.1 mm. For each species, traits were measured on up to six individuals, three males and three females if possible (Fountain-Jones, Baker, and Jordan 2015). These individuals were chosen in a way that attempted to encompass the intraspecific variation in body size observed for the species. To control for variation in beetle body size, relative measurements of all morphological traits were calculated as their ratio to body length for each individual (Ribera et al. 2001).

In addition to measured traits, we utilized the literature to provide information for three additional traits: flight capability, water affinity, and forest affinity (Larochelle and Larivière 2003). Flight capability was coded as 1 if the species is flight-capable, 0 if the species is flight-incapable, and 0.5 if the species exhibits wing dimorphism. Water affinity was coded as 0 for xerophilous species, 1 for hygrophilous species, and 0.5 for intermediate species. Water affinity was treated as a physiological trait, because ground beetle species often have consistent humidity preferences in behavioral studies (Thiele 1977). Forest affinity was coded as “forest-specialist,” “open-habitat,” or “eurytopic” (meaning the species is found in forest clearings or in both forest and open habitats). We treated forest affinity as an ecological performance trait (following the terminology of Fountain-Jones et al. (2015)), and chose to exclude it from calculations of alpha- and beta- functional diversity.

**Table 2**. Morphological traits and literature-based traits used in this study. Forest affinity (the last trait) was excluded from calculations of alpha- and beta-functional diversity.

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| **Trait** | **Connection to habitat** |
| Body length | Shorter body length was found for ground beetles caught in wind-disturbed forests, relative to undisturbed forests (Sklodowski and Garbalinska 2011). Body length is correlated with many other morphological traits (Barton et al. 2011). |
| Antenna length | Tactile hunter species, which rely on sense of touch more than vision, tend to have longer antennae (Bauer and Kredler 1993). Longer antenna length relative to body length was found for ground beetles caught under a tree, versus in the open (Barton et al. 2011). |
| Eye protrusion | A greater eye protrusion was found in a tree-climbing ground beetle, and it may allow partial overlap in the frontal visual field. However, greater eye protrusion might prevent a ground beetle from moving through thick vegetation or soil (Talarico et al. 2007). |
| Eye length | Diurnal ground beetle species and/or those adapted to open environments tend to rely on vision for predator avoidance or prey detection (Talarico et al. 2007), and thus might have longer eyes. |
| Pronotum width | A proportionally wider pronotum can be found in robust-bodied beetles, which tend to be found within open habitats (Barton et al. 2011). A narrow pronotum can be an adaptation to reaching prey within hard-to-reach crevices or shells. A narrow pronotum may also be related to the beetle having an unobstructed view behind its eyes (Forsythe 1991). |
| Abdomen width | Similar pattern to pronotum width, with species having proportionally wider abdomens tending to be found in open habitats (Barton et al. 2011). |
| Rear leg length | Open habitats seem to favor ground beetle species with shorter legs relative to body length (Barton et al. 2011). Ground beetles with longer legs may be weaker at pushing through dense substrates (Forsythe 1991). |
| Rear trochanter length | The rear trochanter connects to the femur of the rear leg. Ground beetles have a bean-shaped rear trochanter that allows them to move between narrow crevices between bark, leaf litter, or soil. The muscle in the rear trochanter allows the rear leg to create a force in the dorsal direction, which enlarges the space and allows the beetle to move through constricted areas. The trochanter is longer, on average, in species that push themselves through soil and underneath leaf litter. It is shorter in species that walk or run above the surface of the substrate (Forsythe 1991, Talarico et al. 2007). |
| Flight capability | Flight-capable species (macropterous and with fully developed flight musculature) can exploit patchy, temporary habitats. Conversely, flight incapable species may have higher fitness within stable habitats (Ribera et al. 2001, Venn 2016). |
| Water affinity | Habitats vary in the saturation of the substrate with water, and water preference varies between ground beetle species, with some species found near riverbanks or other bodies of water, others found in moist leaf litter, and others found in dry soil. A preference for low humidity may be related to overwintering within tree stumps and logs, versus in the soil (Thiele 1977). |
| Forest affinity | Some ground beetle species tend to be caught in forests, underneath trees, whereas other species tend to be caught in fields, prairies, pastures, and other open habitats (Silverman et al. 2008). |

Forest floor environment

Environmental variables on the forest floor were quantified to assess differences among windthrow, salvaged, and undisturbed forest. Percentage canopy openness was measured using a spherical crown densiometer directly above the pitfall traps to assess light availability on the forest floor. Canopy openness was measured on 9-10 June and 5 August in 2015, and on 1-2 June in 2022. Percentage cover of ground-level vegetation, leaf litter, bare ground, fine woody debris (<10 cm diameter at the large end), coarse woody debris (≥ 10 cm diameter), and rocks were estimated in two randomly selected 1 m2 quadrats around each pitfall trap. Understory vegetation height (m) was also measured in the quadrats. Ground cover estimates were collected on 9 June, 7 July, and 5 August in 2015, and on 1-2 June, 13 July, 11 August, and 6 September in 2022. Values from the two quadrats around each pitfall trap were averaged together for a site-level mean. Soil moisture was measured at three locations adjacent to each pitfall trap using a Dynamax Inc. (Houston, Texas) TH20 portable soil moisture meter with a Theta Probe ML2x sensor. Soil moisture measurements were taken biweekly when pitfall samples were collected. The three readings were averaged together for a single mean at each plot-date combination.

Statistical analysis

Data standardization:

Ground dwelling invertebrates vary in how much they move across the forest floor, and movement may be affected by forest management (Perry et al. 2021). Pitfall traps preferentially collect insects that are more active and mobile, and consequently the number of ground beetles caught in pitfalls is reported as activity-abundance, which emphasizes that insect sampling methods have inherent biases towards certain taxa (Gandhi et al. 2008).

To determine if our sampling effort was adequate to understand the ground beetle fauna at the site, we used species accumulation curves (SACs) and Chao estimators. For each year and treatment, we created an SAC with number of sampled plots in the x-axis. This was implemented using the *specaccum* function in the R package ‘vegan’ with the ‘random’ setting, which finds the mean SAC by permuting the order of the plots (Oksanen et al. 2024, R Core Team 2024). To estimate a lower bound on the true species richness of ground beetles, we used an asymptotic approach (Chao and Chiu 2016). We used the Chao1 estimator, which is a nonparametric estimator that gives a lower bound on the true species richness. This estimator incorporates the number of singletons and doubletons to estimate the number of undetected species and was implemented using the function “ChaoSpecies” in the R package “SpadeR” (Anne Chao et al. 2016).

Before doing further analyses, we accounted for occasional loss of trap catch due to animal disturbance. For each species-plot combination, we divided the count by the number of days that the pitfall trap at that plot was operational (Sklodowski and Garbalinska 2011). Thus, all activity-abundance data was corrected for number of operational days.

Taxonomic alpha-diversity

To investigate alpha-diversity at the plot level, we calculated species richness and Shannon diversity using the package “HillR” (Li 2018). Shannon diversity was calculated using the formula exp(-Σpiln(pi)), which is the same as the Hill number of order 1. This metric takes values between 1 and the species richness, depending on the degree to which the relative abundances are equal.

Functional alpha diversity

We used trait data in combination with ground beetle counts to calculate functional alpha-diversity. The eight morphological traits had already been standardized by dividing by body length. After investigating the Pearson correlation coefficients between pairs of traits using the package “corrplot” (Wei and Simko 2024), we determined that eye protrusion and eye length were highly correlated (r = 0.87) and that antenna length and rear leg length were highly correlated (r = 0.81), even after standardization of each variable to body length. To address this, we replaced *standardized\_eye\_protrusion* with *eye\_protrusion to eye\_length ratio*, and we replaced *standardized\_antenna\_length* with *antenna\_length to rear\_leg\_length ratio*. These changes resulted in a set of traits with correlation coefficients ≤ 0.51 between pairs. Trait measurements were averaged across individuals of a species to calculate species-specific means. To address any remaining collinearity within the numerical traits, we performed a principal components analysis (PCA) (Swenson 2014). We centered each numerical trait to a mean of 0, scaled to a variance of 1, and ran the PCA using the function “prcomp” in the R package “stats” (R Core Team 2024). The PCA analysis of the eight numerical traits generated a set of five axes which together explained 89% of the variance. The first PC axis (30% of the variance) was associated with proportionally narrower pronotum, proportionally longer rear legs, and proportionally shorter rear trochanter. The second PC axis (20% of the variance) was associated with longer body length and proportionally shorter eye length. The third PC axis (15% of the variance) was associated with smaller eye protrusion ratio and larger antenna to rear leg ratio. We used the five PC axes, along with the categorical variables *Water\_affinity* and *Flight\_capability* to calculate a Gower distance matrix between all ground beetle species in trait space using the package “FD” (Laliberte et al. 2014). Finally, we calculated functional alpha diversity for each plot by computing the weighted mean pairwise distance in trait space between species found at the plot. Each calculation of distance between a pair of species was weighted by the product of the relative abundances of the two species at the plot (Swenson 2014). The calculation was carried out using the function *mpd* in the R package “picante” (Kembel et al. 2010).

Models

We tested whether forest management treatment (forest control, windthrow, salvaged) was correlated with plot-level metrics of ground beetle biodiversity. Our response variables were total activity-abundance, activity-abundance of open-habitat and eurytopic species, activity-abundance of forest-specialist species, species richness, Shannon diversity, and functional alpha diversity.

We created separate models for each year of sampling, 2015 and 2022. We included transect as a random effect to account for spatial structure in the data.

Taxonomic beta diversity

Functional beta diversity

Comparing open- and forest-adapted ground beetles

Microclimatic variables

**Results**

**Discussion**

Although the percent cover of woody debris did not differ between the windthrow and salvaged treatments, there was higher volume of coarse woody debris in the windthrow in 2014, compared to the salvaged treatment (Perry 2016). The reduction in coarse woody debris volume could last decades. When examining clearcut stands of varying age in New Hampshire, researchers found that the slash from clearcutting decomposed within 20-30 years, leaving low mass of downed wood for an additional 30 years, before the tree regeneration began to contribute downed wood (Gore and Patterson III 1986). Thus, salvage-logging could affect woody debris volume for >50 years.

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