**Title:**

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**Abstract**

Mechanisms that maintain biodiversity remain a focal area of research in ecology. Theory predicts that species diversity is maximized at intermediate levels of disturbance due to trade-offs in traits for competition and colonization ability. To test the competition-colonization trade-off model, ground beetle assemblages were characterized at three levels of forest disturbance intensity (low, intermediate and high) via a manipulative experiment that imposed canopy gap and understory vegetation removal disturbance treatments in factorial combination. Ground beetle assemblages were characterized pre- and post-disturbance treatment implementation. Canopy gaps were identified as a significant factor driving ground beetle assemblage structure. In canopy gaps, ground beetle body size decreased in 2014 and species diversity increased in 2015, with *Chlaenius emarginatus*, *Cyclotrachelus sodalis*, *Platynus angustatus*, and *Pterostichus adoxus* positively correlated to canopy openness, but minimal effects of understory vegetation disturbance were detected. Contrary to model predictions, activity-abundance of macropterous species increased in canopy gaps in 2015, but not in the most disturbed treatments with combined canopy and understory disturbance. Inconsistent responses of ground beetles between years may be explained by temporal changes in the effect sizes of the canopy and understory disturbance treatments. Changes in ground beetle species diversity and composition in response to natural and anthropogenic disturbances has implications for ecosystem services. Therefore, understanding the effects of disturbance on biodiversity is necessary to foster sustainable forest management strategies.

**Keywords**: biological indicators, competition-colonization trade-off, competitive ability, dispersal ability, intensity, perturbation, species diversity

**Introduction**

Species diversity is an emergent property of ecosystems that is important for a multitude of essential processes ([Cardinale et al. 2006](#_ENREF_8); [Harrison et al. 2014](#_ENREF_24)). With the current decline in biological diversity worldwide largely due to anthropogenic disturbances such as climate change, invasive species, and land-use change ([Cardinale et al. 2012](#_ENREF_7); [Sala et al. 2000](#_ENREF_52); [Wilcove et al. 1998](#_ENREF_60)), there is an imminent need to understand the drivers that maintain and promote species diversity in ecosystems ([Essl et al. 2015](#_ENREF_17); [Goulson 2019](#_ENREF_22)). Understanding landscape and local drivers that shape patterns in species diversity is essential for the development of effective management and conservation strategies that foster biodiversity ([Balvanera et al. 2014](#_ENREF_1); [Elmqvist et al. 2003](#_ENREF_16)).

Mechanisms that maintain biodiversity remain a focal area of research in ecology ([Chesson 2000](#_ENREF_10); [Petraitis et al. 1989](#_ENREF_46)). Theory posits that species diversity is maximized at intermediate levels of disturbance. The intermediate disturbance hypothesis (IDH) is often used to explain the effects of disturbance on species diversity ([Connell 1978](#_ENREF_13); [Hutchinson 1961](#_ENREF_26); [Roxburgh et al. 2004](#_ENREF_51); [Shea et al. 2004](#_ENREF_55)). First proposed by Connell (1978), the IDH states that disturbance of intermediate frequency or intensity maintains high diversity in ecosystems by continually changing species composition and reducing competitive dominance. Recently, concerns about the validity and utility of the IDH have been raised, and this mechanism has been debated ([Fox 2013a](#_ENREF_18); [Fox 2013b](#_ENREF_19); [Sheil and Burslem 2013](#_ENREF_56)). One viable mechanism that could produce high species diversity at intermediate levels of disturbance is the competition-colonization trade-off model ([Cadotte 2007](#_ENREF_3); [Fox 2013b](#_ENREF_19); [Hastings 1980](#_ENREF_25)). This model predicts that trade-offs in traits for competition and colonization ability increase species diversity at intermediate disturbances because both early and late successional species, or r- and k-selected species, are able to coexist ([Levin and Paine 1974](#_ENREF_34)). Studies testing the IDH have largely focused on sessile communities ([Kershaw and Mallik 2013](#_ENREF_28); [Shea et al. 2004](#_ENREF_55)), and a variety of diversity-disturbance relationships have been observed ([Mackey and Currie 2001](#_ENREF_36)). However, many of these studies did not directly test potential mechanisms of the IDH and instead, were focused on pattern detection.

In forest ecosystems, natural and anthropogenic disturbances alter habitat structure, energy and nutrient flow, community dynamics, and successional trajectories ([Oliver and Larson 1996](#_ENREF_41); [Pickett and White 1985](#_ENREF_47)). In mixed deciduous forests of eastern North America, natural disturbance regimes commonly affect the canopy and understory through tree mortality. Following tree mortality, gaps are created in the forest canopy, which increase light availability on the forest floor that releases suppressed trees, shrubs, and herbaceous plants in the understory ([Canham et al. 1990](#_ENREF_5); [Oliver and Larson 1996](#_ENREF_41)). The heterogeneous biotic and abiotic environment on the forest floor created by canopy gaps affects the recruitment, colonization, and establishment of plant and animal species ([Canham and Marks 1985](#_ENREF_6); [Collins et al. 1985](#_ENREF_12); [Yamamoto 1992](#_ENREF_61)). However, identifying the primary drivers of community response following these disturbances is often limited due to the combined effects of multiple elements such as canopy and ground-level factors. Isolating the effects of canopy and understory disturbances to discern how these factors may interact to impact communities may elucidate the drivers that are important for the maintenance of species diversity in forest ecosystems. How communities are reorganized following disturbances has significant implications for community dynamics and ecosystem processes, and these responses are largely determined by species’ traits, such as competitive ability, reproductive strategies, dispersal ability, and habitat preferences ([Belyea and Lancaster 1999](#_ENREF_2); [Chase 2003](#_ENREF_9); [Petraitis et al. 1989](#_ENREF_46)).

Ground beetles (Coleoptera, Carabidae) are a diverse insect family that respond quickly to changes in habitat structure and composition ([Lövei and Sunderland 1996](#_ENREF_35); [Thiele 1977](#_ENREF_57)). They are commonly considered biological indicators of environmental change ([Pearce and Venier 2006](#_ENREF_42); [Pohl et al. 2007](#_ENREF_48); [Rainio and Niemelä 2003](#_ENREF_49)) and have been frequently used in studies assessing changes in ecosystem structure and function in response to natural or anthropogenic perturbations ([Cobb et al. 2007](#_ENREF_11); [Koivula and Spence 2006](#_ENREF_30); [Niemelä et al. 1993](#_ENREF_40)). In forest ecosystems, ground beetles respond to changes in light availability ([Gandhi et al. 2014](#_ENREF_20); [Perry and Herms 2016](#_ENREF_45)), vegetation cover ([Jukes et al. 2001](#_ENREF_27); [Leslie et al. 2014](#_ENREF_33)), temperature and moisture ([Neve 1994](#_ENREF_38); [Thiele 1977](#_ENREF_57)), leaf litter depth ([Koivula et al. 1999](#_ENREF_29); [Pearce et al. 2003](#_ENREF_43)), and woody debris ([Latty et al. 2006](#_ENREF_31); [Ulyshen and Hanula 2009](#_ENREF_58)). Changes in these microclimate factors often elicit species-specific responses in ground beetles.

Ground beetles are an ideal group of mobile organisms for testing predictions of the competition-colonization trade-off model owing to their high species diversity and well described taxonomy. In forest ecosystems, many ground beetle species are predators that feed on a variety of invertebrate prey ([Lövei and Sunderland 1996](#_ENREF_35)). Intra- and inter-specific competition for resources between ground beetle adults, between larvae, or between adults and larvae may contribute to assemblage organization or establishment ability ([Lenski 1982](#_ENREF_32); [Niemelä 1993](#_ENREF_39)), especially if disturbances alter prey abundances or distributions on the forest floor. Ground beetles differ in their dispersal abilities, and based on the development of their wings, species are either winged (macropterous), wingless (brachypterous), or wing-dimorphic ([den Boer et al. 1980](#_ENREF_15)). Compared to macropterous species, the dispersal potential of brachypterous ground beetles is limited. Hence, they tend to occur in undisturbed late successional environments ([den Boer 1970](#_ENREF_14); [den Boer et al. 1980](#_ENREF_15); [Roff 1990](#_ENREF_50)). Body size of ground beetles has been linked to their dispersal ability and habitat preference ([Gutiérrez and Menéndez 1997](#_ENREF_23)), and it has been used as an indicator of disturbance or succession ([Gobbi 2014](#_ENREF_21); [Schwerk and Szysyko 2007](#_ENREF_53)). Small macropterous beetles (good dispersers) tend to be abundant in more disturbed early successional forests, while large brachypterous beetles (poor dispersers) are more abundant in stable late successional forests ([Pedley and Dolman 2014](#_ENREF_44); [Šerić Jelaska et al. 2011](#_ENREF_54)).

Based on the competition-colonization trade-off model, ground beetle species diversity is hypothesized to be highest following disturbances of intermediate intensity because both good colonizers and good competitors can survive in these environments. To test this hypothesis, ground beetle assemblages were characterized at three levels of forest disturbance intensity (low, intermediate, and high) via a manipulative experiment that imposed canopy gap and understory vegetation removal disturbance treatments in factorial combination. Additionally, this experiment allowed for the comparison between canopy and understory vegetation disturbances to determine if either is a more significant driving factor influencing ground beetle assemblage diversity and species composition. We predicted that (1) ground beetle species diversity would be highest in treatments that received either canopy or understory vegetation disturbance, compared to undisturbed forest and treatments receiving combined canopy and understory disturbances; (2) ground beetle species composition would change from undisturbed forest to combined canopy and understory disturbance treatments due to a trade-off in traits for competition and colonization ability; (3) the activity-abundance of macropterous ground beetles would increase in combined canopy and understory disturbance treatments compared to undisturbed forest; and (4) body length of ground beetles would decrease in combined canopy and understory disturbance treatments compared to undisturbed forest.

**Methods**

Study Site

This study was conducted at Powdermill Nature Reserve (PNR; 40°09’N, 79°16’W) in Rector, Westmoreland County, Pennsylvania in the Laurel Highlands. PNR has approximately 900 hectares of natural habitat across an elevation range of 392 to 647 m that is largely temperate deciduous forest composed of mesophytic species. PNR was established in 1956 as a nature reserve and the field research station for the Carnegie Museum of Natural History. 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 mined for coal in the 1940s.

Dominant tree taxa were maple (*Acer* spp.), oak (*Quercus* spp.), beech (*Fagus* spp.), poplar (*Populus* spp.), and hickory (*Carya* spp.) ([Murphy et al. 2015](#_ENREF_37)). 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](#_ENREF_4)). However, PNR has a diverse understory of herbaceous plants and woody shrub species, and some of the most abundant 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

A manipulative experiment was established with two disturbance treatments in factorial combination: presence/absence of canopy gaps and presence/absence of understory vegetation removal, resulting in four treatment combinations: (1) canopy gaps absent, understory vegetation present (control, no disturbance and low intensity); (2) canopy gaps absent, understory vegetation absent (intermediate intensity); (3) canopy gaps present, understory vegetation present (intermediate intensity); and (4) canopy gaps present, understory vegetation absent (high intensity). Forest plots (n=6) were randomly selected in 2013 from vegetation survey plots previously established at PNR ([Whitacre 2013](#_ENREF_59)). Plots contained four quadrats (the experimental unit; 30 × 30 m) (n=24). Canopy and understory vegetation treatments were implemented within the quadrats in 2014, and each treatment combination was replicated 6 times in a completely randomized design. The factorial combination of treatments isolated the individual effects of interacting canopy and ground-level vegetation disturbances. Because these disturbance treatments were imposed once, this study focused on intensity rather than frequency as the disturbance property. Ground beetle assemblages were characterized in the experimental plots during the growing seasons of 2013-2015, before and after the disturbance treatments were implemented.

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. The number of trees girdled in each canopy gap treatment was determined by the amount of canopy that needed to be removed to simulate the treatment, and this was dependent on the structure of the forest in the randomly selected plots. Only dominant and codominant trees were girdled to create a patchy distribution of gaps in the forest canopy. A chainsaw was inserted approximately 6-12 cm (depending on tree size) into the tree and a 2 cm ring width was cut around the entire trunk near the base about 1.5 meters above the ground. A second ring was cut into the tree approximately 20-30 cm below the first ring. A total of 117 trees were girdled across all canopy treatments. Girdled tree species (number of individuals girdled) were American beech (*Fagus grandifolia* Ehrh.) (1), American basswood (*Tilia* *americana* L.) (2), yellow birch (*Betula* *alleghaniensis* Britton) (1), black cherry (*Prunus* *serotine* Ehrh) (2), slippery elm (*Ulmus* *rubra* Muhl.) (3), red maple (*Acer* *rebrum* L.) (16), silver maple (*Acer* *saccharinum* L.) (2), sugar maple (*Acer* *saccharum* Marsh.) (27), northern red oak (*Quercus* *rubra* L.) (7), white oak (*Quercus* *alba* L.) (5), cherrybark oak (*Quercus falcata* var. *pagodifolia* Ell.) (1), white ash (*Fraxinus* *americana* L.) (3), tulip poplar (*Liriodendron* *tulipifera* L.) (43), and shellbark hickory (*Carya* *laciniosa* (Michx. F.) Lould.) (4). Canopy condition and overall health of the girdled trees were evaluated monthly during the growing seasons of 2014 and 2015.

To implement the understory vegetation removal treatment, motorized weed trimmers (KM 110 R KombiMotor, Stihl, Inc.; Virginia Beach, VA) 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 units. Woody shrubs and saplings were hauled out of the experimental units 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 all treatments once in 2013, and monthly during the growing seasons of 2014 and 2015.

Ground Beetle Sampling

Ground beetles were sampled using unbaited pitfall traps (Spence and Niemelä 1994, Latty et al. 2006). Although pitfall traps are a standardized method for collecting ground-dwelling invertebrates, this method tends to preferentially collect more active species. Therefore, ground beetle abundances are reported as activity-abundance (beetles per trap). One trap was installed 5 m from the center of each experimental unit in a randomly selected cardinal direction. These methods also were used in the undisturbed reference plots. Based on the size of these experimental units, this level of sampling intensity (one trap per 30 × 30 m plot) was more than adequate for collecting the majority of ground beetle species present (Werner and Raffa 2000). Pitfall traps consisted of two pairs of plastic cups (each pair consisted of an inner 500 mL and outer 1 L plastic cup) placed in holes in the ground such that the rim of the cups were flush with the soil surface and connected by garden edging (Eco Edge, Suncast Corporation, Batavia, Illinois) 1 m in length (Fig. 5.1). 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) along with a few drops of detergent to facilitate collection. Masonite board (100 cm2) was placed 3 cm above each cup to prevent flooding from rainwater, and steel hardware cloth was secured over each trap with 30 cm stakes to limit animal disturbance.

Pitfall trap sampling was conducted continuously over the growing season in 2013, 2014 and 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 beetles were identified to species (Table 5.1) using keys in Lindroth (1961-1969), Freitag (1969), Arnett and Thomas (2001), and Bousquet (2010). Nomenclature follows Bousquet (2012). Species were categorized by dispersal strategies (determined by wing development; macropterous, brachypterous or wing-dimorphic) based on natural history information reported in Larochelle and Larivière (2003), and the sex of each individual was determined. The length of each individual specimen was measured (mm) from the apex of the mandible to the apex of the elytra.

Environmental Conditions

To assess changes in the disturbance treatments over time, percentage cover of understory vegetation and percentage canopy openness were quantified in all treatments once in July 2013 and monthly during the growing seasons in 2014 and 2015. Height and percentage cover of understory vegetation were assessed in a 1 × 1 m quadrat in two randomly selected locations surrounding each pitfall trap. Canopy openness was measured above each pitfall trap using spherical crown densiometer calculations. To follow dieback, the degree of canopy decline for each girdled tree was quantified bi-weekly during the growing season of 2014 and monthly during 2015 using a 1-5 health rating scale (Smith et al. 2015) where 1 corresponded to a healthy tree with a full canopy, 5 corresponded to a dead tree, and 2-4 represented stages of increasing canopy thinning. Additionally, 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.

*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 species activity-abundance data were rank transformed to improve normality. Rank transformations are used in non-parametric tests to correct for normality and variance issues, but this technique can be applied to parametric tests for the same purpose (Quinn and Keough 2002). Trap catches were standardized for 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). Species accumulation curves with rarefaction analyses and first-order jackknife estimates were conducted separately for each year to assess sampling efficiency (McCune and Grace 2002). Species richness (number of species per treatment), Pielou’s *J* evenness index (Pielou 1966), and Shannon (Peet 1974) and Simpson (Simpson 1949) diversity indices 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 beetle assemblages in canopy gap and understory vegetation disturbance treatments using SAS software (SAS Institute 2016). Response variables were total ground beetle activity-abundance, species richness, evenness, and diversity. Predictor variables for the model were canopy gaps (presence/absence) and understory vegetation (presence/absence) as fixed factors, plot as a random factor, and sampling interval as a repeated factor. Each year was analyzed separately.

Activity-abundances of common ground beetle species were analyzed to understand species-specific responses to the disturbance treatments. The activity-abundance of a species was analyzed if ≥ 150 individuals were collected during the study. Responses were only assessed for common ground beetle species because it was clear reproductive populations were established at PNR, and these species were likely driving overall community responses. Repeated measures ANOVA tests similar to those described above were used to analyze the activity-abundance of common ground beetle species with each year analyzed separately using SAS software (SAS Institute 2016).

Indicator species analyses (ISA) were performed to determine if any ground beetle species was associated with canopy gap or understory vegetation disturbance treatments during the study. ISA identifies species that are indicative of a particular habitat or environmental condition based on their abundance and frequency in treatments possessing the characteristic of interest (Dufrêne and Legendre 1997, McCune and Grace 2002). Ground beetle species were included in the analyses if they were present in at least 15% of observations (32 traps) and ≥ 40 individuals were collected. Indicator values were calculated and tested for significance using a Monte Carlo permutation procedure. ISA analyses were conducted using PC-ORD software (McCune and Mefford 2006). ISA provided a quantitative means for categorizing species based on habitat affinity. Spearman rank correlations were used to examine the relationship between the activity-abundances of ground beetle species identified as indicators and percentage canopy openness or percentage cover of understory vegetation using SAS software (SAS Institute 2016).

Multi-response permutation procedures (MRPP) were conducted to test for differences in ground beetle species composition between canopy and understory vegetation disturbance treatments. This procedure is a nonparametric method that tests for differences between *a priori* groups through calculation of a distance matrix (McCune and Grace 2002). Ground beetle assemblages in canopy and understory vegetation disturbance treatments were visualized using non-metric multidimensional scaling (NMDS) (McCune and Grace 2002; McCune and Mefford 2006). NMDS ordinations were conducted with Sørensen’s distance measure using two dimensions, 500 iterations, 500 runs of real data, and 50 runs for the Monte Carlo test. Each year was analyzed separately. MRPP analyses and NMDS ordinations were conducted using PC-ORD software (McCune and Mefford 2006).

For each year, activity-abundances of species categorized as either macropterous or brachypterous were pooled to get total activity-abundance for each dispersal type per trap per sampling interval. Additionally, average ground beetle body length was calculated per trap per sampling interval. Ranked activity-abundance of macropterous and brachypterous ground beetles as well as average ground beetle body size were compared between canopy gap and understory vegetation disturbance treatments using similar repeated measures ANOVA tests as described above using SAS software (SAS Institute 2016). Each year was analyzed separately. Spearman rank correlations was used to further examine the relationship between the activity-abundances of macropterous and brachypterous ground beetles and average ground beetle body length with percentage canopy openness and percentage cover of understory vegetation using SAS software (SAS Institute 2016).

Repeated measure ANOVA tests were used to compare the change in canopy and understory vegetation treatments over the three-year study. Response variables were percentage canopy openness, percentage cover of understory vegetation, and average height of understory vegetation. Again, each year was analyzed separately. Logistic regression analyses with maximum likelihood estimates were conducted to compare canopy decline, using the 1-5 rating scale, of girdled trees over time. Separate analyses were conducted to compare differences between tree species, and between ring- and diffuse-porous trees.

**Results**

A total of 4,640 individuals comprising 30 genera and 59 species were collected via pitfall traps during the growing seasons of 2013-2015 (Table 5.1). Rarefaction analyses and first-order jackknife estimates suggested that the sampling intensity was sufficient to collect over 80% of the ground beetle species present at the study site. In 2013, 46 species were collected and 57 species were estimated to be present; in 2014, 48 species were collected and 55 species were estimated to be present; in 2015, 49 species were collected and 59 species were estimated to be present. The most abundant species (≥ 150 total individuals collected) were *Carabus goryi* Dejean (14.9% of total individuals collected), *Platynus angustatus* Dejean (10.0%), *Pterostichus stygicus* (Say) (8.1%), *Cyclotrachelus fucatus* (Freitag) (8.0%), *Chlaenius emarginatus* Say (7.9%), *Cyclotrachelus sigillatus* (Say) (7.2%), *Pterostichus adoxus* (Say) (5.6%), *Sphaeroderus stenostomus lecontei* Dejean (4.9%), *Dicaelus teter* Bonelli (4.2%) and *Pterostichus lachrymosus* (Newman) (3.8%). Thirteen species were uncommon and collected as singletons (eight species) or doubletons (five species) (Table 5.1).

Ground beetle species diversity

Ground beetle species richness, evenness, diversity and total activity-abundance were similar in all experimental units prior to treatment implementation (*P* = 0.659-0.998) (Table 5.2). Because no pre-treatment differences were detected, ground beetle activity-abundance, species richness, evenness, and diversity were pooled over the growing season for each trap in 2013 and included as a covariate in the corresponding repeated measures ANCOVA tests for 2014 and 2015 to control for pre-treatment ground beetle assemblages.

Following treatment implementation in 2014, ground beetle species evenness decreased in understory vegetation removal treatments compared to undisturbed understory treatments (*F*1,20 = 4.43, *P* = 0.048) (Table 5.2). However, ground beetle species richness, diversity and total activity-abundance were not affected by understory vegetation disturbance in 2014 (*P* = 0.641-0.951), and canopy gap treatments did not affect ground beetle assemblages (*P* = 0.111-0.823). In 2015, ground beetle species evenness (*F*1,20 = 4.42, *P* = 0.045) and diversity (Shannon Index: *F*1,20 = 4.78, *P* = 0.037; Simpson Index: *F*1,20 = 5.40, *P* = 0.028) was higher in canopy gaps than in closed canopy treatments, but species richness and total activity-abundance were not affected (Table 5.2). Differences in ground beetle species diversity between canopy gap and closed canopy treatments was greatest early and late in the growing season, but was not significant during mid-season (Fig. 5.2). No treatment interactions were detected in either year (Table 5.2).

Activity-abundances of the 10 most common ground beetle species were similar in all plots prior to treatment implementation (*P* = 0.082-0.994) (Table 5.3). Because no pre-treatment differences were detected, the activity-abundance of each species was pooled separately over the growing season for each trap in 2013, and used as a covariate in the corresponding repeated measures ANCOVA tests for 2014 and 2015. *Carabus goryi*, the most common species collected, was more abundant in understory vegetation removal treatments in 2014 (*F*1,20 = 4.39, *P* = 0.045) and 2015 (*F*1,20 = 7.33, *P* = 0.013). *Dicaelus teter* was the only other species to be affected by understory disturbance, and activity-abundance was higher in understory vegetation removal treatments in 2015 (*F*1,20 = 4.41, *P* = 0.048). In 2015, activity-abundance of *D. teter* was lower in canopy gaps than in closed canopy treatments (*F*1,20 = 5.38, *P* = 0.028). Activity-abundance of *P. stygicus* was higher in canopy gaps than in closed canopy treatments in 2014 (*F*1,20 = 8.84, *P* = 0.006), while *C. emarginatus* (*F*1,20 = 7.36, *P* = 0.013) and *C. sigillatus* (*F*1,20 = 4.19, *P* = 0.050) increased in canopy gaps in 2015 (Table 5.3).

The interaction between canopy gap and understory vegetation removal treatments affected the activity-abundances of several ground beetle species (Table 5.3). In 2014, activity-abundances of *C. sigillatus* (*F*1,20 = 6.22, *P* = 0.019) and *P. lachrymosus* (*F*1,20 = 6.01, *P* = 0.021) were lowest in closed canopy + understory vegetation removal treatments and canopy gap + undisturbed understory vegetation treatments. Conversely, *D. teter* was marginally more abundant in closed canopy + understory vegetation removal treatments and canopy gap + undisturbed understory vegetation treatments (*F*1,20 = 4.10, *P* = 0.053). In 2015, *P. stygicus* was more abundant in canopy gap + undisturbed understory vegetation treatments than in other treatment combinations (*F*1,20 = 7.96, *P* = 0.009). Activity-abundance of *P. angustatus* was lower in closed canopy + undisturbed understory vegetation treatments than in other treatment combinations in 2014 (*F*1,20 = 5.44, *P* = 0.029), and highest in closed canopy + understory vegetation removal treatments and canopy gap + undisturbed understory vegetation treatments in 2015 (*F*1,20 = 11.9, *P* = 0.001). No significant treatments effects were detected for *C. fucatus*, *P. adoxus* and *S. s. lecontei* (Table 5.3).

Ground beetle species composition

A strong seasonal effect on ground beetle species composition was detected during each year of the study (MRPP: *P* < 0.001 for all years). Therefore, separate analyses were conducted for each sampling interval in 2013, 2014 and 2015. In 2013, ground beetle species composition was similar in all undisturbed experimental plots during every sampling interval (*P* = 0.137-0.989). In 2014 and 2015, the strength of treatment effects on species composition varied over the growing season. In 2014, ground beetle species composition differed between understory vegetation removal and undisturbed understory vegetation treatments from late June through early July immediately following treatment implementation (MRPP: *P* = 0.045), but was similar for all other sampling intervals (*P* = 0.124-0.433). Species composition differed between canopy gap and closed canopy treatments from late August through early September (MRPP: *P* = 0.015), but was similar for all other intervals (*P* = 0.176-0.989). In 2015, ground beetle species composition differed between canopy gap and closed canopy treatments from late May through early June (MRPP: *P* = 0.043) and marginally differed during the last two sampling intervals in late July through mid-August (MRPP: *P* = 0.075; *P* = 0.078). Species composition of understory vegetation removal and undisturbed understory vegetation treatments differed marginally during early August (MRPP: *P* = 0.058), but all other sampling intervals were similar (*P* = 0.147-0.711).

When species composition was analyzed by treatment combination, ground beetle assemblages were similar in all undisturbed experimental units during every sampling interval in 2013 (*P* = 0.160-0.978). In 2014 and 2015, the strength of treatment effects on ground beetle species composition varied over the growing season each year, similar to the effects of each individual treatment. In 2014, ground beetle species composition differed between closed canopy + undisturbed understory vegetation treatments and closed canopy + understory vegetation removed treatments (MRPP: *P* = 0.020) in early to mid-June, but all other treatment combinations were similar (MRPP: *P* = 0.568). During early to mid-July, species composition differed between treatment combinations (Fig. 5.3A; 1-2 July to 15-17 July 2014; 2 dimensions, final stress = 3.47; axis 1 *R*2 = 33.7%, axis 2 *R*2 = 37.7%; MRPP: *P* = 0.042), with closed canopy + undisturbed understory vegetation treatments differing from closed canopy + understory vegetation removal treatments (MRPP: *P* = 0.029) and canopy gaps + understory vegetation removed treatments (MRPP: *P* = 0.038), which also differed from each other (MRPP: *P* = 0.008). Ground beetle species composition was highly variable within canopy gap treatments, especially canopy gaps + undisturbed understory vegetation treatments. Species composition was more similar between closed canopy + undisturbed understory vegetation treatments. These patterns were evident in the clustering of experimental units within the treatments (Fig. 5.3A). Closed canopy + undisturbed understory vegetation treatments differed from canopy gaps + understory vegetation removal treatments during mid to late August (MRPP: *P* = 0.041) and late August to early September (MRPP: *P* = 0.002).

In 2015, ground beetle species composition differed between closed canopy + undisturbed understory vegetation treatments and canopy gaps + undisturbed understory vegetation treatments during late May to early June (MRPP: *P* = 0.039). During late July through early August, species composition differed in canopy gaps + undisturbed understory vegetation treatments and closed canopy + understory vegetation removal treatments (MRPP: *P* = 0.035). Ground beetle species composition in canopy gaps + undisturbed understory vegetation treatments also differed from closed canopy + undisturbed understory vegetation treatments (MRPP: *P* = 0.027), closed canopy + understory vegetation removal treatments (MRPP: *P* = 0.017), and canopy gaps + understory vegetation removal treatments (MRPP: *P* = 0.043) during early to mid-August (Fig. 5.3B; 5-6 August to 17-18 August 2015; 2 dimensions, final stress = 4.14; axis 1 *R*2 = 42.0%, axis 2 *R*2 = 33.8%;). Ground beetle species composition was variable, but the magnitude of variation was similar for all canopy and understory treatment combinations (Fig. 5.3B).

Several species were identified as indicators of canopy treatments and understory vegetation treatments in 2014 and 2015 (Table 5.4). Eight species were found to be good indicators of canopy gap treatments, while only three were considered indicators of closed canopy treatments. Similarly, nine species were indicative of understory vegetation removal treatments, while only four were considered indicators of undisturbed understory vegetation. Over half of the species identified as indicators of canopy or understory treatments were also correlated with canopy openness or understory vegetation cover, although none of these relationships were very strong (Table 5.4). Three ground beetle species, *C. fucatus*, *P. lachrymosus* and *S. s. lecontei*, were considered indicators of closed canopy and/or undisturbed understory vegetation treatments. Interestingly, five species were found to be good indicators of canopy gap and understory vegetation removal treatments, including *C. emarginatus*, *Cyclotrachelus sodalis sodalis* (LeConte), *P. angustatus*, *Platynus hypolithos* (Say), and *P. adoxus*. The four species that were identified as indicators of undisturbed understory vegetation were also found to be indicators of canopy gap or closed canopy treatments, often during the same year. *Carabus goryi*, the most abundant species collected, was identified as an indicator of understory vegetation removal in 2014 and 2015 (Table 5.4).

Ground beetle dispersal

The activity-abundance of macropterous and brachypterous ground beetles was similar in all experimental plots prior to treatment implementation in 2013 (*P* = 0.392-0.711) (Table 5.5). Because no pre-treatment differences were detected, the activity-abundances of macropterous and brachypterous beetles were pooled over the growing season for each trap in 2013, and included as a covariate in the corresponding repeated measures ANCOVA tests for 2014 and 2015. In 2015, the activity-abundance of macropterous beetles was higher in canopy gaps than in closed canopy treatments (Fig. 5.4; *F*1,20 = 7.32, *P* = 0.011) and was positively correlated with percentage canopy openness (*r2* = 0.46, *P* = 0.008). In 2014, the activity-abundance of brachypterous beetles was marginally higher in canopy gaps than in closed canopy treatments (*P* = 0.075), but no other treatment effects were detected (*P* = 0.551-0.678) (Table 5.5).

Average ground beetle body length was similar in all experimental units prior to treatment implementation in 2013 (*P* = 0.215-0.517) (Table 5.6). Average body length was pooled over the growing season for total, female and male ground beetles in 2013 and used as a covariate in the corresponding repeated measures ANCOVA tests for 2014 and 2015. Following treatment implementation in 2014, average body length of all ground beetles decreased in canopy gap treatments (*F*1,20 = 5.94, *P* = 0.023) and was negatively correlated with canopy openness (*r2* = ‒0.57, *P* < 0.001). Average body length of female ground beetles decreased in canopy gap treatments relative to closed canopy treatments (*F*1,20 = 4.76, *P* = 0.041), but only a marginal negative relationship was detected with percentage canopy openness (*r2* = ‒0.32, *P* = 0.070). Additionally, female body length increased in understory vegetation removal treatments (*F*1,20 = 4.22, *P* = 0.049) and was negatively correlated to percentage cover of understory vegetation (*r2* = ‒0.52, *P* = 0.002). Length of male ground beetles was negatively correlated to percentage canopy openness (*r2* = ‒0.48, *P* = 0.004), and males were larger in closed canopy + undisturbed understory vegetation treatments and closed canopy + understory vegetation removal treatments than in other treatment combinations (*F*1,20 = 4.64, *P* = 0.043). No treatment effects were detected in 2015 (*P* = 0.481-0.895) (Table 5.6).

Temporal changes in disturbance treatments

Percentage canopy openness increased over time in canopy gap treatments following tree girdling compared to undisturbed closed canopy forest (Fig. 5.5; *F*1,21 = 48.5, *P* < 0.001). Percentage cover of understory vegetation was lower in removal treatments than in undisturbed understory vegetation treatments (*F*1,27 = 6.67, *P* = 0.015). However, vegetation cover increased over time as plants grew back in the understory (Fig. 5.6; *F*1,162 = 8.49, *P* < 0.001), and plant growth was greater in canopy gap treatments (*F*1,27 = 5.19, *P* = 0.030). Percentage cover of understory vegetation was higher overall in canopy gap treatments (*F*1,27 = 6.01, *P* = 0.021), but less variable in closed canopy treatments (Fig. 5.6). Understory vegetation height increased over time in all treatments (*F*6,126 = 13.9, *P* < 0.001), but was lower in vegetation removal treatments than in undisturbed understory vegetation treatments (*F*1,27 = 4.81, *P* = 0.037). Height of understory vegetation was greater in canopy gap treatments than in closed canopy treatments (*F*1,27 = 5.26, *P* = 0.029).

All trees had a canopy rating of 1 before girdling, which corresponded to a full healthy canopy. After trees were girdled, the canopy of oaks and other species declined more rapidly than the canopy of maples and poplars (Fig. 5.7A; *χ*2 = 62.6, *P* < 0.001; Time *χ*2 = 451.4, *P* < 0.001). As predicted, the canopies of ring-porous species (oaks, ash, cherry, hickory and elm) declined more rapidly following girdling, whereas diffuse-porous species (maples, poplars, basswood, beech and birch) declined more slowly (Fig. 5.7B; *χ*2 = 175.2, *P* < 0.001; Time *χ*2 = 473.7, *P* < 0.001).

**Discussion**

A diverse ground beetle community was present with a total of 59 species collected over the three year study. Prior to treatment implementation, assemblages were similar in all experimental plots. The formation of light gaps in the forest canopy had a greater impact on ground beetle assemblages than disturbance to ground-level understory vegetation, but the effects of the canopy and vegetation disturbances were inconsistent over the two years. Perhaps these patterns can be explained by temporal changes in the effects of the disturbance treatments over the course of the study.

Trade-offs in traits for competition and colonization ability is one potential mechanism that could produce high species diversity at intermediate levels of disturbance (Hastings 1980, Tilman 1994, Cadotte 2007, Fox 2013a). Early and late successional species are predicted to coexist in an environment that has experienced intermediate levels of disturbance, whereas good competitors dominate in undisturbed habitats and good colonizers are more capable of exploiting highly disturbed areas (Levin and Paine 1974). However, this study provided weak support for the predictions of the competition-colonization trade-off model as a mechanism maintaining species diversity in ground-beetle assemblages.

No definitive support was found for the first prediction that ground beetle species diversity would be highest in plots that received only one disturbance, either canopy or understory vegetation disturbance. Ground beetle species diversity was not affected in 2014 following treatment implementation, but was higher in canopy gaps than in closed canopy treatments in 2015. However, when patterns were analyzed over the sampling season, species diversity increased in canopy gaps but only during early and late season. When diversity was pooled over the growing season in 2014 and in 2015, it tended to be higher in combined canopy and understory disturbance treatments, but this pattern was not significant.

Although species diversity was minimally affected by the treatments, nine ground beetle species were associated with canopy and understory treatments, as determined by indicator and correlation analyses. Five species, *A. fidele*, *C. emarginatus*, *C. fucatus*, *C. sigillatus* and *P. lachrymosus*, were identified as indicators of undisturbed ground-level vegetation and were positively correlated with understory vegetation cover. Only one species, *P. tristis*, was associated with understory vegetation removal. Four ground beetle species, *C. emarginatus*, *C. sodalis*, *P. angustatus* and *P. adoxus*, were associated with canopy gaps and positively correlated with canopy openness, but no species were strongly associated with closed canopy treatments. The most common species, *C. goryi*, was consistently more abundant in treatments where understory vegetation was removed, and was considered a good indicator for this treatment, but was weakly negatively correlated with vegetation cover. *Carabus goryi* is commonly found in moist deciduous forests with a thick leaf litter layer (Rykken et al. 1997, Larochelle and Larivière 2003, Jennings and Tallamy 2006). It is unclear why this species responded so strongly to vegetation removal, but it could relate to microclimate factors, such as temperature or moisture (Thiele 1977), or prey availability (Halme and Niemela 1993, Taboada et al. 2006). Overall, there were no clear trends in species’ responses to the different treatment combinations, and some species (*D. teter*, *P. angustatus*, *P. stygicus*) were most abundant in treatment combinations where others species (*C. sigillatus*, *P. lachrymosus*) were least abundant.

The strength of canopy and understory treatment effects on ground beetle species composition varied significantly over the growing season each year. Therefore, some support for the second prediction was found, that ground beetle species composition would change between undisturbed closed canopy forest and the most disturbed treatments. The dominant factor driving these responses was clearly the formation of canopy gaps. Understory disturbance altered species composition immediately following vegetation removal in 2014, but otherwise had no effects. Canopy disturbance had a greater impact overall on ground beetle species composition, but either early or late in the growing season. Similarly, the effects of treatment combinations on species composition changed over the growing season each year as well. In 2014, understory removal altered species composition during early season. During mid- and late season, composition differed between undisturbed closed canopy forest relative to other treatment combinations, with the greatest difference between combined canopy and understory disturbance treatments during late season. In 2015, species composition differed between undisturbed treatments and canopy gaps during early in the growing season. During late season, ground beetle species composition in undisturbed closed canopy treatments differed from all other treatment combinations, while those treatments with canopy gaps were more similar in composition.

No support was found for the third prediction, that the activity-abundance of macropterous ground beetles would increase in combined canopy and understory disturbance treatments compared to undisturbed forest, or the fourth prediction, that the body length of ground beetles would decrease. Activity-abundance of macropterous ground beetles, those individuals capable of flight, increased in canopy gap treatments in 2015, but not in 2014, and not in combined canopy and understory disturbance treatments. This finding suggests that macropterous ground beetles responded to openings in the forest canopy, possibly the increased light availability on the forest floor, as opposed to the combination of canopy and understory disturbance. However, abundances of brachypterous ground beetles that have limited dispersal ability because they are incapable of flight, were not affected by canopy or understory disturbance. Perhaps the size of the treatments (30 × 30 m) were too large for them to emigrate, as movement of forest-inhabiting ground beetles was generally limited within a 48 hr activity period, and/or the removal of understory vegetation reduced their movement (see Chapters 6-7). The response of the forest understory in gaps may have facilitated the movement of brachypterous beetles that disperse by walking or running in canopy gap treatments, as vegetation cover and structure has been shown to influence ground beetle assemblages (Niemelä et al. 1992, Latty et al. 2006, Thomas et al. 2006, Pakeman and Stockan 2014). The presence of both macropterous and brachypterous beetles in canopy gap treatments may explain why ground beetle species diversity was higher there.

The canopy gap treatment had the largest effect on ground beetle body length. Individuals collected in canopy gap treatments were smaller on average in 2014, but this pattern was not observed in 2015. There was also no difference in the most disturbed gap + vegetation removal treatment, which suggests that there was no additional effect of understory disturbance. Patterns in ground beetle body size were not entirely consistent between the sexes because females were affected by each treatment individually, whereas males were affected by the interaction between the two disturbance treatments. On average, male and female individuals were larger in closed canopy treatments, which is consistent with other studies that have found increased in ground beetle size associated with increased habitat heterogeneity and stability (Ings and Hartley 1999, Ribera et al. 2001, Weller and Ganzhorn 2004, Šerić Jelaska et al. 2011).

Canopy and ground-level understory vegetation disturbance treatments had inconsistent effects on ground beetle assemblages over the three-year study. Because the treatments were only implemented once in June 2014, disturbance intensity, but not frequency, was manipulated to investigate the impacts of canopy and understory disturbance. Differences in percentage cover of understory vegetation between undisturbed and removal treatments was greatest initially following implementation, but percentage cover of understory vegetation became more similar between treatments over time in 2014 as plant growth recovered. No difference in percentage cover of understory vegetation was detected between treatments in 2015, but vegetation height was still greater in undisturbed treatments. 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, 1988a,b), but these studies did not remove the understory layer first. Increased light and available growing space from the combined creation of canopy gaps and removal of vegetation resulted in rapid growth of the forest understory to levels of cover higher than pre-treatment measurements.

The opposite temporal pattern was observed for canopy gap treatments because differences in percentage canopy openness between gap and closed canopy treatments increased over time. Girdled trees expressed species-specific rates of canopy decline that was largely associated with differences in their vasculature structure, as ring-porous (oak, ash and hickory) declined faster than diffuse-porous (maple and poplar) species (Wiant and Walker 1961). Therefore, the magnitude effects of understory vegetation removal decreased as plants grew in, while the effects of gaps increased as tree canopies declined over time.

There was some evidence that ground beetles responded to the inverse temporal changes in the effects of canopy and ground-level understory vegetation disturbance, because different effects of the individual treatments were observed over the three-year study. Although the impacts of understory vegetation removal alone were minimal, when they were detected it was usually immediately after treatment implementation in 2014, which was when the effect size of this treatment was greatest. Removal of understory vegetation decreased ground beetle assemblage evenness in 2014, suggesting this type and intensity of disturbance increased the dominance of some species, such as *C. goryi*, which was identified consistently as an indicator of vegetation removal. Additionally, vegetation removal altered community composition early in the growing season in 2014. Consistent with these temporal changes, canopy gaps had a greater effect on ground beetle assemblages in 2015 once a greater percentage of the girdled trees had declined. Ground beetle species evenness and diversity increased in canopy gap treatments in 2015, and gaps were driving the majority of changes in species composition. Canopy and understory disturbances interacted to affect ground beetle assemblages, through either the accelerated regrowth of vegetation in canopy gaps, as understory coverage on the forest floor, or the reduced regrowth of vegetation in closed canopy treatments.

Although this study provided no support for the competition-colonization trade-off model as a mechanism maintaining ground beetle species diversity, at least for the range of disturbance intensities investigated, the results suggest that canopy disturbance is an important driver of assemblage structure for ground beetles in forest ecosystems, as have other studies (Niemelä et al. 1993, Pearce et al. 2003, Gandhi et al. 2008, Silverman et al. 2008, Gandhi et al. 2014, Perry and Herms 2016a,b). Because the effects of canopy and ground-level understory vegetation disturbances were isolated, the relative importance of each disturbance was evaluated as a driving factor shaping patterns in ground beetle assemblage structure and composition. Canopy disturbance alone had a greater impact on ground beetle assemblages than any other treatment or treatment combination, possibly because the understory regenerated quickly following removal. Therefore, the high intensity disturbance treatment was unable to be tested as intended. However, these findings are consistent with other studies that have documented the effects of canopy disturbance on ground beetles.

Understanding the effects of natural and anthropogenic disturbances on biodiversity has clear conservation and management implications. Many ground beetle species have a high affinity for specific microclimate factors, and therefore have been used as environmental indicators of forest management and succession, land-use change, as well as other disturbances (Eyre et al. 1989, Butterfield et al. 1995, Heliölä et al. 2001, Irmler 2003, Rainio and Niemelä 2003, Pearce and Venier 2006, Pohl et al. 2007, Schwerk and Szysyko 2007, Karen et al. 2008, Baker et al. 2009, McCravy and Lundgren 2011, Lange et al. 2014, Leslie et al. 2014). Ground beetles are primarily predatory in forest ecosystems, feeding on a variety of invertebrate prey (Thiele 1977, Lövei and Sunderland 1996), and it is likely that changes in the forest floor microclimate also impact distributions of their prey.

A key concept of the competition-colonization trade-off model not directly evaluated in the study was competition between ground beetle species. Investigating competition in the field has been historically challenging (Shorrocks et al. 1984), especially for burrowing and/or nocturnal species such as ground beetles. Resource partitioning of prey taxa was evaluated for 13 ground beetle species via molecular gut content analysis. Resource overlap between species was high, and largely unaffected by the disturbance treatments (Appendix A, Table 1-2). However, Collembola were detected in the crops of a higher percentage of ground beetles collected in canopy gaps compared to closed canopy treatments (Appendix A, Table 2), where Collembola were also found to be more abundant (see Chapter 8). Land slugs and snails as well as rove beetles were identified as key prey for ground beetles (Appendix A, Table 1), and the activity-abundance of these taxa increased in canopy gaps along with ground beetles (see Chapter 8).

Understanding the mechanisms that promote and maintain species diversity has broad implications for biodiversity conservation and sustainable management of ecosystems on a global scale. The role of natural and anthropogenic disturbances in this process is of particular importance as humans degrade natural habitat (Wilcove et al. 1998) and climate change alters weather patterns (IPCC 2014). These results suggest canopy disturbance is a driver of ground beetle assemblage structure and composition in forest ecosystems. Changes in species diversity and composition in response to forest disturbances that cause tree mortality have implications for ecosystem services such as decomposition and nutrient cycling that are provided by ground-dwelling arthropods such as ground beetles. Therefore, understanding these impacts on biodiversity is critical for fostering sustainable forest management strategies in an era of anthropogenic change.

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