RESEARCH ARTICLE

Localized Effects of Tornado Damage on Ground Beetle Communities and Vegetation in a Forested Preserve

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Natural Areas Journal 37:489–496

ABSTRACT: Natural disturbances, such as tornados, can alter local habitat conditions and have the potential to affect animal communities in preserves. When such disturbances occur in natural areas, understanding these effects can help land managers develop responses and restoration actions following a disturbance. The effects of tornado and other strong wind damage on insect communities is poorly known even though insects comprise the majority of macroscopic diversity in terrestrial systems and are important contributors to ecosystem function. We examined ground beetle (Coleoptera: Carabidae) communities in spring, summer, and fall following an EF-4 tornado that struck a forested preserve in Illinois. We compared the communities and vegetation structure in plots that were affected or unaffected by the tornado. Sites within the tornado's path had reduced canopy cover but increased ground-level vegetation throughout the growing season. Beetle abundance and species richness were unaffected, but Shannon diversity was significantly higher in fall in areas affected by the tornado. Beetle community composition was shifted by tornado effects only in the spring, and tornado-affected areas contained 13 species that were not present in unaffected sites. These sites also contained more seed-eating or omnivorous species and small predators, in contrast to unaffected sites that were dominated by large predatory species. Our results indicate that tornado damage may increase biodiversity in small natural areas by increasing habitat heterogeneity. Land managers may not want to restore tornado-damaged sites to pre-disturbance conditions if maximizing biodiversity is a goal of the preserve.

Index terms: arthropod, canopy, Carabidae, disturbance, Illinois

INTRODUCTION

Natural disturbances, such as fires, hurricanes, and tornados, have obvious effects on vegetation that are well documented (e.g., Liu et al. 1997; Peterson and Rebertus 1997; Peterson 2000; Nelson et al. 2008). Hurricanes and fires often result in widespread destruction, but tornados tend to be damaging on a much smaller, localized scale. In forest stands, tornados alter vegetation and habitat characteristics, and result in fragmentation (Skłodowski and Garbalińska 2011). This generally creates a more heterogeneous environment than had existed previously, with the specific areas affected and unaffected differing greatly in their structure and possibly community composition. For example, shade-intolerant plant species that did not fare well under a canopy of large trees are likely to thrive in areas where a tornado has removed the canopy.

Vegetation structure differences following a tornado or other wind-caused disturbance are very visible, and much research has focused on these effects (Mitchell 2013). These vegetation changes will also alter habitat suitability for consumers, but these effects are poorly known (Prather and Smith 2003; Wolff et al. 2009; McGlinn et al. 2010). This is especially true for arthropods, even though they represent the majority of total macroscopic biodiversity in ecosystems (Maleque et al. 2009) and play important roles in ecosystem processes and services such as nutrient cycling, facilitation of decomposition, and controlling agriculturally noxious arthropod species (McCravy and Lundgren 2011). Tornados and similar small-scale windthrow disturbances reduce canopy cover and may expose soil or litter to sunlight, causing drier conditions and higher temperatures at the ground layer (Bouget and Duelli 2004), which may alter the habitat suitability for ground-dwelling arthropods. Documenting arthropod community changes following a natural disturbance, such as a tornado (Skłodowski and Garbalińska 2011), can provide useful information on how species use microhabitats within a natural area. It may also provide an index for the biodiversity value of different habitat types within a reserve, assist in management decisions where the goal is to maintain high biodiversity (Maleque et al. 2009), and guide management and cleanup actions following a natural disturbance.

One potentially important arthropod group is the family Carabidae (Coleoptera), the ground and tiger beetles (hereafter, "ground beetles"). These insects may be ideal indicators of ecosystem health and biodiversity because of their high richness, morphological variation, and diverse diets (Thiele 1977; Barsoum et al. 2013). Ground beetles play important roles in both arthropod and seed predation, potentially contributing to both insect and weed pest control (Hance

1987; Lang et al. 1999; Lang 2003; Honek et al. 2007; Lundgren 2009; Gaines and Gratton 2010; McCravy and Lundgren 2011). Ground beetle community studies in forest gaps resulting from windthrow have documented shifts in community structure, with higher abundance, richness, or diversity due in part to an influx of seed-eating, open habitat species (Bouget and Duelli 2004; Skłodowski and Garbalińska 2007; Lee et al. 2017). In this way, tornado damage may shift both vegetation and ground beetle communities to an earlier successional stage. Niemelä and Halme (1992) found higher ground beetle species richness in early successional habitats than in forests, and in particular, more rare species (i.e., species that occurred in very low abundances when detected). From this, it may be hypothesized that tornado damage will increase local abundance and species richness in the short term, until habitats develop back into forest.

In this study, we surveyed ground beetles and measured vegetation structure following a tornado event. By sampling in both tornado-affected and -unaffected forest habitats, we are able to document habitat and beetle community changes resulting from this localized natural disturbance.

METHODS

Study Sites

This study was performed at Skare Park (Flagg-Rochelle Community Park District, Ogle County, Illinois) following an EF-4 tornado event on 9 April 2015 (the "Fairdale tornado") (Prevatt et al. 2015). Skare Park is a preserve consisting mostly of riparian forest dominated by oaks (*Quercus* sp.), sugar maple (*Acer saccharum* Marshall), boxelder (*Acer negundo* L.), and hackberry (*Celtis occidentalis* L.), with small grasslands interspersed. The tornado passed through the site and primarily affected forested areas, creating a path of destruction approximately 100 m wide that passed completely through the preserve. We chose five sites within the tornado's path and five sites at least 50 m outside the path in undamaged forest to sample ground beetles and vegetation structure. We avoided grassland areas of the preserve and focused on forested regions. We do not have detailed forest composition data for each site prior to the damage and, thus, cannot verify that the habitats or ground beetle communities in damaged and undamaged sites were initially equivalent. However, the path of the tornado did not change as it moved though the preserve, and damaged tree trunks indicate that affected sites were similarly forested, so we are confident that the presence or absence of tornado damage is the primary difference between these sites.

Sampling and Identification

At each site, we established a 15-m transect with four unbaited pitfall traps spaced 5 m apart. Each trap consisted of a plastic cup (12 cm tall, 24-cm circumference) buried in the ground so that the rim was flush with ground level and half-filled with 50% nontoxic ethylene glycol to preserve the arthropods while minimizing risks to other wildlife (McCravy and Willand 2007). Sampling periods lasted one week each and were carried out in spring (27 May–2 June), summer (4–11 August), and fall (20–27 September) 2015, corresponding to 7, 17, and 24 weeks after the tornado. These sampling dates allowed us to survey beetles across an entire growing season to detect phenological community changes. During each session, traps were checked, emptied, and reset three times during the week (opened Sunday, checked Tuesday, Thursday, and Sunday). Collected insects were brought to the laboratory where ground beetles were sorted and identified to species or morphospecies using keys (Arnett and Thomas 2000; Ciegler 2000; Bousquet 2010).

We also measured vegetation profile and canopy cover at each transect during each trapping session. For vegetation profile, we used a graduated rod placed at five points along the transect and counted vegetation touches at five heights (0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, 2–3 m). This allowed us to determine if vegetation density at each stratum changed following tornado damage. We measured percent canopy cover above each of the four traps using a convex spherical densiometer.

Analysis

We calculated activity density (beetles per trap-day, an index of abundance), species richness, and Shannon diversity for each sampling session. These community metrics were each analyzed using linear mixed models treating tornado status, session, and their interaction as fixed factors and transect as a random factor; this design is analogous to a repeated-measures ANOVA. Linear mixed models used the nlme package (Pinheiro et al. 2015) in R 3.2.3 (R Development Core Team 2015), and fixed factors were evaluated using likelihood ratio tests, which approximate a χ^2 distribution with 1 degree of freedom for tornado and 2 degrees of freedom for session and the interaction term.

To compare community composition between tornado-affected and -unaffected areas in the different sampling sessions, we used permutational MANOVA (PERMANOVA) with the function adonis() in the R package vegan (Oksanen et al. 2016). Bray–Curtis distances were calculated using vegdist() in vegan, and the test used 9999 permutations. We visualized community similarity using nonmetric multidimensional scaling (NMDS) with the function metamds() in vegan.

We calculated the mean number of vegetation touches at each height for each transect and mean canopy cover for each transect. We used linear mixed models as above to determine if canopy cover differed between tornado-affected and -unaffected areas and if they changed over time during the study. Vegetation touches was analyzed in the same way but included height and the two- and three-way interactions with tornado damage and session.

RESULTS

We collected and identified 1221 ground beetles of 42 different species (Table 1). Activity density and species richness did not differ between tornado-affected and -unaffected areas, but these values changed significantly among sampling sessions

Table 1. Activity density of ground beetle species captured during three sampling sessions at sites affected and unaffected by tornado damage. Values are mean activity density, with standard error in parentheses.

Species	Spring		Summer		Fall	
	Tornado-affected	Tornado-unaffected	Tornado-affected	Tornado-unaffected	Tornado-affected	Tornado-unaffected
Agonum melanarium	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.007 (0.007)
Amara aenea	0 (0)	0 (0)	0.007 (0.007)	0 (0)	0 (0)	0 (0)
Amara exarata	0 (0)	0 (0)	0 (0)	0 (0)	0.065 (0.021)	0.007 (0.007)
Amara ovata	0.014 (0.014)	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)
Amphasia interstitialis	0.011 (0.011)	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0.007 (0.007)
Anisodactylus agricola	0.014 (0.009)	0.021 (0.014)	0 (0)	0.036 (0.036)	0.007 (0.007)	0.014 (0.009)
Anisodactylus sanctaecrucis	0 (0)	0 (0)	0 (0)	0 (0)	0.021 (0.021)	0 (0)
Bembidion sp. 1	0 (0)	0 (0)	0.007 (0.007)	0 (0)	0 (0)	0 (0)
Bembidion sp. 2	0 (0)	0 (0)	0 (0)	0 (0)	0.007 (0.007)	0 (0)
Bembidion sp. 3	0 (0)	0 (0)	0 (0)	0 (0)	0.014 (0.009)	0 (0)
Bembidion sp. 4	0 (0)	0 (0)	0 (0)	0 (0)	0.007 (0.007)	0 (0)
Bradycellus lugubris	0 (0)	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)
Bradycellus rupestris	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Chlaenius tricolor	0.082 (0.061)	0.029 (0.021)	0 (0)	0.148 (0.13)	0.007 (0.007)	0.043 (0.026)
Cicindela sexguttata	0.043 (0.017)	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)
Clivina fossor	0.015 (0.009)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Cratacanthus dubius	0 (0)	0 (0)	0.007 (0.007)	0.007 (0.007)	0 (0)	0 (0)
Cyclotrachelus seximpressus	0 (0)	0 (0)	0.043 (0.029)	0.406 (0.176)	0.007 (0.007)	0.03 (0.014)
Cyclotrachelus sodalis	0.007 (0.007)	0.064 (0.02)	0.05 (0.014)	0.119 (0.038)	0.022 (0.014)	0.014 (0.009)
Dicaelus elongatus	0 (0)	0 (0)	0.021 (0.014)	0.015 (0.01)	0 (0)	0.014 (0.009)
Harpalus caliginosus	0 (0)	0 (0)	0.007 (0.007)	0 (0)	0.007 (0.007)	0 (0)
Harpalus herbivagus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.007 (0.007)
Harpalus pensylvanicus	0 (0)	0.007 (0.007)	0.343 (0.19)	0.241 (0.181)	0.136 (0.127)	0.007 (0.007)
Harpalus somnulentus	0 (0)	0 (0)	0 (0)	0.007 (0.007)	0 (0)	0 (0)
Notiobia terminata	0 (0)	0 (0)	0.007 (0.007)	0.014 (0.014)	0.015 (0.009)	0 (0)
Notiophilus aeneus	0.018 (0.011)	0.014 (0.014)	0.007 (0.007)	0 (0)	0.008 (0.008)	0 (0)
Oxypselaphus pusillus	0 (0)	0 (0)	0.007 (0.007)	0 (0)	0 (0)	0 (0)
Patrobus longicornis	0 (0)	0 (0)	0 (0)	0 (0)	0.051 (0.042)	0 (0)
Platynus decens	0.028 (0.02)	0.125 (0.062)	0 (0)	0 (0)	0 (0)	0 (0)
Poecilus lucublandus	0.023 (0.015)	0.039 (0.026)	0.057 (0.057)	0.007 (0.007)	0.05 (0.042)	0 (0)
Pterostichus femoralis	0 (0)	0.007 (0.007)	0 (0)	0 (0)	0 (0)	0 (0)
Pterostichus melanarius	0.007 (0.007)	0.007 (0.007)	0.364 (0.044)	0.713 (0.299)	0.007 (0.007)	0.143 (0.143)
Pterostichus mutus	0 (0)	0.125 (0.125)	0.007 (0.007)	0.23 (0.219)	0.007 (0.007)	0.014 (0.014)

Continued

Table 1. (Cont'd).

Species	Spring		Summer		Fall	
	Tornado-affected	Tornado-unaffected	Tornado-affected	Tornado-unaffected	Tornado-affected	Tornado-unaffected
Pterostichus permundus	0 (0)	0.014 (0.014)	0.057 (0.035)	0.342 (0.271)	0.135 (0.076)	2.129 (1.558)
Pterostichus praetermissus	0 (0)	0 (0)	0.014 (0.014)	0.017 (0.017)	0 (0)	0 (0)
Pterostichus stygicus	0.018 (0.011)	0.046 (0.021)	0.35 (0.204)	1.036 (0.282)	0.153 (0.035)	0.238 (0.139)
Pterostichus tenuis luctuosis	0 (0)	0.025 (0.025)	0 (0)	0 (0)	0 (0)	0 (0)
Stenolophus ochropezus	0 (0)	0 (0)	0 (0)	0 (0)	0.007 (0.007)	0 (0)
Trichotichnus vulpeculus	0 (0)	0 (0)	0.007 (0.007)	0.008 (0.008)	0.036 (0.028)	0.201 (0.126)
Unknown Harpalinii sp.	0 (0)	0 (0)	0 (0)	0 (0)	0.014 (0.009)	0 (0)

(Figure 1A,B, Table 2). Mean activity density and richness were high in some unaffected sites due to a small number of species that reached high abundances, but these values were highly variable. There was a significant interaction effect of tornado and session on Shannon diversity due to a strong increase in diversity in tornado-damaged sites in the final sampling session only (Figure 1C).

PERMANOVA results showed that community composition differed significantly between the three sampling sessions ($F_{2,26} = 5.85$, $P < 0.0001$), indicating that different species were present in spring, summer, and fall. There was a marginally significant effect of tornado damage on ground beetle community composition ($F_{1,26} = 1.59$, $P = 0.076$), which seems to have been driven by the spring session, in which compositional differences between tornado-affected and -unaffected areas were most apparent (Figure 2).

In the habitat measures, canopy cover was significantly reduced by tornado damage; this effect continued all season even though canopy cover increased in the second and third sampling sessions (Table 2, Figure 3A). Vegetation profile was significantly affected by the interaction between height and tornado damage ($\chi^2 = 14.07$, $P = 0.007$), but not season or other interactions (all $P < 0.1$). Wald *t*-tests indicated that tornado-affected sites had significantly more vegetation in the lowest (0–0.5 m) stratum but no difference at all other heights (Figure 3B).

DISCUSSION

Natural disturbances such as tornados can cause significant localized damage in natural areas, altering habitat characteristics and potentially shifting plant and animal communities (Peterson and Rebertus 1997; Peterson 2000). Focusing on ground beetles, a potentially important taxonomic group in terrestrial ecosystems, we documented community and structural vegetation changes after a severe tornado event. We found moderate effects on beetle communities that were likely driven by changes in habitat structure. Both beetle and vegetation effects occurred throughout the growing season, up to five months after the tornado event.

There were significant changes in ground beetle communities across the growing season, with changes in abundance (activity density), species richness, and Shannon diversity between spring, summer, and fall. This reflects typical phenological turnover in which species are active in the community at a given time based on their annual schedule of emergence and breeding (Werner and Raffa 2003; Barber et al. 2017). Tornado damage did not significantly alter activity density or species richness of beetle communities, although the variation in activity density was high in unaffected sites due to some sites consistently having high beetle abundance. Shannon diversity was similar between tornado-affected and -unaffected sites in spring and summer, but in fall, communities were very different because of both an increase in diversity in affected sites and a decrease in unaffected sites. Unaffected sites tended to become dominated by a small number of species in the genus *Pterostichus* in fall, particularly *P. permundus* Say. At the same time, affected sites tended to have distinct species in the fall: 11 species were found exclusively in tornado-affected sites during the last trapping session, versus only four species exclusively in unaffected sites. Nonetheless, these differences did not result in strongly different overall community compositions, as indicated by the overlapping fall points in the NMDS (Figure 2). This is likely because the most common species were present in both types of sites, albeit at different densities.

Spring ground beetle communities, however, had different compositions due to tornado effects, which may not be surprising given that habitat differences may have been greatest shortly after the tornado struck, and vegetation recovery had only just begun. Canopy cover was greatly reduced because of a large number of trees that were knocked over, and this effect persisted throughout the growing season. The slight increase in canopy cover in summer and fall is probably because leaves had not fully expanded in spring. Full canopy recovery is expected to take more than a single season because few large

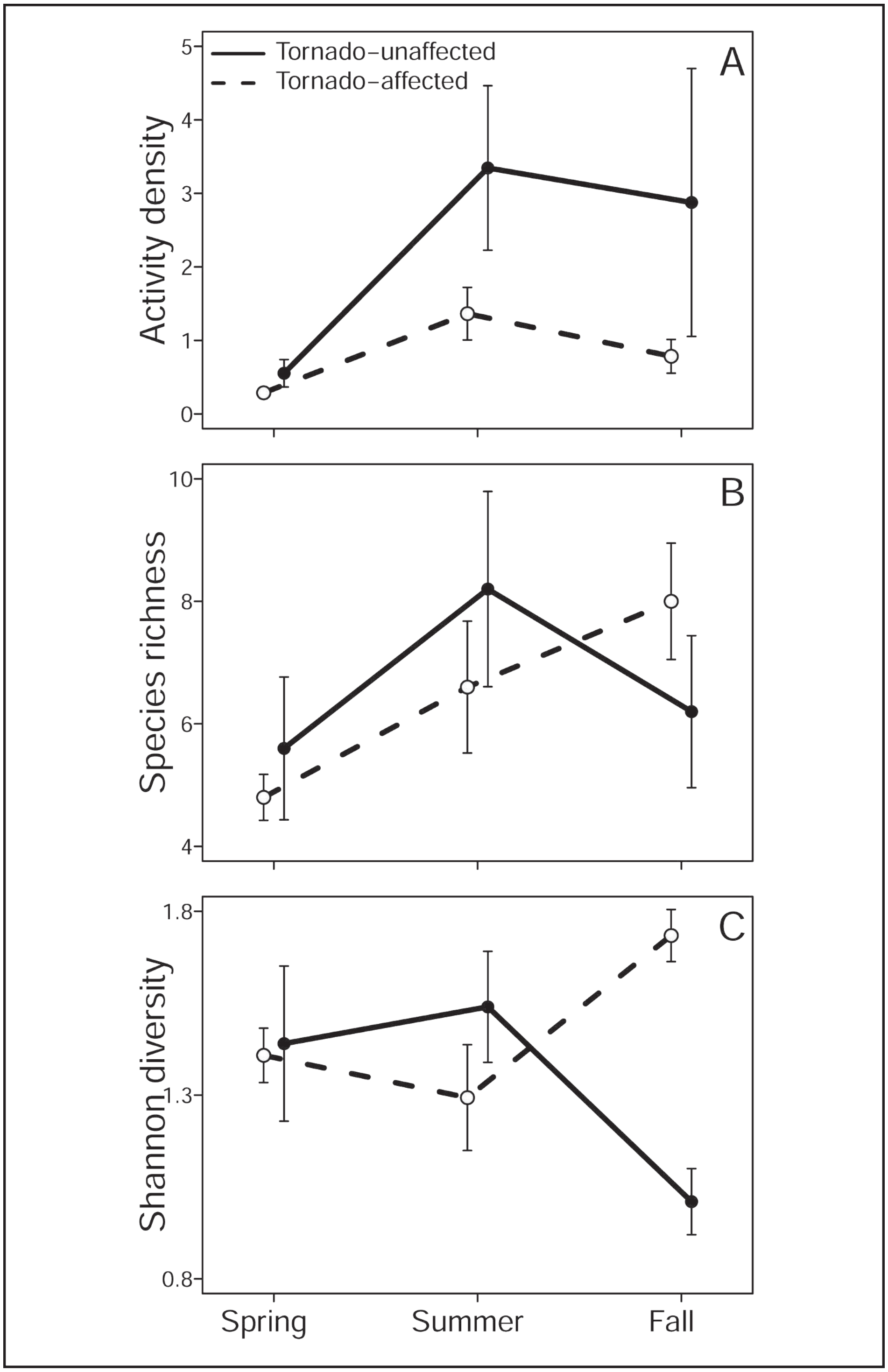

Figure 1. Ground beetle community metrics in transects affected (dashed line) or unaffected (solid line) by tornado damage. (A) activity density, the number of beetle captures per trap-day; (B) species richness; (C) Shannon diversity. Values are means ± 1 SE.

trees survived in the path of the tornado. Canopy changes had consequences for understory vegetation as well. Vegetation density was significantly increased in affected sites, likely because the opened canopy allowed greater sunlight and rapid growth of non-woody understory plants that remained shaded in unaffected sites. This effect was consistent across all sampling sessions, mirroring differences in canopy cover. Thus, although habitat differences were present in all sessions, we saw their effects on beetle communities in different ways: in shifted species composition in spring, in contrasting Shannon diversities in fall, but with no detected differences in summer. High vegetation density can bias activity density estimates if it limits ground beetle mobility and reduces capture rates (Greenslade 1964). But this does not seem to be the case here, as there was no relationship between vegetation density at the lowest (0–0.5 m) stratum and activity density across all seasons ($F_{1,28} = 0.66$, $P = 0.423$).

In some ways, these results contrast with previous surveys of ground beetle communities in forest gaps created by severe wind disturbances. Following tornado damage in a Polish forest, abundances were significantly lower and richness was higher in damaged areas than undamaged areas (Skłodowski and Garbalińska 2011); a similar reduction in abundance followed windstorm damage in sub-boreal forest in Minnesota, USA (Gandhi et al. 2008). Although activity density of beetles was consistently low in our tornado transects, there was high variability in unaffected sites. Like the Polish forest results, species richness of all arthropods also increased in windthrow-damaged areas compared to intact Swiss forest in the years following a storm (Wermelinger et al. 2017). However, increased richness is not universally seen, as demonstrated in Korean pine forests following typhoon damage where gaps had similar ground beetle abundance and richness as undamaged sites (Lee et al. 2017). Like our study, these surveys took place in the year immediately following the disturbance. Increased abundance and richness in gaps may take longer to develop as species colonize and establish robust populations over several seasons.

Examining the particular species that occurred in very different densities between affected and unaffected sites, or that occur only in one site type, may be informative to determine how tornado damage shaped these communities. Colonization of sites relies on both a beetle's ability to reach the site and its habitat preferences, because ground beetle species vary in flight ability as well as in habitat affinity. Several of the species that were present in higher densities

Table 2. **Results of generalized linear mixed models of tornado, sampling session, and their interaction effects on ground beetle community metrics and canopy cover. Fixed factors were evaluated with likelihood ratio tests.**

	Tornado		Session		Tornado × Session	
	c^2	*P*	c^2	*P*	c^2	*P*
Activity density	2.08	0.149	**25.42**	**<0.001**	0.66	0.718
Species richness	0.03	0.864	**7.15**	**0.028**	5.45	0.065
Shannon diversity	–	–	–	–	**14.28**	**<0.001**
Canopy cover	**8.64**	**0.003**	**17.17**	**<0.001**	1.34	0.512

in tornado-affected transects are capable of flight and prefer or are frequently found in open habitats, such as *Amara exarata* Dejean, *Cicindela sexguttata* Fabricius, *Harpalus pensylvanicus* Degeer, and *Poecilus lucublandus* Say (Larochelle and Lariviére 2003). In contrast, several species that prefer forested habitats were more common in the tornado-unaffected area, supporting the idea that they choose habitats with greater canopy cover. These include several *Pterostichus* species that vary in flight ability, such as *P. mutus* Say and *P. stygicus* Say. Other *Pterostichus* have been reported to reach higher abundances in grasslands than forests, such as *P. melanarius* Illiger, a European species introduced to the United States (Magura et al. 2001; Molnár et al. 2001), but this species was more common in our unaffected sites with intact forest. It is also noteworthy that the most abundant species in the study, the flightless *P. permundus*, was far more common in unaffected sites. Although it is found in a variety of habitats (Larochelle and Lariviére 2003), it may have a preference for greater canopy cover like its congeners.

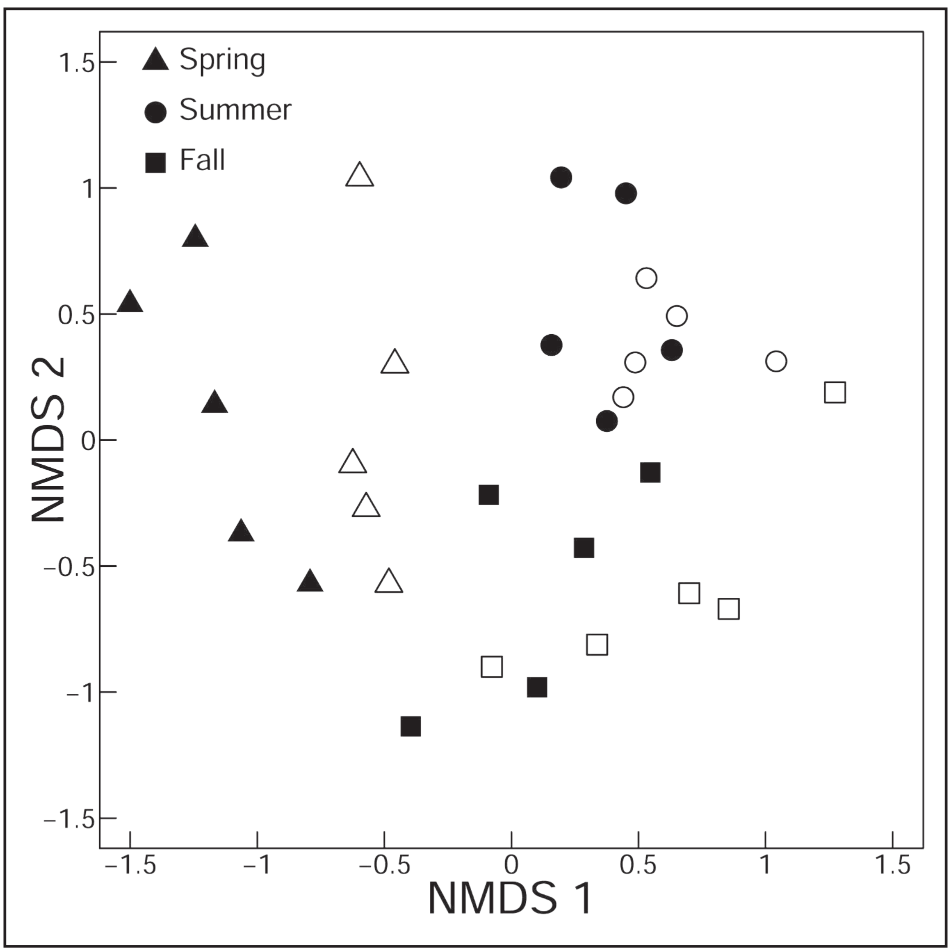

Figure 2. Nonmetric multidimensional scaling ordination of ground beetle community composition (stress = 0.189). Open symbols are tornado-affected transects, and filled symbols are tornado-unaffected.

These *Pterostichus* species, and several other species that were more abundant in unaffected sites such as *Chlaenius tricolor* Dejean, *Cyclotrachelus seximpressus* Leconte, and *C. sodalis* Leconte, are large predatory species (>12 mm average body length). In contrast, most of the predatory species that were exclusively in tornado-affected sites are small: several *Bembidion* species, *Bradycellus rupestris* Say, and *Oxypselaphus pusillus* Leconte (<10 mm body length, although the fairly large *P. lucublandus* is an exception to this pattern). Populations of large carnivorous animals are often reduced or extirpated by habitat disturbances (Estes et al. 2011), and so may be more likely to occur in late-successional habitats. The reduction in large predatory ground beetles that we document here, as well as increases in seed-eating herbivorous and omnivorous species in the genera *Amara* and *Harpalus,* reflect similar patterns following wind damage and other forest disturbances (Gandhi 2008; Skłodowski and Garbalińska 2011).

Management and Research Implications

Tornado damage immediately altered vegetation, and these effects persisted through the season, resulting in changes in ground beetle communities. However, the localized nature of these effects means that total park biodiversity may not have

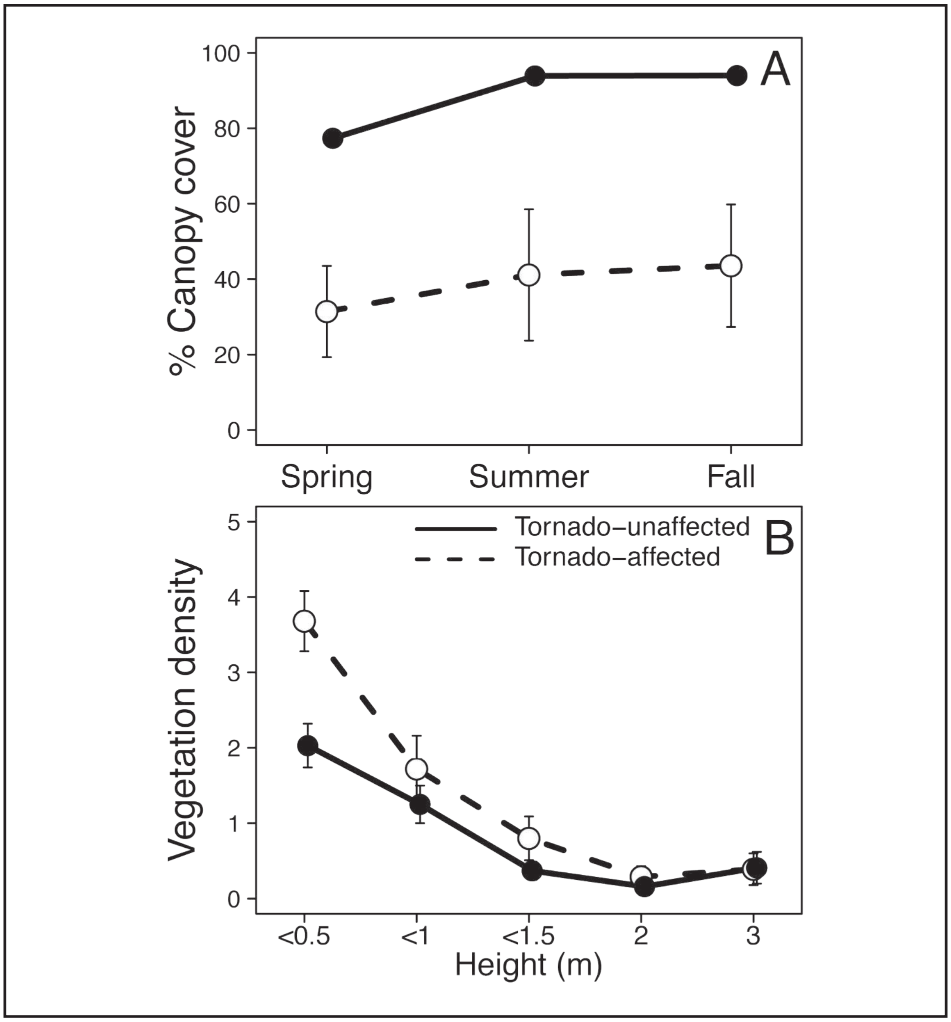

Figure 3. Vegetation structure characteristics of transects affected (dashed line) or unaffected (solid line) by tornado damage. (A) percent canopy cover, where values are means ± 1 SE. Error bars on tornado-affected transects are smaller than width of points. (B) vegetation profile density, showing mean number of vegetation touches at each height ± 1 SE. Values are pooled across the three sampling sessions.

been reduced, and might have increased. Unaffected areas may act as refugia for species that prefer closed-canopy habitats, providing dispersing individuals to recolonize tornado-affected areas once the vegetation has recovered enough to resemble unaffected forest. This may especially be the case for large carnivorous ground beetles. Following damage, managers may not want to immediately restore habitats to their pre-tornado conditions (other than to ensure visitor safety) if the damaged areas represent novel habitats for the site, increasing habitat heterogeneity and potentially increasing diversity. Here, tornado-affected sites provided habitat for 11 species that were not found in unaffected habitat. However, if the goal is to return quickly to a late-successional forest ecosystem, management actions that promote a closed canopy and open understory may be preferable.

Ground beetles may be useful indicator species for understanding the impacts of natural disturbances because of their diverse ecological roles, but more research on other arthropod groups is warranted. This could verify if beetle community patterns are correlated with other taxonomic groups either with similar or different diets or life histories. In particular, focusing on specific trophic groups or guilds might reveal how different compartments within food webs are influenced by the vegetation changes following disturbance. For example, shifts from a ground beetle community dominated by large predatory species to one with mostly herbivorous/omnivorous species and small predators may indicate a change in the relative intensity of seed vs. arthropod predation. Bait experiments examining the frequency of these feeding effects could demonstrate if shifts in the community translate to functional changes as well.

ACKNOWLEDGMENTS

This work was supported by the NIU Office of Student Engagment and Experiential Learning. The Flagg-Rochelle Community Park District generously gave permission to carry out research at the field site. Dylan Luzbetak provided field and lab assistance. Two reviewers provided very helpful comments on earlier drafts that benefited the manuscript.

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