

Carabid beetle responses to herbicide application, shelterwood seed cut and insect defoliator outbreaks

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ABSTRACT

Managing forests to promote biodiversity requires understanding the effects of silvicultural practices on a range of forest species and communities. We evaluated carabid beetle (Coleoptera; Carabidae) responses to operational herbicide and shelterwood seed cut treatments in northern hardwood stands on the Allegheny National Forest, Pennsylvania, USA, from 1992 to 2000. There was substantial defoliation by elm spanworms (*Ennomos subsignarius* Hübner) or cherry scalloped moth (*Hydria prunivora* Ferguson) during four of the 9 years of this study, so we also evaluated effects of these lepidopteran outbreaks on carabids. We found no differences in carabid species richness between herbicide-treated and no herbicide plots overall or in any year, but carabid abundance was higher in herbicide-treated plots in the year following application. Carabid community composition differed among years and increased in dissimilarity over the course of the study but did not differ between herbicide-treated and no herbicide plots. Shelterwood seed cuts had no effects on carabid species richness, abundance or community composition. The relatively few significant effects of experimental treatments on individual carabid species tended to be small and responses we did find differed somewhat from previous studies. In 1992, carabid abundance was significantly correlated with elm spanworm defoliation and in 1995 both species richness and abundance were significantly higher in areas defoliated by cherry scalloped moth. These results support previous findings that forestry practices that have relatively minor and short-term effects on forest vegetation are unlikely to have substantial effects on carabids; however, natural resource variation resulting from forest lepidopteran outbreaks may have important cascading effects for carabid communities that have not been fully explored.

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1. Introduction

Forests are increasingly managed for multiple and potentially conflicting objectives, including timber production and conservation of biodiversity (Perry, 1998). Balancing these goals, or at least making informed decisions regarding potential trade-offs, requires understanding relationships between forest management and the presence and abundance of species associated with forest habitats.

Herbicide application is a common and effective silvicultural practice for removing competing vegetation and promoting growth and survival of desirable tree seedling and saplings (Marquis, 1979; Horsley and Marquis, 1983; Horsley, 1994). In response to scientific questions, regulation, and public concern regarding non-target effects of herbicide use in forest management, numer-

ous studies have evaluated their direct and indirect impacts on individual species and broader measures of biological diversity (Lautenschlager, 1993; Sullivan and Sullivan, 2003; Guynn et al., 2004; Tatum, 2004). The results of such studies vary widely depending on taxa studied, spatial and temporal scale of data collection, chemical formulation used and application frequency and method. However, most effects of herbicide application on animals are mediated through vegetation changes, and habitat use often recovers to pre-treatment levels within 5 years (Sullivan and Sullivan, 2003; Guynn et al., 2004).

Carabid beetles (Coleoptera; Carabidae) are diverse and amenable to study, and research on their responses to forestry practices and natural disturbances has produced abundant data regarding their ecology in managed forests (Work et al., 2008; Koivula, 2011). In general, natural or anthropogenic perturbations that alter habitat structure at large spatial scales (e.g., clearcuts, stand-replacing fire) are associated with the largest shifts in forest carabid communities (Buddle et al., 2006; Gandhi et al., 2008). Conversely, less intensive forest management practices (e.g., group selection, single tree selection, thinning) are usually associated with fewer and

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shorter-duration differences in carabid community composition (Koivula and Niemela, 2002; Ulyshen et al., 2006; Work et al., 2010). Many studies have found higher species richness in intensively managed forests than in old growth stands, and even recently cut or burned areas often have high carabid abundance and diversity due to tolerance of some forest species to disturbance combined with immigration of species that prefer open habitat conditions (Beaudry et al., 1997; Klimaszewski et al., 2005; Buddle et al., 2006). The overall increase in species richness resulting from forest management is often accompanied by population declines of forest specialist species, which may be of concern if carabids are recognized as indicators of forest change (Spence et al., 1996; Beaudry et al., 1997; Duchesne et al., 1999; Gandhi et al., 2008; Work et al., 2008). However, co-occurring carabid species frequently show divergent responses to forest management within studies (e.g., Duchesne et al., 1999; Gandhi et al., 2008; Iglay et al., 2012), demonstrating the importance of considering both community- and species-level effects.

Despite increasing use of herbicides in silviculture and publication of numerous studies evaluating carabid responses to a range of forest management practices, we know little about the effects of operational herbicide application on forest carabid communities (but see Iglay et al., 2012). Laboratory studies have found some direct physiological effects of herbicides on carabids (Kegel, 1989; Brust, 1990), but field studies in agricultural systems have mostly found relatively minor and short-term effects on behavior mediated indirectly through habitat alteration (Brust, 1990; Michalkova and Pekar, 2009). At least two studies that have examined effects of herbicides on carabids in forest systems did not include an appropriate control for identifying herbicide effects when not applied as part of another silvicultural practice (Duchesne et al., 1999; Cobb et al., 2007), making it difficult to interpret the results. Iglay et al. (2012) found community and species-specific effects of a single application of herbicide (imazapyr) on carabid communities in intensively managed pine plantations, suggesting that longer-term studies in a variety of systems are required to better understand the effects of operational herbicide use on forest carabids.

Our study was part of a multi-year experimental assessment of the effects of a single application of glyphosate and sulfometuron methyl on target and non-target taxa in a northern hardwood forest (Ristau et al., 2011; Stoleson et al., 2011). Carabid beetles were collected before, immediately following and for several years after herbicide treatment, allowing us to evaluate potential short-term effects and longer-term carabid community dynamics in herbicide-treated plots compared to untreated forest. Specifically, we examined potential differences in species richness, abundance, community composition and capture frequency of individual species. We also considered potential effects of shelterwood seed cutting and outbreaks of lepidopteran defoliators to better understand the relative importance of herbicide application and other potential sources of environmental variation for carabid community dynamics. Results of this study complement and connect previous research on effects of herbicide on forest biodiversity and effects of forest management practices on carabids.

2. Methods

2.1. Study sites and experimental design

This study was conducted from 1992 to 2000 in ten 6.5 to 8 ha sites in the Allegheny National Forest in northwestern Pennsylvania, USA. All sites were mature second growth northern hardwood stands that originated following clear cutting in the early 1900s. When this experiment was initiated, black cherry (*Prunus serotina* Ehrh.) comprised >25% of the basal area of overstory trees with red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) comprising most of the remaining basal area.

Woody species in the seedling and sapling layers were generally representative of the overstory but were shaded by varying amounts of striped maple (*Acer pensylvanicum* L.), American beech and birch (*Betula lenta* L. and *B. allegheniensis* Britton) in the midstory. Most sites had dense understory vegetation dominated by hayscented fern (*Dennstaedtia punctilobula* (Michx.) T. Moore) or New York fern (*Thelypteris noveboracensis* (L.)), a condition typical of stands in which herbicide is used to increase understory diversity and encourage regeneration of desirable tree species (Horsley and Marquis, 1983; Horsley, 1994). Ristau et al. (2011) provide more detailed description of the sites and their preexisting vegetation.

Each site was divided into two plots to which the herbicide and no herbicide treatments were assigned randomly (the latter is henceforth referred to as the control plot, though it is only a control with respect to herbicide treatment). Sampling was conducted in 1992 and 1994 to assess baseline conditions prior to implementation of the herbicide treatment. In late summer of 1994 (after that year's sampling was completed), a skidder-mounted air blast sprayer was used to apply a tank mix of 364 mL glyphosate and 24 mL sulfometuron methyl in 38 L water per hectare to the understory and midstory of the herbicide treatment plots. This application method and rate is standard operational herbicide use for these stand conditions on the Allegheny National Forest. Five of the sites received a shelterwood seed cut 4–6 years before the experiment was initiated and the other five received this treatment in the winter of 1995–1996. Shelterwood seed cuts reduced stand relative density to approximately 60%, leaving healthy seed trees and creating conditions suitable for recruitment of desirable seedlings (Marquis, 1979). This resulted in an experimental design in which paired herbicide and control plots were nested within sites and sites varied in the time since shelterwood seed cut.

A regional outbreak of elm spanworm (*Ennomos subsignarius* Hübner) resulted in slight to severe defoliation at all of the sites in 1992 and 1993. Elm spanworms are large (~5 cm), polyphagous larvae of a geometrid moth native to the eastern US, where their relatively uncommon outbreaks can cause severe defoliation in mixed hardwood forests. In 1993, at the peak of the outbreak, the defoliated area within the proclamation boundary of the Allegheny National Forest covered approximately 340,000 acres and tended to be most severe in stands dominated by black cherry (Morin et al., 2004). All study sites were within a large area aerially sprayed with the insecticide Thuringicide 48LV in May 1994 to control the outbreak and there was little defoliation from elm spanworm for the remaining years of the study. However, an outbreak of another geometrid, the cherry scalloped moth (*Hydria prunivorata* Ferguson), peaked in 1995 on the Allegheny National Forest and resulted in black cherry defoliation at six sites (Morin et al., 2004).

2.2. Carabid sampling

Pitfall trap arrays consisting of 10 smooth-sided plastic containers (~1 L capacity with a 15 cm diameter) arranged in a “Y” formation and connected by drift fences were placed in each plot to capture carabids. Individual traps were located at the center of the array and then at 2.5, 6 and 15 m out along each of the three drift fences. Containers were filled with approximately 5 cm of 25% formalin and were open for five nights during early growing season (late May – early June) and then again during later growing season (mid late August) each year. For analyses presented here, carabids collected from all 10 traps during each of these two sampling periods were combined. The same trap locations were used throughout the study and sampling effort (e.g., trap days) was equal for all years. Although pitfall trap data are most accurately understood as a function of true density and some capture probability related to frequency and distance of movements (Spence and Niemela, 1994; Thomas et al., 2006), we used the number of individuals captured

as an indicator of abundance because sampling effort did not vary among sites or years and we were not comparing species that may have differed in their capture probability.

Carabids from each trap array were sorted into morpho-species and recorded by REA. RLD provided the taxonomic expertise to identify all carabids to species. Habitat information and flight capacity for each species were based on Lindroth (1961, 1963, 1966, 1968, 1969a,b), Laroche and Larivière (2003), Bousquet (2010) and experience of RLD and REA. Vouchers were deposited at the Carnegie Museum of Natural History.

2.3. Statistical analysis

2.3.1. Species richness and abundance

We tested effects of herbicide treatment and shelterwood seed cut on carabid species richness and abundance with mixed effects models. For these analyses, we modeled year and herbicide treatment as fixed, crossed, categorical variables and time since shelterwood seed cut as a fixed continuous variable. Site and year nested within site were modeled as random grouping variables to account for site- and year-level variation. Parameters were estimated by Penalized Quasi Likelihood with a Poisson distribution to account for potential overdispersion of count data in the response variables. We used planned contrasts to test for differences in species richness and abundance between herbicide and control plots overall and within each year of the study. We assessed pairwise differences between years with linear contrasts using Tukey's adjustment to account for multiple comparisons.

We tested the response of carabid species richness and abundance to the pulse of resources (i.e., insect prey and carrion) resulting from defoliator outbreaks with two separate analyses. For 1992, we tested correlations between carabid richness and abundance and site-level estimates of percent defoliation (which were only available for that year). The cherry scalloped moth outbreak in 1995 was more geographically confined and site- or plot-level defoliation estimates were not available, so we conducted *t*-tests to evaluate the hypothesis that carabid species richness and abundance at sites within the defoliated areas would be higher than at sites that did not experience defoliation that year (using GIS coverage from aerial detection surveys from Morin et al. (2004)).

2.3.2. Community composition

To assess variation in carabid community composition and identify spatial, temporal or treatment-related patterns in species assemblages, we conducted three complementary analyses based on dissimilarity among samples. First, we tested effects of year on the Bray–Curtis dissimilarity of the paired herbicide and control plots with a linear mixed-effect model that included site and year within site as random grouping variables. If dissimilarity between these paired plots increased following herbicide application, it could indicate changes in presence and abundance of species in response to that treatment.

To complement this univariate approach, we conducted two related multivariate analyses based on partitioning dissimilarity among samples according to groupings defined by experimental variables. We used permutational MANOVA based on Bray–Curtis distances to determine if groups of samples differed in multivariate space according to herbicide treatment, year and treatment combinations produced by their interaction. This procedure evaluates explanatory power of variables by comparing the observed intra-group and inter-group dissimilarities to permutations drawn from random assignment of samples to levels of predictor variables (Anderson, 2001). We then tested for differences in heterogeneity of groups with a permutational test of multivariate dispersion (Anderson, 2006). This test uses ANOVA to compare the distances of samples to their group centroids, again using Bray–Curtis dis-

similarity. For our study, groups were defined by herbicide treatment, year and treatment combinations produced by herbicide \times year interaction. This analysis complemented the univariate test of dissimilarity between paired herbicide and control plots by testing dissimilarity of unpaired herbicide and control plots as well as within-group dissimilarity for both treatment levels for each year. That is, the results of the permutational analysis of multivariate dispersion could determine whether apparent convergence or divergence in community composition between paired herbicide and control plots could be attributed to a true treatment effect or simply represent shifts in the entire community at a larger spatial or temporal scale. Additionally, this procedure allowed us to empirically assess patterns in carabid community variability (e.g., to test if communities were more or less variable within and among sites over the course of the study).

The plots designated for herbicide treatment were coded as such for analysis even prior to herbicide application, so a true treatment effect for these analyses would be indicated by a significant interaction between year and herbicide treatment. Post-hoc tests to identify differences among factor levels were conducted for both the permutational MANOVA and the permutational test of dispersion. These tests were based on permutation of data subsets and their significance was assessed by evaluating the *P*-values against Bonferroni-adjusted alpha values. All *P*-values were calculated with 9999 permutations.

2.3.3. Species-level responses

We tested for effects of herbicide application and shelterwood seed cut on the 10 carabid species that accounted for at least 2% of the total number of individuals in this study (=505 individuals). The model specifications for these analyses were the same as those described above for the analyses of overall carabid abundance, though we did not conduct post hoc pairwise analyses among years. We also tested the hypotheses that brachypterous carabids would be less abundant and open-habitat species would be more abundant in sites disturbed by the experimental treatments (Riberia et al., 2001; Mullen et al., 2008).

3. Results

We captured 25,231 individuals from 67 carabid species, including four taxa identified as distinct subspecies or morphs that were treated as species for analysis (Appendix A). Most of the species captured (52 of 67) are considered forest or woodland species, with a smaller number of open-habitat species (11) and four species (comprising only 6 individuals) that are considered riparian species. Captured carabids varied in wing development: 28 were macropterous and likely capable of flight, 14 had polymorphic wing development and 25 were brachypterous or submacropterous and likely incapable of sustained flight.

The most abundant species, *Calosoma frigidum*, occurred in over 75% of samples and accounted for over one-third of all captures (8912 individuals, 5671 of which were captured in 1992). *Pterostichus tristis* and *Myas cyanescens* were the two most ubiquitous taxa, occurring in 116 and 114 out of 120 samples, respectively. The five most frequently captured species (*C. frigidum*, *P. mutus*, *Synuchus impunctatus*, *P. tristis*, and *Platynus decentis*) together comprised approximately two-thirds of all individuals and tended to be most abundant in 1992, 1994 and 1995 (Appendix A). By contrast, eleven species were represented by a single individual and three species were represented by only two individuals.

3.1. Species richness and abundance

Carabid species richness and abundance were positively correlated at the plot level (Pearson product-moment correlation: $r = 0.50$, $t = 6.3$, d.f. = 118, and $P < 0.001$), but both varied

substantially over the course of this study. Species richness varied significantly among years, and pairwise contrasts showed that richness was highest in 1992 and 1994, intermediate in 1995 and lowest in 1996, 1998 and 2000 (Fig. 1A). Herbicide treatment had no significant effects on species richness (overall and within-year contrasts between herbicide and control plots were all $P > 0.05$), nor did time since the shelterwood seed cut ($t = -0.18$, d.f. = 44, and $P = 0.86$). Carabid abundance varied among years in a pattern similar to the pattern of species richness (Fig. 1B). Specifically, time since shelterwood seed cut did not explain significant variation in abundance ($t = 1.48$, d.f. = 44, and $P = 0.15$) and there was no significant difference overall between herbicide and control plots ($z = -2.05$, and $P = 0.29$). However, within-year contrasts showed that in 1995 approximately 30% more beetles were captured in the herbicide plots than the control plots (142.6 vs 109.9, respectively; $z = -3.14$, and $P = 0.01$).

In 1992, site-level canopy defoliation due to elm spanworm was positively correlated with carabid abundance (Fig. 2; $r = 0.58$, $t = 2.0$, d.f. = 8, one-sided $P = 0.04$), but there was no association with spe-

cies richness ($r = -0.21$, $t = -0.6$, d.f. = 8, and one-sided $P = 0.72$). Analysis of the five most abundant species demonstrated that only the abundance of *Calosoma frigidum* (which accounted for over 57% of all individuals collected that year) was positively correlated with elm spanworm defoliation (Fig. 2; $r = 0.55$, $t = 1.9$, d.f. = 8, and one-sided $P = 0.05$). There was no apparent relationship between the shelterwood seed cut treatment and the level of elm spanworm defoliation in 1992 ($t = 0.45$, d.f. = 8, and $P = 0.66$), suggesting that the outbreak was unaffected by the silvicultural treatment that five sites had received. In 1995, an average of 9.3 more species (27.3 vs 18.0) and 350 more individuals (505 vs 155) were captured from sites within the area defoliated by cherry scallophshell moth than from sites not in the defoliated area (richness: $t = 2.62$, d.f. = 8, $P = 0.031$; abundance: $t = 2.66$, d.f. = 8, and $P = 0.029$). Of the six sites affected by cherry scallophshell moth, four had received a shelterwood seed cut and two had not. Additionally, tests that grouped sites the same way but analyzed data from 1996 (after the outbreak ended) did not find significant differences, further suggesting that the 1995 results were related to an effect of the defoliator rather than experimental treatments or site-level variation.

3.2. Community composition

Dissimilarity of species assemblages from paired herbicide and control plots within sites varied significantly among years ($F = 82.27$; d.f. = 6, 45; and $P < 0.001$) and generally increased during the course of the study (Fig. 3A). Dissimilarity of these paired plots was strongly negatively correlated with their combined abundance (Fig. 3B, Pearson product-moment correlation: $r = -0.76$, $t = -8.9$, d.f. = 58, and $P < 0.001$).

Permutational MANOVA indicated that carabid communities were distinct among years, and pairwise post hoc tests showed increasing within-year dissimilarities among plots through the course of the study (Fig. 4). However, dissimilarities among groups defined by herbicide treatment and the herbicide \times year interaction were not significantly different from random assignment of samples to these groups (Table 1). Furthermore, carabid communities were more similar among plots within years – regardless of herbicide treatment – than among plots subjected to the same experimental treatments between years. The permutational test of multivariate dispersion found similar results: there was significant

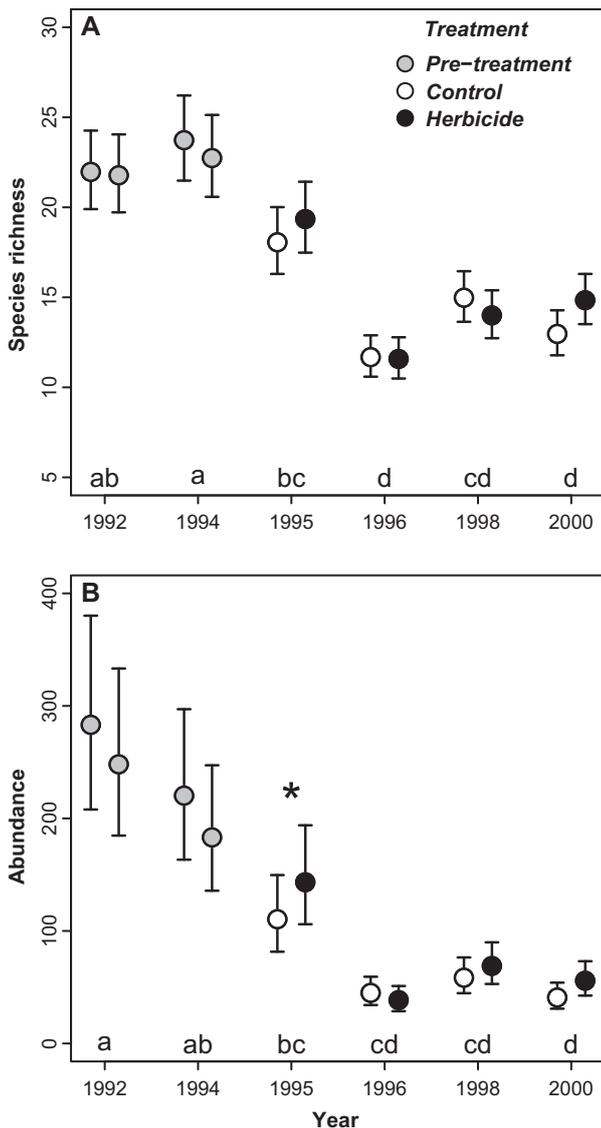


Fig. 1. Carabid species richness (A) and abundance (B) plotted by year and herbicide treatment (means \pm SE). Significant differences among year means are indicated with lowercase letters along the x-axis, and asterisks indicate significant differences between herbicide and control treatments within years. Note that the herbicide and control plots were designated in 1992 and 1994 (allowing for pre-treatment comparisons), but the 1995 samples were the first taken after implementation.

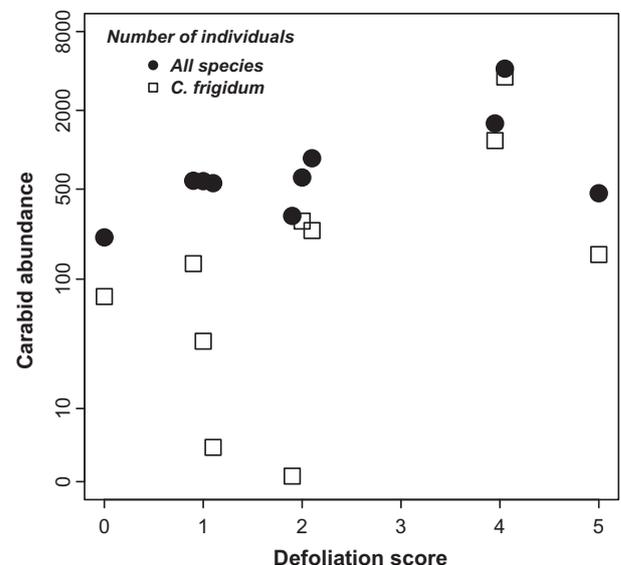


Fig. 2. Relationship between defoliation score and carabid abundance (log scale) in 1992. Data for sites with the same defoliation scores are offset to display data more clearly and allow comparison of the site-level total abundance and abundance of *Calosoma frigidum*.

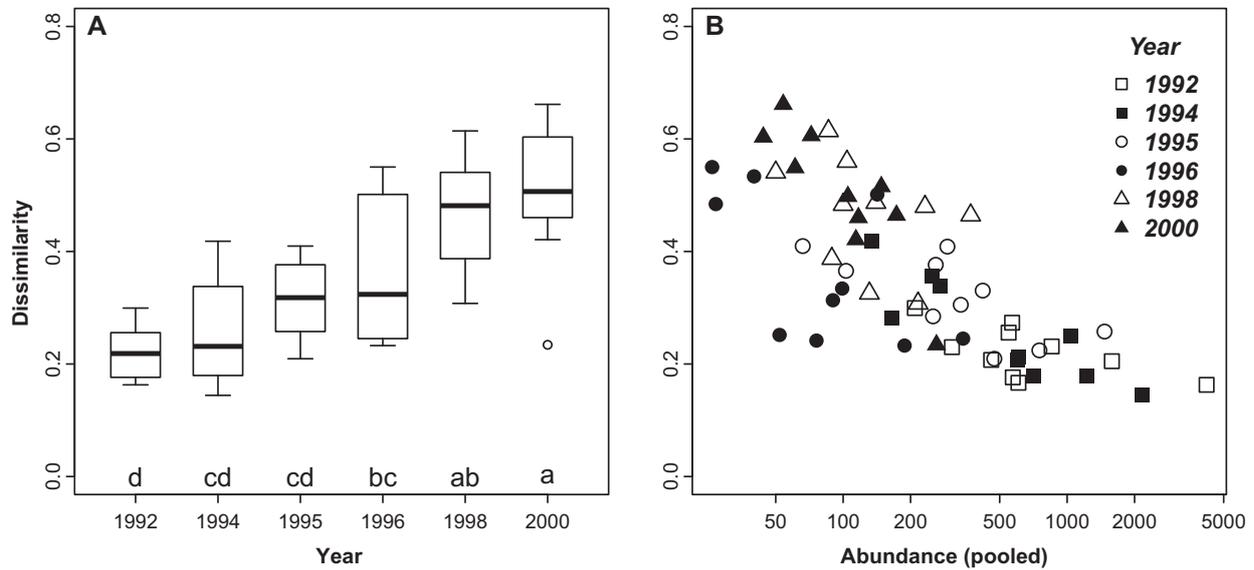


Fig. 3. Dissimilarity of paired, within-site herbicide and control plots varied significantly among years (A) and was strongly associated with site-level carabid abundance (B). Boxplots in (A) show the median (dark line), 25th and 75th percentiles (area within the box), 10th and 90th percentiles (whiskers) and outliers (open circles), with significant differences among year means indicated with lowercase letters along the x-axis.

variation in mean dissimilarities among years but not between herbicide and control plots or treatment combinations produced from herbicide and year interaction (Table 1). The post hoc pairwise tests following that analysis found several significant differences between years, generally showing that carabid communities from the first 2 years of the study were less variable than those from the later years (Fig. 4).

3.3. Species responses

Abundance of four of the ten focal species (*Calosoma frigidum*, *Platynus decentis*, *Pterostichus rostratus* and *P. tristis*) was signifi-

cantly positively related to time since shelterwood seed cut (Table 2). Backtransformed estimates of coefficients for these species correspond to a 1–2% increase in the number of individuals for each year after the shelterwood treatment. Within-year contrasts of the herbicide treatment found higher abundance in herbicide plots than in control plots for *C. frigidum* and *P. mutus*. The parameter estimates from the within-year contrasts correspond to 9.3 and 7.7 more *C. frigidum* individuals in herbicide plots than in control plots in 1998 and 2000, respectively, and 1.7 and 3.5 more *P. mutus* individuals in herbicide plots than in control plots in 1995 and 1998, respectively. Neither the proportion of brachypterous species nor the proportion of open-habitat species was affected by herbicide or shelterwood seed cut treatments.

4. Discussion

Effects of forest management on carabid communities are generally mediated by habitat alteration related to plant structure and diversity (Niemela and Spence, 1994; Latty et al., 2006; Cobb et al., 2007). In this study, herbicide treatment produced a dramatic but short-term reduction in herbaceous plant species richness and cover and the shelterwood seed cut reduced woody vegetation cover initially but increase woody vegetation later in the study due to competitive release of tree seedlings and saplings (Ristau et al., 2011; Stoleson et al., 2011). Given these vegetation changes, we might expect more mobile carabid species and open-habitat specialists to be more abundant following herbicide application and shelterwood seed cuts (Beaudry et al., 1997; Ribera et al., 2001; Buddle et al., 2006; Mullen et al., 2008).

4.1. Variation in carabid communities

Community-level parameters in our study varied substantially among years but were largely unaffected by herbicide or shelterwood seed cut treatments. Species richness and abundance were significantly higher in the first two or three sampling years than in the later years (Fig. 1), and both permutational MANOVA and permutation test of multivariate dispersion showed that carabid assemblages in the first 2 or 3 years of the study were distinct from and less variable than those observed in later years (Table 1 and Fig. 4). Although these differences coincided temporally with herbicide treatment (Fig. 3A), tests of community dissimilarity

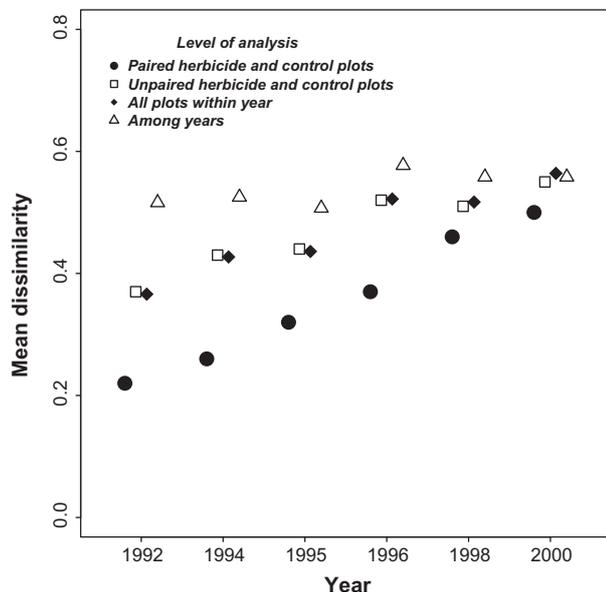


Fig. 4. Mean dissimilarity at different spatial and temporal levels of analysis. The dissimilarity between paired herbicide and control plots (closed circles) was the lowest across all years, followed by the virtually identical within-year dissimilarities between unpaired herbicide and control plots (open squares) and among all plots (closed diamonds). The plot-level dissimilarities at all levels of analysis increased over the course of the study; during the final sampling year the within-year plot-level dissimilarities approached the among-year differences in carabid community composition (open triangles).

Table 1
Results of permutational MANOVA based on distances and permutational test of multivariate dispersion. The two analyses used the same model to partition a matrix containing the Bray–Curtis dissimilarities of all pairs of samples.

Source of variation	Permutational MANOVA					Permutational test of dispersion			
	d.f.	S.S.	M.S.	F	P	S.S.	M.S.	F	P
Herbicide treatment	1	2603	2603	2.28	0.11	10.6	10.6	1.04	0.35
Year	5	40,501	8100	6.88	0.0001	1632	326	6.58	0.0001
Herbicide x year	5	5707	1141	0.97	0.55	51.3	10.3	0.21	0.96
Error	108	127,116	1177			5354	49.6		

Table 2
Results of models testing the effects of time since shelterwood cut and herbicide x year and on abundance of carabid species.

Species or group	Variable ^a	Estimate (SE) ^b	Test statistic	P
<i>Calosoma frigidum</i>	Time since cut	0.023 (0.009)	$t = 2.5$, d.f. = 50	0.016
	Control – herbicide 1998	–2.23 (0.66)	$z = -3.39$	0.005
	Control – herbicide 2000	–2.04 (0.66)	$z = -3.07$	0.016
<i>Myas cyanescens</i>	Time since cut	0.003 (0.004)	$t = 0.70$, d.f. = 50	0.48
<i>Platynus decentis</i>	Time since cut	0.01 (0.005)	$t = 2.1$, d.f. = 50	0.044
<i>Pterostichus adoxus</i>	Time since cut	0.001 (0.003)	$t = 0.37$, d.f. = 50	0.71
<i>Pterostichus lachrymosus</i>	Time since cut	0.008 (0.005)	$t = 1.6$, d.f. = 50	0.12
<i>Pterostichus mutus</i>	Time since cut	–0.004 (0.005)	$t = -0.72$, d.f. = 50	0.48
	Control – herbicide 1995	–0.53 (0.18)	$t = -2.95$	0.024
	Control – herbicide 1998	–1.26 (0.46)	$z = -2.73$	0.045
<i>Pterostichus rostratus</i>	Time since cut	0.018 (0.004)	$r = 4.73$, d.f. = 50	<0.001
<i>Pterostichus tristis</i>	Time since cut	0.011 (0.004)	$r = 2.62$, d.f. = 50	0.012
<i>Sphaeroderus canadensis</i>	Time since cut	0.009 (0.005)	$t = 1.87$, d.f. = 50	0.067
<i>Synuchus impunctatus</i>	Time since cut	0.003 (0.005)	$t = 0.70$, d.f. = 50	0.48
Open-habitat species	Time since cut	–0.004 (0.005)	$t = -0.89$, d.f. = 50	0.38
Brachypterous species	Time since cut	0.002 (0.002)	$t = 1.05$, d.f. = 50	0.30

^a Within-year contrasts (control – herbicide) were tested for all species for all years after herbicide treatment (1995–2000) but only significant differences are reported ($P < 0.05$).

^b Estimates for time since cut are equivalent to coefficients in a Poisson regression in which positive values indicate that abundance increased with time since cut. Estimates for control – herbicide effects are from planned within-year contrasts derived from the mixed effects models described in the methods section; positive values indicate higher abundance in control plots than in herbicide plots.

showed no statistically significant effects of herbicide or herbicide x year interactions (Table 1).

The only effect of herbicide treatment we detected at the community level was the significantly higher abundance of carabids in the herbicide-treated plot in 1995. Because there was no difference in community composition or species richness between herbicide and control plots in 1995, it is unlikely that the increased capture frequency was due to immigration by carabid species that prefer open habitats as has been documented in other studies of forest disturbance (Beaudry et al., 1997; Klimaszewski et al., 2005; Buddle et al., 2006). Instead, it seems more likely that the higher capture frequency of carabids in herbicide-treated plots resulted from increased movement due to the dramatic reduction of herbaceous vegetation in the year following herbicide application (Thomas et al., 2006).

What, then, accounted for significant differences among years? The ubiquity and high abundance of a small number of numerically dominant species during 1992, 1994 and 1995 was responsible for most community-level trends. Although this study was not designed to evaluate carabid responses to population fluctuation of lepidopteran defoliators, outbreaks of elm spanworm and cherry scalloped moth in those years dramatically affected carabid communities (Fig. 2). Most carabid species captured in this study are considered generalist predators (Larochelle and Larivière, 2003) and all of the five most common species are noted predators of lepidopteran larvae (Reeves et al., 1983; Cameron and Reeves, 1990; Dudevoir and Reeves, 1990). Therefore, it is not surprising that carabid abundance was positively correlated with percent defoliation in 1992 and both abundance and richness were higher in sites within the area defoliated by cherry scalloped moth in 1995. Additionally, the abundance of the most common species, *Calosoma frigidum*, was significantly correlated with elm spanworm defoliation in 1992. This large carabid species is highly mobile, commonly hunts in tree canopies and shows strong numerical responses to abundance

of lepidopteran larvae (Burgess and Collins, 1917; Crins, 1980). The defoliator outbreaks may have affected presence and abundance of other carabid species as well; unfortunately, the lack of site-level estimates of defoliator abundance over multiple years limited our analysis of these relationships.

Resource pulses such as defoliator outbreaks are frequently followed by aggregative and reproductive responses of consumers, sometimes through multiple trophic levels (Yang et al., 2010). Two studies on the Allegheny National Forest reported bird responses to the elm spanworm outbreak in 1992 and 1993 (Haney, 1999; Stoleson et al., 2011). Notably, bird abundance in both studies was highest in 1994, the year after peak defoliation (Morin et al., 2004). By contrast, carabid abundance in our study was highest in 1992, before peak elm spanworm defoliation, and then remained high through the peak of the cherry scalloped moth outbreak in 1995. Whereas bird responses to the outbreaks were likely limited by minimum territory size and nest site fidelity, beetle abundance likely represented a combination of rapid aggregation to spatially heterogeneous resources and reproductive responses to the previous year's food resources. The alternative mode and timing of response between birds and carabids were consistent with effects of size and trophic on response lags found in other systems (Yang et al., 2010). Comparing site-level responses of carabids, birds and other potential predators of lepidopteran larvae would further elucidate these relationships and inform our understanding of how consumers respond to these types of resource pulses.

4.2. Individual species responses to forest management

Previous research has found significant effects of forest management practices on many of the species we captured in our study, and some attempts have been made to generalize these results across larger geographic areas (Moore et al., 2004; Work et al.,

2008). We found that two species typical of forest habitats (*Calosoma frigidum* and *Pterostichus mutus*) were more abundant in herbicide plots later in the study, suggesting that this treatment may in some cases increase forest habitat quality. Additionally, four of the ten most abundant species appeared to be significantly negatively affected by the shelterwood seed cut (Table 2), and three of these species – *C. frigidum*, *Platynus decentis* and *Pterostichus tristis* – have responded negatively to forest disturbance or management in other studies (Beaudry et al., 1997; Duchesne et al., 1999; Werner and Raffa, 2000; Klimaszewski et al., 2005; Cobb et al., 2007). However, we found no effects of herbicide or shelterwood seed cut for *Myas cyanescens*, open-habitat species or brachypterous species, results generally inconsistent with those reported elsewhere (Beaudry et al., 1997; Ribera et al., 2001; Koivula et al., 2002; Klimaszewski et al., 2005; Gandhi et al., 2008; Mullen et al., 2008). These findings suggest that it may be difficult to make generalizations about species-specific responses to forest disturbances that vary greatly in context, intensity and duration. It is also important to consider the size of treatment effects we observed; the relatively few effects of herbicide and shelterwood were one or two orders of magnitude less than the year-to-year variation that was at least partially due to lepidopteran outbreaks.

Most species-level responses to forest management are from studies examining effects of clearcut timber harvests, which generally are implemented on large spatial scales and result in dramatic habitat alteration. In contrast, the reduction in basal area from the shelterwood seed cut in our study retained most of the overstory and was within the range of tree removal found to have few effects on carabid community composition (Work et al., 2010). It is important to note, however, that the most common objective of herbicide application and shelterwood seed cutting in northern hardwood forests is to prepare stands for a removal harvest (Marquis, 1979; Horsley, 1994), which would likely have effects on carabid species more similar to those observed in other systems. Maintaining a typical forest carabid community until the overstory removal could facilitate post-harvest recolonization and recovery, particularly because forest management at our study site (the Allegheny National Forest) requires leaving unharvested reserve areas. Our study suggests that even if these reserve areas have been subjected to herbicide and shelterwood seed cut treatments they can likely serve as refugia for many forest-specific carabid species during logging operations and then as source populations for recolonizing the regenerating forest following overstory removal (Gandhi et al., 2004).

4.3. Implications for future studies of carabid responses to forest management

Comparing results from manipulative studies of forest management methods to community dynamics under natural habitat variation or disturbance events is a powerful and intuitive framework for identifying biologically meaningful results (Perry, 1998). Results vary among systems and disturbance types, but carabid communities usually differ substantially among intensively managed forests, naturally disturbed forests and forests that have not experienced large natural disturbances or management (Work et al., 2008). This disparity clearly demonstrates the practical challenges of conserving forest biodiversity by implementing forest management practices that supposedly mimic natural disturbance (Cobb et al., 2007).

Understanding forest management in the context of natural processes requires not only comparing the effects of specific management practices to specific disturbances, but also quantifying the population and community dynamics of the focal taxa under a range of conditions. We found few effects of herbicide application or shelterwood cutting, but two major defoliator outbreaks within 4 years significantly increased carabid species richness and

abundance. In fact, it is possible that the large magnitude of the carabid response to these pulses of food resources obscured effects of the experimental treatments. Most intensive forest management practices simplify vegetation structure and promote colonization by species more typical of open habitats, but we are unaware of any common management practice that increases food availability for forest-associated carabids and other insectivores on a scale comparable to Lepidoptera outbreaks. Although allowing defoliator outbreaks to persist is not feasible in most production-oriented forests, we should perhaps be more aware of cascading effects of defoliator suppression on higher trophic levels if we intend to manage forests for biodiversity.

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Appendix A. Capture frequency and total number of individuals for all carabid species collected in this study

Species	Frequency	No. individuals
<i>Agonum cupripenne</i> (Say 1823)	1	1
<i>Agonum fidele</i> Casey 1920	11	17
<i>Agonum retractum</i> LeConte 1848	32	87
<i>Amara lunicollis</i> Schiödte 1837	8	17
<i>Amphasia interstitialis</i> (Say 1823)	21	41
<i>Anisodactylus nigerrimus</i> (Dejean 1831)	11	26
<i>Apenes lucidulus</i> (Dejean 1831)	7	12
<i>Bembidion lacunarium</i> (Zimmermann 1869)	1	1
<i>Bradycellus lugubris</i> (LeConte 1848)	21	43
<i>Bradycellus nigriceps</i> LeConte 1868	1	1
<i>Calathus gregarius</i> (Say 1823)	16	85
<i>Calosoma frigidum</i> Kirby 1837	93	8912
<i>Carabus goryi</i> Dejean 1831	54	421
<i>Carabus serratus</i> Say 1823	25	88
<i>Carabus vinctus</i> (Weber 1801)	1	1
<i>Chlaenius emarginatus</i> Say 1823	11	44
<i>Cicindela sexguttata</i> Fabricius 1775	24	38
<i>Clinidium sculptile</i> (Newman 1838)	6	6
<i>Colliuris pensylvanica</i> (Linnaeus 1767)	1	1
<i>Cymindis americanus</i> Dejean 1826	5	5
<i>Cymindis cribricollis</i> Dejean 1831	83	306
<i>Cymindis limbatus</i> Dejean 1831	16	30
<i>Cymindis neglectus</i> Haldeman 1843	6	18
<i>Cymindisplaticollis</i> (Say 1823)	10	10
<i>Dicaelus politus</i> Dejean 1826	22	35
<i>Dicaelus teter</i> Bonelli 1813	42	92
<i>Diplocheila obtusa</i> (LeConte 1848)	1	1

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Species	Frequency	No. individuals
<i>Dromius piceus</i> Dejean 1831	2	2
<i>Gastrellarius honestus</i> (Say 1823)	40	80
<i>Harpalus providens</i> Casey 1914	72	483
<i>Harpalus somnulentus</i> Dejean 1829 [morph <i>fallax</i>]	16	40
<i>Harpalus somnulentus</i> Dejean 1829 [morph <i>pleuriticus</i>]	21	37
<i>Harpalus spadiceus</i> Dejean 1829	37	95
<i>Maronetus imperfectus</i> (G.H. Horn 1860)	1	1
<i>Myas cyanescens</i> Dejean 1828	114	1197
<i>Nebria lacustris</i> Casey 1913	1	1
<i>Notiobia nitidipennis</i> (LeConte 1848)	65	272
<i>Notiophilus aeneus</i> (Herbst 1806)	86	492
<i>Notiophilus semistriatus</i> Say 1823	1	1
<i>Olisthopusparmatus</i> (Say 1823)	14	23
<i>Patrobis longicornis</i> (Say 1823)	2	2
<i>Platynus angustatus</i> Dejean 1828	34	111
<i>Platynus decentis</i> (Say 1823)	104	1330
<i>Platynus hypolithos</i> (Say 1823)	7	10
<i>Platynus tenuicollis</i> (LeConte 1848)	1	1
<i>Poecilus lucublandus</i> (Say 1823)	18	33
<i>Pseudamara arenaria</i> (LeConte 1848)		
<i>Pterostichus adoxus</i> (Say 1823)	90	626
<i>Pterostichus coracinus</i> (Newman 1838)	65	365
<i>Pterostichus diligendus</i> (Chaudoir 1868)	10	16
<i>Pterostichus lachrymosus</i> (Newman 1838)	91	757
<i>Pterostichus melanarius</i> (Illiger 1798)	4	31
<i>Pterostichus moestus</i> (Say 1823)	17	27
<i>Pterostichus mutus</i> (Say 1823)	95	3297
<i>Pterostichus pensylvanicus</i> LeConte 1873	53	238
<i>Pterostichus relictus</i> (Newman 1838)	14	58
<i>Pterostichus rostratus</i> (Newman 1838)	99	809
<i>Pterostichus stygicus</i> (Say 1823)	20	55
<i>Pterostichus tristis</i> (Dejean 1828)	116	1459
<i>Scaphinotus andrewsii mutabilis</i> (Casey 1920)	2	2
<i>Scaphinotus viduus</i> (Dejean 1826)	19	28
<i>Selenophorus opalinus</i> (LeConte 1863)	3	3
<i>Sphaeroderus canadensis canadensis</i> Chaudoir 1861	98	997
<i>Sphaeroderus stenostomus lecontei</i> Dejean 1826	19	23
<i>Stenolophus conjunctus</i> (Say 1823)	1	1
<i>Synuchus impunctatus</i> (Say 1823)	110	1870
<i>Trichotichnus autumnalis</i> (Say 1823)	10	16

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