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The response of ground beetles (Coleoptera: Carabidae) to selection cutting in a South Carolina bottomland hardwood forest

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Abstract. We compared the response of ground beetles (Coleoptera: Carabidae) to the creation of canopy gaps of different size (0.13, 0.26, and 0.50 ha) and age (1 and 7 years) in a bottomland hardwood forest (South Carolina, USA). Samples were collected four times in 2001 by malaise and pitfall traps placed at the center and edge of each gap, and 50 m into the surrounding forest. Species richness was higher at the center of young gaps than in old gaps or in the forest, but there was no statistical difference in species richness between old gaps and the forests surrounding them. Carabid abundance followed the same trend, but only with the exclusion of *Semiardistomis viridis* (Say), a very abundant species that differed in its response to gap age compared to most other species. The carabid assemblage at the gap edge was very similar to that of the forest, and there appeared to be no distinct edge community. Species known to occur in open or disturbed habitats were more abundant at the center of young gaps than at any other location. Generalist species were relatively unaffected by the disturbance, but one species (*Dicaelus dilatatus* Say) was significantly less abundant at the centers of young gaps. Forest inhabiting species were less abundant at the centers of old gaps than in the forest, but not in the centers of young gaps. Comparison of community similarity at various trapping locations showed that communities at the centers of old and young gaps had the lowest similarity (46.5%). The community similarity between young gap centers and nearby forest (49.1%) and old gap centers and nearby forest (50.0%) was similarly low. These results show that while the abundance and richness of carabids in old gaps was similar to that of the surrounding forest, the species composition between the two sites differed greatly.

Introduction

Southeastern bottomland hardwood forests are important for water quality and control, nutrient cycling, wildlife habitat, and they support among the most diverse plant and animal communities in North America (Kellison and Young 1997). To protect this unique ecosystem, and to satisfy increasing demand for forest products, the remaining stands must be maintained and managed properly. According to Guldin (1996), proper forest management attempts to imitate natural rates of succession and disturbance in order to

minimize the environmental impacts of timber removal. One promising method for use in bottomland hardwood forests is group selection cutting, an uneven age forest management practice that emulates small-scale natural disturbances (i.e. tree falls, insect outbreaks, wind damage, etc.) to create small openings throughout the forest (Hunter 1990; Guldin 1996; Meadows and Stanturf 1997).

Ground beetles (Carabidae) are taxonomically well known, easily and inexpensively surveyed, and respond quickly to environmental change (Rainio and Niemelä 2003). These attributes have made them useful bioindicators in numerous studies involving disturbance (Allegro and Sciaky 2003; Rainio and Niemelä 2003).

While the response of ground beetles to clearcuts in the conifer forests of Europe and northeastern North America has been well studied Niemelä et al. 1993; Altegrim et al. 1997; Beaudry et al. 1997; Niemelä 1997; Duchesne et al. 1999; Heliola et al. 2001; Koivula 2002a; Koivula et al. 2002; Magura et al. 2003; Pearce et al. 2003), little work has been done on alternative harvesting methods (Altegrim et al. 1997; Werner and Raffa 2000; Koivula 2002b; Koivula and Niemelä 2003; Vance and Nol 2003; Moore et al. 2004), or in hardwood forests (Lenski 1982a; Warriner et al. 2002; Vance and Nol 2003; Moore et al. 2004).

Here we report the results of the first study to examine the response of carabids to group selection cutting in a bottomland hardwood forest in the southeastern United States. We compare the abundance and species richness of carabids in canopy gaps of different size (0.13, 0.26, and 0.50 ha) and age (1 or 7 years) to those at gap edge and in the surrounding forest.

Materials and methods

Study site

This study was conducted from May to November 2001 on the Savannah River Site (SRS), an 80,269-ha nuclear production facility near Aiken, South Carolina. The SRS is owned and operated by the United States Department of Energy (DOE) as a National Environmental Research Park. Our study site was an approximately 120-ha stand of 75–100 year-old bottomland hardwoods. Common forest trees included numerous oak species (*Quercus* spp.), bald cypress (*Taxodium distichum* (L.) Richard), sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), and loblolly pine (*Pinus taeda* L.). The mid-story consisted predominantly of red mulberry (*Morus rubra* L.), ironwood (*Carpinus caroliniana* Walter) and American holly (*Ilex opaca* Aiton). The understory was dominated by dwarf palmetto (*Sabal minor* (Jacquin) Persoon) and switchcane (*Arundinaria gigantean* (Walter) Muhl.). Pre-harvest basal area of the stands was 33 m^2/ha (Pauley et al. 1996). The study site often experiences seasonal flooding (January–April) with some low-lying areas remaining under

water much of the year. Total rainfall in 2001 was 104 cm with the wettest month being June (23.4 cm) and the driest being December (1.2 cm).

Gaps

Of the 24 gaps used in this study, 12 were created in December 1994 ('old gaps') and 12 in August 2000 ('young gaps'). There were four replicates of three different sizes (0.13, 0.26, and 0.50 ha) for each gap age. The gap area was defined as the area surrounded by the boles of the peripheral dominant forest trees. The gaps were located throughout the 120 ha bottomland hardwood forest, and were spaced at least 200 m apart. Vegetation in old gaps was 1–8 m in height and consisted of pioneer species such as sweetgum, sycamore (*Platanus occidentalis* L.), green ash (*Fraxinus pennsylvanica* Marshall), black willow (*Salix nigra* Marshall), tulip poplar (*Liriodendron tulipifera* L.), oaks, switchcane, and dwarf palmetto. Young gaps contained small stump sprouts or seedling of these species as well as fireweed (*Erechtites hieracifolia* (L.) Raf.), blackberries (*Rubus* spp.), and plumegrass (*Erianthus giganteus* (Walter) Muhl.), other native grasses, and various sedge species (*Cyperus* spp.).

Beetle sampling and identification

Ground beetles were sampled at the center and edge of each gap and in the surrounding forest 50 m from gap edges during four 7-day trapping periods (17–23 May, 10–16 July, 7–13 September, and 3–9 November). Each sample location had a malaise and two pitfall traps to capture flying and crawling beetles, respectively. Malaise traps ('Canopy Traps', Sante Traps, Lexington, KY) differed from the traditional design in that they contained collecting jars at the top and bottom so insects that fall when encountering a barrier were also collected. The traps were suspended from 3 m tall metal hangers.

Pitfall traps consisted of a 480 ml plastic cup buried to ground level. A small funnel (8.4 cm diameter) inserted into the cup directed captured beetles into a smaller 120 ml specimen cup below. The pitfall was positioned at the intersection of four 0.5 m long drift fences. Two pitfall traps were placed 5 m apart at each sample station, and the samples from each were combined for each location (center, edge, and forest). The collecting jars for both pitfall and malaise traps were filled with NaCl–2% formaldehyde solution to preserve specimens and a drop of detergent to reduce surface tension (New and Hanula 1998). Once collected, beetles were brought back to the lab and immediately stored in 70% alcohol. Specimens were sorted to morphospecies and later identified using a reference collection and a key to South Carolina Carabidae (Ciegler 2000). In the interest of accuracy, we were unable to assign species-level names to several morphospecies.

We assigned the most abundant species to categories (open-habitat species (fields, meadows, and disturbed areas), generalist species (open or forested areas), and forest species (forested areas)) based on known habitat data (Larochelle and Lariviere 2003). Not all species were classified into these categories due to inadequate information or to the genus-level identification of several morphospecies (Table 1).

Statistical analysis

We combined malaise and pitfall trap captures at each location before analyzing the results. A 3-way analysis of variance with gap age, trap location, and gap size as the main effects showed a significant interaction between gap age and trap location so we analyzed the data for each gap age separately. The General Linear Model procedure of SAS (SAS Institute 1985) was used for all analyses and the Ryan–Einot–Gabriel–Welsch Multiple Range Test was used to determine differences ($\alpha < 0.05$ unless otherwise stated) in relative abundance of insects between trap locations or gap sizes for each gap age (Day and Quinn 1989). We used Raabe's percent similarity (Southwood 1966) to compare similarity among trap locations and trap types.

Results

In total, 5498 ground beetles were collected representing 26 tribes, 60 genera, and 87 species. Species richness was higher at the center of young gaps than in old gaps or in the forest, but there was no statistical difference in species richness between old gaps and the forests surrounding them (Figure 1). Carabid abundance followed the same trend (Figure 2), but only with the exclusion of *Semiardistomis viridis* (Say), a very abundant species (23% of the total number) that differed in its response to gap age compared to most other species (Table 1). There was no statistical difference in abundance or species richness among gaps of differing size (Figure 3).

We were able to classify 19 of the 31 most abundant (>25 individuals) species as open-habitat species, generalists, or forest dwellers (Table 1). In general, carabids associated with open-habitat responded positively to canopy gap creation, and were more abundant at the centers of young gaps than at other young or old gap locations (center, edge, or forest) (Figure 4). The number of open-habitat species at the centers of old gaps was comparable to that of the surrounding forest. Likewise, the abundance of generalist carabids was similar among both young and old gap locations (Figure 4). Carabids that prefer forest habitats were less abundant at the centers of young and old gaps than in their respective forest locations, but this was only significant ($p < 0.1$) for old gaps (Figure 4).

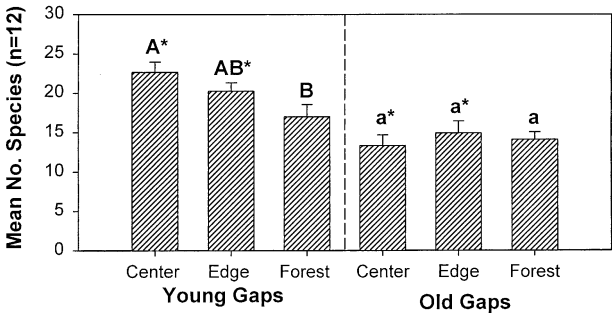

Figure 1. Mean (±SE) richness of carabids collected in malaise and pitfall traps in a bottomland hardwood forest, South Carolina, USA in 2001. The traps were placed at the center, edge, and in the forest surrounding 'young' (created in 2000) and 'old' (created in 1994) canopy gaps. Within graphs (for each gap age), bars with the same letter above them are not significantly different (Ryan–Einot–Gabriel–Welsch Multiple Range Test, $p < 0.05$). Asterisks denote significant differences ($p < 0.05$) between the same trap locations (e.g. center vs. center) in old and young gaps.

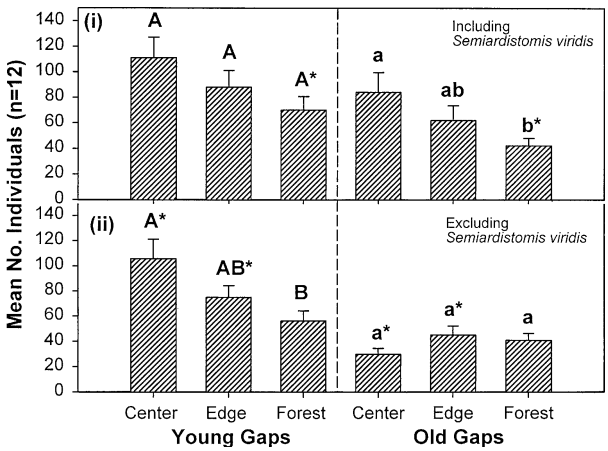

Figure 2. Mean (±SE) number of carabids collected in malaise and pitfall traps in a bottomland hardwood forest, South Carolina, USA in 2001. The traps were placed at the center, edge, and in the forest surrounding 'young' (created in 2000) and 'old' (created in 1994) canopy gaps. (b) depicts total beetle abundances excluding *Semiardistomis viridis*. Within graphs (for each gap age), bars with the same letter above them are not significantly different (Ryan–Einot–Gabriel–Welsch Multiple Range Test, $p < 0.05$). Asterisks denote significant differences ($p < 0.05$) between the same trap locations (e.g. center vs. center) in old and young gaps.

Of the 31 most abundant species, ten species exhibited a significant difference among young gap locations and five differed significantly among old gap locations (Table 1). Eight of the ten species that differed among young gap locations were more abundant in the centers of young gaps than in the surrounding forest. Conversely, only two (*Acupalpus* sp. 2 and *S. viridis*) were more abundant at the center of old gaps than in the surrounding forest

Table 1. Mean (±SE) number of the most abundant (>25 specimens collected) carabid species collected in malaise and pitfall traps in 2001 at different locations in bottomland hardwood forest gaps (n = 12) created in 1994 (old) and 2000 (new).

Species	Young gaps			Old gaps		
	Center	Edge	Forest	Center	Edge	Forest
Open-habitat species						
Acupalpus testaceous Dejean	A 1.50 ± 1.04	A 1.17 ± .63	A .42 ± .23	a 1.17 ± .56	a 2.25 ± 1.92	a 0
Clivina bipustulata (Fabricius)	A* 5.50 ± 1.64	A 2.33 ± .67	A 3.67 ± .96	a* .92 ± .36	a 2.25 ± .72	a 2.00 ± .28
Harpalus pennsylvanicus (De Geer)	A* 2.00 ± .77	B .25 ± .18	B .08 ± .08	a* .17 ± .11	a .08 ± .08	a .17 ± .17
Notiobia terminata (Say)	A* 1.92 ± .74	B* .42 ± .19	B 0	a* 0	a* 0	a 0
Poecilus chalcites (Say)	A .33 ± .19	A .33 ± .19	A .83 ± .39	a .17 ± .11	a .42 ± .23	a .50 ± .29
Scarites spp. Fabricius	A* 3 ± .70	B* 1.17 ± .37	B .92 ± .29	a* .17 ± .11	a* .17 ± .17	a .58 ± .26
Generalist species						
Brachinus alternans Dejean	A* 21.83 ± 4.93	A* 16.25 ± 5.05	A 9.50 ± 3.48	a* 5.33 ± 2.25	a* 4.08 ± 1.74	a* 3.67 ± 1.97
Carabus sylvosus Say	A 1 ± .66	A 1.5 ± .87	A .58 ± .23	a .25 ± .13	a .17 ± .11	a .42 ± .19
Dicaelus dilatatus Say	A .08 ± .08	AB .58 ± .19	B 1.08 ± .36	a .17 ± .11	a .83 ± .34	a .92 ± .36
Dicaelus elongatus Bonelli	A* .08 ± .08	A .75 ± .33	A 1.17 ± .56	a* 1.00 ± .35	a .5 ± .26	a .33 ± .14
Galerita spp. Fabricius	A .58 ± .34	A .75 ± .33	A .42 ± .26	a 1.08 ± .36	a .42 ± .26	a .67 ± .43
Stenolophus ochropezus (Say)	A 1.75 ± .62	A* 1.08 ± .42	A .33 ± .26	a 1.42 ± .74	a .08 ± .08	a 0
Forest species						
Chlaenius aestivus Say	A 5.08 ± 1.39	A 7.58 ± 2.92	A 5.67 ± 2.60	a 5.42 ± 1.78	a 3.92 ± 1.49	a 3.50 ± 1.98
Chlaenius erythropus Germar	A 1.42 ± .71	A 1.25 ± .65	A .83 ± .21	a .58 ± .29	a 1.58 ± .99	a .42 ± .19

Cyclotrachelus brevoorti (LeConte)	A .25 ± .13	A .75 ± .28	A 1.08 ± .80	a .08 ± .08	a 1.00 ± .83	a .5 ± .34
Diplocheila assimilis (LeConte)	A .83 ± .58	A .50 ± .42	A .75 ± .35	a .25 ± .13	ab 1.33 ± .61	b 2.25 ± .72
Lophoglossus gravis LeConte	A 2.50 ± .77	A 6.58 ± 2.28	A 5.17 ± 1.36	a 2.42 ± .82	a 4.92 ± 1.32	a 4.25 ± 1.49
Olisthopus spp. Dejean	A .33 ± .19	A .92 ± .67	B 4.83 ± 1.10	a 0.58 ± .19	b 1.67 ± .64	b 4.08 ± .88
Piesmus submarginatus (Say)	A .75 ± .75	A 1.83 ± .76	A .67 ± .36	a .08 ± .08	a 1.5 ± .60	a 3.67 ± 1.77
Unknown habitat requirements						
Acupalpus sp. 2	A* 8.67 ± 2.81	B* 3.00 ± 1.04	B 1.33 ± 0.80	a* 1.17 ± 0.32	b* 0.50 ± 0.15	b 0.25 ± 0.13
Agonum aeruginosum Dejean	A .67 ± .28	A .25 ± .18	A .83 ± .21	a .08 ± .08	a .08 ± .08	a .33 ± .19
Agonum decorum (Say)	A* 3.17 ± .89	AB* 2.33 ± .69	B .42 ± .26	a* .08 ± .08	a* .58 ± .36	a .33 ± .19
Chlaenius sp. 3	A .92 ± .42	A 4.17 ± 1.73	A 3.75 ± 1.41	a .75 ± .45	a 1.42 ± .68	a 1.58 ± .63
Clivina rubicunda LeConte	A* 2.0 ± .62	B .42 ± .15	B 0	a* 0	a .17 ± .11	a .08 ± .08
Cymindis spp. Latreille	A .33 ± .14	A 0.75 ± .33	A .92 ± .36	a .33 ± .19	a 1.17 ± .34	a 1.5 ± .65
Loxandrus sp. LeConte	A* 4.83 ± 1.09	A 2.58 ± 0.50	A 2.42 ± 0.70	a* 0.67 ± 0.22	a 2.08 ± 0.82	a 1.75 ± 0.73
Micratopus aenescens (LeConte)	A* 14.83 ± 5.96	A 7.17 ± 1.67	A* 2.67 ± .53	b* 1.08 ± .34	a 5.33 ± 1.80	ba* 4.25 ± .84
Oodes amaroides Dejean	A* 3.42 ± .92	B* 1.50 ± .54	B .25 ± .18	a* .42 ± .19	a* .25 ± .13	a .17 ± .11
Oodes sp. 2	A .83 ± .59	A .83 ± .59	A .83 ± .44	a .25 ± .18	a .17 ± .11	a .17 ± .11
Paratachys spp. Casey	A* 4.33 ± 1.51	B .58 ± .19	AB 2.08 ± 1.02	a* .92 ± .51	a 1.67 ± .90	a .83 ± .30
Semiardistomis viridis (Say)	A* 5.42 ± 1.90	A 13.25 ± 5.54	A* 14.08 ± 3.40	a* 54.33 ± 12.29	b 16.67 ± 6.27	b* 1.58 ± .43

For each species and gap age, values with the same letter are not significantly different (Ryan–Einot–Gabriel–Welsch Multiple Range Test, $p < 0.05$).
*denotes significant differences ($p < 0.05$) between the same trap locations (e.g. center vs. center) in young and old gaps.

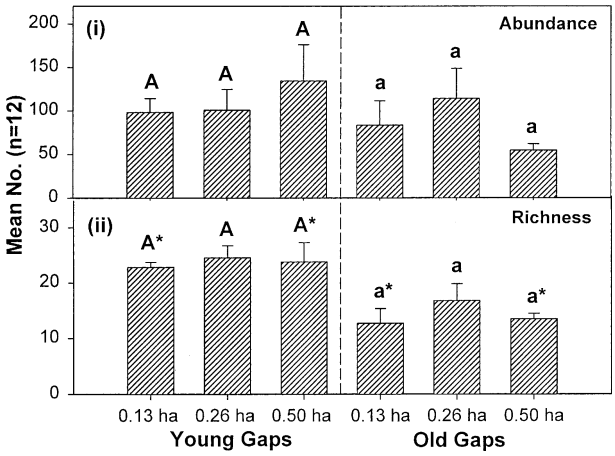

Figure 3. Mean (±SE) abundance (a) and richness (b) of carabids collected in malaise and pitfall traps in 2001 in bottomland hardwood forest gaps of different size (0.13, 0.26, and 0.50 ha) created in 1994 and 2000 in South Carolina, USA. Within graphs (for each gap age), bars with the same letter above them are not significantly different (Ryan–Einot–Gabriel–Welsch Multiple Range Test, $p < 0.05$). Asterisks denote significant differences ($p < 0.05$) between the same trap locations (e.g. center vs. center) in old and young gaps.

(Table 1). While *Acupalpus* sp. 2 was more abundant at the centers of both young and old gaps, *S. viridis* was much more numerous in old gap centers than at the edge or in the forest. It was also significantly more abundant in old gap centers than in young gap centers. Several abundant species appeared to respond positively to recent disturbance, but only *Notiobia terminata* (Say) was found exclusively in young gaps (Table 1).

The most similar carabid assemblages were those at the edges of gaps and the forests surrounding them (Table 2). The edges of old and young gaps also had a high degree of similarity (72%). The least similar carabid communities were those at the centers of young and old gaps (Table 2), but carabid assemblages in gap centers and surrounding forests also had relatively low similarity.

Discussion

Many studies have shown an overall increase in the species richness and/or abundance of carabids following disturbance (Eryschov and Trophimova 1984; Niemelä et al. 1993, 1994; Thompson and Allen 1993; Beaudry et al. 1997; Heliola et al. 2001; Warriner et al. 2002; Koivula et al. 2002). While some studies have found no overall change in carabid abundance or species richness, they have identified significant affects at the species level (Atlegrim et al. 1997) as well as differences in species composition between disturbed and undisturbed sites (Greenburg and Thomas 1995; Butterfield 1997; Werner and Raffa 2000).

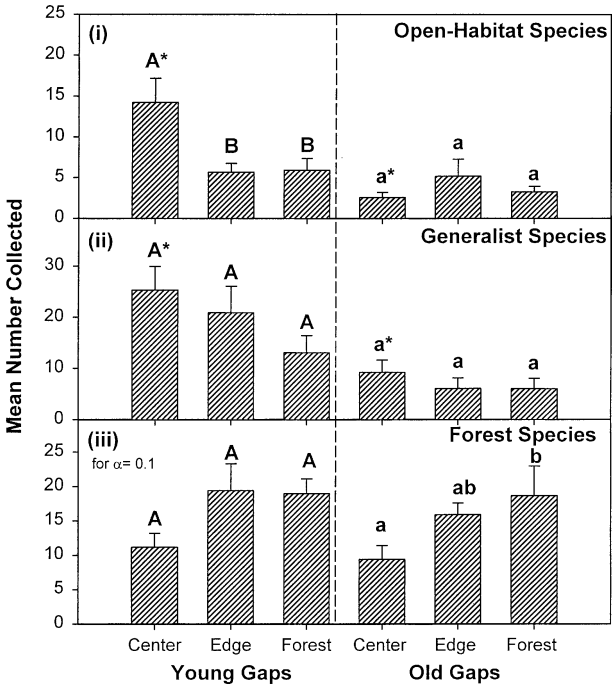

Figure 4. Mean (±SE) number of carabids collected in malaise and pitfall traps in a bottomland hardwood forest, South Carolina, USA in 2001. The traps were placed at the center, edge, and in the forest surrounding 'young' (created in 2000) and 'old' (created in 1994) canopy gaps. The species (Table 2) were categorized as preferring open-habitat (a), being generalists (b), or preferring intact forests (c) based on information in Larochelle and Lariviere (2003). Within graphs (for each gap age), bars with the same letter above them are not significantly different (Ryan–Einot–Gabriel–Welsch Multiple Range Test, $p < 0.05$). Asterisks denote significant differences ($p < 0.05$) between the same trap locations (e.g. center vs. center) in old and young gaps.

Table 2. Raabe's percent similarity of carabids in new (1 year) vs. old (7 years) canopy gaps by location (center, edge, or 50 m into surrounding forest) in a South Carolina bottomland hardwood forest, 2001.

Comparison	Percent similarity
New Edge vs. New Forest	76.21
Old Edge vs. Old Forest	75.30
New Edge vs. Old Edge	72.33
New Forest vs. Old Forest	67.66
New Center vs. New Edge	60.64
Old Center vs. Old Edge	58.47
Old Center vs. Old Forest	50.01
New Center vs. New Forest	49.11
New Center vs. Old Center	46.49

As might be expected, habitat specificity appears to determine the response of many carabids. The abundance of open-habitat species, for example, has been shown to increase in disturbed areas, while the numbers of forest-dwelling species often decreases or disappears following disturbance (Niemelä et al. 1993).

Our results are generally consistent with these trends, but there appears to be substantial differences in the abundance, species richness, and community composition of carabids with time after disturbance. For example, the carabid abundance, richness, and species composition differed greatly between the centers of young and old gaps. Furthermore, while species composition differed greatly between both young and old gaps centers and their respective forest locations, differences between the abundance and species richness of carabids at the centers of gaps and the forests surrounding them was significant only for young gaps. Open-habitat species were more abundant at the centers of young gaps than in the surrounding forest, but there was no difference in abundance between the centers of old gaps and the forests surrounding them. Conversely, forest species were less abundant at the centers of gaps than in the forest, but only for old gaps was this difference significant. Thus, the carabid communities present at the centers of old gaps differed greatly from those found at the centers of young gaps as well as from those in the forests surrounding old gaps.

Past studies have also noted changes in carabid communities with time after disturbance. For example, in a study involving single-tree selection cutting, Vance and Nol (2003) found reduced activity densities in recently (0.5–3 years) cut stands compared to reference stands, while the activity densities for certain species was higher in older (15–20 years) cut stands. The authors attribute these differences to significant reductions in leaf litter in the recently cut stands, and to differences in the vegetation in older stands. The importance of factors such as vegetation structure, temperature, humidity, light intensity, and soil moisture to ground beetles is well supported by past research (Lenski 1982a; Cardenas and Bach 1989; Thompson and Allen 1993; Magura et al. 1997; Antvogel and Bonn 2001; Warriner et al. 2002).

Reduced competitive exclusion may have played a role in the higher abundance and species richness of carabids observed in young gaps (Allen and Thompson 1977; Lenski 1982a, b), but we suspect that it had relatively little effect in this study. The increase in habitat heterogeneity following disturbance was probably much more important. For example, timber removal created large amounts of coarse woody debris and greatly increased the complexity of the gap floor. While young gaps contained an abundance of CWD, little remained in the old gaps. Differences in vegetation between young and old gaps were similarly dramatic. In contrast to young gaps in which there were scattered clumps of grasses, tree sprouts, and herbaceous growth, old gaps were covered in a dense growth of young trees competing for sunlight. Because young and old gaps were so different in habitat structure, it is not surprising that carabid abundance, species richness, and composition differed greatly between the two locations.

Because the carabid communities at the edges of young and old gaps were so similar to those in the surrounding forest, we have little indication of a distinct edge community. Although researchers in Hungary reported unique edge communities as well as several species unique to edge habitats (Magura and Tothmeresz 1997; Magura et al. 2001; Magura 2002), the results from other studies are similar to our own (Spence et al. 1996; Heliola et al. 2001; Kotze and Samways 2001).

The carabid community in seven-year old gaps is far from recovered, despite comparable abundance and species richness between old gaps and the surrounding forest. This is indicated by the low degree of similarity between the two sites. In fact, carabids at the centers of old gaps are only slightly more similar to those in the forest than are the carabids at young gap centers (50.0 and 49.1% similar, respectively). These results emphasize the fact that abundance should not be used alone (Moore et al. 2004) to determine the recovery time of carabid assemblages.

Although Vance and Nol (2003) found an increase in both open-habitat species and forest generalists 0.5–3 and 15–20 years after single-tree selection harvests, we could identify no common trend among carabids between young and old canopy gaps. The response of carabids to young and old gaps differed greatly, even among species with similar habitat preferences. For example, of the six common open-habitat species in this study, three were significantly more abundant at young gap centers than at the edges or in the forest surrounding young gaps, but there were no differences among old gap locations. Furthermore, of the 31 most abundant morphospecies collected, 13 exhibited a significant difference among either young or old gap locations. Of these, only five differed significantly among old gap locations and just two responded similarly to young and old gaps.

These differences in abundance between young and old gaps are probably due to the specific habitat requirements of each species. Given this, it is interesting to note that just two species (*S. viridis* and an *Acupalpus* species) were more abundant at the centers of old gaps than in the nearby forest. While the *Acupalpus* species was more abundant at the center of young gaps than old gaps, *S. viridis* was more abundant at the centers of old gaps than at any other young or old gap location. This result further emphasizes the importance of time considerations when studying the effects of disturbance on ground beetles, as well as the species-specific response of carabids to disturbance.

While many species tend to be more abundant in disturbed habitats, several have been shown to exist there exclusively (Niemelä et al. 1993; Thompson and Allen 1993; Beaudry et al. 1997; Warriner et al. 2002). For example, in this study, *N. terminata* was collected only in the center or at the edge of young gaps. Similarly, a number of forest species were found in much greater numbers in the forest than elsewhere. While we found no substantial evidence for the presence of strict forest specialists, such species may have been collected in low numbers (and could not be analyzed statistically) or not at all. Since total carabid abundance in the forest near young gaps was different from that near old gaps, gap creation had a definite effect on the carabid community at least 50 m into the surrounding

forest. Because of this, obligate forest species, if present, may have found the forests surrounding the gaps to be unsuitable. Although many carabids will eventually recolonize an area after disturbance (Koivula et al. 2002) some forest specialists are unable to reestablish populations in regenerating clear-cut stands (Beaudry et al. 1997) and old growth species with poor dispersal ability may face local extinction if stands of mature forest are not preserved (Halme and Niemelä 1993; Spence et al. 1996; Beaudry et al. 1997; Heliola et al. 2001; Koivula et al. 2002). Because group selection harvesting disturbs smaller patches of bottomland hardwood forest at any one time and is more similar to natural levels of disturbance, it may lessen the detrimental effects of disturbance on these sensitive forest species.

How group selection cutting compares to other forestry practices, remains unclear. Recent work in Finland has found small (0.16 ha) openings to be less disruptive of community structure than larger clear-cut stands (Koivula 2002b; Koivula and Niemelä 2003) but much more comparative work is needed to ascertain the advantages of various harvesting techniques with respect to environmental health. Different forests have different natural rates of disturbance (Hunter 1990; Guldin 1996) so the effects of a particular management technique may depend upon the forest type under consideration. Because few carabids were negatively affected by gap creation, and none seemed to be completely eliminated by the disturbance, we feel that group selection cutting may be particularly well suited to bottomland hardwood forests and deserves further consideration.

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