Changes in Ground Beetle (Coleoptera: Carabidae) Species Assemblages after Removal of Red Pine (*Pinus resinosa*) Overstory on Dry Sand Prairie Sites in Michigan

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Abstract

Ground beetle (Coleoptera: Carabidae) species assemblages were studied at sites on the Huron-Manistee National Forests in Newaygo County, Michigan. The goal was to monitor changes in carabid diversity on areas where mature red pine (*Pinus resinosa* Sol. ex Aiton) was removed during the 1996–1997 winter and compare with carabid diversity at nearby natural dry sand prairie sites, natural oak-pine barrens, and uncut red pine stands. The red pine had been planted on dry sand prairie sites during 1940–1950. Sampling with pitfall traps occurred during May-August in both 1996 and 1997, but only July–August in 1999. Overall, 16,259 carabid specimens were collected, representing 92 species of which one was a new state record for Michigan: *Dicaelus furvus furvus* Dejean. Of the 92 species, 27 were collected in the uncut red pine stands, 41 in the natural dry sand prairie sites, 28 in the natural oak-pine barrens, and 77 in the clearcut areas. Of all 41 species collected in the dry sand prairie sites, 27 (66%) of these were collected in the clearcut sites in 1997, 30 (73%) in 1999, and 34 (81%) for both years combined. Carabid abundance peaked in June in the red pine and oak-pine sites, compared with August for the clearcut sites. Non-metric multidimensional scaling (NMDS) ordination indicated considerable overlap in the carabid composition for the red pine and oak-pine collections, but more distinct assemblages for the dry sand prairie and clearcut sites. Of the 92 species, 41 (45%) were significant indicator species for a particular habitat.

Keywords: Carabidae, biodiversity, state records, tree harvesting, Michigan

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The family Carabidae, including both the ground beetles and tiger beetles, contains about 40,000 described species worldwide, making it the third most speciose family of beetles (Coleoptera), following the Staphylinidae and Curculionidae (Bouchard et al. 2017). The Carabidae of North America are well-known with about 2500 species now recognized (Bousquet 2012), of which at least 528 occur in Michigan (Ruesink et al. 2023). Carabids are usually abundant and occur in many terrestrial habitats, from rainforests to deserts, and from sea level to mountain tops (Larochelle and Larivière 2001, 2003). Many carabids are sensitive to environmental change, which makes them useful as bioindicators (Lövei and Sunderland 1996, Pearce and Venier 2006, Work et al. 2008, Koivula 2011). Furthermore, they are also highly suitable as bioindicators because: (1) carabids are relatively easy to sample and quantify with pitfall traps; (2) pitfall trapping is relatively inexpensive and passive; (3) carabids are relatively well-known taxonomically and identification keys exist, especially for the north temperate species; and (4) most species are localized with only a few migrating long distances (Rainio and Niemelä 2003, Langor and Spence 2006). However the limitations of pitfall trapping should be recognized as well, such as their reduced ability to collect arboreal species (Woodcock 2005).

There is a large body of research documenting changes in carabid assemblages in response to various forestry practices, such as logging, which can alter tree age structure and composition, herbaceous plant cover, level of sun exposure, and near-ground microclimate. Most studies have compared carabid communities in mature native forests with nearby areas that had been logged and then replanted at various times with either native or exotic tree species (Niemelä et al. 1993, Magura et al. 2003, Yu et al. 2006, Fuller et al. 2008, Work et al. 2008, Koivula et al. 2019). Other researchers have explored the impact of both logging and various levels of slash removal or live tree retention on carabids communities (Work et al. 2010, 2013, 2014, 2023; Venier et al. 2017; Wu et al. 2020), as well as the impact of gap size during small selective logging operations (Vance and Nol 2003, Klimaszewski et al. 2005, Ulyshen et al. 2006).

By contrast, little research has been conducted on carabid assemblages in dry sand prairie habitats in the northcentral United States. Learning that the Huron-Manistee National Forests in Michigan planned to convert several mature red pine (*Pinus resinosa* Sol. ex Aiton) stands back to dry sand prairie, which was the original natural plant community, we decided to conduct this study to learn how carabid species assemblages would change after logging.

The Huron National Forest was established in northeastern Lower Michigan in 1909 and the Manistee National Forest in northwestern Lower Michigan in 1938. Later, in 1945, the two were combined administratively to form the Huron-Manistee National Forests (HMNF), which together cover almost one million acres (ca. 400,000 ha). Much of the original HMNF acreage came from tax-delinquent lands that were abandoned farms or had been logged and sometimes burned (Conrad 1997, Stearns 1997). In response to the Great Depression of the 1930s, the Civilian Conservation Corps (CCC) was formed in 1933. Tree planting was a major activity of the CCC crews. In Michigan, CCC crews planted nearly 485 million trees, more than any other US State (Dickmann and Leefers 2016). In Lower Michigan, there were 36 CCC camps on the HMNF (Conrad 1997). Thousands of acres of land in both the Huron and Manistee National Forests were planted to pine, primarily red pine, during the 1930s and early 1940s (Conrad 1997, Haack and Mattson 1993). These tree planting efforts slowed during World War II on the HMNF but then increased during the late 1940s through the 1960s, again planting primarily red pine (Haack and Mattson 1993, Dickmann and Leefers 2016).

Many of the areas planted to pine on the HMNF were former prairies and savannas. On HMNF lands in Newaygo County, in western Lower Michigan (Fig. 1A), many of these sites would have been classified as dry sand prairie or oak-pine barrens (Chapman and Crispin 1984, Chapman and Brewer 2008). Detailed descriptions of Michigan's dry sand prairie and oak-pine barrens habitats are given in Cohen (2000) and Kost (2004). Several dry sand prairie remnants still occur in Newaygo County on HMNF lands and are often surrounded in part by oak-pine barrens. In these areas, the pines are mostly eastern white pine, *Pinus strobus* L., and the oaks are mostly black oak, *Quercus velutina* Lam., northern pin oak, *Quercus ellipsoidalis* E.J. Hill, and white oak *Quercus alba* L.

As part of a national effort to restore natural habitats within the National Forest System, efforts have been underway since the early 1990s to convert some HMNF red pine stands back to prairie and savanna. The Karner blue butterfly, *Plebejus samuelis* (Nabokov) (Lepidoptera: Lycaenidae), which was federally listed as endangered in 1992, is one of the key target species in these oak savanna restoration efforts on the HMNF (Keough 2023). Karner blue larvae feed only on foliage of wild lupine (*Lupinus perennis* L.; Fabaceae), which grows readily in open sandy sites (Haack 1993). The HMNF continues to maintain these sites and others as open oak savanna through various combinations of burning, woody vegetation control, and seeding with herbaceous native plants (USDA Forest Service 2004, 2013; Keough 2023; Fig. 1B).

The current study was conducted in the late 1990s on HMNF lands in Newaygo County, MI. At that time, several red pine stands planted during 1940–1950 were under consideration for conversion to native prairie. Some of these stands were adjacent to HMNF lands that had been set aside for research or as a natural area. These included portions of the Lower Peninsula Experimental Forest, established in 1954 (Adams et al. 2004) and the Newaygo Prairies Research Natural Area, established in 1988 (USDA Forest Service 1988). The initial plan after logging was to conduct spring burns at some sites, fall burns at others, and leave some logged areas unburned. The primary objective of the study was to determine if certain carabid species could serve as useful indicators during the conversion of red pine plantations to dry sand prairie habitats that are typical of western Lower Michigan. Therefore, we documented and compared carabid abundance and diversity in four habitat types over a 4-year period: (1) red pine stands the summer prior to logging and again during the first and third summer after logging, and (2) nearby dry sand prairies, oak-pine barrens, and uncut red pine stands during the same period. We also analyzed the numerical relationships of the carabid assemblages by habitat using non-metric multidimensional scaling and conducted indicator species analysis.

Materials and Methods

Study area. The study was conducted on portions of the HMNF in Newaygo

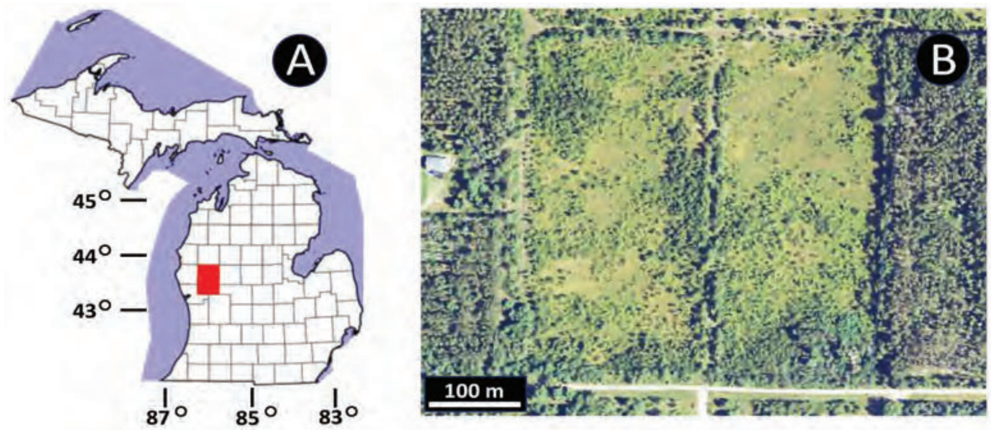

Figure 1. A: County outline map of Michigan with Newaygo County highlighted in red. **B:** Aerial photo from 2022 (25 years post-logging), showing two of the ten sampled blocks that had been clearcut during the winter of 1996–1997. The 15-acre block on the left originally received the "slash free" treatment, whereas the 14-acre block on the right received the "leave slash" treatment. (Image source: USDA National Agriculture Imagery Program.)

County, centering near N 43.4658° Lat, W 85.7045° Long (Fig. 1). The trapping efforts in this study, especially those on the dry sand prairie (Fig. 2D) and oak-pine barrens sites, occurred on the Lower Peninsula Experimental Forest and Newaygo Prairies Research Natural Area. By contrast, trapping in the red pine stands, either logged or unlogged, occurred in the Lower Peninsula Experimental Forest as well as on nearby actively managed lands of the HMNF. The two principal soils in the study area are Sparta loamy sand and Plainfield sand, the former of which is a true prairie soil (USDA Forest Service 1988, Adams et al. 2004).

Winter logging during 1996-1997. Several individual red pine stands were cut during the winter months of 1996–1997. The cut stands (blocks) were rectangular in shape and measured about 12–15 ac (4.8–6.1 ha) each (Fig. 1B). Ten of these cut stands (blocks) were selected to sample in 1997.

Post-logging treatments. The original plan after logging was to divide each of the 10 selected blocks into four quadrants to create 40 units of roughly equal size and then impose assorted treatments on each unit involving the residual slash (limbs and tree tops) and burning. Two treatments involved either mechanically removing the logging slash (Figs. 2E, 2F) or leaving the slash in place (Fig. 2C). On 24 of the 40 units, the slash was removed (slash free), while on 16 units the slash was left on site (leave slash). The removal of slash was conducted in late spring 1997. The other treatments involved burning, including spring burns, fall burns, or no burning. Unfortunately, weather conditions did not allow the original burn plan to be followed. As a result, the fall burn occurred in September 1997 and the spring burn not until April 1999.

Carabidae trapping methods. We used barrier pitfall traps to collect carabids in all years of the study. The use of a barrier increases the trap catch by directing ground invertebrates towards the collection cups and thereby increases the chances of collecting more species at a site (Durkis and Reeves 1982, Skvarla et al. 2014). The traps consisted of a 1-m long strip of plastic garden edging that was partially buried in the soil with a 32-oz (0.95 L) plastic collection cup at each end of the barrier (Figs. 2A, 2B). The collection cups, ca. 10-cm wide at the top, were buried so that the upper rim was level with the surrounding soil and with the garden edging touching near the cup center. A second 32-oz collection cup with its rim removed was placed inside the first cup, which allowed removal of the second cup when collecting the insects without causing much disturbance to the first cup. The cups were filled about halfway with 70% ethanol, which served as both a killing agent and preserving solution. Then, a shorter 16-oz plastic cup of similar diameter, with rim removed and with a ca. 2 × 2 cm hole cut in its bottom was placed inside the two 32-oz cups. The smaller cup fit snugly inside the larger cup, and generally kept leaves out of the alcohol while allowing the insects to fall through. After the cups, alcohol, and barrier were assembled, a plastic plate, ca. 25 cm diameter, was placed over each cup and sup-

Figure 2. A: Installing a barrier pitfall trap in one of the prairie sites in May 1996. **B:** Installing a trap in a red pine site in May 1997. **C:** Example of a "leave slash" site in August 1997. **D:** View of one of the open prairie sites that was sampled in 1996. **E:** One of the "slash free" sites in May 1997. **F:** One of the slash free sites in October 1998.

ported about 8 cm above the soil using two nails along the outer edge of the plate and the top of the plastic barrier. These plates provided protection from rain and reduced animal disturbance. Samples were collected every 9 days on average (range: 5 to 15 days) during May to August in 1996 and 1997, and during July and August in 1999 (Table 1).

1996 Trapping program. We installed 45 barrier pitfall traps on 9 May 1996 in three habitats: (1) 15 traps in 14 red pine stands, most of which were scheduled for logging later that winter; (2) 15 traps in six open areas of nearby dry sand prairie sites; and (3) 15 traps in five nearby oak-pine barrens that surrounded some of the sampled prairies (Table 1). All 45 traps were visited and emptied every 5 to 14 days up until 20 August when sampling ended.

1997 Trapping program. We installed 50 barrier pitfall traps on 20 May 1997, including 10 in three unlogged red pine stands, and 40 traps in ten of the clearcut blocks. The traps in the ten clearcut blocks were positioned so that one trap occurred in each of the four treatment units in each block. Traps were emptied every 6 to 15 days, ending on 27 August (Table 1). We did not sample the nearby dry sand prairie nor oak-pine barrens sites in 1997.

Table 1. Temporal and spatial sampling design for the 1996 to 1999 carabid study in Newaygo County, Michigan, including year of sampling; annual sampling period (month in Roman, day in Arabic); number of times study area was visited; time intervals between sampling dates; number of pitfall traps established by habitat type; total trap days; and total number of carabid species collected by year.

Sample year	Sample period (month & day)	No. of site visits	Interval length between pitfall samples (days)	No. of pitfall traps established by habitat type				Total trap days	Total No. carabid species collected
				Pine	Oak	Prairie	Clearcut		
1996	V 9–VIII 20	11	5–14	15	15	15	No sites logged yet	4635	47
1997	V 20–VIII 27	10	6–15	10	Not sampled	Not sampled	40	4950	68
1999	VII 9–VIII 31	7	6–10	6	6	6	30	2544	65

1999 Trapping program. Trapping in 1999 occurred in July and August, which allowed targeting the summer months with the greatest carabid diversity, based on our sampling experiences in 1996 and 1997. We installed 48 barrier pitfall traps on 9 July 1999, including six traps in three unlogged red pine stands (two traps per stand), six traps in three nearby dry sand prairies (two traps each), and six traps in three nearby oak-pine barrens (two traps each). The remaining 30 traps were placed in ten of the original 40 clearcut units, three traps per unit. The selected units represented five different treatments (two units per treatment): (1) leave slash only; (2) slash free only; (3) leave slash and fall burn; (4) leave slash and spring burn; and (5) slash free and spring burn (where primarily vegetation that grew during the previous two summers, stumps, and small wood pieces were burned). Traps were emptied every 6 to 10 days, ending on 31 August (Table 1).

Sample processing and carabid identification. When the samples were collected, the contents from both cups at the ends of each barrier were combined into a single, labeled sealed plastic container. Samples were transported first to the US Forest Service laboratory at Michigan State University, East Lansing, MI, where carabid specimens were removed from each sample and stored in 70% ethanol within separate sealed jars to maintain sample integrity. After this initial sorting, all samples were transported to Morgantown, WV, for final sorting by REA to morphospecies from which representatives were pinned and labelled. These representatives were identified to species by RLD to develop a reference collection that REA could use to tentatively identify all further specimens to species. Final species confirmation was made by RLD, who has broad taxonomic expertise with the Carabidae and a large reference collection at the Carnegie Museum of Natural History (CMNH) in Pittsburgh, PA. Nearly all specimens from this study were deposited at the CMNH with a few voucher specimens sent to TRP in East Lansing, MI.

Carabid species characteristics. For each identified carabid species, we obtained traits and ecological information from the literature. The feeding habits for adults of each species was categorized as: (1) seed eater (herbivore), (2) predator (carnivore), or (3) exhibiting both of these feeding habits based on Larochelle and Larivière (2001, 2003). When no information was found for a species, then the typical food for the entire genus was used based on Lindroth (1961, 1963, 1966, 1968, 1969). We also used information from Larochelle and Larivière (2001, 2003) to further characterize each species by: (1) eco-tolerance based on its occurrence in many habitat types (eurytopic) or restricted to a few (stenotopic); (2) typical adult habitat preference as being graminephilous (grassland, prairie, meadow or field sites), psammophilous (open sand, clay, organic litter sites), or silvicolous (forest or woodland sites); (3) typical soil moisture requirements as hygrophilous (wet or usually moist conditions), mesophilous (moderate moisture conditions), or xerophilous (dry conditions); and (4) adult flight ability as being able to fly (macropterous), likely unable to fly (brachypterous), or having both brachypterous and macropterous forms. Differences by habitat type in the proportion of adults in each of the above categories were compared by Chi-square test (χ^2).

Data management and analyses. The data were assembled into a spreadsheet by species, specimen count, trap number, collection date, year, habitat, and treatment. For each year of the study, the mean (±SE) number of carabid individuals per trap and carabid species per trap were calculated for each habitat or treatment type, using all collection data for the entire trapping season. Each trap was considered an independent experimental unit in all analyses. Depending on the variable being tested, means were compared with ANOVA followed by the Tukey HSD test or the Kruskal–Wallis non-parametric analysis of variance test followed by the Dunn's test for post hoc pairwise comparisons. An alpha level of 0.05 was used for significance in all tests.

To explore differences in carabid assemblages by habitat and year, species abundance data were examined with non-metric multidimensional scaling (NMDS) ordination using PC-ORD v.7 for Windows (McCune and Mefford 2017). The data matrix consisted of log10 (x + 1) transformed, season-long specimen counts by trap, habitat or treatment, and year. We weighted the species equally and used the NMDS ordination default program settings, e.g., 250 randomized runs and a Bray-Curtis distance measure (McCune and Mefford 2017). For each determined axis a Monte Carlo test was conducted to evaluate its difference from a random ordination structure (Dexter et al. 2018).

The Indicator Value Index (IndVal) developed by Dufrêne and Legendre (1997), was calculated for each species, using the program PC-ORD to identify indicator species associated with the various habitats sampled. This method uses a combination of the percentage of habitats in which a particular species occurs along with the average abundance of that species within each habitat divided by the average abundance of that species in all habitat types to determine a species' indicator value. Values for IndVal range from 0 to 100, where values close to zero reflect little indicator value, while those closer to 100 indicate near perfect association between a species and a particular habitat (Dufrene and Legendre 1997). A Monte Carlo test of observed (IVobs) indicator values relative to those of a randomized group (IVran) are used to determine the significance of a particular indicator value.

Results

For all years combined, 16,259 carabid specimens were collected and identified to 92 species, representing the following number of species within six subfamilies: 7 Carabinae; 5 Cicindelinae; 70 Harpalinae; 2 Loricerinae; 3 Scaritinae; and 5 Trechinae (Table 2). The five most collected species were *Harpalus pensylvanicus* (DeGeer) (4,094 specimens), *Carabus goryi* Dejean (3,909), *Synuchus impunctatus* (Say) (1,679), *Pterostichus pensylvanicus* LeConte (1,248), and *Harpalus lewisii* LeConte (1,032) (Table 2). By contrast, 39 of the 92 species were represented by five specimens or fewer, with 19 species represented by a single specimen. The two *Dicaelus furvus furvus* Dejean specimens collected in this study represent a new state record for Michigan based on data in Ruesink et al (2023). Four of the 92 species are exotic introductions now established in North America: *Amara apricaria* (Paykull) (3 specimens), *Clivina fossor fossor* (Linnaeus) (9), *Harpalus affinis* (Shrank) (164), and *Pterostichus melanarius melanarius* (Illiger) (6). Of the 16,259 carabids, 4,482 were collected in 1996 (47 species), 3,852 in 1997 (68 species), and 7,925 in 1999 (65 species). Considering the four major habitat types for all years combined, 311 specimens (41 species) were collected in the natural dry sand prairie sites, 5,048 specimens (27 species) in the red pine sites, 1,718 specimens (28 species) in the natural oak-pine barrens sites, and 9,182 specimens (77 species) in the clearcut sites (Table 2).

Venn diagrams were used to display various combinations of the carabid species collected in this study by habitats and treatments (Fig. 3, data from Table 2). Of the 64 species collected in the red pine (pine), dry sand prairie (prairie), and oak-pine barrens (oak) sites combined, 10 species were collected in all three habitats, as well as 7 found only in red pine sites, 26 only in dry sand prairie sites, and 9 only in oak-pine barrens sites (Fig. 3A). Of the 88 species collected in the red pine, dry sand prairie, and clearcut sites combined, 13 species were collected in all three habitats, as well as 4 found only in the red pine sites, 7 only in the dry sand prairie sites, and 33 only in the clearcut sites (Fig. 3B). For the 81 species collected in the red pine sites and the clearcut sites in the initial year after logging (1997) and third year post-logging (1999), 12 species were found in all habitats, as well as 4 found only in the red pine sites, 13 found only in the clearcut sites 1-year post logging, and 10 found only in the clearcut sites 3-years post logging (Fig. 3C). Similarly, for the 84 species collected in the dry sand prairie and the clearcut sites one (1997) and three years (1999) post-logging, 23 species were found in all habitats, as well as 7 found only in the prairie openings, 18 found only in the clearcut sites 1-year post logging, and 5 found only in the clearcut sites 3-years post logging (Fig. 3D).

Table 2. Summary data for the carabid species collected in pitfall traps in Newaygo County, MI, including ecological and life history data, number of specimens collected by habitat type, number of specimens collected by year, and months of collection.

	Species ecological attributes						Percent of specimens collected by habitat type				Number of specimens collected by year			
Species	Adult food[1]	Species eco-tolerance[2]	Adult habitat type[3]	Soil moisture[4]	Adult flight ability[5]	Total number of specimens collected	Red pine	Clear-cut	Prairie	Oak-pine	1996	1997	1999	Numeric calendar of months collected
Carabinae														
Carabini														
Calosoma calidum (Fabricius)	Pr	E	G	X	YES	96	1	99	0	0	1	15	80	6 7 8
Calosoma frigidum Kirby	Pr	E	S	M	YES	1	100	0	0	0	1	0	0	6
Carabus goryi Dejean	Pr	E	S	H	NO	3909	74.3	0.9	2.8	22.0	3214	640	55	5 6 7 8
Carabus serratus Say	Pr	E	S	X	BOTH	5	0	100	0	0	0	5	0	6 7
Carabus sylvosus Say	Pr	E	S	H	NO	9	66.7	22.2	0	11.1	6	2	1	6 7 8
Cychrini														
Scaphinotus bilobus (Say)	Pr	E	S	H	NO	18	66.7	33.3	0	0	11	7	0	6 7 8
Sphaeroderus stenostomus lecontei Dejean	Pr	E	S	H	NO	9	22.2	0	0	77.8	6	3	0	5 6 7 8
Cicindelinae														
Cicindelini														
Cicindela formosa generosa Dejean	Pr	S	P	X	YES	27	0	92.6	7.4	0	0	18	9	6 7 8
Cicindela patruela patruela Dejean	Pr	S	S	M	YES	3	0	0	100	0	3	0	0	5 6
Cicindela purpurea purpurea Olivier	Pr	E	G	X	YES	5	0	100	0	0	0	4	1	5 6 8
Cicindela scutellaris lecontei Haldeman	Pr	S	P	X	YES	11	0	100	0	0	0	3	8	6 7 8
Cicindelidia punctulata punctulata (Olivier)	Pr	E	P	X	YES	162	0	96.9	3.1	0	0	21	141	7 8
Harpalinae														
Chlaeniini														
Chlaenius brevilabris LeConte	Pr*	S	P	H	YES	1	100	0	0	0	1	0	0	**6**
Chlaenius impunctifrons Say	Pr	S	P	H	YES	1	100	0	0	0	0	1	0	6
Chlaenius nemoralis Say	Pr	S	P	H	YES	2	0	50	0	50	1	1	0	5 6
Chlaenius tomentosus (Say)	Pr	E	P	X	YES	20	0	65	35	0	3	5	12	6 7 8
Galeritini														
Galerita janus (Fabricius)	Pr	E	S	M	YES	6	0	66.7	16.7	16.7	2	1	3	5 6 7 8
Harpalini														
Agonoleptus conjunctus (Say)	Pr	E	P	X	BOTH	6	0	66.7	33.3	0	2	0	4	5 7
Anisodactylus merula (Germar)	S Pr	E	P	X	YES	105	0	96.2	3.8	0	4	18	83	5 6 7 8
Anisodactylus rusticus (Say)	S Pr	E	P	X	YES	20	0	95	5	0	1	0	19	7 8

(Continued on next page)

Table 2. (Continued).

Species	Species ecological attributes					Total number of specimens collected	Percent of specimens collected by habitat type				Number of specimens collected by year			Numeric calendar of months collected
	Adult food[1]	Species eco-toler-ance[2]	Adult habitat type[3]	Soil mois-ture[4]	Adult flight ability[5]		Red pine	Clear-cut	Prairie	Oak-pine	1996	1997	1999	
Anisodactylus sanctaecrucis (Fabricius)	S Pr	E	P	M	YES	1	0	100	0	0	0	1	0	6
***Harpalus affinis* (Shrank)†**	S Pr	E	P	X	YES	164	0	100	0	0	0	3	161	6 7 8
Harpalus caliginosus (Fabricius)	S Pr	E	P	X	YES	13	0	84.6	15.4	0	0	0	13	7 8
Harpalus compar LeConte	S Pr	E	G	X	YES	155	0	100	0	0	0	2	153	7 8
Harpalus erraticus Say	S Pr	S	P	X	YES	262	0	99.2	0.4	0.4	0	11	251	7 8
Harpalus faunus Say	S Pr	E	P	X	YES	26	3.8	92.3	3.8	0	2	10	14	6 7 8
Harpalus fulvilabris Mannerheim	Pr	E	S	M	YES	2	0	100	0	0	0	2	0	6
Harpalus herbivagus Say	S Pr	E	G	X	YES	521	0	99.8	0.2	0	0	2	519	5 6 7 8
Harpalus indigens Casey	Pr	E	G	X	YES	256	0	94.1	5.9	0	4	30	222	6 7 8
Harpalus laticeps LeConte	S*	E	G	X	YES	4	0	100	0	0	0	3	1	7 8
Harpalus lewisii LeConte	S*	E	G	X	YES	1032	0	99.6	0.4	0	4	37	991	5 7 8
Harpalus opacipennis (Haldeman)	S*	E	P	X	YES	1	0	0	100	0	1	0	0	7
Harpalus pensylvanicus (DeGeer)	S Pr	E	G	X	YES	4094	0	99.7	0.3	0	3	103	3988	7 8
Harpalus plenalis Casey	S*	E	P	X	YES	221	0	100	0	0	0	9	212	7 8
Harpalus providens Casey	Pr	S	S	M	YES	77	2.6	49.4	45.5	2.6	26	19	32	5 6 7 8
Harpalus somnulentus Dejean	Pr	E	P	M	YES	5	60	20	20	0	2	3	0	6 7
Notiobia terminata (Say)	S Pr	E	P	X	YES	6	0	100	0	0	0	5	1	8
Ophonus puncticeps Stephens	S Pr	E	P	X	YES	1	0	100	0	0	0	1	0	8
Selenophorus hylacis (Say)	S*	S	S	M	YES	1	0	0	100	0	0	0	1	8
Selenophorus opalinus (LeConte)	S*	E	P	X	YES	110	0	92.7	7.3	0	3	1	106	7 8
Selenophorus planipennis LeConte	S*	E	P	X	YES	5	0	100	0	0	0	0	5	7 8
Stenolophus lineola (Fabricius)	S Pr	E	P	M	YES	1	0	100	0	0	0	0	1	8
Trichotichnus autumnalis (Say)	S*	S	S	H	YES	45	0	0	0	100	45	0	0	6 7 8
Helluonini														
Helluomorphoides nigripennis (Dejean)	Pr*	S	S	H	YES	1	0	0	0	100	0	0	1	8
Helluomorphoides praeustus bicolor (T.W. Harris)	Pr*	S	S	X	YES	1	0	100	0	0	0	0	1	8
Lebiini														
Cymindis cribricollis Dejean	Pr	E	P	X	BOTH	3	33.3	33.3	0	33.3	0	2	1	8
Cymindis limbata Dejean	Pr	S	S	M	YES	4	0	50	0	50	0	1	3	7 8
Cymindis pilosa Say	Pr*	E	P	X	BOTH	3	0	66.7	33.3	0	0	1	2	8

Cymindis platicollis platicollis (Say)	Pr	S	S	M	YES	3	0	33.3	0	66.7	2	1	0	5 6
Microlestes linearis (LeConte)	Pr	E	G	X	BOTH	7	0	85.7	14.3	0	0	0	7	7 8
Syntomus americanus (Dejean)	Pr	E	G	X	BOTH	62	3.2	88.7	6.5	1.6	4	1	57	5 7 8
Licinini														
Dicaelus furvus furvus Dejean	Pr*	S	S	M	NO	2	0	50	0	50	1	1	0	5 6
Platynini														
Agonum cupripenne (Say)	Pr	E	G	X	YES	2	0	100	0	0	0	1	1	6 7
Agonum harrisii LeConte	Pr	S	G	H	YES	1	0	100	0	0	0	1	0	6
Agonum placidum (Say)	Pr	E	G	X	YES	1	0	0	100	0	1	0	0	6
Agonum retractum LeConte	Pr	S	S	M	BOTH	14	0	0	0	100	13	0	1	5 6 7
Platynus decentis (Say)	Pr	S	S	H	NO	1	0	0	0	100	1	0	0	6
Sericoda quadripunctata (DeGeer)	Pr	S	S	M	YES	1	0	100	0	0	0	1	0	7
Pterostichini														
Myas coracinus (Say)	Pr	S	S	M	NO	580	47.8	26.9	4.7	20.7	153	268	159	6 7 8
Myas cyanescens Dejean	Pr	E	S	M	NO	490	34.5	27.6	3.7	34.3	170	256	64	5 6 7 8
Poecilus chalcites (Say)	Pr	E	P	M	YES	3	0	66.7	33.3	0	1	1	1	5 8
Poecilus lucublandus (Say)	Pr	E	P	X	YES	42	0	97.6	2.4	0	1	30	11	6 7 8
Pterostichus adstrictus Eschscholtz	Pr	S	S	M	YES	23	60.9	34.8	0	4.5	3	20	0	5 6 7 8
Pterostichus commutabilis (Motschulsky)	Pr	E	G	M	YES	9	0	100	0	0	0	6	3	6 7 8
Pterostichus femoralis (Kirby)	Pr	E	G	M	BOTH	2	50	50	0	0	0	2	0	6
Pterostichus luctuosus (Dejean)	Pr	S	S	H	YES	1	0	100	0	0	0	1	0	5
***Pterostichus melanarius melanarius* (Illiger)†**	Pr	E	P	M	BOTH	6	16.7	66.7	16.7	0	2	4	0	7 8
Pterostichus mutus (Say)	Pr	S	S	X	YES	118	28.8	33.9	0	37.3	66	39	13	5 6 7 8
Pterostichus novus Straneo	Pr	S	S	M	NO	23	78.3	21.7	0	0	10	13	0	6 7 8
Pterostichus pensylvanicus LeConte	Pr	S	S	M	YES	1248	52.2	31	0.2	16.6	480	691	77	5 6 7 8
Pterostichus stygicus (Say)	Pr	S	S	H	NO	16	25	56.3	12.5	6.3	5	7	4	7 8
Pterostichus tristis (Dejean)	Pr	S	S	H	NO	118	73.7	18.6	0	7.6	37	64	17	6 7 8
Sphodrini														
Calathus gregarius (Say)	Pr	E	S	X	BOTH	137	17.5	5.1	2.9	74.5	17	10	110	6 7 8
Calathus ingratus Dejean	Pr	E	S	M	BOTH	87	42.5	3.4	2.3	51.7	42	37	8	6 7 8
Calathus opaculus LeConte	Pr	E	P	X	YES	9	0	88.9	0	11.1	0	3	6	8
Synuchus impunctatus (Say)	S Pr	E	S	M	BOTH	1679	47.1	48.2	0.1	4.5	108	1369	202	6 7 8
Zabrini														
Amara aenea (DeGeer)	S Pr	S	P	X	YES	3	0	33.3	66.7	0	2	1	0	7 8
***Amara apricaria* (Paykull) †**	Pr	S	P	X	YES	3	0	100	0	0	0	2	1	8
Amara convexa LeConte	Pr	S	P	X	YES	19	0	100	0	0	0	18	1	5 6 7 8
Amara littoralis Dejean	Pr	S	P	X	YES	3	0	100	0	0	0	3	0	7 8

(Continued on next page)

Table 2. (Continued).

Species	Species ecological attributes					Total number of specimens collected	Percent of specimens collected by habitat type				Number of specimens collected by year			Numeric calendar of months collected
	Adult food[1]	Species eco-tolerance[2]	Adult habitat type[3]	Soil moisture[4]	Adult flight ability[5]		Red pine	Clear-cut	Prairie	Oak-pine	1996	1997	1999	
Amara musculis (Say)	S	S	P	X	YES	1	0	100	0	0	0	1	0	8
Amara obesa (Say)	Pr	S	P	X	BOTH	7	0	100	0	0	0	3	4	7 8
Loricerinae														
Notiophilini														
Notiophilus aeneus (Herbst)	Pr	S	S	M	YES	6	16.7	33.3	0	50	1	1	4	7 8
Notiophilus semistriatus Say	Pr	S	P	X	BOTH	2	0	0	100	0	0	0	2	8
Scaritinae														
Clivinini														
***Clivina fossor fossor* (Linnaeus)†**	Pr	E	P	M	BOTH	9	0	100	0	0	0	7	2	6 7 8
Dyschiriini														
Dyschirius globulosus (Say)	Pr	E	P	M	BOTH	18	0	11	89	0	15	0	3	5 6 7 8
Pasimachini														
Pasimachus elongatus LeConte	Pr	S	G	M	NO	6	0	0	100	0	1	0	5	7
Trechinae														
Bembidiini														
Bembidion mimus Hayward	Pr*	S	P	H	YES	1	0	100	0	0	0	0	1	7
Bembidion quadrimaculatum oppositum Say	Pr	E	P	M	BOTH	1	0	100	0	0	0	0	1	7
Bembidion rapidum (LeConte)	Pr	E	P	H	YES	23	0	100	0	0	0	1	22	7 8
Bembidion transparens transparens (Gebler)	Pr*	S	P	H	BOTH	1	0	0	100	0	0	0	1	7
Elaphropus anceps (LeConte)	Pr*	S	P	X	YES	40	0	95.0	5.0	0	0	1	39	7 8

[1] Adult food: Pr = predator, S = seed eater, S Pr = primarily a seed eater, and based on Larochelle and Larivière (2001, 2003); and Pr* or S* indicate that the adult food was not listed by Larochelle and Larivière (2003), so the general food type for the entire genus was used based Lindroth (1961-1969).

[2] Species eco-tolerance based on data in Larochelle and Larivière (2001, 2003): E = Eurytopic (wide range of many, different habitat types), S = Stenotopic (narrow range of few, specific habitat types)

[3] Typical adult habitat type based on data in Larochelle and Larivière (2001, 2003): G = gramiophilous (grassland, prairie, meadow or field sites), P = psammophilous (open sand, clay, organic litter sites), and S = silvicolous (forest or woodland sites).

[4] Typical soil moisture where species is found based on data in Larochelle and Larivière (2001, 2003): H = hygrophilous (wet or usually moist conditions), M = mesophilous (moderate moisture conditions), and X = xerophilous (dry conditions).

[5] Adult flight ability based on Larochelle and Larivière (2001, 2003): YES = adults able to fly, macropterous, NO = adults not able to fly, brachypterous, and BOTH = both brachypterous and macropterous forms occur.

† The four species in bold and followed by † are adventive to North America.

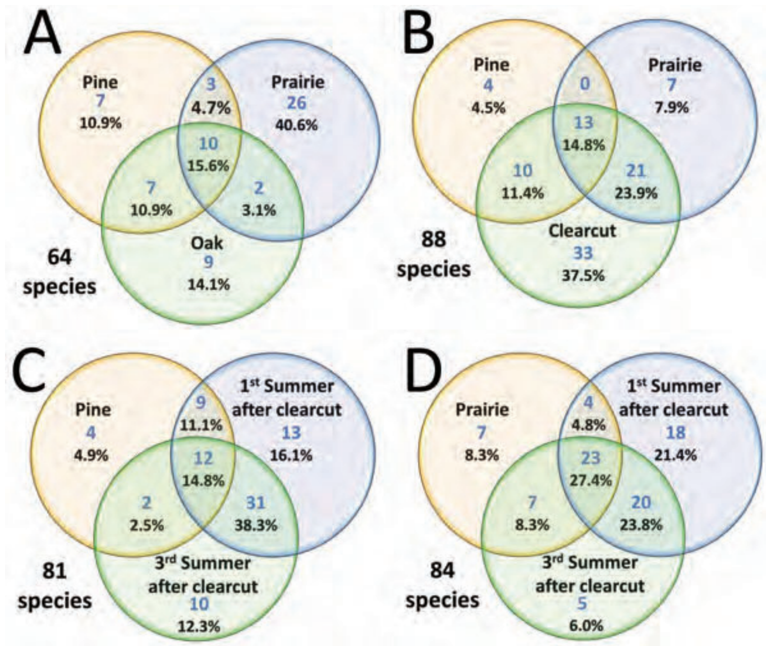

Figure 3. Venn diagrams indicating the number of carabid beetle species and corresponding percent of the total for A: the 64 species collected in all years (1996, 1997, and 1999) in the red pine (pine), oak-pine barrens (oak), and dry sand prairie (prairie) sites in Newaygo County, MI; B: the 88 species collected in all years in the pine, prairie, and clearcut (cut winter of 1996) sites; C: the 81 species collected in the pine habitat (1996, 1997, and 1999) and in the pine clearcuts in 1997 (1st summer post-clearcut) and 1999 (3rd summer post-clearcut); and D: the 84 species collected in the prairie openings (1996 and 1999) and in the pine clearcuts in 1997 (1st summer post-clearcut) and 1999 (3rd summer post-clearcut).

An NMDS ordination of all 143 traps (from all habitats and years combined) produced a two-dimensional solution (Fig. 4A; final stress 0.09). We recognize that the experimental design was not balanced and that this situation could have affected the final ordination. Nevertheless, the red pine and oak-pine barrens traps showed considerable overlap, whereas the dry sand prairie and clearcut traps assemblages were more distinct. In fact, the 1997 and 1999 clearcut assemblages were distinct from each other, with no overlap. Of all the treatments imposed on the clearcut sites, the 1999 carabid assemblage from the “leave slash” plots was visually nearest (i.e., least distinct) the 1997 clearcut assemblages (compare Figs. 4A and 4B).

Overall, 41 of the 92 (45%) carabid species had significant indicator values ($P < 0.05$) (Table 3). Typically, a species with a significant indicator value is one that is common and abundant in one habitat, but not in the others. Of these 41 species, 8 were significantly associated with the red pine stands, 7 with the oak-pine barren sites, 4 with the dry sand prairie sites, and 22 with the clearcut sites. Also included in Table 3 for each species is the number of carabid specimens collected in the clearcut sites in 1997 and 1999 after mathematically standardizing the counts to 100 traps. These latter values show that for the eight species that had significant indicator values for the red pine stands, several were collected in the clearcut sites the first season after clearcutting (1997), but very few to none were collected in the clearcut sites three years post-logging (1999; Table 3). By contrast, collections of 18 of the 22 species that had significant indicator values for the clearcut sites increased from 1997 to 1999, with some increasing dramatically such as eight of the *Harpalus* species.

When considering the five treatments imposed on the clearcut sites, carabid abundance throughout the sampling period in 1999 was higher in the two “slash free”

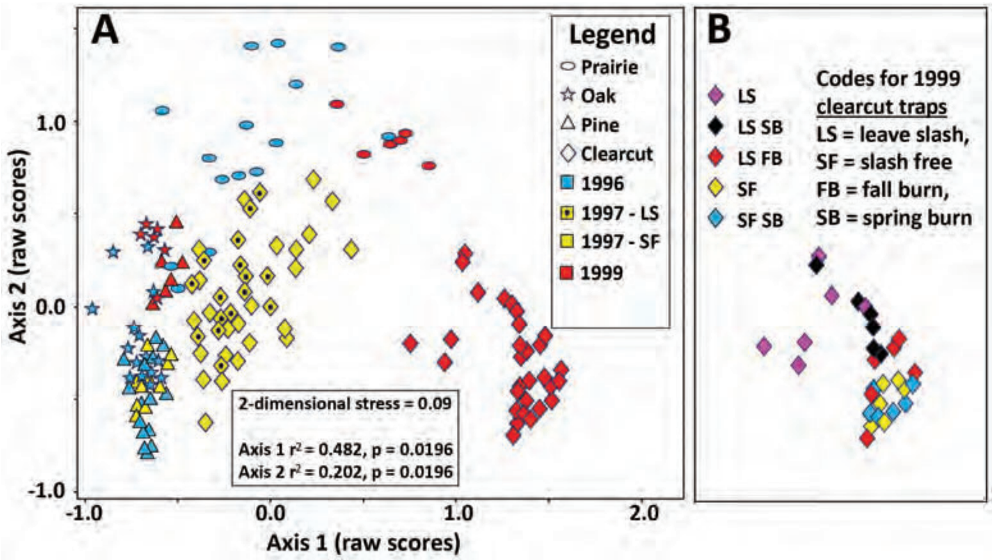

Figure 4. A. Non-metric multidimensional scaling (NMDS) ordination of the 143 pitfall samples based on carabid log10 abundance per species per pitfall sample and grouped by habitat and year of collection. *P*-values from a Monte Carlo test of non-random ordination structure. The solid yellow diamonds in part A indicate the clearcut traps that were in the slash free sites (SF), whereas the yellow diamonds with a black dot indicate traps in sites where slash was left after logging (LS). **B:** Indicates details on the traps in the clearcut sites in 1999 that had been treated in five different ways: LS = slash left on site after logging in winter of 1996-1997, SF = slash removed spring 1997, FB = fall burn in September 1997, and SB = spring burn in April 1999.

treatments compared with the three "leave slash" treatments, with the "leave slash and spring burn" treatment being intermediate (Tables 4 and 5). Over 55% of all specimens collected on the clearcut sites in 1999 were *H. pensylvanicus* (3,980 of 7,196). In large part, the differences in abundance among the five treatments was due to the *H. pensylvanicus* collections, with 1,424 specimens collected in the three "leave slash" treatment sites (an average of 79 individuals per trap for 18 traps), and 2,556 specimens collected in the two "slash free" treatment sites (an average of 213 individuals per trap for 12 traps; Table 4).

Carabid abundance during the May to August trapping period, as reflected by the number of carabid specimens captured per trap per day, was highest in late June at the red pine sites (Fig. 5). Similarly, carabid abundance peaked in early summer in the oak-pine barren sites, but not until late summer in the clearcut sites. Abundance at the dry sand prairie sites was relatively low throughout the entire trapping period, with only a slightly higher count in absolute terms recorded in late May.

The species accumulation curves shown in Fig. 6 indicate that new species were collected during every trapping period (except one) from May through August for each of the four habitats. The only time when two consecutive periods did not add a new species was in the pine sites where only three carabid species were collected in both early and late May. The species accumulation curves tended to flatten earlier in the season for collections in the pine and oak-pine barrens sites compared with collections in the clearcut sites (Fig. 6), likely reflecting the differences in peak seasonal abundance in these habitats (Fig. 5).

Season-long carabid abundance, as measured by mean number of specimens collected per trap, was highest in the pine sites in both 1996 and 1997, but not 1999 (Table 5). Average season-long abundance in the clearcut sites generally increased from 1997 to 1999, even though the 1997 trapping season was six weeks longer. For example, mean abundance per trap significantly increased from 1997 to 1999 for both the slash free (SF: $H = 11.26$; df = 1; $P < 0.0008$) and leave slash (LS: $H = 13.94$; df = 1; $P < 0.0002$) treatment sites. In absolute terms, mean seasonal abundance was lower at the dry sand prairie sites compared with the red pine and oak-pine barren sites, but this difference was only significant in 1996.

Table 3. Overall indicator values (IV) and associated *P* values for the 41 carabid species with significant indicator values sorted by habitat. Species are arranged by IV (high to low) within the habitat in which they were significant. In addition, the total number of carabid specimens collected in the clearcut sites in both 1997 and 1999 are given for each of the 41 species, after standardizing the collection values to 100 traps.

Habitat Species	Indicator value (IV)	*P* =	No. collected per 100 traps in all clearcut sites 1997	 1999
Pine				
Carabus goryi	66.7	0.0002	85	3
Pterostichus tristis	66.3	0.0002	55	0
Synuchus impunctatus	58.5	0.0002	2015	13
Pterostichus pensylvanicus	57.6	0.0002	928	53
Myas coracinus	49.2	0.0002	340	67
Pterostichus adstrictus	16.6	0.0098	20	0
Scaphinotus bilobus	15.8	0.0122	15	0
Oak				
Calathus ingratus	49.9	0.0002	8	0
Calathus gregarious	46.9	0.0002	0	23
Myas cyanescens	46.9	0.0004	335	3
Pterostichus mutus	29.2	0.0064	85	20
Trichotichnus autumnalis	23.8	0.0002	0	0
Sphaeroderus stenostomus lecontei	19.9	0.0014	0	0
Agonum retractum	19.0	0.0008	0	0
Prairie				
Harpalus providens	53.6	0.0002	43	70
Pasimachus elongatus	23.8	0.0004	0	0
Dyschirius globulosus	18.4	0.0020	0	7
Cicindela patruela patruela	9.5	0.0432	0	0
Clearcut				
Harpalus pensylvanicus	87.8	0.0002	258	13267
Harpalus lewisii	73.3	0.0002	93	3303
Harpalus indigens	56.8	0.0002	75	703
Cicindelidia punctulata punctulata	50.4	0.0002	53	453
Harpalus erraticus	44.6	0.0002	28	830
Calosoma calidum	41.9	0.0002	38	267
Anisodactylus merula	40.4	0.0002	45	277
Harpalus affinis	40.0	0.0002	8	537
Harpalus plenalis	37.1	0.0002	23	707
Harpalus herbivagus	35.5	0.0004	5	1727
Selenophorus opalinus	31.7	0.0006	3	337
Harpalus compar	31.4	0.0006	5	510
Poecilus lucublandus	30.4	0.0002	75	37
Harpalus faunus	22.0	0.0030	25	47
Cicindela formosa generosa	18.0	0.0114	45	23
Amara convexa	17.1	0.0074	45	3
Syntomus americanus	16.5	0.0372	0	183
Anisodactylus rusticus	15.8	0.0132	0	63
Bembidion rapidum	14.3	0.019	3	73
Cicindela scutellaris lecontei	14.3	0.0132	8	27
Clivina fossor fossor	12.9	0.0214	18	7
Elaphropus anceps	12.1	0.0494	3	123

Table 4. Total number of carabid specimens collected in the clearcut sites in 1999 by treatment for the 22 species with significant indicator values for the clearcut habitat as listed in Table 3.

		Habitat treatments*				
Species	**Total**	**LS**	**LSFB**	**LSSB**	**SF**	**SFSB**
Amara convexa	1	0	0	0	0	1
Anisodactylus merula	83	2	8	3	38	32
Anisodactylus rusticus	19	2	8	1	5	3
Bembidion rapidum	22	0	14	2	3	3
Calosoma calidum	80	4	36	9	23	8
Cicindela formosa generosa	7	0	0	3	3	1
Cicindela scutellaris lecontei	8	0	2	2	2	2
Cicindelidia punctulata punctulata	136	17	34	22	46	17
Clivina fossor fossor	2	1	0	0	0	1
Elaphropus anceps	37	0	11	10	16	0
Harpalus affinis	161	21	20	15	13	92
Harpalus compar	153	1	43	9	72	28
Harpalus erraticus	249	3	21	14	69	142
Harpalus faunus	14	4	1	1	2	6
Harpalus herbivagus	518	3	234	9	178	94
Harpalus indigens	211	88	15	38	31	39
Harpalus lewisii	991	74	168	138	251	360
Harpalus pensylvanicus	3980	247	719	458	1441	1115
Harpalus plenalis	212	13	58	13	29	99
Poecilus lucublandus	11	2	3	1	2	3
Selenophorus opalinus	101	30	12	13	34	12
Syntomus americanus	55	29	0	9	8	9
Total No. indicator specimens	7051	541	1407	770	2266	2067
No of indicator species	22	17	18	20	20	21
Total No. species collected	55	32	31	31	32	35

* Treatment codes: LS = slash left on site after logging in winter of 1996-1997, SF = slash removed spring 1997, FB = fall burn in September 1997, and SB = spring burn in April 1999.

The mean number of carabid species collected throughout the season per trap varied from a low of 5.5 species for the dry sand prairie sites in 1996 to a high of 18.3 species for the slash-free clearcut sites in 1999 that had been burned in spring 1999 (Table 5). In 1996, the mean number of carabid species collected per trap was higher in the forested sites (red pine and oak-pine barrens) compared with the open dry sand prairie sites. In 1997, there were no significant differences between the habitats sampled (see *P* values in Table 5). In 1999, traps in all five clearcut treatments captured significantly more species per trap than the traps in the red pine, oak-pine barrens, and dry sand prairie sites.

The ecological and life history data presented in Table 2 were used to compare the carabid assemblages between habitats. Proportional comparisons between traits of the species collected in the two forested habitats, red pine sites vs. the oak-pine barrens sites, showed no differences in adult food, eco-tolerance, habitat type, soil moisture, and adult flight ability (Table 6). Similarly, no differences were noted in these traits for the species collected in the more open habitats, i.e., clearcut (all treatments combined) vs. dry sand prairie sites. By contrast, when comparing the more forested sites (after pooling the red pine and oak-pine barrens data) to the more open sites (after pooling the clearcut and dry sand prairie data), significant differences were noted in all traits except for eco-tolerance (Table 6). In general, (1) more species were seed eaters in the open habitats (27%) compared with the forested habitats (11%), (2) most species in the forested habitats were forest specialists (68%) while most species in the open habitats were open-sand specialists (49%), (3) most species in the forested habitats were usually found in mesic soils (47%) while most in the open habitats were found in xeric soils (54%), and (4) more of the species in the open habitats (88%) were able to fly than those in the forested habitats (71%) (Table 6).

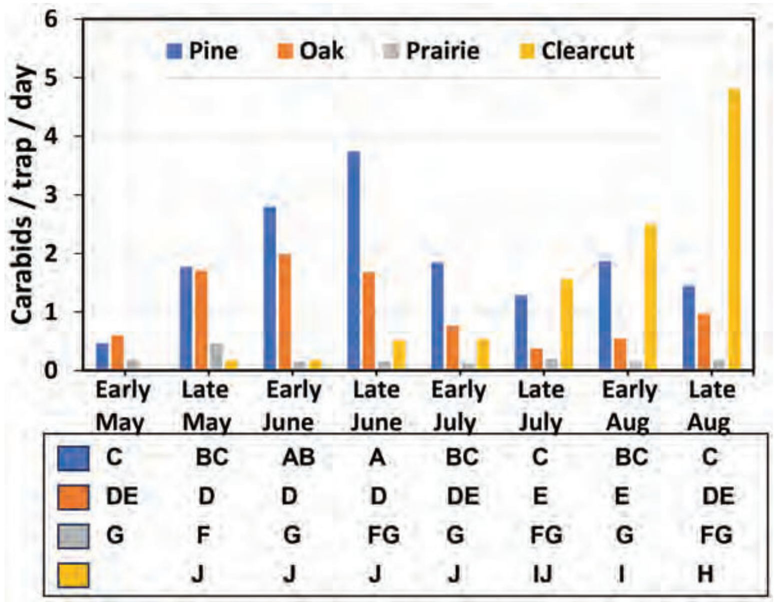

Figure 5. Average number of carabids collected per trap per day in pitfall traps in four habitats sampled in 1996, 1997, and 1999 (data combined for all years of trapping: see Table 1). Results of mean separation tests are given in the box below for each habitat individually (use the color codes for habitat type). ANOVA results followed by the Tukey HSD test for the red pine (pine) trap data were df = 7, 299, $F = 6.60$, $P < 0.0001$, and similarly the results for the clearcut trap data were df = 6, 603, $F = 32.35$, P < 0.0001. Kruskal-Wallis non-parametric test results followed by the Dunn's test for the oak-pine barrens (oak) trap data were df = 7, $H = 43.14$, $P < 0.0001$ and similarly the results for the dry sand prairie (prairie) trap data were df = 7, $H = 18.92$, $P < 0.008$.

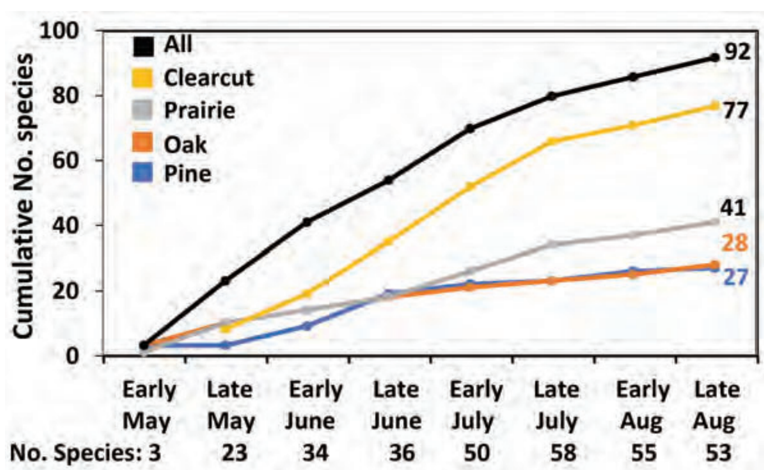

Figure 6. Cumulative number of distinct carabid species collected from early May to late August based on three years of sampling in four habitats in Newaygo County, MI. Data shown for all years combined by each habitat type (Clearcut, Prairie, Oak, Pine) and for all habitats combined (All). Shown below the X-axis label are the number of distinct carabid species collected for all habitats combined during each of the eight time periods.

Table 5. Mean number of individual carabids and number of species collected per trap by treatment throughout the trapping periods in 1996, 1997, and 1999.

Year	Habitat (No. of traps)[1]	No. individual carabids per trap Mean ± SE (Range)		No. carabid species per trap Mean ± SE (Range)	
1996	Pine (15)	187.8 ±24.9 (36–337)	a[2]	7.5 ± 0.4 (5–10)	a
	Oak (15)	95.3 ± 9.9 (24–152)	b	8.4 ± 0.7 (4–15)	a
	Prairie (15)	15.7 ± 3.6 (3–50)	c	5.5 ± 0.6 (2–12)	b
		df = 2; H = 31.9; P < 0.0001[3]		df = 2; H = 13.5; P < 0.002	
1997	Pine (16)	186.6 ± 10.4 (138–227)	a	9.8 ± 0.6 (7–12)	a
	SF (24)	55.0 ± 7.7 (11–177)	b	11.7 ± 0.8 (5–21)	a
	LS (10)	41.7 ± 4.3 (19–77)	b	11.6 ± 0.7 (6–16)	a
		df = 2; H = 23.1; P < 0.0001		df = 2; H = 2.8; P = 0.2502	
1999	Pine (6)	60.8 ± 13.9 (35–135)	bc	7.8 ± 0.4 (6–9)	b
	Oak (6)	48.2 ± 4.0 (34–59)	bc	8.8 ± 1.1 (6–13)	b
	Prairie (6)	12.5 ± 1.5 (8–17)	c	7.7 ± 0.6 (6–10)	b
	SF (6)	382.5 ± 30.8 (297–509)	a	17.3 ± 1.3 (16–22)	a
	SFSB (6)	348.5 ± 49.4 (161–497)	a	18.3 ± 1.0 (14–23)	a
	LSFB (6)	238.5 ± 38.2 (134–344)	ab	14.5 ± 1.1 (12–19)	a
	LSSB (6)	131.3 ±29.5 (47–243)	b	16.7 ± 1.2 (12–19)	a
	LS (6)	98.5 ± 13.5 (59–148)	b	14.5 ± 1.1 (11–18)	a
		df = 7; H = 41.2; P < 0.0001		df = 7; H = 35.3; P < 0.0001	

[1] Habitat codes: Pine = red pine stands, Oak = oak-pine barrens, Prairie = dry sand prairie, LS = leave slash, SF = slash free, FB = fall burn in September 1997, SB = spring burn in April 1999 (see Methods for details).

[2] Means followed by the same letter within years are not significantly different based on Kruskal–Wallis non-parametric analysis of variance with Dunn's test for post hoc pairwise comparisons, p < 0.05).

[3] Summary statistics for Kruskal-Wallis rank sum test, including degrees of freedom (df), Kruskal-Wallis chi-squared statistic H, and p-value.

Discussion

Carabid diversity and abundance dramatically changed after removal of the red pine overstory, with most forest specialists in the clearcut sites declining in numbers, while the open-habitat species increased. Similar patterns of decreasing forest specialists and increasing open-habitat species have been documented in many carabid studies following logging in both conifer (Niemelä et al. 1993; Beaudry et al. 1997; Heliölä et al. 2002; Koivula et al. 2002, 2019; Pedley et al. 2023; Work et al. 2023) and hardwood habitats (Buddle et al. 2006, Magura et al. 2015, Kriska et al. 2020).

In the present study, all eight species with significant indicator values for the red pine stands showed large decreases after the sites were logged (Table 3), and this was especially true for most of the flightless species. For example, after the season-long collection data were standardized to 100 traps, numbers of *C. goryi* dramatically dropped from 9,371 specimens in the red pine sites, to 85 in the same sites during 1997 after they had been clearcut, and to 3 in 1999 in these same clearcut sites. Similar patterns were also observed during these same years for the following flightless species: *Myas coracinus* (Say) (894 to 340 to 67), *Pterostichus novus* Straneo (58 to 13 to 0), *Pterostichus tristis* (Dejean) (281 to 55 to 0), and *Scaphinotus bilobus* (Say) (39 to 15 to 0). However, lower catch rates of these species in 1999 could also reflect the later start date for trapping in 1999 (July) compared to 1996 and 1997 (May), i.e., recognizing that daily carabid abundance peaked in June at the pine sites in 1996 and 1997 (Fig. 5). Nevertheless, over time, many flightless species will reestablish in cutover sites as forests regrow (Niemelä et al. 1993, Koivula et al. 2002, Rainio and Niemelä 2003, Pearce and Venier 2006, Fuller et al. 2008, Riley and Browne 2011).

About equal numbers of the forest generalist species *S. impunctatus* were captured in the red pine and clearcut sites in the present study (Table 2). However, of those captured in the clearcut sites, almost all were captured in 1997 (Table 3), the first summer post-logging. This scenario suggests

Table 6. Number of carabid species collected in each habitat for all years combined and categorized by various ecological and life history traits as shown in Table 2.

		Forested habitats		Open habitats		Combined habitats	
Parameter	**Grouping***	**Pine**	**Oak**	**Clearcut**	**Prairie**	**Pine + Oak**	**Clearcut + Prairie**
No. species		27	28	77	41	38	84
Adult food	Predator	25	25	56	28	34	61
	Seed	2	3	21	13	4	23
X^2 test		X^2 =0.18, P = 0.669		X^2 = 0.26, P = 0.613		X^2 = 4.31, P = 0.0378	
Ecotolerace	Eurytopic	16	11	49	28	18	51
	Stenotopic	11	17	28	13	20	33
X^2 test		X^2 =2.19, P = 0.139		X^2 = 0.2558, P = 0.613		X^2 = 1.90, P = 0.1685	
Habitat	G	3	1	14	8	3	18
	P	6	4	38	21	9	41
	S	18	23	25	12	26	27
X^2 test		X^2 =1.99, P = 0.369		X^2 = 0.13, P = 0.936		X^2 = 14.86, P = 0.0006	
Soil moisture	H	8	9	10	3	12	11
	M	13	13	25	14	18	28
	X	6	6	42	24	8	45
X^2 test		X^2 =0.041, P = 0.979		X^2 = 0.88, P = 0.6443		X^2 = 12.48, P = 0.0019	
Flight ability	No	9	9	9	5	11	10
	Yes	18	19	68	36	27	74
X^2 test		X^2 =0.0088, P = 0.925		X^2 = 0.007, P = 0.935		X^2 = 5.331, P = 0.0209	

*Groupings are based on information given in footnotes in Table 2. For Habitat: G = gramiophilous, P = psammophilous, and S = silvicolous. For soil moisture: H = hygrophilous, M = mesophilous, and X = xerophilous. For flight ability: No = adults brachypterous, and Yes = adults macropterous or having both brachypterous and macropterous forms.

that most *S. impunctatus* captured in 1997 had developed at these sites the previous year when the area was still forested rather than migrating to the sites in 1997. *Synuchus impunctatus* has been among the most commonly collected carabids in other studies as well. For example, in Ohio, *S. impunctatus* was primarily collected within the forest and along the ecotone compared to within an open pipeline corridor that was created the year before sampling (Silverman et al. 2008). In Ontario where coniferous areas were clearcut and then variously treated the following year, and then replanted with pine the next, Beaudry et al. (1997) reported that *S. impunctatus* increased in abundance from the first to the second-year post-logging, suggesting that *S. impunctatus* was reestablishing in the newly planted sites. As reported above, abundance and diversity of open-habitat carabids tends to increase in clearcut sites in the years immediately following logging. For example, in Alberta, Canada, Niemelä et al. (1993) reported that 18 species of *Amara* Bonelli, *Bembidion* Latreille, and *Harpalus* Latreille all increased dramatically in the first few years after clearcutting of pine-spruce forests. Similarly, Beaudry et al. (1997), found that 15 species of *Amara* and *Harpalus* increased significantly in pine forests following clearcutting along with other possible treatments such as prescribed burning and soil scarification in Ontario, Canada. We noted similar increases in the abundance of nearly all 25 species of *Amara*, *Bembidion*, and *Harpalus* collected in the clearcut sites in this study (Table 2).

Of the various habitats sampled in the present study, the clearcut sites had the greatest number of new species added during the late summer sampling periods (Fig. 6). This situation resulted from the large number of Harpalinae species that occurred primarily in the clearcut sites, many of which were only collected in late summer (Table 2).

Of the five tiger beetle species (Cicindelinae) collected in this study (Table 2), four were collected in the clearcut sites (N = 198 specimens; 2.8/trap) and three in the dry sand prairie sites (N = 10; 0.5/trap). None were collected in the forested sites. Only *Cicindela formosa generosa* Dejean and *Cicindelidia punctulata punctulata* (Olivier) were collected in both the clearcut and dry sand prairie sites. Graves (1963) considered *C. p. punctulata* to be one of the two most common tiger beetle species in Michigan, which was reflected in it representing 78% of 208 tiger beetle specimens collected in our study.

Several studies have examined how removing various amounts of slash after clearcutting affects species diversity and abundance of ground invertebrates (Pearce et al. 2003; Nittérus et al. 2007; Work et al. 2013, 2014, 2023; Venier et al. 2017). For example, Nittérus et al. (2007) found that carabid species richness was higher in slash-free plots compared to plots where logging slash remained on site during the first year after logging in spruce stands in Sweden. Similarly, Work et al. (2013) noted that species abundance of carabids and staphylinids (rove beetles) was greater in slash-free plots the first year after clearcutting in boreal forests (balsam fir and paper birch) in Quebec, Canada. By contrast, Pearce et al. (2003) and Work et al. (2014) noted that several carabid species were positively associated with increasing levels of retained slash. In the present study, we did not find significant differences in species abundance between the "slash free" (SF) and "leave slash" (LS) plots during the first year after clearcutting (1997) (Table 5). However, by 1999, both species abundance and diversity were greater on the "slash free" plots (compare SF vs. LS in Table 5 for species abundance; for SF vs. LS species diversity: $H = 4.05$; df = 1; $P = 0.044$).

One of the original goals of the HMNF when deciding to clearcut the red pine stands in the 1990s was to restore those sites to near their original state, i.e., a mixture of dry sand prairie and oak-pine barrens. Based on the carabid assemblages collected in the clearcut sites that goal was largely met in just the first few years post-logging. That is, of the 41 species collected in the dry sand prairie sites, 27 (66%) of those species were collected in the clearcut sites in 1997, 30 (73%) in 1999, and 34 (81%) for both years combined (Figs. 3B, 3D). Although not directly comparable, some researchers today are cautioning against the widespread efforts to plant trees on naturally treeless habitats as a means to mitigate climate change given that such actions can have negative impacts on biodiversity, such as pollinators (Moyano et al. 2024, Pérez-Gómez et al. 2024).

The HMNF has continued to maintain many of the clearcut sites from 1996-1997, as well as many others, as a network of prairies, savannas, and barrens (Keough 2023, Fig. 1B). As mentioned above, improving habitat for the Karner blue butterfly has been the main focus of these efforts. Maintaining habitats in early successional stages requires considerable effort and resources (USDA Forest Service 2013, Hess and Hess 2015, Abella et al. 2017). Site management by the HMNF has been accomplished through prescribed burning, hand cutting and mechanical removal of woody plants, mowing, and planting of native wildflowers (Larsen et al. 2016, Reinhardt et al. 2017, Keough 2023).

Given that nearly three decades have now passed since the initial logging of these sites in 1996-1997, it would be interesting to sample the carabids on some of the original clearcut sites again and compare the species assemblages found today to those now existing nearby in the original dry sand prairie sites. For comparison, in a recent 10-year study where agricultural land was restored to grassland, Lange et al. (2023) found that in the latter years of that study both plant and carabid diversity tended to stabilize. The extent to which carabid diversity in the original clearcut sites has begun to coincide with the diversity in the original open sand prairie sites could provide the HMNF a means to measure the success of their restoration efforts.

Moreover, extending any trapping efforts into October in the dry sand prairie sites might document the occurrence of *Hartonymus hoodi* Casey, an elusive Harpalini restricted to deep sandy habitats in the Midwest. Currently, *H. hoodi* is only known in Michigan from collections made in 2011 from Berrien and Van Burren Counties in the extreme southwest part of the state in the sand dunes along Lake Michigan (R. L. Davidson, unpublished data; specimens are held at the Carnegie Museum of Natural History). Although those detections of *H. hoodi* represent the first Michigan state records for this carabid it likely occurs in other locations along Lake Michigan and possibly in some dry sand prairie habitats in western Lower Michigan.

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