Initial Responses of Carabidae (Coleoptera) to Intensive Biomass Harvesting and Soil Compaction in Aspen Stands of the Huron-Manistee National Forest, Oscoda County, Michigan

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Abstract

During the 1990s, the United States Forest Service implemented several studies to measure the impacts of organic matter removal and soil compaction on forest productivity in forest ecosystems throughout the country. One site was in northeastern Lower Michigan on the Huron-Manistee National Forest in Oscoda County. This site was dominated by mature quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.) growing on sandy loam soils. The three organic-matter removal treatments at the site included: 1. stem-only harvesting (SOH); 2. whole-tree harvesting (WTH); and 3. whole-tree harvesting plus forest floor removal (FFR). The three soil compaction treatments also at the site included: 1. no compaction beyond normal levels from tree harvesting during winter; 2. moderate compaction; and 3. heavy compaction, i.e., increasing surface soil bulk density by about 0%, 15%, or 30%, respectively. These silvicultural treatments were conducted during the winter and spring of 1994, and thus offered an opportunity to determine how carabid beetles (Coleoptera: Carabidae) would initially respond to these forest management practices. Thus, carabids were collected the year following treatment with pitfall traps from June to September in 1995 on all treatment sites and in nearby uncut forest stands. Overall, 3690 carabid specimens were collected, representing 46 species. Many carabids showed a significant response to the organic matter removal treatments, some positively and some negatively, but few showed a response to the compaction treatments. An NMDS ordination indicated that the carabid assemblages from the uncut aspen stands were distinct from all treatment plots, but most distinct from the FFR-plot assemblages. Catch rates of the Harpalini (12 species) were highest on the FFR plots. For some of the most collected species, catch rates of *Myas cyanescens* Dejean (540 specimens), *Pterostichus pensylvanicus* LeConte (208), and *Synuchus impunctatus* (Say) (473) were generally highest in the uncut aspen stands and lowest in the FFR plots; for *Cyclotrachelus sodalis* (LeConte) (638) and *Pterostichus stygicus* (Say) (307) catch rates were highest in the SOH and WTH plots and lowest in the uncut aspen stands; and for *Pterostichus mutus* (Say) (392) catch rates were highest in the FFR plots and lowest in the uncut aspen stands. Of the 46 species, 8 were significant indicator species: 2 for the FFR plots and 6 for the uncut aspen plots.

Keywords: Carabidae, ground beetles, biodiversity, degree of biomass removal, tree harvesting

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There are about 2500 species of Carabidae (Coleoptera) in North America (Bousquet 2012), and at least 530 have been recorded in Michigan (Ruesink et al. 2023, Haack et al. 2024). Carabids are found in many terrestrial habitats and are typically abundant in or on the soil surface (Larochelle and Larivière 2001, 2003). Carabids are good bioindicators because many species are sensitive to environmental change (Lövei and Sunderland 1996, Pearce and Venier 2006, Work et al. 2008). Moreover, carabids are considered reliable bioindicators because they are relatively easy to sample and quantify with pitfall traps and are well-known taxonomically.

Tree harvesting, especially clearcutting, can greatly alter the biodiversity of many soil invertebrates such as carabids. One common response to clearcutting by carabids is the loss of forest specialists and an increase in open-habitat specialists (Niemelä et al. 1993, Beaudry et al. 1997, Heliölä et al. 2002, Magura et al. 2015, Koivula et al. 2019, Kriska et al. 2020, Pedley et al. 2023, Belluz et al. 2022). In addition, some studies have investigated how carabid assemblages change in response to varying levels of biomass removal during tree harvesting (Work et al. 2013, 2014, 2023; Venier et al. 2017; Haack et al. 2024). Typically, the greatest reductions in forest specialists occurred where clearcutting was followed by other site disturbances such as stump removal and soil scarification (Beaudry et al. 1997, Klimaszewski et al. 2005, Work et al. 2023).

Long-term forest productivity is important to forest managers who desire to maintain steady wood production over multiple rotations on a particular site (Grier et al. 1989). There are several management activities that can affect future forest productivity. These include: 1. the degree of biomass removal (e.g., stem only vs. whole-tree harvesting); 2. soil compaction from harvesting equipment that can occur during logging; and 3. burning of slash and soil scarification that are often conducted during site preparation for the next rotation of trees (Standish et al. 1988, Thiffault et al. 2011, Mayer et al. 2020).

The USDA Forest Service is obligated by the National Forest Management Act of 1976 to manage land so that its long-term productivity is not impaired (Powers et al. 2005, Powers 2006). As a result of this mandate, Forest Service scientists and managers developed a national Long-Term Soil Productivity (LTSP) study to investigate how reductions in soil organic matter and soil porosity would affect future productivity of a site. Productivity was defined in terms of a site's capacity to capture carbon and grow vegetation (Powers 2006).

Beginning in the 1990s, several LTSP studies were initiated throughout the United States and in two Canadian provinces to investigate long-term soil productivity by altering biomass removal and soil compaction (Tiarks et al. 1993, Powers et al. 2005, Powers 2006). Similar methods were used at all sites. Three test sites were established in Michigan and Minnesota in mature aspen forests dominated by quaking aspen (*Populus tremuloides* Michx.) and bigtooth aspen (*P. grandidentata* Michx.) (Stone 2001). Quaking aspen and bigtooth aspen are early successional tree species that are often managed by clearcutting mature stands, allowing aspen to retake the site from root suckers, and then clearcutting again once the new stand matures (Cleland et al. 2001).

The first of these aspen sites was established in 1992 on clay loam soils located on the Ottawa National Forest in the Upper Peninsula of Michigan. The second site was established in 1993 on silt loam soils on the Chippewa National Forest in northern Minnesota. The third site was established in 1994 on sandy loam soils on the Huron-Manistee National Forest (HMNF) in northeastern Lower Michigan. Stone (2001) reported vegetative growth responses after five growing seasons post-treatment at the HMNF site, and others have reported various vegetative and soil responses after 10 to 25 growing seasons post-treatment (Voldseth et al. 2011; Curzon et al. 2014, 2016; Slesak et al. 2017; Lewandowski et al. 2019; Adams et al. 2021; Curzon et al. 2022). The main objective of the current study was to document initial changes in the carabid assemblages in response to varying levels of organic matter removal and soil compaction at the HMNF LTSP site. In addition, we wanted to compare the carabid assemblages in the treatment plots to those in the surrounding uncut aspen stands. We analyzed variables such as carabid catch rate and species richness, as well as tested whether any carabid species were good indicator species for a particular treatment. The study was conducted in 1995, which corresponded to the second growing season post-treatment.

Methods and Materials

Stand and site conditions. The LTSP experimental plots were installed in mature aspen stands on the Huron-Manistee National Forest in Oscoda County, Michigan (44.57° N Latitude, 83.98° W Longitude) in 1994. The soils were classified as Graycalm-Grayling sand. The site index (average height at age 50) of these stands was 19 m (62 ft). Quaking aspen and bigtooth aspen dominated the overstory of the selected stands, but also included some associated red maple (*Acer rubrum* L.), northern red oak (*Quercus rubra* L.), eastern white pine (*Pinus strobus* L.), and black cherry (*Prunus serotina* Ehrh.) (Stone 2001).

Plot design and treatments. Following the standard procedures for the LTSP network, three levels of organic matter removal and three levels of soil compaction were applied, using a completely randomized 3 × 3 factorial design, to 27 plots that each measured 50 × 50 m (0.25 ha, 0.62 acre). A detailed account of the treatments and how they were conducted was given by Stone (2001). Briefly, the three levels of organic matter removal included: 1. stem-only harvesting (SOH) where the merchantable tree bole was removed to an upper diameter of 10 cm (4 in) with the treetops and branches retained on site; 2. whole-tree harvesting (WTH) where all aboveground woody material was removed; and 3. whole-tree harvesting plus forest floor removal (FFR). The soil compaction treatments were: 1. minimal compaction beyond that from cutting the trees and harvesting during winter (see details below); 2. medium, which aimed at increasing bulk density of upper 10 to 20 cm of soil by 15%; and 3. heavy, which aimed to increase soil bulk density by 30%. Bulk density is measured as the dry weight of soil divided by its volume (g/cm^3), where higher values indicate greater compaction, which can inhibit water and air infiltration as well as root growth.

All stands were harvested in January 1994 at which time there was 35–40 cm (14–16 in) of snow present and the soil was frozen to a depth of 20–25 cm (8–10 in) (Stone 2001). For the plots targeted for minimal soil compaction, the trees were cut with a tracked Bobcat shear while a Hydro-Ax feller-buncher was used on the other plots. The merchantable stems were skidded off the plots using Caterpillar 518 and Timberjack 380B grapple skidders. On the SOH plots scheduled for soil compaction, the tree tops were moved adjacent to the plots and replaced near their original locations soon after completing the compaction treatments. In mid-April, on the FFR plots, the coarse woody debris was removed manually and then the forest floor materials were removed using a power-driven sidewalk sweeper with a revolving wire-brush head (Stone 2001). In late April 1994, the compaction treatments were conducted when the soil was near field capacity (i.e., when soil is saturated with water after any excess water has drained away). The compaction treatments were applied using a Hough Model H60 front-end loader that travelled over the plot by moving one tire width with each pass. The loader, with the bucket empty and tire pressure at 172 kPa (25 psi), made a single pass over the plots for the medium compaction treatment. For the heavy compaction treatment, a second pass was made at right angles to the original direction, with the bucket filled with sand and a tire pressure at 276 kPa (40 psi) (Stone 2001). For the SOH plots that were compacted, the treetops were moved off the plots and then replaced after compaction was completed.

Carabidae trapping methods. Barrier pitfall traps were used to collect carabids because the barriers increase trap catch by directing ground invertebrates towards the collection cups (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. 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 center of the cup touching the garden edging. A second 32-oz collection cup, with rim removed, was placed inside the first cup, which allowed removal of the second cup when collecting the insects with little disturbance to the first cup. The second 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 a ca. 2 × 2 cm hole cut in the bottom, was placed inside the two 32-oz cups. The smaller cup fit snugly inside the larger cup and helped keep leaves and other material out of the alcohol while allowing insects to fall through the hole. This three-cup design was modified from Reeves (1980). Lastly, a plastic plate, ca. 25 cm diameter, was placed over each cup and supported about 8 cm above the soil using two nails along the outer edge of the plate and the top of the plastic barrier. The plates provided protection from rain and reduced animal disturbance.

Two barrier pitfall traps were placed in each of the 27 treatment plots, one in the northwest portion of the plot and one in the southwest portion. Although more traps per plot would have been desirable, we were restricted on the degree of soil disturbance that we could make in each plot by concurrent studies of other researchers. However, given that barrier pitfall traps are recognized as superior to standard pitfall traps (i.e., cups without barriers) in collecting more carabid individuals and species (Durkis and Reeves 1982, Hansen and New 2005, Boetzl et al. 2018, Horn 2020), we considered two barrier pitfall traps per plot to be adequate in the current study. In addition, 10 other traps were installed in the surrounding uncut mature aspen forest, with two traps in each of five separate areas. Pitfall samples were collected seven times at 7–16 day intervals, from 4 June to 6 September 1995 (Table 1).

Sample processing and carabid identification. When collecting the samples the contents from both cups of each barrier trap were combined into a single, labeled sealed plastic container. The samples were transported to the USDA Forest Service laboratory at Michigan State University, East Lansing, MI, for initial sorting and stored in 70% ethanol in separate labeled jars. Later, all samples were transported to Morgantown, WV, for final sorting to morphospecies. Final species confirmation was made at the Carnegie Museum of Natural History in Pittsburgh, PA, with most specimens being deposited there.

Data management and analyses. The data were assembled into a spreadsheet by species, specimen count, treatment, trap number, plot, collection date, and trap days. Recall that the contents from each of the two cups per barrier trap were combined. Moreover, because each plot was considered an independent experimental unit in the analyses below, the data for the two traps in each plot were combined. Similarly, for the traps installed in the uncut aspen stands, the values for the two traps in each of five separate stands were combined. Given that some traps were disturbed during various trapping periods, catch rates were standardized by the total number of trap days per trap and then pooled by plot. These values were standardized to catch rates per day for 100 plots. Because of the skewness of the data the values were $\log_{10}$ (x + 1) transformed prior to analysis. Initially, we used a two-way ANOVA (www.statskingdom.com) to test for significance in the two main factors (degree of organic matter removal and soil compaction) and their interaction. We ran tests on mean catch rate for several carabid groupings: 1. all carabids combined; 2. all Harpalini species combined; 3. the nine most commonly collected carabid species (i.e., those representing about 4% or more of the total catch); and 4. the total number of species collected per plot. We selected the Harpalini because most species are open-habitat specialists (Larochelle and Larivière. 2003). We used an alpha level of 0.1 in these analyses because the N value for each treatment combination was only three after the two traps per plot were pooled.

After conducting the initial two-way analyses on the above carabid groupings, we noted that organic matter removal was a significant factor in 8 of the 12 tests, but soil compaction was only significant for 1 test (see Results). Therefore, we focused subsequent analyses on just the organic matter removal treatments after pooling by soil compaction level. In these latter analyses, we compared mean catch rates by treatment. Means were compared among treatments, without transformation, using the non-parametric Kruskal-Wallis rank sum test followed by post-hoc pairwise comparisons using Dunn's test. The analyses were first conducted comparing catch rates among the three levels of organic matter removal, and then again after including data from the uncut aspen plots.

To explore differences in carabid assemblages by treatment, 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 season-long, log10 (x + 1) transformed, catch rates per day by plot (after pooling the data from both traps in each plot). We weighted the species equally and used the NMDS ordination default program settings and a Bray-Curtis distance measure (McCune and Mefford 2017). A Monte Carlo test, using 250 randomized runs, was conducted in PC-ORD to create a null distribution which was compared to each determined axis to test for significance.

Carabid species accumulation curves for species richness (Hill number q = 0) were calculated using pooled, season-long abundance data for each organic matter removal treatment and the uncut aspen stands using the online iNEXT package (https://chao.shinyapps.io/iNEXTOnline/; Chao et al. 2024). Sample-size-based rarefaction and extrapolation curves were generated for each 'habitat' with 95% confidence intervals based on 100 bootstrap replicates.

Indicator species analysis (IndVal), developed by Dufrêne and Legendre (1997). was used to identify carabids that were indicator species for a particular treatment. The analyses were conducted in PC-ORD, using log-transformed, season-long catch rates for each carabid species by plot. Values for IndVal range from 0 to 100, where values close to zero signify 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 (5000 permutations) of the observed indicator values relative to those of a randomized group was used to determine the significance of each indicator value.

Results

Overall, 3690 carabid specimens were collected during the study and identified to 46 species that represented 5 subfamilies, including 6 species in Carabinae, 37 in Harpalinae, 1 in Loricerinae, 1 in Patrobinae, and 1 in Trechinae (Table 2). The nine most collected species were *Cyclotrachelus sodalis* (LeConte) (638 specimens), *Myas cyanescens* Dejean (540), *Synuchus impunctatus* (Say) (473), *Pterostichus mutus* (Say) (392), *Carabus nemoralis* O.F. Mueller (385), *Pterostichus stygicus* (Say) (307), *Pterostichus pensylvanicus* LeConte (208), *Calathus gregarius* (Say) (181), and *Carabus sylvosus* Say (144). By contrast, 20 of the 46 species were represented by five or fewer specimens, with 11 species represented by a single individual. All species collected were previously known from Michigan based on Ruesink et al. (2023). Three of the 46 species collected are adventive in North America: *C. nemoralis*, *Harpalus affinis* (Schrank), and *Pterostichus melanarius* (Illiger).

Table 1. Abundance and seasonality of the Carabidae species collected during 1995 at the LTSP study site on the Huron-Manistee National Forest, Oscoda County, Michigan.

SUBFAMILY		Total	No. specimens by collection period (CP)*						
Tribe	**Species**	**collected**	**CP1**	**CP2**	**CP3**	**CP4**	**CP5**	**CP6**	**CP7**
CARABINAE									
Carabini	*Calosoma calidum* (Fabricius)	3	0	0	0	3	0	0	0
Carabini	*Calosoma frigidum* Kirby	1	1	0	0	0	0	0	0
Carabini	***Carabus nemoralis* O.F. Mueller†**	385	82	18	14	56	126	81	8
Carabini	*Carabus serratus* Say	37	0	2	11	5	7	11	1
Carabini	*Carabus sylvosus* Say	144	3	1	5	21	13	61	40
Cychrini	*Sphaeroderus stenostomus lecontei* Dejean	9	1	0	7	0	0	0	1
HARPALINAE									
Harpalini	*Anisodactylus merula* (Germar)	1	0	0	0	1	0	0	0
Harpalini	*Anisodactylus rusticus* (Say)	1	0	1	0	0	0	0	0
Harpalini	***Harpalus affinis* (Schrank) †**	1	0	0	1	0	0	0	0
Harpalini	*Harpalus indigens* Casey	11	0	1	5	2	2	1	0
Harpalini	*Harpalus lewisii* LeConte	5	2	0	1	0	1	1	0
Harpalini	*Harpalus laticeps* LeConte	9	1	0	1	4	1	1	1
Harpalini	*Harpalus opacipennis* (Haldeman)	10	0	0	10	0	0	0	0
Harpalini	*Harpalus pensylvanicus* (DeGeer)	28	0	0	0	0	0	15	13
Harpalini	*Harpalus providens* Casey	27	0	0	9	2	8	5	3
Harpalini	*Harpalus somnulentus* Dejean	21	0	1	5	5	2	7	1
Harpalini	*Notiobia terminata* (Say)	1	0	0	0	0	0	1	0
Harpalini	*Selenophorus opalinus* (LeConte)	5	0	0	1	2	2	0	0
Lebiini	*Cymindis americana* Dejean	1	0	0	0	0	1	0	0
Lebiini	*Cymindis cribricollis* Dejean	13	0	0	0	0	1	5	7
Licinini	*Dicaelus purpuratus* Bonelli	1	0	0	0	0	1	0	0
Lebiini	*Lebia pulchella* Dejean	1	0	0	0	0	0	0	1
Lebiini	*Syntomus americanus* (Dejean)	5	0	0	1	1	3	0	0
Platynini	*Agonum cupripenne* (Say)	2	0	0	0	0	1	0	1
Platynini	*Agonum placidum* (Say)	5	0	0	4	1	0	0	0
Platynini	*Agonum retractum* LeConte	1	0	0	0	1	0	0	0

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Table 1. Abundance and seasonality of the Carabidae species collected during 1995 at the LTSP study site on the Huron-Manistee National Forest, Oscoda County, Michigan (*Continued*).

SUBFAMILY		Total	No. specimens by collection period (CP)*						
Tribe	**Species**	**collected**	**CP1**	**CP2**	**CP3**	**CP4**	**CP5**	**CP6**	**CP7**
Platynini	*Calathus gregarius* (Say)	181	0	0	0	1	25	54	101
Platynini	*Synuchus impunctatus* (Say)	473	0	1	16	36	57	205	158
Pterostichini	*Cyclotrachelus sodalis* (LeConte)	638	25	11	48	125	190	190	49
Pterostichini	*Myas cyanescens* Dejean	540	20	20	85	195	106	91	23
Pterostichini	*Poecilus lucublandus* (Say)	77	6	8	35	19	4	2	3
Pterostichini	*Pterostichus coracinus* (Newman)	6	0	0	0	0	1	3	2
Pterostichini	*Pterostichus corvinus* (Dejean)	3	0	0	1	0	0	0	2
Pterostichini	***Pterostichus melanarius* (Illiger) †**	56	0	2	4	9	17	13	11
Pterostichini	*Pterostichus mutus* (Say)	392	91	38	203	36	7	5	12
Pterostichini	*Pterostichus novus* Straneo	29	0	3	4	4	11	6	1
Pterostichini	*Pterostichus pensylvanicus* LeConte	208	27	31	51	22	15	20	42
Pterostichini	*Pterostichus permundus* (Say)	13	0	0	4	0	1	5	3
Pterostichini	*Pterostichus stygicus* (Say)	307	13	52	92	29	26	71	24
Pterostichini	*Pterostichus tristis* (Dejean)	11	0	0	4	1	3	3	0
Zabrini	*Amara angustata* (Say)	8	1	0	5	1	0	0	1
Zabrini	*Amara cupreolata* Putzeys	1	0	0	0	0	0	1	0
Zabrini	*Amara lunicollis* Schodte	1	0	0	0	0	0	1	0
LORICERINAE									
Notiophilini	*Notiophilus aeneus* (Herbst)	5	0	1	2	0	2	0	0
PATROBINAE									
Patrobini	*Patrobus longicornis* (Say)	11	1	2	0	1	2	5	0
TRECHINAE									
Bembidionini	*Bembidion quadrimaculatum oppositum* Say	2	0	0	0	0	1	1	0
Total specimens		3690	274	193	629	583	637	865	509
Distinct species		46	14	17	28	26	30	28	25
Species accumulation			14	22	31	35	41	45	46

* 1995 Collection Periods (CP): 1 = 4-20 June; 2 = 20–27 June; 3 = 27 June – 12 July; 4 = 12–26 July; 5 = 26 July – 9 August; 6 = 9–24 August; and 7 = 24 August – 6 September.

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

Table 2. Total number of carabid specimens collected in 1995 by treatment at the LTSP study site.

		Number of specimens collected by treatments*									
		Stem only harvesting (SOH)			Whole-tree harvesting (WTH)			Forest floor removal (FFR)			
CARABIDAE: SUBFAMILY ***Species***	**Total collected**	C_0	C_1	C_2	C_0	C_1	C_2	C_0	C_1	C_2	**Control (uncut aspen forest**
CARABINAE											
Calosoma calidum	3	0	0	0	0	0	0	0	2	1	0
Calosoma frigidum	1	0	0	0	0	0	0	0	1	0	0
Carabus nemoralis	385	38	142	70	5	17	34	3	5	23	48
Carabus serratus	37	5	3	2	4	8	2	3	1	6	3
Carabus sylvosus	144	9	18	13	27	15	11	27	6	6	12
Sphaeroderus stenostomus lecontei	9	0	0	0	1	0	0	0	0	0	8
HARPALINAE											
Anisodactylus merula	1	0	0	0	0	0	0	1	0	0	0
Anisodactylus rusticus	1	1	0	0	0	0	0	0	0	0	0
Harpalus affinis	1	0	0	0	0	0	0	0	0	1	0
Harpalus indigens	11	0	4	2	0	0	1	1	1	2	0
Harpalus lewisii	5	0	0	1	0	0	0	1	0	3	0
Harpalus laticeps	9	1	0	1	3	0	0	2	1	1	0
Harpalus opacipennis	10	1	1	0	1	0	1	5	0	1	0
Harpalus pensylvanicus	28	3	0	0	0	2	1	5	9	8	0
Harpalus providens	27	1	1	4	3	2	2	4	4	5	1
Harpalus somnulentus	21	2	2	1	3	0	4	3	2	4	0
Notiobia terminata	1	0	0	0	0	0	0	0	0	1	0
Selenophorus opalinus	5	0	0	2	0	0	0	0	3	0	0
Cymindis americana	1	0	0	0	0	1	0	0	0	0	0
Cymindis cribricollis	13	0	0	0	0	0	0	0	0	0	13
Dicaelus purpuratus	1	0	0	0	0	0	0	0	1	0	0
Lebia pulchella	1	0	0	1	0	0	0	0	0	0	0
Syntomus americanus	5	0	1	0	1	1	1	0	0	1	0
Agonum cupripenne	2	1	1	0	0	0	0	0	0	0	0
Agonum placidum	5	0	0	0	0	0	0	1	1	3	0
Agonum retractum	1	0	0	0	0	0	0	0	0	0	1
Calathus gregarius	181	7	21	10	19	35	41	3	12	14	19
Synuchus impunctatus	473	57	36	17	30	23	67	8	18	37	180
Cyclotrachelus sodalis	638	52	112	58	67	84	70	30	42	82	41
Myas cyanescens Dejean	540	51	70	77	59	41	33	22	13	15	159
Poecilus lucublandus	77	16	2	9	2	7	10	1	5	24	1
Pterostichus coracinus	6	0	2	0	0	0	1	0	1	0	2
Pterostichus corvinus	3	1	0	0	0	0	0	0	0	0	2
Pterostichus melanarius	56	5	9	6	12	7	3	3	5	3	3
Pterostichus mutus	392	13	26	45	17	55	58	51	70	53	4
Pterostichus novus	29	5	7	2	2	0	2	5	1	2	3
Pterostichus pensylvanicus	208	21	17	15	16	21	15	2	5	11	85
Pterostichus permundus	13	1	0	1	1	0	5	1	4	0	0
Pterostichus stygicus	307	42	30	40	37	25	29	30	20	23	31
Pterostichus tristis	11	0	0	0	0	0	4	0	2	0	5
Amara angustata	8	1	1	1	0	4	0	0	0	1	0
Amara cupreolata	1	0	0	0	1	0	0	0	0	0	0
Amara lunicollis	1	0	0	0	0	0	1	0	0	0	0
LORICERINAE											
Notiophilus aeneus	5	1	0	0	1	2	0	0	0	1	0

(*Continued on next page*)

Table 2. Total number of carabid specimens collected in 1995 by treatment at the LTSP study site (*Continued*).

CARABIDAE: SUBFAMILY *Species*	**Total collected**	**Number of specimens collected by treatments*** Stem only harvesting (SOH) C_0	C_1	C_2	Whole-tree harvesting (WTH) C_0	C_1	C_2	Forest floor removal (FFR) C_0	C_1	C_2	**Control (uncut aspen forest**
PATROBINAE											
Patrobus longicornis	11	2	2	0	1	0	2	0	2	1	1
TRECHINAE											
Bembidion quadrimaculatum oppositum	2	0	0	0	0	0	1	0	0	1	0
Total specimens collected	3690	337	508	378	313	350	399	212	237	334	622
Total species collected	46	25	22	22	23	18	25	23	27	29	21
Number of plots (2 traps/plot)	32	3	3	3	3	3	3	3	3	3	5

*Treatments occurred in early 1994. Levels of organic matter removal were: SOH = stem-only harvesting where the merchantable tree bole was removed to an upper diameter of 10 cm with the treetops retained on site; WTH = whole-tree harvesting where all aboveground woody material was removed; and FFR = whole tree harvesting plus forest floor removal. Soil compaction levels: C_0 = minimal soil compaction; C_1 = medium: increased bulk density of upper soil by 15%; and C_2 =heavy: increased soil bulk density by 30%. See Methods for details.

Of the 3690 carabids, 622 specimens (21 species) were collected in the uncut aspen stands and 3068 specimens (44 species) in the 27 treatment blocks (Table 2). New carabid species were added with each collection throughout the entire sampling period, starting with 14 distinct species during the first period in June and ending with one new species added during the last collection period in late August and early September (Table 1). The sampling period when the most carabid species (30) were collected occurred during 26 July–9 August.

The two-way ANOVA tests on the 12 selected carabid groupings indicated that 'organic-matter-removal' significantly affected mean catch rate in 8 tests, but 'soil compaction' was only significant in one test and the interaction term in two (Table 3). No factors were significant in four of the tests. The one test where soil compaction was significant involved the combined catch rate for all Harpalini. However, in a subsequent analysis of mean Harpalini catch rate per plot, after pooling the data within each level of soil compaction, no significant differences were detected (Kruskal-Wallis test: $H = 2.6$; df = 2; $P = 0.2763$). Given the above results, soil compaction was not included in the succeeding analyses. After pooling the data within each level of organic matter removal, 31 species had been collected in the SOH (1223 specimens) and WTH (1062) plots and 36 species in the FFR (783) plots.

An NMDS ordination of all 32 plots, including all treatment plots and the uncut aspen stands, produced a two-dimensional solution that explained 84.5% of the variation (final stress = 0.16; Fig. 1). The species composition of the carabid assemblages from the uncut aspen stands were distinct (not overlapping) from all treatment plots. By contrast, the FFR assemblages were the least similar to (furthest from) the uncut aspen assemblages, with the SOH and WTH assemblages being intermediate and often overlapping (Fig. 1).

When considering mean species richness per plot, no significant differences were detected among treatments when comparing the three levels of organic matter removal (Table 4). However, when including the uncut aspen plots, significantly more carabid species were collected in the treatment plots than in the aspen plots.

The species accumulation curves generated in iNEXT revealed that the FFR plots consistently had the highest richness as sample size increased, with the control (uncut) plots having the lowest rarified species richness and the SOH and WTH plots being intermediate (Fig. 2). The fact that the 95% confidence intervals for the FFR and control plot curves did not overlap indicates that the carabid diversity in these two communities were significantly different.

Table 3. Summary statistics for two-way ANOVA analyses for the number of carabid specimens collected per day per plot (2 traps per plot) standardized to 100 plots and the number of carabid species collected per plot. Showing results for the two main effects (level of organic matter removal and level of soil compaction), and the interaction term.

Carabid grouping and most common species	Total collected	Summary results of two-way ANOVA *					
		Organic matter (OM) removal		Compaction (C)		OM × C interaction	
		F, df	*P* =	F, df,	*P* =	F, df,	*P* =
All Carabidae	3690	2.21, 2	0.1386	0.00, 2	1.0000	0.34, 4	0.8400
All Harpalini	120	7.67, 2	**0.0039**	5.61, 2	**0.0128**	0.96, 4	0.4531
Calathus gregarius	181	2.67, 2	**0.0965**	0.36, 2	0.7026	0.33, 4	0.8542
Carabus nemoralis	385	0.77, 2	0.4777	0.19, 2	0.8286	0.24, 4	0.9120
Carabus sylvosus	144	3.5, 2	**0.0520**	0.45, 2	0.6446	2.19, 4	0.1112
Cyclotrachelus sodalis	638	2.22, 2	0.1375	0.55, 2	0.5863	0.66, 4	0.6277
Myas cyanescens	540	15.08, 2	**0.0001**	0.34, 2	0.7162	0.96, 4	0.4531
Pterostichus mutus	392	2.95, 2	**0.0780**	0.44, 2	0.6508	2.47, 4	**0.0817**
Pterostichus pensylvanicus	208	6.67, 2	**0.0068**	0.00, 2	1.0000	0.95, 4	0.4582
Pterostichus stygicus	307	4.93, 2	**0.0196**	1.93, 2	0.1740	0.54, 4	0.7083
Synuchus impunctatus	473	5.25, 2	**0.0160**	1.31, 2	0.2943	3.66, 4	**0.0238**
Number of species/plot		0.64, 2	0.5389	0.00, 2	1.0000	0.96, 4	0.4531

* Data were log10 (x+1) transformed prior to analysis. The two traps in each plot were averaged together, resulting in three values for each of the 9 separate treatment combinations. Significant *P* values are shown in bold.

Mean carabid abundance per plot was significantly greater in the SOH and WTH plots compared with the FFR plots (Table 4). A similar pattern appeared after including the uncut aspen plots, with the aspen plots being intermediate.

After pooling the data from the 12 Harpalini species collected in this study (Tables 1 and 2), mean Harpalini catch was significantly greater in the FFR plots compared with the WTH plots, with SOH plots being intermediate (Table 4). A similar ranking occurred when including the uncut aspen plots, with the mean catch rate in the aspen plots being significantly lower than all the treatment plots.

Treatments significantly affected mean catch rates for six of the nine most commonly collected carabids species, with significant effects to four species when comparing only the three organic matter removal treatments and to six species when comparing the treatment plots and the uncut aspen plots (Table 4). Three general catch-rate patterns were evident among these six species. First, for *M. cyanescens*, *P. pensylvanicus*, and *S. impunctatus,* catch rates were generally highest in the uncut aspen stands, intermediate in the SOH and WTH plots, and lowest in the FFR plots (Table 4). Second, for *C. sodalis* and *P. stygicus,* catch rates were generally highest in the SOH and WTH plots, lower in the FFR plots, and lowest in the aspen stands. Third, catch rates of *P. mutus* were highest in the FFR plots, intermediate in the SOH and WTH plots, and lowest in the aspen stands.

Overall, 8 of the 46 (17%) carabid species in this study had significant indicator values ($P < 0.05$) (Table 5). 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 eight species, two were significantly associated with the FFR plots and six with the uncut aspen stands. However, of these eight species, only two had relatively high indicator values (IndVal > 40), and both were collected at relatively low numbers: *Cymindis cribricollis* Dejean (IndVal = 100; 13 specimens) and *Sphaeroderus stenostomus lecontei* Dejean (IndVal = 73.4; 9 specimens).

Discussion

During the second post-logging growing season in the present study, carabid diversity and abundance had changed in several ways, especially between the uncut aspen stands and the treatment plots. For example, several forest specialists (based on Larochelle and Larivière 2003), such as *M. cyanescens*, *P. pensylvanicus*, and *S. impunctatus,* dramatically declined in numbers after logging, especially in the FFR plots, while open-habitat species, such as most Harpalini, increased greatly, especially in the FFR plots. Similar patterns of decreasing catch rates of forest specialists and increasing catch rates of open-habitat species have been documented in many carabid studies

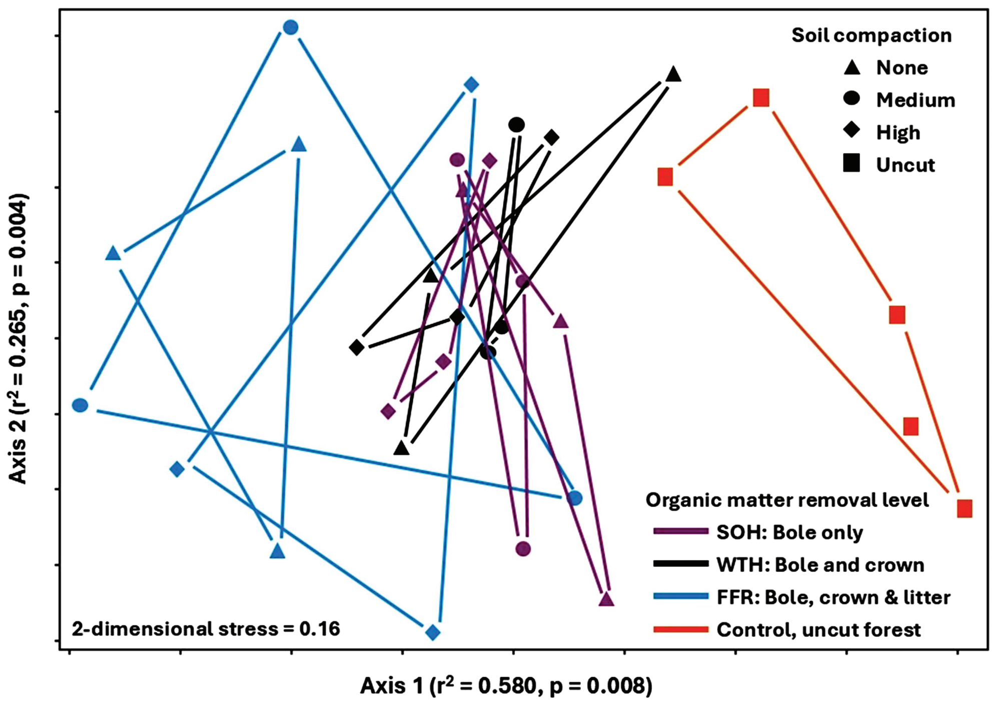

Figure 1. Non-metric multidimensional scaling (NMDS) ordination of the 32 season-long pitfall samples (pooling two traps per plot) based on carabid catch rates per day after log10 (x + 1) transformation, Convex hulls unite plots of similar level of organic matter removal and soil compaction as well as the nearby uncut aspen forest. Colors are used to signify similar levels of organic matter removal, while symbols signify different soil compaction levels. SOH = stem-only harvesting where the merchantable tree bole was removed to an upper diameter of 10 cm with the treetops retained on site; WTH: whole-tree harvesting where all aboveground woody material was removed; and FFR: whole tree harvesting plus forest floor removal.

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; Haack et al. 2024) and hardwood habitats (Buddle et al. 2006, Magura et al. 2015, Kriska et al. 2020). Some of the reasons given in the above publications as to why carabid forest specialists decline after clearcutting include: 1. increases in sunlight raise near-ground temperatures and lower humidity; 2. changes to the litter layer and understory vegetation reduce places for some carabids to shelter, hide, and hunt; and 3. interspecific competition with open-habitat species that quickly colonize new openings.

In an Ontario study, carabids and other ground invertebrates were monitored in jack pine (*Pinus banksiana* Lamb.) stands after two (Venier et al. 2017) and seven years (Work et al. 2023) following treatments similar to those in our study. At that Ontario site, forested plots were subjected to stem-only harvesting (SOH), whole-tree harvesting (WTH), WTH plus stump removal, and WTH plus stump removal and blading, where the forest floor was removed. Even after seven years post-treatment, catch rates of the forest specialists such as *M. cyanescens*, *P. pensylvanicus*, and *S. impunctatus* were still lowest in the plots that had been most disturbed, i.e., WTH and bladed (Work et al. 2023). In both studies (Venier et al. 2017, Work et al. 2023), as well as generally in ours (Fig. 2, Table 4), the community responses of the arthropods studied were similar in the SOH and WTH plots.

In other studies, forest specialists declined in numbers following both human-caused and natural disturbance events. For example, forest specialists declined following the selective cutting of oaks (*Quercus* spp.) to create more open savanna-like habitat in Ohio (Kriska et al. 2020), the removal of mature red pine (*Pinus resinosa* Sol. ex Aiton) to restore sites to prairie in Michigan (Haack et al. 2024), as well as following a severe ice storm in hardwood forests in Quebec

Table 4. Mean (± SE) number of carabid species collected per plot (2 traps per plot) and mean number of carabid specimens collected per day per plot standardized to 100 plots in 1995 by treatment after pooling data within each level of organic matter removal. Data shown for all species combined, for all Harpalini combined, and for the nine most commonly collected carabid species.

CARABIDAE: FAMILY TRIBE Most common species	Total Collected	Treatments: Stem only harvesting (SOH)	Whole-tree harvesting (WTH)	Forest floor removal (FFR)	Control (uncut aspen forest)	Kruskal-Wallis rank sum test statistic *H*: Test results for only the first three treatments	Test results for the three treatments and the uncut control forest
		Number of plots (2 traps per plot)					
		9	9	9	5		
		Mean number of species per plot					
		12.1 ± 0.5 Aa*	11.2 ± 0.4 Aa	10.9 ± 1.0Aa	8.7 ± 0.7 b	H = 2.1, df = 2, P = 0.3513	H = 9.3, df = 3, P = 0.0253
		Mean number specimens per day per plot × 100					
CARABIDAE	3690	84.9 ± 8.6 Aa	71.0 ± 9.3 Aa	53.7 ± 5.9 Bb	70.3 ± 10.1 ab	*H* =6.3, df = 2, ***P* = 0.0425**	*H* =6.3, df = 3, ***P* = 0.0961**
HARPALINI	120	2.4 ± 0.4 ABab	1.8 ± 0.4 Bb	5.0 ±1.1 +Aa	0.1 ± 0.1 c	*H* =6.86, df = 2, ***P* = 0.0327**	*H* =16.1, df = 3, ***P* = 0.0011**
Calathus gregarius	181	2.9 ± 0.9 Aa	7.5 ±2.2 Aa	2.3 ± 0.6 Aa	2.3 ± 1.1 a	*H* =4.4, df = 2, *P* = 0.1135	*H* =5.3, df = 3, *P* = 0.1542
Carabus nemoralis	385	13.1 ± 5.8 Aa	3.4 ± 1.3 Aa	2.0 ± 0.9 Aa	5.1 ± 3.8 a	*H* =0.9, df = 2, *P* = 0.6340	*H* =1.0, df = 3, *P* = 0.7943
Carabus sylvosus	144	3.9 ± 1.0 Aa	3.8 ± 0.8 Aa	2.0 ± 0.9 Aa	1.3 ± 0.7 a	*H* =3.4, df = 2, *P* = 0.1788	*H* =6.2, df = 3, *P* = 0.1015
Cyclotrachelus sodalis	638	16.2 ± 2.4 Aa	15.6 ± 3.0 Aa	10.4 ± 2.6 Aab	4.5 ± 1.9 b	*H* = 3.1, df = 2, *P* = 0.2133	*H* = 9.2, df = 3, ***P* = 0.0273**
Myas cyanescens	540	14.4 ± 1.9 Aab	10.2 ± 2.0 Ab	3.7 ± 0.7 Bc	18.6 ± 3.1 a	*H* = 15.4, df = 2, ***P* = 0.0005**	*H* = 19.4, df = 3, ***P* = 0.0002**
Pterostichus mutus	392	6.6 ± 1.8 Ab	10.0 ± 2.1 Aab	12.2 ± 1.2 Aa	0.4 ± 0.3 c	*H* = 3.6, df = 2, *P* = 0.1643	*H* = 14.6, df = 3, ***P* = 0.0022**
Pterostichus pensylvanicus	208	3.5 ± 0.6 Ab	3.8 ± 0.8 Ab	1.3 ± 0.5 Bc	10.4 ± 2.6 a	*H* = 8.9, df = 2, ***P* = 0.0116**	*H* = 16.8, df = 3 ***P* = 0.0008**
Pterostichus stygicus	307	8.4 ± 0.6 Aa	7.0 ± 1.0 ABab	4.8 ± 0.8 Bbc	3.6 ± 0.8 c	*H* = 7.1, df = 2, ***P* = 0.0294**	*H* = 11.5, df = 3, ***P* = 0.0093**
Synuchus impunctatus	473	7.0 ± 1.1 Ab	8.4 ± 1.5 Ab	4.2 ± 1.2 Bc	21.9 ± 3.7 a	*H* = 4.8, df = 2, ***P* = 0.0890**	*H* = 13.3, df = 3, ***P* = 0.0040**

* Means followed by the same letter within rows were not significantly different at $P = 0.1$ level (Kruskal-Wallis rank sum test followed by the Dunn's test for post-hoc pairwise comparisons). Upper case letters refer to tests with only the three treatments, whereas the lower-case letters refer to the three treatments and control plots. Significant P values are shown in bold.

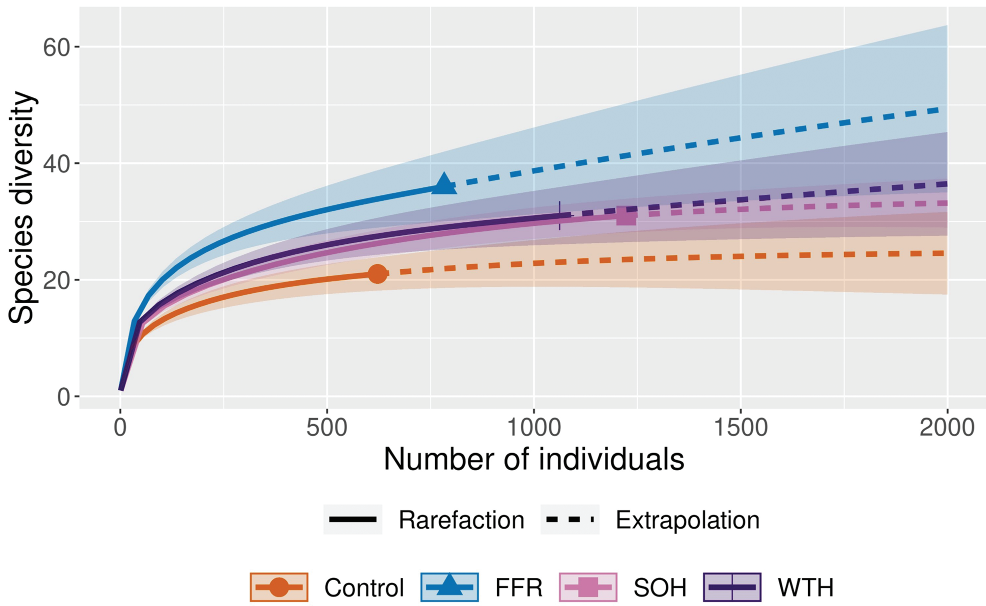

Figure 2. Sample-size-based rarefaction (solid lines) and extrapolation curves (dashed lines) with 95% confidence intervals (shaded areas) for species richness, a species diversity index (Hill's number q=0), for carabids collected in 1995 by pitfall traps the year after logging in aspen stands in Michigan. The treatments were: SOH = stem-only harvesting where the merchantable tree bole was removed to an upper diameter of 10 cm with the treetops retained on site; WTH = whole-tree harvesting where all aboveground woody material was removed; and FFR = whole tree harvesting plus forest floor removal See Methods for details. Figure generated in iNEXT online.

that created large gaps in the former closed tree canopy (Saint-Germain and Mauffette 2001). In the case of *P. pensylvanicus*, several authors have reported that it highly prefers forest sites with leaf litter (Epstein and Kulman 1990, Niemela et l. 1992, Pearce et al. 2003), likely explaining its lowest levels in the FFR treatment plots of the present study.

With respect to the two species with higher catch rates in the SOH and WTH plots compared with the FFR and uncut aspen plots, *C. sodalis* and *P. stygicus*, both are considered more open-habitat species, being associated with both forests and fields in the Midwestern USA (Epstein and Kulman 1990, Larsen et al. 2003, Gandhi et al. 2011). In Illinois, Willand et al. (2011) reported high catch rates of *C. sodalis* in early successional forests and *P. stygicus* in recently burned forests. In Ohio, where a 17-m-wide corridor was created in a hardwood dominated forest the year before sampling, most *P. stygicus* were collected in the corridor compared with the forest edge or interior forest (Silverman et al. 2014).

The trapping pattern for *P. mutus* along with the Harpalini, showed highest catch rates in the FFR plots, intermediate in the SOH and WTH plots, and lowest in the aspen stands. Epstein and Kulman (1990) consider *P. mutus* a generalist that is common in xeric, upland forests. In an Ontario study, Work et al. (2023) reported that *P. mutus* catch rates increased as site disturbance levels increased.

There were three commonly collected species in the present study that showed no significant differences in catch rates among all treatments: *C. gregarious*, *C. nemoralis*, and *C. sylvosus*. Of these three species, *C. gregarious* and *C. nemoralis* are considered habitat generalists, while *C. sylvosus* is more a forest specialist, but also occurs in fields adjacent to forested areas (Larochelle and Larivière 2003). In some studies, *C. gregarious* was reported from both uncut and clearcut forested areas, as well as in open fields (Epstein and Kulman 1990, Beaudry et al. 1997, Haack and Ruesink 2020, Kriska et al. 2020, Haack et al. 2024). In forested areas, *C. nemoralis* was more common in managed forests compared with old growth forests (Werner and Raffa 2000, Latty et al. 2006), suggesting it is a good colonizer of disturbed sites. By contrast, Latty et al. (2006) reported that *C. sylvosus* was common in old growth forests in Wisconsin. whereas Riley and Browne (2011) collected most *C.*

Table 5. Overall indicator values (IndVal) and associated *P* values for 8 carabid species with significant indicator values sorted by treatment. Species are arranged by IndVal (high to low) within the habitat in which they were significant. In addition, the total number of test plots (2 traps per plot) and carabid specimens collected in 1995 are given by treatment.*

Treatment or habitat	Indicator value		No. carabids collected in all plots for each level of organic matter removal aTab lecut control plots				
Species	(IndVal)	*P* =	No.	SOH	WTH	FFR	Control
Number of test plots (2 traps/plot)				9	9	9	5
FFR							
Harpalus pensylvanicus	38.8	0.0296	28	3	3	22	0 (0)**
Pterostichus mutus	36.8	0.0012	392	84	130	174	4 (7)
Control (uncut aspen stands)							
Cymindis cribricollis	100.0	0.0004	13	0	0	0	13 (23)
Sphaeroderus stenostomus lecontei	73.4	0.0008	9	0	1	0	8 (14)
Pterostichus tristis	39.5	0.0174	11	0	4	2	5 (9)
Pterostichus pensylvanicus	38.3	0.0002	208	53	52	18	85 (153)
Synuchus impunctatus	34.8	0.0012	473	110	120	63	180 (324)
Myas cyanescens	31.5	0.0042	540	198	133	50	159 (286)

* Treatment codes: SOH = stem-only harvesting; WTH = whole-tree harvesting; FFR = whole tree harvesting plus forest floor removal; and Control = uncut aspen stands.

** The number in parentheses represents the number of specimens captured in the 5 control plots after adjustment to 9 plots to aid in comparison among all treatments.

sylvosus in a wide-range of younger forested sites ranging from some that were recently clearcut up to others that had been clearcut 50 years earlier, but was rarely found in stands that were 85- and 150-years-old in North Carolina.

Although we found no strong evidence that carabid catch rates were significantly impacted by the soil compaction treatments in the present study, others have reported that increasing soil compaction negatively altered carabid abundance and diversity. For example, Magura et al. (2003), working in Hungary, found a significant negative correlation between the degree of soil compaction and carabid species richness. These authors argued that compacted soil could have negatively affected digging in the soil by carabids during oviposition, aestivation and hibernation. In the study by Belskaya et al. (2020), in Russia, carabid abundance and diversity were lowest at forested sites open to the public compared to similar sites that were mostly closed to the public. The authors suggested that high recreational use resulted in greater soil compaction that negatively influenced carabid reproduction.

It is possible that the soil compaction of sandy loam soils that occurred at our study sites does not negatively effects carabids. As evidence, consider that vegetative measurements taken five years post-treatment at our study site indicated a positive, although not significant, response to increasing soil compaction (Stone 2001). That is, average aspen above-ground biomass and sapling height both tended to increase with increasing level of soil compaction (Stone 2001). These trends were attributed to increased bulk density of the sandy loam soils caused by the higher levels of soil compaction, thereby enhancing soil water holding capacity. By contrast, increasing levels of organic matter removal on the same plots after five years showed significantly reduced average aspen biomass and height (Stone 2001). By 10 years post-treatment, soil bulk density levels at the HMNF study site had recovered to normal (pre-harvest) levels in the upper 0–10 cm of soil but were still significantly compacted at the 10–20 cm and 20–30 cm levels (Voldseth et al. 2011). A similar finding for soil bulk density was reported at 25 years post-treatment (Curzon et al. 2022).

At the other LTSP aspen study sites in Minnesota (on silt loam) and the Upper Peninsula of Michigan (on clay loam), the compaction treatments, especially heavy soil compaction, resulted in reduced tree biomass even after 10- and 25-years post-treatment (Voldseth et al. 2011, Curzon et al. 2022). Perhaps if carabids had been monitored at these other two study sites with finer soil textures that were more impacted by the compaction treatments, the carabid assemblages would have shown stronger responses to compaction.

As mentioned above, in the present study as well as the studies by Venier et al. (2017) and Work et al. (2023), the community responses of the ground arthropods were similar in the SOH and WTH plots. Likewise, the SOH and WTH treatments had similar and minimal impacts on above-ground woody biomass production 25 years post-logging at the aspen LTSP study sites in Minnesota and Upper Michigan on the silt loam and clay loam soils (Curzon et al. 2022). However, on the sandy HMNF LTSP site, above-ground woody biomass production was reduced on the WTH plots compared with SOH. Such findings indicate that impacts from biomass removal on ground invertebrates and subsequent biomass production may not always be directly correlated, suggesting that site conditions, such as soil texture, need to be considered when comparing the potential impacts of WTH to SOH on biodiversity and long-term forest sustainability.

Unfortunately, carabid trapping only occurred once at the HMNF LTSP sites during the year after the silvicultural treatments were completed, and therefore no long-term trends can be analyzed. Nevertheless, the current study documents carabid species diversity and abundance at a particular time and place that gives a baseline about forest habitat conditions at these sites. Furthermore, the present study indicates that many carabid species were sensitive to the treatments imposed, especially the varying levels of organic matter removal. Because of their high species diversity and sensitivity to environmental conditions, carabids are considered useful bioindicators (Work et al. 2008, Koivula 2011) and therefore could be used to monitor long-term site productivity of forests.

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