Initial Changes in Ground Beetle (Carabidae: Coleoptera) Assemblages after Creating Gaps of Varying Sizes in Mature Northern Hardwood Forests in Wisconsin

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Abstract

Managers of northern hardwood forests in the Great Lakes region create gaps in the forest canopy of various sizes during harvesting to achieve different silvicultural objectives. Single-tree harvesting favors recruitment of shade-tolerant tree species by creating small gaps in the canopy, whereas group selection creates larger gaps that can favor shade-intolerant tree species. We evaluated changes in carabid beetle abundance and diversity in harvest-created gaps of five sizes (gap diameters of 6, 10, 20, 30, and 46 m) and uncut forests in northern Wisconsin where sugar maple (*Acer saccharum*) was the dominant tree species. Gaps were cut during the fall/winter of 1994 and 1995. Pitfall traps were used to sample carabids during the summers of 1994 (pre-harvesting) and 1997 (2nd or 3rd summer post-harvesting). Overall, 27,111 carabids (60 species) were collected in both years, with 15,036 (25 species) collected in 1994 and 12,075 (55 species) collected in 1997. Carabid species richness increased while catch rate decreased with increasing gap size. Similarly, as gap size increased, carabid abundance declined for forest specialists but increased for open-habitat species. The carabid assemblages in the 6- and 10-m-diameter gaps were most like the intact forest, while those in the 30- and 46-m-diameter gaps were most distinct. Results are discussed in terms of harvesting strategies in northern hardwood forests to maintain high biodiversity.

Keywords Carabidae, ground beetles, richness, rarefaction, harvest-created gaps, northern hardwoods

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Gaps in the forest canopy result from the death of one or more trees, or at times from the death of a single large branch of a dominant tree (Runkle 1985, Yamamoto 2000, Muscolo et al. 2014). Gaps can be caused by a variety of natural disturbances, such as tree death or upper crown breakage following fire, high winds, ice storms, and disease and insect outbreaks. In addition, various silvicultural systems create canopy gaps of different sizes, from small gaps following single-tree and small group harvesting to larger gaps following group selection cutting or clearcutting. The environmental conditions within a gap can be considerably different from that in the surrounding intact forest. For example, within a gap, especially near the center, light levels and daytime temperatures are typically higher than within the surrounding intact forest. In response to these environmental changes, plant and animal diversity within gaps has been found to increase (Denslow 1987, Shields et al. 2008, Kern et al. 2013a, Muscolo et al. 2014, Lewandowski et al. 2021). However, over time, as gaps close, diversity usually returns to that which was found prior to disturbance.

Forest gaps vary widely in size. The smallest gaps reported in many studies is about 4 m^2, while the largest gaps studied have reached 2 ha in size (Schliemann and Bockheim 2011, Zhu et al. 2015). In temperate hardwood forests in Japan, most natural forest gaps were 30–140 m^2 in size, with only a few exceeding 400 m^2 (Yamamoto 2000). Gap size has a strong influence on which plants become the most successful colonizers. Shade-tolerant species are generally more

Table 1. Summary information for five selected studies on carabid responses to forest gaps of various sizes.

Reference	Study location	Dominant tree species, genus, or forest type	Gap sizes (m^2)	Year of cutting	Year of sampling	General findings for gaps relative to uncut forests*
Koivula and Niemelä 2003	Finland	*Picea*	1,600	1995–1996	1996–1998	OHS ↑
Klimaszewski et al. 2005	Quebec, Canada	*Betula alleghaniensis*	628, 1,257, 2,513	1999	2000	FS ↓, OHS ↑, species richness ↑
Ulyshen et al. 2006	South Carolina, USA	*Quercus*	1,300, 2,600, 5,000	1994, 2000	2001	FS lowest in oldest gaps, species richness highest in youngest gaps
Lee et al. 2017	South Korea	*Pinus*	2,500, 2,800, 3,200	2010 (typhoon-created)	2011	Species richness and trap catch ↑
Haack et al. 2024b	Michigan, USA	*Populus*	2,500	1994	1995	FS ↓, OHS ↑

* Codes: FS = forest specialists, OHS = open-habitat specialists, ↓ = decreased, and ↑ = increased.

successful in small gaps, whereas shade-intolerant species establish themselves better in larger gaps where more sunlight is available. Forest managers routinely use this knowledge to adjust their silvicultural harvesting systems to favor recruitment of certain tree species (Tubbs 1977, Hewitt 1998, Kern et al. 2013b, Leak et al. 2014, Kern et al. 2017, WI DNR 2018, Rogers et al. 2022). For example, in the northern hardwoods of the Great Lakes region, single tree or small group harvesting is practiced to favor shade tolerant tree species such as sugar maple (*Acer saccharum* Marshall) and American beech (*Fagus grandifolia* Ehrh.). By contrast, creation of larger gaps is promoted to favor tree species that are more intermediate in shade tolerance like yellow birch (*Betula alleghaniensis* Britt.).

One of the common forest types in the northern hardwoods of the Great Lakes region and northeastern North America is referred to as the "maple-beech-birch" type. This forest type is usually dominated by sugar maple, American beech, and yellow birch along with many minor tree species (Eyre 1980). The maple-beech-birch type is common on moist, well-drained, loamy soils. Sugar maple is usually the dominant tree species in these forests and because of its high degree of shade tolerance this species can form self-perpetuating climax plant communities. Sugar maple and yellow birch commonly regenerate by seed, whereas American beech can grow from seed as well as sprout from stumps.

Ground beetles (Coleoptera: Carabidae) are considered good bioindicators because they are relatively easy to sample and quantify with pitfall traps, are well-known taxonomically, and are sensitive to environmental disturbances such as forest management activities (Pearce and Venier 2006, Work et al. 2008). Numerous carabid studies have found that abundance of forest specialists usually declines following large-scale clearcutting of trees while abundance of open-habitat specialists increases (Niemelä et al. 1993, Beaudry et al. 1997, Fuller et al. 2008, Venier et al. 2017, Koivula et al. 2019, Haack et al. 2024a). Relatively few studies have investigated carabid responses to creation of forest gaps (Koivula and Niemelä 2003, Klimaszewski et al. 2005, Ulyshen et al. 2006, Lee et al. 2017, Haack et al. 2024b). The authors of the preceding studies generally described their study sites in terms of gaps or patch harvesting and reported similar patterns of transition from fewer forest-specialists to more open-habitat specialists during the first few years following gap creation (Table 1). Moreover, Klimaszewski et al. (2005) studied three sizes of gaps and found carabid species richness was higher in gaps compared with the intact forests. They also found carabid species composition in gaps became more like the intact forest as gap size decreased. However, the smallest gap size investigated in the Klimaszewski et al. (2005) study, as well as in any of the studies listed in Table 1, was 628 m^2, which is similar in area to a 28-m-diameter circle. The sizes of gaps studied to date are relatively large and not representative of the smaller openings that would be created by single-tree and small group harvesting. Therefore, our study provides an opportunity to build on

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previous studies by including much smaller gaps to investigate how a wider range of gaps sizes influences faunal diversity within a northern hardwood forest.

A well-replicated study was initiated in the 1990s in northern hardwood stands in Wisconsin where five sizes of forest gaps were created, i.e., 6, 10, 20, 30 and 46 m in diameter. Several studies have been conducted at this site during the past few decades, primarily on gap microclimate, seedling survival, tree regeneration, ground-layer plant diversity, and deer browse (Strong et al. 1997, 1998; Kern et al. 2012, 2013a, 2013b, 2014, 2023; Knapp et al. 2019; 2021, VanderMolen et al. 2021). Two of the first reports focused on differences in microclimate and plant diversity among gap sizes (Strong et al. 1997, 1998). In 1996, average maximum daily air temperatures (at 1 m above ground) for the month of July averaged about 4 °C higher in the center of the 46-m gap compared to the intact forest. Similarly, average July temperatures were also 4–6 °C warmer in the 46-m gaps than the forest when measured at 10 cm above ground as well as 3 and 15 cm below ground (Strong et al. 1997). Average temperatures in the 20-m gaps were intermediate between the 46-m gaps and intact forest. As for tree seedlings and forbs, total plant diversity in 1997 was greatest in the 10–30 m gaps but declined in the 46-m gaps because of widespread growth of red raspberry (*Rubus idaeus* L.) (Strong et al. 1998). Interestingly, diversity of the ground-layer plant community was still highest in the 20–30 m gaps after 13 years post-harvesting (Kern et al. 2014), and raspberry continued to dominate many of the 46-m gaps even after 23 years post-harvesting (Knapp et al. 2021).

In the present study, we investigated initial changes in ground beetle assemblages at the Wisconsin study site. We sampled the summer before harvesting was initiated as well as 2–3 growing seasons post-harvesting. Our main objectives were to document changes in the carabid assemblages over a wide range of gap sizes, and determine if there was a clear break in gap size when forest specialists declined and open-habitat specialists increased.

Methods and Materials

Study site. The study area covered 136 ha of second-growth, northern hardwood forest on the Chequamegon-Nicolet National Forest, in northern Wisconsin (Forest County; 45.94065 °N, 88.97712 °W). The dominant trees were about 60 years old at the time the study was initiated (1994). having developed in areas that were heavily logged in the early 1900s (Rhemtulla et al. 2009). There had been no recent management activities conducted in the study area prior to 1994. The forest canopy was closed with only a few small canopy gaps created by recent single-tree blowdowns. Sugar maple dominated the study area (ca. 85% of stems), with over a dozen minor tree species present, such as American basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.), and yellow birch (2–4% of stems each). The general topography was a hummocky (uneven) kame-kettle complex. The dominant soils were classified as Stambaugh silt loam loess, which is a deep, well-drained soil.

Plot design and treatments. In 1993, the study area was divided into seven units (15–25 ha each), of which five were selected for future harvesting (Fig. 1). The habitat type for Unit 1 was classified as AOCa (Acer/Osmorhiza-Caulophyllum), which has soil conditions characterized as mesic and rich to very rich in nutrients (Kotar et al. 2002). The habitat type for the other four units scheduled for harvesting were all classified as ATD (Acer-Tsuga/Dryopteris), which has mesic soil conditions that are medium to rich in nutrients. Five sizes of canopy gaps were created (diameters of 6, 10, 20, 30 and 46 m, or about 28, 79, 314, 707, and 1662 m^2, respectively) as well as uncut reference areas to serve as controls. These sizes were selected to span the range found in silvicultural guidelines for northern hardwood forests. The 6- and 10-m gaps represented openings made from single-tree removals, while the 20- to 46-m gaps represented openings from group selection cuts.

Within each of the five units scheduled for harvesting, 18 plots were marked, each 1 acre (0.4 ha) in size, resulting in 90 plots total. Next, the six gap treatments were randomly assigned within each unit with three replicates of each gap size (Fig. 1). Logging occurred in Units 4 and 7 during fall–winter of 1994–1995, and in Units 3 and 5 after the next growing season during fall and early winter 1995. Unit 1 was not cut until 1999. All trees in the gaps with stems greater than 2.5 cm diameter at breast height were cut. The merchantable boles of larger trees were removed, with the upper crown and branches left on site. The plot centers of the canopy gaps and the corners of the 1-acre control plots were marked with aluminum pipes.

Carabidae trapping methods. We used barrier pitfall traps to collect carabids because they increase trap catch by directing surface-active invertebrates towards the collection cups (Durkis and Reeves 1982, Skvarla et al. 2014). Each trap 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 cup at each end of the

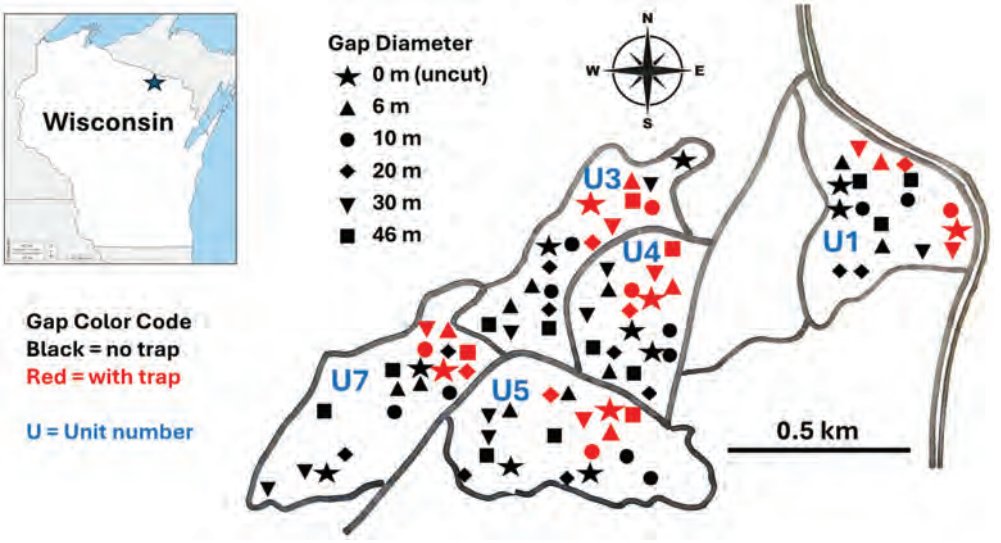

Figure 1. Location of study area in northern Wisconsin, showing layout of the original 90 research plots (black and red), and the ones selected for sampling in 1994 (red). In 1997, sampling only occurred in Units 3, 4 and 7, using the same plots as in 1994. Gap sizes are signified by different symbols.

barrier. The collection cups were ca. 10-cm wide at their top. We buried the cups so that the center of each cup touched the garden edging and was flush with the surrounding soil. A second 32-oz collection cup, with its rim removed, was placed inside the first cup, which allowed it to be removed later when collecting insects with little disturbance to the first cup. The inner cups were filled about halfway with 70% ethanol, which served as both a killing agent and preserving solution. Next, a shorter 16-oz plastic cup of similar diameter, with rim removed and a ca. 2 × 2 cm hole cut in its bottom, was placed inside the set of two 32-oz cups. The smaller cup fit snugly near the opening of the larger cups and helped keep leaves and other material out of the alcohol while allowing insects to fall through. This three-cup design was modified from Reeves (1980). Lastly, a 25-cm-diameter plastic plate 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.

Trapping protocol in 1994 (pre-harvesting). We used 90 traps in 1994. We selected six of the 18 plots in each of the five units slated for harvesting and installed three traps per plot (Fig. 1). In each unit, the six plots selected would each become a gap of a different size after harvesting later in 1994 or 1995. The traps were installed in different directions around each plot center, generally at distances of 8 to 10 m from the center. Trapping began on 12 June and ended on 21 September 1994, which covered the months of peak carabid activity in the Great Lakes region (Epstein and Kulman 1990; Haack et al. 2024a,b). There were seven trapping periods that spanned 9 to 18 days each for a total trapping season of 102 days (Table 2).

Timing of gap creation. Harvesting occurred within one unit at a time in 1994 and 1995. The Unit 4 gaps were created during August–December 1994, followed by Unit 7 (December 1994–February 1995), Unit 3 (August–September 1995), and Unit 5 (October–November 1995). Unit 1 was harvested in 1999.

Trapping protocol in 1997 (post-harvesting). We used 72 traps in 1997. We used the same plots in 1997 as we did in 1994, but only trapped in Units 3, 4, and 7 (Fig. 1). We installed four traps per plot. For those plots that were now gaps, we installed the traps at a distance about half the length of the gap radius. The traps were placed along SW, NW, NE, and SE lines measured from plot center. For the plots in uncut forest, the traps were placed in similar directions at distances of 8 to 10 m from plot center. As a result of the harvesting schedule, local flora and fauna in Unit 4 and 7 gaps had two summer seasons (1995 and 1996) to respond before our trapping in 1997, while only one season (1996) for gaps in Unit 3.

Sample processing and carabid identification. The contents from both cups

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Table 2. Summary data for the carabid collections made in 1994 and 1997 in the Chequamegon-Nicolet National Forest in northern Wisconsin.

Parameter	1994	1997
No. traps	90	72
No. forest units sampled	5	3
No. gaps per unit sampled	6	6
No. traps per gap installed	3	4
No. sampling periods	7	6
Sampling period dates (Roman numerals signify months)	VI 12–26, VI 27–VII 13, VII 14–27, VII 28–VIII 5, VIII 6–23, VIII 24–IX 9, IX 10-21 (= 101 trap days)	VI 5-18, VI 19-VII 1, VII 2–17, VII 18 –30, VII 31–VIII 13, VIII 14–VIII 26 (= 82 trap days)
Total trap days (traps ×days)	9,180	5,976
Total No. carabids collected	15,036	12,075
Total No. carabid species	25	55

of each barrier trap were combined into a single, labeled sealed plastic container during each collection. The samples were transported to the US 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 and then to the Carnegie Museum of Natural History (CMNH) in Pittsburgh, PA, for final species confirmation. Most specimens from this study were deposited at the CMNH.

Data management and analyses. The data were assembled into a spreadsheet by species, specimen count, trap, gap, collection date, and treatment (gap size). The mean (± SE) number of carabid species was calculated on a per gap basis. Each unit in 1994 or gap in 1997 was considered an independent experimental unit in the analyses, with the data averaged for all traps within each unit or gap. 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 averaged. Mean species richness and abundance (catch rates) were compared among units and gaps using the non-parametric Kruskal-Wallis rank sum test followed by the Dunn's test for post-hoc pairwise comparisons (https://www.statskingdom.com). The relationship between abundance of various carabid species and genera and gap size was explored with linear regression. An alpha level for significance of 0.1 was used because the N value was relatively low after the trap data were pooled by unit or gap. In addition, the Sørensen similarity index for the carabid species composition was calculated for each combination of gap sizes. This index measures the degree of species overlap between two populations with values ranging from 0 (no overlap) to 1 (perfect overlap).

We compared mean species richness among the five sampled units in 1994 to see how uniform the carabid community was over the experimental area. For the 1997 data, we first compared mean abundance and species richness between the gaps in Unit 3 with the gaps in Units 4 and 7 to compare gaps of the same size but different ages (1 vs. 2 seasons post-harvest). Based on the lack of significant differences for gaps of different ages in 1997 (see below), we combined the three units in all subsequent analyses.

Carabid species accumulation curves for species richness (Hill number q = 0) were calculated using pooled, season-long abundance data by carabid species for each unit (in 1994) and gap size (in 1997) using the online iNEXT package (https://chao.shinyapps.io/iNEXTOnline/; Chao et al. 2024). Sample-size-based rarefaction and extrapolation curves were generated with 95% confidence intervals based on 100 bootstrap replicates. As suggested by Chao et al. (2024), the 95% confidence intervals were visually inspected for overlap (i.e., non-significance) at the X-axis value that was double the smallest sample size for all curves in the analysis.

To explore differences in carabid assemblages by treatment (gap size), 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 rate per trap per day by species after averaging all traps within a particular unit (1994) or gap (1997). Log transformation was used because the original dataset was skewed. 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-

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Table 3. Summary data for the carabid species collected in 1994 (pre-harvest) and 1997 (post-harvest) in the gap study conducted in the Chequamegon-Nicolet National Forest in northern Wisconsin. The 1997 collection totals are given by month of collection and gap size.

SUBFAMILY Tribe Species	No. specimens collected			No. specimens collected by month in 1997			No. specimens collected by gap diameter in 1997					
	1994	1997	Total	June	July	August	0 m	6 m	10 m	20 m	30 m	46 m
CARABINAE												
Carabini												
Calosoma frigidum Kirby	16	3,595	3,611	3,588	5	2	1,148	1,692	665	88	1	1
Carabus nemoralis O.F. Mueller	0	46	46	34	0	12	9	5	0	1	14	17
Carabus sylvosus Say	712	119	831	3	8	108	49	14	14	19	8	15
Cychrini												
Scaphinotus bilobus (Say)	0	1	1	0	0	1	0	0	0	1	0	0
Sphaeroderus stenostomus lecontei Dejean	141	37	178	26	8	3	16	10	6	3	1	1
HARPALINAE												
Chlaeniini												
Chlaenius emarginatus Say	1	0	1	0	0	0	0	0	0	0	0	0
Elaphrini												
Elaphrus clairvillei Kirby	0	1	1	1	0	0	0	0	1	0	0	0
Harpalini												
Anisodactylus harrisii LeConte	0	3	3	3	0	0	0	0	0	0	7	3
Bradycellus lugubris (LeConte)	0	67	67	45	17	5	0	4	3	25	25	10
Bradycellus nigrinus (Dejean)	0	2	2	0	0	2	0	0	0	0	2	0
Bradycellus semipubescens Lindroth	0	5	5	2	0	3	0	0	0	0	3	2
Harpalus affinis (Schrank)	0	3	3	2	1	0	0	0	0	0	1	2
Harpalus compar LeConte	0	1	1	1	0	0	0	0	0	0	1	0
Harpalus fulvilabris Mannerheim	32	18	50	10	6	2	3	4	0	2	3	6
Harpalus herbivagus Say	0	9	9	6	3	0	0	0	0	0	7	2
Harpalus innocuus LeConte	0	1	1	0	1	0	0	0	0	0	0	1
Harpalus laticeps LeConte	0	17	17	10	4	3	0	0	0	0	0	17
Harpalus nigritarsis C.R. Sahlberg	0	1	1	0	1	0	0	0	0	0	1	0
Harpalus pensylvanicus (DeGeer)	0	1	1	0	1	0	0	0	0	0	0	1
Harpalus providens Casey	0	8	8	3	4	1	1	4	0	1	0	2
Harpalus solitaris Dejean	0	11	11	10	1	0	1	0	0	0	0	10
Harpalus somnulentus Dejean	1	218	219	65	112	41	0	3	1	13	89	112
Stenolophus conjunctus (Say)	0	1	1	1	0	0	0	0	0	0	0	1
Xestonotus lugubris (Dejean)	0	15	15	10	5	0	0	0	0	0	10	5
Patrobini												
Patrobus longicornis (Say)	1	0	1	0	0	0	0	0	0	0	0	0
Platynini												
Agonum cupripenne (Say)	0	11	11	10	1	0	0	0	0	0	6	5
Agonum gratiosum (Mannerheim)	0	2	2	2		0	0	0	1	0	0	1

Agonum melanarium Dejean	0	5	5	4	1	0	0	0	0	2	3	0
Agonum placidum (Say)	3	0	3	0	0	0	0	0	0	0	0	0
Agonum retractum LeConte	302	537	839	170	334	33	60	84	118	144	89	42
Agonum sordens Kirby	0	1	1	1	0	0	0	0	0	0	1	0
Calathus ingratus Dejean	1,371	280	1,651	89	132	59	167	40	41	21	10	1
Platynus decentis (Say)	892	632	1,524	591	39	2	251	174	146	37	17	7
Synuchus impunctatus (Say)	7,122	2,522	9,644	17	1,191	1,314	409	422	484	418	457	332
Pterostichini												
Myas cyanescens Dejean	349	683	1,032	198	189	296	258	105	167	71	36	46
Poecilus lucublandus lucublandus (Say)	0	59	59	42	14	3	0	0	0	0	4	55
Pterostichus adstrictus Eschscholtz	322	424	746	352	27	45	56	159	83	58	18	50
Pterostichus adoxus (Say)	9	0	9	0	0	0	0	0	0	0	0	0
Pterostichus caudicalis (Say)	0	18	18	12	3	3	0	1	0	1	2	14
Pterostichus commutabilis (Motschulsky)	0	1	1	1	0	0	0	0	0	1	0	0
Pterostichus coracinus (Newman)	1,775	840	2,615	446	215	179	313	92	194	105	79	57
Pterostichus femoralis (Kirby)	1	0	1	0	0	0	0	0	0	0	0	0
Pterostichus melanarius (Illiger)	1,002	441	1,443	170	182	89	36	112	23	33	57	180
Pterostichus mutus (Say)	28	389	417	347	24	18	24	42	31	47	70	175
Pterostichus pensylvanicus LeConte	460	590	1,050	420	132	38	221	120	110	77	28	34
Pterostichus tristis (Dejean)	191	37	228	20	13	4	15	3	7	7	3	2
Zabrini												
Amara angustata (Say)	0	16	16	7	9	0	0	0	0	14	1	1
Amara erratica (Duftschmid)	0	16	16	12	2	2	0	0	0	0	4	12
Amara familiaris (Duftschmid)	0	4	4	2	2	0	0	0	0	0	2	2
Amara littoralis Mannerheim	0	46	46	25	20	1	0	0	0	0	0	17
Amara lunicollis Schiodte	0	38	38	19	7	12	0	0	1	4	29	26
Pseudamara arenaria (LeConte)	1	206	207	166	37	3	0	6	4	39	71	86
LEBIINAE												
Lebiini												
Cymindis cribricollis Dejean	302	65	367	16	17	32	19	18	23	5	0	0
Syntomus americanus (Dejean)	1	1	2	1	0	0	0	0	0	0	0	1
LORICERINAE												
Loricerini												
Loricera pilicornis pilicornis (Fabricius)	0	1	1	0	1	0	0	0	0	0	1	0
SCARITINAE												
Scaritini												
Clivina fossor (L.)	0	13	13	9	4	0	0	0	2	1	7	3
Dyschirius globulosus (Say)	0	2	2	2	0	0	0	0	0	0	0	2
TRECHINAE												
Bembidiini												
Amerizus wingatei (Bland)	1	1	2	1	0	0	0	0	0	0	0	1
Bembidion quadrimaculatum oppositum Say	0	13	13	13	0	0	0	0	0	0	2	11
Bembidion stephensii Crotch	0	1	1	1	0	0	0	0	0	0	1	0
Totals	15,036	12,075	27,111	6,986	2,773	2,316	3,056	3,114	2,125	1,238	1,171	1,371

Table 4. Kruskal-Wallis rank sum test results by gap size for comparisons of mean carabid abundance and species richness in 1997 between traps in Unit 3 (1 season post-harvesting; N = 4 traps) vs. Units 4 and 7 (2 seasons post-harvesting; N = 8).

	Carabid comparisons for Unit 3 vs. Units 4 and 7	
Gap diameter (m)	Abundance Kruskal-Wallis H, df, p	Species richness Kruskal-Wallis H, df, p
0 (uncut)	$H = 1.22$, df = 1, $p = 0.27$	$H = 2.34$, df = 1, $p = 0.13$
6 m	$H = 1.41$, df = 1, $p = 0.23$	$H = 0.00$, df = 1, $p = 1.00$
10 m	$H = 1.85$, df = 1, $p = 0.17$	$H = 0.19$, df = 1, $p = 0.66$
20 m	$H = 0.35$, df = 1, $p = 0.55$	$H = 0.37$, df = 1, $p = 0.54$
30 m	$H = 1.03$, df = 1, $p = 0.31$	$H = 0.00$, df = 1, $p = 1.00$
46 m	$H = 0.03$, df = 1, $p = 0.86$	$H = 1.44$, df = 1, $p = 0.23$

ORD to create a null distribution which was compared to each determined axis to test for significance.

Results

Overall, 15,036 (25 species) carabid specimens were collected in 1994 and 12,075 specimens in 1997 (55 species). For the two seasons combined, 27,111 carabids (60 species) were collected. The 60 species represented 6 subfamilies of Carabidae, including 5 species of Carabinae, 47 Harpalinae, 2 Lebiinae, 1 Loricerinae, 2 Scaritinae, and 3 Trechinae. The top 5 species collected in 1994, when all sampling occurred in intact forests, were *Synuchus impunctatus* (Say) (7,122 specimens; 47.4% of 1994 total), *Pterostichus coracinus* (Newman) (1,775; 11.8%), *Calathus ingratus* Dejean (1,371; 9.1%), *Pterostichus melanarius* (Illiger) (1,002; 6.7%), and *Platynus decentis* (Say) (892; 5.9%). Similarly, in 1997, for all gaps and uncut forest sites combined, the top five species were *Calosoma frigidum* Kirby (3,595; 29.8%) *S. impunctatus* (2,522; 20.9%), *P. coracinus* (840; 7.0%), *Myas cyanescens* Dejean (683; 5.7%), and *P. decentis* (632; 5.2%) (Table 3). By contrast, 25 of the 60 species were represented by five or fewer specimens, with 14 species represented by a single individual. All species collected were previously known from Wisconsin based on Messer (2009).

In the initial analyses to compare mean carabid abundance and species richness per trap in the gaps that had one year to respond to harvesting (Unit 3) vs. two years (Units 4 and 7), no significant differences were detected for any of the six gap sizes (Table 4). Moreover, the species overlap (Sørensen similarity index) among all three units was very similar: 81% overlap for Unit 3 and Unit 4, 80% for Unit 3 and Unit 7, and 76% for Unit 4 and Unit 7. Given these results, the data from the three forest units were combined in all subsequent analyses (Table 2).

Most carabid species were collected during the first few sampling periods in both 1994 and 1997. In 1994, 22 of the 25 (88%) species collected that year were captured during the first sampling period (VI 12–26). For the remaining three species, *Bembidion wingatei* (Bland) was collected first in the second sampling period (VI 27–VII 13), with *Chlaenius emarginatus* Say and *Pterostichus femoralis* (Kirby) collected first in the third sampling period (VII 14–27). In 1997, when 55 carabid species were collected, new species were added during each sampling period, with the last few new species being detected in the largest gaps (Tables 3 and 5). The species accumulation curves generated by iNEXT should be compared along the X-axis at the value that is double the smallest sample size for all curves being analyzed (Chao et al. 2024), which equates to 4,474 individuals for the 1994 data in Fig. 2A and 2,476 individuals for the 1997 data in Fig. 2B. For 1994, the 95% confidence intervals overlapped for all curves, indicating no significant differences in the carabid assemblages among the five units sampled (Fig. 2A). The curve for the uncut gaps sampled in 1997, was also similar to all the 1994 unit curves (Fig. 2A). However, for the curves generated with 1997 data the rarefied species richness was highest in the 30- and 46-m gaps, intermediate in the 20-m gaps, and lowest for the 0-, 6- and 10-m gaps (Fig. 2B). A similar ranking emerged when comparing mean species richness per trap (after pooling) among units in 1994 and gaps in 1997, i.e., no significant differences among units in 1994, but with significantly higher mean richness values in the 30- and 46-m gaps compared to the 0-, 6-, and 10-m gaps (Fig. 3).

Although mean species richness was greatest in the largest gaps in 1997 (Fig. 3), mean carabid catch rate per trap decreased with increasing gap size (Fig. 4). Mean catch

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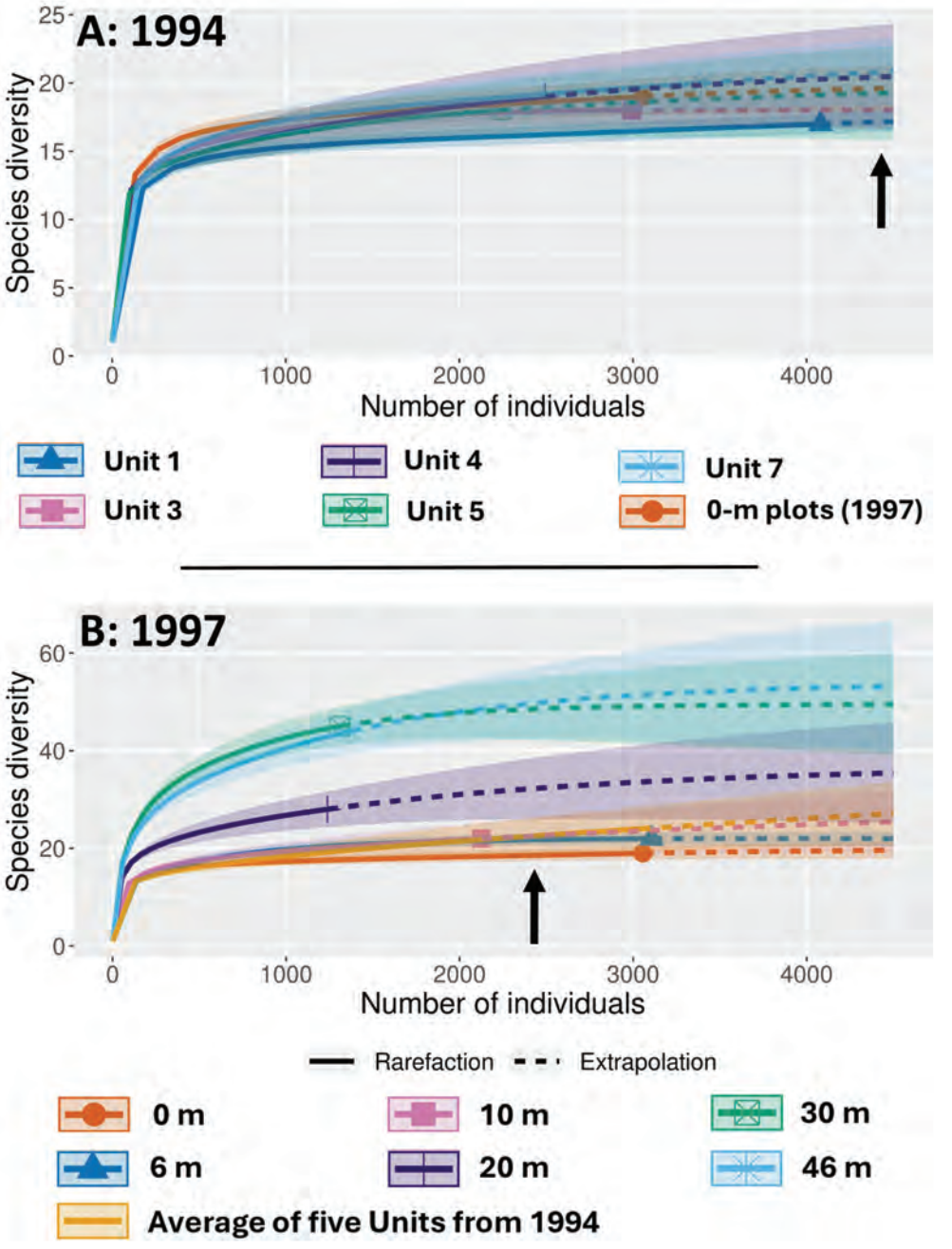

Figure. 2. Sample-size-based rarefaction (solid lines) and extrapolation (dashed lines) curves with 95% confidence intervals (shaded areas) for rarefied species richness for carabids collected by pitfall traps (A) in 1994 in five forest units in northern hardwoods forests in Wisconsin prior to harvesting as well as the curve for the 1997 uncut plots for reference, and (B) in 1997 in gaps of five different sizes and uncut plots (= 0 m) as well as the curve for the average of all uncut units sampled in 1994 for reference. Arrows indicate the values where the curves should be compared at 4,474 individuals in A and 2,476 individuals in B. Figure generated in iNEXT online.

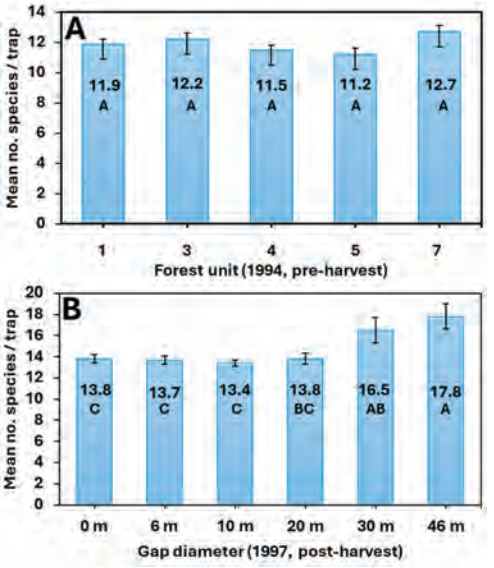

Figure 3. Mean species richness by trap for carabids collected by pitfall traps (A) in 1994 in five forest units in northern hardwoods forests in Wisconsin prior to harvesting (Kruskal-Wallis test: $H = 4.4$, df = 4, $p = 0.35$), and (B) in 1997 in gaps of five different sizes and uncut plots (= 0 m) (Kruskal-Wallis test: $H = 10.6$, df = 5, $p = 0.0589$).

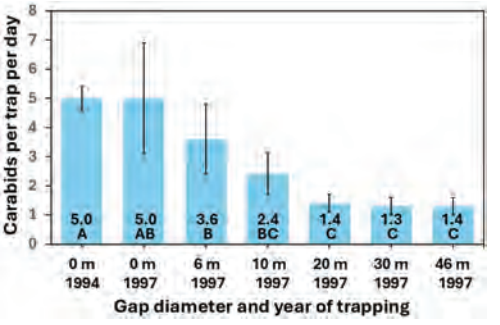

Figure 4. Mean catch rate (carabids/day/trap) for carabid beetles collected by pitfall traps in 1994 (pre-harvesting; all units combined) and 1997 (post-harvesting) by gap size in northern hardwood forests in Wisconsin (Kruskal-Wallis test: $H = 23.0$, df = 6, $p = 0.0008$).

rates per unit in 1994, which was prior to harvesting, was the same as the mean catch rate for the uncut gaps in 1997, i.e., both averaged 5.0 carabids per trap per day (Fig. 4).

An NMDS ordination of carabid catch rates for the sampling units in 1994 and the gaps in 1997 produced a two-dimensional solution that explained 91.5% of the variation (final stress = 0.12; Fig. 5). The species composition of the carabid assemblages in 1994 for the four uncut units (3, 4, 5, and 7) on the ATD habitat type generally overlapped, whereas the assemblage on Unit 1, which was on the richer AOC habitat type, was close but did not overlap the other four units (Fig. 5). By contrast, in 1997, the uncut (0 m) gaps were closest (most similar) to the

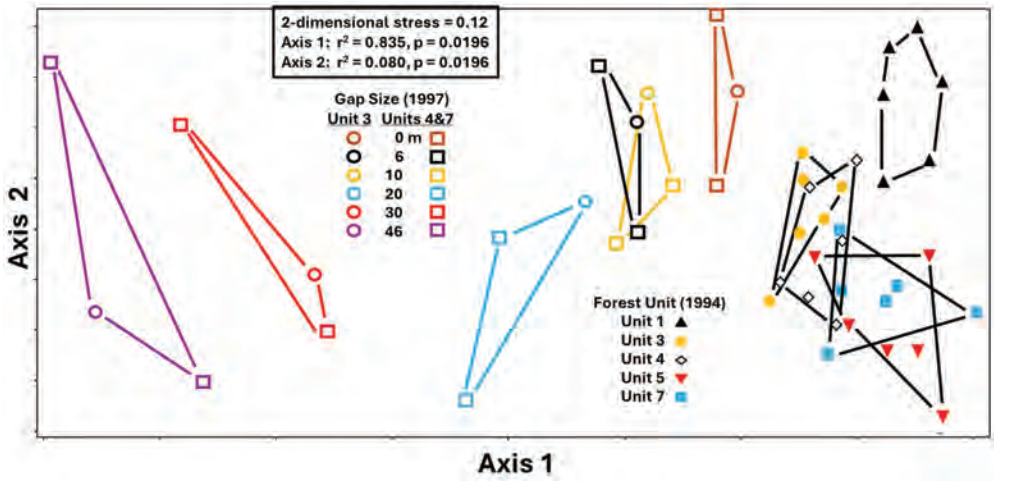

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of the 48 season-long pitfall samples (averaging either 3 traps per unit in 1994 or 4 traps per gap in 1997) based on carabid catch rates per day after log10 (x + 1) transformation. Convex hulls unite samples of the same unit in 1994 (N = 30) or same gap in 1997 (N = 18). Samples for 1997 are shown with two symbols: squares for samples where harvesting took place two growing seasons prior to sampling in 1997, whereas circles represent samples where harvesting occurred one growing season prior to 1997.

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Table 5. Number of carabid species collected in 1997 by gap size and collection period, and the cumulative percent of all carabid species collected within each gap size and overall.

	No. species collected by period in 1997 (cumulative % of total species collected within row)						
Gap size (diameter, m)	**Total**	**VI 5–18**	**VI 19–VII 1**	**VII 2–17**	**VII 18 –30**	**VII 31–VIII 13**	**VIII 14–VIII 26**
0 m (uncut)	19	14 (74 %)	19 (100 %)	14	10	11	11
6 m	22	17 (77 %)	19 (95 %)	16 (95 %)	10 (100 %)	14	12
10 m	22	17 (77 %)	15 (91%)	14 (95 %)	11 (100 %)	12	11
20 m	28	17 (61 %)	20 (78 %)	18 (89 %)	12 (93 %)	14 (100 %)	9
30 m	40	26 (65 %)	27 (90%)	22 (93 %)	16 (98 %)	13 (100 %)	14
46 m	44	29 (66 %)	32 (93 %)	24 (98 %)	15 (98 %)	17 (98 %)	17 (100 %)
All traps	55	42 (76 %)	42 (89 %)	36 (94 %)	23 (96 %)	26 (100 %)	23

1994 assemblages, but as gap size increased the carabid community became more distant (more distinct) from the uncut stands in 1994 and 1997 (Fig. 5).

The top 10 most collected carabid species in 1997 are listed for each gap size in Table 6. The top 10 species were the same and in the same rank order in the uncut stands and smallest gaps (0 and 6 m). *Calosoma frigidum* was the most frequently collected species in the 0, 6, and 10-m gaps. Moreover, it is noteworthy that only 16 *C. frigidum* were collected in 1994, compared with 3,595 in 1997 (Table 2). In the larger gaps (20, 30, and 46 m), *S. impunctatus* was the most frequently collected species. There were four species that were among the top 10 in all gap sizes: *Agonum retractum* LeConte, *M. cyanescens*, *Pt. coracinus*, and *S. impunctatus*. Compared to the top 10 carabids in the 0- and 6-m gaps, there was 1 different species in the 10-m gaps, 3 in the 20-m gaps, 5 in the 30-m gaps, and 6 in the 46-m gaps. The Sørensen similarity index values for each gap-size combination (Table 6), showed generally high degrees of overlap among the 0-, 6-, and 10-m gaps (73–88%), but lower when compared to the 30- and 46-m gaps (54–65%). The degree of species overlap was again relatively high between the 30- and 46-m gaps (79%).

Collections of carabids generally classified as forest-specialists or open-habitat specialists (Larochelle and Larivière 2003) demonstrated opposing trends with respect to gap size (Table 7). For four species typically considered forest specialists (*C. frigidum*, *M. cyanescens*, *P. decentis*, and *Pt. pensylvanicus* LeConte) there were significant negative linear relationships for each species between abundance and increasing gap size. By contrast, for species in the genera *Amara* Bonelli, *Bembidion* Latreille, and *Harpalus* Latreille, which are mostly open-habitat specialists, there were significant positive linear relationships for each genus between abundance and increasing gap size.

Discussion

Many studies in recent decades have documented reductions in carabid forest-specialists following tree harvesting, often with a concurrent increase in open-habitat specialists. Most of these studies were conducted in large clearcuts (e.g., Niemelä et al. 1993, Beaudry et al. 1997, Fuller et al. 2008, Koivula et al. 2019, Venier et al. 2017, Haack et al. 2024a), but similar trends were also documented in smaller forest gaps (Koivula and Niemelä 2003, Klimaszewski et al. 2005, Haack et al. 2024b; Table 1). In the study by Klimaszewski et al. (2005) in Quebec, three sizes of gaps were used with areas, if considered circles, would have diameters of about 28, 40, and 57 m. In both our earlier study and Klimaszewski et al. (2005), carabid catch rate was higher in intact forest plots compared with the gaps. In our study, this trend was most influenced by relatively high collections of *C. frigidum*, *C. ingratus*, *M. cyanescens*, *P. decentis, Pt. coracinus*, and *Pt. pensylvanicus* in the forest plots compared with the gaps, especially the larger 20-, 30-, and 46-m gaps (Table 3). Another similarity in the preceding two studies was that the carabid community in gaps became more like the intact forest as gap size decreased. In the present study, the 20-m gaps appeared to be near the breaking point where carabid assemblages in gaps of smaller size were most like the intact forest, favoring forest specialists, while gaps larger than 20 m were most distinct from the intact forest and favored open-habitat specialists.

It is important to note that Digweed et al. (1995) reported that pitfall traps should be placed at least 25 m apart to ensure independence of catches between traps. That

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Table 6. Top 10 carabid species collected in 1997 in the Chequamegon-Nicolet National Forest in northern Wisconsin by gap size, and the Sørensen similarity index for each gap size combination.

Parameter	Uncut forest (0 m)	6-m gaps	10-m gaps	20-m gaps	30-m gaps	46-m gaps
Total No. carabids collected	3,056	3,114	2,125	1,238	1,171	1,371
Total No. carabid species	19	22	22	28	40	44
Top 10 most collected carabid species: species code* (number collected, percent of total within each column)]						
	CAFR (1,148, 38%)	CAFR (1,692, 54%)	CAFR (665, 31%	SYIM (418, 34%)	SYIM (457, 39%)	SYIM (332, 24%)
	SYIM (409, 13%)	SYIM (422, 14%)	SYIM (484, 23%)	AGRE (144, 12%)	AGRE (89, 8%)	PTME (180, 13%)
	PTCO (313, 10%)	PTCO (174, 6%)	PTCO (194, 9%)	PTCO (105, 8%)	HASO (89, 8%)	PTMU (175, 13%)
	MYCY (258, 8%)	MYCY (159, 5%)	MYCY (167, 8%)	CAFR (88, 7%)	PTCO (79, 7%)	HASO (112, 8%)
	PLDE (251, 8%)	PLDE (120, 4%)	PLDE (146, 7%)	PTPE (77, 6%)	PSAR (71, 6%)	PSAR (86, 6%)
	PTPE (221, 7%)	PTPE (112, 4%)	AGRE (118, 6%)	MYCY (71, 6%)	PTMU (70, 6%)	PTCO (57, 4%)
	CAIN (167, 5%)	CAIN (105, 3%)	PTPE (110, 5%)	PTAD (58, 5%)	PTME (57, 5%)	POLU (55, 4%)
	AGRE (60, 2%)	AGRE (92, 3%)	PTAD (83, 4%)	PTMU (47, 4%)	MYCY (36, 3%)	PTAD (50, 4%)
	PTAD (56, 2%)	PTAD (84, 3%)	CAIN (41, 2%)	PSAR (39, 3%)	AMLU (29, 2%)	MYCY (46, 3%)
	CASY (49, 2%)	CASY (42, 1%)	PTMU (31, 1%)	PLDE (37, 3%)	PTPE (28, 2%)	AGRE (42, 3%)
Sørensen similarity index						
0 m		0.878	0.732	0.766	0.542	0.571
6 m			0.773	0.840	0.645	0.636
10 m				0.800	0.613	0.606
20 m					0.676	0.667
30 m						0.786

* Species codes: AGRE = *Agonum retractum*, AMLU = *Amara lunicollis*, CAFR = *Calosoma frigidum*, CAIN = *Calathus ingratus*, CASY = *Carabus sylvosus*, HASO = *Harpalus somnulentus*, MYCY = *Myas cyanescens*, PLDE = *Platynus decentis*, POLU = *Poecilus lucublandus*, PSAR = *Pseudamara arenaria*, PTAD = *Pterostichus adstrictus*, PTCO = *Pterostichus coracinus*, PTME = *Pterostichus melanarius*, PTMU = *Pterostichus mutus*, PTPE = *Pterostichus pensylvanicus*, and SYIM = *Synuchus impunctatus*.

Table 7. Percentage of four forest-specialist carabid species and three genera of mostly open-habitat carabids collected in the Chequamegon-Nicolet National Forest in northern Wisconsin in 1997 by gap size, and linear regression results for the actual number of carabids collected in 1997 vs. gap diameter.

Carabid genus or species	No. collected	Percent of specimens collected by gap size (%)						Linear regression (df = 1,4 for all)
		0 m	6 m	10 m	20 m	30 m	46 m	r =, F =, p =
Forest specialists								
CAFR*	3,595	31.9	47.1	18.5	2.4	0.03	0.03	–0.81, 7.4, 0.053
MYCY	683	37.8	15.4	24.5	10.4	5.3	6.7	–0.80, 7.2, 0.055
PLDE	632	39.7	27.5	23.1	5.9	2.7	1.1	–0.91, 18.3, 0.013
PTPA	590	37.5	20.3	18.6	13.1	4.7	5.8	–0.87, 11.9, 0.026
Open-habitat specialists								
Amara (5 spp)	113	0	0	0.9	15.9	31.9	51.3	+0.98, 115.2, 0.0004
Bembidion (2 spp)	14	0	0	0	0	21.4	78.6	+0.89, 14.8, 0.018
Harpalus (11 spp)	288	1.7	3.8	0.3	5.6	35.4	53.1	+0.94, 31.0, 0.0051

* Species codes: CAFR = *Calosoma frigidum*, MYCY = *Myas cyanescens*, PLDE = *Platynus decentis*, and PTPE = *Pterostichus pensylvanicus*.

goal was not reached in our study because we placed traps near the midpoint of the gap radius, and therefore the traps within the same gap were about 2 m apart in the 6-m gaps and 16 m apart in the 46-m gaps. Nevertheless, in all cases, the traps within any single gap were always more than 25 m away from the traps in all other gaps.

It is noteworthy that the carabid assemblages in the five units sampled in 1994 separated neatly in the NMDS analysis by habitat type (Fig. 5). The AOC habitat type (Unit 1) is recognized as having more nutrient-rich soils and a more species-rich herb layer than the ATD type (Units 3, 4, 5, and 7) (Kotar et al. 2002). The three main differences among the carabid assemblages in these two habitat types were (1) most *Pt. melanarius* were collected in AOC (356 in Unit 1 vs. an average of 39 in each of the four ATD units), (2) no *C. frigidum* were collected in AOC (Unit 1) compared with 2-8 individuals in each of the four ATD units, and (3) the singleton *Patrobus longicornis* (Say) individual collected in the present study was collected in the AOC type.

The similarity in carabid richness and catch rates between Unit 3 (which had one growing season before sampling) compared with Units 4 and 7 (which had two growing seasons before sampling) (Table 4), suggests that open-habitat specialists, which are typically capable of flight (Venn 2016), quickly colonize new openings. This finding is supported by the results from Koivula and Niemelä (2003) and Huber and Baumgarten (2005) where several open-habitat carabid species colonized new forest openings the first summer after winter harvesting.

As mentioned in the Methods, the upper crowns and branches of the merchantable trees in our study were left on site after harvesting. It is not clear to what degree our results would have changed if all logging slash had been removed at the time of harvest. Logging slash is known to provides structure, complexity, and refugia to certain carabids (Pearce et al. 2003, Nittérus and Gunnarsson. 2006). Some carabids respond positively to increasing levels of retained slash (Pearce et al. 2003, Work et al. 2014). However, as a group, carabid species richness tends to be higher in slash-free plots compared to plots with slash (Nittérus et al. 2007, Haack et al. 2024a). Moreover, in the studies by Venier et al. (2017), Work et al. (2023), and Haack et al. (2024b), carabid community responses were similar in both stem-only harvested plots (i.e., with slash) and whole-tree harvested plots (i.e. slash free).

The dramatic increase in numbers of *C. frigidum* collected in 1997 (3,595 individuals collected) compared to 1994 (16 individuals) is noteworthy. This increase did not appear linked to creation of the gaps given that 98% of the *C. frigidum* collected in 1997 were trapped in the intact forest plots and the smaller 6- and 10-m gaps (Table 3). It is more likely that the increase in *C. frigidum* adults was related to building populations of defoliating insects in the area. Although we noted large numbers of caterpillars (Lepidoptera) at the study site when collecting samples in 1997, we did not identify any of them. How-

ever, we suspect that most were the native Bruce spanworm, *Operophtera bruceata* (Hulst) (Lepidoptera: Tortricidae), which did cause heavy defoliation in the area in 1998 (WI DNR 1998). In eastern North America, *O. bruceata* larvae consume primarily foliage of sugar maple and American beech in May and June (Brown 1962). Adult *C. frigidum* have been reported feeding on *O. bruceata* larvae and pupae in Ontario, both on the forest floor as well as climbing trees and flying between trees to locate larvae (Crins 1980). High populations of *C. frigidum* have also been documented during outbreaks of many other forest Lepidoptera (Burgess and Collins 1917, Trager et al. 2013).

The results from our study and others (e.g., Klimaszewski et al. 2005, Ulyshen et al. 2006) indicate that creating a range of gap sizes increases carabid diversity. That is, smaller gaps aid in preserving populations of forest specialist species, especially those that are flightless, with larger gaps recruiting many open-habitat species. Some of the flightless forest-specialist carabids collected in the present study were *C. sylvosus* Say, *M. cyanescens*, and *Pterostichus tristis* (Dejean) (Larochelle and Larivière 2003). Knowing how carabids respond to changes in gap size allows forest managers to adjust gap size to meet their economic productivity goals while at the same time achieving a desired level of biodiversity as indicated by the carabids species assemblages. Gaps will close over time, with smaller gaps closing sooner primarily from lateral growth of perimeter trees, whereas larger gaps will close more slowly mostly from sapling height growth within the gaps (Runkle 1985, Webster and Lorimer 2005). As a result of plant succession and microclimatic changes within gaps over time, the community of associated carabids will also change (Ulyshen et al. 2006). Besides carabids, creation of forest gaps can affect many other forest animals, including spiders (Samu 2023), reptiles and amphibians (Greenberg 2001), birds (Lewandowski et al. 2021), and mammals (Gitzen and West 2002). There is likely no optimal gap size that benefits all or even most plants and animals, and therefore producing gaps of several sizes should help maintain and enhance high biodiversity of all organisms throughout a forest ecosystem (Kuuluvainen et al. 2012, Kern et al. 2013b).

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