Initial Changes in Ground Beetle (Coleoptera: Carabidae) Species Assemblages Near Seasonal Ponds Surrounded by Forests Under Different Harvesting Practices

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Abstract

Seasonal ponds often form after spring snowmelt in forests of the Great Lakes region. Although such seasonal ponds are common, few US states set buffer-width guidelines to protect them when harvesting the adjacent upland forest. The objectives of this study were to determine if the carabid beetle assemblages near seasonal ponds differed from those in the adjacent upland forests prior to any logging, and then if these assemblages changed in response to various levels of tree harvesting within and adjacent to the 15-m-wide buffers that surrounded the seasonal ponds. The traps were placed within the buffers at about 7.6 m from the pond edge, and in the adjacent upland forest at about 46 m from the pond. The study was conducted in northern hardwood forests in Minnesota, using a replicated block design with four pond buffer treatments (uncut control in both the buffer and upland forest, or a clearcut upland forest with the buffer remaining uncut, partially harvested, or clearcut). The clearcut blocks varied from 6–26 ha in size. Carabids were collected with pitfall traps in 2000 (prior to winter logging in 2000–2001) and 2002 (1-year after logging). Overall, 15,857 carabid specimens were collected, representing 99 species. In 2000, before logging, 51 species were collected, including 15 riparian species. An NMDS ordination indicated high similarity between the species assemblages near and adjacent to the seasonal ponds. However, more riparian species were collected near ponds. In 2002, after logging, 92 species were collected, including 33 riparian species. Among the four buffer treatments, NMDS ordination indicated that the species assemblages in the clearcut buffers were the most distinct from the control buffers. In addition, although the clearcut buffers had the most species and the most riparian species, forest-associated carabids were present in all four buffer treatments. Although retaining forested buffers around seasonal ponds was not required to maintain high carabid diversity in the short-term following tree harvesting, such practices would ensure protection for the ponds themselves as well as associated flora and fauna.

Keywords: Carabidae, biodiversity, vernal pools, riparian habitats, tree harvesting, Minnesota

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Seasonal ponds, which are also called vernal pools or seasonal forest pools, are isolated wetlands that form in depressions usually in spring after snowmelt or during periods of heavy precipitation (Kolka et al. 2011). Seasonal ponds, as the name implies, have an annual wet and dry phase and typically are 0.01 to 0.3 ha in size in the Great Lakes region and New England (Brooks and Hayashi 2002, Palik et al. 2003, Schrank et al. 2015). Seasonal ponds are important to many amphibians and invertebrates, allowing them to breed and develop in this type of wetland that lack major predators such as fish (Hofmeister et al. 2022). However, given their small size and temporary nature, seasonal ponds are challenging to protect when harvesting trees in forested landscapes, especially when logging occurs in winter or when ponds are dry. Nevertheless, the value of seasonal ponds in maintaining both plant and animal biodiversity is well recognized (Hofmeister et al. 2022). As evidence, some U.S. states have implemented

logging restrictions around seasonal ponds. For example, Minnesota requires a 15 m (50 ft) minimum buffer around all wetlands, including seasonal ponds, during logging operations (MFRC 2014). By contrast, the states of Maine and Massachusetts impose a 30 m (100 ft) buffer around seasonal ponds (Calhoun and deMaynadier 2004, MA-DEP 2017).

Ground beetles (Coleoptera: Carabidae) occur in many terrestrial habitats including riparian areas, which are lands that occur along the edges of water bodies (Larochelle and Larivière 2001, 2003). There are about 40,000 described species of Carabidae worldwide, including both ground beetles and tiger beetles (Bouchard et al. 2017), with about 2500 species recognized in North America (Bousquet 2012). Carabids are generally univoltine (Thiele 1977, Lott 2001) and sensitive to environmental changes in light, temperature, vegetation structure, and soil moisture (Lövei and Sunderland 1996, Pearce and Venier 2006, Work et al. 2008, Koivula 2011). Carabids are useful bioindicators because they are (1) relatively easy to sample and quantify with pitfall traps; (2) well-known taxonomically; and (3) highly localized with few migrating long distances (Rainio and Niemelä 2003, Langor and Spence 2006). In addition, pitfall trapping is relatively inexpensive and passive, although such traps do not evenly collect all carabid groups, such as the arboreal species (Woodcock 2005).

Many carabid species occur in riparian areas (Larochelle and Larivière 2001, 2003; Dearborn et al. 2014). Most carabid studies in riparian habitats have focused on species found near banks and shores of rivers, streams, and lakes (Andersen and Hanssen 2005, Kirichenko-Babko et al. 2020, Middendorf et al. 2025), while others have targeted permanent ponds (Kosewska and Nietupski 2015, Ludwiczak et al. 2022), floodplains (Cartron et al. 2003, Ballinger et al. 2005, Shepherd 2014), and seasonal ponds (Lott 2001, Brose 2003). Although carabids are primarily terrestrial insects, species that inhabit riparian areas often feed on aquatic insects, especially those that are washed ashore or come to shore soon after the adults emerge from the water bodies (Hering and Plachter 1997, Paetzold et al. 2005).

Harvesting trees alters both the forest and environmental features within it, such as tree age structure and composition, herbaceous plant cover, light intensity, and near-ground microclimate (Thiffault et al. 2025, Woodcock et al. 2025). In response, species assemblages often change after logging, especially clearcutting, with declines commonly reported for species that are forest specialists and increases in the numbers and diversity of open-habitat species (Niemelä et al. 1993; Beaudry et al. 1997; Magura et al. 2015; Koivula et al. 2019; Work et al. 2023; Haack et al. 2024a, 2024b).

A large-scale study focusing on the effects of forest harvesting on seasonal ponds was conducted in northcentral Minnesota, USA, beginning in 2000. A replicated block design was used that consisted of four treatments: (1) uncut and (2) partially cut buffers with the adjacent upland forest clearcut, (3) clearcut buffers with residual patches of uncut forest in the otherwise clearcut upland, and (4) control plots where both the buffers and nearby uplands were uncut (Fig. 1). To date, four studies conducted at these sites have been published. The topics addressed in those studies included pond hydrology (Kolka et al. 2011), pond invertebrates (Hanson et al. 2010), breeding bird communities (Hanowski et al. 2006), and plant communities (Palik and Kastendick 2010).

The current study was designed to survey and compare the species assemblages both near and upland from seasonal ponds prior to logging as well as during the second summer after logging. We hypothesized (1) that the species assemblages near and upland from seasonal ponds would be similar prior to logging, but more riparian species would be present near ponds. After logging, we hypothesized (2) that the species assemblages in the clearcut buffers would be most distinct from the other buffer treatments, with the uncut and control buffers being most similar, and the partial-cut buffers intermediate. Similarly, after logging, we hypothesized (3) that the species assemblages in the upland clearcuts would be most distinct, with those in the residual patches and control plots being similar.

Materials and Methods

Study site. The study area in northcentral Minnesota has experienced multiple glaciations events that created landforms such as drumlins, lake plains, moraines, and outwash plains. The seasonal ponds in this study were mostly elliptical in shape and located on gently rolling ground moraines (Kolka et al. 2011). The upland forests where the ponds were located were dominated by trembling aspen (*Populus tremuloides* Michx.) mixed with other common northern hardwood trees such as northern red oak (*Quercus rubra* L.), sugar maple (*Acer saccharum* Marshall), and basswood (*Tilia americana* L.). Black ash (*Fraxinus nigra* Marshall) was the dominant tree species growing in the seasonal ponds. Additional details on average temperature, length of

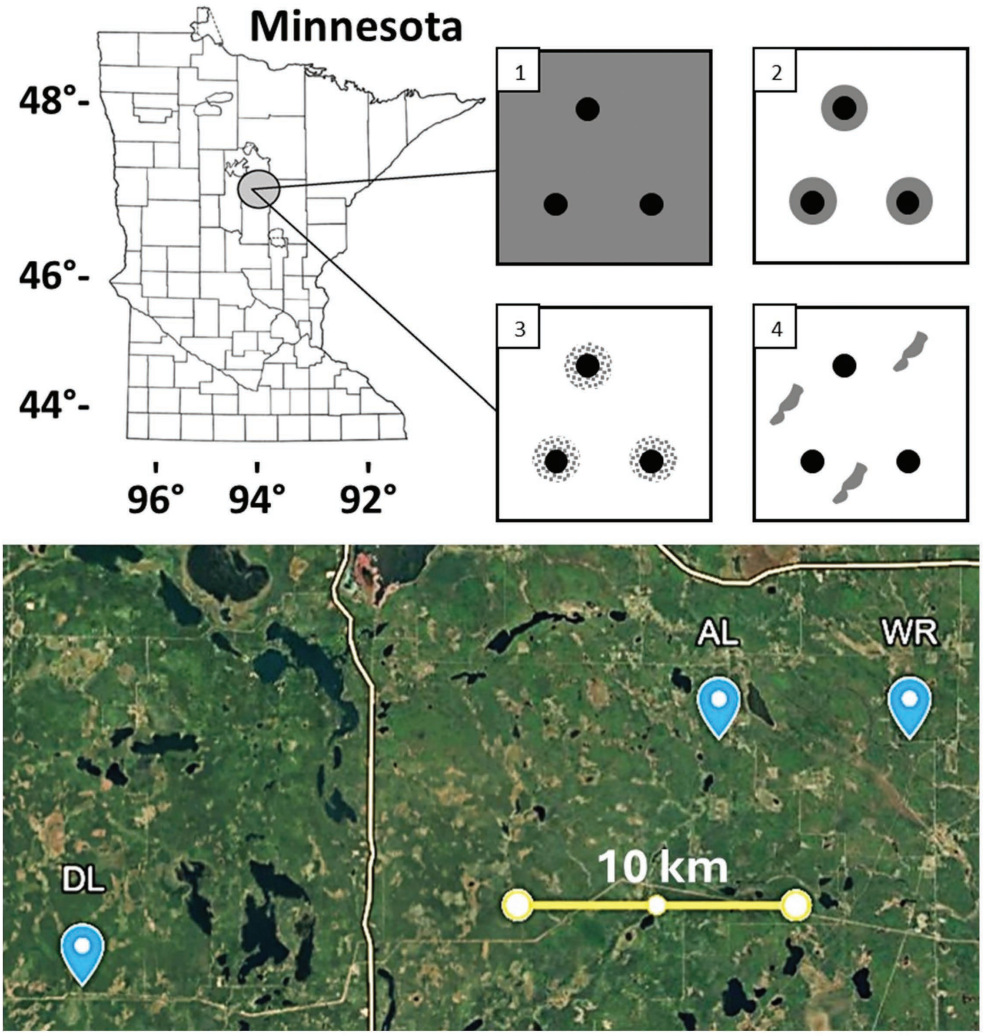

Figure 1. General location of the three study sites (blue teardrops) in Minnesota and diagrams of the four treatments imposed at each site: (1) control (uncut pond buffer and uncut upland forest); (2) uncut buffer and clearcut upland; (3) partially cut buffer and clearcut upland; and (4) clearcut pond buffer, clearcut upland, with residual patches of uncut forest. Site names: AL = Ahseburn Lake, DL = Dog Lake, and WR = Willow River. (Satellite image from Google Earth.)

growing season, and annual precipitation were given in Kolka et al. (2011).

General study design. Adult Carabidae were collected in 2000 and 2002 at three sites in north central Minnesota: Willow River (Atkin Co., 46.93 N 93.69 W), Ahseburn Lake (Cass Co., 46.93 N 93.78 W), and Dog Lake (Cass Co., 46.85 N 94.08 W) (Fig. 1). At each site, four or more seasonal ponds were selected that met the following criteria: (1) the surrounding forest was more than 50 years old; (2) ponds and surrounding forests had no evidence of recent disturbance; (3) initial pond area was between 0.02 and 0.1 ha in surface area; (4) ponds had a mineral or muck bottom rather than peat; (5) maximum water depth in the ponds was more than 15 cm when the initial selection was made in spring 2000, and (6) ponds had no inlets or outlets (Kolka et al. 2011). The cutting units that surrounded the seasonal ponds varied in size from 6 to 26 ha (average 12 ha), with some of the larger units containing multiple ponds. The three study sites were separated

by about 7–31 km, and the 4 ponds within each site were separated by about 200–1500 m.

Four ponds were randomly selected at each of the three sites and each pond was assigned to one of the following treatments: (1) uncut forest (control); (2) upland clearcut with 15 m (50 ft) uncut buffers surrounding each pond (uncut buffer); (3) upland clearcut with 15 m buffers surrounding each pond that were thinned to about 50% of the original stem basal area (partially cut buffer); and (4) upland clearcut with residual patches of uncut forest (0.13 ha) left in the upland but no buffer was retained around each pond (clearcut buffer) (Fig. 1). Trees along the outer margin of each pond, buffer or patch were marked in spring and summer 2000 prior to any logging. Logging occurred during December 2000 and January 2001 on frozen ground that usually had a 60-cm-thick snowpack. Therefore, collections in 2000 represented baseline, preharvest conditions, whereas collections in 2002 represented conditions during the second summer postharvest.

Sample year 2000. We installed four pitfall traps near each of the 12 ponds for a total of 48 traps. Two traps were positioned within the future 15-m-wide buffer of each pond at about 7.6 m (25 ft) from the pond edge and generally on opposite sides of the pond. Two additional traps were placed about 46 m (150 ft) beyond the pond edge in the surrounding upland forest. The two traps in the uplands were on the same side of the pond as the two traps placed within the buffer areas. Each pitfall trap consisted of a 1-m-long strip of garden edging partially buried in the soil with a 0.95 l (32 oz) plastic collection cup at each end. The collection cups were buried so that their rim was level with the forest floor and touching the garden edging. Inside each collection cup, we placed another 0.95 l cup with its rim removed. About 500 ml of ethanol (70%) was placed in the inner cup to serve as a killing agent and preserving solution. In addition, a shorter 0.47 l (16-oz) cup with its rim removed and a ca. 3-cm by 2-cm hole cut in its bottom was fitted inside of the inner cup. Insects could easily fall through the hole in the smaller cup where they were killed and preserved in the alcohol, but most leaves and twigs were kept out of the alcohol. All pitfall traps were installed during 16–18 May 2000. This three-cup design was modified from Reeves (1980).

The pitfall samples were collected at approximately 2-week intervals until 12–13 July 2000. 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, Michigan. Initially all carabid beetles were removed from each plastic container and placed in 70% ethanol within separate jars. These were labeled with pertinent information needed to associate each specimen with the study parameters of space, time, and treatment. Later, all samples were transported to Morgantown, West Virginia, for final sorting to morphospecies. Final species determinations for all carabid adults were made at the Carnegie Museum of Natural History in Pittsburgh, Pennsylvania, with voucher specimens of each species deposited there.

Sample year 2002. Using methods like those used in 2000, we installed all traps during 20–21 May 2002. Again, traps were emptied at about 2-week intervals through 15–16 July 2002. Overall, 64 traps were installed in 2002, with 48 traps installed near the same locations used in 2000, and 16 traps installed in the forest patches (treatment 4, Fig. 1). We installed 2 traps within the interior of each patch, using two patches at the Willow River site and three patches each at the Ahseburn Lake and Dog Lake sites.

Data management and analyses. The data were assembled into a spreadsheet of these study parameters: number of carabid species, specimen count, site, trap number, location (e.g., buffer, upland, patch), collection date, year, and treatment (e.g., clearcut, partially cut, no cut, control). Using primarily data from Larochelle and Larivière (2003), we also characterized the flight ability of each carabid species as well as its occurrence in riparian habitats because these attributes were thought to be potentially useful in explaining shifts in the species assemblages after logging. With respect to flight ability, each species was classified as (1) all or most adults being flight-capable, (2) most adults not flight-capable, or (3) all adults unable to fly. Species classified as "riparian" were those that occurred primarily in riparian habitats.

For most analyses, each trap was considered independent because they were separated by at least 30 – 50 m around the seasonal ponds (Digweed et al. 1995). However, given the configuration of the individual upland patches, the distance between each pair of traps within a single patch was less: 12–20 m; average = 14 m. Using individual trap data, we calculated and compared mean (± SE) number of species and specimens for all species, riparian species, and flightless species collected by year and treatment. We also calculated and compared catch rates (adults/day/100 traps) among treatments for three of the most frequently

collected species, which are all commonly associated with forests: *Platynus decentis* (Say), *Pterostichus pensylvanicus* LeConte, and *Synuchus impunctatus* (Niemelä et al. 1992, Beaudry et al. 1997, Graham-Sauvé et al. 2013).

We used the non-parametric Mann-Whitney U test when comparing two variables or the Kruskal-Wallis rank sum test followed by the Dunn's test for post-hoc pairwise comparisons when comparing three or more variables (https://www.statskingdom.com; Ashour 2024). These nonparametric tests were used because the datasets were often not normally distributed. In addition, we log10 (x + 1) transformed the data prior to analysis to reduce heteroscedasticity. Various percentage values were compared using the Chi-square test (https://www.socscistatistics.com). An alpha level for significance of 0.05 was used for all analyses. In addition, we calculated the Sørensen similarity index for the carabid species composition for various combinations of sites, locations, and treatments. This index measures the degree of species overlap between two populations with values ranging from 0 (no overlap) to 1 (perfect overlap).

We used carabid abundance data for the entire eight-week collection period in each year to calculate the Chao1 estimate of total carabid richness for each location or treatment in 2000 and 2002 (Colwell 2013). The Chao1 index estimates total species richness of a community by calculating the number of new (undetected) species at a "site" based on the initial number of species observed at that site and how many of those species were relatively rare, being represented by only one or two individuals each.

To explore differences in species assemblages by location, treatment, and year, species abundance data were examined with non-metric multidimensional scaling (NMDS) ordination using PC-ORD v.7 for Windows (McCune and Mefford 2017). The data matrix consisted of log10 (x + 1) transformed, catch rate data by species (carabids/day/100 traps). Given that some traps were disturbed during various trapping periods, catch rates were averaged for each pair of traps prior to analysis. Log transformation was used because the original datasets were skewed. The NMDS ordination default program settings and Bray-Curtis distance measure were used with each species weighted equally (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.

Results

Overall, 15,857 carabid adult specimens were collected in both years of this study, representing 15 tribes and 99 species (Table 1). For both years combined, the eight species most often collected were *Pl. decentis* (5,501 specimens), *Pt. pensylvanicus* (1,938), *Sy. impunctatus* (1,078), *Agonum retractum* LeConte (985), *Agonum cupripenne* (Say) (928), *Poecilus lucublandus* (Say) (750), *Pterostichus caudicalis* (Say) (640), and *Sphaeroderus stenostomus lecontei* Dejean (508). Of the 99 species, 48 of the species were represented by 5 or fewer specimens and 27 were singletons. According to Bousquet (2012), *Badister reflexus* LeConte represents a new state record for Minnesota.

2000: pre-harvest results. Overall, 6,988 carabid specimens were collected in 2000, representing 51 species: 47 species were collected near ponds and 40 in the upland forests (Table 1). The five species most often collected in all traps were *Pl. decentis* (2,212 specimens), *Pt. pensylvanicus* (891), *Sy. impunctatus* (800), *Ag. retractum* (778), and *Sp. stenostomus lecontei* (267). Of the 51 species, 18 were represented by 5 or fewer specimens and 8 were singletons. The top four species most often collected were the same, and in the same rank order, for both the buffer and upland areas. The fifth most common species was *Oxypselaphus pusillus* (LeConte) in the buffer areas and *Agonum palustre* Goulet in the upland forests. The average number of carabid species and specimens collected per trap did not vary significantly between traps near ponds and the upland forests (Table 2). Similarly, catch rates of *Pl. decentis*, *Pt. pensylvanicus*, and *Sy. impunctatus* did not vary significantly between traps located near and upland from the seasonal ponds (Table 2). The Chao1 index estimated four new species could occur near the ponds and nine in the upland forests (Table 1). The overall Chao1 estimates of total carabid richness were similar for these two habitats and overall (51–57 species).

New carabid species were collected during each of the four, two-week-long, sampling periods in 2000 (Fig. 2). Most species were collected during the first period (57%), with 80% of all species collected during the first two sampling periods. The overall Sørensen similarity index between the carabid species found near ponds vs. uplands for all sites combined was generally high (0.828) but varied among sites: 0.762 at Ahseburn Lake (39 total species collected), 0.630 at Dog Lake (37 species), and 0.886 at Willow River (39 species).

The NMDS ordination of carabid abundance for the traps near ponds and in the

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Table 1. Summary data for the carabid species collected near or adjacent to seasonal ponds in Minnesota by location or treatment in 2000 and 2002.

	2000: year prior to treatment			2002: 1-year post-treatment							
Parameter or species	**All traps in 2000**	**Pond traps**	**Upland forests traps**	**All traps in 2002**	**Uncut buffer traps**	**Partially cut buffer traps**	**Clearcut buffer traps**	**Control buffer traps**	**Upland patch traps**	**Upland clearcut traps**	**Upland control traps**
No. traps (before pooling pairs of traps)	48	24	24	64	6	6	6	6	16	12	12
Total No. species collected	51	47	40	92	45	39	57	30	40	67	31
No. species that are all or mostly flight-capable	34	31	25	72	33	26	41	19	27	52	21
Percent of species that are mostly flight-capable (%)	66.7	66.0	62.5	78.3	73.3	66.7	71.9	63.3	67.5	77.6	67.7
No. completely flightless species	9	8	9	9	5	6	8	7	7	7	5
Total riparian species†	15	15	9	35	15	13	21	11	9	16	8
Percentage of species considered riparian (%)	29.4	31.9	22.5	35.9	33.3	33.3	36.8	36.7	22.5	23.9	25.8
Total specimens	6988	4128	2860	8869	864	571	1014	781	1949	2844	846
No. specimens that can likely fly	2278	1259	1019	4494	227	253	468	276	790	2210	270
Percent of specimens that can likely fly (%)	32.6	30.5	35.6	50.7	26.3	44.3	46.2	35.3	40.5	77.7	31.9
No. specimens of flightless species	2949	1929	1020	3776	589	279	478	387	963	540	540
Percent of flightless specimens (%)	42.2	46.7	35.7	42.6	68.2	48.9	47.1	49.6	49.4	19.0	63.8
Total riparian specimens	808	561	247	826	51	46	204	144	97	201	83
Percentage of specimens considered riparian (%)	11.6	13.6	8.6	9.3	0.6	0.5	2.3	1.6	1.1	2.3	0.9
Chao1 index											
Chao1 estimate of total carabid richness	57	51	55	157	135	103	77	38	43	103	68
Number of new species predicted by Chao1	6	4	9	65	90	64	20	8	3	36	36
No. carabid species or subspecies by tribe											
Bembidiini											
Amerizus wingatei (Bland)‡‡	17	8	9	1			1				
Bembidion frontale (LeConte)*‡	0			2	1		1				
Bembidion mimus Hayward*‡	0			9	3		2			4	
Bembidion mutatum Gemminger & Harold‡	0			41	2	1	5			32	1

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Table 1. (Continued).

Parameter or species	2000: year prior to treatment			2002: 1-year post-treatment							
	All traps in 2000	Pond traps	Upland forests traps	All traps in 2002	Uncut buffer traps	Partially cut buffer traps	Clearcut buffer traps	Control buffer traps	Upland patch traps	Upland clearcut traps	Upland control traps
Amerizus wingatei (Bland)‡‡	17	8	9	1			1				
Bembidion occultator Notman*‡	0			1			1				
Bembidion praticola Lindroth*‡-	147	91	56	34	4		4	7	16	2	1
Bembidion quadrimaculatum oppositum Say‡	0			39			4	1	5	28	1
Bembidion rapidum (LeConte)‡	1		1	3		1		1		1	
Bembidion versicolor (LeConte)*‡	0			1	1						
Elaphropus anceps (LeConte)‡	0			1						1	
Trechus apicalis Motschulsky‡-	29	18	11	2		1		1			
Brachinus cyanochroaticus Erwin*‡	0			1			1				
Carabini											
Calosoma calidum (Fabricius) ‡	0			1						1	
Calosoma frigidum Kirby‡	51	16	35	219	9	61	4	30	77	24	14
Carabus maeander maeander Fischer von Waldheim*‡	0			5	1					4	
Chlaeniini											
Chlaenius alternatus G. Horn*‡	0			1			1				
Chlaenius emarginatus Say‡	1		1	14	1		3		2	7	1
Chlaenius impunctifrons Say*‡	0			1		1					
Chlaenius sericeus sericeus (Forster)‡	1	1		26	1		1		1	23	
Cychrini											
Sphaeroderus stenostomus lecontei Dejean‡‡	267	146	121	241	17	24	14	46	65	59	16
Elaphrini											
Elaphrus clairvillei Kirby*‡	3	3		7	1		4	1			1
Harpalini											
Acupalpus carus (LeConte)*‡	0			1						1	
Amphasia sericea (T. W. Harris)‡	1	1		0							
Anisodactylus kirbyi Lindroth*‡	0			1			1				
Anisodactylus nigrita Dejean*‡	0			1						1	
Anisodactylus rusticus (Say)‡	0			3						3	
Anisodactylus sanctaecrucis (Fabricius)‡	0			1						1	

Bradycellus badipennis (Haldeman)*‡	0			1			1											
Bradycellus lecontei Csiki*‡	0			1					1									
Bradycellus lugubris (LeConte)*‡	5	3	2	0														
Bradycellus neglectus (LeConte) ‡	0			1		1												
Dicheirotrichus cognatus (Gyllenhal)‡	0			1											1			
Discoderus parallelus (Haldeman)‡	0			3											3			
Harpalus fulvilabris Mannerheim‡	47	25	22	42			5		9	2	14				8	4		
Harpalus herbivagus Say‡	0			3											3			
Harpalus laticeps LeConte‡	0			5							1				4			
Harpalus lewisii LeConte‡	0			1							1							
Harpalus opacipennis (Haldeman)‡	0			1											1			
Harpalus plenalis Casey‡	0			1											1			
Harpalus paratus Casey‡	1		1	0														
Harpalus providens Casey‡	0			1											1			
Harpalus somnulentus Dejean‡	13	8	5	26	4		1		3	1	2				12	3		
Stenolophus fuliginosus Dejean*‡	0			1											1			
Xestonotus lugubris (Dejean)‡	1	1		2					1						1			
Lebiini																		
Cymindis cribricollis Dejean‡-	23	15	8	39	7		4		8		15				4	1		
Dromius piceus Dejean‡	0			2	1										1			
Syntomus americanus Dejean‡-	0			17	1		1		2		1				12			
Licinini																		
Badister obtusus LeConte‡	13	6	7	12			1		2		4				4	1		
Badister parviceps Ball*‡	30	16	14	13	3		1		1	1	5				1	1		
Badister reflexus LeConte*‡	0			1					1									
Loricerini																		
Loricera pilicornis pilicornis (Fabricius)*‡	9	9		6	1		1		3	1								
Notiophilini																		
Notiophilus aeneus (Herbst)‡	14	8	6	11	2					2	4				3			
Patrobini																		
Patrobus longicornis (Say)‡-	0			2												2		
Patrobus septentrionis septentrionis Dejean*‡	2	2		0														
Platynini																		
Agonum affine Kirby*‡	0			3			1				2							
Agonum cupreum Dejean‡	0			3			1		2									

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Table 1. (Continued).

Parameter or species	2000: year prior to treatment			2002: 1-year post-treatment							
	All traps in 2000	Pond traps	Upland forests traps	All traps in 2002	Uncut buffer traps	Partially cut buffer traps	Clearcut buffer traps	Control buffer traps	Upland patch traps	Upland clearcut traps	Upland control traps
Platynini (continued)											
Agonum cupripenne (Say)‡	0			928	10	22	15		13	834	34
Agonum gratiosum (Mannerheim)*‡	11	9	2	14	1	1	4	3	2	2	1
Agonum harrisii LeConte*‡	0			1							1
Agonum melanarium Dejean*‡	67	56	11	111	15	4	22	21	2	27	20
Agonum metallescens (LeConte)*‡	0			1			1				
Agonum muelleri (Herbst)‡	0			56						56	
Agonum palustre Goulet‡	237	76	161	14	3				6	5	
Agonum placidum (Say)‡	8	4	4	3	1					2	
Agonum propinquum (Gemminger & Harold)*‡	2	2		1		1					
Agonum retractum LeConte‡-	778	417	361	207	9	21	19	63	52	33	10
Agonum sordens Kirby*‡	3	2	1	4	1		2			1	
Agonum trigeminum Lindroth*‡	71	58	13	135	7	4	32	23	3	47	19
Calathus ingratus Dejean‡-	126	49	77	31	1	5	4	1	16	4	
Olisthopus species‡§	2	2		0							
Oxypselaphus pusillus (LeConte)*‡‡	237	157	80	19		3	3	4	4	3	2
Platynus decentis (Say)‡‡	2212	1500	712	3289	539	225	417	315	839	451	503
Platynus mannerheimii (Dejean)**‡‡	0			10		2	4	3		1	
Synuchus impunctatus (Say)‡-	800	437	363	278	28	6	31	53	109	29	22
Pterostichini											
Myas cyanescens Dejean‡‡	47	25	22	104	17	16	19	4	19	18	11
Poecilus lucublandus (Say)‡	28	19	9	722	13	25	44	11	105	486	38
Pterostichus adoxus (Say)‡‡	3		3	0							
Pterostichus adstrictus Eschscholtz‡	9	8	1	9	1		1			6	1
Pterostichus caudicalis (Say)*‡	216	150	66	424	10	23	113	77	61	102	38
Pterostichus commutabilis (Motschulsky)‡	0			4	1		1			2	
Pterostichus coracinus (Newman)‡‡	121	63	58	96	13	9	16	13	32	5	8
Pterostichus femoralis (Kirby)‡-	2	1	1	5	1		1			3	
Pterostichus luctuosus (Dfossejean)*‡	7	3	4	13	1	3	2	2	2	3	

Pterostichus melanarius melanarius (Illiger)‡	68	32	36	106	10	7	2	17	17	37	16
Pterostichus mutus (Say)‡	69	23	46	215	8	13	14	10	60	83	27
Pterostichus novus Straneo‡‡	40	29	11	10			4		3	3	
Pterostichus patruelis (Dejean)*‡-	2	2		1	1						
Pterostichus pensylvanicus LeConte‡	891	498	393	1047	103	66	134	64	377	259	44
Pterostichus tenuis (Casey)*‡	1	1		1						1	
Pterostichus tristis (Dejean)‡‡	5	1	4	6	3			2	1		
Scaritini											
Clivina fossor fossor (Linnaeus)‡	248	126	122	13		2	4		1	2	4
Dyschirius globulosus (Say)‡	0			2		1				1	
Zabrini											
Amara angustatoides Hieke‡	0			1			1				
Amara cupreolata Putzeys‡-	0			11			2			8	1
Amara impuncticollis (Say)‡	0			83	5	5	11		2	60	
Amara lunicollis Schiødte‡	0			26			9		5	12	
Amara patruelis Dejean‡	0			6	1		1			4	
Amara species‡?	1	1		0							
Pseudamara arenaria (LeConte)‡-	0			6		1	1		3	1	

† = A carabid species was considered "riparian" if it was listed as primarily occurring in any type of riparian habitat by Larochelle and Larivière (2003) or Dearborn et al. (2014).

* = Carabids species that occur primarily in riparian habitats as reported by Larochelle and Larivière (2003).

** = Carabids species that occur primarily in riparian habitats as reported by Dearborn et al. (2014), but not so listed in Larochelle and Larivière (2003).

‡ = All or most adults capable of flight; ‡- = some adults able to fly but most cannot; ‡‡ = adults not capable of flight; ‡? = flight ability unknown based on Larochelle and Larivière (2003) for all species except *Amara angustatoides*, which was based on Levesque and Levesque (2022); ‡§ = Specimens of *Olisthopus* spp. were considered likely flight capable because the only species of this genus known from Minnesota is *O. parmatus* (Say) (Epstein and Kulman 1990, Bousquet 2012), which can fly. Likewise, *Olisthopus micans* LeConte is the only other member of this genus in nearby Iowa, Michigan, Wisconsin, and Ontario (Bousquet 2012), which can also fly.

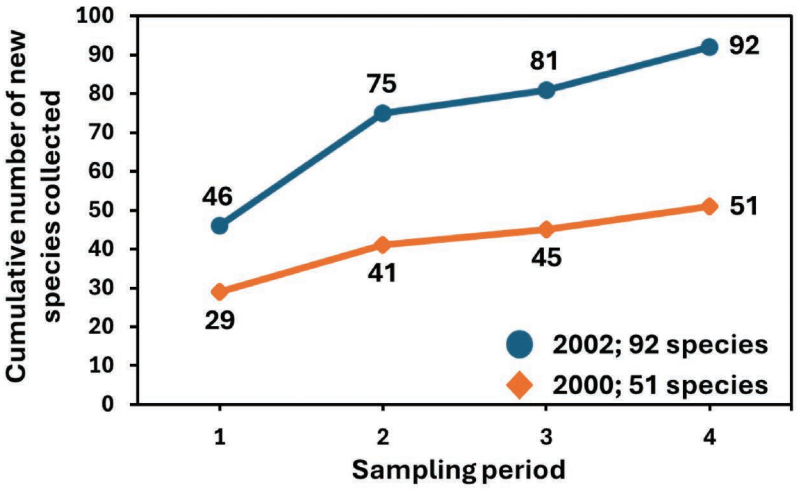

Figure 2. Cumulative number of new carabid species collected during four 2-week-long sampling periods from mid-May to mid-July in 2000 and 2002 for all treatments combined.

upland forests produced a two-dimensional solution that explained 92.4% of the variation (final stress = 0.11; Fig. 3). The species assemblages at the three study sites were somewhat distinct from each other, with the least overlap between the two sites that were furthest apart: Dog Lake and Willow River (Fig. 1). By contrast, there was greater overlap (higher similarity) in the species assemblages near ponds (buffers) and the adjacent upland forests within each site.

Overall, 15 of the 51 (29%; Table 1) species collected in 2000 were classified as riparian species based on Larochelle and Larivière (2003). Of the 15 riparian species,

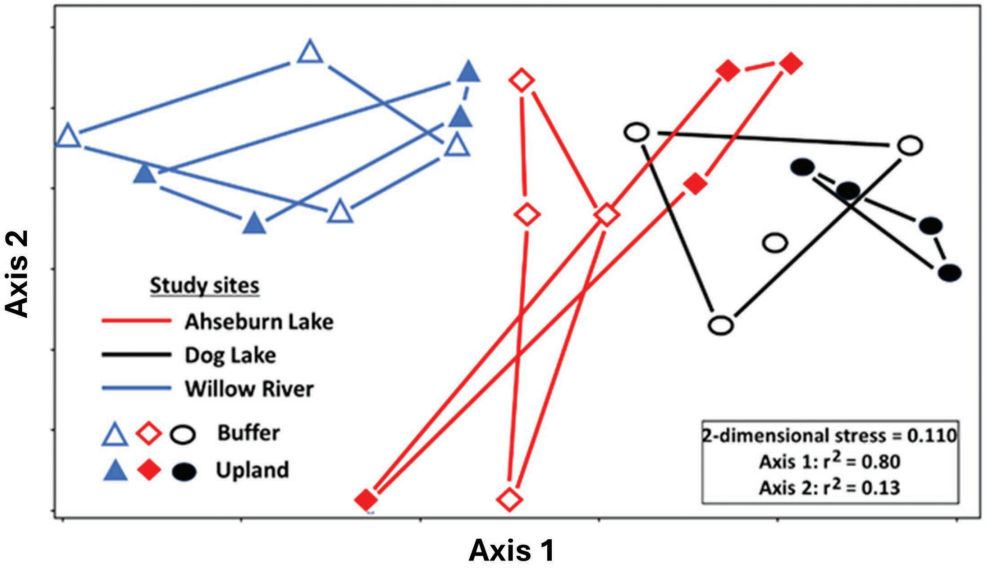

Figure 3. Non-metric multidimensional scaling (NMDS) ordination of 24 pitfall samples (after averaging the two traps at each location) in 2000 based on catch rate data (carabids per day for 100 traps) after log10 (x + 1) transformation. Convex hulls unite samples of the same habitat (near ponds within the future pond buffer areas or in the upland forests) around seasonal ponds at three sites in Minnesota.

Table 2 Various pre-logging comparisons for carabid collections in 2000 between traps located near and upland from seasonal ponds.

Parameter	Traps near seasonal ponds	Traps upland from seasonal ponds	Mann-Whitney U test results
Mean No. species per trap	16.2 ± 0.9 a*	14.4 ± 0.8 a	U = 227, z= 1.2, P = 0.211
Mean No. specimens. per trap	166 ± 20 a	125 ± 12 a	U = 219, z= 1.4, P = 0.162
Mean No. riparian species per trap	4.5 ± 0.5 a	2.4 ± 0.4 b	U = 142, z = 3.0, P = 0.003
Mean No. riparian specimens per trap	23.4 ± 6.5 a	10.4 ± 3.2 b	U = 171, z= 2.4, P = 0.016
Mean % of specimens per trap considered riparian.	13.2 ± 3.1 a	6.8 ± 1.9 b	U = 177, z = 2.3, P = 0.023
Mean No. flightless species per trap	4.5 ± 0.3 a	4.5 ± 0.2 a	U =278, z = 0.2, P = 0.834
Mean No. flightless specimens. per trap	79 ± 16 a	44 ± 8 a	U = 219, z = 1.4, P = 0.156
Mean No. carabids /day/100 traps			
Platynus decentis	82.9 ± 22.4 a	35.8 ± 11.3 a	U = 44, z = 1.58, P = 0.114
Pterostichus pensylvanicus	19.2 ± 3.0 a	17.9 ± 3.7 a	U = ,065 z = 0.38, P = 0.707
Synuchus impunctatus	16.4 ± 3.2 a	17.0 ± 3.6 a	U = 69, z = 0.12, P = 0.908

* Means followed by the same letter (within rows) are not significantly different.

all 15 (100%) were collected near ponds, compared with 9 (60%) in the uplands. Similarly, of the 808 riparian specimens collected in 2000, 561 (69.4%) were collected near ponds compared with 247 (30.6%) in the upland forests. Overall, the average number of riparian species and specimens collected per trap were significantly greater in traps near ponds compared with the upland forests, as well as the average percent of all carabids collected per trap that were classified as riparian (Table 2).

In 2000, 66.7% of the species collected were flight-capable, with similar percentages found for species collected near ponds (66.0%) and in the upland forests (62.5%; Table 1) [X^2 (1, N = 87) = 0.113, P = 0.737]. Of the 51 species collected, 9 were flightless (Table 1). *Platynus decentis* was the dominant flightless species collected near ponds (78%) and in the upland forests (71%). The average number of flightless carabid species and specimens collected per trap did not vary significantly between traps near ponds and the upland forests (Table 2).

2002: general post-harvest results. Overall, 8,869 carabid specimens were collected in 2002, representing 92 species of which 44 had been collected previously in 2000 with 48 being new in 2002 (Table 1). Of these 92 species, 73 were collected in the various buffer treatments, and 72 in the various upland treatments. The five species most often collected in 2002 were *Pl. decentis* (3,289 specimens), *Pt. pensylvanicus* (1,047), *Ag. cupripenne* (928), *Po. lucublandus* (722), and *Pt. caudicalis* (424). Of the 92 species, 46 of the species were represented by five or fewer specimens and 28 were singletons. Of the 8,869 specimens, 864 were collected in the uncut buffers (45 species), 571 in the partially cut buffers (39 species), 1,014 in the clearcut buffers (57 species), 780 in the control buffers (30 species), 1,949 in the upland patches (40 species), 2,844 in the clearcut uplands (67 species), and 847 in the upland control sites (32 species). Of the 48 species collected only in 2002, 43 (90%) were species where all or most adults can fly, and one was a flightless species (Table 1).

As in 2000, new species were collected during each of the four, 2-week-long, sampling periods in 2002 (Fig. 2). Again, most new species were collected during the first period (50%), with 82% of all species collected during the first two sampling periods. There was wide variation in the Chao1 estimates for total carabid richness in the various treatment areas. For example, the index estimated as few as 3 new species for the upland patch sites to as many as 90 new species for the uncut buffers (Table 1). For all sites combined, the Chao1 estimate for 2002 was 157 species, compared with 57 species in 2000 (Table 1).

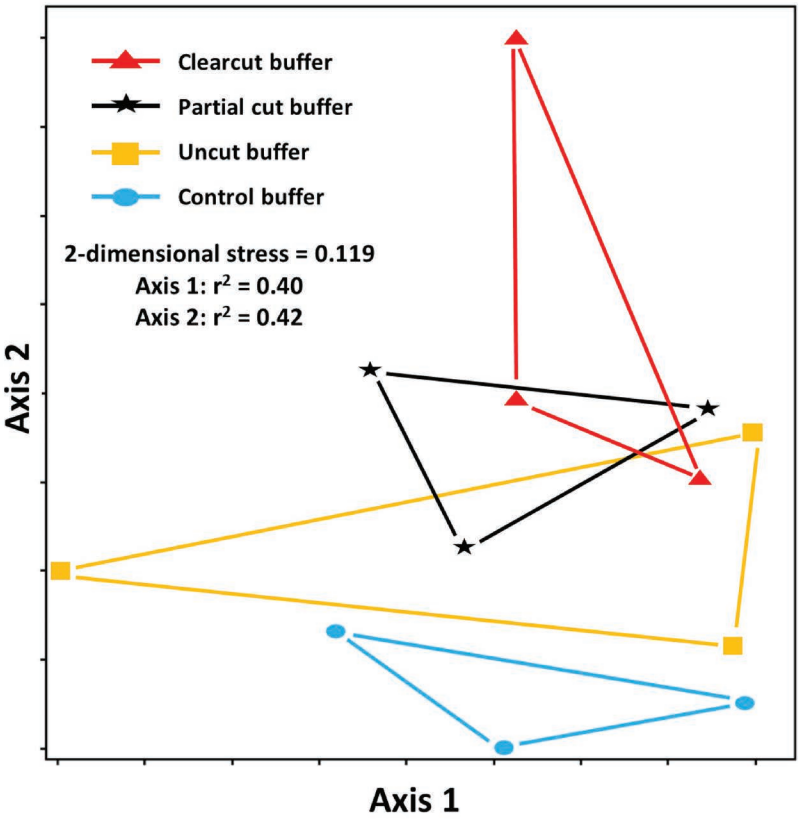

Figure 4. Non-metric multidimensional scaling (NMDS) ordination of 12 pitfall samples (after averaging the paired traps at each location) in the four buffer treatments in 2002 based on catch rate data (carabids per day for 100 traps) after log10 (x + 1) transformation. Convex hulls unite samples of the same treatments (same color).

2002: buffer treatment comparisons. The NMDS ordination of carabid abundance for traps in the four buffer treatments produced a two-dimensional solution that explained 82% of the variation (final stress = 0.12; Fig. 4). The species assemblages in the control buffers (where no logging occurred near or upland from the ponds) were distinct (no overlap) from the other three buffer treatments where the upland forests were clearcut. By contrast, some overlap occurred among the three other buffer treatments, with the assemblages in the uncut buffers being nearest (most similar) to the control buffers, while those in the clearcut buffers being furthest (most distinct) from the control buffers.

Although not significant ($H = 7.5$, df = 3; $P = 0.057$) mean percent similarity (based on Sørensen similarity index) of the carabid species collected at the same locations before (2000) and after (2002) treatment was highest in absolute terms in the control buffers (71.3%). For the other three buffer treatments, percent similarity before and after treatment averaged 50.3, 54.3, and 57.7% in the no cut, partially cut, and clearcut buffers, respectively.

Overall, 33 of the 92 (29%) species collected in 2002 were considered riparian species (Table 1). Of these 33 species, 28 (85%) were collected in the buffer areas. Of the four buffer treatments the mean number of riparian species collected per trap was significantly higher in clearcut buffers compared to partially cut and uncut buffers. Also, the mean percentage of all specimens collected that were classified as riparian was significantly higher in the clearcut buffers compared to uncut buffers (Table 3).

Overall, 54 of the 73 (74.0%) species collected in the buffer areas were fully or mostly flight-capable, with percentages varying for the individual buffer treatments from 63.3% to 73.3% (Table 1). Of the 92 species

Table 3 Various post-logging comparisons for carabid collections in 2002 among traps located in buffer areas surrounding seasonal ponds that underwent four harvesting treatments (clearcut, partially cut, and uncut buffers surrounded by clearcut uplands; and control buffers surrounded by uncut upland forests).

Parameter	Clearcut buffer traps	Parially cut buffer traps	Uncut buffer traps	Control buffer traps	Kruskal-Wallis test results
Mean No. species per trap	25.3 ± 1.7 a*	16.8 ± 1.9 b	17.3 ± 2.0 b	14.8 ± 1.5 b	H = 11.1, df = 3, P = 0.011
Mean No. specimens. per trap	169 ± 46 a	95 ± 19 a	144 ± 29 a	139 ± 26 a	H = 1.5, df = 3, P = 0.674
Mean No. riparian species per trap	7.8 ±1.1 a	4.2 ±0.5 b	4.5 ± 1.2 b	4.8 ± 0.8 ab	H =8.5, df = 3, P = 0.037
Mean % of specimens per trap considered riparian.	16.8 ± 3.1 a	8.8 ± 1.8 ab	5.6 ± 1.6 b	12.2 ± 6.0 ab	H = 8.3, df = 3, P = 0.039
Mean No. flightless species per trap	4.5 ± 0.6 a	4.2 ± 0.5 a	3.0 ± 0.3 a	4.2 ± 0.5 a	H = 5.6, df = 3, P = 0.130
Mean No. flightless specimens per trap	80 ± 31 a	47 ± 12 a	98± 24 a	65 ± 16 a	H =2.7, df = 3, P = 0.445
Mean No. carabids /day/100 traps					
Platynus decentis	50.1 ± 21.2 a	29.0 ± 7.8 a	73.7 ± 21.4 a	40.4 ± 11.7 a	H = 2.5, df = 3, P = 0.470
Pterostichus pensylvanicus	17.7 ± 3.7 a	8.8 ± 2.7 a	14.4 ± 5.4 a	8.4 ± 2.4 a	H = 3.7, df = 3, P = 0.291
Synuchus impunctatus	3.8 ± 1.8 a	0.9 ± 0.5 a	3.6 ± 1.8 a	7.1 ± 3.4 a	H = 4.4, df = 3, P = 0.221

* Means followed by the same letter (within rows) are not significantly different.

collected in 2002, 9 were flightless, and all 9 were collected in the buffer areas (Table 1). Again, *Pl. decentis* was the dominant flightless species collected in all buffer treatments, ranging from 81–92% of the flightless specimens. There were no significant differences among the four buffer treatments for mean number of flightless species or specimens collected per trap (Table 3). Similarly, there were no significant differences among the four buffer treatments with respect to mean catch rates of *Pl. decentis*, *Pt. pensylvanicus*, and *Sy. impunctatus* (Table 3).

2002: upland treatment comparisons. An NMDS ordination of carabid abundance for traps in the three upland treatments produced a two-dimensional solution that explained 92% of the variation (final stress = 0.10; Fig. 5). The species assemblages in the upland clearcuts and upland patches were generally distinct (no overlap), while some assemblages in the upland control sites were similar to the other two upland treatments (some overlap with each). The average number of species collected per trap was highest in the upland clearcuts, although there were no significant differences in the average number of carabid specimens collected per trap (Table 4). Similarly, there were no significant differences among the three upland treatments with respect to mean catch rates of *Pl. decentis*, *Pt. pensylvanicus*, and *Sy. impunctatus* (Table 4).

Of the 33 riparian species collected in 2002, 18 (54%) were collected in the three upland treatments (Table 1). Of the three upland treatments there were no significant differences in the mean number of riparian species collected per trap nor the mean percentage of all specimens collected that were classified as riparian (Table 4).

Overall, 55 of the 72 (76.4%) species collected in the upland treatment sites were fully or mostly flight-capable, with percentages for the individual upland treatments varying from 67.5% to 77.6% (Table 1). Of

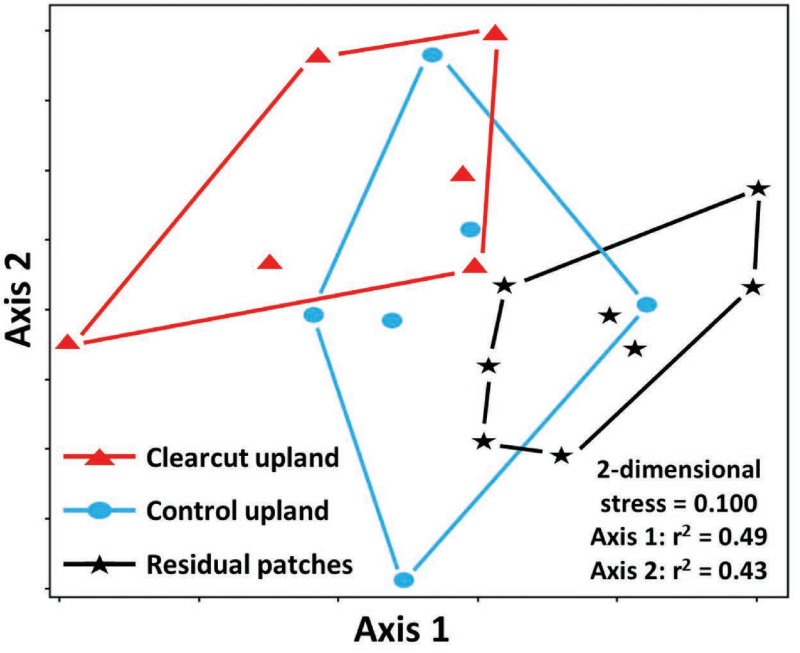

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of 20 pitfall samples (after averaging the paired traps at each location) in the three upland treatments in 2002 based on catch rate data (carabids per day for 100 traps) after log10 (x + 1) transformation. Convex hulls unite samples of the same treatments (same color).

the nine flightless species collected in 2002, eight were collected in the upland treatment areas (Table 1). Again, *Pl. decentis* was the dominant flightless species collected in all upland treatments, ranging from 84–93% of the flightless specimens. There were no significant differences among the three upland treatments for mean number of flightless species collected per trap (Table 4). However, the mean number of flightless specimens per trap was highest in the upland control sites, lowest in the upland clearcuts, and intermediate for the upland patches (Table 4).

Discussion

This study is unique in that we are unaware of any other studies that experimentally manipulated the buffer area and adjacent upland forests around small seasonal ponds to quantitatively analyze changes in carabid assemblages found in these riparian habitats. Our first objective was to compare the species assemblages in forested areas near seasonal ponds with those in the adjacent upland forests. We hypothesized that the species assemblages would be similar in these two areas prior to any logging, but more riparian species would be present near ponds. Our findings support these hypotheses. For example, we found that the species assemblages near and upland from seasonal ponds showed considerable overlap at each site (Fig. 3) and that catch rates of carabid species and specimens were statistically similar in both areas (Table 3). In addition, more riparian species and specimens were collected near ponds (Table 2).

Our second objective was to determine how various levels of tree harvesting within the pond buffers would affect the species assemblages the second summer after logging. We hypothesized that the species assemblages in the clearcut buffers would be the most distinct, while those in the uncut and control buffers would be most similar. Our findings provide partial support for these hypotheses. For example, of the four buffer treatments, the NMDS analysis indicated that the species assemblages in the control buffers were nearest (more similar) to the uncut buffers and furthest (more distinct) from the clearcut buffers (Fig 4). In addition, the clearcut buffers had highest catch rates of all species as well as those classified as riparian species (Table 3).

Table 4. Various post-logging comparisons for carabid collections in 2002 among traps located upland from seasonal ponds that underwent various treatments (clearcut, residual patches within clearcuts, and uncut control forests).

Parameter	Upland clearcut traps	Upland patch traps	Upland control traps	Kruskal-Wallis test results
Mean No. species per trap	18.1 ± 1.2 a*	14.3 ± 1.0 b	12.0± 1.2 b	H =10.1, df = 2, P = 0.006
Mean No. specimens. per trap	157 ± 28 a	122 ± 22 a	141 ± 31 a	H = 1.9, df = 2, P = 0.378
Mean No. riparian species per trap	2.6 ± 0.5 a	1.9 ± 0.4 a	2.2 ± 0.8 a	H = 1.0, df = 2, P = 0.603
Mean % of specimens per trap considered riparian.	5.8 ± 1.2 a	4.8 ± 1.5 a	6.1 ± 4.4 a	H = 0.8, df = 2, P = 0.686
Mean No. flightless species per trap	2.9 ± 0.3 a	3.4 ± 0.3 a	2.8 ± 0.3 a	H = 1.4, df = 2, P = 0.504
Mean No. flightless specimens. per trap	29 ± 8 b	60 ± 16 ab	90 ± 22 a	H = 7.8, df = 2, P = 0.021
Mean No. carabids /day/100 traps				
Platynus decentis	13.7 ± 4.9 a	40.2 ± 11.3	53.0 ± 20.2	H = 2.5, df = 3, P = 0.289
Pterostichus pensylvanicus	10.9 ± 3.7 a	18.4 ± 5.2 a	11.6 ± 4.2	H = 1.0, df = 3, P = 0.604
Synuchus impunctatus	2.4 ± 1.9 a	5.6 ± 1.5 a	1.9 ± 0.9 a	H = 5.5, df = 3, P = 0.063

* Means followed by the same letter (within rows) are not significantly different.

Our third objective was to compare the species assemblages in the three upland treatments. We hypothesized that the species assemblages in the upland clearcuts would be distinct from those in the residual patches and control plots. Again, our findings provided some support for this hypothesis. For example, collections in the clearcut uplands had the highest species richness as well as the lowest numbers of flightless individuals (Tables 1 and 4). However, the NMDS analysis indicated that the species assemblages in the clearcut uplands were most distinct from those in the residual patches but less so from the control plots (Fig. 5).

Many carabid studies in both North America and Europe have reported reductions in forest specialists and increases in open-habitat species following clearcutting (Niemelä et al. 1993; Beaudry et al. 1997; Heliölä et al. 2002; Koivula et al. 2002, 2019; Buddle et al. 2006; Fuller et al. 2008; Magura et al. 2015; Venier et al. 2017; Pedley et al. 2023; Work et al. 2023; Haack et al. 2024a, 2024b). In the present study, average catch rates in absolute terms of the three most frequently collected forest-associated carabids were generally higher before logging (Table 2) than after logging (Tables 3 and 4). Interestingly, catch rates of *Sy. impunctatus* were relatively low in all buffer and upland treatments in 2002, compared with 2000.

Niemelä et al. (1993) noted that many species of *Amara*, *Bembidion*, and *Harpalus* are open-habitat specialists and that they quickly colonize sites soon after clearcutting. We noted a similar pattern in the present study with the number of *Amara* species collected increasing from one in 2000 to five in 2002, and similarly for species of *Bembidion* (two to eight) and *Harpalus* (three to eight). Adults of nearly all North American species of these three genera can fly (Larochelle and Larivière 2003), which would enable them to quickly colonize new habitats. In addition to species in the above three genera, we noted large increases in collections from 2000 to 2002 for *Ag. cupripenne* (0 to 928) and *Po. lucublandus* (28 to 722). Both species are common in grasslands, fields, and open forests, with *Po. lucublandus* also having been collected along river and lake shorelines (Larochelle and Larivière 2003, Dearborn et al. 2014). Working at the same Minnesota study sites as in the present study, Palik and Kastendick (2010) reported that sedges

and grasses became the dominant ground cover in both the buffer clearcuts and upland clearcuts soon after logging, which would favor many seed-consuming carabids, such as many species of *Amara* and *Harpalus* (Honek et al. 2003).

Relatively little is known about the impact of tree harvesting on carabids that are strongly associated with riparian habitats. Most riparian carabids can fly and usually reproduce during spring, i.e., they overwinter as adults (Thiele 1977, Lott 2001). For most riparian carabids that are strongly associated with rivers, adults overwinter high on the banks or more inland, and then migrate, often by flight, to the water's edge in spring where they mate and oviposit. In a Finnish study of riparian carabids near a lake shoreline, as reported by Lott (2001), adult carabids did not migrate from their inland overwintering sites to the lake margin until late May or June. Such findings may help explain why we collected many riparian species both near and upland from seasonal ponds. That is, given that we collected from mid-May to mid-July, we could have collected some riparian carabids at both their breeding and overwintering sites. In addition, given that seasonal ponds often go dry by mid-to-late summer could force adults of some riparian species to disperse.

As expected, adults of nearly all new species collected in 2002 were all or mostly flight-capable (43 of 48 species). The ability to fly allows species to quickly colonize new habitats (Venn 2016), such as recently logged areas, and possibly those near water bodies as well. Perhaps the relatively high richness of riparian species being found in the clearcut buffers (Table 3) was due to seasonal ponds with clearcut buffers being more easily detected during their dispersal flight compared to ponds with forested edges. In the studies by Koivula and Niemelä (2003) and Huber and Baumgarten (2005), several open-habitat carabid species colonized new forest openings the first summer after winter-time tree harvesting.

The upland forest patches appeared to provide refugia for both flightless carabid species and forest specialists when compared to the upland clearcuts (Table 4). For example, in absolute terms, the mean number of flightless species and specimens per trap was higher in the forest patches compared with the upland clearcuts. Similarly, in absolute terms, mean catch rates of *Pl. decentis*, *Pt. pensylvanicus*, and *Sy. impunctatus* were all higher in the residual patches compared with the upland clearcuts. Others have reported on the value of residual patches, either those caused naturally by fire or through active management, in providing refugia for forest-specialist carabids (Gandhi et al. 2004, Matveinen-Huju et al. 2006, Grove 2010, Toivanen et al. 2014).

It is noteworthy that species richness was highest in the clearcut buffers among the four buffer treatments (Table 3) and in the upland clearcuts among the three upland treatments (Table 4). Among the species collected in the clearcuts were several forest specialists and flightless species. Perhaps we would have detected more distinct treatment differences if we had sampled in 2001, the year immediately following clearcutting when forest conditions were most dramatically altered by harvesting. Note that suckering from existing aspen root systems is stimulated soon after harvesting (Frey et al. 2003). For example, in the same study sites as ours, Palik and Kastendick (2010) reported that almost no aspen suckers had reached 0.5 m in height by early summer 2001. However, by early summer 2002, average densities of aspen suckers greater than 0.5 m in height were about 2,000 stems/ha in the uncut and partially cut buffers, and over 8,000 stems/ha in the clearcut buffers. Possibly, such high densities of aspen suckers and their associated foliage in summer 2002, especially in the clearcut areas, provided suitable levels of shade and soil moisture to some carabids that are typically associated with forests.

Leaving forested buffers around seasonal ponds when harvesting trees in the adjacent upland forests is often recommended as a method to reduce disturbance to seasonal ponds given their importance as breeding sites for various frogs and salamanders (Dodd and Cade 1998, Semlitsch 1998, MFRC 2012, Hofmeister et al. 2022). Although we did not find evidence that retaining forested buffers around seasonal ponds was required to maintain high carabid diversity around ponds in the short-term following tree harvesting, such practices would certainly help protect the ponds themselves and provide habitat for associated flora and fauna. As mentioned in our Introduction, Minnesota currently requires a 15 m minimum buffer around seasonal ponds during logging operations (MFRC 2014), whereas both Maine and Massachusetts require a 30 m minimum buffer (Calhoun and deMaynadier 2004, MA-DEP 2017). Given that many riparian carabids overwinter upland from the shorelines of water bodies where they developed as larvae (Lott 2001), a wider buffer would likely provide more opportunities for suitable overwintering habitats for a wider variety of such species. Therefore, retaining buffers around seasonal ponds during harvesting of adjacent upland forests should help maintain a diversity of carabid species, especially some species commonly

associated with mature forests. Such buffers would not only benefit certain carabids but would also serve as refugia for many other animals and plants, as well as the flora and fauna associated with the ponds themselves (Hanowski et al. 2006, Hanson et al. 2010, Palik and Kastendick 2010, Hofmeister et al. 2022).

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