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A Five-Year Study of the Ground-Dwelling Beetles (Coleoptera) from a Grassland and an Adjacent Woods in Southern Québec (Canada)

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Abstract

We present results of the first long-term study on spatiotemporal variations in the composition and structure of ground-dwelling beetle (Coleoptera) assemblages from a grassland and adjacent woods in eastern Canada. It is the third part of an investigation on the beetle biodiversity using diverse methods between 2006 and 2012. During the entire snow-free season (April/May to October) in 2006–2010, we collected by pitfall trapping 67,694 individuals representing 386 Coleoptera species and morphospecies belonging to 35 families in southern Québec. Adventive species represented at least 51.9% of individuals. Carabidae and Staphylinidae were the most abundant families and had the highest species richness in all seven pitfall trap lines (two lines in a grassland, one line at the edge of the woods, two lines in the woods, and two lines near a ditch parallel to the woods). We did not detect a trend in annual variations of total catches and species richness in each pitfall trap line. A large part of the species (42.2%) occurred as singletons or doubletons over all sampling months. We collected at least 100 individuals for 50 species, including four eudominant species: *Tachinus limbatus* Melsheimer (14.0% of the total catches), *Pterostichus melanarius* (Illiger) (10.5%), *Drusilla canaliculata* (Fabricius) (9.6%) and *Anotylus rugosus* (Fabricius) (5.3%). Over all sampling years, between 49 and 63% of species from one pitfall trap line were sporadically collected *(i.e.*, during one to three months only over five years), whereas only a few species were active during at least 26 months over all the 33 sampling months in each pitfall trap line. Fourteen species were dominant in at least one pitfall trap line; we observed strong year-to-year fluctuations in the relative abundance of dominant and subdominant species in each line, and spatiotemporal variations of each of these species. We determined the sex-ratio for 42 abundant species, including 17 species with a female biased sex-ratio, and 13 species with a predominance of males. Adults of the most abundant species were mostly macropterous (73% of catches), and we discuss on their dispersal power by flight.

Keywords: Carabidae, Coleoptera, long-term monitoring, phenology, pitfall traps, Québec, sex-ratio, Staphylinidae, wing polymorphism.

Epigaeic Carabidae and Staphylinidae (Coleoptera) are regarded as good bioindicators of environmental changes (Luff 1996, Bohác 1999, Rainio and Niemelä 2003, Scott and Anderson 2003, Pohl et al. 2008, Brunke et al. 2014). They are influenced by agricultural and forestry practices, habitat fragmentation and loss, heavy metal pollution, soil acidification, urbanization, etc. These beetles are also of a great interest in long-term studies to promote the conservation of insect biodiversity. For example, Irmler (2018a, 2018b) presented the results of a 15 years investigation after the conversion from conventional to organic farming for the families Carabidae and Staphylinidae. He observed that 1) the number of staphylinid species remained on the same level in the first eight years, but increased from the eighth to the 15th year, and 2) the direction of the succession of carabids and rove beetles was similar: the change after the conversion was primarily based on the loss of forest species and the invasion of open grassland species. In Canada, a few long-term studies presented results on epigaeic beetles from boreal forests (e.g., Holliday 1992, Pohl et al. 2007, Lee et al. 2023, Work et al. 2023), but none on beetles from a grassland and adjacent woods in eastern Canada.

Among epigaeic Carabidae and Staphylinidae in north-temperate regions, it is not unusual for a few species to be most numerous and representing 60–90% of the catches in a site during consecutive years (Byers et al. 2000, Scott and Anderson 2003, Schwerk and Szyszko 2009, Sushko 2014); nevertheless, there are strong year-to-year fluctuations in the relative abundance of species and a large percentage of species are observed only sporadically. McCravy and Willand (2020) showed that pitfall sampling throughout the growing season during multiple years provides a substantial contribution for assessments of carabid diversity in Illinois.

Venn (2016) provides a comprehensive overview of the role of flight capacity or its absence in carabid species and populations in the temperate regions from the perspective of ecological studies. The carabid macroptery seems primarily an adaptation for dispersal and there exists a mechanism for subsequently reducing the ratio of macropterous to brachypterous species under stable conditions, due to the competitive advantage of brachyptery. Brachypterous species tend to disappear from disturbed habitats. Some macropterous species do not possess functional flight muscles.

We investigated the beetle biodiversity using diverse methods in southern Québec (Canada) between 2006 and 2012, including flight interception traps (FIT) and a blacklight trap (Levesque and Levesque 2019, 2023). In the present manuscript, we report the spatiotemporal variations in the composition and structure of ground-dwelling beetle assemblages collected by pitfall traps from a grassland and the adjacent woods in southern Québec, and the edge effects, during 2006–2010. Furthermore, we discuss on factors driving the large percentage of species observed only sporadically, and the dispersal power by flight of some abundant species.

Materials and Methods

Study site. We sample beetles at Scotstown (45°32′ N, 71°17′ W, about 370 m above sea level), in a forest region of southern Québec. This site, about 350 m by 60 m, on a wet soil, includes a grassland (pasture for horses during many years and abandoned since 2004) (40%), and a mixed woods dominated by alders (*Alnus* sp.) (60%). A ditch, generally partially or totally shaded by shrubs and trees, runs parallel to the grassland and the woods.

Five-year study. During the entire snow-free season (April/May to October) in 2006–2010 (total of 33 sampling months), we used pitfall traps consisted of plastic white jar (750 ml, 11.5 cm diameter at the top), with a plywood roof (20 by 20 cm), and filled with 100 ml of 50% ethylene-glycol solution plus a drop of soap. We installed seven lines of nine pitfall traps (5 m apart): at the edge of the woods (**EDGE**); at 20 and 50 m from the edge, in the grassland (**GR–20** and **GR–50**) and in the woods (**WO–20** and **WO–50**); and in two locations alongside the ditch, the first in a shaded zone (**DI–SH**), and the second in a herbaceous zone (**DI–HE**). Pitfall traps were in place continuously during the sampling period and emptied once weekly.

The beetles collected in pitfall traps were identified using about 90 taxonomic publications (revisions, keys, notes) and, in several cases, we had taxonomic specialists help to confirm or complete our identification. A list of main taxonomic references includes Kevan (1967), Smetana (1971, 1982, 1989, 1995), Campbell (1973, 1975, 1979, 1988), Stibick (1978), Anderson and Peck (1985), Downie and Arnett (1996), Peck and Cook (2002), Bright and Bouchard (2008), Bousquet (2010), Brunke et al. (2011), and Klimaszewski et al. (2018). We identified a morphospecies when the taxonomy of certain North American beetle groups is poorly known (e.g., for the staphylinid genus *Carpelimus* Leach), or when the available taxonomy is very difficult (e.g., for a single sex, for some Staphylinidae Aleocharinae groups); we used a local numbering for morphospecies of a taxon (e.g., *Carpelimus* sp. S01 for the first recorded morphospecies of this genus from Scotstown). The identification of adventive and Holarctic species was based on Bousquet et al. (2013) and Klimaszewski et al. (2012, 2013, 2015, 2017, 2020). For all species, voucher specimens were deposited in the Canadian National Collection of Insects, Arachnids, and Nematods (Central Experimental Farm, Agriculture and Agri-Food Canada, Ottawa, Ontario), or in our personal collection.

Data analysis. We assessed the similarity of ground-dwelling beetles from two pitfall trap lines with the Renkonen's percent similarity (Levesque and Levesque 1992); the percent similarity is the sum of minimum (x_i, y_i) where x_i and y_i are the percentages representing species "i" in the two lines. A dominant taxon (family or species) represented at least 5% of catches in a line of pitfall traps during 2006–2010, and a subdominant taxon, between 2 and 5%. We used a chi-square test to determine whether the sex-ratio differed from a 1:1 ratio for some abundant species.

Results

Abundance and species richness. We collected by pitfall trapping 67,694 individuals representing 386 Coleoptera species and morphospecies belonging to 35 families from Scotstown in 2006–2010. We recorded at least 74 adventive species (51.9% of individuals) and at least 25 Holarctic species (2.0% of individuals). Adventive species represented at least 63% of catches in the grassland, 55% at the edge, 43% in

Table 1. Renkonen's percent similarity between beetle assemblages from pitfall trap lines at Scotstown during 2006–2010

Line	GR–50	GR–20	EDGE	WO–20	WO–50	DI–SH	DI–HE
GR–50							
GR–20	**77**						
EDGE	56	59					
WO–20	43	45	**82**				
WO–50	35	37	66	**75**			
DI–SH	26	28	47	46	50		
DI–HE	27	27	44	43	49	**76**	

the woods, and 46% alongside the ditch. We caught mainly zoophagous beetles (nearly 85% of individuals and 60% of species), representing 70% of catches in GR–50, 77% in GR–20, and more than 90% in five other pitfall trap lines.

A strong similarity occurred 1) between beetle assemblages from the two pitfall trap lines in the grassland (GR–50 and GR–20) (77%), 2) between beetles collected at the edge and the ones in WO–20 (82%), 3) between beetles caught in WO–20 and WO–50 (75%), and 4) between beetles captured in the two lines alongside the ditch (DI–SH and DI– HE) (76%) (Table 1). Whereas, the lower similarity was observed between beetles from the grassland and the ones near the ditch (Table 1).

We collected 11,620 individuals of 222 species in 2006, 11,694 individuals of 224 species in 2007, 16,046 individuals of 210 species in 2008, 12,970 individuals of 201 species in 2009, and 15,364 individuals of 203 species in 2010 (Table 2). We cannot detect a trend in annual variations of total catches and species richness in each pitfall trap line (Table 2).

The number of individuals per species over the five years ranged from 1 to 9,447 adults. The number of species occurring as singletons or doubletons were 131 (33.9% of species) and 32 (8.3%), respectively. Four species were dominant in this study: the carabid *Pterostichus melanarius* (Illiger) (10.5% of total beetle catches), and three rove beetle species, *Anotylus rugosus* (Fabricius) (5.3%), *Drusilla canaliculata* (Fabricius) (9.6%) and *Tachinus limbatus* Melsheimer (14.0%); *T. limbatus* is a Nearctic species and the three others are adventive species.

Over 2006–2010, the species richness per pitfall trap line ranged from 149 to 203 species (Table 2). At the end of the first sampling year (2006), we recorded between

Table 2. Total catches and species richness of beetles in each pitfall trap line at Scotstown during 2006–2010

Line	2006	2007	2008	2009	2010	Total
			Individuals			
GR–50	1309	1573	3177	2178	2130	10367
GR–20	1569	1820	2760	1978	2265	10392
EDGE	1278	913	1531	1283	1809	6814
WO–20	1029	861	1009	843	1622	5364
WO–50	905	768	921	883	1522	4999
DI–SH	2833	2996	3341	2880	3291	15341
DI–HE	2696	2763	3307	2925	2726	14417
Total	11620	11694	16046	12970	15364	67694
			Species			
GR–50	87	97	92	89	89	160
GR–20	82	93	72	80	76	158
EDGE	96	80	88	67	91	171
WO–20	74	81	77	69	80	149
WO–50	84	80	89	77	86	169
DI–SH	85	98	92	96	92	181
DI–HE	108	96	105	95	99	203
Total	222	224	210	201	203	386

Table 3. Total catches and species richness of dominant and subdominant beetle families in each pitfall trap line at Scotstown during 2006–2010

		INDIVIDUALS		SPECIES	
Line	**Family**	**N**	**%**	**n**	**%**
GR–50	Staphylinidae	5084	**49.0**	63	39.4
	Carabidae	3923	**37.8**	51	31.9
	Elateridae	943	**9.1**	6	3.8
GR–20	Staphylinidae	6042	**58.1**	69	43.7
	Carabidae	3707	**35.7**	52	32.9
	Elateridae	362	3.5	4	2.5
EDGE	Staphylinidae	3455	**50.7**	70	40.9
	Carabidae	3046	**44.7**	52	30.4
WO–20	Staphylinidae	2740	**51.1**	69	46.3
	Carabidae	2388	**44.5**	38	25.5
WO–50	Carabidae	2550	**51.0**	38	22.5
	Staphylinidae	2182	**43.6**	79	46.7
	Curculionidae	111	2.2	11	6.5
DI–SH	Staphylinidae	8360	**54.5**	80	44.2
	Carabidae	6352	**41.4**	48	26.5
DI–HE	Staphylinidae	7588	**52.6**	86	42.3
	Carabidae	5918	**41.0**	56	27.6
	Silphidae	352	2.4	5	2.5
All lines	Staphylinidae	35451	**52.4**	160	41.5
	Carabidae	27884	**41.2**	86	22.3
	Elateridae	1609	2.4	12	3.1
	Silphidae	753	1.1	7	1.8
	Curculionidae	474	0.7	25	6.5

74 and 108 species per line; after five years of trap operation, this cumulative number of species in a specific line had nearly increased twofold. Over all sampling years, between 49 and 63% of species from a line were collected during one to three months only, whereas only a few species (four to eight) were active during at least 26 months over all the 33 sampling months in each pitfall trap line.

Dominant and subdominant families. Five families were dominant (at least 5% of catches in a line) or subdominant (between 2 and 5%) in at least one pitfall trap line (Table 3); both Staphylinidae and Carabidae were dominant families in all lines, and Elateridae were dominant only in GR–50. We caught 35,451 individuals of 160 Staphylinidae species and 27,884 individuals of 86 Carabidae species; both families together represented 93.6% of total catches and 63.7% of all species. Adults of Staphylinidae were more abundant than Carabidae in all lines except in WO–50 with closer canopy (Table 3); the catches of Staphylinidae and Carabidae together were higher near the ditch (about 14,000 per trap line). The species richness of Staphylinidae was higher than for the Carabidae in all lines (Table 3). The number of ground beetle species was lower in the woods (WO–20 and WO–50) (Table 3).

Dominant and subdominant species. Fourteen species were dominant (at least 5% of catches) in at least one pitfall trap line over 2006–2010 (Table 4). The elaterid *Hypnoidus abbreviatus* (Say) was dominant only in GR–50. The rove beetle *Tachinus rufipes* (DeGeer) was dominant in the grassland (GR–50 and GR–20). The carabids *Agonum gratiosum* (Mannerheim) and *Agonum muelleri* (Herbst), and the staphylinids *A. rugosus* and *Quedius curtipennis* Bernhauer were dominant in the grassland and at the edge. *Quedius molochinus* (Gravenhorst) was dominant in the grassland, at the edge and in WO–20. *Agonum palustre* Goulet was dominant in the woods (WO–20 and WO–50), *Liogluta intermedia* Klimaszewski & Langor was dominant in WO–20 and DI–HE, and *Platynus decentis* (Say) was dominant in WO–50. The carabid *P. melanarius* and the rove beetle *D. canaliculata* were dominant at the edge, in the woods and near the ditch (DI–SH and DI–HE). *Tachinus limbatus* was dominant in WO–50 and along the ditch, and *Blemus discus* (Fabricius) was dominant only near the ditch. Strong year-to-year fluctuations occurred in the relative abundance of the following species: *A. muelleri* (between 5.8 and 26.8% in GR–50; 3.2–25.2% in GR–20), *A. palustre* (2.3–18.7% in WO–50), *A. rugosus* (2.1–22.6% in GR–50; 1.9–27.6% in

GR–20), *B. discus* (4.8–22.2% in DI–HE), *T. limbatus* (3.5–20.2% in WO–50, 16.5–42.4% in DI–SH, 12.2–41.3% in DI–HE) and *T. rufipes* (5.9–24.3% in GR–20) (Table 4).

Over 2006–2010, many species showed a habitat preference (Table 5): *A. gratiosum*, *A. muelleri*, *A. rugosus, H. abbreviatus* , *Q. curtipennis, Q. molochinus* and *T. rufipes* in the grassland; *Agonum retractum* LeConte in the woods; *Lesteva pallipes* LeConte at the edge and in the woods; *Carabus nemoralis* O.F. Müller and *P. decentis* in the shaded places (Edge, WO–20, WO–50, DI–SH); *B. discus*, *D. canaliculata, Oxypselaphus pusillus* (LeConte), *P. melanarius* and *T. limbatus* near the ditch; and *L. intermedia* and *Necrophila americana* Linnaeus in DI–HE. No clear preference was observed for *A. palustre* and *Agonum sordens* Kirby (Table 5). Finally, *Dinothenarus badipes* (LeConte) was a habitat generalist (Table 5).

The most abundant species. We collected at least 100 adults for 50 species representing 94.2% of individuals in all pitfall traps during 2006–2010 (Table 6).

The activity patterns of the most abundant species were rather synchronous independently of the pitfall trap lines or years. Some species were mainly active in May–June (e.g., the carabids *C. nemoralis* and *P. decentis*, and the staphylinids *Devia prospera* (Erichson), *D. badipes* and *Gyrohypnus angustatus* Stephens); the ground activity peak for the majority of species was observed in June and/or July; whereas some species were primarily active later in season (August–October) (e.g., the ground beetle *B. discus,* the leaf beetle *Longitarsus luridus* (Scopoli), and the rove beetles *L. pallipes, L. intermedia, Q. molochinus* and *T. limbatus*) (Table 6).

We determined the sex-ratio for 42 species on the basis of external morphological characteristics. Seventeen species presented a female-biased sex-ratio (e.g., 75% of females for *A. palustre*), and we caught mainly males in 13 species (e.g., only 13% of females for *Carabus maeander* Fischer von Waldheim) (Table 6).

Macropterous beetles represented 73% of adults from the study site. Adults of 36 species were all macropterous (Table 6). *Clivina fossor* Linnaeus showed a wing polymorphism (70% of macropterous adults) (Table 6). We observed the predominance of micropterous or brachypterous adults in eight carabid species, the chrysomelid *L. luridus*, and three staphylinid species including *D. canaliculata* (Table 6).

Discussion

Brunke et al. (2019) reported that 8,302 species of Coleoptera have been recorded in Canada, firstly the Staphylinidae (1,774 spp.) and Carabidae (983 spp.). In the present study, Staphylinidae was the better represented family, followed by Carabidae in terms of both species richness and abundance, the only exception being more carabid individuals in WO–50 (Table 3). We observed similar results during an investigation with pitfall traps on the beetle activity in a raspberry agroecosystem (raspberry plantation, woods edge, pine woods) at Johnville (about 40 km from Scotstown) over 1987–1989 (Levesque and Levesque 1994,1995). For ground beetles in temperate regions, higher species richness has generally been found in forest edges and surroundings than in forest interiors along forest-field transects and forest-grassland transects (Jung and Lee 2016); we observed a similar situation for Carabidae at Scotstown (Table 3). We suspect that the soil vegetation under the canopy (open or closed) of woodlands has possibly an important influence on the activity of ground-dwelling beetles.

Abundance and species richness of beetles using various sampling methods. To collect more species and cover a more complete spectrum of species traits, many researchers recommend to combine complementary sampling techniques in a single study (e.g., Work et al. 1998, Muona 1999, González et al. 2020, Iannuzzi et al. 2020, Knapp et al. 2020). We used three methods at Scotstown to understand the overall beetle diversity: pitfall traps (PF) (33 months, 2006–2010), four flight interception traps (FIT) (33 months, 2006–2010) and a blacklight trap (LT) (34 months, 2007–2012). We collected 67,694 individuals of 386 species in PF (Table 2), 34,629 individuals of 848 species in FIT (Levesque and Levesque 2019), and 33,382 individuals of 625 species in LT (Levesque and Levesque 2023). The total annual number of beetle species using the three sampling methods varied between 590 and 748 species during 2007–2010. We collected nearly 1,200 species in 2006–2010, whereas at least 4,127 species of Coleoptera have been recorded in Québec (Bousquet et al. 2013).

With a combination of PF, FIT and LT, we collected yearly between 50 and 60% of species recorded at Scotstown during 2006–2010. Muona (1999) had observed similar results. Beetles have been collected in the general area of the Oulanka National Park in Eastern Finland since more than 90 years; the beetle fauna of this region, about 450 km^2, was regarded to be as well known as early as the 1950s (Muona 1999). This

Table 4. Total catches of dominant and subdominant beetle species in each pitfall trap line during 2006–2010, and variations in annual percentages (minimum-maximum)

Species	Fam.[a]	N	%	Range
	GR–50			
Anotylus rugosus (Fabricius)	STA	1319	**12.7**	2.1–22.6
Agonum muelleri (Herbst)	CAR	1316	**12.7**	5.8–26.8
Hypnoidus abbreviatus (Say)	ELA	936	**9.0**	3.7–16.5
Quedius curtipennis Bernhauer	STA	818	**7.9**	4.4–12.3
Tachinus rufipes (DeGeer)	STA	740	**7.1**	0.6–15.2
Quedius molochinus (Gravenhorst)	STA	732	**7.1**	4.1–14.2
Agonum gratiosum (Mannerheim)	CAR	701	**6.8**	3.2–9.8
Pterostichus melanarius (Illiger)	CAR	390	3.8	2.4–7.7
Agonum sordens Kirby	CAR	248	2.4	0.8–4.3
Liogluta intermedia Klim. & Langor	STA	241	2.3	0.2–4.6
Drusilla canaliculata (Fabricius)	STA	238	2.3	0.4–4.3
Total		7679	74.1	64.9–80.4
	GR–20			
Tachinus rufipes (DeGeer)	STA	1586	**15.3**	5.9–24.3
Anotylus rugosus (Fabricius)	STA	1551	**14.9**	1.9–27.6
Agonum gratiosum (Mannerheim)	CAR	1084	**10.4**	6.8–14.9
Agonum muelleri (Herbst)	CAR	862	**8.3**	3.2–25.2
Quedius curtipennis Bernhauer	STA	693	**6.7**	3.1–8.7
Quedius molochinus (Gravenhorst)	STA	563	**5.4**	2.5–8.6
Pterostichus melanarius (Illiger)	CAR	435	4.2	2.2–6.1
Drusilla canaliculata (Fabricius)	STA	401	3.9	2.9–5.9
Agonum sordens Kirby	CAR	372	3.6	2.4–6.0
Hypnoidus abbreviatus (Say)	ELA	359	3.5	0.5–8.3
Tachinus limbatus Melsheimer	STA	231	2.2	0.1–5.6
Total		8137	78.4	70.0–85.2
	EDGE			
Drusilla canaliculata (Fabricius)	STA	1063	**15.6**	13.3–18.8
Agonum muelleri (Herbst)	CAR	550	**8.1**	3.3–18.0
Pterostichus melanarius (Illiger)	CAR	455	**6.7**	4.8–12.0
Agonum gratiosum (Mannerheim)	CAR	382	**5.6**	3.4–7.0
Anotylus rugosus (Fabricius)	STA	356	**5.2**	1.0–9.2
Quedius molochinus (Gravenhorst)	STA	352	**5.2**	3.1–7.2
Quedius curtipennis Bernhauer	STA	338	**5.0**	2.2–7.0
Agonum palustre Goulet	CAR	272	4.0	1.0–7.1
Liogluta intermedia Klim. & Langor	STA	250	3.7	0.8–7.1
Oxypselaphus pusillus (LeConte)	CAR	242	3.6	2.3–4.8
Agonum sordens Kirby	CAR	223	3.3	2.0–4.0
Platynus decentis (Say)	CAR	216	3.2	0.9–5.5
Tachinus limbatus Melsheimer	STA	212	3.1	0.6–5.0
Carabus nemoralis O.F. Müller	CAR	203	3.0	2.3–3.9
Lesteva pallipes LeConte	STA	188	2.8	0.0–7.4
Dinothenarus badipes (LeConte)	STA	143	2.1	0.6–3.5
Total		5445	79.9	73.1–87.9
	WO–20			
Drusilla canaliculata (Fabricius)	STA	880	**16.4**	12.9–20.3
Agonum palustre Goulet	CAR	524	**9.8**	5.3–17.4
Pterostichus melanarius (Illiger)	CAR	334	**6.2**	3.7–9.5
Liogluta intermedia Klim. & Langor	STA	275	**5.1**	2.4–9.2
Quedius molochinus (Gravenhorst)	STA	275	**5.1**	4.5–6.0
Quedius curtipennis Bernhauer	STA	260	4.8	3.4–5.9
Carabus nemoralis O.F.Müller	CAR	258	4.8	2.8–6.9

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Table 4. (Continued)

Species	Fam.[a]	N	%	Range
	WO–20			
Agonum gratiosum (Mannerheim)	CAR	244	4.5	2.8–7.5
Anotylus rugosus (Fabricius)	STA	212	4.0	1.0–8.0
Platynus decentis (Say)	CAR	191	3.6	2.8–4.6
Tachinus limbatus Melsheimer	STA	181	3.4	0.6–4.8
Lesteva pallipes LeConte	STA	171	3.2	0.4–6.3
Agonum muelleri (Herbst)	CAR	165	3.1	1.5–4.3
Oxypselaphus pusillus (LeConte)	CAR	132	2.5	0.7–3.5
Dinothenarus badipes (LeConte)	STA	121	2.3	0.6–4.2
Total		4223	78.7	76.6–80.8
	WO–50			
Tachinus limbatus Melsheimer	STA	513	**10.3**	3.5–20.2
Drusilla canaliculata (Fabricius)	STA	433	**8.7**	6.7–12.6
Agonum palustre Goulet	CAR	402	**8.0**	2.3–18.7
Pterostichus melanarius (Illiger)	CAR	399	**8.0**	5.8–10.5
Platynus decentis (Say)	CAR	251	**5.0**	3.7–7.9
Carabus nemoralis O.F.Müller	CAR	225	4.5	3.1–6.8
Agonum gratiosum (Mannerheim)	CAR	182	3.6	1.1–6.9
Liogluta intermedia Klim. & Langor	STA	175	3.5	0.9–11.0
Lesteva pallipes LeConte	STA	166	3.3	0.3–5.7
Quedius molochinus (Gravenhorst)	STA	166	3.3	2.2–4.5
Agonum retractum LeConte	CAR	160	3.2	0.3–6.0
Quedius curtipennis Bernhauer	STA	140	2.8	1.5–5.0
Anotylus rugosus (Fabricius)	STA	110	2.2	1.2–4.1
Blemus discus (Fabricius)	CAR	108	2.2	1.2–2.5
Dinothenarus badipes (LeConte)	STA	102	2.0	0.5–4.0
Oxypselaphus pusillus (LeConte)	CAR	98	2.0	0.9–3.0
Total		3630	72.6	67.1–77.5
	DI–SH			
Tachinus limbatus Melsheimer	STA	4459	**29.1**	16.5–42.4
Pterostichus melanarius (Illiger)	CAR	3272	**21.3**	13.9–26.6
Drusilla canaliculata (Fabricius)	STA	2031	**13.2**	9.4–17.4
Blemus discus (Fabricius)	CAR	966	**6.3**	3.6–11.2
Oxypselaphus pusillus (LeConte)	CAR	416	2.7	1.0–4.5
Agonum palustre Goulet	CAR	407	2.7	0.8–7.0
Total		11551	75.3	70.8–77.9
	DI–HE			
Tachinus limbatus Melsheimer	STA	3756	**26.1**	12.2–41.3
Blemus discus (Fabricius)	CAR	1842	**12.8**	4.8–22.2
Pterostichus melanarius (Illiger)	CAR	1809	**12.5**	6.4–18.0
Drusilla canaliculata (Fabricius)	STA	1455	**10.1**	7.5–15.0
Liogluta intermedia Klim. & Langor	STA	1104	**7.7**	4.5–12.2
Oxypselaphus pusillus (LeConte)	CAR	505	3.5	0.9–5.2
Agonum gratiosum (Mannerheim)	CAR	468	3.2	0.9–4.5
Agonum palustre Goulet	CAR	344	2.4	0.3–9.0
Necrophila americana Linnaeus	SIL	331	2.3	0.6–6.3
Total		11614	80.6	75.9–83.8

[a] Families: CAR Carabidae; ELA Elateridae; SIL Silphidae; STA Staphylinidae

Table 5. Spatial distribution of each dominant or subdominant beetle species in pitfall trap lines during 2006–2010 (+ = line where less than 1% of catches)

		Total catches (%)						
Species	**N**	**GR–50**	**GR–20**	**ED–GE**	**WO–20**	**WO–50**	**DI–SH**	**DI–HE**
Agonum gratiosum (Mannerheim)	3355	**21**	**32**	11	7	5	9	14
Agonum muelleri (Herbst)	3014	**44**	**29**	18	5	3	1	+
Agonum palustre Goulet	2077	3	3	13	25	19	20	17
Agonum retractum LeConte	222	1	0	5	**21**	**72**	1	0
Agonum sordens Kirby	1319	19	28	17	6	6	17	7
Anotylus rugosus (Fabricius)	3571	**37**	**43**	10	6	3	1	+
Blemus discus (Fabricius)	3067	1	1	1	2	4	**31**	**60**
Carabus nemoralis O.F. Müller	1054	5	3	**19**	**24**	**21**	**16**	11
Dinothenarus badipes LeConte	854	12	11	17	15	12	18	16
Drusilla canaliculata (Fabricius)	6501	4	6	16	14	7	**31**	**22**
Hypnoidus abbreviatus (Say)	1496	**63**	**24**	6	+	1	1	6
Lesteva pallipes LeConte	562	+	4	**33**	**30**	**30**	2	1
Liogluta intermedia Klim. & Langor	2314	10	3	11	12	8	9	**48**
Necrophila americana Linnaeus	614	19	7	1	+	2	17	**54**
Oxypselaphus pusillus (LeConte)	1551	4	6	16	9	6	**27**	**33**
Platynus decentis (Say)	895	3	3	**24**	**21**	**28**	**20**	1
Pterostichus melanarius (Illiger)	7094	6	6	6	5	6	**46**	**26**
Quedius curtipennis Berhnauer	2489	**33**	**28**	14	10	6	6	4
Quedius molochinus (Gravenhorst)	2353	**31**	**24**	15	12	7	7	4
Tachinus limbatus Melsheimer	9447	1	2	2	2	5	**47**	**40**
Tachinus rufipes (DeGeer)	2673	**28**	**59**	1	+	+	7	5

beetle fauna includes about 850 species, 630 of these being true forest dwellers. A combination of pitfall traps and FIT showed the presence of 55 to 60% of these in one year (Muona 1999).

The species in small numbers. At Scotstown, the species occurring as singletons or doubletons represented 42.2% of species in PF, 45.7% in FIT and 43.3% in the LT over all sampling months (33 or 34). Species sporadically collected (during 1–3 months only over 33 or 34 sampling months) represented between 49 and 63% of species from one pitfall trap line, between 66 and 74% of species from one FIT, and 59% of species in LT. We believe that the presence of species in small numbers may be associated with behavior of insects, particular habitat preferences, methodology, distribution of a species, migration, food availability and/or long larval development (two years or more).

Most of the small Carabidae (e.g., Bembidiini) and Staphylinidae (under 2 mm long) are often missed in pitfall traps (Pohl et al. 2008, Jocque et al. 2016); however, we caught small beetles in large numbers using FIT and the blacklight trap (Levesque and Levesque 2019, 2023). Among the 50 most abundant epigaeic species at Scotstown, we noted the occurrence of one or two adults only for nine taxa in FIT and six taxa in the light trap over 2006–2010. In north-temperate forests and in agricultural landscapes, the vertical stratification of flying Coleoptera may be observed (Levesque and Levesque 2019), and some species may be in small numbers at a level at a certain time. A vertical subterranean stratification of Coleoptera, such as observed by Jászayová et al. (2022) in Slovakia, is also plausible in North America.

Some rare species have a distribution by patches often associated with the last glaciation periods; among the beetles of this group, the staphylinid *Acidota crenata* (Fabricius) (2 adults at Scotstown) can tolerate a wide range of temperatures and is found from northern boreal or colder habitats south to southernmost Canada (Motz and Morgan 1997). Certain other species are apparently rare in southern Québec because this region is at the periphery of their distribution area; for example, *Scaphinotus viduus* (Dejean) is a carabid recorded from Québec to Florida (Downie and Arnett 1996). A true endangered Nearctic species in North America is rare nearly on its entire geographical range, independently of geo-political frontiers (country, provinces, states).

During a migration (*i.e.*, between two breeding sites, between a breeding site and an overwintering site, or within a single site), it is possible that an individual becomes a tourist in an unusual habitat (macro- or microhabitat) and this species will be apparently rare during a study. At Scotstown, we collected only one individual of the carabid *Platypatrobus lacustris* Darlington; this species was regarded as an old relict because of its great rarity until its habitat requirements were discovered, *i.e.*, wet places exclusively in inhabited or recently deserted beaver houses (Bousquet 2010). We collected six adults of *Dromius piceus* Dejean (forest canopy species) only by the light trap in the center of the grassland (Levesque and Levesque 2023).

A species may be rare in a site where its preferred food sources (host-plant, moss, fungus, seed, deadwood, prey, carrion, dung, etc.) are scarce or absent. In 2006–2010, we observed the ground activity for only three adults of *Agriotes mancus* (Say), common elaterid having a larval development of three years in Canada and a distribution governed by soil moisture (Campbell et al. 1989). We suspect that the evaluation of the rarity of a species with a long larval development (two years or more) may be problematic in the context of a short-term study (one or two years), particularly if the number of newly emerged adults is very variable from year to year.

The most abundant species. The number of most abundant species (at least 100 adults) collected at Scotstown during 33 or 34 months was 50 in PF, 48 in FIT and 57 in LT, and these species varied with the sampling method (Table 6; Levesque and Levesque 2019, 2023). Nevertheless, catches of certain ground-active species were also abundant in FIT and the blacklight trap over 2006–2010. We observed the flight of at least 100 adults for the eleven following species: the carabids *B. discus, C. fossor* and *Harpalus rufipes* (DeGeer), the elaterid *H. abbreviatus*, the silphid *N. americana,* and the staphylinids *A. rugosus, Atheta crenuliventris* Bernhauer, *Carpelimus* sp. S02, *Gabrius subnigritulus* (Reitter), *Mocyta fungi* (Gravenhorst) and *Q. curtipennis* (Levesque and Levesque 2019, 2023). We caught also 3660 adults of the Chrysomelidae Alticini *L. luridus* (5.5% of macropterous individuals) in FIT during 2006–2010 (Levesque and Levesque 2019).

With each method, we observed important variations in annual percentages for dominant species at Scotstown (Table 4; Levesque and Levesque 2019, 2023). The maximal fluctuations were between 12.2 and 41.3% for the staphylinid *T. limbatus* in pitfall traps, between 10.3 and 59.6% for the nitidulid *Fabogethes nigrescens* (Stephens) in FIT, and between 0.7 and 39.8% for the carabid *Bembidion versicolor* (LeConte) in LT. Species-level responses are probably driven by differences in behavior, various physiological factors, dispersal ability, ecological interactions, abundance of ephemeral habitats, various environmental factors (e.g., photoperiod, soil pH, soil moisture, soil texture, vegetation, microclimate), time of day or night, season, spatial heterogeneity in food quality and quantity, and the nature of the trap installation (Matalin 1998, Pohl et al. 2008, Janssen et al. 2009, Maguire et al. 2014, Pohe et al. 2018,).

Sex-ratio of some species. We can compare the sex-ratio for 13 species captured at Scotstown in pitfall traps (2006–2010) (Table 6), FIT (2006–2010) and/or the light trap (2007–2010) (Levesque and Levesque 2019, 2023). The assumed sex-ratio of 1:1 was observed in pitfall traps and FIT for *Catops alsiosus* (Horn) only. We collected primarily males by pitfall trapping and females in flight traps for *B. discus* (in LT: 62% of females) and *G. subnigritulus* (in FIT: 72% of females). The predominance of females occurred in *A. rugosus* (three methods), *Agonum thoreyi* Dejean (pitfall traps and light trap), *A. sordens, H. abbreviatus, Stenus erythropus* (Reitter) and *T. limbatus* (pitfall traps only), and *H. rufipes* (light trap only). Whereas, the predominance of males occurred in *N. americana* (pitfall traps and FIT), *Q. curtipennis* (pitfall traps only), and *A. crenuliventris* (in FIT only).

In a previous study, we investigated with pitfall traps and FIT the beetle activity in a raspberry agroecosystem at Johnville (about 40 km from Scotstown) over 1987–1989. Among the carabids in pitfall traps, we collected mainly males of *B. discus* and *P. melanarius,* and the sex-ratio of *A. muelleri* and *Poecilus lucublandus* (Say) was not significantly different of 1:1 (Levesque and Levesque 1994). At Scotstown, our observations were similar for *B. discus*, *P. lucublandus* and *P. melanarius*, but not for *A. muelleri* (Table 6). At Johnville, the predominance of males in pitfall traps and females in FIT occurred in staphilinids *A. rugosus* and *G. subnigritulus*, and females of *S. erythropus* were primarily collected in pitfall traps and FIT (Levesque and Levesque 1995). At Scotstown, we confirmed previous observations for *G. subnigritulus*. We observed the predominance of females of *B. discus* and *H. rufipes*, but not of *A. rugosus*, in light trap at Compton (about 50 km from Scotstown) over 2014–2017 (Levesque and Levesque 2022). The sex-ratio of *A. rugosus* was variable in different studies, in possible relation with trophic preferences of this saprophilic species. Finally, the colonization by flight in new breeding sites seems mainly dependent on females in species *B. discus, G. subnigritulus* and *H. rufipes*.

Wing polymorphism in some adventive species. Among the most abundant

Table 6. Total and monthly catches, wing length, and female ratio of the 50 most abundant beetle species from Scotstown during April-October 2006–2010, and probability for an assumed sex-ratio of 1:1

		Monthly catches[b] (%)							Wings[c] (%)		Fem.	
Family and species [a]	**N**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	**M**	**B**	**%[d]**	***P***
Carabidae												
Agonum gratiosum (Mannerheim)	3355	0	1	9	**56**	**26**	4	4	100	0	**63**	< 0.001
Agonum melanarium Dejean	131	1	2	23	**32**	20	12	10	100	0	57	0.097
Agonum muelleri (Herbst)*	3014	1	10	**27**	**41**	18	2	1	100	0	**60**	< 0.001
Agonum palustre Goulet	2077	0	3	**32**	**57**	1	4	4	100	0	**75**	< 0.001
Agonum retractum LeConte	222	0	1	22	**70**	3	2	3	**4**	**96**	**69**	< 0.001
Agonum sordens Kirby	1319	+	4	**32**	**47**	7	5	5	100	0	**59**	< 0.001
Agonum thoreyi Dejean**	105	0	0	1	**41**	**30**	10	18	100	0	**64**	0.005
Agonum trigeminum Lindroth	394	1	9	19	**30**	16	15	10	100	0	**62**	< 0.001
Amara neoscotina Casey	379	11	19	**34**	20	6	7	3	100	0	**39**	< 0.001
Bembidion semicinctum Notman	229	4	17	**46**	**25**	3	2	2	**0**	**100**	45	0.165
Blemus discus (Fabricius)*	3067	0	0	1	13	**40**	**38**	8	100	0	**41**	< 0.001
Carabus maeander Fischer von W.**	121	12	**60**	17	7	3	1	0	**17**	**83**	**13**	< 0.001
Carabus nemoralis O.F. Müller*	1054	12	**45**	18	5	11	6	2	**0**	**100**	**38**	< 0.001
Clivina fossor (Linnaeus)*	479	1	22	**35**	22	10	6	5	**70**	**30**	na	
Harpalus rufipes (DeGeer)*	125	0	2	**55**	**34**	7	2	0	100	0	42	0.089
Loricera pilicornis (Fabricius)**	311	1	9	**39**	**37**	12	0	1	100	0	**66**	< 0.001
Oxypselaphus pusillus (LeConte)	1551	+	1	24	**60**	7	4	4	**+**	**100**	50	0.899
Patrobus longicornis (Say)	222	0	0	1	**40**	**44**	14	1	**2**	**98**	**38**	< 0.001
Platynus decentis (Say)	895	8	**44**	**43**	3	1	1	+	100	0	**62**	< 0.001
Poecilus lucublandus (Say)	399	0	21	**54**	13	5	7	1	100	0	49	0.802
Pterostichus luctuosus (Dejean)	199	0	11	**33**	**33**	2	6	16	100	0	55	0.178
Pterostichus melanarius (Illiger)*	7094	1	7	16	**57**	16	2	+	**10**	**90**	**43**	< 0.001
Pterostichus patruelis (Dejean)	106	8	13	8	9	8	15	**39**	**2**	**98**	59	0.052
Stenolophus fuliginosus Dejean	113	5	5	20	24	20	8	17	100	0	46	0.393
Chrysomelidae												
Longitarsus luridus (Scopoli)*	479	4	3	1	10	**30**	**32**	20	**4**	**96**	**56**	0.007
Curculionidae												
Exomias pellucidus (Boheman)*	186	0	3	**80**	15	3	1	0	na		na	
Elateridae												
Hypnoidus abbreviatus (Say)	1496	2	17	**38**	**42**	2	0	+	100	0	**58**	< 0.001
Leiodidae												
Catops alsiosus (Horn)**	119	0	1	20	**49**	**27**	1	3	100	0	43	0.119

Ptiliidae												
Ptenidium sp. S	172	0	1	1	1	4	**37**	**58**	100	0	na	
Silphidae												
Necrophila americana (Linnaeus)	614	0	3	**56**	**34**	6	1	0	100	0	**42**	< 0.001
Staphylinidae												
Anotylus rugosus (Fabricius)*	3571	+	9	22	**42**	22	2	3	100	0	**58**	< 0.001
Atheta crenuliventris Bernhauer	100	0	0	3	**55**	**40**	2	0	100	0	40	0.041
Carpelimus sp. S02	189	4	**31**	17	**27**	11	5	4	100	0	na	
Devia prospera (Erichson)**	296	1	**59**	**34**	6	0	0	0	100	0	na	
Dinothenarus badipes (LeConte)	834	1	**34**	**46**	9	4	4	1	100	0	**30**	< 0.001
Drusilla canaliculata (Fabricius)*	6501	+	7	22	**36**	24	8	3	**2**	**98**	**63**	< 0.001
Gabrius subnigritulus (Reitter)*	106	13	**52**	17	6	6	3	4	100	0	**30**	< 0.001
Gyrohypnus angustatus Stephens*	213	7	**44**	**36**	10	1	1	1	100	0	na	
Lesteva pallipes LeConte	562	8	6	4	1	+	5	**77**	100	0	46	0.043
Liogluta intermedia Klim. & Langor	2314	0	+	+	+	2	**42**	**55**	100	0	**41**	< 0.001
Mocyta fungi (Gravenhorst)*	451	1	7	14	**30**	**30**	11	8	100	0	na	
Oxypoda perexilis Casey	152	2	**42**	13	3	18	13	9	**19**	**81**	na	
Quedius curtipennis Bernhauer*	2489	6	13	10	3	6	23	**38**	100	0	**35**	< 0.001
Quedius molochinus (Gravenhorst)*	2353	0	+	1	21	**50**	**26**	1	100	0	**27**	< 0.001
Stenus erythropus Melsheimer	792	2	14	**31**	**33**	11	5	4	100	0	**65**	< 0.001
Tachinus corticinus Gravenhorst*	479	5	19	18	**30**	1	3	**26**	**35**	**65**	46	0.049
Tachinus limbatus Melsheimer	9447	0	0	2	7	16	**62**	13	100	0	**55**	< 0.001
Tachinus rufipes (DeGeer)*	2673	+	6	**41**	**43**	7	1	1	100	0	**42**	< 0.001
Tachyporus canadensis Campbell	107	13	18	7	20	14	7	21	100	0	42	0.120
Tinotus caviceps Casey	106	7	**27**	**48**	7	0	5	7	100	0	**68**	< 0.001

[a] Adventive species marked with * and Holarctic species marked with **
[b] + for month with less than 1% of catches
[c] Wings: B micropterous (vestigial wings) and/or brachypterous (reduced wings); M macropterous adults (fully developed wings); + one single adult
[d] Female ratio in bold when the sex-ratio is significantly biased

adventive species, adults of *A. muelleri, B. discus, H. rufipes, A. rugosus, G. subnigritulus, G. angustatus, M. fungi, Q. curtipennis* and *T. rufipes* are macropterous in Europe and in North America (Table 6; Levesque and Levesque 1994, 1995; Kunze and Kache 1998). Whereas, *C. fossor*, *P. melanarius, L. luridus* and *Tachinus corticinus* Gravenhorst show a wing polymorphism in Europe and in North America (Table 6; Levesque and Levesque 1994, 1995, 1998). In Europe, *D. canaliculata* is wingless and *Q. molochinus* is wing-dimorphic (Assing 1994, Kunze and Kache 1998); at Scotstown, we observed the macropterous morph in few *D. canaliculata* (2% of individuals) and all *Q. molochinus* (Table 6).

Some European studies (e.g., in the Dutch polders) show that young assemblages of carabids (recently occupying new areas) consist predominantly of macropterous species and macropterous individuals of wing-dimorphic species; also, populations of wing-dimorphic carabid species at the periphery of their geographical range contain high proportions of macropterous individuals (Venn 2016). In *P. melanarius* populations from southern Québec, we observed 16% of macropterous adults in a raspberry agroecosystem at Johnville (Levesque and Levesque 1994), and 10% at Scotstown (Table 6). In Canadian regions that have established populations of *P. melanarius*, the proportions of short-winged individuals are greater than long-winged (Larson and Langor 1982, Bourassa et al. 2011, Cottrell-Callbeck et al. 2019). Macropterous beetles in wing-dimorphic species are important for ea rly colonization of unexploited territory, but that flightless individuals replace the flying morph relatively rapidly once populations are established (Bourassa et al. 2011).

Dispersal power by flight of some abundant species. Among the dominant and subdominant species in PF at Scotstown (Table 5), adults of sixteen species were all macropterous, and the predominance of micropterous or brachypterous adults occurred in *A. retractum, C. nemoralis, D. canaliculata O. pusillus* and *P. melanarius* (Table 6). We have been surprised to capture one macropterous adult of *O. pusillus*; Lindroth (1966) suspected that macropterous individuals may exist in this species. During 2006–2010, we did not observe the flight of *A. retractum, C. nemoralis, L. pallipes, O. pusillus* and *Q. molochinus*. Only *A. rugosus* and *B. discus* were collected in large numbers in the light trap (Levesque and Levesque 2023). Whereas we caught in FIT a very small number of macropterous adults for some abundant epigaeic species (e.g., four *B. discus*, five *D. badipes*, three *D. canaliculata*, two *L. intermedia* and four *P. melanarius*).

The Nearctic macropterous species *D. badipes* is broadly distributed over eastern North America, and collected in a wide variety of habitats including anthropogenic habitats (Brunke et al. 2011). The adventive species *D. canaliculata* and *P. melanarius* are often found in large numbers in Canadian disturbed sites including synanthropic habitats (Klimaszewski et al. 2012, 2013). At Scotstown, we did not detect habitat preferences of *D. badipes*; whereas *D. canaliculata* and *P. melanarius* occurred mainly alongside the ditch (Table 5). Across a period of ten years, Andorkó and Kádár (2006) have observed the eurytopic species *P. melanarius* associated with high level of soil moisture and dense shrub vegetation; similar conditions occurred in DI–SH of the present study, and *P. melanarius* was the dominant carabid species in raspberry rows of southern Québec (Levesque and Levesque 1994). Some species, with high environmental plasticity, may occur in large numbers in disturbed habitats, independently of their dispersal power by flight. It is possibly the case of *D. badipes, D. canaliculata* and *P. melanarius*, three generalist species (Bohác and Bezdek 2004, Andorkó and Kádár 2006, Brunke et al. 2011), and practically not flying beetles at Scotstown.

During the present study, the phytophagous and saprophagous ground-dwelling species were more abundant in the grassland. Among the species often soil-active in the grassland, we caught in FIT 569 adults of the phytophagous chrysomelid *Hydrothassa vittata* (Olivier), and many adults of saprophilic species (e.g., 113 *A. rugosus*, 247 *A. crenuliventris,*100 *Carpelimus* sp. S02*,* 97 *C. alsiosus* and 189 *N. americana* (Levesque and Levesque 2019)). We suspect that the flight may be very important in the food search for these species. Furthermore, we collected 3,413 *H. vittata* adults by sweeping net during 2011–2012, mainly in the grassland (unpublished data).

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Literature Cited

Anderson, R. S., and S. B. Peck. 1985. The carrion beetles of Canada and Alaska (Coleoptera: Silphidae and Agyrtidae). The Insects and Arachnids of Canada. Part 13. Agriculture Canada, Ottawa, Ontario, 121 pp.

Andorkó, R., and F. Kádár. 2006. Carabid beetle (Coleoptera: Carabidae) communities in a woodland habitat in Hungary. Entomologica Fennica 17: 221–228.

Assing, V. 1994. Zur Kurzflügelkäferfauna xerothermer Flächen im südlichen Niedersachsen (Coleoptera: Staphylinidae). Göttinger Naturkundliche Schriften 3: 7–31.

Bohác, J. 1999. Staphylinid beetles as bioindicators. Agriculture, Ecosystems and Environment 74: 357–372.

Bohác, J., and A. Bezdek. 2004. Staphylinid beetles (Coleoptera, Staphylinidae) recorded by pitfall and light trapping in Mrtvý Luh peat bog. Silva Gabreta 10: 141–150.

Bourassa, S., J. R. Spence, D. J. Hartley, and S. I. Lee. 2011. Wing-dimorphism and population expansion of *Pterostichus melanarius* (Illiger, 1798) at small and large scales in central Alberta, Canada (Coleoptera, Carabidae, Pterostichini). ZooKeys 147: 545–558.

Bousquet, Y. 2010. Illustrated identification guide to adults and larvae of northeastern North American ground beetles (Coleoptera: Carabidae). Pensoft Series Faunistica No. 90. Pensoft Publishers, Sofia, Bulgaria. 562 pp.

Bousquet, Y., P. Bouchard, A. E. Davies, and D. S. Sikes. 2013. Checklist of beetles (Coleoptera) of Canada and Alaska. Second edition. Pensoft Series Faunistica No. 109. Pensoft Publishers, Sofia, Bulgaria. 402 pp.

Bright, D. E., and P. Bouchard. 2008. The weevils of Canada and Alaska. Volume 2. Coleoptera Curculionidae, Entiminae. The Insects and Arachnids of Canada. Part 25. NRC Research Press, National Research Council Publications, Ottawa, Ontario. xiii + 327 pp.

Brunke, A., C. A. Bahlai, J. Klimaszewski, and R. H. Hallett. 2014. Rove beetles (Coleoptera: Staphylinidae) in Ontario, Canada soybean agroecosystems: assemblage diversity, composition, seasonality, and habitat use. Canadian Entomologist 146: 652–670.

Brunke, A. J., P. Bouchard, H. B. Douglas, and M. Pentisaari. 2019. Coleoptera of Canada. ZooKeys 819: 361–376.

Brunke, A., A. Newton, J. Klimaszewski, C. Majka, and S. Marshall. 2011. Staphylinidae of eastern Canada and the adjacent United States. Keys to subfamilies; Staphylininae: tribes and subtribes, and species of Staphylinina. Canadian Journal of Arthropod Identification No. 12: 1–110.

Byers, R. A., G. M. Barker, R. L. Davidson, E. R. Hoebeke, and M. A. Sanderson. 2000. Richness and abundance of Carabidae and Staphylinidae (Coleoptera), in northeastern dairy pastures under intensive grazing. The Great Lakes Entomologist 33: 81–105.

Campbell, J. M. 1973. A revision of the genus *Tachinus* (Coleoptera: Staphylinidae) of North and Central America. Memoirs of the Entomological Society of Canada No. 90: 1–137.

Campbell, J. M. 1975. New species and records of *Tachinus* (Coleoptera: Staphylinidae) from North America. Canadian Entomologist 107: 87–94.

Campbell, J. M. 1979. A revision of the genus *Tachyporus* Gravenhorst (Coleoptera: Staphylinidae) of North and Central America. Memoirs of the Entomological Society of Canada No. 109: 1–95.

Campbell, J. M. 1988. New species and records of North American *Tachinus* Gravenhorst (Coleoptera: Staphylinidae). Canadian Entomologist 120: 231–295.

Campbell, J. M., M. J. Sarazin, and D. B. Lyons. 1989. Canadian beetles (Coleoptera) injurious to crops, ornamentals, stored products, and buildings. Publication 1826. Agriculture Canada, Research Branch, Ottawa, Ontario. iv + 491 pp.

Cottrell-Callbeck, S., M. MacDonald, and M. Evenden. 2019. Wing polymorphism of *Pterostichus melanarius* (Coleoptera: Carabidae) (Illiger, 1978) in Alberta pulse crops. Alberta Academic Review 2: 23–24.

Downie, N. M., and R. H. Arnett, Jr. 1996. The beetles of northeastern North America. An American insect projects. The Sandhill Crane Press, Publisher, Gainesville, Florida. xiv +1721 pp.

González, E., A. Salvo, and G. Valladares. 2020. Insects moving through forest-crop edges: a comparison among sampling methods. Journal of Insect Conservation 24: 249–258.

Holliday, N. J. 1992. The carabid fauna (Coleoptera: Carabidae) during postfire regeneration of boreal forest: properties and dynamics of species assemblages. Canadian Journal of Zoology 70: 440–452.

Iannuzzi, L., C. Nunes Liberal, T. Bezerra de Souza, T. G. Pellegrini, J. C. Siqueira da Cunha, R. Koroiva, L. S. Corrêa de Alburquerque, F. Correia Costa, R. Portela Salomao, A. C. Dália Maia, and F. W. Trevisan Leivas. 2020. Sampling methods for beetles (Coleoptera) (pp. 125–185). *In*: Measuring arthropod biodiversity—A handbook of sampling methods (J. C. Santos, and G. W. Fernandes, editors). Springer.

Irmler, U. 2018a. Which carabid species (Coleoptera: Carabidae) profit from organic farming after a succession of 15 years? Agriculture, Ecosystems and Environment 263: 1–6.

Irmler, U. 2018b. The succession of Staphylinidae (Coleoptera) after 15 years of conversion from conventional to organic farming. Biodiversity and Conservation 27: 3233–3246.

Janssen, P., D. Fortin, and C. Hébert. 2009. Beetle diversity in a matrix old-growth boreal forest: influence of habitat heterogeneity at multiple scales. Ecography 32: 423–432.

Jászayová, A., T. Jászay, and A. Csanády. 2022. Subterranean biodiversity and the depth distribution of beetles (Coleoptera) in forested scree slopes in the Western Carpathians (Slovakia). Journal of Insect Conservation 26: 735–750.

Jocque, M., T. M. Teofilova, and N. D. Kodzhabashev. 2016. Light trapping as a valuable rapid assessment method for ground beetles (Carabidae) in Bulgarian wetland. Acta Zoologica Bulgarica 68: 529-534.

Jung, J. K., and J. H. Lee. 2016. Forest-farm edge effects on communities of ground beetles (Coleoptera: Carabidae) under different landscape structures. Ecological Research 31: 799–810.

Kevan, D. K. 1967. The British species of the genus *Longitarsus* Latreille (Coleoptera, Chrysomelidae). Entomologist's Monthly Magazine 103: 83–110.

Klimaszewski, J., A. Brunke, V. Assing, D. W. Langor, A. F. Newton, C. Bourdon, G. Pelletier, R. P. Webster, L. Herman, L. Perdereau, A. Davies, A. Smetana, D. S. Chandler, C. Majka, and G. G. E. Scudder. 2013. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 2: Staphylinidae. Pensoft Series Faunistica No. 104. Pensoft Publishers, Sofia, Bulgaria. 360 pp.

Klimaszewski, J., E. R. Hoebeke, D. W. Langor, H. B. Douglas, L. Borowiec, H. E J. Hammond, A. Davies, C. Bourdon, and K. Savard. 2020. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 5: Chrysomeloidea (Cerambycidae, Chrysomelidae, and Megalopodidae). Pensoft Series Faunistica No. 119. Pensoft Publishers, Sofia, Bulgaria. 175 pp.

Klimaszewski, J., D. Langor, R. Batista, J. A. Duval, C. G. Majka, G. G. E. Scudder, and Y. Bousquet. 2012. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 1: Carabidae. Pensoft Series Faunistica No. 103. Pensoft Publishers, Sofia, Bulgaria. 96 pp.

Klimaszewski, J., D. W. Langor, H. E. J. Hammond, G. Pelletier, Y. Bousquet., C. Bourdon, R. P. Webster, L. Borowiec, G. G. E. Scudder, and C. G. Majka. 2015. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 3: Cucujoidea. Pensoft Series Faunistica No. 113. Pensoft Publishers, Sofia, Bulgaria. 171 pp.

Klimaszewski, J., D. W. Langor, A. B. T. Smith, E. R. Hoebeke, A. Davies, G. Pelletier, H. B. Douglas, R. P. Webster, C. Bourdon, L. Borowiec, and G. G. E. Scudder. 2017. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 4: Scarabaeoidea, Scirtoidea, Buprestoidea, Byrrhoidea, Elateroidea, Derodontoidea, Bostrichoidea, and Cleroidea. Pensoft Series Faunistica No. 116. Pensoft Publishers, Sofia, Bulgaria. 215 pp.

Klimaszewski, J., R. P. Webster, D. W. Langor, A. Brunke, A. Davies, C. Bourdon, M. Labrecque, A. F. Newton, J. A. Dorval, and J. H. Frank. 2018. Aleocharine rove beetles of eastern Canada (Coleoptera, Staphylinidae, Aleocharinae): a glimpse of megadiversity. Springer. xiv + 902 pp.

Knapp, M., J. Knappová, P. Jakubec, P. Vonicka, and P. Moravec. 2020. Incomplete species lists produced by pitfall trapping: how many carabid species and which functional traits are missing? Biological Conservation 245, art. 108545, 9 pp.

Kunze, M., and P. Kache. 1998. Zonationszönosen vin Kurzflügelkäfern (Coleoptera, Staphylinidae) on Flussufern Nordwestdeutschlands. Zeitschrift für Ökologie und Naturschutz 7: 29–43.

Larson, D. J., and D. W. Langor. 1982. The carabid beetles of insular Newfoundland (Canada) (Coleoptera: Carabidae: Cicindelidae): 30 years after Lindroth. Canadian Entomologist 114: 591–597.

Lee, S. I., D. W. Langor, J. R. Spence, J. Pinzon, G. R. Pohl, D. J. Hartley, T. T. Work, and L. Wu. 2023. Rapid recovery of boreal rove beetle (Staphylinidae) assemblages 16 years after variable retention harvest. Ecography (e06347), 13 pp.

Levesque, C., and G. Y. Levesque. 1992. Epigeal and flight activity of Coleoptera in a commercial raspberry plantation and adjacent sites in southern Québec (Canada): introduction and Nitidulidae. The Great Lakes Entomologist 25: 271–285.

Levesque, C., and G. Y. Levesque. 1994. Abundance and seasonal activity of ground beetles (Coleoptera: Carabidae) in a raspberry plantation and adjacent sites in southern Québec (Canada). Journal of the Kansas Entomological Society 67: 73–101.

Levesque, C., and G. Y. Levesque. 1995. Abundance, diversity and dispersal power of rove beetles (Coleoptera: Staphylinidae) in a raspberry plantation and adjacent sites in Eastern Canada. Journal of the Kansas Entomological Society 68: 355–370.

Levesque, C., and G. Y. Levesque. 1998. Faunal composition, wing polymorphism and seasonal abundance of some flea beetles (Coleoptera: Chrysomelidae) in southern Québec, Canada. The Great Lakes Entomologist 31: 39–48.

Levesque, C., and G. Y. Levesque. 2019. A five-year study of the flying beetles (Coleoptera) from a grassland and an adjacent woods in southern Québec (Canada). The Great Lakes Entomologist 52: 45–52.

Levesque, C., and G. Y. Levesque. 2022. Complementarity of blacklight trap and flight interception trap in a multi-year study of flying Coleoptera near a farm pond in southern Québec (Canada). The Great Lakes Entomologist 55: 76–109.

Levesque, C., and G. Y. Levesque. 2023. Six-year study of a nocturnal flying Coleoptera community in southern Québec, Canada. The Coleopterists Bulletin 77: 35–45.

Lindroth, C. H. 1966. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 4. Opuscula Entomologica Supplementum No. 29: 409–648.

Luff, M. L. 1996. Use of carabids as environmental indicators in grasslands and cereals. Annales Zoologici Fennici 33: 185–195.

Maguire, D. Y., K. Robert, K. Brochu, M. Larrivée, C. Buddle, and T. A. Wheeler. 2014. Vertical stratification of beetles (Coleoptera) and flies (Diptera) in temperate forest canopies. Environmental Entomology 43: 9–17.

Matalin, A. V. 1998. Influence of weather conditions on migratory activity of ground beetles (Coleoptera, Carabidae) in the steppe zone. Biology Bulletin 25: 485–494.

McCravy, K. W., and J. E. Willand. 2020. Seasonal occurrence of adult carabid beetles (Coleoptera: Carabidae) in west-central Illinois. Journal of Entomological Science 55: 329–343.

Motz, J.E., and A. V. Morgan. 1997. Late-glacial climate and ecology of a kettle section at Brampton, Ontario, Canada, as determined from fossil Coleoptera. Canadian Journal of Earth Sciences. 34: 926–934.

Muona, J. 1999. Trapping beetles in boreal coniferous forest—how many species do we miss? Fennia, International Journal of Geography 177: 11–16.

Peck, S. B., and J. Cook. 2002. Systematics, distributions, and bionomics of the small carrion beetles (Coleoptera: Leiodidae: Cholevinae: Cholevini) of North America. Canadian Entomologist 134: 723–787.

Pohe, S. R., M. J. Winterbourn, and S. Harding. 2018. Comparison of fluorescent lights with differing spectral properties on catches of adult aquatic and terrestrial insects. New Zealand Entomologist 41: 1–11.

Pohl, G., D. Langor, J. Klimaszewski, T. Work, and P. Paquin. 2008. Rove beetles (Coleoptera: Staphylinidae) in northern Nearctic forests. Canadian Entomologist 140: 415–436.

Pohl, G. R., D. W. Langor, and J. R. Spence. 2007. Rove beetles and ground beetles (Coleoptera: Staphylinidae, Carabidae) as indicators of harvest and regeneration practices in western Canadian foothills forests. Biological Conservation 137: 294–307.

Rainio, J., and J. Niemelä. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity and Conservation 12: 487–506.

Schwerk, A., and J. Szyszko. 2009. Distribution and spatial preferences of carabid species (Coleoptera: Carabidae) in a forest-field landscape in Poland. Baltic Journal of Coleopterology 9: 5–15.

Scott, W. A., and R. Anderson. 2003. Temporal and spatial variation in carabid assemblages from the United Kingdom Environmental Change Network. Biological Conservation 110: 197–210.

Smetana, A. 1971. Revision of the tribe Quediini of America north of Mexico (Coleoptera: Staphylinidae). Memoirs of the Entomological Society of Canada No. 79: 1–303.

Smetana, A. 1982. Revision of the subfamily Xantholininae of America north of Mexico (Coleoptera: Staphylinidae). Memoirs of the Entomologcal Society of Canada No. 120: 1–394.

Smetana, A. 1989. *Gabrius subnigritulus* (Reitter), a Palearctic species recently introduced into North America (Coleoptera: Staphylinidae). Naturaliste Canadien 116: 175–178.

Smetana, A. 1995. Rove beetles of the subtribe Philonthina of America north of Mexico (Coleoptera: Staphylinidae). Classification, phylogeny and taxonomic revision. Memoirs on Entomology, International. No. 3. Associated Publishers, Gainesville, Florida. 946 pp.

Stibick, J. N. L. 1978. A revision of the Hypnoidinae of the world (Col. Elateridae): Part II. The Hypnoidinae of North and South Americana. The genera *Ascoliocerus, Desolakerrus, Margaiostus, Hypolithus* and *Hypnoidus*. EOS, Revista Espanola de Entomologia 52: 309–386.

Sushko, G. 2014. Spatial distribution of epigeic beetles (Insecta, Coleoptera) in the "Yelnia" peat bog. Baltic Journal of Coleopterology 14: 151–161.

Venn, S. 2016. To fly or not to fly: factors influencing the flight capacity of carabid beetles (Coleoptera: Carabidae). European Journal of Entomology 113: 587–600.

Work, T. T., D. G. McCullough, and W. J. Mattson. 1998. Moth and carabid beetle species associated with two ecological landtype phases in northern Michigan. General Technical Report NC-201. United States Department of Agriculture, Forest Service, North Central Research Station. St. Paul, Minnesota, USA. 25 pp.

Work, T. T., D. M. Morris, S. Loboda, J. Klimaszewski, K. Wainio-Keizer, and L. Vernier. 2023. Cumulative effects of biomass harvesting and herbicide application on litter-dwelling arthropod communities in jack pine-dominated forests: 7th year postharvest assessment. Canadian Journal of Forest Research 53: 931–952.

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