GROUND BEETLES (COLEOPTERA: CARABIDAE) FROM ALVAR HABITATS IN ONTARIO

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Abstract

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An inventory of ground beetles (Coleoptera: Carabidae) was conducted in ten alvar sites, representing four alvar types, in southern Ontario. We identified 142 species from 8647 specimens. Species richness and numbers of specimens were generally higher in alvar grasslands. Alvar pavement and alvar shrubland generally had lower species richness and specimen numbers. Each site had between four and seven dominant (over 5% of individuals collected at the site) species, which varied between alvar types and localities. Three of the dominant species (*Agonum nutans*, *Chlaenius purpuricollis,* and *Pterostichus novus*) have rarely been collected in non-alvar sites in the region. Most of the species collected are associated with open habitats or grassy meadows. The carabid fauna collected was dominated by widespread or eastern North American species, although some northern and southern species were near the limits of their range. The known distribution of *Cicindela denikei* was extended eastward from northwestern Ontario. Nine introduced European species were collected, and only two (*Carabus nemoralis* and *Pterostichus melanarius*) were dominant at any site.

Introduction

Alvars are naturally open areas of thin soil overlying flat limestone or dolostone. The vegetation is generally sparse and dominated by grasses (Poaceae), sedges (Cyperaceae), and shrubs. Trees are rare because there are few areas with sufficient soil accumulation. Six types of alvars are recognized based on the percentage of exposed bedrock, herb and shrub cover, and tree cover (Catling and Brownell 1995). North American alvars are concentrated in the Great Lakes region, where the limestone was denuded by glaciation and the sites have been maintained as natural openings by multiple factors including fires, grazing by large herbivores, lack of soil, and a seasonal pattern of flood-drought-flood in spring, summer, and fall, respectively. There are 250 to 300 known alvar sites in the Great Lakes region,

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mostly in southern Ontario, but also in New York, Michigan, Ohio, Quebec, and Vermont (Catling and Brownell 1995; Reschke et al. 1999).

The flora of alvars is well known: 347 species of native plants have been identified in Great Lakes alvars, of which 28% are considered characteristic of alvars. There are also several endemic species. The lack of introduced European flora is notable, although many of these species have invaded alvars recently because of artificial or man-made stresses. Due to the combination of present conditions (geology, hydrology, etc.) and postglacial history of alvars, plant species with northern, western, and southern Nearctic affinities coexist in these sites (Catling and Brownell 1995).

Surveys of arthropods in North American alvars have been sporadic compared to surveys in Europe. Approximately 1800 species of arthropods, including more than 700 species of Coleoptera, have been recorded in the Great alvar of Öland (Sweden) alone (Lundberg 1983; Coulianos and Sylvén 1983). As for North America, Catling and Brownell (1995) documented a number of rarely collected species of Lepidoptera, Coleoptera, and Hymenoptera in Ontario alvars. There are also 18 species of leafhoppers (Hemiptera: Auchenorrhyncha) occurring in Great Lakes alvars that are normally associated with prairie habitats (Bouchard et al. 2001). Bouchard et al. (1998) provided phenology and habitat data on three species of Carabidae (Coleoptera) that are abundant in Ontario alvars but rarely collected elsewhere in Ontario.

As part of the International Alvar Conservation Initiative (Reschke et al. 1999), the objective of this study was to conduct a faunal inventory of the ground beetles (Coleoptera: Carabidae) in southern Ontario alvars to provide baseline data on the species and communities in this unique ecosystem.

Methods

Ten sites, representing four alvar types (pavement, shrubland, savanna grassland, grassland) were sampled in southern Ontario in 1996-1997 (Table 1). Sample sites were described and mapped in Bouchard et al. (1998; 2001). Examples of each alvar type are shown in Figure 1.

Sampling methods at each site consisted of one Malaise trap, 16 uncovered pitfall traps (white plastic beer cups, 9 cm in diameter), 16 pan traps (355 ml yellow plastic bowls, 15 cm in diameter), and two flight intercept traps, distributed randomly throughout the site. Pan traps and pitfall traps were set with their upper rim flush with the ground surface, which in alvars with thin soil cover restricted their use to cracks in the bedrock. Propylene glycol or ethylene glycol was used as the preserving fluid and a drop of liquid detergent or Kodak Photoflo® was added as a wetting agent. All traps were serviced twice a month and specimens were preserved in 70% ethanol prior to mounting. Hand collecting and sweeping were used to supplement trap catches at every visit to the sites. All traps operated from mid-May until mid-September. At Site 9, small mammals disturbed the pitfall traps and pan traps frequently throughout the summer. Although the data from this site were included in the species list and calculation of overall numbers of beetles, the site was omitted from the calculation of dominant species and rarefied estimates of species richness.

In order to determine whether certain species of carabids were characteristic of

TABLE 1. Location of study sites in Ontario alvars.

Site	Location	Alvar region	Coordinates	Alvar type	Sampling
1	Misery Bay Prov. Nat. Res.	Manitoulin Island	N 45°47'26" W 082°45'00"	alvar pavement	June - Sept 1996
2	10 km W Evansville	Manitoulin Island	N 45°49'18" W 082°41'04"	alvar shrubland	June - Sept 1996
3	10 km SW Gore Bay	Manitoulin Island	N 45°52'12" W 082°31'48"	alvar savanna grassland	June - Sept 1996
4	10 km W Gore Bay	Manitoulin Island	N 45°53'45" W 082°34'41"	alvar grassland	June - Sept 1996
5	5 km E Camden East	Napanee Plain	N 44°20'19" W 076°47'49"	alvar grassland	June - Sept 1997
6	3 km N Miller Lake	Bruce Peninsula	N 45°07'46" W 081°26'44"	alvar pavement	June - Sept 1997
7	Cabot Head	Bruce Peninsula	N 45°14'44" W 081°18'28"	alvar grassland	June - Sept 1997
8	1.5 km NE Dalrymple	Carden Plain	N 44°41'02" W 079°05'31"	alvar grassland	June - Sept 1997
9	7.5 km E Seabright	Carden Plain	N 44°38'27" W 079°03'59"	alvar shrubland	June - Sept 1997
10	5 km N Almonte	Smith Falls Plain	N 45°16'14" W 076°10'58"	alvar grassland	June - Sept 1997

all alvars sampled, characteristic of particular types of alvars, or whether communities are more affected by the fauna at the regional scale, we identified the species found in dominant numbers at each site. Dominant species were defined as any species comprising more than 5% of carabid specimens collected at that site (Frank and Nentwig 1995). Dominant species were identified for each alvar site and for all sites pooled.

Buddle et al. (2005) provided strong arguments for including rarefaction curves in biodiversity studies. We used EstimateS, version 6.0bl (Colwell 2001) to generate individual-based rarefied estimates of observed species richness for all sites sampled (except site 9, see comments above). Each curve is the result of 100 randomizations without replacement. Measures of standard deviation were obtained from all randomizations for each site.

Carabidae were identified using Lindroth (1961; 1963; 1966; 1968; 1969a; 1969b). Classification and geographic distribution follow Bousquet and Larochelle (1993). Habitat preferences were based primarily on data in Lindroth (1961; 1963; 1966; 1968; 1969a; 1969b), although other recent information was incorporated when available (Freitag 1999;

FIGURE 1. Examples of the four alvar types sampled during this study: A) alvar savanna, Manitoulin Island; B) alvar grassland, LaCloche Island; C) alvar pavement, Manitoulin Island; D) alvar shrubland, Manitoulin Island.

Larochelle and Larivière 2003). Species known to occupy four or more of the eight habitat categories were recorded as generalists.

In order to assess the potential interactions of carabid species in different alvar sites, we report on the dispersal ability of each species as determined by the condition of their hind wings. The condition of the hind wings (brachypterous or macropterous) was recorded from Lindroth (1961; 1963; 1966; 1968; 1969a; 1969b) and Larochelle and Larivière (2003). All specimens are deposited in the Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, Quebec, or the Canadian National Collection of Insects, Ottawa, Ontario.

Results

Species richness and abundance

We collected 8647 ground beetles, representing 142 species (Table 2). Excluding site 9, in which most traps were lost during the sampling period, the number of specimens collected per site ranged from 324 (site 8) to 2188 (site 10), and the number of species ranged from 21 (site 2) to 67 (site 5). The four sites with the highest species richness were alvar grasslands (sites 5, 10, 8, 4; Table 2). Sites 5 and 10 had the highest numbers of specimens (1841 and 2188, respectively) and species (67 and 57, respectively). Species richness and numbers of specimens collected were also high in the alvar savanna grassland

TABLE 2. Carabidae collected in Ontario alvars. Hab - habitat (G = generalist, F = forest, M = marsh, Mg = grassy meadow, Mw = wet meadow, Ob = open bare ground, Osw = open wet sand, R = riparian). Site numbers correspond to those in Table 1. Length of the hind wings was recorded as a measure of dispersal ability (+ = macropterous, - = brachypterous, +/- = dimorphic). * = introduced species.

			Alvar site										
Species	**Wings**	**Hab**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Total**
Acupalpus canadensis Casey	+	M								1			1
Ac. nanellus Casey	±	M					2						2
Ac. partiarius (Say)	+	M				1				1	2		4
Agonum crenistriatum (LeConte)	+	ObMg					13		15			85	113
Ag. cupreum Dejean	±	ObMg			3	35							38
Ag. cupripenne (Say)	+	Ob	4		218	64	202	8	92	32		74	694
Ag. gratiosum (Mannerheim)	+	M							1	1			2
Ag. harrisii LeConte	+	M				3	1			1			5
Ag. lutulentum (LeConte)	+	M					1		1				2
Ag. melanarium Dejean	+	MR			2	2							4
Ag. metallescens (LeConte)	+	M			1								1
Ag. muelleri (Herbst)*	+	Mg			1								1
Ag. nutans (Say)	+	Mg				370	45		2	2		26	445
Ag. placidum (Say)	+	Ob	5			1	1	1	1	1		1	11
Ag. rufipes Dejean	+	Ob					39		22			1	62
Ag. trigeminum Lindroth	+	MR				2	19	1		12		3	37
Amara aeneopolita Casey	+	Mg	1										1
Am. angustata (Say)	+	Mg								1			1
Am. cupreolata Putzeys	±	Mg	7		12	12	8	2	4	1	2	10	58
Am. familiaris (Duftschmid)*	+	Mg					2					1	3
Am. impuncticollis (Say)	+	Mg			1	7	8	10	11	1		5	43
Am. laevipennis Kirby	+	Mg					2			2			4

TABLE 2. Continued

Species	Wings	Hab	Alvar site 1	2	3	4	5	6	7	8	9	10	Total
Am. latior (Kirby)	+	MgOb	2										2
Am. lunicollis Schiødte*	+	Mg								5			5
Am. obesa (Say)	-	Ob	6									11	17
Am. pallipes Kirby	+	Mg				7	2			23			32
Am. pennsylvanica Hayward	+	Mg					57					367	424
Anisodactylus carbonarius (Say)	+	Mg					41					13	54
An. harrisii LeConte	+	MwMg			1			28	8	14		36	87
An. nigerrimus (Dejean)	+	Mg					49	2	13	9		152	225
An. rusticus (Say)	+	Mg					19			2		9	30
An. sanctaecrucis (Fabr.)	+	MRMg					1					1	2
Badister neopulchellus Lindroth	+	M			1	4					1		6
Ba. notatus Haldeman	±	Mg	1			1	1	3	7	5		29	47
Bembidion castor Lindroth	+	MR						1					1
Be. concretum Casey	+	M					1						1
Be. mimus Hayward	+	MR				4	3	39	1	3	1	10	61
Be. mutatum Gemminger & Harold	±	Osw			1					1			2
Be. nitidum (Kirby)	+	Ob			1								1
Be. patruele Dejean	+	MR						3	1			3	7
Be. praticola Lindroth	±	FMw								1			1
Be. rapidum (LeConte)	+	Osw	1				1	12					14
Be. versicolor (LeConte)	+	RM			2	3							5
Brachinus cyanochroaticus Erwin	+	M				2			1			1	4
Br. tenuicollis LeConte	+	M					2						2
Bradycellus lecontei Csiki	+	M				1							1
Bd. neglectus (LeConte)	+	Ob								2		1	3
Bd. nigriceps LeConte	+	M					3	2		1		3	9

TABLE 2. Continued

Species	Wings	Hab	Alvar site 1	2	3	4	5	6	7	8	9	10	Total
Bd. nigrinus (Dejean)	+	MwMg								1			1
Calathus gregarius (Say)	±	ObF	114	47	256	7	1		19	4		6	454
Ca. opaculus LeConte	+	Ob					1					4	5
Calosoma calidum (Fabr.)	+	MgOb	1		7	6	6		1	2		36	59
Carabus maeander Fischer von Waldheim	±	M		1		4	58		17	39		2	121
Cr. nemoralis O.F. Müller*	-	G			9		127					2	138
Cr. serratus Say	±	Ob	36	3	6	2		24	8			5	84
Cr. sylvosus Say	-	F	10							3			13
Chlaenius emarginatus Say	+	F								1	5	1	7
Ch. impunctifrons Say	+	MFR				6							6
Ch. l. lithophilus Say	+	M				1							1
Ch. p. pennsylvanicus Say	+	M				1	1		1	1			4
Ch. p. purpuricollis Randall	+	Ob	13		115	6	8			7		125	274
Ch. s. sericeus (Forster)	+	MRMg			2	1	2	1					6
Ch. t. tomentosus (Say)	+	Ob			1							7	8
Ch. t. tricolor Dejean	+	MgOb	1			3	1						5
Cicindela denikei Brown	+	Ob		14	7								21
Ci. limbalis Klug	+	Ob		3							1	69	73
Ci. l. longilabris Say	+	Ob		9	3								12
Ci. p. purpurea Olivier	+	Ob	2		3					2	7	3	17
Ci. punctulata Olivier	+	Ob									4	2	6
Ci. sexguttata Fabr.	+	FMg					1			1	2		4
Clivina fossor (L.)*	±	Ob				1	5	15	3	2	1	32	59
Cyclotrachelus s. sodalis (LeConte)	-	Mg								12			12
Cymindis americanus Dejean	±	ObMg	1										1

TABLE 2. Continued

Species	Wings	Hab	Alvar site 1	2	3	4	5	6	7	8	9	10	Total
Cm. cribricollis Dejean	±	Ob	1					1					2
Cm. neglectus Haldeman	±	FOb	1		1		4		1		1		8
Cm. pilosus Say	±	Ob					2						2
Dicaelus teter Bonelli	-	F									1		1
Diplocheila obtusa (LeConte)	+	Ob	1		1	1	13	6		3		28	53
Dp. striatopunctata (LeConte)	+	M		1		8							9
Dromius piceus Dejean	+	F	1				1	1			1		4
Dyschirius globulosus (Say)	±	Ob	1		6	1	4	22	6	3	1	15	59
Elaphropus anceps (LeConte)	+	Ob					1	2	1	3		11	18
El. granarius (Dejean)	±	Ob			3		8			2		7	20
El. incurvus (Say)	+	Ob				2			1			2	5
Elaphrus clairvillei Kirby	+	M								1			1
Eu. fuliginosus Say	+	M								1			1
Galerita janus (Fabr.)	+	F					8	1					9
Harpalus affinis (Shrank)*	+	Mg					3	1					4
H. caliginosus (Fabr.)	+	MgOb		1									1
H. compar LeConte	+	Mg	9		4	4							17
H. erythropus Dejean	+	Mg					4			2		109	115
H. faunus Say	+	Mg	1		20	8	486					341	856
H. herbivagus Say	+	MgOb	3				18	1		1		7	30
H. indigens Casey	+	Ob										1	1
H. opacipennis (Haldeman)	+	ObMg	4	1	2			1					8
H. pensylvanicus (DeGeer)	+	Mg	7	1	2		45	4	1	5		45	110
H. plenalis Casey	+	MgOb		2			1	12	1		3		19
H. somnulentus Dejean	+	Mg	21		8	12	20	3	20	11	1	31	127
Lebia atriventris Say	+	Mg								1			1

TABLE 2. Continued

Species	Wings	Hab	Alvar site 1	2	3	4	5	6	7	8	9	10	Total
Le. fuscata Dejean	+	Mg		1			1						2
Le. moesta LeConte	+	Mg					1						1
Le. pumila Dejean	+	Mg		1				11			2		14
Le. viridis Say	+	Mg								1			1
Lophoglossus scrutator (LeConte)	+	M				5							5
Microlestes linearis (LeConte)	±	Ob					1						1
Myas cyanescens Dejean	-	F	3										3
Notiophilus aeneus (Herbst)	+	F			2								2
N. aquaticus (L.)	±	FOb						4					4
N. semistriatus Say	±	Ob	25	2									27
Oodes fluvialis LeConte	+	M							1				1
Ophonus puncticeps Stephens*	+	Mg	4		1	2		2	1				10
Patrobus longicornis (Say)	±	Mw		1			1						2
Platynus decentis (Say)	-	FR						1					1
Poecilus chalcites (Say)	+	MgOb					1	1				1	3
Po. l. lucublandus (Say)	+	MgOb	1	1	309	322	416	1	31	25	1	235	1342
Pterostichus caudicalis (Say)	+	M				2							2
Pt. commutabilis (Motschulsky)	+	Mg			22	26	22	2	17	21		74	184
Pt. coracinus (Newman)	-	F	63	329		1		5	11		1		410
Pt. corvinus (Dejean)	+	M				1	2						3
Pt. femoralis (Kirby)	±	Ob			1	34				22			57
Pt. lachrymosus (Newman)	-	F						2					2
Pt. luctuosus (Dejean)	+	M				23	4		2	1		3	33
Pt. melanarius (Illiger)*	±	G	5	24	43	138	1	3				2	216
Pt. mutus (Say)	+	MgF			1								1
Pt. novus Straneo	-	FObMg	294	33	108	2	22	86	35	16	2	107	705

TABLE 2. Continued

			Alvar site										
Species	**Wings**	**Hab**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**Total**
Pt. patruelis (Dejean)	±	M								3			3
Pt. pensylvanicus LeConte	+	F				1	2		1				4
Pt. tenuis (Casey)	+	M					1		7			1	9
Pt. tristis (Dejean)	-	F		1				1					2
Selenophorus gagatinus Dejean	+	Ob					2			2		24	28
Se. opalinus (LeConte)	+	Ob						1					1
Sphaeroderus c. canadensis Chaudoir	-	F									3		3
Sp. nitidicollis brevoorti LeConte	-	F	1										1
Sp. stenostomus lecontei Dejean	-	F	5			1		3	3			1	13
Stenolophus comma (Fabr.)	+	Ob	3										3
St. conjunctus (Say)	±	Ob			2	2	10			2	2	6	24
St. fuliginosus Dejean	+	M			1	1	2	1				1	6
St. ochropezus (Say)	+	M	2					1					3
Syntomus americanus (Dejean)	±	Ob	1		3	1		2			1		8
Synuchus impunctatus (Say)	±	ObF	39	2	7					1			49
Trechus apicalis Motschulsky	±	F						3					3
T. quadristriatus (Schrank)*	+	Ob	2		1	1		1	3				8
Total species			**41**	**21**	**44**	**52**	**67**	**47**	**39**	**56**	**23**	**57**	**142**
Introduced species			**3**	**1**	**5**	**4**	**5**	**5**	**3**	**2**	**1**	**4**	**9**
Percent introduced species			**7.3**	**4.8**	**11.4**	**7.7**	**7.4**	**10.6**	**7.7**	**3.6**	**4.3**	**7.0**	**6.3**
Total specimens			**703**	**478**	**1201**	**1156**	**1841**	**338**	**372**	**324**	**46**	**2188**	**8647**
Introduced specimens			**11**	**24**	**55**	**142**	**138**	**22**	**7**	**7**	**1**	**37**	**444**
Percent introduced specimens			**1.6**	**5.0**	**4.6**	**12.3**	**7.5**	**6.5**	**1.9**	**2.2**	**2.2**	**1.7**	**5.1**

(site 3), with 44 species and 1201 specimens. Species richness was lowest in the alvar shrubland (site 2, 21 species) although more specimens were collected in that site than in sites 6 (alvar pavement), 7 and 8 (alvar grasslands) (Table 2).

Dominant species

A total of 24 carabid species were collected in dominant numbers. Each site had between four and seven dominant carabid species (Table 3). Only two of the dominant species (*Poecilus l. lucublandus* (Say) and *Pterostichus novus* Straneo) were present at all sites (Table 3). *Poecilus l. lucublandus* was the most frequently collected species overall (1342 specimens, Table 2). *Agonum cupripenne* (Say) was dominant in five sites and present in all except one. *Calathus gregarius* (Say) was dominant in four sites. Of the remaining 20 species, five were dominant in two sites and 15 were dominant only in one. Eight different species ranked first in dominance at the nine sites analyzed (Table 3).

Estimates of species richness

Rarefied estimates of species richness are presented in Figure 2. Overall rarefaction curves (Fig. 2a) show that sampling was incomplete in several sites and additional carabid species remained undetected. Site 10 (alvar grassland, Smith Falls Plain) was the only site for which the accumulation of new species begins to level off (at about 1500-2000 specimens). Six of the sites (1, 3, 4, 5, 7, 10) have overlapping or similar richness based on the subsamples common to all sites (Fig. 2b; N = 300 specimens). These sites include the only alvar savanna sampled, one of the alvar pavements, and most alvar grasslands. Site 2 (alvar shrubland, Manitoulin Island) appears to be significantly less diverse than all other sites while site 8 (alvar grassland, Carden Plain) is the most species rich of all sites (Fig. 2b). The species richness of site 6 (alvar pavement, Bruce Peninsula) is slightly lower than at site 8 but greater than at all other sites.

Introduced species

Nine introduced European species were collected comprising 6.3% of the total species richness: *Agonum muelleri* (Herbst), *Amara familiaris* (Duftschmid), *Am. lunicollis* Schiødte, *Carabus nemoralis* O. F. Müller, *Clivina fossor* (L.), *Harpalus affinis* (Shrank), *Ophonus puncticeps* Stephens, *Pterostichus melanarius* (Illiger), and *Trechus quadristriatus* (Shrank). The number of introduced carabid species collected at each site (Table 2) ranged between one (sites 2 and 9) and five (sites 3, 5, 6). The two sites with the highest proportion of introduced species were sites 6 and 3, representing 10.6% and 11.4% of the species collected at those sites, respectively. Conversely, less than 5% of the carabid species collected on sites 2, 8 and 9 were introduced. Only three species (*Cr. nemoralis, Cl. fossor,* and *Pt. melanarius*) were represented by more than ten specimens (Table 2). There was no consistent pattern in the distribution of introduced species between sites.

For all sites combined, 5.1% of the specimens collected belonged to introduced species. The proportion of introduced species was highest at site 4 (12.3% of all specimens), whereas introduced species comprised less than 2.5% of all specimens at sites 1, 7, 8, 9, and 10 (Table 2).

TABLE 3. Dominant species of Carabidae collected in Ontario alvars. Site numbers correspond to those in Table 1. Dn = rank of dominant species at site (e.g. D1 = most dominant species at site); P - species present but not dominant at site * = introduced species.

	Alvar site									
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**10**	**Total**
Agonum cupripenne	P		D3	D4	D3	P	D1	D2	P	D4
Agonum nutans				D1	P		P	P	P	D6
Agonum rufipes					P		D4		P	
Amara pallipes				P	P			D4		
Amara pennsylvanica					P				D1	
Anisodactylus harrisii			P			D3	P	P	P	
Anisodactylus nigerrimus					P	P	P	P	D4	
Bembidion mimus				P	P	D2	P	P	P	
Calathus gregarius	D2	D2	D2	P	P		D6	P	P	D5
Carabus maeander		P		P	P		P	D1	P	
*Carabus nemoralis**			P		D4				P	
Carabus serratus	D5	P	P	P		D4	P		P	
Chlaenius p. purpuricollis	P		D4	P	P			P	D5	
Dyschirius globulosus	P		P	P	P	D5	P	P	P	
Harpalus erythropus					P			P	D6	
Harpalus faunus	P		P	P	D1				D2	D2
Harpalus somnulentus	P		P	P	P	P	D5	P	P	
Poecilus l. lucublandus	P	P	D1	D2	D2	P	D3	D3	D3	D1
Pterostichus commutabilis			P	P	P	P	P	D6	P	
Pterostichus coracinus	D3	D1		P		P	P			
Pterostichus femoralis			P	P				D5		
*Pterostichus melanarius**	P	D4	P	D3	P	P			P	
Pterostichus novus	D1	D3	D5	P	P	D1	D2	D7	P	D3
Synuchus impunctatus	D4	P	P					P		
Number of dominant species	**5**	**4**	**5**	**4**	**4**	**5**	**6**	**7**	**6**	**6**
Total number of species	**41**	**21**	**44**	**52**	**68**	**47**	**39**	**56**	**57**	**142**

Vagility

Fully developed hind wings are known in at least some specimens of 91% of the species collected (Table 2). Thirteen species are brachypterous (Table 2).

Habitat associations and geographic affinities

A large number of carabids have previously been associated with open, bare ground (50 species, Table 2). A similar number of species occur in grassy meadows (48 species). The third and fourth most common habitats are marshes and forests (37 and 25

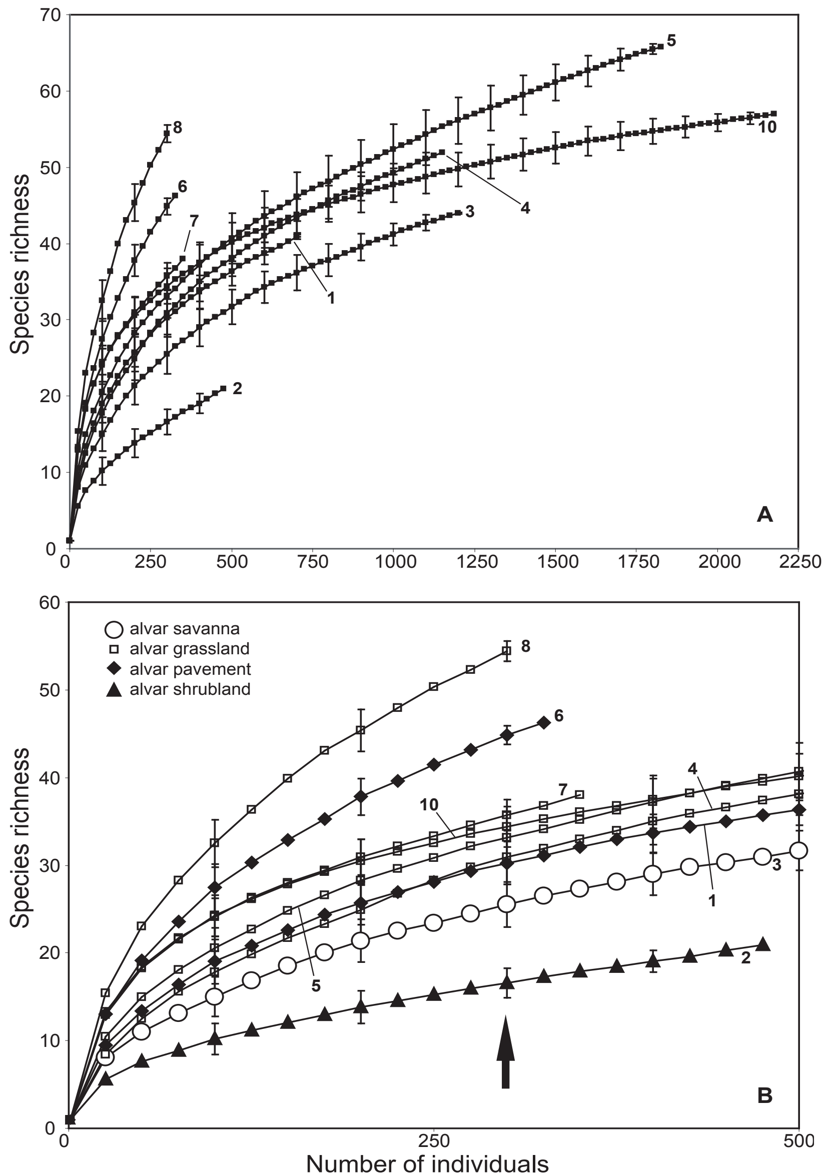

FIGURE 2. Rarefied estimate of species richness for ground beetles (Carabidae) sampled in nine Ontario alvar sites. Data points were plotted for every 25th specimen and measure of variance (± SD) for every 100th specimen. A) rarefaction including all specimens sampled; B) rarefaction based on first 500 specimens (arrow indicates subsample sizes for comparison of species richess). Sites are separated by alvar type.

species, respectively). Less than ten percent of the species occur in either riparian habitats, wet meadows, open wet sand, or are generalists in their habitat requirements.

Most of the species collected are widespread in North America, the rest are restricted to eastern North America. Some species are near the limits of their distribution in the study sites. Species such as *Agonum metallescens* (LeConte), *Amara lunicollis*, *Bradycellus lecontei* Csiki, *Cicindela l. longilabris* Say, and *Lebia moesta* LeConte are boreal species near the southern limit of their ranges. In contrast, species like *Brachinus tenuicollis* LeConte*, Carabus sylvosus, Cyclotrachelus s. sodalis, Cymindis americanus* Dejean*, Dicaelus teter*, *Lophoglossus scrutator* (LeConte)*,* and *Selenophorus opalinus* (LeConte) are southern or southeastern species near the northern limit of their ranges. Most of these species were collected in very low numbers. Of the above-mentioned species only three (*Ci. l. longilabris, Cr. sylvosus*, and *Cy. s. sodalis*) were represented by more than five specimens (Table 2).

All the species collected have previously been recorded in Ontario and few range extensions were noted. *Cicindela denikei* Brown was previously known only from a small area near the borders of Ontario, Manitoba, and Minnesota (Kaulbars and Freitag 1993; Freitag 1999). Manitoulin Island represents a significant southeastern extension of the known range and the species appears to be abundant in appropriate alvar sites on the island. We did not collect *Ci. denikei* in alvars on the mainland.

All of the introduced species are widespread in North America except *Ophonus puncticeps,* which is at the western edge of its North American range in Ontario, and *Trechus quadristriatus*, which is known in North America only from Quebec, Ontario, Michigan, and Wisconsin (Bousquet and Larochelle 1993).

Discussion

Species richness and abundance

The total number of carabid species recorded in each alvar site sampled ranged from 21 to 67. The lowest species richness occurred in the alvar shrubland of Manitoulin Island (site 2, Table 2). Approximately 65% of this site is covered with shrubs such as common juniper (*Juniper communis* L. Cupressaceae) whereas the rest is composed almost entirely of large blocks of limestone separated by narrow and deep cracks. This type of habitat can be compared to similar alvars with poor vegetation diversity in Sweden (Sylvén 1983). In Europe, this alvar type, although not as rich in carabid species as sites that are more diverse botanically, is thought to support a unique insect fauna and should not be discarded from a conservation point of view based on low species number (Coulianos and Sylvén 1983).

Carabid species richness was consistently higher in alvar grasslands, with most sites supporting more than 50 species each (Table 2). These results are comparable to those reported for European alvars (Coulianos and Sylvén 1983) where the highest number of arthropod species was recorded in sites with rich vegetation. Alvar pavement and alvar savanna sites were also species-rich with between 40 and 50 carabid species each.

Recent investigations of carabid diversity in different types of open habitats in northeastern North America have reported between 26 and 76 carabid species from a single site (Table 4). Additionally, Canadian agroecosystems typically support between 40 and 60 carabid species at a single site (Goulet 2003). The two alvar shrublands sampled during our study fall below the carabid species richness values recorded in other open habitats. On the other hand, alvar grasslands occupy the higher end of the scale of carabid species richness with more than 50 species. The alvar pavements as well as the alvar savanna support carabid species richness similar to that of typical agroecosystems.

Generally speaking, the more species-rich sites (grasslands, savanna, and pavements) support larger populations of ground beetles based on our trap catches. More than 1000 specimens were collected on sites 3, 4, and 5, and more than 2000 specimens at site 10 (Table 2). However, carabid abundance was not closely correlated with species richness in all sites. For example, the species-rich alvars at Miller Lake (site 6) and Dalrymple (site 8) supported comparatively very low numbers of specimens (less than 400 each).

Dominant species

Species such as *Poecilus l. lucublandus* and *Pterostichus novus* were dominant in several sites and present in all alvars sampled. Whereas *Po. l. lucublandus* is a species commonly encountered in grassy meadows throughout its range (Lindroth 1966; Tyler and Ellis 1979; Levesque and Levesque 1987, 1994; Boivin and Hance 1994; Byers et al. 2000), the presence of *Pt. novus* in Ontario alvars in such numbers was not expected. The latter species has been collected in high numbers in different types of forests outside of Ontario (e.g. Snider and Snider 1986; Epstein and Kulman 1990). The numerous captures of this species in southern Ontario alvars (> 700 specimens) indicate that this species is closely associated with this type of habitat (Bouchard et al. 1998). Three species (*Agonum cupripenne*, *Dyschirius globulosus*, and *Harpalus somnulentus*) were recorded in dominant numbers in some alvars and were present in all sites except for the alvar shrubland on Manitoulin Island (Table 3). As mentioned above, the alvar shrublands support the lowest carabid beetle species richness of all alvars sampled. The harsh microclimatic conditions in alvar shrublands seem to be an important factor in excluding certain species found commonly in all other sites sampled.

Five dominant species were collected only in alvar grasslands: *Agonum nutans*, *Ag. rufipes*, *Amara pallipes*, *Am. pennsylvanica*, and *Harpalus erythropus*. Of these, *Ag. nutans* was the most numerous carabid in the alvar grassland of Manitoulin Island and was the only species present in all other alvar grasslands. Although widespread in North America, most of the specimens of *Ag. nutans* recorded in Canada prior to this study were from the shore of Lake Erie (Lindroth 1966). Based on the uncommon catches of this species outside of alvars in Ontario, it now appears that *Ag. nutans* is very closely associated with alvar grasslands in the province (Bouchard et al. 1998). The presence of *Carabus serratus* in dominant numbers only in alvar pavements is also noteworthy. This species, although collected in small numbers in other alvar types, seems to prefer sites with moss or lichen-covered, flat limestone with sparse grasses and shrubs growing in cracks.

Some species of dominant ground beetles were either only recorded in or only dominant in the two alvars of eastern Ontario (*Amara pennsylvanica* and *Harpalus faunus*). Other species such as *Pterostichus coracinus* and *Pt. melanarius* were collected in dominant numbers only in alvars of Manitoulin Island. These observations indicate that the ground beetle community of Ontario alvars can also be influenced by regional assemblages.

TABLE 4. Recent studies on carabid fauna in open habitats in northeastern North America. a = old plants; b = young plants; NY = New York; PA = Pennsylvania; QC = Quebec; VM = Vermont. All studies used pitfall traps to collect the carabid fauna.

	Levesque & Levesque (1987)	Boivin & Hance (1994)	Levesque & Levesque (1994)	Levesque & Levesque (1994)	Byers et al. (2000)	Byers et al. (2000)	Byers et al. (2000)
Habitat	Meadow	Carrot field & field edges	Raspberry[a] plantation	Raspberry[b] plantation	Pasture	Pasture	Pasture
Province or state	QC	QC	QC	QC	PA	NY	VM
Number localities sampled	1	1	1	1	5	3	3
Total species	26	76	45	32	85	40	54
Introduced species	4	5	10	7	6	10	13
Percent introduced species	15.4	6.6	22.2	21.9	7.1	25.0	24.1
Total specimens	1127	7700	5375	3806	4365	618	1366
Introduced specimens	113	2266	4493	3085	2653	334	792
Percent introduced specimens	10.0	29.4	83.6	81.1	60.8	54.0	58.0

Estimates of species richness

The majority of alvar sites sampled in this study have overlapping or similar rarefaction curves when estimates are standardized to sampling effort (Fig. 2b). The two major exceptions to this trend are sites 2 and 8. Site 2 (the only alvar shrubland included in the analysis) is significantly less diverse than all other sites. This result is consistent with studies on Swedish alvars (Coulianos and Sylvén 1983) and is thought to reflect the lower microhabitat diversity available to ground beetles in alvar shrublands. Site 8 (alvar grassland, Carden Plain) is the most species-rich alvar sampled. The high number of singletons (N=22) and doubletons (N=11) in this site, combined with the low number of specimens (N=324) result in a rarefaction curve that show no signs of leveling off (Fig. 2a).

Introduced species

Of the approximately 470 species of ground beetles that occur in eastern Canada, 41 (8.7%) are introduced European species that have become established predominantly in disturbed ecosystems. Although the number of introduced carabid species in disturbed sites may represent a small proportion of the overall species richness (when compared to native species), these species can often dominate trap catches (Goulet 2003).

The number of introduced ground beetle species in the sampled Ontario alvars ranged between one, in the alvar shrubland sites, and five, in sites on Manitoulin Island, the Napanee Plain and the Bruce Peninsula, respectively (Table 2). The number of introduced species recorded in other recent studies on the carabid fauna of various open habitats in eastern North America ranged between 4 and 13 (Table 4). The alvar shrublands in Ontario, as for similar alvars in Sweden (Coulianos and Sylvén 1983), can be considered relatively undisturbed by human activity. This hypothesis is supported the current study by the very low number of introduced species that have invaded these harsh habitats. The alvar sites with four or five introduced species are usually sites with rich vegetation that have been used in the past as pastures for farm animals (e.g. alvar savanna and alvar grassland on Manitoulin Island).

Ground beetle communities, such as those recorded by Levesque and Levesque (1994) in raspberry plantations, can be composed of more than 80% introduced species in some sites. The overall percentage of introduced specimens in the Ontario alvars was low in most sites with values below 5% (Table 2). The site with the greater percentage of introduced specimens was the alvar grassland of Manitoulin Island (12.3%), a site that has been used in the past for grazing. Even with a value of more than 12%, the alvar grassland of Manitoulin Island supports what can be considered a relatively undisturbed ground beetle community when compared to those reported in other studies (Table 4).

Vagility

The majority of ground beetles collected in Ontario alvars have the ability to fly at some stage during their life cycle. Of the thirteen brachypterous species recorded during our study, only three occur in dominant numbers in at least one site (*Carabus nemoralis*, *Pterostichus coracinus*, and *Pt. novus*). *Carabus nemoralis* is an introduced species that has a large population in the alvar grassland of the Napanee Plain. *Pterostichus coracinus* occurs in large numbers on the alvar pavement and alvar shrubland on Manitoulin Island. Because alvar pavement sites on Manitoulin Island are now preserved, and because this species has close associations with forested areas neighboring alvar sites, its survival on the island seems secure. *Pterostichus novus*, however, is closely associated with alvars in southern Ontario (Bouchard et al. 1998) and the reduced dispersal ability of this species could pose a threat to local populations in certain areas.

Habitat associations and geographic affinities

Given the nature of alvars, it is reasonable to predict that the carabid fauna would be dominated by species associated with open dry habitats. Because of the occurrence of spring flooding and the frequent persistence of temporary pools in many of the sites, hygrophilous species would be expected to comprise another important component of the fauna. Forest species and those associated with riparian habitats would be expected in lower numbers, usually as a result of movement from adjacent suitable habitats that border or surround many of the alvar sites.

These predictions were largely confirmed by our results (Table 2). More than thirty percent of all species are known to occur in open bare ground or grassy meadows throughout their North American range (e.g. *Amara* spp.). Nineteen of the twenty-four dominant species in Table 3 (79.2%) typically occur in dry open habitats or grassy meadows. The presence of seasonal flooding has a major influence on the ground beetle communities of most alvars, with 26% of all species recorded being associated with marsh habitats (e.g. some *Agonum* spp.). Populations of *Ag. nutans*, a species rarely collected in Ontario which seems closely associated with alvar grasslands, are thought to increase with the presence of small bodies of water in those habitats (Bouchard et al. 1998). *Bembidion mimus* and *Carabus meander* are typically associated with wet habitats throughout their ranges and are found in dominant numbers in one Ontario alvar site each (Table 3). Forest ground beetles make up a lesser component of the alvar fauna (18% of all species). Most of the forest species were collected in small numbers except for *Pterostichus coracinus* which was found in dominant numbers at two sites on Manitoulin Island. Both sites are surrounded by forests. Ground beetles known to occur in riparian habitats, open wet sand, and wet meadows make up only a small percentage of the Ontario alvar communities.

The Carabidae, dominated by widespread and eastern Nearctic species, do not show the same geographic pattern as the plants. The flora of Ontario alvars consists of a combination of southern, northern, and western species, along with some endemic species (Catling and Brownell 1995). The presence of boreal and western plant species probably resulted from range expansion of this flora in periglacial communities along the front of the continental ice sheet. Following glacial retreat, relict populations remained in suitable open habitats such as alvars. The southern flora probably colonized alvars later, during the expansion of prairie communities in the Hypsithermal (Catling and Brownell 1995). The presence of western carabid species such as *Chlaenius p. purpuricollis* in Great Lakes alvars probably results from the existence of more continuous prairie habitat during the Hypsithermal. This pattern is also seen in the distribution of several species of leafhoppers (Homoptera: Cicadellidae) (Bouchard et al. 2001).

Most ground beetles are generalized predators, and their patterns of distribution and habitat association are generally associated with climatic and physical features of the habitat rather than the distribution of prey species or plant communities (Campbell et al. 1979). As a result, close correspondence between geographic or habitat affinities of carabids and plants was not expected in this study. Nevertheless, a small number of species showed notable patterns of distribution.

Agonum nutans, *Chlaenius p. purpuricollis*, and *Pterostichus novus* were all dominant in this study and have rarely been collected in Ontario except in alvars. Because of this, Bouchard et al. (1998) considered them alvar-associated species in the region. However, all three have been collected in other habitats outside of Ontario.

Agonum nutans was present in all the alvar grasslands, but was dominant in only one. It was not collected in other alvar types. Based on the few published records of this species, Bouchard et al. (1998) considered *Ag. nutans* associated with open grassy areas in the Great Lakes region.

Pterostichus novus was collected at all alvar sites, and was one of the most dominant species. Although it is apparently associated with alvars in Ontario (Bouchard et al. 1998), many specimens have been collected in a range of habitats including upland and mesic deciduous forests and mesic old fields in Michigan and Minnesota (Snider and Snider 1986; Epstein and Kulman 1990). Because of variation in habitat use, phenology, and morphological characters throughout its range, Bouchard et al. (1998) suggested that *Pt. novus* may represent a complex of species.

Chlaenius purpuricollis purpuricollis was collected in six of the sites and was dominant in two. The main range of *Ch. p. purpuricollis* extends over the prairie ecotone and they are found in well drained, open grasslands. In Ontario it has been recorded only from alvars.

Cicindela denikei has a restricted range in northwestern Ontario, southeastern Manitoba, and northeastern Minnesota and is associated with dry open substrates, usually near forest stands (Kaulbars and Freitag 1993). The Manitoulin Island population is apparently disjunct from the western population and given its apparent habitat preferences, *Ci. denikei* may be restricted to alvars in Ontario.

The major obstacle to characterizing the carabid community of the Great Lakes alvars is the lack of similar studies on native, open habitats other than alvars in the region. If the dominant species identified in this study are also dominant elsewhere in the region, it may be in habitats such as savannas, tallgrass prairie outliers, or sand beach and dune ecosystems. Comprehensive inventories of Carabidae using standardized sampling programs should be undertaken in more of those habitats in order to establish the distribution, abundance, and habitat preferences of "alvar" carabids in the Great Lakes region.

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