Diversity and seasonal density of carabid beetles (Coleoptera: Carabidae) in relation to the soybean aphid in soybean crop in Québec, Canada

Annabelle Firlej,[1] Annie-Ève Gagnon, Simon Laurin-Lemay, Jacques Brodeur

Abstract—We studied the diversity and summer seasonal activity-density of Carabidae associated with soybean fields infested by the soybean aphid (*Aphis glycines* Matsumura; Hemiptera: Aphididae) in Québec, Canada. Carabid beetles were sampled in six to seven fields from June to September 2004 and 2005 using pitfall traps. A total of 33 species from 15 genera were identified, with the exotic *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae), representing 75.8% and 84.5% of all individuals trapped in 2004 and 2005, respectively. Large variations in species richness and diversity indexes were observed between fields within and between years. Multivariate analyses showed that carabid activity-density varied as a function of field location and sampling period, with individuals belonging to species overwintering as adults being more abundant early in the growing season. There was no relationship between carabid trap catches and *A. glycines* density, suggesting that carabid beetles do not respond numerically to soybean aphid populations at the spatial scale studied.

Résumé—Nous avons étudié la diversité et l'activité densité-dépendante de Carabidae présents dans des champs de soya infestés par le puceron du soya (*Aphis glycines* Matsumura; Hemiptera: Aphididae) en saison estivale au Québec, Canada. Les carabes ont été échantillonnés dans 6–7 champs de juin à septembre 2004 et 2005 en utilisant des pièges fosses. Un total de 33 espèces appartenant à 15 genres ont été identifiés, avec l'espèce exotique *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) représentant 75.8% et 84.5% de tous les individus capturés en 2004 et 2005 respectivement. De grandes variations dans la richesse spécifique et les indices de diversité ont été observées entre les champs, dans et entre les années. Des analyses multivariées ont montré que l'activité densité-dépendante des carabes varie en fonction de la localité du champ et de la période d'échantillonnage, avec des individus qui appartiennent aux espèces diapausantes sous forme adulte plus abondants en début de saison. Il n'y a pas de relation entre les captures de carabes dans les pièges et la densité de *A. glycines* dans les champs: ceci suggère que les carabes ne répondent pas numériquement aux populations de pucerons du soya à l'échelle spatiale étudiée.

Introduction

Carabid beetles (Coleoptera: Carabidae) represent a large and diverse group of generalist predators, with more than 40 000 described species (Capinera 2008). Their diversity and abundance depend mainly on food resources, habitat type/structure, and farming practices (Symondson *et al.* 1996; Kromp 1999; Menalled *et al.* 1999). Carabids are ubiquitous in arable lands and can significantly reduce populations of crop pests (Kromp 1999; Menalled *et al.* 1999; Symondson *et al.* 2002; Lang 2003). For instance, their role as biological control agents of cereal aphids has been documented in grain fields in Europe, where control of aphid populations occurs mainly early in the season (reviewed by Kromp 1999). Some carabid species can be particularly voracious, consuming aphids that fall off plants or climbing onto the plant to catch their prey (Chiverton 1988; Winder 1990; Losey and Denno 1998). Most carabids are ground dwelling and forage nocturnally; their contribution

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A. Firlej,[1] S. Laurin-Lemay, J. Brodeur, Institut de Recherche en Biologie Végétale, Université de Montréal, 4101 rue Sherbrooke est, Montréal, Québec H1X 2B2, Canada
A.-È. Gagnon, Département de phytologie, Université Laval, 2480 Boul. Hochelaga, Québec, Québec G1 V 0A6, Canada

[1] Corresponding author (e-mail: annabelle.firlej@gmail.com).

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as biological control agents is often considered complementary to that of diurnal foliar predators (Losey and Denno 1998, 1999; Grez *et al.* 2007).

Since its invasion of North America in 2000, the soybean aphid, *Aphis glycines* Matsamura (Homoptera: Aphididae), has become the most important pest species in soybean fields (Ragsdale *et al.* 2011). Large populations of *A. glycines* can reduce soybean yield and generate additional economic and environmental costs through insecticide applications (Ragsdale *et al.* 2006). Much work has been done on the identity and impact of natural enemies of this invasive pest throughout infested regions (Brown *et al.* 2003; Fox *et al.* 2004; Rutledge *et al.* 2004, Rutledge and O'Neil 2005; Costamagna and Landis 2006). In Québec, Canada, the community of generalist foliar predators, both indigenous and naturalised, is dominated by four species of Coccinellidae (Coleoptera) (Mignault *et al.* 2006) and exerts top-down control of *A. glycines* populations (Rhainds *et al.* 2007). Assemblages of ground arthropod predators, mostly carabid beetles in association with *A. glycines* populations, were studied in soybean fields in Illinois (United States of America) (Rutledge *et al.* 2004) and New York (United States of America) (Hajek *et al.* 2007). According to Hajek *et al.* (2007), carabid beetles likely contribute to a reduction in soybean aphid populations since negative correlations between carabid and aphid densities are found.

The objectives of this study were (1) to characterise the species diversity and the summer seasonal activity-density of carabid beetles associated with soybean fields infested by *A. glycines* in Québec and (2) to investigate how time (sampling date), space (field location), and food resource (*A. glycines* density) influence carabid assemblages.

Methods

Field survey

The study was conducted in commercial soybean fields in Québec (Canada) in 2004 and 2005. Carabids were sampled in six fields from 14 June to 7 September (13 weeks) in 2004 and in seven fields from 30 June to 24 August (5 weeks) in 2005. Fields in 2004 were in Nicolet-Sud, St-Augustin-de-Dermaures, Maskinongé, Hérouxville, St-Mathias-sur-Richelieu, and St-Denis-sur-Richelieu. Another sampling site, St-Constant, was added in 2005. Fields differed in their planting dates (from early May to early June) and followed commercial agricultural practices. In both years, carabid sampling started prior to the arrival of *A. glycines* to soybean fields.

Carabid beetles were sampled using pitfall traps (12 per field). Traps consisted of a plastic container with a top diameter of 10 cm and a depth of 7 cm buried in the soil such that the top of the trap was at ground level. Four traps were placed on three rows 10 m away from each other and 10 m away from field margins. Traps on a same row were separated by 10 m from each other. Rows were aligned perpendicular to the proximate road. In 2004, traps were filled with a solution of ethylene glycol and water (1:1) rather than with alcohol because the content of the traps was collected once a week and alcohol would have evaporated. Because overcrowding occurred in traps in 2004, sampling in 2005 was conducted once every 2 weeks and traps were left open only for 24 hours. These traps were filled with 70% alcohol. Samples were returned to the laboratory and Carabidae adults were identified to species using the key in Larochelle (1976). Identifications were confirmed by the Laboratoire de Diagnostic en Phytoprotection (Ministère de l'Agriculture des Pêcheries et de l'Alimentation du Québec, Québec, Canada). Specimens have been deposited at the Collection d'insectes du Québec, Sainte-Foy (Québec), Canada. The abundance of each species used in statistical analyses (multivariate analysis of variance [MANOVA]) was calculated as the number of individuals per trap over 24 hours for each week sampled.

Aphis glycines populations were estimated in parallel with carabid sampling throughout the season. All aphids on five plants were counted at 10 stations; stations were separated by approximately 100 m along a zigzag transect in the same field but not within the carabid sampling zone to avoid disturbance (Roy and Mignault 2003). Aphid density was calculated as the mean number of *A. glycines* per plant (±SE) per week of sampling. Aphids were identified using Mignault and Roy (2003).

Statistical analyses

Total carabid abundance was calculated for each field sampled in 2004 and 2005 and species richness was calculated for pooled data (all fields combined) for each year. We used rarefaction curves to evaluate species richness per field in both years. Individual-based rarefaction analysis provides an estimate of community richness by showing the accumulation of expected species richness as a function of individuals sampled (Gotelli and Colwell 2001). This method can be used to compare sampling sites with different sampling efforts and is complementary to traditional diversity indexes, which can provide inconsistent results (Buddle *et al*. 2005). In our study, we relied on rarefaction curves to determine if we collected enough samples to characterise carabid assemblages in soybean fields. Total abundance of each carabid species over the weeks of sampling in both years were used to calculate expected species richness values with EcoSim 7.72 (on a base of 1000 permutations) (Gotelli and Entsminger 2009).

For all further analyses, we used data from only 11 weeks of sampling in 2004 because two fields (St-Mathias-sur-Richelieu and St-Denis-sur-Richelieu) were sampled during 11 weeks from 21 June to 2 September 2004. We also selected the nine dominant carabid species in both 2004 and 2005. Data used for analysis were the standardised abundance calculated as the number of individuals per trap over 24 hours for each sampling period.

MANOVA without replication (Model 3) was used to test for the influence of space (field sampled) and time (sampling date) as well as their interactions on carabid assemblages. We used the space–time interaction (STI) function in the principal coordinates of neighbour matrices package (http://sites.google.com/site/miquelde-caceres/software) before conducting further multivariate analyses (Legendre *et al*. 2010) to test STI. Because data from 2004 to 2005 were not compared with each other, we performed distinct multivariate analyses by pooling numbers of carabid individuals from the six fields sampled during each of the 11 sampling weeks in 2004 and from the seven fields sampled during 5 weeks in 2005. Prior to the analyses, species data were transformed with the Hellinger distance adapted for the analysis of community composition (Legendre and Gallagher 2001). To visualise the interaction between time and space variables within a year, data were analysed by K-means partitioning (Legendre *et al*. 2010) using the cascade KM function of the vegan package (Oksanen *et al*. 2007) in the R statistical language. K-means partitioning is used to identify interactions between time and space among sampling sites. We used the simple structure index rather than Calinski index, to identify the best number of clusters with a minimum of variance (Legendre *et al*. 2010): the index was maximal for six groups in 2004 and for four groups in 2005. The spatiotemporal representations of the partitioning only include the nine most abundant carabid species in both years (see Table 1 for species).

We conducted a partial canonical redundancy analysis (RDA) to examine the relative contribution of the time variable (sampling date) for the nine most abundant species for each year. Species with more than four individuals collected over the 2005 season were considered as dominant. We removed the confounding effects of the space variable and the STI since they were significant factors in the MANOVA analysis for both years (see Table 2). Finally, to obtain the relative contribution of each variable to carabid species activity-density, we partitioned the explained variation by including time, space, and *A. glycines* density for each year (Peres-Neto *et al*. 2006) with the varparts function of the vegan package (Oksanen *et al*. 2007) in the R statistical language.

Results

Carabid species diversity and abundance

We collected 26 208 adult carabid specimens in 2004 from 31 different species and 4591 specimens in 2005 from 19 species (Table 1). Out of the combined total of 33 species from 15 genera, six species are non-native: *Pterostichus melanarius* (Illiger), *Clivina fossor* (Linnaeus), *Harpalus rufipes* (De Geer), *Harpalus affinis* (Schrank), *Agonum muelleri* (Herbst), and *Amara aulica* (Panzer). *Pterostichus melanarius* numerically dominated the carabid assemblage in soybean, making up 75.8% and 84.5% of the total individuals in 2004 and 2005, respectively (Table 1). Rarefaction curves in 2004 reached asymptotes in the six fields, indicating that our sampling effort was sufficient to characterise the entire carabid assemblage (Fig. 1A and 1B). In contrast, rarefaction curves in 2005 suggest

Table 1. List of carabid beetle species and number of individuals collected in soybean fields in 2004 and 2005 in Québec, Canada.

		2004		2005	
	Abbreviation	Abundance	Proportion	Abundance	Proportion
Pterostichus melanarius (Illiger)*,†	Ptemel	19 888	0.754	3880	0.845
Poecilius lucublandus (Say)*	Poeluc	2852	0.109	71	0.015
Poecilius chalcites (Say)*	Poecha	912	0.035	213	0.046
Clivina fossor (Linnaeus)*,†	Clifos	512	0.02	22	0.005
Notiobia terminata (Say)*	Notter	509	0.019	37	0.8
Anisodactylus sanctaecrucis (Fabricius)*	Anisan	407	0.016	29	0.006
Bembidion quadrimaculatum oppositum (Say)*	Bemqua	399	0.015	101	0.022
Harpalus rufipes (De Geer)*,†	Harruf	326	0.012	150	0.033
Agonum cupripenne (Say)*	Agocup	164	0.006	68	0.015
Harpalus affinis (Schrank)†	Haraff	53	0.002	1	0
Chlaenius sericeus (Forster)	Chlser	33	0.001	3	0.001
Bembidion incrematum (LeConte)	Beminc	29	0.001	0	0
Blemus discus (Fabricius)	Bledis	29	0.001	1	0
Agonum muelleri (Herbst)†	Agomue	28	0.001	1	0
Stenolophus comma (Fabricius)	Stecom	12	0	4	0.001
Amara aenea (De Geer)	Amaaen	12	0	1	0
Syntomus americanus (Dejean)	Syname	11	0	0	0
Amara littoralis (Mannerheim)	Amalit	6	0	0	0
Harpalus pensylvanicus (De Geer)	Harpen	5	0	0	0
Clivina collaris (Herbst)	Clicol	3	0	2	0
Amara obesa (Say)	Amaobe	3	0	3	0.001
Patrobus longicornis (Say)	Patlon	3	0	0	0
Bembidion nitidum (Kirby)	Bemnit	2	0	0	0
Chlaenius lithophilus lithophilus (Say)	Chllit	2	0	0	0
Chlaenius pennsylvanicus pensylvanicus (Say)	Chlpen	2	0	0	0
Dyschirius sphaericollis (Say)	Dyssph	1	0	0	0
Harpalus herbivagus (Say)	Harher	1	0	0	0
Amara impuncticollis (Say)	Amaimp	1	0	0	0
Chlaenius impunctifrons (Say)	Chlimp	1	0	0	0
Amara aulica (Panzer)†	Amaaul	1	0	0	0
Harpalus bicolor (Fabricius)	Harbic	1	0	0	0
Synuchus impunctatus (Say)	Synimp	0	0	1	0
Agonum placidum (Say)	Agopla	0	0	3	0.001
Total		26 208	1	4591	1

*Indicates dominant species used for multivariate and partial canonical redundancy analysis.
† Indicates species not native to North America.

that too few individuals were collected to adequately describe carabid community composition in three fields (SMR, SDR, and HER; Fig. 1C). Then, we observed a large variation in species richness among fields within and between years. The total species richness was consistently greater in 2004 (31 species) than in 2005 (19 species).

Carabid assemblage composition in relation to time, space, and *A. glycines* density

The MANOVA revealed that variation in carabid activity-density is influenced by time and space factors and that both interact (Table 2), hence, sites of sampling varied each other independently. To illustrate this interaction pattern, the

Fig. 1. Rarefaction curves for the soybean fields sampled for carabid species diversity in 2004 and 2005. Curves result from plotting the expected number of species as a function of the number of individuals for fields in 2004 having fewer (A) and more (B) than 1200 individuals sampled and in fields in 2005 having fewer (C) and more (D) than 500 individuals sampled duals sampled. Field locations: NIS = Nicolet Sud, SAU = St-Augustin-de-Desmaures, MAS = Maskinongé, HER = Hérouxville, SMR = St-Mathias-sur-Richelieu, SDR = St-Denis-sur-Richelieu, SCO = St-Constant.

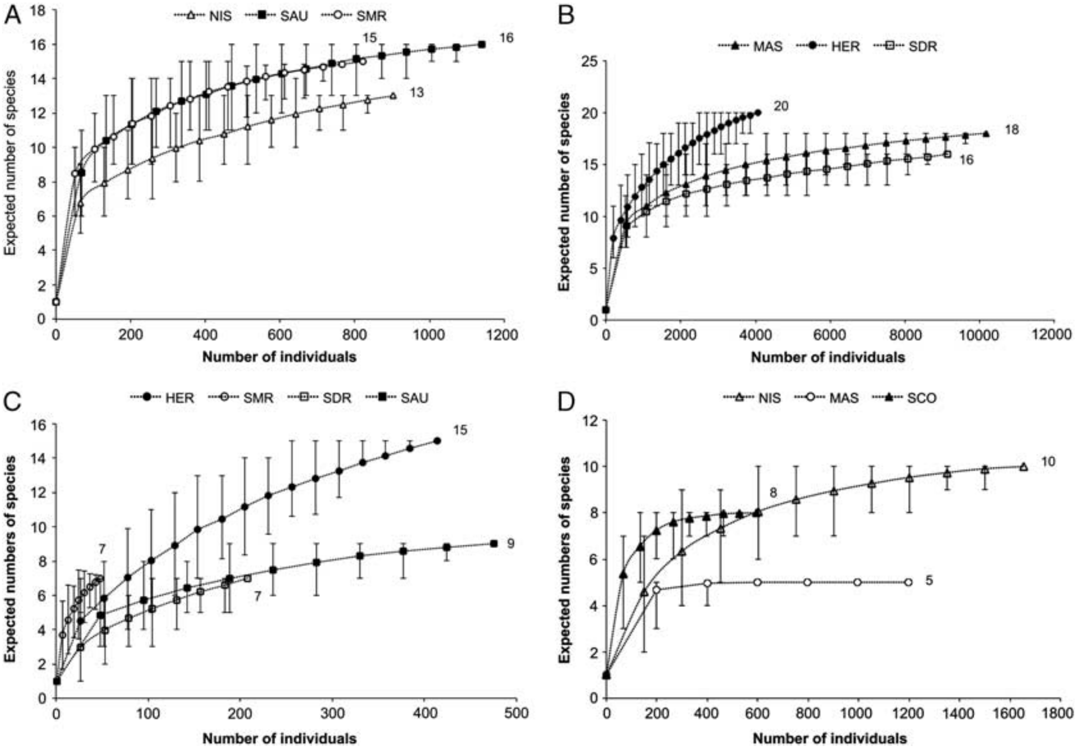


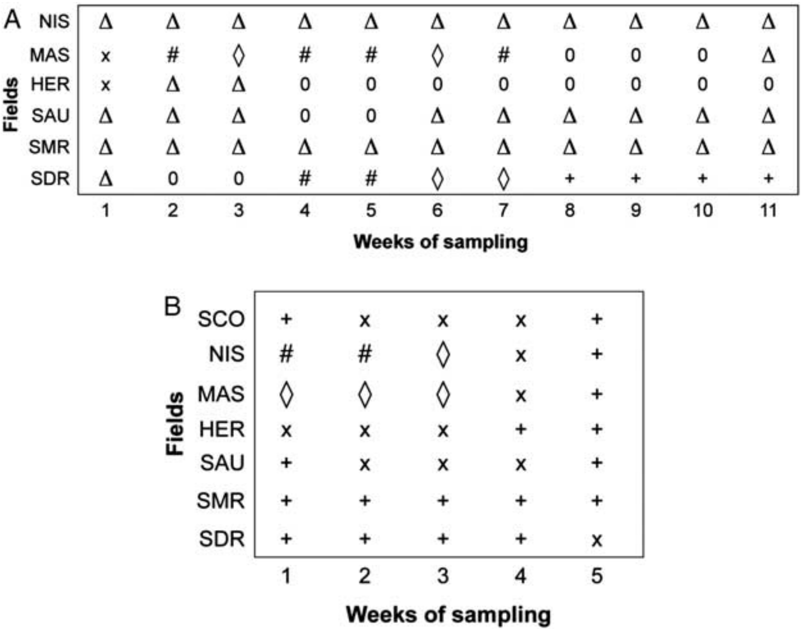
Table 2. Multivariate analysis of variance results on the effect of time (sampling date), space (field), and the time × space interaction on activity-density of the nine most abundant carabid beetles.

Year	Variable	R^2	F	df	P-value
2004	Time	0.106	15.90	5	0.001
	Space	0.448	32.29	5	0.001
	Time ×Space	0.246	3.54	25	0.001
2005	Time	0.106	6.11	2	0.001
	Space	0.523	10.01	6	0.001
	Time × Space	0.247	2.36	12	0.001

K-means partitioning in Fig. 2A and 2B show the variation in carabid activity-density (nine most abundant species) between fields and sampling dates for both years. In 2004, some fields (NIS, HER, SAU, and SMR) were relatively consistent in their number of specimens collected throughout the sampling period (dominance of Δ and 0), but other fields (MAS and SDR) showed large variations (community changes in five different groups) (Fig. 2A). In 2005, fields SCO, HER, SAU, SDR, and SMR only showed variations between two levels of abundance (dominance of X and +), whereas NIS, and MAS showed large variations throughout the summer season (from 3 to 4 groups) (Fig. 2B).

The effect of the time variable on carabid activity-density was significant in 2004 (RDA; $F = 17.403$, $P = 0.001$) but not in 2005 ($F = 2.81$, $P = 0.115$). The sampling period explained 16.22% of the carabid activity-density variation observed in 2004. Six carabid species (*Poecilius lucublandus*, *Poecilius chalcites*, *Anisodactylus sanctaecrucis*, *C. fossor*, *Agonum cupripenne*, and *Bembidion quadrimaculatum oppositum*) appear

Fig. 2. Spatiotemporal representation showing the K-means partitioning of the six fields sampled (A) in 2004 and (B) seven fields in 2005 as a function of sample week into six groups of observations.



A

Fields	1	2	3	4	5	6	7	8	9	10	11
NIS	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ
MAS	x	#	◊	#	#	◊	#	0	0	0	Δ
HER	x	Δ	Δ	0	0	0	0	0	0	0	0
SAU	Δ	Δ	Δ	0	0	Δ	Δ	Δ	Δ	Δ	Δ
SMR	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ	Δ
SDR	Δ	0	0	#	#	◊	◊	+	+	+	+

Weeks of sampling

B

Fields	1	2	3	4	5
SCO	+	x	x	x	+
NIS	#	#	◊	x	+
MAS	◊	◊	◊	x	+
HER	x	x	x	+	+
SAU	+	x	x	x	+
SMR	+	+	+	+	+
SDR	+	+	+	+	x

Weeks of sampling

in the fields early in the summer season while the three others (*P. melanarius*, *Notiobia terminata*, and *H. rufipes*) became common later in the mid-summer season (RDA; Fig. 3). In 2004, carabid activity-density was strongly influenced by space (0.41) and time (0.23), but not by aphid density (0) (Fig. 4A). In 2005, carabid activity-density was also strongly influenced by space (0.39), but not by time (0.06) or aphid density (0) (Fig. 4B).

Figs. 5 and 6 show summer seasonal variations in *A. glycines* density in 2004 and 2005 in relation to the activity-density of the nine most common carabid species with a focus on *P. melanarius*. Patterns of activity-density response were similar for the nine carabid species and *P. melanarius*, as expected from the dominance of *P. melanarius* in carabid assemblages. Population activity-density patterns differed greatly between carabids/*P. melanarius* and *A. glycines*, with predators reaching their maximal activity-density in late July, just when aphid populations started to increase (Figs. 5 and 6). In 2004, aphid populations were maximal in mid-August, when carabid populations had decreased to half their maximum activity-density (Fig. 5).

Discussion

Carabid assemblage in Québec soybean fields

The diversity of carabid species observed in Québec soybean fields is similar to those previously reported in Michigan (United States of America) (Rutledge *et al.* 2004) and New York (United States of America) (Hajek *et al.* 2007). In 2004, we collected from 13 to 20 different species per field for a total of 31 species, with a clear dominance of *P. melanarius* in all fields. In comparison, Rutledge *et al.* (2004) observed between 21 and 29 species per field and year in Michigan, with *Agonum placidum* (Say) or *Clivina impressifrons* LeConte being the most common. In New York, Hajek *et al.* (2007) collected from 11 to 35 species per field, with *A. muelleri* (Herbst) being the dominant species. Differences in sampling methods between studies may account for a bias in the dominant species observed. Work *et al.* (2002) showed that pitfall traps of small diameter preferentially trap smaller species. Rutledge *et al.* (2004) used pitfall traps of 8.5 cm in diameter, which are likely to have preferentially trapped smaller species such as

Fig. 3. Redundancy analysis (RDA) biplot depicting relationships between the nine dominant carabid species (black vector) and the time variable (black arrow) (RDA result: $F = 17.403$, $P = 0.001$, $R^2 = 16.22\%$). Numbers represent the sample week for a given field. See Table 1 for carabid species abbreviations.

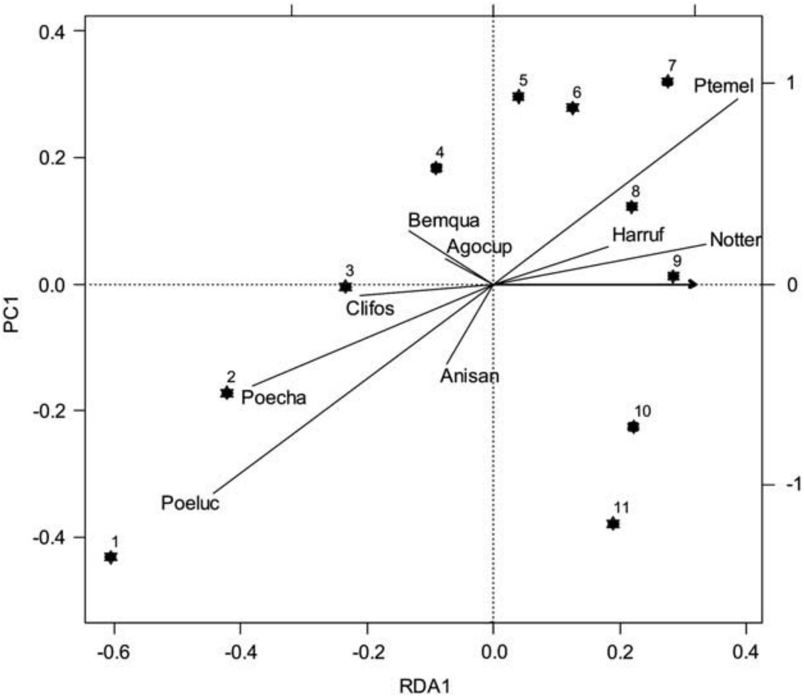
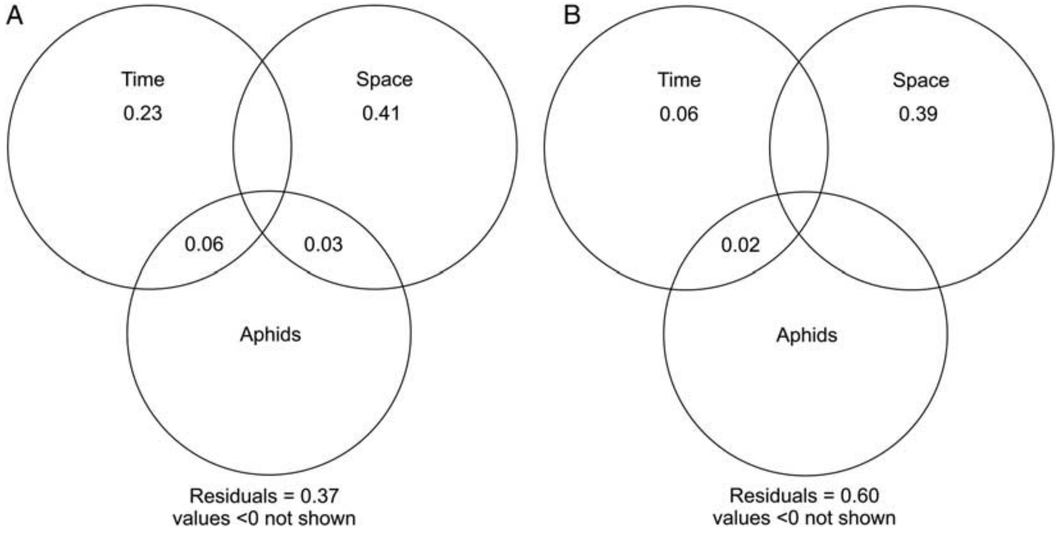


Fig. 4. Variation partitioning diagrams representing the contribution of time, space, and *A. glycines* density to the activity-density of the nine dominant carabid species in (A) 2004 and (B) 2005.



C. impressifrons (5.9–7.0 mm) and *A. placidum* (6.9–8.8 mm). The large pitfall traps used by Hajek *et al.* (2007) (11.5 cm) and in our study (10 cm) are better designed to catch bigger individuals such as *A. muelleri* (7.0–9.5 mm) and *P. melanarius* (12–20 mm). Characteristics of

Fig. 5. Mean activity-density of carabids (nine dominant species), *Pterosticus melanarius*, and density of *Aphis glycines* in soybean fields in 2004 (bars represent standard deviation). Mean carabid numbers are per trap per field for each sampling period. Mean numbers of aphids are per plant per field for each sampling period.

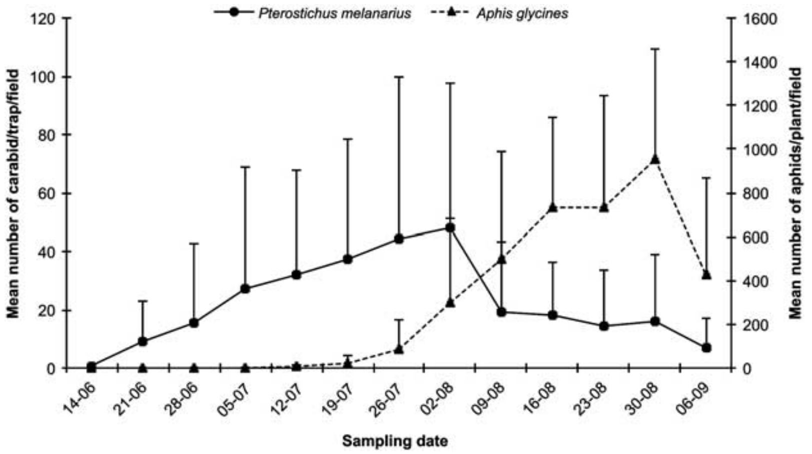
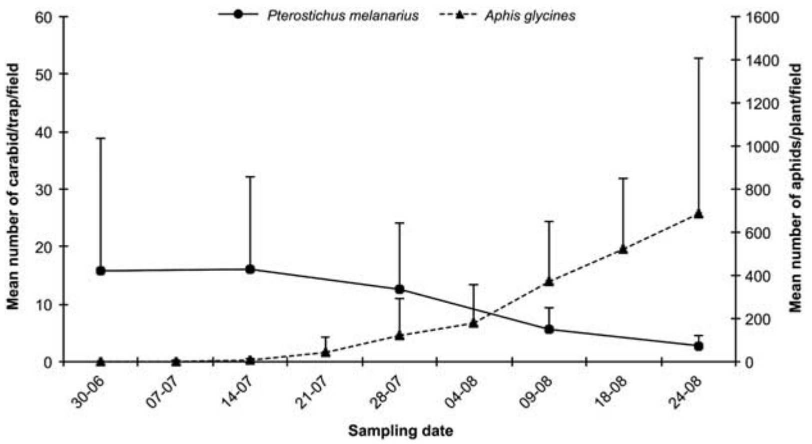


Fig. 6. Mean activity-density of carabids (nine dominant species), *Pterosticus melanarius*, and density of *Aphis glycines* in soybean fields in 2005 (bars represent standard deviation). Mean carabid numbers are per trap per field for each sampling period. Mean numbers of aphids are per plant per field for each sampling period.



the crops and farming practices might also contribute to explain why *P. melanarius* is dominant in our fields over other carabid species. Crop rotation, organic or conventional farming, type of field margins, and tillage can influence carabid richness and abundance (Rochefort *et al.* 2006; Menalled *et al.* 2007; Bourassa *et al.* 2008; O'Rourke 2008; Davis *et al.* 2009). *Pterostichus melanarius* has been shown to be more abundant in conventional farming than other carabid species (Kromp 1990).

A careful evaluation of carabid diversity requires exhaustive sampling and *post-hoc* verification through the use of rarefaction curves. Observed carabid richness and abundance in 2005 were lower than in 2004, and rarefaction curves revealed that the carabid assemblage in 2005 was only partially sampled in some fields (three out of seven). Pitfall traps remained open all week for 13 weeks in 2004, with samples collected once a week, but only for 24 hours during each of the 5 weeks in 2005. Some studies have tried to determine the minimum sampling effort necessary to obtain a reliable description of carabid diversity within an ecosystem. For example, trapping conducted for 10 days in both early and late season is sufficient to capture the most common ground beetle species in coniferous forest (Niemelä *et al*. 1990). A large number of pitfall traps (from 25 to 50 per 15 000 m^2) is required to provide a good estimate of carabid diversity in agroforests (Vennila and Rajagopal 1999). In agricultural crops, carabid species with different overwintering strategies colonise fields at different times during the season (Kromp 1999). As observed in soybean fields, species overwintering as adults, such as *P. lucublandus* or *P. chalcites*, are collected early in the summer season compared with species with a larval overwintering strategy, such as *P. melanarius* or *H. rufipes* (Fig. 4). Our analysis suggests that sampling ground beetles throughout the soybean growing season is necessary to provide a realistic picture of carabid biodiversity and summer seasonal activity-density.

In soybean fields in Québec, the carabid assemblage is dominated by exotic species. The six non-native species colonising soybean fields have all been introduced from Europe and represented 79% and 88% of the total number of carabid beetles captured in 2004 and 2005, respectively. *Pterostichus melanarius* accounts for more than 95% of the exotic individuals captured during our study. A similar pattern of exotic species dominance was observed in turfgrass lawns of Québec, with *H. rufipes* (De Geer), a European Palaearctic species, being the most common species (Rochefort *et al*. 2006). Carabid assemblages observed in soybean fields in other regions of North America also include exotic species but to a lesser extent: 16.7% in New York state (Hajek *et al*. 2007) and 10.3% in Michigan (Rutledge *et al*. 2004).

In Canada, *P. melanarius* dominates carabid assemblages in numerous habitats: meadows in Alberta (Cárcamo *et al*. 1995), woodlands in Ontario (Pearce *et al*. 2002), and raspberry fields and vineyards in Québec (Levesque and Levesque 1994; Goulet *et al*. 2004). The flight ability of *P. melanarius*, its flexibility in habitat use and its association to human modified habitats could explain its important colonisation of disturbed as well as undisturbed habitats (Niemelä and Spence 1991). The competition with native carabid species is also put forward to explain the widespread of *P. melanarius* (Hokkanen and Holopainen 1986; Spence and Spence 1988, Niemelä *et al*. 1997), whereas others favour the hypothesis of the biological community unsaturated permitting the exploitation of abundant resources or the occupation of niche free from native species by *P. melanarius* (Niemelä and Spence 1991). Because conventional farming practices such as tillage and pesticide applications are less detrimental to *P. melanarius* than other carabid species (Kromp 1990; Hatten *et al*. 2007), these factors may have also favoured the colonisation and exploitation of soybean fields by *P. melanarius*.

Influence of temporal, spatial, and food resource variables on carabid assemblages

The significant STI in 2004 and 2005 revealed that soybean fields differed greatly between each other in their carabids activity-density response. Also, our analysis revealed that carabid assemblages are more influenced by space (field sampled) and time (sampling date) than by the presence and density of *A. glycines*. Farming practices, habitat structure, and the presence of refuge strips and corridors are examples of field characteristics that have an impact on diversity, abundance, and Carabidae activity in crops (Carmona and Landis 1999; Östman *et al*. 2001; Weibull and Östman 2003; Weibull *et al*. 2003; Purtauf *et al*. 2005).

The life history traits of carabid species explain much of the influence of the time variable on their activity-density. Adult carabids colonise fields at different periods depending on their overwintering strategies and breeding period. Those that overwinter as adults (called spring breeders) are often the first species observed in the field whereas species that overwinter as larvae (called summer/autumn breeders) are usually more abundant later in the season (Kromp 1999). Among the nine dominant species we collected, *P. lucublandus*, *P. chalcites*, *C. fossor*, *A. sanctaecrucis*, *A. cupripenne*, and *B. quadrimaculatum oppositum* overwinter as adults (Lindroth 1992) and, accordingly, have an early activity-density peak, i.e., from mid-June to mid-July. In contrast, the three other species, *P. melanarius*, *H. rufipes*, and *N. terminata*, overwinter as larvae (Lindroth 1992) and are more abundant later in the summer season, i.e., from late July to mid-August.

There was no correlation between carabid activity-density and aphid density in soybean fields in either 2004 or 2005, as shown by the variation partitioning analysis. Carabid beetles are generalist predators, feeding on many invertebrate preys (Larochelle 1990). For example, the strongly generalist predator *P. melanarius* feeds on aphids (Winder *et al.* 2005) as well as on slugs (Symondson *et al.* 2000) and earthworms (King *et al.* 2010); its fitness is enhanced when it develops on a mixed diet of prey (Harwood *et al.* 2009). Because of low prey specificity, carabids probably do not have a strong response to variations in prey density (Symondson *et al.* 2002). To clarify the potential of *P. melanarius* to prey on *A. glycines* and its role in reducing aphid population early in the season, experiments using molecular gut content analysis (as in King *et al.* 2010) have been conducted.

Aphis glycines is a relatively new – first discovered in Québec in 2001 – and abundant food source for ground beetles. It has rapidly become the principal pest of soybeans within the agroecosystem (Ragsdale *et al.* 2011). Although we observed no summer seasonal response in carabid population activity-density related to *A. glycines* density, this exotic aphid may have favoured populations of generalist predators over the years. This hypothesis has recently been put forward by Heimpel *et al.* (2010), who argued that the arrival of *A. glycines* in North America has likely contributed to an increase in the abundance of the aphid's natural enemies, namely exotic species such as *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and the carabid beetle *A. muelleri*. Detailed population studies conducted over several years are needed to explore how *A. glycines* may impact the short-term and long-term population dynamics and community structure of carabid beetles.

Carabid beetles are abundant early in the soybean growth period and have the potential to slow the growth of *A. glycines* populations before the arrival of other aphidophagous predators, as suggested by Sunderland and Vickerman (1980). Our data showed that carabid populations reached an activity-density peak a few days before the colonisation of soybean fields by *A. glycines*. The presence of resident predators that buffer aphid populations could occur in conditions of high predator/prey ratio, as has been observed with the carabid *Bembidion* spp. (Holopainen and Helenius 1992) and the anthocorid bug *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) (Harwood *et al.* 2007). Although Sunderland and Vickerman (1980) suggested that *P. melanarius* has a low potential for reducing increases in aphid populations because of its low density during the early phase of aphid population growth, the pattern is different in Québec soybean fields because *P. melanarius* is abundant during the increasing phase (Fig. 5). This period is characterised by a high predator/prey ratio for *P. melanarius*/*A. glycines*, thus conditions are suitable for *P. melanarius* to act as a buffer to aphid populations. This scenario remains to be tested experimentally, for example, by using exclusion cages with low aphid density that mimics the situation occurring when *A. glycines* colonises crops.

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