Acta Soc. Zool. Bohem. **79**: 83–94, 2015
ISSN 1211-376X

Differential responses of granivorous, omnivorous and carnivorous species of ground beetles (Coleoptera: Carabidae) to local and landscape characteristics in a Canadian landscape

Éric Lucas & Julie-Éléonore Maisonhaute

Département des Sciences Biologiques, Université du Québec à Montréal,
C.P. 8888, Succ. Centre-ville, Montréal, Québec, Canada H3C 3P8
Corresponding author: e-mail: lucas.eric@uqam.ca

Received 4 March 2015; *accepted 20 May 2015*
Published 17 August 2015

Abstract. Landscape structure affects the abundance, richness and species composition of many arthropods in agriculture, including ground beetles. However, this effect of the landscape can be quite variable between different species and functional groups. In this study, we aimed to understand whether the trophic functional groups of ground beetles were affected by the agricultural landscape in the same way or whether significant differences occur between different groups (granivorous, carnivorous, and omnivorous). Ground beetles were sampled weekly using pitfall traps along a ditch border adjacent to cornfields in 2006 and 2007, in the Vacher creek watershed (Québec, Canada). Landscape characteristics were studied at the local scale (the sampled border and the adjacent cornfield) and at the landscape scale per se (500 m around fields). We draw three primary conclusions from our results. Firstly, the different functional groups seem to be associated with a specific scale (local or landscape). The granivorous group was not associated with either local or landscape components. Carnivorous species were associated with landscape components but not the local context and omnivorous species with both landscape and local context. Secondly, when considering the significant landscape/local components, the association of each species within a functional group can differ. Thirdly, specific results are highly variable among years, as a focal species can respond to a specific component in a completely opposite way depending on the year.

Key words. Carabidae, landscape, granivorous, functional groups, trophic groups.

INTRODUCTION

Insect biology and ecology remain a blackbox. Even in disturbed agricultural landscapes several hundreds of terricolous species (ground, tiger and rove beetles, spiders...) are commonly found. The trophic biology of both adult and larval stages are beginning to be investigated (see for example for granivorous carabids in Honek et al. 2003), but assessing the natural dynamics or anthropocentric values and of these assemblages of species is very difficult (Lucas & Maisonhaute 2014).

Ground beetles (Carabidae) constitute one of the main components of the terricolous assemblage in agrosystems, with dozens of different species (for example, USA: Byers et al. 2000, 83 species, Sweden: Weibull et al. 2003, 18–38 species, Canada: Maisonhaute et al. 2010, 72 species). Ground beetles constitute also one of the main biocontrol agents of pest and weeds in agricultural landscapes. They may be involved in the predation of both ground-dwelling arthropods (Luff et al. 1987, Lovei & Sunderland 1996) and canopy arthropods (Losey & Denno 1998, Snyder & Ives 2001), and also weed seeds (Honek et al. 2003, 2007, Bohan et al. 2011, Trichard et al. 2013, 2014). For example, seed predation in arable fields can reach 1000 seeds per m^2 per day (Honek et al. 2003). On the other hand, carabids may be involved in "noxious" interactions, which may hamper or reduce the magnitude of these ecological services. As an example, ground beetles are commonly involved in cannibalism, intraguild predation, and/or non-pest predation (Snyder & Ives 2001, Traugott et al. 2012).

These ecosystem services are provided by different trophic functional groups of carabids: carnivorous, omnivorous and/or granivorous. Numerous factors affect ground beetle populations and their activity in the field including agricultural land use and management (Cole et al. 2002, Menalled et al. 2007), landscape structure (Aviron et al. 2005, Werling & Gratton 2008, Maisonhaute et al. 2010), seasonal dynamics (Honek et al. 2006, Trichard et al. 2014), pesticide application (Nash et al. 2008, Diekötter et al. 2010, Trichard et al. 2013), tillage (Carcamo 1995, Trichard et al. 2013) and biotic interactions (Trichard et al. 2013). At the landscape level, it has been demonstrated in Germany that the species richness of the carnivorous group is more affected by landscape simplification than that of the phytophagous group and that of the omnivorous group is not affected (Purtauf et al. 2005). In France, Trichard et al. (2013) showed that landscape composition has a greater affect than local practices on weed seed predation by ground beetles, which was positively related to granivorous diversity and negatively to omnivorous richness. In a study carried out in eight European countries, the activity of phytophagous carabids increased with landscape habitat richness, whereas that of zoophagous carabids was not affected (Vanbergen et al. 2010). The response of the different functional groups differed in these studies. This may be linked to the local context of the study (specific landscape at a specific location with specific resource availability), or to species specific responses within the same functional groups (see for example Maisonhaute & Lucas 2011).

The purpose of the present study was to evaluate, in a typical agricultural North-American landscape, how the most common species of the different functional groups of ground beetles, that is, granivorous, omnivorous and carnivorous, are affected by the surrounding landscape and local environment. Also, we aimed to test if species of the same functional group would respond in the same way to different landscape/local conditions.

MATERIAL AND METHODS

Sampling area

Twenty sites were sampled in the Vacher creek watershed (Lanaudière, Quebec, Canada), about 40 km north from Montreal. The watershed area covers 69 km^2 and the landscape configurations differ, from intensive farming areas, characterized by large fields and many cultivated areas, to more extensive areas composed of small fields and extensive areas of woodland (Ruiz et al. 2008). Twenty sites distributed throughout the entire watershed were sampled during the summers of 2006 and 2007. At each site, four pitfall traps were placed along a ditch border adjacent to a cornfield, at 10 m intervals and filled with 100 ml of a propylene glycol diluted with water (total of 80 pitfall traps each year). Ground beetles in the pitfall traps were collected weekly from the beginning of June until the end of September in 2006 and 2007, totaling 16 weeks of sampling. For more details of the methods, see Maisonhaute et al. (2010).

Ground beetle communities

Not all the beetles collected were identified only those collected every two weeks (8 weeks). Ground beetles were identified using Larochelle (1976) and the identifications confirmed by an expert at Agriculture and Agri-food Canada. Information about the species diet was extracted from Larochelle and Larivière's guide (2003) and Lundgren (2009). Ground beetles were classified into 3 groups according to their diet: mainly granivores, omnivores (which can also consume seeds) and carnivores. Within each group, we selected the 2 or 3 species that were most abundant (Table 1). Mainly granivore beetles belonging to the genus *Amara* and the species *Ophonus rufibarbis* (Fabricius, 1792). Because of the difficulty of identifying species of *Amara* and the short time available for identification, the ground beetles of the genus *Amara* were not identified to species. However, the few species identified at the beginning of the identification process revealed the presence of *A. aulica* (Panzer, 1796), *A. avida* Say, 1823, *A. bifrons* Gyllenhal, 1810, *A. ellipsis* (Casey, 1918), *A. latior* (Kirby, 1837), *A. pallipes* Kirby, 1837, *A. quenseli* (Schönherr) and *A. rubrica* Haldeman, 1843. Most of these species are granivorous. From this pool of specimens, it seems that the most abundant species of *Amara* were *A. rubrica*, *A. latior* and *A. avida*. Among the omnivores, we studied the species *Pterostichus melanarius* (Illiger, 1798), *Poecilus lucublandus lucublandus* (Say, 1823) and *Harpalus pensylvanicus* (DeGeer, 1774). Finally, included in the carnivorous beetle group were the species *Chlaenius tricolor tricolor* Dejan, 1826 and *Bembidion quadrimaculatum oppositum* Say, 1823.

Table 1. Biological and ecological characteristics of the different species of ground beetles included in this study. G: Granivore, O: Omnivore, C: Carnivore. In 2006 and 2007, 7 species/genera studied made up nearly 80% of the total number of ground beetles collected. Mean population density = mean number of specimens collected per trap per site (mean population density ± standard error). In brackets: minimum and maximum population density. References: Larochelle and Larivière 2003 (diet, brachyptery, flight) and Larochelle 1976 (size)

species	diet	size [mm]	polymorphism	flight	2006 number collected	%	mean population density	2007 number collected	%	mean population density	% both years
Amara spp.	G	5.3–11	mostly macropterous	occasionnal or frequent	77	2.4	0.12±0.04 (0–0.56)	180	4.3	0.28±0.1 (0–2.16)	3.5
O. rufibarbis	G	6.3–9.5	macropterous	occasional	37	1.2	0.14±0.13 (0–2.69)	89	2.1	0.14±0.13 (0–2.69)	1.7
P. melanarius	O-G	12.2–19	polymorphic	ocasionnal	1247	39.6	1.95±0.83 (0.03–14.53)	1035	24.9	1.62±0.49 (0.03–8.94)	31.2
P. lucublandus	O-G	9.3–13.8	macropterous	frequent	433	13.8	0.68±0.14 (0.03–1.91)	298	7.2	0.47±0.09 (0.06–1.34)	10.0
H. pensylvanicus	O-G	10–15	macropterous	frequent	298	9.5	0.47±0.14 (0–2.56)	783	18.8	1.22±0.37 (0.13–6.09)	14.8
B. quadrimaculatum	C	2.9–3.7	polymorphic	frequent	251	8.0	0.39±0.08 (0.06–1.31)	737	17.7	1.15±0.24 (0.19–4.38)	13.5
C. tricolor	C	10.1–13.3	macropterous	frequent	81	2.6	0.13±0.03 (0–0.53)	110	2.6	0.17±0.05 (0–0.78)	2.6
total number of the seven species					2424	77.0		3232	77.7		77.4
total collected					3147	100		4156	100		100

Table 2. Description of the local and landscape components included in this study. Local components are those of the ditch border and adjacent cornfield. Landscape components are those within 500 m of the fields

variables	description	code
local variables	**variables recorded in the field border and adjacent cornfield**	
focal area	area of the cornfield adjacent to the border sampled (m^2)	area
focal perimeter-to-area ratio	perimeter-to-area ratio of the cornfield adjacent to the border sampled (m^{-1})	pa
ditch width	ditch width (m)	width
presence of water	presence of stream or river in the border (0/1)	water
presence of tree	presence of trees in the border (0/1)	tree
vegetation richness	mean vegetation richness in the border (within 1 m^2 around pitfall traps)	rich
landscape variables	**landscape variables recorded within a 500 m-radius from the fields**	
percentage of the area under crops	percentage of the area under crops (%)	CROP
percentage of the area under grassland	percentage of the area under grassland (%, includes hay crops, pasture, fallow, riparian vegetation)	GRASS
percentage of the area under woodland	percentage of the area under woodland (%)	WOOD
landscape richness	number of different landscape elements (maximum of 27 categories)	RICH
crop diversity	simpson index of crop diversity (based on 18 crop categories)	DIV
extent of field borders	extent of field borders (m/ha)	BORDER
landscape patchiness	total number of patches of landscape elements	PATCHES
non-crop patchiness	total number of non-crop patches	NCP
mean field area	mean field area of all the fields in the landscape (m^2)	AREA
mean field perimeter-to-area ratio	mean field perimeter-to-area ratio of all the fields in the landscape (m^{-1})	PA

Local environment

Each year, characteristics of the field border were evaluated in order to determine the effect of local components on beetle density. Components recorded in the field included the ditch width, the presence of water in the ditch (stream), the presence of trees and vegetation richness (Table 2). The vegetation richness was evaluated within 1 m^2 around each pitfall trap. Then, the area and the perimeter-to-area ratio of the adjacent cornfield were determined using ArcGIS (ESRI 2005).

Landscape structure

Landscape structure within 500 m around each field was analyzed using MapInfo (ESRI 2000) and ArcGIS (ESRI 2005). This scale was chosen based on previous studies that found an effect of landscape structure on ground beetles at similar scales (Weibull & Östman 2003: 400 m, Purtauf et al. 2005: 750 m). Aerial photographs of the study area and land use information came from the Ministère du Développement durable, de l'Environnement et des Parcs du Québec. Land use within the study area (especially information on the crops) was updated with information gathered in the field. Variables of landscape composition included the proportion of the landscape under crops within the 500 m radius, the proportion of corn, grassland, woodland, landscape richness and crop diversity. Variables related to landscape configuration included the density of field borders, landscape patchiness, non-crop patchiness, the mean field area and mean field perimeter-to-area ratio (Table 2).

Statistical analyses

Analysis of the population density of ground beetles was done using the mean number of specimens collected per trap and per field during the eight weeks when the beetles were identified. Each genus/species was analyzed individually. Then, since sampling sites were not exactly the same in 2006 and 2007 (but close to each other), analyses were performed on each year separately. A forward selection was initially carried out in the local and landscape matrices separately, and only significant variables were retained (permutation tests based on 999 permutations, α=0.05) (Blanchet et al. 2008). In a second step, regression models were used to determine the best model accounting for the beetle density (calculation of adjusted R^2, p and regression coefficients, Crawley 2007). The different models were compared with each other using ANOVA test (Crawley 2007) and only the best model was retained. When significant variables were found in both the local and the landscape matrices, a variation partitioning was performed. This procedure was applied to determine the unique contribution of local and landscape components in determining the variation in beetle population density (Borcard et al. 1992, Peres-Neto et al. 2006).

RESULTS

Ground beetle communities

A total of 3147 ground beetles were collected in 2006 and 4156 in 2007 (Table 1). Both years combined, 72 species were identified, with 66 species in 2006 (mean±SE: 17.2±1.27), 67 species in 2007 (mean±SE: 19.0±1.51) and 60 species common to both years. The seven species (genus for *Amara*) studied represented nearly 80% of the total number of specimens collected with other species often making up less than 1% of the total. The population peaks of each of the species were recorded at different times in a year and even differed between years (Fig. 1). *Pterostichus melanarius*, *P. lucublandus* and *B. quadrimaculatum* were present at the 20 sites in 2006 and 2007, whereas *Amara*, *O. rufibarbis* and *C. tricolor* were not found at all the sites. *Harpalus pensylvanicus* was present at the 20 sites in 2007 and most of the sites in 2007 (16 sites).

Local versus Landscape effect

In both years, the granivorous ground beetles were not associated with either local or landscape components whereas the carnivorous species were associated with only the landscape components (Table 3). Two of the omnivorous species (*P. melanarius* and *P. lucublandus*) were associated with components of the local and/or landscape scales (Fig. 2), whereas the third omnivorous species was only associated with landscape components in 2007. The principal component analysis (Fig. 3) reveals the relation between the significant variables at the local and landscape scales and the mean population densities of the different species of ground beetles.

Granivorous Ground Beetles

Both in 2006 and 2007 *Amara spp*. and *O. rufibarbis* were not associated with local or landscape components (Table 3).

Omnivorous Ground Beetles

Pterostichus melanarius was associated with local and/or landscape components. In 2006, the mean population density of *P. melanarius* was negatively associated with vegetation richness in the field border (R^2=0.16, Table 3, Fig. 3). In 2007, positively associated with the perimeter-to-area ratio of the adjacent cornfield (R^2=0.17) and the proportion of area under crops at the landscape

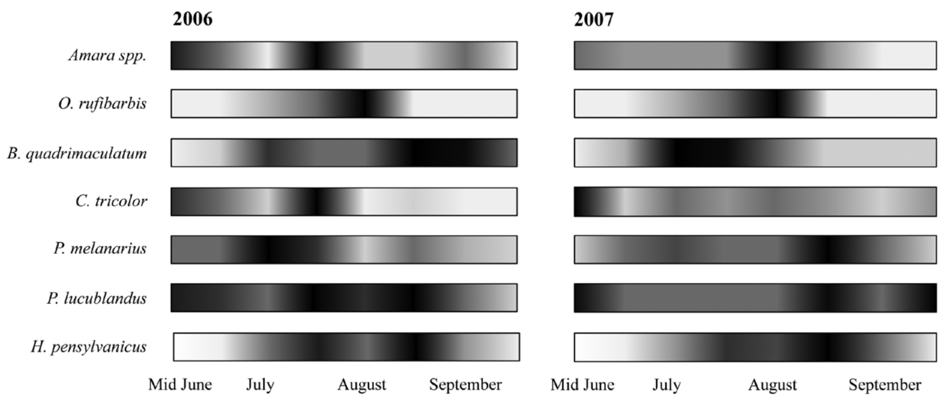

Fig. 1. Population density of the different species of ground beetles recorded at different times during 2006 and 2007. For each species, the darker the shading the greater the population density (black: peak abundance).

Table 3. Associations between ground beetle population density and local environment and landscape structure. Only significant variables retained after forward selection are presented. Regressions only included the significant variables. R^2 corresponds to adjusted values. No effect was recorded for the granivorous (G) *Amara* spp. and *Ophonus rufibarbis*. O-G: Omnivore-Granivore, C: Carnivore

species	diet	year	R^2	p	scale	model
Amara spp.	G	2006	–	>0.05	–	–
		2007	–	>0.05	–	–
O. rufibarbis	G	2006	–	>0.05	–	–
		2007	–	>0.05	–	–
P. melanarius	O-G	2006	0.159	0.046	local	–0.67rich +7.92
		2007	0.169	0.040	local	–74.63pa +3.66
			0.191	0.031	landscape	5.52CROP –1.83
P. lucublandus	O-G	2006	0.191	0.031	local	–0.12rich +1.75
			0.434	0.001	landscape	2.20CROP –0.64
		2007	0.425	0.004	landscape	–1.34CROP +0.07RICH +0.41
H. pensylvanicus	O-G	2007	0.360	0.009	landscape	7.83GRASS –4.86DIV +2.47
B. quadrimaculatum	C	2006	0.436	0.003	landscape	8.08GRASS^2 –5.46GRASS +1.11
		2007	0.277	0.001	landscape	3.11WOOD +0.76
C. tricolor	C	2006	0.186	0.033	landscape	0.01NCP +0.041
		2007	0.111	0.083	landscape	0.015NCP +0.048

scale (R^2=0.19), see Table 3 and Fig. 3. These two variables together accounted for 19.8% of the variation and an equivalent part of the variation (Fig. 2).

Poecilus lucublandus was associated with either local or landscape components. In 2006, the mean population density of *P. lucublandus* was negatively associated with vegetation richness in the field border (R^2=0.19, Table 3, Fig. 3) and positively with area under crops (R^2=0.43). Variation partitioning revealed that these two variables accounted for 45.2% of the variation and that the landscape component (CROP) accounted for the greatest part of the variation (Fig. 2). In 2007, the mean population density of *P. lucublandus* was negatively associated with the proportion of the area under crops (R^2=0.29, p=0.009, –1.19CROP +1.21, Fig. 3) and positively with landscape richness (R^2=0.17, p=0.041, 1.27e^{-8}exp(RICH) +0.41). These 2 variables together accounted for 43% of the variation (Table 3).

Regarding *Harpalus pensylvanicus*, variables were significant only in 2007. The mean population density of *H. pensylvanicus* was positively associated with the proportion of grassland

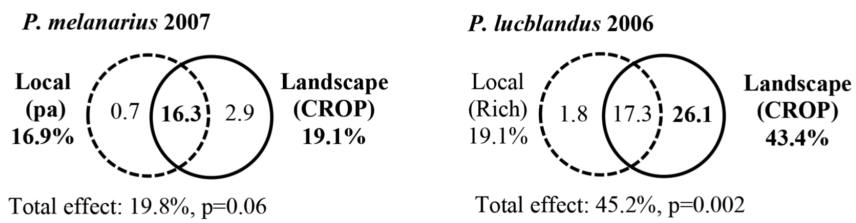

Fig. 2. Variation partitioning between the local and landscape components that are associated with two species of omnivorous ground beetles. Variation partitioning was performed only when significant associations were recorded at both local and landscape scales, which only occurred in the case of *P. melanarius* in 2007 and *P. lucublandus* in 2006. In bold: greatest associations.

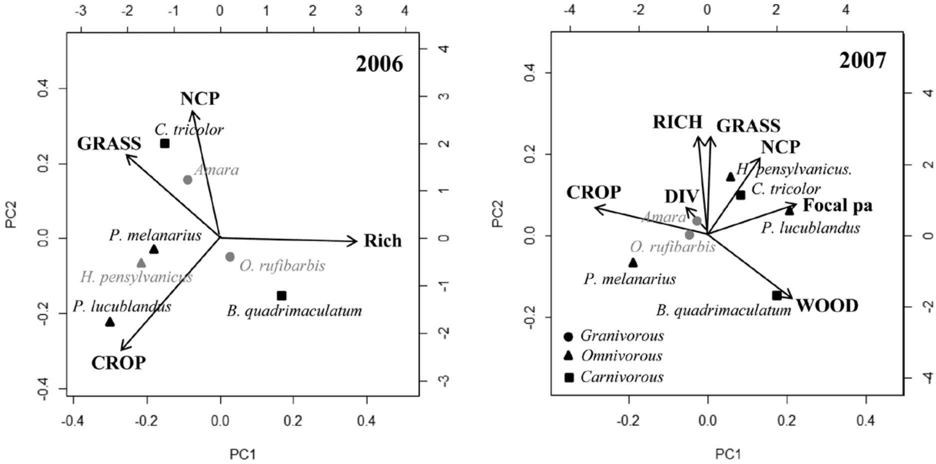

Fig. 3. Principal component analysis of the association of the different species of ground beetles with the significant landscape variables. Species for which there was no association with local or landscape components are coloured grey. Rich: vegetation richness (local matrix), Focal pa: focal perimeter-to-area-ratio (local matrix), CROP: percentage of the area cultivated by CROP: percentage of the area under crops; GRASS: percentage of the area under grassland, WOOD: percentage of the area under woodland, RICH: landscape richness, DIV: crop diversity, NCP: Non-crop patchiness.

in the landscape (R^2=0.21 p=0.023, 5.839GRASS +0.013, Figs. 3, 4) and negatively with crop diversity (simple regression non-significant). These two variables together accounted for 36% of the variation (Table 3).

Carnivorous Ground Beetles

Both years, *B. quadrimaculatum* was only associated with components at the landscape scale. In 2006, the mean population density of *B. quadrimaculatum* was positively associated with the proportion of grassland in the landscape (R^2=0.44, Table 3, Figs. 3–5) whereas in 2007 it was positively associated with the proportion of woodland (R^2=0.28).

In both years, the mean population density of *C. tricolor* was only associated with non-crop patchiness at the landscape scale (2006: R^2=0.19, 2007: R^2=0.11, Table 3 and Figs. 3–5).

DISCUSSION

Model species in the different functional groups of ground beetles were differently associated with components of the local/landscape. Carnivorous species were associated with only components of the landscape, while granivorous species were not associated with either local or landscape characteristics, and omnivorous species mainly with landscape and local characteristics. The responses recorded for specific functional groups were relatively similar among species but the components of the landscape-local effects differed drastically among species and sometimes in the two years for the same species.

Our results demonstrate that the effect of local and landscape context on ground beetle species seems to differ depending on the functional group. The effect of the functional group may be linked to the resource exploited by members of this group (availability in time and space, competition ...). The temporal and spatial availability of the resources used by the different trophic functional

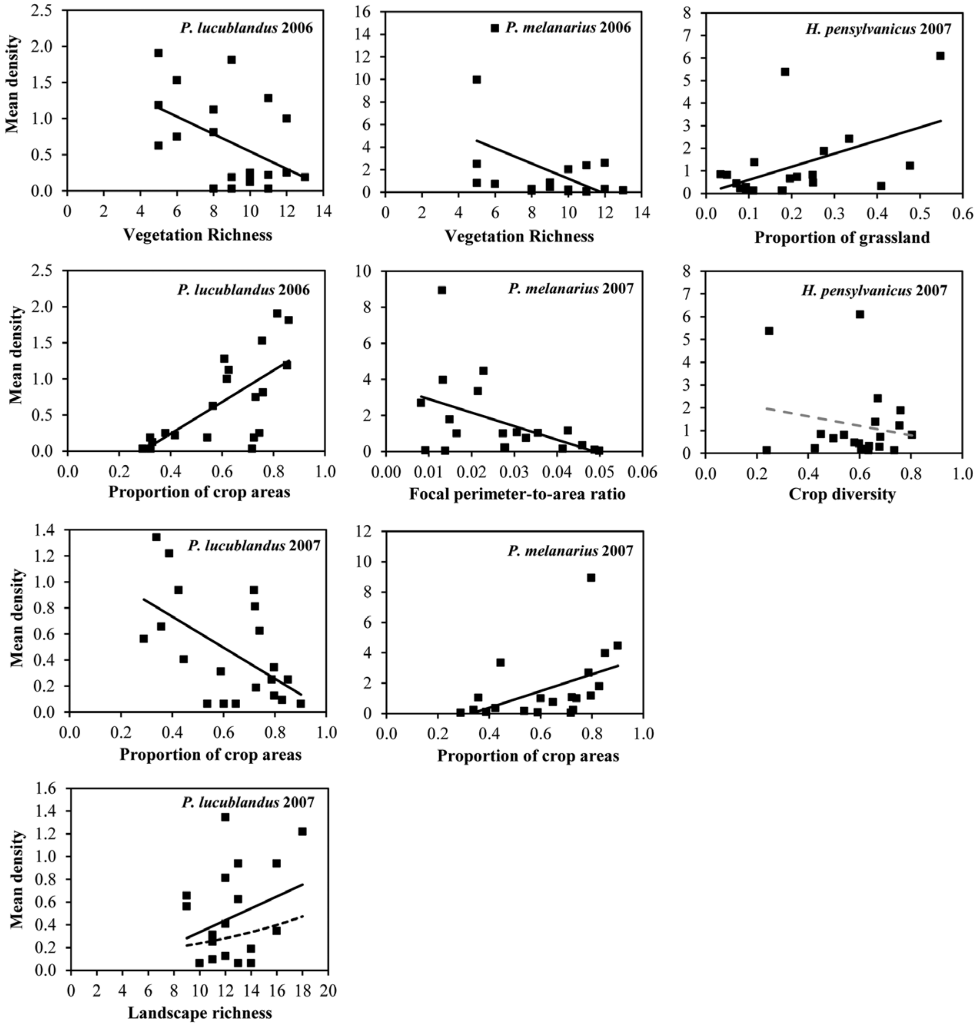

Fig. 4. Association of omnivorous ground beetles with local and landscape components. Mean population density is the mean number of ground beetles collected per trap per site. *Poecilus lucublandus* 2007: exponential model (dotted line) significantly accounted for a greater proportion of the variation than the linear model (plain line). *Harpalus pensylvanicus* 2007: crop diversity was significant in the global model that included the proportion of the area under grassland but not in the simple regression.

groups should be drastically different, and also the diversity and abundance (and consequently competition) of the consumers in each group. However, it is highly speculative to draw such conclusions as there is no information on the availability of these resources.

Within the three functional groups, the different species were differently associated with specific variables. Granivorous ground beetles were not associated with either landscape or local conditions. It is very difficult to evaluate the absence of an association. In comparison, a French study found that seed predation and granivorous richness were more associated with landscape structure than agricultural practices, such as tillage, pesticide or crop residue (Trichard et al. 2013). In contrast, in Germany, Diekötter et al. (2010) found that seed predation was only associated with the farming system (conventional versus organic) and not with landscape. Thus, components associated with granivorous species appear to differ in these two studies. In an excellent paper, Honek et al. (2003) reveal the complexity of the functioning of a granivorous guild and the effect of crop, season, seed type and site on ground beetle granivory. They also demonstrated that the different carabid species had different specific preferences and the effect of adult size and seed size (Honek et al. 2007, 2011). Since we worked with an "*Amara*" group that included several different species of different sizes it is highly speculative to try to explain the situation *in situ*. It would be interesting to analyse specifically some of the *Amara* species (e.g., *A. rubrica*, *A. latior* or *A. avida*) to verify whether presence of these species is associated with local or landscape variables. This would verify the effect of the absence of local or landscape conditions recorded for the *Amara* group in our study. The other species, *O. rufibarbis*, was not recorded at numerous sites, which may account for the absence of landscape effects. As *O. rufibarbis* commonly feeds on plants of the family Apiaceae (Larochelle & Larivière 2003), its presence at some sites could be related to the abundance of plants of this family. In fact, we noted that *O. rufibarbis* was present at some sites where the abundance of wild carrot, *Daucus carota*, was quite high, which is in accordance with the hypothesis previously mentioned. As previously stated it is very difficult

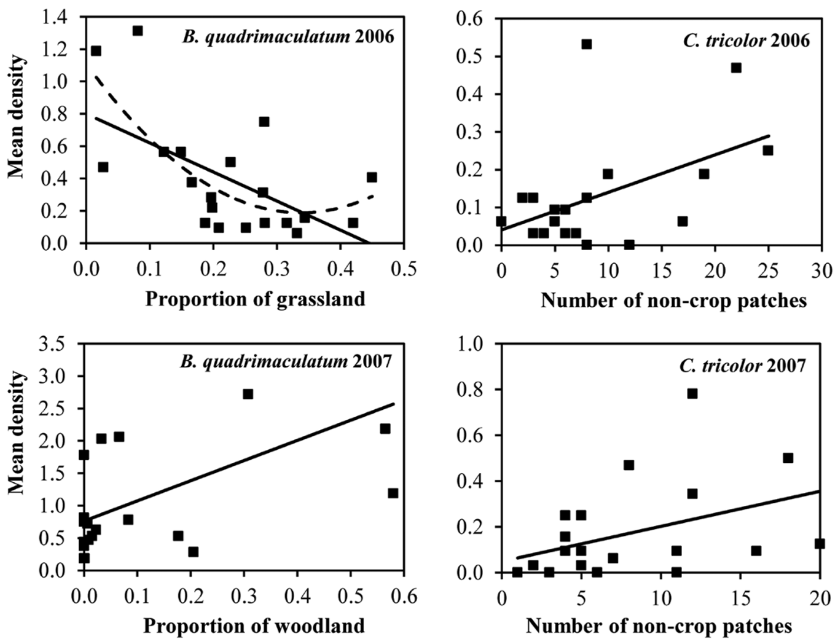

Fig. 5. Association of the carnivorous species of ground beetles with landscape structure. Mean population density is the mean number of ground beetles collected per trap per site. *B. quadrimaculatum* 2006: polynomial model (dotted line) significantly accounted for a greater proportion of the variation than the linear model (plain line).

to draw strong conclusions since the availability of seeds in the landscape is unknown and may be linked not only to crop type but also to the vegetation in field margins.

Carnivorous species were only associated with landscape characteristics. This is similar to the results of Purtauf et al. (2005), which indicate that carnivorous species are more associated with landscape structure than the omnivorous and phytophagous species. In particular, we found that the abundance of *C. tricolor* increased with increase in the number of non-crop patches, reflecting a positive association of abundance with the fragmentation of non-crop areas. The other carnivorous species, *B. quadrimaculatum*, increased in number with decrease in the proportion of grassland (2006) and increase in the proportion of woodland (2007). *Bembidion quadrimaculatum* is one of the most abundant species in agricultural landscapes (Melnychuk et al. 2003; the present study). Similar interactions with woodland and grassland are recorded in the U.K., with a negative association with heath grassland and a positive association with deciduous woodland (Eyre & Luff 2004). While both species are associated with components of the landscape, each is specifically associated with different components of the landscape, which may illustrate their habitat preferences.

Finally, the omnivorous group was associated with both landscape and local characteristics. Previous studies also show that both local components (agricultural practices) and landscape affect the distribution of some polyphagous ground beetles (Östman et al. 2001). Although both local and landscape characteristics are associated with the distribution of the species in the omnivorous group in our study, the specific components of the landscape/local area affecting the different species differ. While both *P. lucublandus* and *P. melanarius* were negatively associated with vegetation richness at the local scale, each species respond differently in 2007 to the proportion of the area under crops. *Pterostichus melanarius* is a species often associated with disturbed habitats, as found in intensive agricultural landscapes. In our study, the abundance of *P. melanarius* increased with increase in the proportion of area under crops, which is in accordance to its preference for open habitats (Fournier & Loreau 2001, Aviron et al. 2005). Also, it is unclear why the effect of the proportion of the area under crops on *P. lucublandus* differed in 2006 and 2007. Regarding *H. pensylvanicus*, it was more abundant in a landscape with a high proportion of grassland. This association between *H. pensylvanicus* abundance and grassland (in particular field borders) is also recorded in the USA (Varchola & Dunn 2001). In that study, *H. pensylvanicus* was more abundant in cornfields bordered by grass than cornfields bordered by hedges. It may also reflect the positive effect of extensive farming on *H. pensylvanicus* populations.

Our study also revealed great variability between years, which makes it dangerous to reach a conclusion based on a one season study of ground beetles assemblages. Food availability (prey, seed or other food items) may vary greatly between years and account for the differences observed. It is also known that seed predation varies throughout the season each year (Honek et al. 2006), so it could also be assumed that it also varies between years. Interestingly, the habitat preferences of some species of ground beetle can also vary throughout the season, for instance, due to variations in temperature (Crist & Ahern 1999). In particular, seasonal shifts between habitats are recorded for the omnivorous species, *H. pensylvanicus*. Thus, differences in climate between years may play an important role, and strong conclusions should not be drawn unless based on results collected over many years.

Acknowledgements

First, our acknowledgements go to Yves Bousquet (Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-food Canada) for taxonomic assistance. Then, we would like to thank Karine Gauthier, Simon Paradis, Maryse Desrochers, Noémie Charest-Bourdon, Félix Bureau-Primeau, Dominique Dubreuil, Anik Pelletier-Leboeuf and Adriana Puscasu for help with field sampling and in the laboratory. Our acknowledgements also go to the farmers involved in this project and the members of the laboratory of biological control of UQAM. Finally, we would like to thank the Prof. Anthony Dixon for language editing. The funding came from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) and the Ministère du Développement durable, de l'Environnement et des Parcs du Québec (MDDEP).

REFERENCES

Aviron S., Burel F., Baudry J. & Schermann N. 2005: Carabid assemblages in agricultural landscapes: impacts of habitat features, landscape context at different spatial scales and farming intensity. *Agriculture, Ecosystems and Environment* **108**: 205–217.

Blanchet F. G., Legendre P. & Borcard D. 2008: Forward selection of explanatory variables. *Ecology* **89**: 2623–2632.

Bohan D. A., Boursault A., Brooks D. R. & Petit S. 2011: National-scale regulation of the weed seedbank by carabid predators. *Journal of Applied Ecology* **48**: 888–898.

Borcard D., Legendre P. & Drapeau P. 1992: Partialling out the spatial component of ecological variation. *Ecology* **73**: 1045–1055.

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

Carcamo H. A. 1995: Effect of tillage on ground beetles (Coleoptera: Carabidae): A farm-scale study in central Alberta. *Canadian Entomologist* **127**: 631–639.

Cole L. J., McCracken D. I., Dennis P., Downie I. S., Griffin A. L., Foster G. N., Murphy K. J. & Waterhouse T. 2002: Relationships between agricultural management and ecological groups of ground beetles (Coleoptera: Carabidae) on Scottish farmland. *Agriculture, Ecosystems & Environment* **93**: 323–336.

Crawley M. J. 2007: Analysis of Variance. Pp.: 449–488. In: Sons J. W. (eds): *The R Book*. West Sussex, England: Wiley, 950 pp.

Crawley M. J. 2007: Regression. Pp.: 387–448. In: Sons J. W. (eds): *The R Book*. West Sussex, England: Wiley, 950 pp.

Crist T. O. & Ahern R. G. 1999: Effects of Habitat Patch Size and Temperature on the Distribution and Abundance of Ground Beetles (Coleoptera: Carabidae) in an Old Field. *Environmental Entomology* **28**: 681–689.

Diekötter T., Wamser S., Wolters V. & Birkhofer K. 2010: Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems and Environment* **137**: 108–112.

ESRI (Environmental Systems Research Institute) 2005: *ArcGIS Version 9.1*. Redlands, CA: ESRI.

Eyre M. D. & Luff M. L. 2004: Ground beetle species (Coleoptera, Carabidae) associations with land cover variables in northern England and southern Scotland. *Ecography* **27**: 417–426.

Fournier E. & Loreau M. 2001: Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape. *Landscape Ecology* **16**: 17–32.

Honek A., Martinkova Z. & Jarosik V. 2003: Ground beetles (Carabidae) as seed predators. *European Journal of Entomology* **100**: 531–544.

Honek A., Martinkova Z. & Saska P. 2011: Effect of size, taxonomic affiliation and geographic origin of dandelion (Taraxacum agg.) seeds on predation by ground beetles (Carabidae, Coleoptera). *Basic and Applied Ecology* **12**: 89–96.

Honek A., Martinkova Z., Saska P. & Pekar S. 2007: Size and taxonomic constraints determine the seed preferences of Carabidae (Coleoptera). *Basic and Applied Ecology* **8**: 343–353.

Honek A., Saska P. & Martinkova Z. 2006: Seasonal variation in seed predation by adult carabid beetles. *Entomologia Experimentalis et Applicata* **118**: 157–162.

Larochelle A. 1976: *Manuel d'identification des Carabidae du Québec*. Rigaud, 127 pp.

Larochelle A. & Larivière M.-C. 2003: A natural history of the ground-beetles (Coleoptera: Carabidae) of America north of Mexico. *Pensoft Series Faunistica* **27**: 1–584.

Losey J. E. & Denno R. F. 1998: Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* **79**: 2143–2152.

Lovei G. L. & Sunderland K. D. 1996: Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae). *Annual Review of Entomology* **41**: 231–256.

Lucas É. & Maisonhaute J.-É. 2014: Paysage et services écosystémiques, une nouvelle dimension dans la lutte aux insectes nuisibles. Pp.: 175–196. In: Domon G. & Ruiz J. (eds): *Agriculture et paysage. Aménager autrement les territoires ruraux*. Montréal (Québec, Canada): Presses de l'Université de Montréal, 338 pp.

Luff M. L., Thiele H. U. & Allen R. T. 1987: Biology of polyphagous ground beetles in agriculture. *Agricultural Zoology Reviews* **2**: 237–278.

Lundgren J. G. 2009: Relationships of Natural Enemies and Non-Prey Foods. *Progress in Biological Control* **7**: 453.

MAISONHAUTE J.-É. & LUCAS É. 2011: Influence of landscape structure on the functional groups of an aphidophagous guild: Active-searching predators, furtive predators and parasitoids. *European Journal of Environmental Sciences* **1**: 41–50.
MAISONHAUTE J.-É., PERES-NETO P. & LUCAS É. 2010: Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. *Agriculture*, *Ecosystems and Environment* **139**: 500–507.
MELNYCHUK N. A., OLFERT O., YOUNGS B. & GILLOTT C. 2003: Abundance and diversity of Carabidae (Coleoptera) in different farming systems. *Agriculture*, *Ecosystems and Environment* **95**: 69–72.
MENALLED F. D., SMITH R. G., DAUER J. T. & FOX T. B. 2007: Impact of agricultural management on carabid communities and weed seed predation. *Agriculture*, *Ecosystems and Environment* **118**: 49–54.
NASH M. A., THOMSON L. J. & HOFFMANN A. A. 2008: Effect of remnant vegetation, pesticides, and farm management on abundance of the beneficial predator Notonomus gravis (Chaudoir) (Coleoptera: Carabidae). *Biological Control* **46**: 83–93.
ÖSTMAN Ö., EKBOM B., BENGTSSON J. & WEIBULL A.-C. 2001: Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. *Ecological Applications* **11**: 480–488.
PERES-NETO P. R., LEGENDRE P., DRAY S. & BORCARD D. 2006: Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* **87**: 2614–2625.
PURTAUF T., DAUBER J. & WOLTERS V. 2005: The response of carabids to landscape simplification differs between trophic groups. *Oecologia* **142**: 458–464.
RUIZ J., DOMON G., LUCAS E. & CÔTÉ M.-J. 2008: Vers des paysages multifonctionnels en zone d'intensification agricole: une recherche interdisciplinaire au Québec (Canada). *Revue Forestière Française* **5**: 589–601.
SNYDER W. E. & IVES A. R. 2001: Generalist predatorsdisrupt biological control by a specialist parasitoid. *Ecology* **82**: 705–716.
TRAUGOTT M., BELL J. R., RASO L., SINT D. & SYMONDSON W. O. C. 2012: Generalist predators disrupt parasitoid aphid control by direct and coincidental intraguild predation. *Bulletin of Entomological Research* **102**: 239–247.
TRICHARD A., ALIGNIER A., BIJU-DUVAL L. & PETIT S. 2013: The relative effects of local management and landscape context on weed seed predation and carabid functional groups. *Basic and Applied Ecology* **14**: 235–245.
TRICHARD A., RICCI B., DUCOURTIEUX C. & PETIT S. 2014: The spatio-temporal distribution of weed seed predation differs between conservation agriculture and conventional tillage. *Agriculture*, *Ecosystems and Environment* **188**: 40–47.
VANBERGEN A. J., WOODCOCK B. A., KOIVULA M., NIEMELÄ J., KOTZE D. J., BOLGER T. O. M., GOLDEN V., DUBS F., BOULANGER G., SERRANO J., LENCINA J. L., SERRANO A., AGUIAR C., GRANDCHAMP A.-C., STOFER S., SZÉL G., IVITS E. V. A., ADLER P., MARKUS J. & WATT A. D. 2010: Trophic level modulates carabid beetle responses to habitat and landscape structure: a pan-European study. *Ecological Entomology* **35**: 226–235.
VARCHOLA J. M. & DUNN J. P. 2001: Influence of hedgerow and grassy field borders on ground beetle (Coleoptera: Carabidae) activity in fields of corn. *Agriculture*, *Ecosystems and Environment* **83**: 153–163.
WEIBULL A.-C. & ÖSTMAN Ö. 2003: Species composition in agroecosystems: The effect of landscape, habitat, and farm management. *Basic and Applied Ecology* **4**: 349–361.
WEIBULL A.-C., ÖSTMAN Ö. & GRANQVIST A. 2003: Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity and Conservation* **12**: 1335–1355.
WERLING B. P. & GRATTON C. 2008: Influence of field margins and landscape context on ground beetle diversity in Wisconsin (USA) potato fields. *Agriculture*, *Ecosystems and Environment* **128**: 104–108.