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AGEE-3710; No. of Pages 8
ARTICLE IN PRESS

Agriculture, Ecosystems and Environment xxx (2010) xxx–xxx

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

# Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage

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ARTICLE INFO

*Article history:*
Received 15 March 2010
Received in revised form 6 September 2010
Accepted 7 September 2010
Available online xxx

*Keywords:*
Agronomic practices
Ground and tiger beetles
Landscape structure
Local environment
Non-crop areas
Variation partitioning

ABSTRACT

In this study, two main hypotheses were tested: (1) whether landscape structure explains a greater part of the variation in predatory beetle assemblage than agronomic practices and local environment; and (2) whether non-crop areas and landscape heterogeneity have a positive effect on predatory beetle abundance and diversity. Ground and tiger beetles were sampled in ditch borders adjacent to 20 cornfields in 2006 and 2007 in Quebec (Canada). For each site, agronomic practices performed in the border and adjacent field, local border characteristics and landscape cartography (at 200 and 500-m radii) were measured. Compared with agronomic practices and the local environment, landscape structure was globally the main factor driving predatory beetle abundance and diversity, explaining 7.9–24.6% of the variation (unique contribution) depending on the variable and year. In most cases, non-crop areas and landscape heterogeneity had a positive influence on predatory beetle abundance and diversity. Our results showed that variables acting at large scales represent an essential factor influencing predatory beetle assemblage and they validate the importance of conserving non-crop areas and landscape heterogeneity in agricultural landscapes.



## 1. Introduction

In agroecosystems, natural pest control depends on field colonization by natural enemies from non-crop areas (Wissinger, 1997; Tscharntke et al., 2005). Many studies found that ground beetles, rove beetles and spiders are efficient biological control agents that are directly responsible for aphid mortality in fields (Östman, 2004; Schmidt et al., 2004; Van Alebeek et al., 2006). Ground beetles, in particular, consume a large variety of crop pest (Thiele, 1977; Kromp, 1999; Sunderland, 2002) and are often used as bioindicators to assess the impact of farming methods (Kromp, 1990) or environmental disturbances (Luff, 1996; Rainio and Niemelä, 2003).

Several studies have shown that ground beetles are influenced by agronomic practices (Hance and Grégoire-Wibo, 1987; Kromp, 1999; Holland and Luff, 2000), generally with a greater abundance or diversity in less intensive land-use systems or systems with reduced chemical input (Attwood et al., 2008). For instance, ground beetle assemblage is influenced by the farming system (organic versus conventional farm), usually showing greater abundance and diversity in organic farms (Kromp, 1989; Cárcamo et al., 1995; Bengtsson et al., 2005). In addition, ground beetle assemblage can be affected by crop rotation and land use (Booij and Noorlander, 1992; Ellsbury et al., 1998; Dauber et al., 2005), tillage (Cárcamo, 1995; Menalled et al., 2007; Nash et al., 2008), fertilization (Söderström et al., 2001) and the use of pesticides (Ellsbury et al., 1998; Epstein et al., 2001; Nash et al., 2008). Regarding seed characteristics, the effect of genetically modified plants on non-target organisms such as ground beetles is not clear (Floate et al., 2007). However, it has been found that ground beetles are actually exposed to the Bt toxin (Zwahlen and Andow, 2005).

On a local scale, the characteristics of field borders (vegetation composition, richness and width) and border management (mowing and/or fertilization) can explain differences in ground beetle assemblage in the border region (Sotherton, 1985; Woodcock et al., 2005, 2007; Griffiths et al., 2007) as well as in the adjacent field (Lys et al., 1994; Varchola and Dunn, 2001). For instance, Van Alebeek et al. (2006) found twice as many ground beetles in uncut field borders than in bare soils, providing evidence for the need to conserve the vegetation beside fields.

Beyond the local scale, it has been found that ground beetles can be affected by landscape structure independently of farming practices (Purtauf et al., 2005a). Many studies involving landscape have underlined the positive effect of non-crop areas (Purtauf et al., 2005a; Werling and Gratton, 2008; Perovic et al., 2010) and landscape heterogeneity (Weibull and Östman, 2003; Weibull et al., 2003; Ekroos et al., 2010) on ground beetle assemblage. In particular, Dauber et al. (2005) showed that ground beetle richness was positively correlated with the length of forest edges, and Hendrickx

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doi:10.1016/j.agee.2010.09.008

et al. (2007) showed that ground beetle diversity increased with the proximity of semi-natural habitat patches, confirming the need to conserve non-crop areas in agricultural landscapes.

Few studies have integrated different factors and scales to understand ground beetle assemblage (Weibull and Östman, 2003; Aviron et al., 2005; Schweiger et al., 2005), and there is still much uncertainty about which of these factors influence the assemblage of ground beetle communities. Moreover, given that most rural landscapes are perturbed by human activities, it is also crucial to quantify the impacts of anthropic variables. Therefore, the aim of this study was to understand the relative effects of agronomic practices, local environment and landscape structure on predatory beetle abundance and diversity (Coleoptera: Carabidae and Cicindelidae). First, we hypothesized that ground and tiger beetle abundance and diversity were more strongly influenced by landscape structure than by agronomic practices and local environment. Second, we wanted to verify whether ground and tiger beetle abundance and diversity were positively related to non-crop areas (fallow, woodland, border, riparian vegetation) and landscape heterogeneity (richness and diversity), as mentioned in previous studies.

## 2. Methods

### 2.1. Study area and sampling

The study was conducted in the Vacher creek watershed (Lanaudière, Quebec, Canada), located approximately 40 km northeast from Montreal, covering 69 km$^2$ and including the town of Saint Jacques (45°56′N, 73°34′O) and Sainte Marie Salomé (45°55′N, 73°29′O) (Domon et al., 2005). The Vacher creek watershed present landscapes with different land use configurations (Ruiz et al., 2008) and as a consequence, sampled sites were positioned throughout the entire watershed so that we could assess the potential effects of these configurations on predatory arthropods. Twenty sites were sampled in the watershed during the summers of 2006 and 2007, each site representing a ditch bordering a cornfield. We considered as field borders any elements that represented a limit between a field and another landscape element (e.g., simple herbaceous field margins, hedgerows, woody borders or ditches).

Ground and tiger beetles were collected weekly from the beginning of June until the end of September in 2006 and 2007, covering a span of 16 weeks over a period of two years. These sampling periods allowed us to collect both autumn-breeding and spring-breeding species, maximizing the representation of ground and tiger beetle abundance and diversity. A total of 80 pitfall traps (four traps per site, 20 sites) were installed each year. Pitfall traps consisted of Multipher I traps (⌀ 12.5 × H 24 cm) used without pheromone. A cover (⌀ 26 cm) was used to avoid water entering the trap and to limit the access to small mammals. Four openings (2.6 cm × 8.4 cm) allowed ground and tiger beetles to fall inside the traps. Traps were buried in the ground so that openings were at the ground level, and they were placed in the edge of the ditch, between the ditch and the field margin. The first trap was placed at approximately 10 m from the beginning of the field, and the other traps were placed every 10 m along a transect parallel to the ditch. A plastic container filled with approximately 100 ml of propylene glycol (car antifreeze with low toxicity) diluted with water (1:1) was placed inside each trap to preserve insects. Due to identification logistics, only ground and tiger beetles sampled every other week were identified to species based on Larochelle (1976), with Agriculture and Agri-food Canada's expert confirmation.

### 2.2. Agronomic practices

Agronomic descriptors included variables regarding the studied field border (ditch) and the agronomic practices conducted in the field next to it (see Appendix A for details of all the descriptors). Because we focused on ground-dwelling predators, soil characteristics and soil perturbations were considered as well. Border descriptors included soil type (sand, loam-clay, clay) and binary codes describing whether the border was mowed or not during the season. Regarding the cornfield, seed characteristics included corn heat unit (C.H.U.) that serves as a proxy for corn precocity. In order to determine whether genetically modified corn could influence ground and tiger beetles, two variables were taken into account: corn borer resistance (i.e., Bt corn) and herbicide tolerance. We also considered descriptors linked to the agronomic practices performed in the cornfield included crop rotation (i.e., whether or not the field was cultivated with crop other than corn in the previous year), sowing date, sowing rate, soil perturbation which included the type of tillage (superficial vs deep) and hoeing, soil fertilization (organic fertilization, post-emergence fertilization, quantity of nitrogen, potassium and phosphorus applied to the field) and phytosanitary treatment, including the type of herbicide used (amino acid, sulfonylurea, triazine) and the application date. In 2007, three agronomic descriptors were added due to changes in relation to 2006: the practice of direct-sowing (not performed in 2006) involved three categories of variables for tillage instead of two (direct sowing, superficial tillage and deep tillage), the application of pre-sowing mineral fertilizer (pre-sowing fertilization) and the addition of one group of herbicides (other herbicide). In total, 21 agronomic variables were estimated in 2006 and 24 in 2007. Note that no insecticide or fungicide was applied to the fields during the two-year study period.

### 2.3. Local environment

Local environment included descriptors related to the sampled ditch, the cornfield adjacent to the ditch (=focal field) and the landscape element located on the other site of the ditch (see Appendix B). The following local characteristics were measured regarding the ditch: width, tree presence, creek presence and vegetation richness. Data from the cornfield next to the border included field area and spatial orientation. Finally, the type of landscape element located on the other side of the ditch was characterized (corn, fodder crop, other crop, fallow, woodland or road). In 2007, none of the studied borders was located next to a road, so the road variable was removed from the local descriptors in 2007. Overall, 12 local variables were estimated in 2006 and 11 in 2007.

### 2.4. Landscape structure

Aerial photos of the Vacher creek watershed, dated from 1998, were obtained from the Minister of Environment du Québec (MDDEP) and were updated using information gathered directly in the field. Circles of 200 and 500-m radii were plotted around each site to delimit landscape descriptors. Only three descriptors were not measured at the 200-m level (see Appendix B) as these variables were based on the entire field which extension expands beyond 200 m. In 2006 and 2007, landscape composition within each circle was determined by field observation. Then, spatial analyses of landscape structure (composition and configuration) were performed using MapInfo (ESRI, 2000) and ArcGIS (ESRI, 2005). Regarding landscape composition, the areas of the different landscape elements were calculated at both scales (200 and 500 m): corn, leguminous crop (soybean or beans = bean), cereal (wheat, barley, oat or mixed cereals), fodder crop (grass, alfalfa, clover or mixed fodder), other crop (potatoes, berries or other vegetable crops), fallow, pasture, woodland, riparian vegetation, water (pool, creek or river), constructed area, road or path and sand pit. Landscape heterogeneity at 200 and 500 m was evaluated by landscape richness, representing the number of different landscape elements

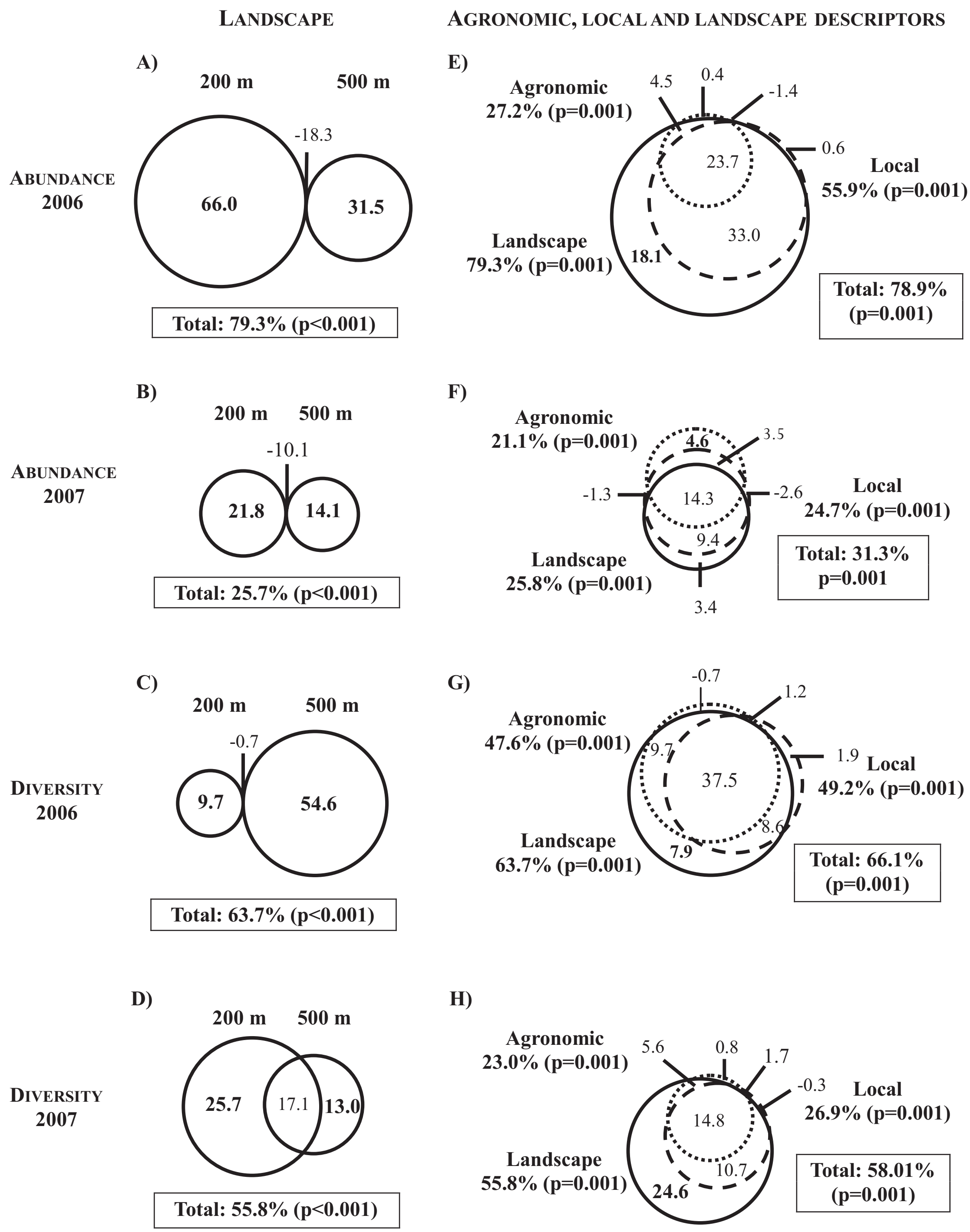


**Fig. 1.** Variation partitioning between landscape descriptors (A–D) and between agronomic (dotted line), local (dashed line) and landscape descriptors (solid line; E–H), explaining differences in predatory beetle abundance and diversity in two consecutive years, 2006 and 2007. Values inside circles (proportional to the explained variation) correspond to the explained fractions whereas values outside circles represent the total variation. Numbers inside one circle only represent the unique contribution whereas numbers inside two or three circles represent shared variation between respective sets. Percentages in bold were significant.

(maximum of 13 different landscape elements, as described above), and landscape diversity, based on the proportion of the 13 landscape elements around each site and assessed by the Shannon index (Yoshida and Tanaka, 2005). Landscape configuration at both scales included the density of field borders, estimated as the density (in m ha$^{-1}$) of non-cultivated corridors available for insect dispersion, landscape patchiness, expressed by the number of landscape elements, and the number of non-crop patches. Then, three descriptors were integrated to the 500-m circle: the mean area of fields, the perimeter-to-area ratio of landscape elements (p/a), which provides information about the form of landscape elements and quantity of frontiers between elements, and finally, the shortest distance to woodland, due to its potential to shelter ground beetles over the winter. We felt that it was more appropriate to integrate these three descriptors to the 500-m circle because this scale usually included the entire field area and distance to woodland was greater than 200 m in more than half of the sites. Note that the entire area and the entire perimeter of landscape elements were

Please cite this article in press as: Maisonhaute, J.-É., et al., Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. Agric. Ecosyst. Environ. (2010), doi:10.1016/j.agee.2010.09.008

taken into account, even if they overlapped with the focal radius of 500 m. Overall, 18 landscape variables were estimated at 200 m and 21 at 500 m (see Appendix B for further details).

### 2.5. Statistical analyses

Ground and tiger beetle abundance was calculated using the total number of individuals collected during the entire sampling season (16 weeks). Predatory beetle abundance data were square root transformed prior to analyses. Given the high number of specimens collected and the identification logistics, ground and tiger beetle diversity was estimated using the Shannon index (Magurran, 2004) from half of the samples (every other week). Because sampling sites were not the same in 2006 and 2007 (except for 7 sites), data from the two years were analyzed separately. Data were regrouped per site and per trap (20 sites, four traps per site, $n = 80$). Analyses were performed using MATLAB® (MathWorks, 2000) (most functions are available from the authors upon request). Abundance and diversity were analyzed separately and were based on a two-step procedure. First, a variable selection procedure (forward selection with permutation tests based on 999 permutations, alpha = 0.05; see Legendre and Legendre, 1998 for computational details) was used to produce a model containing only variables that had a significant and an independent effect when contrasted to other candidate predictors (hence reducing collinearity among predictors) on predatory beetle abundance or diversity. Forward selection allows us to conduct predictor selection in the presence of several candidate variables, but most importantly, it allows us to find a model in which high levels of predictive redundancy (collinearity) is reduced. Because we measured an extensive number of candidate predictors and that we knew that a number of them would be probably collinear (as they were), our strategy in retaining predictors that provided a significant independent contribution was related to the point of being able to argue more strongly for the importance of these predictors than the redundant ones. Note that a separate selection procedure was performed for each of the agronomic, local and landscape set of descriptors. Appendix B presents other predictors that were highly collinear with the ones selected but that were not retained by model selection.

Given the high collinearity of some predictors, we wanted first to determine the significant predictor within these sets and then understand how they were correlated across sets. Following this rationale, our second step was to conduct a variation partitioning scheme (see Peres-Neto et al., 2006 for details), which was applied to quantify the unique contribution of each matrix (agronomic, local and landscape) on predatory beetle abundance or diversity. Results of variation partitioning were based on adjusted variation which take into account the number of predictors and number of observations (akin to adjusted $R^2$; see Peres-Neto et al., 2006). In the partitioning, only significant descriptors within each set selected by the forward selection procedure were used. Additionally, a variation partitioning scheme was also performed with the selected predictors within the landscape set to assess the relative influence of descriptors at 200 and 500-m scales.

It is important to note that samples within sites were not treated independently. Although abundance and diversity (response variables) varied within sites, predictors assumed the same values within sites and therefore statistical tests are not affected at this level of variation (see Peres-Neto and Legendre, 2010 for further details).

## 3. Results

In total, 23,820 beetles were trapped in 2006, including 6575 ground and tiger beetles (27.6%), whereas 32,290 beetles were trapped in 2007, including 8207 ground and tiger beetles (25.4%). In 2006, the total abundance per site (=per ditch) varied from 104 to 1119 individuals, with a mean value of 328.75 ± 265.66. In 2007, it ranged from 169 to 749 individuals, with a mean value of 410.35 ± 178.50. The analyses of ground beetle diversity, based on 8 weeks, included 3147 ground and tiger beetles in 2006 and 4156 in 2007. Overall, 72 carabid species were identified: 66 species in 2006, 67 in 2007 and 58 species that were common to both years. In 2006, the total diversity per site varied from 0.86 to 3.08, with a mean value of 1.95 ± 0.59. It ranged from 0.74 to 2.56, with a mean value of 1.89 ± 0.45, in 2007.

### 3.1. Variation partitioning

In both years, ground and tiger beetle abundance was more influenced by variables at 200 m than at 500 m (Fig. 1A and B). In 2006, the global model explained 78.85% of the variation in ground and tiger beetle abundance ($p = 0.001$, Fig. 1E and Table 1). In this year, landscape structure was the most important factor, explaining 18.13% of the variation (unique contribution, $p = 0.001$), whereas agronomic practices and local environment had almost no effect and appeared non-significant compared to landscape structure (explaining 0.40% and 0.58% of the variation, respectively). However, the total amount of variation explained by the three groups combined (i.e., agronomic, local, landscape) was significant (Fig. 1E) though the effect of landscape structure remained as the most important. In 2007, the global model explained 31.32% of the variation in ground and tiger beetle abundance ($p = 0.001$, Fig. 1F and Table 1). In this year, although the effects of agronomic practices and landscape structure were quite comparable, only the effect of agronomic practices appeared significant (4.62% of variation, $p = 0.043$). The effects of local environment and landscape structure were not significant (−2.56% and 3.36% of the variation, respectively). The total amounts of variation of the three groups of variables appeared significant and were quite similar (Fig. 1F).

In 2006, ground and tiger beetle diversity was mainly influenced by variables at 500 m, whereas in 2007, it was more influenced by variables at 200 m (Fig. 1C and D). In 2006, the global model explained 66.05% of the variation in ground and tiger beetle diversity ($p = 0.001$, Fig. 1G and Table 2). In this year, landscape structure was the most important factor influencing ground and tiger beetle diversity explaining 7.93% of unique variation whereas agronomic practices and local environment had no (or very low) effects and did not appeared significant (−0.74% and 1.93% of variation, respectively). However, the total variation explained by the three groups of variables combined appeared significant and the effect of landscape structure was the most important (Fig. 1G). In 2007, the global model explained 58.01% of the variation in ground and tiger beetle diversity ($p = 0.001$, Fig. 1H and Table 2). In this year, landscape structure was the most important factor explaining alone 24.64% of the variation, whereas agronomic practices and local environment had no (or very low) effect (0.84% and −0.26% of variation, respectively). The total variation of the three groups of variables also appeared significant and the effect of landscape structure remained the most important (Fig. 1H).

### 3.2. Agronomic and local variables

In 2006, ground and tiger beetle abundance was positively influenced by crop rotation, the use of an amino acid herbicide and by the focal area of the field but negatively influenced by sandy and loamy-clay soil, vegetation richness, presence of tree in the ditch and presence of fodder crop in the other side of the ditch (Table 1). In 2007, ground and tiger beetle abundance was positively influenced by the presence of fodder crop and fallow in the other side of the ditch but negatively influenced by pre-sowing fertilization, the

**Table 1**
Model selection within agronomic, local and landscape descriptor sets explaining variation in predatory beetle abundance in 2006 and 2007.

| Year | Selected variables | *F* | *P* | Slope | Total variation (%) |
|---|---|---|---|---|---|
| 2006 | **Agronomic practices** | | 0.001 | | 27.18 |
| | Rotation | 11.18 | 0.002 | 0.90 | |
| | Sand | 10.09 | 0.003 | −2.09 | |
| | Loam-clay | 4.29 | 0.041 | −1.62 | |
| | Amino acid | 4.40 | 0.047 | 0.78 | |
| | **Local environment** | | 0.001 | | 55.86 |
| | Vegetation richness | 22.40 | 0.001 | −2.16 | |
| | Fodder | 28.86 | 0.001 | −1.42 | |
| | Tree | 13.58 | 0.001 | −0.94 | |
| | Focal area | 10.81 | 0.002 | 0.82 | |
| | **Landscape descriptors** | | 0.001 | | 79.27 |
| | Road 200 m | 15.34 | 0.002 | 4.18 | |
| | Bean 200 m | 22.91 | 0.001 | 3.89 | |
| | Road 500 m | 8.11 | 0.013 | −3.53 | |
| | Riparian vegetation 500 m | 14.50 | 0.002 | −1.97 | |
| | Richness 200 m | 19.00 | 0.001 | 2.87 | |
| | Bean 500 m | 17.24 | 0.001 | −3.69 | |
| | Woodland 500 m | 13.84 | 0.001 | −0.12 | |
| | Pasture 500 m | 8.75 | 0.008 | 0.85 | |
| | Corn 200 m | 7.01 | 0.014 | 0.83 | |
| | Other crop 200 m | 7.04 | 0.011 | −0.84 | |
| | Non-crop patches 200 m | 5.69 | 0.020 | −0.63 | |
| 2007 | **Agronomic practices** | | 0.001 | | 21.07 |
| | Pre-sowing fertilization | 11.71 | 0.002 | −0.96 | |
| | *N* | 10.03 | 0.004 | −0.90 | |
| | **Local environment** | | 0.001 | | 24.67 |
| | Fodder | 11.81 | 0.002 | 0.99 | |
| | Vegetation richness | 6.82 | 0.011 | −0.80 | |
| | Fallow | 7.67 | 0.007 | 0.77 | |
| | **Landscape descriptors** | | 0.001 | | 25.75 |
| | Fallow 200 m | 8.39 | 0.006 | 0.87 | |
| | Woodland distance | 6.92 | 0.010 | 1.08 | |
| | Corn 200 m | 7.96 | 0.005 | −0.99 | |
| | Richness 500 m | 4.78 | 0.037 | −0.62 | |

quantity of nitrogen applied in the field and by vegetation richness (Table 1).

In 2006, ground and tiger beetle diversity was positively influenced by the spread of a triazine herbicide, the quantity of nitrogen applied in the field, the presence of woodland and corn in the other side of the ditch and border width but negatively influenced by the use of a corn borer resistant seed, hoeing, field orientation and the presence of fallow in the other side of the ditch (Table 2). In 2007, ground and tiger beetle diversity was positively influenced by direct sowing, the use of an herbicide tolerance seed and a triazine herbicide but negatively influenced by the presence of other crop (potato, berry or vegetable crop) in the other side of the ditch and by field orientation (Table 2).

### 3.3. Landscape variables

In 2006, area in bean, corn and road within 200 m, landscape richness within 200 m and area in pasture within 500 m positively influenced ground and tiger beetle abundance whereas area in other crop and non-crop area patchiness within 200 m (number of non-crop patches) and area in bean, woodland, riparian vegetation and road within 500 m had negative effects (Table 1). In 2007, area in fallow within 200 m and distance to woodland positively influenced ground and tiger beetle abundance whereas area in corn within 200 m and landscape richness within 500 m had negative effects (Table 1).

In 2006, area in cereal and pasture within 200 m and area in other crop and riparian vegetation within 500 m positively influenced ground and tiger beetle diversity whereas landscape diversity within 200 and 500 m and area in cereal within 500 m had negative effects (Table 2). In 2007, area in woodland within 200 and 500 m, landscape diversity within 500 m and distance to woodland positively influenced ground and tiger beetle diversity whereas area in other crop, landscape diversity and density of field borders within 200 m had negative effects (Table 2).

## 4. Discussion

Overall, our results showed that landscape structure is an important factor driving ground and tiger beetle assemblage, with a contribution usually greater than either agronomic practices or local environment. These findings suggest that in the studied agricultural landscapes, predatory beetle communities respond strongly to variables acting at larger scales (200 and 500 m). Note that similar studies also found an influence of landscape structure on ground beetles at similar scales (Weibull et al., 2003: 400 m × 400 m; Aviron et al., 2005: 500 m × 500 m; Dauber et al., 2005: 250 m radius). As only few studies were performed on even greater scales (Schweiger et al., 2005), it is still uncertain how far landscape structure may influence predatory beetle assemblages.

Moreover, our results showed that landscape composition was more important than landscape configuration in explaining differences in ground and tiger beetle abundances and diversity observed in the Vacher creek watershed. Most of the significant landscape variables were related to landscape composition (area in corn, bean, cereal, other crop, fallow, pasture, riparian vegetation, woodland, road, landscape richness and diversity, Tables 1 and 2) and only few variables were related to landscape configuration (number of non-crop patches, density of field borders, distance to woodland).

**Table 2**
Model selection within agronomic, local and landscape descriptor sets explaining variation in ground beetle diversity in 2006 and 2007.

| Year | Selected variables | *F* | *P* | Slope | Total variation (%) |
|---|---|---|---|---|---|
| 2006 | **Agronomic descriptors** | | 0.001 | | 47.63 |
| | Triazine | 18.06 | 0.001 | 0.43 | |
| | Corn borer | 23.58 | 0.001 | −0.15 | |
| | *N* | 5.16 | 0.027 | 0.18 | |
| | Hoeing | 12.81 | 0.001 | −0.25 | |
| | **Local descriptors** | | 0.001 | | 49.17 |
| | Field orientation | 33.28 | 0.001 | −0.29 | |
| | Fallow | 12.79 | 0.002 | −0.17 | |
| | Woodland | 6.95 | 0.009 | 0.13 | |
| | Corn | 5.52 | 0.027 | 0.13 | |
| | Border width | 5.73 | 0.024 | 0.11 | |
| | **Landscape descriptors** | | 0.001 | | 63.65 |
| | Riparian vegetation 500 m | 43.38 | 0.001 | 0.28 | |
| | Diversity 500 m | 14.54 | 0.001 | −0.08 | |
| | Cereal 500 m | 9.83 | 0.003 | −0.45 | |
| | Cereal 200 m | 10.07 | 0.004 | 0.37 | |
| | Other crop 500 m | 9.29 | 0.009 | 0.20 | |
| | Diversity 200 m | 5.26 | 0.031 | −0.23 | |
| | Pasture 200 m | 4.01 | 0.048 | 0.09 | |
| 2007 | **Agronomic descriptors** | | 0.001 | | 22.96 |
| | Direct sowing | 13.88 | 0.001 | 0.15 | |
| | Herbicide tolerance | 5.99 | 0.017 | 0.11 | |
| | Triazine | 4.77 | 0.032 | 0.10 | |
| | **Local descriptors** | | 0.001 | | 26.91 |
| | Other crop | 12.72 | 0.002 | −0.18 | |
| | Field orientation | 15.94 | 0.001 | −0.17 | |
| | **Landscape descriptors** | | 0.001 | | 55.76 |
| | Woodland 200 m | 27.66 | 0.001 | 0.01 | |
| | Field borders 200 m | 11.60 | 0.005 | −0.12 | |
| | Other crop 200 m | 12.82 | 0.002 | −0.11 | |
| | Diversity 500 m | 5.72 | 0.018 | 0.36 | |
| | Woodland distance | 4.58 | 0.038 | 0.25 | |
| | Diversity 200 m | 6.23 | 0.021 | −0.22 | |
| | Woodland 500 m | 7.03 | 0.009 | 0.51 | |

Except for the abundance analysis for 2007, landscape structure represented the most influential factor explaining the variation in predatory beetle abundance and diversity. When considering the total variation (including the contribution shared with agronomic and local descriptors), landscape structure was still the most influential factor (Fig. 1). Our results confirm that variables acting at large scales are more important for ground and tiger beetles than local parameters. On one hand, this result contradicts previous European studies in which habitat (i.e., local environment) was the principal factor influencing ground beetle assemblage. For example, in Germany, Dauber et al. (2005) found that ground beetle richness was more influenced by habitat characteristics such as land use (40% of variance) than by landscape variables on 200 m scale (15% of variance). This was also the case for Jeanneret et al. (2003) in Switzerland (habitat: 16% of variance, landscape: 3% of variance, 200 m scale). Weibull and Östman (2003) also found that "habitat type" was the main factor influencing the species composition of ground beetles (28% of variance), but landscape heterogeneity on 400 m scale also explained a significant component of the variation (25% of the variance). On the other hand, some studies have found that variables acting on a large scale were more important than the local environment. According to Schweiger et al. (2005), whose study covered seven European countries, ground beetle assemblage was mostly influenced by large-scale landscape variables (land use intensification and semi-natural elements on a $4 \times 4$-km scale: 16% of variance) than by local variables (habitat composition and diversity on a 50-m scale: 3% of variance). In France, Aviron et al. (2005) found that landscape unit (corresponding to a 25 km$^2$ landscape) represented the most important factor influencing ground beetle assemblage, explaining 10% of the variation, whereas habitat characteristics explained 9% of the variation, and landscape elements (woodland within 500 m) explained only 4%.

Agronomic practices had only a small contribution. This result is in agreement with studies that found no effect of the farming system (Melnychuk et al., 2003; Purtauf et al., 2005a) or agronomic practices (Lalonde et al., 2008; Ekroos et al., 2010) on ground beetle diversity or abundance. However, several studies demonstrated that ground beetles were influenced by agronomic practices, showing a greater abundance in reduced tillage and reduced chemical use systems (Nash et al., 2008). Furthermore, results can depend on the species considered, as some ground beetle species are more sensitive to agronomic practices than others (Cárcamo et al., 1995), which can hide the effect of agronomic practices when studying the total abundance. In our study, the relative influence of agronomic practices varied among species, being more important for some species than for others (unpublished data) but when considering all species, ground and tiger beetle assemblage is only slightly influenced by agronomic practices. The differences between years regarding agronomic practices may be partially explained by the pre-sowing fertilization (not performed in 2006), that appeared significant in the abundance analysis for 2007. Thus, it appears that fertilization early in the season negatively influenced ground beetle abundance, perhaps because natural vegetation around fields is not sufficiently developed to provide shelter. In some regions, it has been shown that landscape structure can be directly associated with agronomic practices. For instance, Millàn de la Peña et al. (2003) observed that landscape openness was highly correlated with corn areas, which was characteristic of milk farms. In our case, the variance shared between agronomic and landscape descriptors was usually low. This indicates that agronomic and landscape descriptors are usually independent in our study, reinforcing our results regarding the influence of landscape structure alone.

Local environment had no or a very small contribution in explaining predatory beetle assemblage. Although the characteristics of the sampled ditches were quite different (for example, in terms of vegetation richness and width), it seems that these characteristics did not affect predatory beetle assemblage. These results are in agreement with Marshall et al. (2006), who found no effect of field border characteristics on ground beetle assemblage. However, vegetation may influence ground beetle assemblage depending on the trophic group as herbivorous beetles prefer habitats with greater plant diversity (Harvey et al., 2008). The variance shared between local and landscape descriptors was quite relevant when compared to the variation shared between agronomic and landscape descriptors, indicating that local and landscape descriptors were more strongly related. This was somewhat expected given that landscape descriptors can indirectly include some of the local descriptors. Then, local environment and landscape structure can be related. For instance, it has been found that the local diversity of weeds in wheat fields increased with landscape complexity (i.e., the percentage of non-crop areas) (Gabriel et al., 2005).

Variation partitioning helps to provide an overall picture of the differences in sets of predictors. The influence of each independent variable can be analyzed, but they may correlate with each other very strongly in some cases, reducing their importance in the regression model. Indeed, given the somewhat high levels of shared variation across predictor sets and that the influence of different predictors was not necessarily consistent between the two years, it is not possible to determine the exact independent role of many variables. Finally, differences between years could be explained by external factors that were not taken into account in the study like the weather or other abiotic factors, or the presence of preys in the surrounding crops.

Several studies have shown a positive effect of non-crop areas and landscape heterogeneity on predatory arthropods. Non-crop areas are found to increase ground beetle richness (Purtauf et al., 2005b) and spider abundance and richness (Clough et al., 2005; Schmidt et al., 2005; Thorbek and Topping, 2005), whereas landscape diversity was related to a greater diversity of spiders (Clough et al., 2005) and ground beetles (Weibull and Östman, 2003). Recently, in the US, Werling and Gratton (2008) confirmed these results, in which ground beetle diversity in potatoes fields increased with the amount of non-crop areas at large scales (1.5 km). Unfortunately, our results could not provide a strong support to the idea that non-crop areas and landscape heterogeneity (landscape richness and diversity) are related to a great abundance and diversity of predatory beetles. However, non-crop areas appeared to have a greater positive effect on predatory beetle diversity (effect of riparian vegetation, pasture, woodland) than on abundance (effect of fallow and pasture). Conversely, predatory beetle diversity was often more negatively related to landscape diversity. In fact, predatory beetle abundance appeared to be both positively and negatively affected by the surrounding crops, non-crop areas and landscape heterogeneity.

Concluding, our study showed that both ground and tiger beetle assemblage respond globally to large-scale variables such as landscape structure and is less sensitive to agronomic practices and local environment. Therefore, environmental management, with the goals of increasing predatory beetle abundance and diversity, should take into account not only the local characteristics of the habitat but also the characteristics of the surrounding landscape.

## Acknowledgements

We would like to thank Yves Bousquet (Eastern Cereal and Oilseed Research Centre, Agriculture and Agri-food Canada) for taxonomic assistance, Yann Roche and Samy Bouma for their help in cartography and GIS and Pierre Drapeau and Christopher Buddle for their comments. The help of Karine Gauthier, Simon Paradis, Maryse Desrochers, Noémie Charest-Bourdon, Félix Bureau-Primeau, Dominique Dubreuil, Anik Pelletier-Leboeuf and Adriana Puscasu in field sampling and in the lab are much appreciated, as well as Nathalie Roullé and all members of the laboratory of biological control of UQAM for their general support of this research. Finally, we would like to thank the farmers involved in this project, 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, for funding.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.09.008.

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Please cite this article in press as: Maisonhaute, J.-É., et al., Influence of agronomic practices, local environment and landscape structure on predatory beetle assemblage. Agric. Ecosyst. Environ. (2010), doi:10.1016/j.agee.2010.09.008