

## Seasonal modulation of landscape effects on predatory beetle assemblage

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### Abstract

Arthropod assemblages are influenced by various factors including landscape structure. In temperate areas, agricultural landscapes undergo drastic seasonal changes, which can directly affect arthropod communities and their responses to landscape structure. In this study, we aimed to test whether the effects of landscape structure vary throughout the summer season, using predatory beetles as a model system (Coleoptera Carabidae: Carabinae and Cicindelinae). Our main hypothesis was that predatory beetle assemblages were more influenced by landscape structure at mid-season (July-August) when the vegetation is fully grown. Then, we hypothesized that differences between species would be related to their biological and ecological characteristics. Ground and tiger beetles were sampled with pitfall traps in 20 ditch borders adjacent to cornfields, from early June to the end of September in 2006 and 2007, in the Vacher creek watershed (Quebec, Canada). Landscape cartography was measured at 200 m and 500 m radius around each site. As predicted, landscape structure had a strong seasonal component in structuring these communities, with the greatest influence observed at mid-season. Regarding species abundances, landscape structure mainly had the highest influence at mid-season, but variations were observed between species. Landscape effect on *Harpalus pensylvanicus* (DeGeer) appeared the most variable throughout the season (0-53.8%) whereas landscape effect on *Poecilus lucublandus lucublandus* (Say) appeared the most consistent (13.9-41.0%). Overall, our results demonstrate the importance of considering seasonality when assessing the effects of landscape structure on arthropod assemblage in temperate areas, but further studies are needed to determine species ecological characteristics that explain their differential responses.

**Key words:** species assemblage, *Bembidion quadrimaculatum oppositum*, *Harpalus pensylvanicus*, *Poecilus lucublandus lucublandus*, *Pterostichus melanarius*, landscape structure, seasonality.

### Introduction

Agricultural landscapes show great variations across geographical locations and human activities. In temperate areas, agricultural landscapes are often a mosaic of crop and non-crop patches with different levels of management intensity (Blackshaw and Vernon, 2006). In such landscapes, many predatory arthropods, including ground beetles, are known to move cyclically between fields and non-crop areas (Wissinger, 1997; Thomas *et al.*, 2001). In agricultural landscapes, herbaceous non-crop areas comprise alternative food resources and offer reproductive or overwintering sites for numerous predatory arthropods (Sotherton, 1985; Dennis *et al.*, 1994; Landis *et al.*, 2000; Geiger *et al.*, 2009).

The importance of non-crop areas in agro-ecosystems has been demonstrated by several studies. First, non-crop areas were generally related to lower crop pests and a more efficient biological control in fields (Veres *et al.*, 2013). In fact, increasing the proportion of non-crop areas in the landscape can enhance the abundance or diversity of many predatory arthropods such as spiders (Clough *et al.*, 2005), ladybirds (Burgio *et al.*, 2004; 2006) and ground beetles (Purtauf *et al.*, 2005b). It can also increase parasitism rates (Thies *et al.*, 2003; Plečaš *et al.*, 2014) and reduce aphid establishment (Östman *et al.*, 2001). Landscape heterogeneity or diversity is another landscape component that affects arthropod populations. Past researches show a positive effect of landscape heterogeneity or diversity on the arthropod abundance or richness, with effects observed on butterflies (Kerr *et al.*, 2001), moths (Scalercio *et al.*, 2012), spiders (Thorbeck and Topping, 2005), epigaeic

beetles (Romero-Alcaraz and Ávila, 2000), some coccinellid species (Maisonhaute and Lucas, 2011) and ground beetles (Weibull *et al.*, 2003; Werling and Gratton, 2008; Ekroos *et al.*, 2010). Overall, a heterogeneous or diversified landscape likely supports a greater diversity of arthropods, which can increase ecosystem stability (Altieri, 1994). Diverse landscapes were also found related to higher biological control in fields (Gardiner *et al.*, 2009). In addition to the effect of non-crop areas and landscape heterogeneity, arthropod populations can also be influenced by landscape fragmentation. Landscape fragmentation can have either positive effects on predatory arthropods, e.g., when increasing species richness and density of ladybirds (Grež *et al.*, 2004; Zaviezo *et al.*, 2006) or negative effects, e.g., when reducing the viability of forest ground beetles (Pichancourt *et al.*, 2006).

Temporal effect is also important to consider when studying arthropods. In fact, it is well known that ground beetle assemblage and activity density can undergo seasonal modulation and disparity across habitats (Niemelä *et al.*, 1992; Carmona and Landis, 1999; French and Elliott, 1999; Boivin and Hance, 2003; Juen and Traugott, 2004). In particular, beetle assemblages show greater seasonal modulations in canopy in contrast to ground layer (Hardersen *et al.*, 2014). Moreover, seasonal effects had also been observed on seed predation by ground beetles (Honek *et al.*, 2006). Finally, although seasonal modulations of the landscape effects had been reported, very few studies have tackled this subject. Some studies performed on aphids found that different landscape effects occur depending on crop phenology (Thies *et al.*, 2005) or sampling period

(Roullé *et al.*, 2015). For instance, different landscape effects on aphids and their natural enemies were observed in early versus late season (Alignier *et al.*, 2014). Regarding ground beetle populations, only a single study assessed the effects of grassy field borders and hedgerows and found that they differed throughout the season (Varchola and Dunn, 2001), but the effects of landscape structure in the surroundings has never been evaluated. Overall, no study to date has really focused on the seasonal modulation of the landscape effects on predatory arthropods. However, in temperate countries, agricultural landscapes change drastically along the crop season and as a function of the crop (and non-crop plant) growth. In Quebec (Canada), lands are covered by snow in the winter and regrowth of natural vegetation occurs just after the thaw in spring, becoming fully grown in the summer then withering in the fall. Crops are also fully grown in the summer, starting to grow in the spring (sowing in April-June depending on the crop) and being harvested at the end of the summer or in the fall (August-November). This cyclic development of both crop and non-crop vegetation may then influenced the arthropod abundance.

Besides the temporal effects, landscape effects on predatory arthropod populations can also vary between species. Differences can be due to biological and ecological characteristics, in which differences can be observed across functional groups (Maisonhaute and Lucas, 2011) or trophic guilds (Schweiger *et al.*, 2005; Lucas and Maisonhaute, 2015). For instance, carnivorous beetles are more affected by landscape simplification (i.e. decrease of non-crop areas) than phytophagous, whereas omnivorous beetles do not seem to be affected (Purtauf *et al.*, 2005a). Furthermore, it appears that ground beetles are differently influenced by landscape structure depending on their size and mobility, with larger species, often apterous, being favoured by less perturbed landscapes and landscapes composed of high density of hedgerows, whereas small ones, more mobile, appear more abundant in open and perturbed landscapes (Millán de la Peña *et al.*, 2003; Aviron *et al.*, 2005).

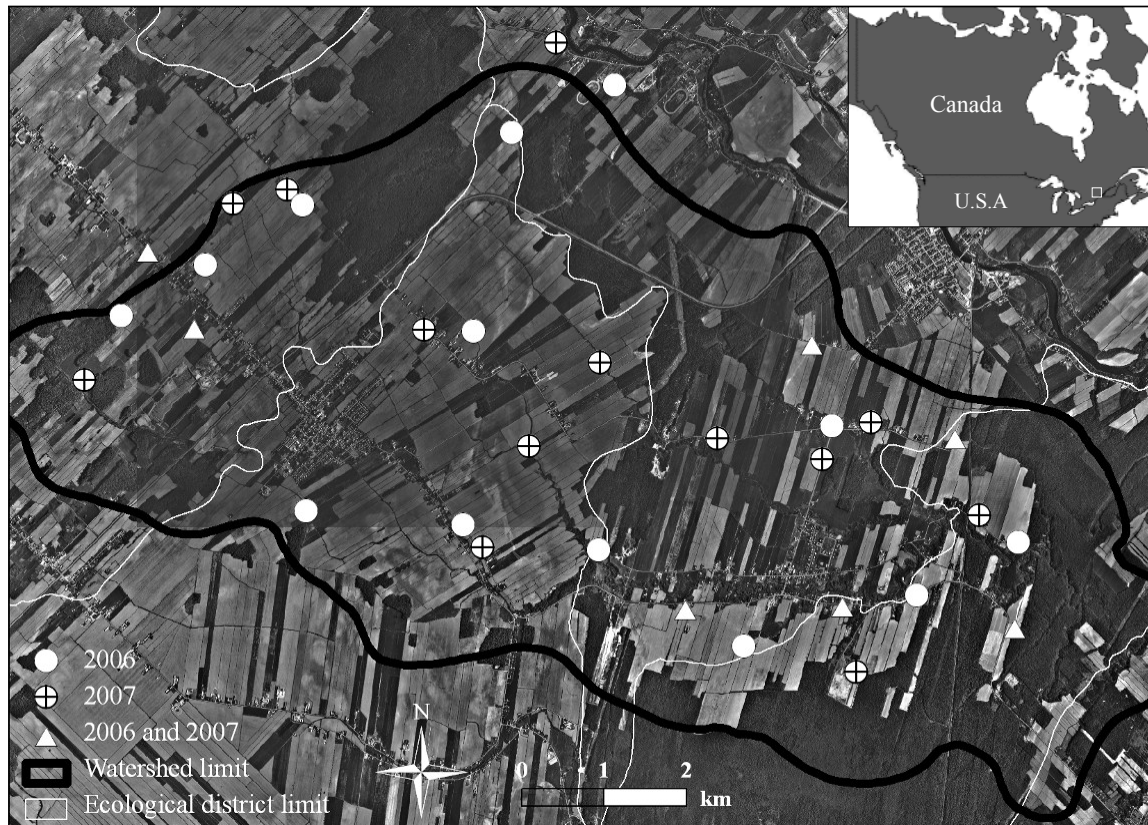
The aim of the present study was to determine whether landscape effects vary throughout the crop growing season, using as a model the ground and tiger beetle species found in ditch borders adjacent to cornfields. Our main hypothesis was that landscape effects would be maximal in the middle of the season (July-August) when the crop and non-crop vegetation is fully grown, contrary to the beginning of the season when bare soils are frequent and crop has just emerged (June) or to the end of the season when some crops (e.g., cereals) are harvested (September) or when other crops are mature and begin to wither. First, we were interested in the modulation of the effect of landscape structure on the species assemblage (i.e., the whole ground and tiger beetle species). Secondly, we wanted to verify the individual responses, focusing on some specific species. We aimed to determine whether the seasonal modulation of the landscape effects would be the same for all these species or if some differences could be related to their biological and ecological characteristics (size, flight ability and feeding group).

## Materials and methods

### Studied area and sampling

Predatory beetles were sampled in the Vacher creek watershed (Quebec, Canada, 45°5'N 73°3'W, figure 1), which was the focal area for a larger project on landscape management (Ruiz *et al.*, 2008) and previous studies investigating on the relative influence of landscape structure on ground beetles (Maisonhaute *et al.*, 2010), aphidophagous predators (Maisonhaute and Lucas, 2011) and aphids (Roullé *et al.*, 2015). This area is characterised by different landscape and land-use configurations (Ruiz *et al.*, 2008), so the sampling was performed throughout the entire watershed in order to maximize landscape heterogeneity. Sampling, including both ground and tiger beetles, was performed during the summers of 2006 and 2007 and was conducted on 20 ditch borders adjacent to cornfields (seven ditches common in both years). A total of 80 pitfall traps, initially filled with about 100 ml of propylene glycol (car antifreeze, low toxicity) diluted with water (1:1), were installed across the watershed at the rate of four traps per ditch border. The traps were installed along the ditch border, placed 10 m away from each other (for further information about the sampling protocol, see Maisonhaute *et al.*, 2010). The sampling period was the same for all the traps, and the sampling was performed weekly from the beginning of June to the end of September. This sampling period allowed us to collect both spring-breeding and autumn-breeding species. In the lab, ground and tiger beetles were identified at the species or morphotype levels for samples collected every two week (totalling 8 weeks), and the identification was confirmed later on by an expert (Agriculture and Agri-food Canada).

Four species were by far the most abundant ones: *Pterostichus melanarius* (Illiger), *Poecilus lucublandus lucublandus* (Say), *Harpalus pensylvanicus* (DeGeer) and *Bembidion quadrimaculatum oppositum* Say. In both years, they represented around 70% of all the total abundance (table 1), whereas the other species accounted for less than 5% each. As a result, in the second part of the study, we focused only on these four species. The biological and ecological characteristics of these species were listed in table 2. Three main hypotheses were proposed regarding the seasonal modulation of the landscape effects on these four species. We expected that the species that were the most affected by landscape structure would also show the greatest seasonal modulation of landscape effects. Thus, based on the feeding group hypothesis (Purtauf *et al.*, 2005a), the seasonal modulation of landscape effects should be greater for the carnivorous beetle than for the omnivorous species (*B. quadrimaculatum* > *P. melanarius*, *P. lucublandus*, *H. pensylvanicus*). Based on the size hypothesis (small species less affected by landscape structure: Aviron *et al.*, 2005), a greater seasonal modulation of landscape effects should be observed for the largest species (*P. melanarius* > *H. pensylvanicus* > *P. lucublandus* > *B. quadrimaculatum*). Finally, based on the flight hypothesis (more mobile species less affected by landscape structure: Millán de la Peña *et al.*, 2003; Aviron *et*



**Figure 1.** Distribution of the 20 sites sampled in 2006 and 2007 across the Vacher creek watershed (Lanauidière, Quebec, Canada). The watershed covers 69 km<sup>2</sup> and is located about 40 km north-east of Montreal. Hierarchical classification of the territory was performed using the Ecological Reference Framework which divided the watershed into four major ecological districts. Each site represents a ditch border adjacent to a cornfield. Seven sites were common in both years. Aerial photography: Gouvernement du Québec.

**Table 1.** Total abundance of the main ground and tiger beetles species trapped in 2006 and 2007. Sampling occurred in the Vacher creek watershed (Quebec, Canada) in the summers (June-September).

Species	2006	2007	Total
<i>P. melanarius</i>	1247 (39.6%)	1035 (24.9%)	2282 (31.2%)
<i>P. lucublandus</i>	433 (13.8%)	298 (7.2%)	731 (10.0%)
<i>H. pensylvanicus</i>	298 (9.5%)	783 (18.8%)	1081 (14.8%)
<i>B. quadrimaculatum</i>	251 (8.0%)	737 (17.7%)	988 (13.5%)
Total of the 4 species	2229 (70.8%)	2853 (68.7%)	5082 (69.6%)
<i>Agonum palustre</i>	33 (1.0%)	25 (0.6%)	58 (0.8%)
<i>Agonum muellieri</i>	15 (0.5%)	45 (1.1%)	60 (0.8%)
<i>Agonum placidum</i>	24 (0.8%)	46 (1.1%)	70 (1.0%)
<i>Amara</i> sp.	77 (2.4%)	180 (4.3%)	257 (3.5%)
<i>Anisodactylus harrisi</i>	109 (3.5%)	93 (2.2%)	202 (2.8%)
<i>Chlaenius tricolor</i>	81 (2.6%)	110 (2.6%)	191 (2.6%)
<i>Clivina fossor</i>	32 (1%)	36 (0.9%)	68 (0.9%)
<i>Diplocheila obtusa</i>	46 (1.5%)	36 (0.9%)	82 (1.1%)
<i>Harpalus compar</i>	73 (2.3%)	63 (1.5%)	136 (1.9%)
<i>Harpalus herbivagus</i>	46 (1.5%)	44 (1.1%)	90 (1.2%)
<i>Harpalus rufipes</i>	15 (0.5%)	56 (1.3%)	71 (1.0%)
<i>Harpalus somnulentus</i>	8 (0.3%)	63 (1.5%)	71 (1.0%)
<i>Ophonus rufibarbis</i>	37 (1.2%)	89 (2.1%)	126 (1.7%)
<i>Poecilus chalcites</i>	79 (2.5%)	56 (1.3%)	135 (1.8%)
Other species	243 (<1% each)	361 (<1% each)	604 (<1% each)
<b>Total</b>	<b>3147</b>	<b>4156</b>	<b>7303</b>

**Table 2.** Biological and ecological characteristics of the fourth most abundant ground beetle species trapped in the Vacher creek watershed in 2006 and 2007. References: <sup>1</sup>Larochelle and Larivière (2003), <sup>2</sup>Larochelle (1976), <sup>3</sup>Kromp (1999).

Characteristics	<i>P. melanarius</i>	<i>P. lucublandus</i>	<i>H. pensylvanicus</i>	<i>B. quadrimaculatum</i>
Tribe <sup>1</sup>	Pterostichini	Pterostichini	Harpalini	Bembidiini
Mean size (mm) <sup>2</sup>	15.6	11.6	12.5	3.3
Feeding group <sup>1</sup>	Omnivorous	Omnivorous	Omnivorous	Carnivorous
Wings <sup>1</sup>	Dimorphic (mostly macropterous)	Submacropterous	Macropterous	Dimorphic
Flight <sup>1</sup>	Occasionally	Occasionally	Frequently	Frequently
Runner <sup>1</sup>	Moderate	Moderate	Moderate	Moderate
Climber <sup>1</sup>	Occasionally (trees)	Occasionally (plants)	Occasionally (plants and trees)	Occasionally (plants and trees)
Ground <sup>1</sup>	Open or slightly shaded	Open (mostly) or slightly shaded	Open	Open
Activity <sup>1</sup>	Nocturnal	Mostly nocturnal, sometimes diurnal	Mostly nocturnal, sometimes diurnal	Mostly nocturnal, sometimes diurnal
Seasonality <sup>1</sup>	April-November	January-December	January-December	January-December
Reproduction <sup>1</sup>	July-October (autumn breeder)	April-July (spring breeder)	June, August-September (spring and autumn breeder)	May-beginning of July (spring breeder)
Overwintering <sup>1</sup> (adult)	Cultivated field, roadside, sand pit	Cultivated field, fallow, pasture, hill, sand pit, wood edge, wood	Cultivated field, fallow, sand or gravel pit, wood edge, wood clearing	Fallow, roadside, gravel pit, hillock, wood edge, wood
Other information <sup>1</sup>	Strongly favoured by human activities, strong colonialist	Favoured by human activities	Strongly favoured by human activities	Strongly favoured by human activities
Pest controlled <sup>1,3</sup>	Lepidopterous caterpillars, aphids, gall midges, cabbage root fly eggs, apple maggot, leatherjackets, potato beetle larvae, teneral and adult weevil, cabbage white caterpillars	Earwigs, Lepidopterous caterpillars	Crop pests	Onion maggot, aphids, midge larvae, weevil

*al.*, 2005), we expected a greater seasonal modulation of landscape effects for the occasional flyers versus frequent flyers (*P. melanarius*, *P. lucublandus* > *H. pensylvanicus*, *B. quadrimaculatum*).

### Landscape structure

Aerial photos of the Vacher creek watershed dating from 1998 (Gouvernement du Québec) were updated using information gathered in the field in 2006 and 2007. Circles of 200 m and 500 m radius were plotted around each site and matrix descriptors were assessed at each of these two scales. Land occupation within each circle was determined by field observations. These scales were chosen according to a previous study on landscape effects on aphids that was also performed in the Vacher creek watershed (Roullé *et al.*, 2015). Moreover, other studies found that ground beetles are influenced by landscape structure at similar scales (e.g., Dauber *et al.*, 2005: 250 m). Landscape composition and configuration at 200 and 500 m were analysed using MapInfo (ESRI, 2000) and ArcGIS (ESRI, 2005). First, landscape composition around field was determined in terms of the area (in m<sup>2</sup>) of following landscape elements: cornfields, leguminous crops (soya and beans), cereals (wheat, barley, and oat), fodder crops (grass, leguminous and mixed), other crops (potatoes, berries and other vegetable crops), fallow, pasture, woodland, riparian vegetation, water, sand pit, constructed area (house and other buildings) and road (road and path). Land-

scape heterogeneity was evaluated by calculating landscape richness (number of different landscape elements, based on the 13 landscape elements mentioned above) and landscape diversity assessed using the Shannon index of diversity. Landscape configuration was determined by the density of field borders (meters of borders per hectare), landscape patchiness (number of landscape element patches) and non-crop patchiness (number of patches of fallow, pasture, woodland and riparian vegetation). The following landscape descriptors were exclusively associated with the 500 m matrix: the shortest distance to woodland (in m), the mean field area (in m<sup>2</sup>) and the mean perimeter-to-area ratio (p/a, in m<sup>-1</sup>) of landscape elements. For more information on the landscape descriptors, see Maisonhaute *et al.*, 2010.

### Statistical analyses

The variation in beetle abundance throughout the season was evaluated in R (R Core Team, 2013). As *P. melanarius*, *P. lucublandus*, *H. pensylvanicus* nor *B. quadrimaculatum* were found non-normally distributed (Shapiro-Wilk normality test:  $p < 0.0001$ ), differences in abundance throughout the season (June, July, August, September) were evaluated using the Kruskal-Wallis rank sum test (Yau, 2013).

The effect of landscape structure at 200 and 500 m was evaluated monthly (June, July, August and September) focusing on 1) the species assemblage (i.e., the abundance matrix of all species) then 2) the abundance

of one specific species (*P. melanarius*, *P. lucublandus*, *H. pensylvanicus* and *B. quadrimaculatum*). Analyses were performed on the total abundance of ground beetles collected per trap per site each month (June = weeks 1-2, July = week 3-4, August = weeks 5-6, August = weeks 7-8, identification performed on samples collected every two weeks). Data were transformed using the Hellinger transformation (Legendre and Gallagher, 2001) given the presence of zeroes in the species matrix (species assemblage analysis only). Analyses were performed using MATLAB® (MathWorks, 2000) (most of the functions are available upon request) and were based on a two-step procedure as mentioned below (for more details about the statistical analyses, see Maisonhaute *et al.*, 2010). First, a forward selection (entrance criteria based on permutation tests, 999 permutations,  $\alpha = 0.05$  as criteria for each individual variable) was performed to select an important subset of landscape descriptors at each scale (200 m and 500 m). Then, linear regression slopes were calculated for each significant variable to determine the direction of the relationship between the landscape descriptor and the species assemblage or the abundance of each ground beetle species individually. Adjusted  $R^2$  was calculated for the models including all the significant variables at 200 m and 500 m. Finally, a variation partitioning (Peres-Neto *et al.*, 2006) between landscape descriptors at 200 m and 500 m was performed to evaluate the contribution of landscape structure at each of these scales in explaining ground beetle assemblage composition.

## Results

### Landscape structure

Information on all landscape descriptors at 200 m and 500 m cannot be detailed in this paper, but the data are available upon request. Marked differences in landscape structure among sites were observed. Focusing on the landscape structure at 500 m around sampled sites, it can be noticed that cornfields were the dominant crop every year, with a mean proportion accounting respectively for  $29.4 \pm 15.0\%$  and  $29.4 \pm 15.7\%$  in 2006 and

2007 (mean  $\pm$  standard deviation) respectively, while the mean proportion of fodder crops accounted for  $12.4 \pm 12.4\%$  in 2006 and  $13.4 \pm 14.7\%$  in 2007. The mean proportion of woodland represents  $14.1 \pm 16.1\%$  of the landscape area in 2006 and  $12.5 \pm 19.3\%$  in 2007. In both years, the mean crop diversity value was  $1.83 \pm 0.3$  (Shannon index). Finally, the mean area of all the fields that intercepted the 500 m radius around the sites was  $5.46 \pm 0.45$  in 2006 and  $5.0 \pm 0.39$  in 2007.

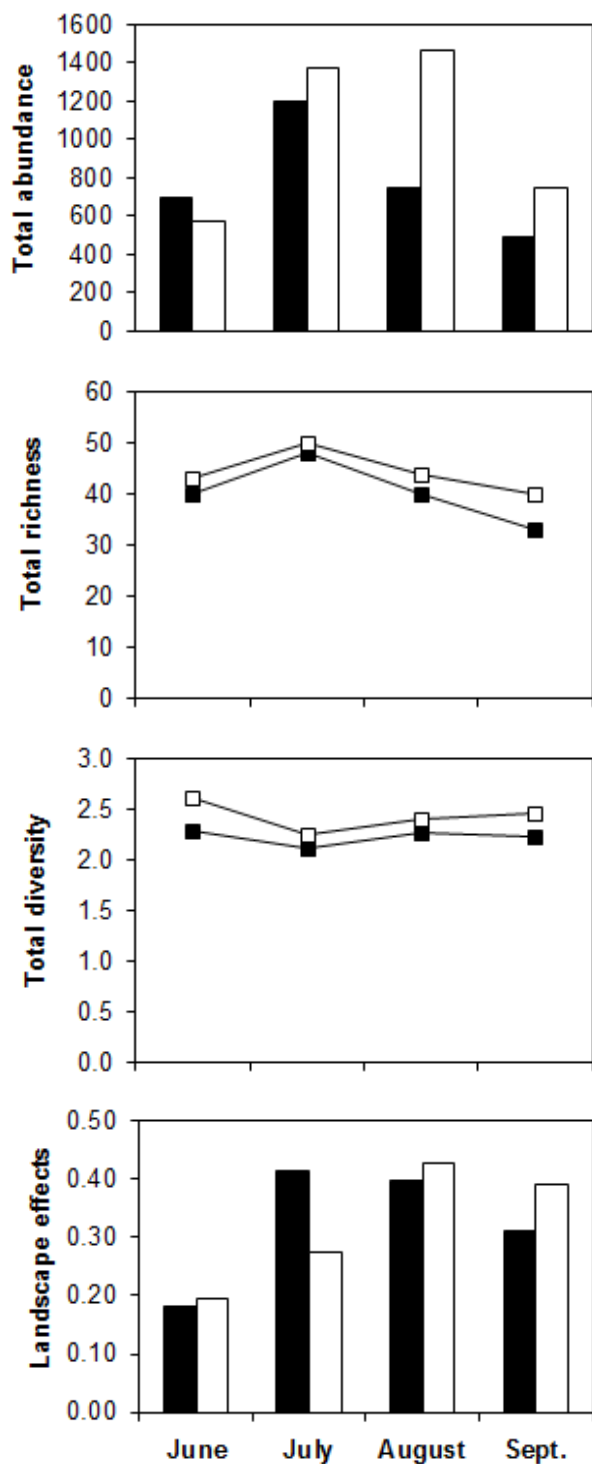
### Beetle abundance throughout the season

In total for sampling period of 8 weeks, 3147 ground and tiger beetles individuals were captured in 2006 and 4156 in 2007, including 72 species (66 in 2006 and 67 in 2007). Both years, *P. melanarius*, *P. lucublandus*, *H. pensylvanicus* and *B. quadrimaculatum* represented about 70% of the total abundance (table 1). Mean abundances of ground beetles collected per trap per site and per day throughout the season were provided in table 3. When considering all species, the total abundance was maximum in July (2006) or August (2007) (table 3 and figure 2). The species richness was lowest in June, increased in July (maximal species richness) and then decreased in August and September (figure 2). Ground beetle diversity (Shannon index) was minimal in July in both years (figure 2).

The abundance of *P. melanarius* showed significant differences between months (Kruskal-Wallis rank sum test, 2006:  $p = 0.0001$ , 2007:  $p = 0.0002$ ), with maximal abundance observed in July 2006 and August 2007 (figure 2 and table 3). The abundance of *P. lucublandus* did not show significant differences between months neither in 2006 nor 2007 (2006:  $p = 0.27$ , 2007:  $p = 0.055$ ). However, the maximal abundance was observed in August 2006 and September 2007 (figure 2 and table 3). The abundance of *H. pensylvanicus* showed significant differences between months ( $p < 0.0001$  both years), with a maximal abundance occurring in August in both years (figure 2 and table 3). Finally, the abundance of *B. quadrimaculatum* also showed significant differences between months ( $p < 0.0001$  both years), with a maximal abundance observed in August and September 2006 and July 2007 (figure 2 and table 3).

**Table 3.** Mean abundance of ground and tiger beetles observed throughout the season 2006 and 2007. Sampling occurred in the Vacher creek watershed (Quebec, Canada) in the summers (June-September). The abundances correspond to the mean abundance per site per trap per day (mean  $\pm$  standard error).

2006	June	July	August	September
All species	0.621 $\pm$ 0.149	1.072 $\pm$ 0.242	0.672 $\pm$ 0.127	0.444 $\pm$ 0.084
<i>P. melanarius</i>	0.258 $\pm$ 0.137	0.529 $\pm$ 0.227	0.193 $\pm$ 0.076	0.134 $\pm$ 0.056
<i>P. lucublandus</i>	0.104 $\pm$ 0.025	0.100 $\pm$ 0.026	0.122 $\pm$ 0.034	0.060 $\pm$ 0.015
<i>H. pensylvanicus</i>	0.003 $\pm$ 0.001	0.112 $\pm$ 0.028	0.121 $\pm$ 0.045	0.030 $\pm$ 0.015
<i>B. quadrimaculatum</i>	0.021 $\pm$ 0.011	0.058 $\pm$ 0.016	0.074 $\pm$ 0.019	0.071 $\pm$ 0.026
2007				
All species	0.509 $\pm$ 0.089	1.223 $\pm$ 0.163	1.313 $\pm$ 0.156	0.666 $\pm$ 0.093
<i>P. melanarius</i>	0.148 $\pm$ 0.067	0.278 $\pm$ 0.118	0.322 $\pm$ 0.086	0.176 $\pm$ 0.069
<i>P. lucublandus</i>	0.068 $\pm$ 0.015	0.049 $\pm$ 0.013	0.071 $\pm$ 0.018	0.078 $\pm$ 0.026
<i>H. pensylvanicus</i>	0.002 $\pm$ 0.001	0.203 $\pm$ 0.086	0.358 $\pm$ 0.116	0.137 $\pm$ 0.053
<i>B. quadrimaculatum</i>	0.056 $\pm$ 0.014	0.398 $\pm$ 0.087	0.136 $\pm$ 0.042	0.068 $\pm$ 0.015



**Figure 2.** Species assemblage and landscape effects throughout the season in 2006 (black) and 2007 (white). Analyses of landscape effects were performed on information for all species. Total abundance = total number of specimens collected. Total richness = total number of species collected. Total diversity = Shannon index. Landscape effects = adjusted  $R^2$ ,  $p = 0.001$  for all the models.

### Landscape effects throughout the season

The maximal landscape effect on the whole species assemblage (abundance matrix of all species) was observed in July 2006 (adjusted  $R^2 = 41.3\%$ ,  $p = 0.001$ ) and August 2007 (adjusted  $R^2 = 42.6\%$ ,  $p = 0.001$ , figure 2). For both years, variation partitioning showed no strong tendencies regarding the scales that were most important in influencing species assemblage composition. In 2006, landscape effects at 200 m explained between 1.8-11.0% of the variation, while effects at 500 m explained between 3.9-21.6% of the variation (shared variation by the two scales varied between 5.9-29.6%). In 2007, landscape effects at 200 m explained 0-18.0% of the variation, while effects at 500 m explained between 0-18.7% (shared variation between 8.3-22.9%).

Landscape effects on *P. melanarius* reached a maximum in June 2006 (adjusted  $R^2 = 75.6\%$ ,  $p = 0.001$ ) and August 2007 (adjusted  $R^2 = 40.3\%$ ,  $p = 0.001$ , figure 3). Variation partitioning revealed that *P. melanarius* was most influenced by the 200 m scale all months in 2006 (adjusted  $R^2$  10.2-56.3%, unique contribution) and by the 500 m scale all months in 2007 (adjusted  $R^2$  4.8-15.9%). However, the variation shared between the 2 scales was also important (2006: 14.0-33.7%, 2007: 11.0-36.7%). The abundance of *P. melanarius* was positively influenced by landscape diversity, crop areas (corn, bean, cereal), area in water, density of field borders and patchiness and negatively influenced by area in other crops, riparian vegetation, woodland and constructed areas (supplemental material table S1).

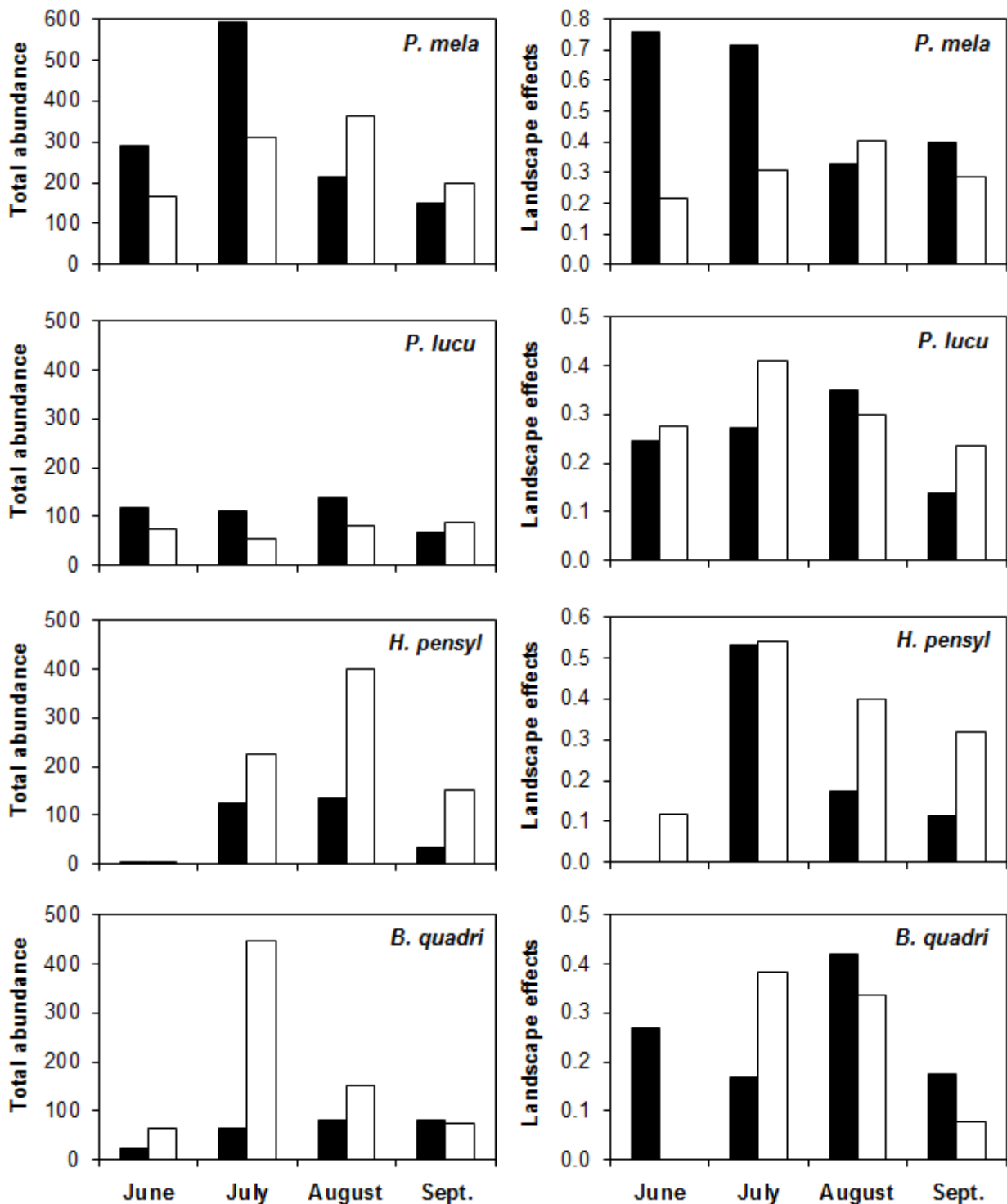
Landscape effects on *P. lucublandus* reached a maximum in August 2006 (adjusted  $R^2 = 35.0\%$ ,  $p = 0.001$ ) and in July 2007 (adjusted  $R^2 = 41.0\%$ ,  $p = 0.001$ , figure 3). Variation partitioning revealed that *P. lucublandus* was overall most influenced by the 500 m scale in 2006 (adjusted  $R^2$  0-11.9%, unique contribution), and by either the 200 m or the 500 m scale in 2007 (200 m: adjusted  $R^2$  0-10.6%, 500 m: adjusted  $R^2$  0.02-23.5%). However, in almost all cases, the variation shared between the 200 m and the 500 m scales explained the greatest part of the variation (2006: 4.2-29.9%, 2007: 18.8-32.7%). The abundance of *P. lucublandus* was positively influenced by area in cereal, other crops, fodder crop, fallow and riparian vegetation and negatively influenced by area in constructed area and landscape diversity (supplemental material table S2).

Landscape effects on *H. pensylvanicus* reached a maximum in July in both years (2006: adjusted  $R^2 = 53.3\%$ ,  $p = 0.001$ , 2007: adjusted  $R^2 = 53.8\%$ ,  $p = 0.001$ , figure 3). Both years, the abundance of *H. pensylvanicus* was most influenced by the 500 m scale (2006: 7.2-11.6%, 2007: 2.7-19.6%), but in some cases, the variation shared between the two scales was also important (2006: 2.7-36.1%, 2007: 9.8-31.8%). The abundance of *H. pensylvanicus* was positively influenced by area in bean, fodder crop, pasture, riparian vegetation, density of field borders, patchiness and the mean perimeter-to area ratio, and negatively influenced by area in woodland and constructed area (supplemental material table S3).

Landscape effects on *B. quadrimaculatum* reached a maximum in August 2006 (adjusted  $R^2 = 41.9\%$ ,  $p = 0.001$ ) and July 2007 (adjusted  $R^2 = 38.2\%$ ,  $p = 0.001$ ,

figure 3). In both years, the abundance of *B. quadrimaculatum* was generally most influenced by the 200 m scale (2006: adjusted  $R^2$  4.5-12.6%, 2007: adjusted  $R^2$  0-19.5%), but the variation shared between the two scales often represented the greatest part of the variation

(2006: 7.2-26.3%, 2007: 8.9-20.7%). The abundance of *B. quadrimaculatum* was positively influenced by crop area (corn, bean, other crops), area in pasture, fallow, woodland and water and negatively influenced by fodder crop (supplemental material table S4).



**Figure 3.** Seasonal modulation of ground beetle abundance and landscape effects on the four most abundant species found in the Vacher creek watershed in 2006 (black) and 2007 (white). *P. mela* = *Pterostichus melanarius*, *P. lucu* = *Poecilus lucublandus*, *H. Pensyl* = *Harpalus pensylvanicus*, *B. quadri* = *Bembidion quadrimaculatum*. Landscape effects = adjusted  $R^2$ ,  $p = 0.001$  for most of the models (except *P. mela* in July, *B. quadri* in June and July 2006 and *P. lucu* in June 2007:  $p = 0.002$ ; *P. mela* in June 2007, *P. lucu* in September 2006 and *H. pensyl* in August 2006:  $p = 0.003$ ; *H pensyl* in September 2006:  $p = 0.004$ ; *B. quadri* in September 2007:  $p = 0.024$ ; *H. pensyl* in June 2007:  $p = 0.013$ ).



### Trophic group, size and flight hypotheses

Overall, our results showed that the seasonal modulation of the landscape effects followed the order: *H. pensylvanicus* > *B. quadrimaculatum*, *P. melanarius* > *P. lucublandus*. Thus, none of the hypotheses initially formulated fully explain our results (Trophic group hypothesis: *B. quadrimaculatum* > *P. melanarius*, *P. lucublandus*, *H. pensylvanicus*. Size hypothesis: *P. melanarius* > *H. pensylvanicus* > *P. lucublandus* > *B. quadrimaculatum*. Flight hypothesis: *P. melanarius*, *P. lucublandus* > *H. pensylvanicus*, *B. quadrimaculatum*).

### Discussion

Many studies found that landscape structure significantly influences ground beetle assemblage (Weibull and Östman, 2003; Gaucherel *et al.*, 2007; Werling and Gratton, 2008). Yet, no study has really evaluated the seasonal modulation of these landscape effects. Our results show that landscape effects on ground beetle assemblage actually vary throughout the season, which had never been documented. This result was obtained for the whole ground beetle species assemblage, but also when considering the most abundant species individually. In both cases, ground beetle abundance was more influenced by landscape structure at mid-season (July or August). Then, landscape effects throughout the season showed variations between species. In addition, as effects at both 200 m and 500 m significantly influenced ground beetle abundance and the variation shared between the two scales were often quite large, one should conclude that these two scales do not differ enough.

As predicted, landscape effects on ground beetle assemblage (species matrix) were maximal at mid-season (July-August) when crop plants were fully developed. This seasonal modulation of the landscape effects may be explained by both the characteristics of the crop and non-crop vegetation in the surroundings. First, non-crop areas are important landscape elements for ground beetles, representing refuges and shelters when field perturbation occurs (e.g., due to pesticide application or tillage), but also reproduction or overwintering sites (Zangger *et al.*, 1994; Jopp and Reuter, 2005). In our study, several non-crop elements significantly affected ground beetle assemblage throughout the season (e.g., pasture, fallow, riparian vegetation, border density, data not showed), but it was quite complex to determine a general tendency between the two years studied. Secondly, crop plants can shelter significant food resources for ground beetles (preys), so landscape effects may then rely on the availability of these preys over time and the growing season.

When considering each species individually, landscape effects were also maximal at mid-season (35-71%), except for *P. melanarius* in 2006 for whom maximal effect was observed in June. Overall, the four species studied presented some seasonal modulation of the landscape effects, with the magnitude following the order: *H. pensylvanicus* > *B. quadrimaculatum*,

*P. melanarius* > *P. lucublandus*. Thus, none of the three hypotheses we proposed exactly predicts our results. First, the seasonal modulation of the landscape effects on the carnivorous species (*B. quadrimaculatum*) was not the most variable throughout the season, and the seasonal modulation of the landscape effects on the omnivorous species (*P. melanarius*, *P. lucublandus* and *H. pensylvanicus*) were much more important than expected. Regarding the size hypothesis, we expected the greatest seasonal modulation for the largest species, *P. melanarius*. Actually, landscape effects on *P. melanarius* were the most important but not the most variable throughout the season. On the contrary, *B. quadrimaculatum*, which was the smallest species, showed a great seasonal modulation of the landscape effects. Then, the greatest seasonal modulation of the landscape effects was observed for *H. pensylvanicus*, although it was not the largest of the four species. However, the fact that we did not measure all the specimens collected but use the mean size for each species based on the literature, may explain why our results did not follow the size hypothesis. It is then possible that *H. pensylvanicus* is as large as *P. melanarius*. Finally, when considering the flight hypothesis, we obtained results contrary to expected, with frequent flyers (*H. pensylvanicus*, *B. quadrimaculatum*) showing greater seasonal modulation of the landscape effects than occasional flyers (*P. melanarius*, *P. lucublandus*). Overall, a combination of several biological and ecological characteristics, which were not all evaluated here, may better predict the seasonal modulation of the landscape effects on ground beetle.

Differences observed among species may also be explained by the habitat preference and a significant association with some landscape components throughout the season. Regarding *H. pensylvanicus*, some studies revealed that its abundance actually showed some seasonal modulations (Crist and Ahern, 1999) and was higher in low-input areas where more weeds occurred (Ellsbury *et al.*, 1998). Therefore, the seasonal modulation of the landscape effects on *H. pensylvanicus* we found may be related to the schedule of the phytosanitary treatments performed in the adjacent cornfield (e.g. herbicide application), the vegetation growth (productivity) or the prey availability in non-crop areas throughout the season. Our results would fit this hypothesis, as we found that the abundance of *H. pensylvanicus* was mainly positively influenced by the amount of non-crop areas and grassland throughout the season.

Very few studies focused on *B. quadrimaculatum*. One performed in Finland, showed that *B. quadrimaculatum* was more frequent in crop fields (potato and cereal fields) versus leys (Kinnunen *et al.*, 2001), thus suggesting a preference for crops instead of non-crop areas. In comparison, in our study we found such positive relation between the abundance of *B. quadrimaculatum* and some crop areas (corn, bean, other crops). But contrary to Kinnunen *et al.* (2001), we found the abundance of *B. quadrimaculatum* also positively influenced by non-crop areas (pasture, fallow and woodland). Thus, the seasonal modulation of the landscape effects on



*B. quadrimaculatum* may rely on seasonal characteristics of both crop and non-crop areas (e.g., vegetation growth, variation in prey availability or phytosanitary treatment performed in fields).

The seasonal modulation of the landscape effects on ground beetles may also be explained by different dispersal ability throughout the season, which can be the case for *P. melanarius*. Some European studies revealed that *P. melanarius* dispersal depends on various factors including the habitat type and satiation state (Wallin and Ekbom, 1988; Fournier and Loreau, 2002), the sex, and the season (Thomas *et al.*, 1998). Others studies found that *P. melanarius* dispersal depends on the landscape structure (Wallin and Ekbom, 1988: field versus woodland in the surroundings). In particular, Retho *et al.* (2008) found a greater dispersal from small fields surrounded by few large-size patches. Overall, in the case of *P. melanarius*, the seasonal modulation of the dispersal ability may help explaining the seasonal modulation of the landscape effects we observed.

Finally, *P. lucublandus* was found as the dominant species in wheat and soybean fields in the USA (Ellsbury *et al.*, 1998). Thus, it can be supposed that the seasonal modulation of the landscape effects may be related to the characteristics of these crops throughout the season (e.g., plant growth, variation in prey availability). This would fit our results because we found that the abundance of *P. lucublandus* was positively influenced by the area in cereals during the 2 years of the study and the area in soybean (2006 only). In addition, we found that the abundance of *P. lucublandus* was positively influenced by non-crop areas and grassland (fodder crop, fallow, pasture, riparian vegetation) but this effect was not documented.

## Conclusion

This study showed that there is an important seasonal modulation of the landscape effects on ground beetle assemblage, landscape effects being the most important at mid-season. Ground beetle species generally responded in the same way, but differences between species occur, with a greatest seasonal modulation of the landscape effects for *H. pensylvanicus*, and a lower seasonal modulation for *P. lucublandus*. None of the hypotheses tested regarding the feeding group, size or flight ability of the species exactly predicted our results. However we found that frequent flyers showed a greater seasonal modulation of the landscape effects than occasional flyers. Then, variations between species may be explained different responses to landscape components throughout the season. Finally, it would be interesting to determine whether predatory arthropods other than ground beetles also present some modulations of the landscape effects throughout the season. This would be essential to habitat management for biological control purposes.

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