Seasonal and environmental variability of ground beetle (Coleoptera:Carabidae) assemblages at Mont St-Hilaire, QC

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ABSTRACT

Seasonal and environmental variability of ground beetle (Coleoptera:Carabidae) assemblages at Mont St-Hilaire, QC

Christopher Adlam

In order to study the seasonal variation and habitat preference of carabids, I sampled using pitfall traps in various habitat types at Mont-St-Hilaire, southern Quebec, from the beginning of June until the end of October 2007. I caught 1193 individuals belonging to 53 species. Among the 16 most abundant species, nine were caught predominantly in early summer, five in mid summer, and four showed two peaks of activity, one in the early summer and one in the fall. There was no significant difference in terms of species richness or abundance between hardwood and mixed forests. On the other hand, ground beetle populations differed between wet and dry areas, and between forested and open or ecotonal areas. The ecotone between forest and meadow had the highest diversity and the highest abundance of carabids. Furthermore my analysis showed that several species were reliable indicators for various habitat characteristics such as proximity to a water body, forest type, and openness.

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Table of Contents

List of figures

List of tables

Preface

The thesis that follows presents the results of the main part of my master's research. It does not, however, cover my entire progression over the past two-and-a-half years, which is why I will present first a succinct account of the trajectory of my master's work. My original project was not focused on ground beetles (Coleoptera: Carabidae), but rather on mites. I was drawn to the possibility of starting a new project with Dr. Emma Despland and Dr. Fred Beaulieu, on *Antennoseius janus* (Acari: Mesostigmata), a mite phoretic on carabids. This mite is remarkable in that it has two adult female morphs, which are distinct morphologically and behaviorally. While the default morph is free-living and soil-dwelling, the alternative morph is phoretic, and will actively seek out carabids for dispersal. The phoretic female will then delay reproduction and feeding activity until dismounting from the carabid. High population densities are known to trigger maturation into the phoretic morph, but the exact mechanism is yet a subject of debate. My project would have been concerned with attempting experimentally to find out what mediates this trigger (physical contact, chemical cues, etc.).

Antennoseius janus is found on a variety of carabids, but disperses in high numbers on *Sericoda quadripuncata*, a carabid found in burnt forest areas. Unfortunately, despite two field trips, I failed to locate one of the rare burnt forests in southern Québec (the first trip not only revealed the importance of an accurate estimation of distances, but also left me at the end of the day on a forest road locked behind a metal barrier that had been open the same morning, while the second ended when the path ran into a lake that had not been on any map). After this, I gave up trying to locate burnt forests, and sampled near Mont Rigaud, QC, in the hope of collecting carabids carrying *A. janus*. Several of the beetles collected did carry phoretic mites, and it was decided that I should try to rear these in the hopes that they would be *A. janus* (identifying them would have required killing some to observe them, but I had too few to risk this). I tried feeding them with various prey: collembolans *Folsomia candida*, nematodes *Caenorhabditis elegans* (that I reared in Petri dishes) and *Turbatrix aceti*, and spider mites. None of this worked and they died without reproducing.

After this, I decided to sample for a whole season in diverse habitats in order to maximize my chances of finding *A. janus*. This way, if I didn't find *A. janus*, I would still have data on mite-beetle associations, including seasonal and environmental factors that influence these associations. However, at the end of my sampling period I had collected only 12 mites. Some of these had dismounted when I found them, meaning that I could not identify the original carrier, some were dead, and a few were destroyed during handling. Most of those still alive died soon after being transferred to a rearing container.

This new setback made me reluctant at first to fully investigate the carabid data I had collected. The few mites that survived were *Poecilochirus carabi*, which are usually phoretic on burying beetles (Coleoptera: Silphidae: *Nicrophorus*), but will disperse on ground beetles if none of their preferred hosts are available. This prompted me to look for more burying beetles, since they can carry dozens of *P. carabi*, which I could then use for behavioral experiments. I set up baited traps and left mouse corpses at Mont St-Hilaire, and drove about investigating roadkill. I was able to collect some burying beetles, but since it was already late in the season I did not find many. The ones that I did catch died soon after, which left me with many mites but no burying beetles. After a great deal of enquiry, I located one researcher at the University of New Hampshire who reared *Nicrophorus defodiens*. I drove there to collect some, and after much waiting and anxiety at the border upon my return (I had a permit, but it turned out that was not enough), brought them back to the lab. I provided them with mouse corpses and peat moss in a container, in which they formed their burying chambers and reproduced successfully. The mites also reproduced in the process, and I now had a very large number of them. I was able to keep them alive by feeding them *Rhabditis* sp. nematodes reared in an oatmeal-wheat germ medium, and subsequently realized that they would even reproduce if given access to meat (which I used to feed the beetles), even without the presence of a host.

I attempted a number of experiments to evaluate the cues mediating the attraction of the mites for the beetles, including visual tests in glass containers, and chemical tests using a Y-tube or cuticle extracts. These experiments were only mildly successful. The one experiment that yielded a tangible result was one that tested the preference of the mites for a piece of paper towel that had been in contact with either meat, burying beetles, or both, and a control imbibed only with distilled water. It appeared from my results that the mites were only attracted to the paper towel that had been in contact with beetles and meat at the same time. This is an interesting result, but without any follow-up experiments any conclusions made from this experiment would not be very strong. The beetles unfortunately died before any further experiments could be done. I did not include a chapter on this experiment as it is unrelated to the body of the thesis, and, as I say, rather weak as a stand-alone experiment (it may however be considered for publication later).

Putting my preference for behavioral studies behind, I returned to the carabid data that I had accumulated from Mont St-Hilaire, as this would be the only way for me to present sufficient results for my master's. Though I had at first lacked trust in this data as I had had some minor setbacks during sampling (such as traps being damaged), it became apparent that I could still make a good analysis, and, in fact, such setbacks are an unavoidable part of fieldwork in ecology. Therefore this is the data that I am presenting in this thesis.

This project has challenged me far more than I first expected, and far more than I had ever been challenged in the course of my prior studies. I have felt at times immensely discouraged, put off by delays and setbacks, and hopeless to find solutions to my problems. I have also had to balance the empowerment of directing my own project with at times ailing motivation levels. I think that this experience has led me to be a great deal more mature and autonomous; I have learnt self-confidence in designing projects and deciding upon what direction I wished to take, and determination in the face of adverse circumstances. I have become a great deal more familiar with the process of ecological fieldwork, with its variables and challenges, the extraction and synthesis of results from a large volume of data, and with the rigor of experiments, though this may not be apparent in my final thesis.

Introduction

Ground beetles or carabids are a vast and common family of beetles, with about 40,000 known species worldwide (Lövei et al. 1996) that share a high degree of morphological uniformity (Thiele 1977). In North America, carabids are the third largest family of Coleoptera with over 2,600 species in 189 genera (Triplehorn et al. 2005). Since Lindroth's seminal work on Canadian carabids (Lindroth 1969), the systematics of this group have been studied extensively, resulting in the collection of a large body of taxonomical, behavioral and quantitative knowledge of ground beetles. In addition, as a group of mainly solitary, nocturnal, predaceous (though also often carrion-consuming) and flightless (or at least seldom flying) beetles, their study is not complicated by considerations of host plants or intricate social behavior (Thiele 1977). This combination of a fairly extensive understanding of the biology of carabids and their relatively simple, homogenous life history has made them attractive objects of research. Yet despite the fruits of these past decades of studies, there are still gaps in the knowledge of the phenology and habitat preferences of a number of species (or, in many cases, no more than anecdotal reports), and extensive studies of local carabid faunae of North-America are relatively few, leaving us at times with only a vague understanding of the response of carabids to various environmental factors on a local scale.

Though the distribution of ground beetles has been well studied throughout various habitats in Europe (Thiele 1977), there have been comparatively few summer-long studies in North-America that have attempted to draw a complete picture of the phenological and ecological habits of carabids. In addition to this, carabid assemblages are characterised by considerable regional variability, rendering comparisons between distant studies difficult, especially with regards to eastern and western parts of the continent (Work et al. 2008). Still, a handful of studies stand out in their relevance to the biogeographic and climatic conditions of southern Quebec: Werner et al. (2003) have contributed an insightful overview of the seasonal activity of carabids in Northern Wisconsin and the Upper Peninsula of Michigan, while Bailey et al. (1994) succinctly attempt the same work in Maryland. Epstein et al.'s (1990) oft-cited study of East-Central Minnesota carabids gives a very thorough insight into their seasonal patterns as well as spatial distribution and the impact of environmental factors, a subject also touched on by Larsen et al. (2003) in Northeastern Iowa.

As with these studies, my research will attempt to present a general picture of the ecological habits of carabids in the Mont St-Hilaire area, with special emphasis on seasonal variation and spatial distribution. Understanding the seasonal variation and phenology of ground beetle populations is useful for a number of reasons. Fairly obviously, knowing carabid seasonal activity is necessary to develop adequate sampling strategies, and to assess optimal sampling periods (Werner et al. 2003). Furthermore, carabids play a role in pest control, and therefore the overlap of their activity periods with those of pests is a key factor in assessing their suitability as biological control agents (Suenaga et al. 2001). Lastly, assessing the impact of invasive species on the native beetle fauna requires a knowledge of the phenology of the native species before and after the exotic species establish. The risk of displacement of native fauna can be lowered if there is little overlap in seasonal activity between native and introduced species, and therefore reduced levels of interspecific competition between species with otherwise similar ecological niches. This idea of temporal niche partitioning was put forth by Loreau (1985) and has been used to explain why the European native *P. melanarius* does not displace species with similar ecological requirements such as *P. pensylvanicus* and *P. adstrictus* in North-America (Niemela et al. 1997). In contrast, *P. coracinus* is more likely to be negatively affected by interspecific competition from *P. melanarius* as a result of overlapping activity periods (Barlow 1970). Whether and how invasive species affect the seasonal occurrence, population stability and habitat use of native species needs to be further studied and, for this purpose, it is necessary to first have a thorough understanding of the phenology of the different species involved.

Seasonal activity of carabids is affected by a number of factors, one of the most important of which is breeding behavior (Goulet 1974; Thiele 1977; Loreau 1985; Bousquet 1986). Several general works have shed light on the reproductive habits of carabids, starting most notably with Larsson (1939) and Lindroth (1945). These studies laid out the classical subdivision of carabids into "spring breeders" ("adult hibernators") and "autumn breeders" ("larval hibernators"). This perspective was later refined by Thiele (1977), who recognized the influence of external environmental factors on the breeding patterns of carabids, and the flexibility in the reproductive strategies of some species. Loreau (1985) further recognized the complexity of the breeding strategies of ground beetles, finding evidence for a substantial number of species that do not fit into either of the two classical categories. Notably, Loreau found species with continuous reproduction and hibernation in both adult and larval stages, species with variable reproductive periods, species with a facultative breeding period in the autumn continuing the next spring and species with winter reproduction. In addition, the results from Loreau's study highlighted the geographic variability in breeding strategies, especially along a latitudinal gradient. For this reason, the degree to which the results of studies of carabid seasonal activity from other areas of eastern North-America can be generalized to the carabid populations of southern Québec remains to be determined. A major aim of this study was to acquire a better knowledge of the seasonal patterns of activity of carabids in this area and to provide data for comparison with studies of similar scope.

The role of environmental variables in shaping the spatial distribution of carabids has been the subject of much research. Antvogel et al. (2001) found several abiotic factors to influence carabids in alluvial forests of northern Germany: carabid communities there varied with soil moisture, light intensity and pH, even over a distance of a few meters. Moisture in particular is a factor whose prime importance in determining carabid assemblages has been recognized (Thiele 1977; Epstein et al. 1990; Niemelä et al. 1992; Sroka et al. 2006). Other factors that appear to influence carabids include temperature (Thiele 1977; Magura 2002), forest area (Burke et al. 1998; Sroka et al. 2006), leaf litter (Koivula 1999; Antvogel et al. 2001; Magura 2002; Sroka et al. 2006), amount of dead wood (Sroka et al. 2006), distance to forest edge (Sroka et al. 2006), canopy cover (Magura 2002), type of ground cover (Niemelä et al. 1992; Antvogel et al. 2001; Magura 2002) and habitat heterogeneity (Liebherr et al. 1979; Niemela et al. 1996).

Despite correlations between carabid assemblages and vegetation cover (Niemelä et al. 1992; Antvogel et al. 2001), the exact effect of plant communities on ground beetles is still debated. For example, it has been suggested that correlations exist between carabid and plant assemblages not primarily because vegetation mediates ground beetle diversity but because both respond to the same environmental factors (Thiele 1977; Antvogel et al. 2001). The microclimate, especially water balance, but also soil acidity and temperature, are important determinants of both plant and carabid communities, suggesting that the association is not causal in nature (Thiele 1977). On the other hand, it has been proposed that vegetation structure has more importance in determining carabid assemblages than vegetation taxonomy (Brose 2003). In particular, Brose found that dense vegetation, by decreasing the vulnerability of carabids to predators (the "enemy-free space hypothesis"), provided preferred habitat to some species, notably the larger ones. Plant stem density also affects carabids by reducing their locomotory abilities (Heydemann 1957, in Thiele 1977). Such structural properties affect the habitat choices of carabids, with different species favoring either dense or sparse vegetation (Novák 1971, in Thiele 1977). Leaf litter similarly exerts a resistance to carabid motion, a factor that may explain the prevalence of more slender coleopterans in dense litter, such as the Staphylinidae (Heydemann 1957, in Thiele 1977). However, leaf litter also offers protection from adverse climatic effects and variation, as well as increasing prey density, such that leaf litter characteristics can be important determinants of carabid assemblages (Koivula 1999). These are some examples of the complexity of the relationship between vegetation and carabid populations that every study of the spatial distribution of ground beetles must face. One of the questions I will attempt to address in this study is how the cumulative effects of this multitude of environmental factors shape carabid populations at the scale of forest stands.

One approach to this issue is the use of bioindicators to identify links between particular species and broad habitat categories, based on forest type, canopy cover and proximity to a water body. McGeoch (1998, in Rainio et al. 2003) defines a bioindicator as "a species or a species group that reflects the abiotic or biotic state of the environment, represents the impact of environmental change on a habitat, community or ecosystems, or indicates the diversity of other species". Carabids have several characteristics of good indicators as laid out by several authors (e.g. Pearson et al. 1992; Niemelä 2000): a well known taxonomy, life history and biology, broad geographical distribution, ease and low cost of sampling and a degree of specialization to certain habitat requirements. While the interest in bioindicators lies mainly in the ability to evaluate environmental change and anthropogenic disturbances and to monitor the diversity of other species within the ecosystem for conservation purposes (Rainio et al. 2003), carabids have also been used in the past to distinguish between related habitats. In one instance they were used to separate several grassland types (Eyre et al. 1990), while Dufrêne and Legendre (1997) show that it is possible to use carabid species as indicators of a variety of different wet and dry sites. With this approach it is possible to evaluate the degree of specialization of carabids with regards to various habitat types and to gather information on their ecological requirements, both of which are critical to understand their biology and therefore their usefulness as bioindicators for conservation purposes.

I have, therefore, three major aims in this study: 1) to characterise carabid assemblages at Mont-St-Hilaire, by presenting a list of species present in the sampling area that covers a diversity of different habitat types, along with a measure of their abundance and diversity; 2) to assess the seasonal patterns of the most abundant species and to compare them with previous studies; and 3) to evaluate the correlation between broad habitat characteristics and ground beetle species diversity and composition and their use as predictors of carabid assemblages and to assess the usefulness of carabids as indicators of these habitat types.

Materials and Methods

1. Study sites

Sampling was performed from May 30th until October 26th 2007 at the Gault Nature Reserve at Mont St-Hilaire, southern Québec, Canada (study sites located from 45°32'18'' to 45°32'40'' north and 73°09'25'' to 73°09'45'' west). Traps were distributed in as many different environments as possible. In particular, I placed them throughout various kinds of mixed and deciduous forest stands (there were no pure conifer stands in the area) as well as in a meadow and in the young regenerating forest between the meadow and the established forest (hereafter called "ecotone"). The dominant tree species in the deciduous forest varied, the main forest communities being *Acer saccharum/Fagus grandifolia* and *Acer saccharum/Fagus grandifolia/Quercus rubra*. In addition to deciduous tree species (*Acer/Fagus* mainly), the mixed forests were dominated by the Eastern Hemlock (*Tsuga canadensis*) and were characterized by having a needle-based litter and generally sparser undergrowth. In addition to sampling in various forest types, I took special care to have traps in dry locations as well as close to water bodies (<1m from a stream, pond or marsh). The meadow was dominated by grasses, with some brambles (*Rubus* sp.). The ecotone between the meadow and forest areas was characterized by vegetation typical of intermediary stages of succession (low trees, bushes, grasses, herbaceous plants and trees typical of regenerating forests, such as Staghorn Sumac (*Rhus typhina*) and Trembling Aspen (*Populus tremuloides*)). Traps were separated by at least ten meters, and were kept at least five meters away from obstacles such as logs or large rock formations that might skew beetle catches by channelling their movement towards or away from the traps.

For the analysis, the traps were divided into habitat types (See Table 1). The two main criteria used to distinguish between habitat types were the forest type (mixed forest, deciduous forest, ecotone/regenerating forest and meadow) and wetness (dry or wet).

2. Sampling method

Fifty-five pitfall traps were installed in May (one was subsequently lost, see "Results"), as soon as the snow had melted, in an area of approximately 0.5 km^2. Each trap consisted of a clean 750 ml yogurt container, inside which was fastened a funnel constructed from acetate transparencies. The funnel was smooth enough not to provide a grip for passing beetles, and prevented them from climbing up the side of the trap or from flying out. The traps were inserted into the ground such that the rim of the trap was level with the ground surface. Over the top was placed a roof consisting of a full-sized transparency (8 ½ X 11 inches) held 5 cm above the ground by four wooden dowels. The roof prevented rain from falling into the traps, as well as leaves and other objects that might obstruct the trap opening. I used acetate rather than other materials such as masonite (Liebherr et al. 1979) because its transparent nature makes it less easy to detect and therefore potentially less liable to affect the behavior of carabids.

In the forested sites, the leaf litter immediately surrounding the trap (within 30 cm) was removed (following Liebherr et al. 1979), which rendered the comparison of catches more relevant between sites, since the locomotory activity of ground-dwelling beetles was not hampered by debris. However, this was not possible in the meadow and in areas with dense herbaceous vegetation; due to the nature of such vegetation and the rapidity of its growth, efficient clearing of the ground around the trap would have required digging, which would have heavily disturbed the environment and therefore affected the results of the sampling.

The traps were designed in this way to catch live specimens, for reasons tied to the fact that my original project was concerned with phoretic mites. Since I had the hope of establishing mite cultures, I wanted to catch the mites live. Secondly, if the traps had contained a preserving solution, it would have been likely that mites would have fallen off their hosts, therefore making it impossible to reliably study the association of mites with their hosts. With the system I decided to use, the problem remained that mites may have disembarked and mounted other beetles, therefore skewing my results slightly. Nevertheless, it was decided that combined with frequent visits to the traps, this system would be the most dependable.

Werner and Raffa (2000) found that the minimum sampling effort required to collect most of the species theoretically present in the habitat was to use four traps per site of 250x250 m. In light of this, I used either four or five traps per study site. Each site was no more than 200x200 m in size, within which traps were distributed in a way to maximise environmental variation (by personal estimation). For each habitat type, I sampled in at least two sites separated by over 300 meters. The only exceptions to this were the meadow and the forest edge (ecotone), which were too small to allow such a distance between sites.

Table 1.: Number of pitfall traps and sampling sites for each habitat type. The ecotone was continuous all around the meadow, making the "number of sites" irrelevant.

	Dry Hardwood	Wet Hardwood	Dry Mixed	Wet Mixed	Ecotone	Open
No. sites	3	2	2	2	N/A	1
No. traps	13	10	10	8	9	4

Traps were checked 34 times between May 30th and October 26th, every 2 to 7 days (on average every 4 days), and all Coleoptera were placed individually in vials and brought back to the lab. They were examined for the presence of mites, including under the elytra, and were then placed in 70% alcohol. Carabid specimens were later pinned, air-dried and identified to species (Lindroth 1969). My identifications were corroborated with the help of Dr. Yves Bousquet at the Canadian National Collection of Insects and Nematodes (Agriculture and Agri-Food Canada) in Ottawa.

Trap catches were sometimes lost due to damage by racoons and other mammals, heavy rain running along the forest floor and filling them up, and wetland traps being flooded or floating up on ground water so that they were no longer flush with the soil. In total, 10% of sampling days were lost. Attempts to reduce racoon-related damage were made, such as using chicken-manure as a repellent, but these had little effect and were abandoned.

3. Data analysis

- ***Seasonal variation***

I observed the seasonal variation in abundance of the 16 most abundant species ($n \geq 18$) by comparing the number of catches in early summer (June 2nd to July 12th), mid-summer (July 16th to August 8th), late summer (August 13th to September 19th), and fall (September 27th to October 26th). The results were compared to other studies; in particular, the patterns of activity of these species were analysed in light of the classic distinction between spring breeders and autumn breeders (Larsson 1939; Lindroth 1945).

- *Spatial variation*

Characterizing habitats according to carabid species composition

Ordination of traps based on species composition were obtained by performing a multi-dimensional scaling (MDS) using the statistical computer program PATN (Belbin 1993), which grouped the trap locations according to the sample of carabids they caught. MDS was used because it is generally robust to non-linear effects and conceptually simple. Within a predetermined number of dimensions (three in this case), the software constructs a set of points in a way that the plotted distance optimally reflects the dissimilarity between the carabid composition at each trap. In order to maximize the correspondence between the measured data (input) and the derived data (output), the software PATN uses metric multi-dimensional scaling (MMDS), which takes into account the measured distances, when there is a presumed linear relationship between input and output distances, and non-metric multi-dimensional scaling (NMDS), which takes into account the rank order of distances, above that region. It is therefore considered to be a hybrid technique (HMDS) (Belbin 1993). The 3-dimensional ordination obtained is based on the Bray-Curtis index of dissimilarity between each trap, and produced groups of traps with the most similar carabid assemblages. In addition, we performed an analysis of similarity (ANOSIM) to evaluate the similarity between each habitat type.

Comparison of carabid species diversity and abundance across habitats

After log-transforming the data to achieve normality, one-way analyses of variance (ANOVA) were performed using the software PopTools (Hood 2008) to test the variation in species richness and abundance (number of specimens per trap) between the different habitats. Accumulation curves comparing cumulative species number as a function of sampling effort were computed for each habitat using the software EstimateS, at 1,000 randomizations (Colwell 1997).

Indicator species

To test whether some species were representative of certain habitats, an analysis was conducted using the software IndVal, developed by Dufrêne and Legendre (1997), which calculates an "indicator value" for each species. To do this, the software uses a randomization-based test that compares the relative species' abundance and frequency of occurrence across sampling groups. Good indicator species are therefore those that are found mostly in a single sample group and in a majority of traps from that group. The indicator value expresses a species' affinity as a percentage (Dufrêne et al. 1997).

To run the software, I grouped the habitats hierarchically according to their similarity in species composition of carabids, based on the results obtained using PATN. This produced the following dendrogram:

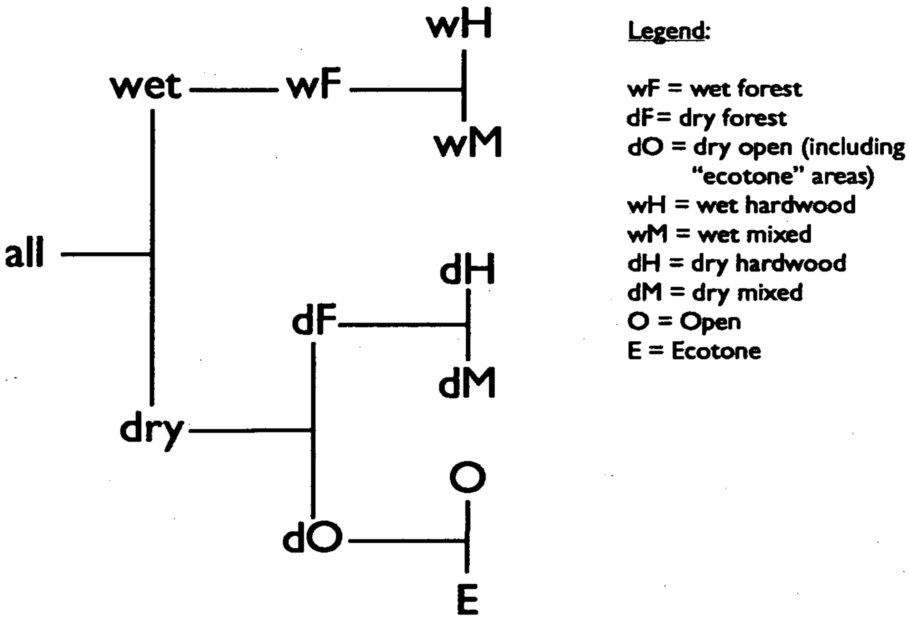


Fig.1: Dendrogram used for carabid indicator species analysis.

IndVal gives an indicator value for each species at every partitioning level. For example, a species may be an indicator of a wet environment, or of a more terminal partition such as "wet mixed forest" or sometimes both, in which case it is useful to consider for which habitat it gets the highest indicator value.

Results

A total of 1193 carabids belonging to 53 species were collected. One trap from the meadow was lost amid the rapid spring growth; overall 10% of trap/days were lost due to damage, which, as stated previously, was mostly due to animal activity or flooding.

1. Seasonal variation

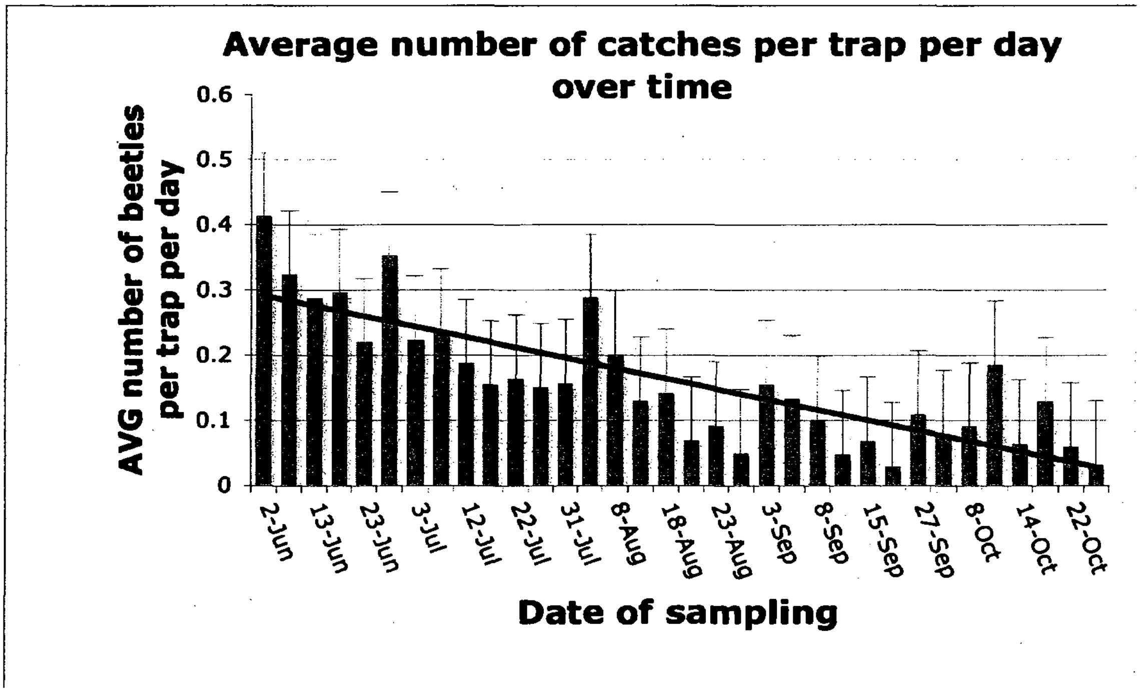


Fig. 2: Total carabid abundance over time sampled at Mont-Saint-Hilaire, QC, in 2007, using pitfall traps. Bars represent standard deviation.

The overall trend was a slight decline of carabid catches throughout the summer (Fig. 2). Some species followed this general trend such as *Agonum fidele*, of which 89% of individuals were collected between June 2nd and July 12th, but many species exhibited other patterns of activity (Fig. 3, Table 2). *Pterostichus melanarius* and *Synuchus impunctatus* showed what looked like a normal pattern of activity, being rare at the beginning and end of the summer and peaking around the end of July and beginning of August respectively (with 59% and 75% respectively being collected between July 16th and August 18th). The other trend was a bimodal pattern of activity, shown for example by *Sphaeroderus lecontei* (42% collected in early summer and 43% in the fall), *Pterostichus pensylvanicus* (25% collected in the early summer and 65% in the fall), and *Pterostichus mutus* (68% collected in early summer and 22 % in the fall).

Among the species which had a bimodal activity pattern, only *P. pensylvanicus* had a significantly higher level of activity in the fall. *S. lecontei* had two roughly equivalent peaks of activity, while *P. mutus* and *P. decentis* were both significantly more active in the early summer, with only a small resurgence of activity in the fall.

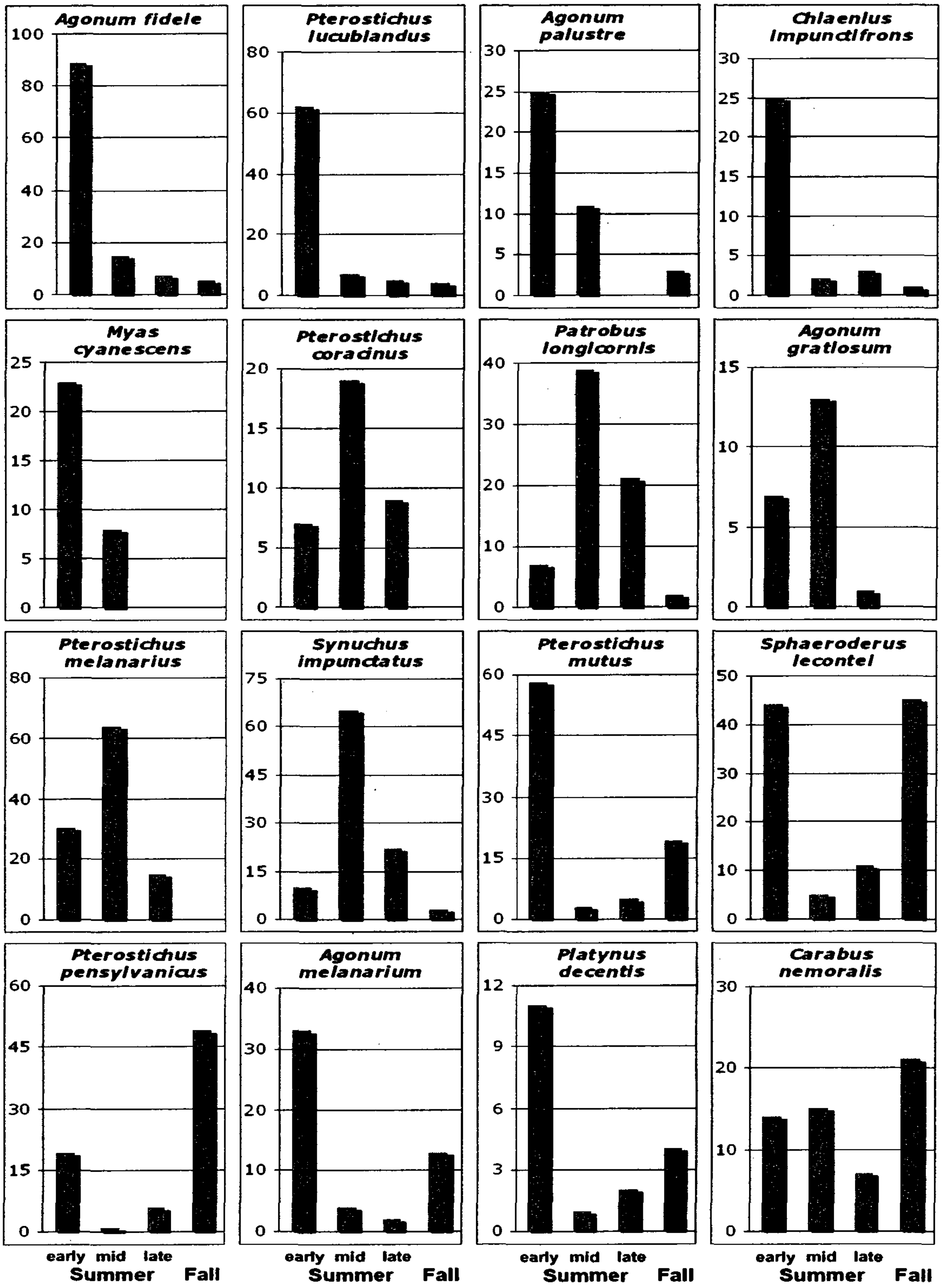


Fig. 3: Seasonal activity of the most abundant species of carabids collected at Mont-Saint-Hilaire, QC, in 2007, using pitfall traps. *Y-axis: number of individuals. Early summer = June 2nd-July 12th; mid-summer = July 16th-August 18th ; late summer = August 21st- September 19th; fall = September 27th–October 26th.*

Table 2: Main activity periods for the most abundant species of carabids collected at Mont-Saitn-Hilaire, QC, in 2007, using pitfall traps.

Early summer and fall	Early summer	Mid-summer	Constant
Sphaeroderus lecontei	*Agonum palustre*	*Pterostichus melanarius*	*Carabus nemoralis*
Pterostichus mutus	*Agonum fidele*	*Pterostichus coracinus*	
Pterostichus pensylvanicus	*Poecilus lucublandus*	*Patrobus longicornis*	
Platynus decentis	*Myas cyanescens*	*Synuchus impuncatus*	
Agonum melanarium	*Chlaenius impunctifrons*	*Agonum gratiosum*	

Early summer = June 2 - July 12
Mid-summer = July 16 - August 18
Fall = September 27th – October 26th

Table 3. Comparison of the species activity periods of most abundant carabid species collected in this study with other studies. *Early summer = June to early July; mid summer = mid July to mid August; fall = mid August to late October. Carabids collected in 2007 at Mont-Saint-Hilaire, using pitfall traps.*

Species	**Present study**	**(Werner et al. 2003)**	**Other studies**
Chlaenius impunctifrons	Early summer		
Agonum fidele			
Pterostichus. lucublandus			Early s. + Fall[2,3]
Myas cyanescens		erratic	Constant[1]
Agonum palustre			
Platynus decentis	Early s. + Fall	Early summer	Early s. + Fall[2,3,8]
Sphaeroderus lecontei		Early summer	Constant[1]; Early s. + Fall[2,4,8]
Pterostichus mutus		Early summer	Early s. + Fall[2,5,8]
Pterostichus pensylvanicus		Early summer	Early s. + Fall[2,3,5,6,7,8]
Agonum. melanarium			Early s. + Fall[3]
Pterostichus melanarius	Mid summer	Mid-late summer	
Pterostichus coracinus		erratic	Mid summer [8]
Synuchus impunctatus		Mid-late summer	Mid summer [3,8]
Agonum gratiosum			
Patrobus longicornis			
Carabus nemoralis	constant	Early summer	

[1]: (Bailey et al. 1994)

[2]: (Bousquet et al. 1977)

[3]: (Epstein et al. 1990)

[4]: (Bousquet et al. 1980)

[5]: (Liebherr et al. 1979)

[6]: (Goulet 1974)

[7]: (Bousquet 1986)

[8]: (Levesque et al. 1986)

2. Spatial variation

- ***Characterizing habitats according to carabid species composition***

The HMDS ordination indicated that the samples can be divided into three main habitats based on carabid species composition: open and ecotone sites, dry forest sites, and wet forest sites. Figure 4 shows that the traps from each of these three habitat types tend to cluster together in groups, reflecting the increased similarity in their catches. A simplification of this can be seen in the dendrogram produced by PATN (Fig. 5). The three basal groups segregate the traps into dry open or ecotone traps, dry forest traps, and wet forest traps (from top to bottom in the dendrogram). The open and ecotone sites and dry forest sites are more similar to each other than they are to the wet forest sites, and there is no significant difference in carabid species composition between the mixed and hardwood forests. The ANOSIM confirms that species composition does not differ significantly between the wet areas of mixed and hardwood forests ($p= 0.08$), or between the dry areas ($p= 0.61$) of each forest type. In addition, the ordination shows that the dry forest sites are more similar to the dry ecotonal and open areas, than they are to the wet forest sites. Wetness therefore appears to be a more important factor in determining carabid communities than forest type.

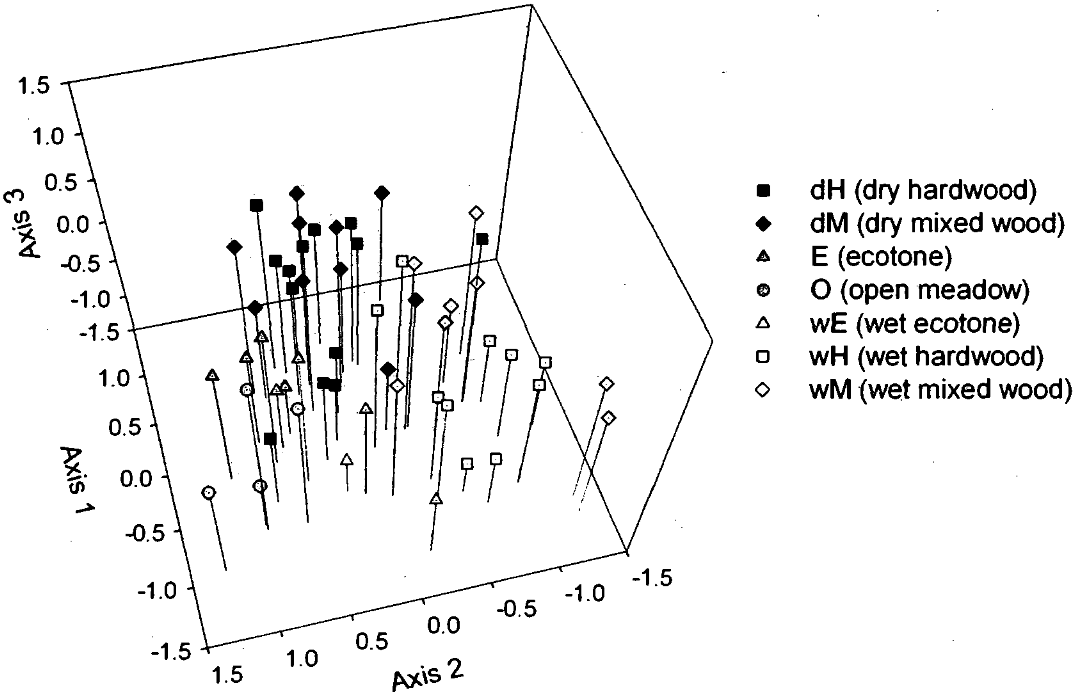
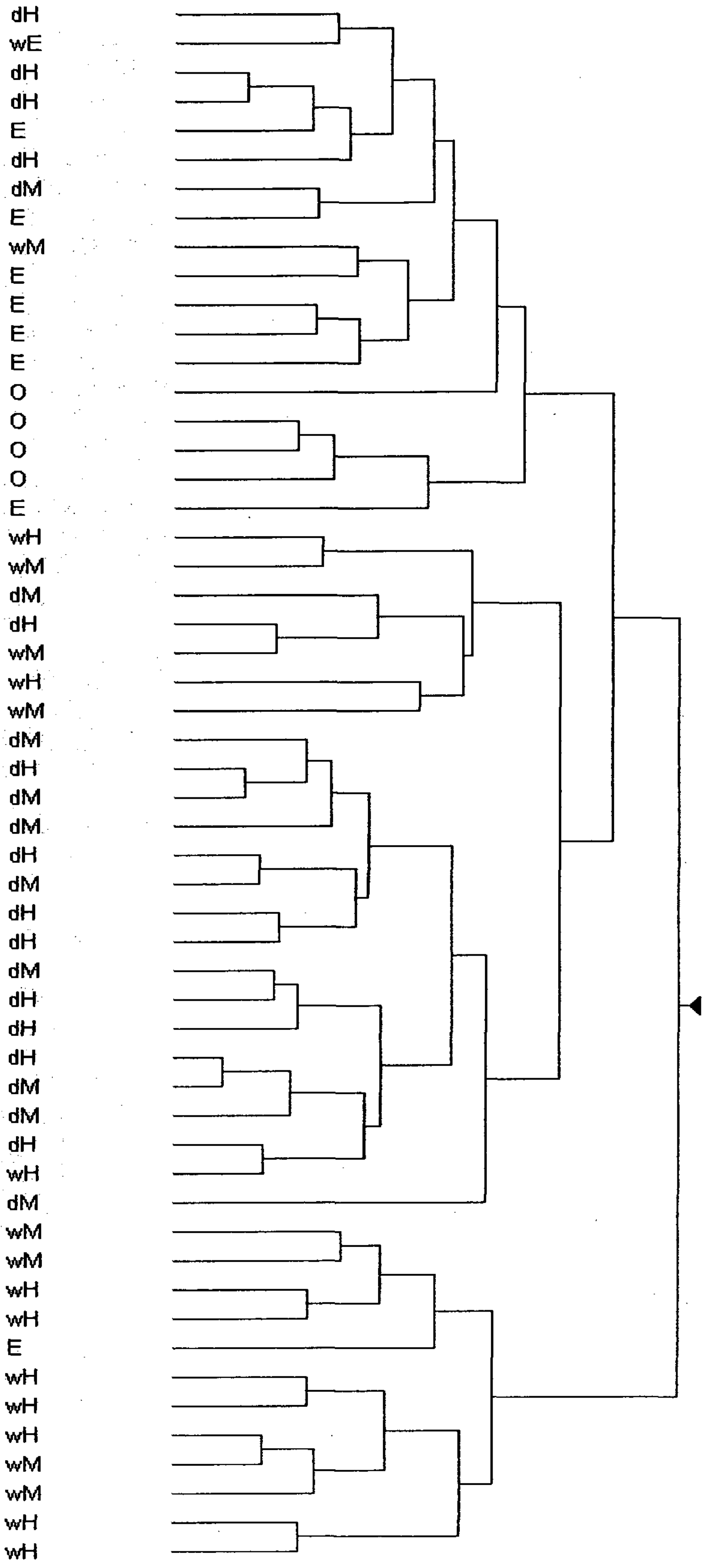


Fig. 4: Three-dimensional representation of the traps according to the Bray-Curtis distance between the communities of carabids sampled by each one. Dry forest traps (black) are at the top, while open and ecotone traps (gray) are grouped on the bottom left, and wet forest traps (white) are on the bottom right. Note that there is no segregation based on forest type (hardwood=squares, mixed=diamonds).



<u>Fig. 5</u>: Dendrogram of traps according to the similarity in their carabid catches. This figure is a simplified, two-dimensional version of the above three-dimensional ordination.

Legend:

dH = dry hardwood
wH = wet hardwood
dM = dry mixed
wM = wet mixed
E = ecotone
wE = wet ecotone (one trap)
O = open

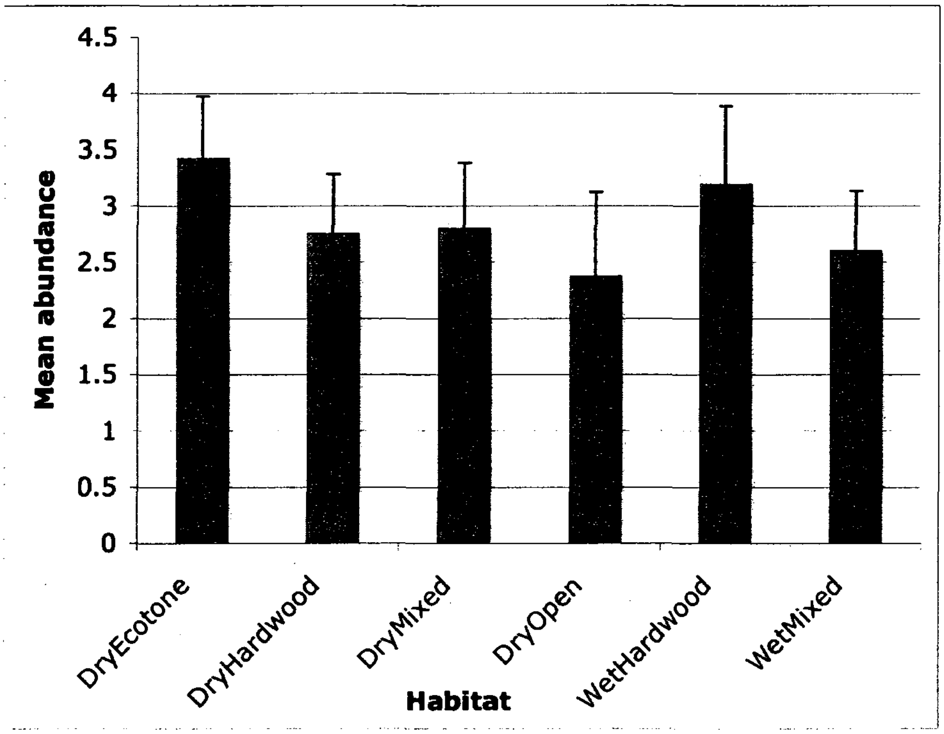


Fig. 6: Mean carabid abundance per trap per visit for each habitat type. Bars represent standard deviation.

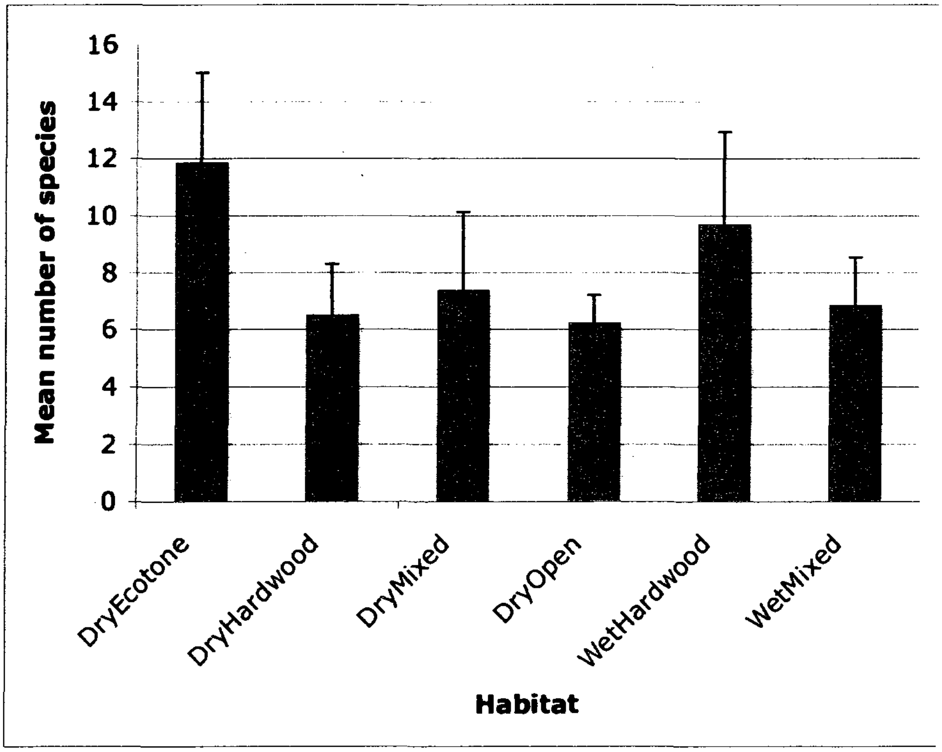


Fig. 7: Carabid species richness per trap per visit for each habitat type. Bars represent standard deviation.

- ***Comparison of carabid species diversity and abundance across habitats***

The abundance of carabids was higher in the ecotone sites (3.4±0.5 catches per trap per visit) than all other sites (one-way ANOVA, $0.005<p<0.04$) except those in the wet hardwood forest ($p= 0.41$). These sites had a significantly higher abundance (3.2±0.7 catches per trap per visit) than the wet mixed forest and the open areas, which had the lowest abundances (2.6±0.5 and 2.4±0.7 respectively; $p=0.04$ and $p=0.02$ respectively) (Fig. 6). A similar pattern was observed for species richness: the ecotone had the highest number of species per trap, except when compared with the wet hardwood forest sites ($p=0.07$) (Fig. 7). Rarefaction curves give similar results, with the ecotone having the highest species richness, followed by wet hardwood forest (Fig. 8).

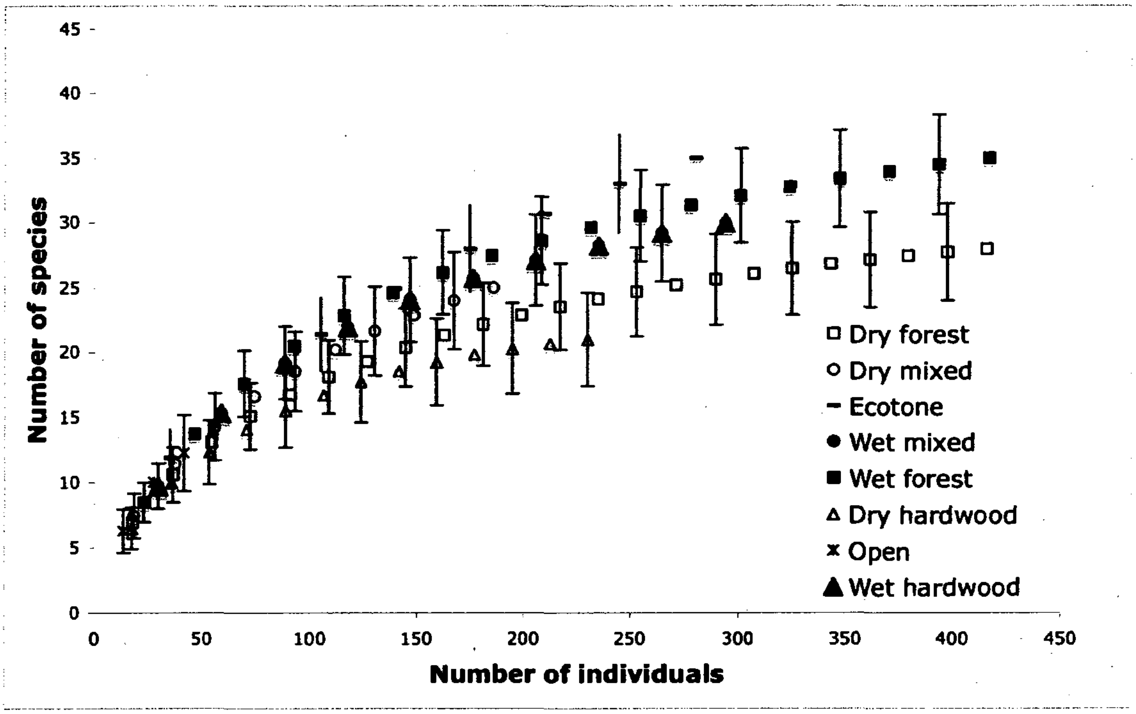


Fig. 8: Rarefaction curves for each habitat type for carabids collected at Mont-Saint-Hilaire, summer 2007. Bars represent the standard deviation.

Table 4: Preferred habitats of some of the carabid species sampled at Mont-Saint-Hilaire during summer 2007 according to other studies.

Open	Mixed forest	Deciduous forest	Dry	Wet
Pterostichus mutus[4] *Carabus nemoralis*[4] *Poecilus lucublandus*[4] *Pterostichus melanarius*[4,5] *Pterostichus coracinus*[4] *Patrobus longicornis*[4]	*Pterostichus coracinus*[1] *Sphaeroderus lecontei* *Platynus decentis*[6]	*Pterostichus pensylvanicus*[1] *Synuchus impunctatus*[1] *Sphaeroderus lecontei*[1] *Agonum retractum*[1,4] *Pterostichus melanarius*[3] *Patrobus longicornis*[4]	*Synuchus impunctatus*[4] *Poecilus lucublandus*[4] *Pterostichus mutus*[2]	*Patrobus longicornis*[2,4] *Bembidion graciliforme*[2] *Platynus decentis*[2,4] *Agonum melanarium*[2] *Chlaenius impunctifrons*[4] *Agonum fidele*[4] *Agonum palustre*[4]

[1]: (Work et al. 2008)

[2]: (Epstein et al. 1990)

[3]: (Niemela et al. 1997)

[4]: (Lindroth 1969)

[5]: (Magura 2002)

[6]: (Werner et al. 2000)

[7]:(Bousquet et al. 1980)

(underlined: same findings as this study)

- ***Indicator species***

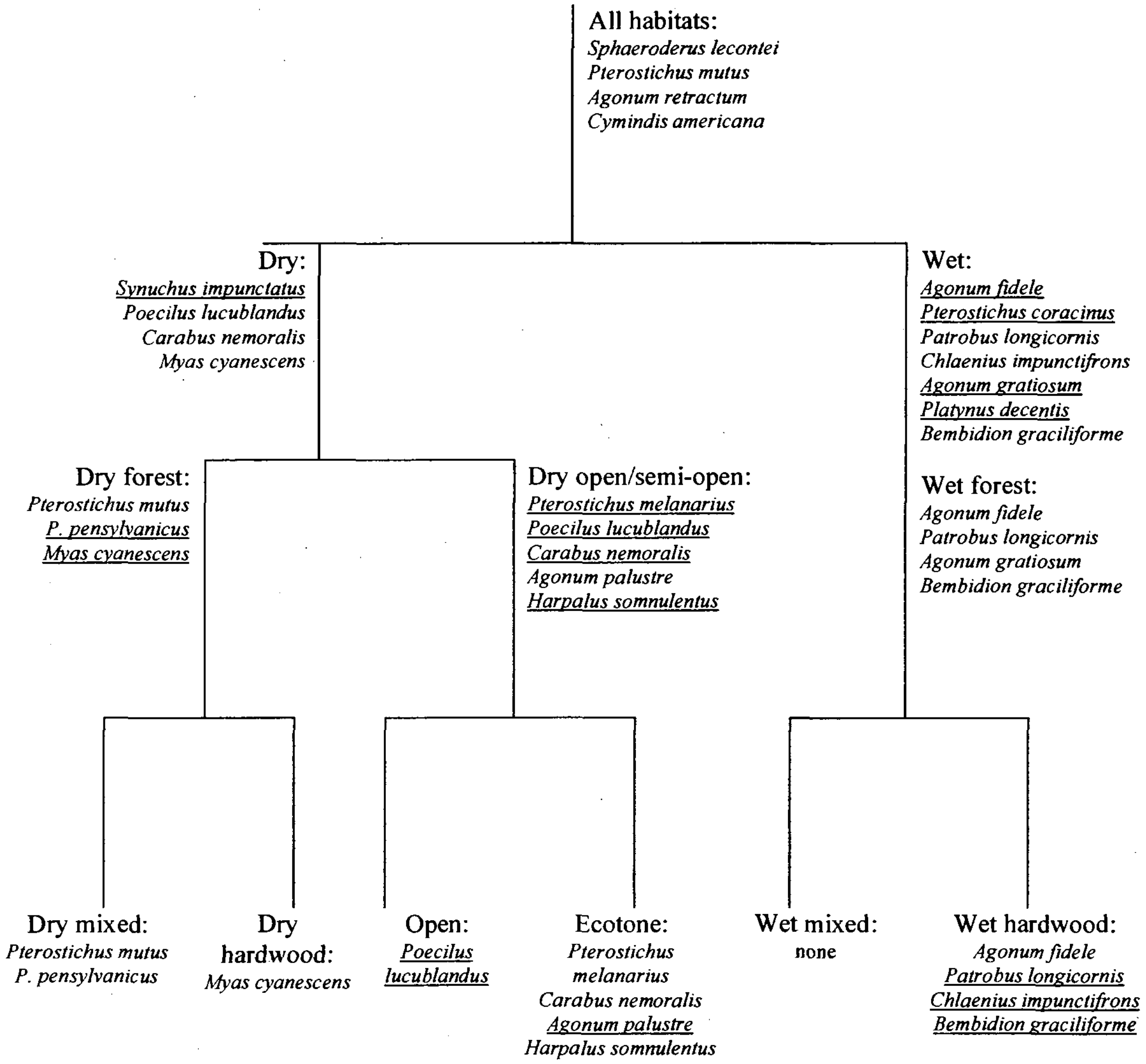


Fig. 9: Dendrogram of habitats showing carabid indicator species for each partitioning level. Species underlined where they have their maximal indicator value.

The most generalist species were *Sphaeroderus lecontei* (IV=73.6), and *Pterostichus mutus (IV=60.4)*, since their indicator value (IV) is maximal in the first partition, corresponding to all habitats (Fig. 9).

Synuchus impunctatus is a habitat indicator species for dry areas (IV= 63.4); the best indicator for wet areas is *Agonum fidele* (IV= 91.4), and to a lesser extent *Pterostichus coracinus* (IV=29), *Agonum gratiosum* (IV=31.6) and *Platynus decentis* (IV=31.8).

Pterostichus pensylvanicus is an indicator of dry forest areas (IV=63.65), as is *Myas cyanescens* (IV=46.89), while indicators of open or semi-open areas (meadow and ecotone together) are *Pterostichus melanarius* (IV=50.02), *Poecilus lucublandus* (IV=77.92), *Carabus nemoralis* (IV=68.74) and *Harpalus somnulentus* (IV=37.33).

Agonum palustre is an indicator of an ecotonal area (IV=86.41), the presence of *Poecilus lucublandus* (IV=41.79) indicates an open area and *Patrobus longicornis*, *Chlaenius impunctifrons* and *Bembidion graciliforme* indicate the wet hardwood area (IV=56.78, IV=43.33, IV=55.38).

Discussion

Seasonal variation:

By virtue of the length of the sampling period, especially into the fall, I found distinct patterns of activity for many of the most abundant species. It is one of a rather limited number of studies that have been conducted for a whole season in Eastern North America. The studies of Bailey et al. (1994) in Western Maryland and of Werner et al. (2003) in Northern Wisconsin and the Upper Peninsula of Michigan ended in August. Even the otherwise very comprehensive study by Epstein et al. (1990) of Eastern-Central Minnesota carabids ended in late September. Bailey et al. (1994) acknowledged that, had they continued their research into the fall, the patterns they found may have been more marked, while Werner et al. (2003) hypothesized that a longer study period would have led them to find bimodal activity patterns for several species, including those that I found to have such patterns. Indeed, I found significant peaks of activity for several species during the month of

October, long after many other studies, such as those previously cited, have stopped sampling. This is the case for *Sphaeroderus lecontei* (43% of individuals collected in the fall, between September 27th and October 26th), *Pterostichus pensylvanicus* (65% collected in the fall), *Pterostichus mutus* (22% collected in the fall) and *Platynus decentis* (22% collected in the fall). Studies that end before the first heavy frosts might miss valuable data on late season activity of some carabid species. Perhaps if Bailey et al. (1994) had continued sampling past the month of August they would not have found the activity levels of *S. lecontei* to be relatively constant throughout the season.

To interpret seasonal patterns, it is necessary to understand the life cycle of ground beetles. Carabids overwinter either as adults or as larvae (Thiele 1977) or, occasionally, in both stages (Loreau 1985). Those that breed during the spring are likely to hibernate as adults, whereas those that breed during the fall are likely to hibernate as larvae, only to mature the following season (Lindroth 1949, in Thiele 1977).

Some species hibernating as adults will have one peak of activity during their spring breeding period, and one in the autumn which corresponds to the emergence of the new generation. This new generation seeks prey to increase fat reserves for hibernation, and either mates then or during the following spring (Larsson 1939, in Thiele 1977; Goulet 1974). This second period of activity has been observed in this study, as mentioned above, for *S. lecontei, P. pensylvanicus, P. mutus, P. decentis,* and to a certain extent *A. melanarium.* These species hibernate as adults, as confirmed for *P. pensylvanicus* (Goulet 1974; Bousquet 1986; Epstein et al. 1990), *P. mutus* (Bousquet 1986), *A. melanarium* (Lindroth 1969; Epstein et al. 1990), *P. decentis* (Larochelle 1972; Epstein et al. 1990) and *S. lecontei* (Bousquet et al. 1980). Adult hibernation has also been reported for *Poecilus lucublandus* (Kirk 1971; Bousquet 1986), which explains the strong activity level during early summer (79% of individuals were caught before July 12th). Following this period, activity levels remained low, in contrast with the study by Epstein and Kuhlman (1990), which found a second peak of activity in the late summer (See Table 3 for comparison of present data with other studies).

Synuchus impunctatus and *Pterostichus melanarius*, on the other hand, hibernate in the larval stage (Lindroth 1969), which explains the mid to late summer peak of activity observed for these species, similar to trends found by other studies (Epstein et al. 1990; Werner et al. 2003). Late summer breeders may in some cases hibernate in both larval and adult stages, as is the case for *P. coracinus* (Lindroth 1969; Bousquet 1986) and *Agonum gratiosum* (Epstein et al. 1990), two species that were also observed mainly in mid and late summer. In fact, many of the species that reproduce from the height of the summer onwards (those termed "autumn breeders" by Lindroth (1945), slightly misleadingly given how early the reproductive period can start) hibernate in both stages, with the adults sometimes entering into a second reproductive period the following year (Thiele 1977). All five species characterized by a mid to late summer activity are known to hibernate in the larval stage, with or without adult hibernation in addition (Lindroth 1969; Epstein et al. 1990). My data supports the idea that the stage at which a particular species hibernates will determine its period of activity; larval hibernation leading to mid to late summer activity, while adult hibernation is correlated with early summer activity, with or without a second peak during the fall.

I found that most species had their highest peak of activity early in the season (among the 15 most abundant species, eight had their highest activity levels before mid-July, and five between mid-July and mid-August) which agrees with the findings of other studies (e.g. Epstein et al.

1990). It has been hypothesized that the reason for this pattern is that in northern latitudes, spring breeding is favored so that the offspring have more time to develop before winter (Loreau 1985).

Several other factors have been found to influence carabid seasonal activity, such as prey availability (Goulet 1974), breeding activity, as described above (Goulet 1974; Thiele 1977; Loreau 1985; Bousquet 1986), interspecific competition and microhabitat parameters such as soil moisture, temperature and humidity (Epstein et al. 1990). In addition, a correlation between the breeding strategy and habitat type has been reported, at least within the genus *Pterostichus*: spring breeders within that genus are typically from wet or open habitats (such as *Poecilus lucublandus* (sometimes classified in the genus *Pterostichus*) and *Pterostichus mutus*), whereas autumn breeders (such as *Pterostichus coracinus*) are more likely to be from forests (Bousquet 1986).

Spatial variation

- ***Scope and scale***

Factors affecting carabid distribution have been studied on a regional scale (Thiele 1977; Work et al. 2008), landscape level (mesoscale) (Judas et al. 2002) and within stands (microscale) (Niemela et al. 1996; Antvogel et al. 2001). The scope of this study is situated somewhat between the landscape level and the microscale level, with an area roughly 0.5 km^2 in size.

The scale of this study was designed to sample a wide variety of species from differing habitat types, rather than to evaluate micro-spatial environmental factors affecting their distribution (e.g. pH, soil moisture, light intensity, etc.). As such, the resolution of the sampling was coarser than in some studies of the distribution of ground beetles within stands, and did not permit a good survey of the effect of micro-habitats. For instance, in order to test the effect of specific environmental factors such as soil pH, humidity, light intensity, litter depth, and vegetation type, Antvogel et al. (2001) used 152 traps within a 100 x 120 m plot. Indeed, carabid communities sometimes vary over very short distances, of the order of only a few meters, even within a single forest stand, as a result of subtle fluctuations in environmental conditions (Niemela et al. 1996; Antvogel et al. 2001).

On the other hand, the scope of microscale studies does not allow any conclusions to be made on differences between biotopes. Fully aware of the limitations of not using specific, measurable environmental factors (humidity, soil pH, etc.) in the analysis of carabid distribution, I attempted instead in this study to evaluate the correlation between ground beetle communities and the broader habitat type. This approach has two major benefits, in that it enables us to look for species that are indicators of certain habitat types and to compare different habitats in terms of species composition, richness and abundance.

- ***Forest type***

My data showed that mixed and deciduous forests do not differ markedly in terms of their carabid communities. This came somewhat as a surprise, given the seeming difference between the two in terms of litter quality (leaves vs. needles) and amount, and other factors relating to the different tree compositions such as soil pH, which is usually lower in the mixed forests than in hardwood forests (Finzi et al. 1998). Werner et al. (2000) assert that hardwood-hemlock mixed forests are cooler and wetter and they found accordingly that some species, most notably *Platynus decentis*, prefer these conditions. Only a few species seemed to be significantly affected by the forest type, such as *Chlaenius impunctifrons*, found primarily in hardwood sites (38% of individuals *after correcting for the number of traps per habitat* (19 out of 31)), with no individuals collected in the mixed forest sites, and *Pterostichus pensylvanicus*, which showed a preference for mixed forests (71% (50 individuals) in the mixed forest and 27% (24 individuals) in the deciduous forest).

This is unlike the findings of Work et al. (2008), whose study found forest type to be the most important determinant of carabid assemblages after geographic location (either Eastern or Western Canada). Of course, their study was done on a regional scale, and it may not be surprising that studies on different scales will yield different results. It may be also that the scale used in the present study was coarse enough to overlook microscale variability of abiotic factors, yet not broad enough to catch subtle differences between habitat types. However, another interpretation could be rather that the results of very large scale studies do not always apply on the landscape level. Just as the resolution of this study makes it difficult to catch variations stemming from subtle intra-stand abiotic factors, the coarseness of regional-scale studies might make smaller, mesoscale factors harder to assess by merging them together. This would indicate that much caution is necessary when attempting to apply the findings of large-scale studies to specific landscapes. Despite the difficulties in reconciling findings obtained at different scales of observation, studies can and need to be done at every spatial scale and level of resolution, and each will yield different kinds of information (Judas et al. 2002) (See Table 4 for a comparison of the present data with the findings of other studies).

Interestingly, it should also be mentioned that according to Work et al. (2008), the distinction between deciduous stands and mixed forests is only significant in Eastern Canada. Indeed, their data led them to pool the mixed forest data with deciduous stands rather than with the conifer stands in Western Canada, which suggests that the influence of the forest type is variable and dependant upon other environmental factors rather than all important in determining carabid assemblages.

Curiously, Work et al. (2008) found that *Pterostichus pensylvanicus* was found primarily in deciduous stands, which also contradicts my findings. This too seems to indicate that caution is necessary when applying conclusions from very large scale studies to the landscape level. Other environmental factors may overrule the effect of the dominant tree-type on a local scale.

- ***Wetness***

The most significant factor affecting carabid assemblages in this study was the proximity to a water body (stream or marsh). This factor appeared to be even more important than the openness of the site (i.e. forest vs. meadow vs. forest edge), the other factor that had a significant impact on carabid population structure. Wet areas in the deciduous stands had a significantly higher abundance and species richness, and several species were shown to be indicators of wet habitats: *Agonum fidele, Patrobus longicornis, Pterostichus coracinus, Chlaenius impunctifrons, Platynus decentis, Agonum gratiosum* and *Bembidion graciliforme*. These species have long noted to be correlated with moist areas (Lindroth 1969; Epstein et al. 1990). Our findings corroborate the conclusion of others that moisture is an important factor in determining the range of habitats used by carabids (Epstein et al. 1990; Niemelä et al. 1992).

- ***Openness and edge effect***

Dry forest areas appeared to be more similar to open or ecotonal areas than to wet forest areas, but there were species that were significant indicators of the more open areas: *Pterostichus melanarius, Poecilus lucublandus, Carabus nemoralis, Agonum palustre*, and *Harpalus* *somnulentus*. Of these, only *P. lucublandus* was found to be an indicator of fully open grassland areas, the others being more common in the ecotone. As in other studies (e.g. Burke et al. 1998), *P. melanarius* and *C. nemoralis* were found more in the open areas than the forested habitats; these species are both European natives, and as such would be expected to thrive in the more disturbed or unstable environments (Spence et al. 1988). This includes artificial meadows such as the one found at Mont-Saint-Hilaire, which is undergoing succession as it regenerates.

A strong edge effect has been reported for carabids (Magura et al. 2001; Magura 2002), and the results of the present study support this observation. As in other studies (Halme et al. 1993; Butterfield et al. 1995; Magura 2002), the forest edge (that I call ecotone in this study) had a higher species richness than either the adjoining grassland or forest areas. The overall abundance of ground beetles was also higher. Moreover, in addition to finding species from the grassland and the forest in the ecotonal areas, there were also ecotone-preferring species, suggesting that the characteristics of this area give rise to habitats that are distinct from either of the adjacent areas. Notably, the presence of both herbaceaous vegetation from the grassland and shrubs from the forest interior provides a unique habitat for carabids by creating microclimates that differ from either grassland or forest in terms of temperature, air moisture, etc., and by increasing the amount and diversity of prey available (Magura 2002). An alternative or complementary explanation for the existence of species that favor forest edges is that these species require the close proximity of two different habitat types (Odum 1971). This study does not yield any results that would allow a test of which these explanations, if either, is the most important in explaining the patterns found. Forest edges around the meadow at Mont St-Hilaire were often characterized by higher plant diversity following the effect of vegetation succession, with trees such as Staghorn Sumac (*Rhus typhina*) and Trembling Aspen (*Populus tremuloides*) that were not found deeper within the forest, as well as grasses and herbaceaous plants from the grassland. This supports the microsite hypothesis, but we must leave it to further studies to elucidate this question.

The effect of forest edges has been studied in depth by other researchers, and in comparison this study provides only descriptive data. In addition, the forest edge was identified rather "subjectively", in the words of Tibor Magura (2002), as opposed to employing a systematic transect method that could yield results about the environmental factors affecting the species composition in these areas. Nevertheless my results provide anecdotal support for the observations and studies that have already examined the importance and specificity of forest edges for carabids (Halme et al. 1993; Butterfield et al. 1995; Molnár et al. 2001; Magura 2002). Forest edges play a key role in maintaining diversity and provide a source habitat for small-scale dispersal (Molnár et al. 2001). On the other hand forest-specialist species are likely to be negatively affected by the proximity of a forest edge (Halme et al. 1993). In the case of the sampling location of this study, the meadow, which once was an apple orchard, is being gradually overtaken by other plants as succession proceeds, and will likely disappear within a few decades. This could have a positive impact on some forest specialists, but will likely diminish overall ground beetle diversity in the local area.

- ***Indicator species***

Our data showed that several species were reliable indicators of habitat types. For instance, finding *Agonum fidele* most likely signifies that a body of water is close (IV = 91.4). *Patrobus longicornis* can be used even more precisely as an indicator that the site is wet *and* in a hardwood forest (IV = 56.8). This kind of data is useful both to expand our knowledge of the habitat preferences of these species and to be enable us to characterize habitats based on their carabid assemblages. For instance, trap numbers 1 to 4, which were grouped with the hardwood forest category due to the distance to the forest edge being over 25m, were more similar to the ecotone/open traps than to the other hardwood forest traps, according to the multivariate pattern analysis, as a result of the large proportion of species from more open habitats (*Pterostichus melanarius, Carabus nemoralis, Poecilus lucublandus*, for instance). In this case, the carabid assemblage of the site suggests that the forest edge still affects the habitat conditions this far into the forest, suggesting that the influence of the edge varies depending on factors other than simply the distance, such as possibly vegetation structure, edge type, and other biotic and abiotic factors. Similarly, the multivariate pattern analysis indicates that trap number 36, situated in the forest edge, caught a carabid assemblage similar to those captured in wet sites, which is illustrated by the high proportion of *Agonum fidele* and *Patrobus longicornis*, two wet area indicator species, as well as *Agonum palustre*, a species that has been found elsewhere to favor wet areas (Lindroth 1969). In the case of this trap, I had noted that the ground surrounding it was constantly moist, but this did not fit my criteria for a "wet area" (the proximity of a water body). The carabid assemblages found at these sites help to determine the dominant environmental characteristics driving species composition.

The difficulties of reconciling data obtained at different scales have already been discussed, but this extends to the question of indicator species. Work et al. (2008) found that carabids were better suited as fine-scale bioindicators of environmental disturbance than as regional or national indicators. Regional variation, patchy species distribution and variation in the effect of local biotic and abiotic factors are largely responsible for decreasing the effectiveness of carabids as indicators at a coarse scale. Despite these problems, carabids appear to make suitable environmental indicators on a local or landscape scale (Rainio et al. 2003; Work et al. 2008).

Sampling methods

Firstly, it is very important to remember that pitfall traps measure a composite of abundance and the level of searching activity of the carabids (Mitchell 1963). Therefore some species that show a peak of activity at the beginning of the season do not necessarily disappear afterwards, and those with two peaks of activity might still be present in between; they may simply be less active. Pitfall trap efficiency also varies between habitats due to differences in vegetation structure and density (which might explain the very low catch rate in the meadow area) (Lang 2000). Denser vegetation impedes locomotion for ground beetles, constricting their movements and therefore reducing their likelihood of being caught in pitfall traps. Other studies have found that carabids are more diverse in grasslands than in forested areas (e.g. Magura 2002), but this study found quite the opposite. This result may be due in part to the relatively low number of traps in the meadow, but probably has a lot more to do with the thickness of the grass and the consequently reduced locomotory activity of the beetles.

Larger species, which move faster, are also over-represented compared to smaller ones by pitfall-trapping, which renders comparisons of relative abundance somewhat difficult (Andersen 1995; Lang 2000). Interspecific comparisons should especially be made with caution due to the effect of differences in size, mobility and behavior towards traps (Thiele 1977).

Despite these deficiencies, several researchers have argued in favor of pitfall traps. Topping et al. (1992) suggest that sampling over an entire season can reduce biases in relative abundance, while direct trap comparisons within species have long been considered reliable (Thiele et al. 1962, in Judas et al. 2002). Paje et al. (1985, in Judas et al. 2002) conclude that despite the shortcomings of this method, presence/absence data and coarse abundance data from pitfall traps can be used in the analysis of distribution patterns. Lastly, the cheapness, ease of use and repair, and replicability of pitfall traps also makes them an attractive technique to use over long periods of time, over big areas, or in large numbers.

Alternate sampling regimes that could have been used include discontinuous sampling, by sampling for several short "observation windows" throughout the season (Niemela et al. 1990; Niemela et al. 1996; Antvogel et al. 2001). This would have eased the sampling, but could potentially have led to losing some data, especially at the end of the season when many studies "miss" the fall activity peaks of some carabids. In addition, the relatively low daily rate of catches made an interval of a few days between each visit more adequate than short, intensive, daily sampling windows.

An easy and reliable alternative to pitfall traps is the use of wooden coverboards left on the ground, under which carabids take refuge. This is especially useful for live trapping (which was my original aim), and is less work and as efficient as pitfall traps (Dávalos et al. 2006). Other advantages include reduced disturbance, decreased sensitivity to damage by flooding and animal activity, reduced catch of non-target organisms, and the possibility of leaving the boards in place for longer periods of time between sampling (especially for live trapping purposes).

If my original project had not required live trapping, using a killing agent would have been preferable in some ways, notably by reducing the risk of specimens escaping (though this was reduced by the design of the traps) and enabling less frequent visits, as the specimens would not be at risk of dying, eating each other, or attracting mammalian predators. Using coverboards instead of pitfall traps might have been problematic due to the relative lack of research on this method, as well as making it difficult to compare with other studies that overwhelmingly use pitfall traps. However, using coverboards to complement the results from the pitfall traps could have helped to ensure the capture of the widest variety of species. Indeed, each technique has its own species-specific bias: pitfalls, as discussed above, are more likely to catch carabids based on their activity levels rather than their abundance only, while coverboards are likely to be biased towards slow-moving, ground-dwelling and nocturnal species (given that the sampling is likely to be done during the day, when diurnal species are more likely to be active and away from the shelter of the coverboard) (Dávalos et al. 2006). Grouped or barrier pitfall traps are also optimal for different species (Dávalos et al. 2006). However, multiplying sampling techniques complicates data analysis.

Conclusion

Like many ecological surveys faced with a variety of environmental conditions and research subjects of diverse sizes, phenologies and behaviors, this study met with some difficulties and challenges, some unique, some inherent to all field work. In addition to providing an inventory of ground beetle species found in the Mont St-Hilaire Nature Reserve, this study has provided further evidence for the phenology and habitat preferences of several species, attempted to elucidate the role of several landscape-level environmental factors in determining carabid assemblages, and to identify indicator species for these factors. The relative scarcity of studies performed at the landscape scale requires that further studies be made before being able to draw strong links between broad habitat types and particular carabid assemblages. Further studies are needed to determine whether reliable predictions of species composition can be made from easily observable, landscape-scale environmental characteristics (e.g. forest type, wetland type, etc.), or, on the other hand, the degree to which species composition can be used to identify the dominant environmental forces that affect a site.

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Appendices

Appendix 1: List of species caught, with number of individuals for each habitat type

	Total	Hardwood	Mixed	Ecotone	Open	Dry forest	Wet forest
Agonum fidele Casey	116	58	44	14	0	4	98
Pterostichus melanarius Illiger	109	46	8	49	6	37	17
Sphaeroderus lecontei Dejean	105	55	32	16	2	66	21
Synuchus impunctatus Say	100	50	26	22	2	66	10
Pterostichus mutus Say	85	33	37	15	0	54	16
Pterostichus lucublandus Say	78	12	6	32	28	11	7
Pterostichus pensylvanicus LeConte	75	24	50	1	0	64	10
Patrobus longicornis Say	69	58	7	4	0	1	64
Carabus nemoralis O.F. Müller	57	9	7	36	5	15	1
Agonum melanarium Dejean	52	26	11	15	0	9	28
Agonum palustre Goulet	39	3	3	33	0	2	4
Pterostichus coracinus Newman	35	21	14	0	0	14	21
Chlaenius impunctifrons Say	31	19	0	12	0	2	17
Myas cyanescens Dejean	31	18	10	2	1	28	0
Agonum gratiosum Mannerheim	21	15	5	1	0	1	19
Platynus decentis Say	18	8	6	4	0	5	9
Bembidion graciliforme Hayward	16	15	0	1	0	0	15
Agonum retractum LeConte	12	4	8	0	0	5	7
Harpalus somnulentus Dejean	11	3	1	6	1	2	2
Bembidion frontale LeConte	9	6	2	1	0	0	8
Clivina fossor Linnaeus	9	2	0	7	0	0	2
Notiophilus aeneus Herbst	9	3	1	5	0	4	0
Pterostichus rostratus Newman	9	3	6	0	0	8	1
Pterostichus luctuosus Dejean	8	6	1	0	1	0	7
Pterostichus vernalis Panzer	8	0	0	6	2	0	0
Agonum tenuicolle Leconte	6	2	4	0	0	0	6
Amphasia interstitialis Say	6	4	0	2	0	2	2
Pterostichus tristis Dejean	6	2	4	0	0	6	0
Loricera pilicornis Fabricius	6	4	2	0	0	1	5
Bembidion obtusum Audinet-Serville	5	0	0	5	0	0	0
Cymindis americana Dejean	5	1	2	1	1	2	1
Elaphrus clairvillei Kirby	5	4	1	0	0	1	4
Amara Lunicollis Schiodte	4	0	0	1	3	0	0
Pterostichus patruelis Dejean	4	4	0	0	0	0	4
Acupalpus carus LeConte	3	1	0	1	1	0	1
Gastrellarius honestus Say	3	0	3	0	0	3	0
Pterostichus corvinus Dejean	3	3	0	0	0	0	3
Pterostichus femoralis Kirby	3	0	0	3	0	0	0
Trechus apicalis Motschulsky	3	0	3	0	0	0	3

Chlaenius emarginatus Say	2	0	0	2	0	0	0
Amara cupreolata Putzeys	2	0	0	1	1	0	0
Bradycellus kirbyi G.H. Horn	2	0	1	1	0	0	1
Olisthopus parmatus Say	2	1	1	0	0	2	0
Agonum muelleri Herbst	1	0	0	1	0	0	0
Amara angustata Say	1	0	0	1	0	0	0
Calleida punctata LeConte	1	0	0	1	0	0	0
Pterostichus adoxus Say	1	0	1	0	0	0	1
Scaphinotus viduus Dejean	1	0	1	0	0	1	0
Bembidion mimus Hayward	1	0	1	0	0	0	1
Notiobia nitidipennis LeConte	1	0	0	1	0	0	0
Stenolophus conjunctus Say	1	0	0	0	1	0	0
Bembidion muscicola Harward	1	1	0	0	0	0	1
Xestonotus lugubris Dejean	1	0	0	1	0	0	0
Bradycellus semipubescens Lindroth	1	0	0	1	0	0	0
	1193	524	309	305	55	416	417

Appendix 2: Table of indicator species

Partition	Species	Habitat type	Indicator Value	
1	Sphaeroderus lecontei	All habitat	73.58	Max
	Pterostichus mutus	All habitat	60.38	Max
	Agonum retractum	All habitat	15.09	Max
	Cymindis americana	All habitat	9.43	Max
2	Synuchus impunctatus	Dry	63.44	Max
	Carabus nemoralis	Dry	49.67	
	Myas cyanescens	Dry	42.86	
	Pterostichus lucublandus	Dry	43.06	
	Agonum fidele	Wet	91.37	Max
	Patrobus longiconis	Wet	48.07	
	Agonum gratiosum	Wet	31.62	Max
	Bembidion graciliforme	Wet	32.23	
	Pterostichus coracinus	Wet	28.96	Max
	Platynus decentis	Wet	31.75	Max
	Chlaenius impunctifrons	Wet	28.21	
3	Pterostichus pensylvanicus	Dry forest	63.65	Max
	Myas cyanescens	Dry forest	46.89	Max
	Pterostichus mutus	Dry forest	40.95	
	Pterostichus lucublandus	Dry open	77.92	Max
	Carabus nemoralis	Dry open	68.74	Max
	Agonum palustre	Dry open	59.74	
	Pterostichus melanarius	Dry open	50.02	Max
	Harpalus somnulentus	Dry open	37.33	Max
	Agonum fidele	Wet forest	80.24	
	Patrobus longicornis	Wet forest	45.21	

	Agonum gratiosum	Wet forest	29.76	
	Bembidiongraciliforme	Wet forest	30.3	
4	Myas cyanescens	Dry hardwood	29.54	
	Pterostichus pensylvanicus	Dry mixed	54.9	
	Pterostichus mutus	Dry mixed	32.85	
	Agonum palustre	Dry ecotone	86.41	Max
	Carabus nemoralis	Dry ecotone	54.37	
	Pterostichus melanarius	Dry ecotone	38.95	
	Harpalus somnulentus	Dry ecotone	34.04	
	Pterostichus lucublandus	Dry open	41.79	
	Patrobus longicornis	Wet hardwood	56.78	Max
	Chlaeniusimpunctatus	Wet hardwood	43.33	Max
	Bembidion graciliforme	Wet hardwood	55.38	Max
	Agonum fidele	Wet hardwood	43.23	