



*Research*

## The Trade-off Between Housing Density and Sprawl Area: Minimizing Impacts to Carabid Beetles (Coleoptera: Carabidae)

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**ABSTRACT.** Increasing housing density has negative effects on native biodiversity. This implies that we should build at low density to conserve native species. However, for a given human population, low-density development must cover a large area, resulting in sprawl. A pertinent question is then, at what housing density are the impacts of a given human population on native biodiversity minimized? We addressed this question with carabid beetles in Ottawa and Gatineau, Canada. First, we collected beetles at 22 sites representing a range of housing densities. We then used these data to estimate beetle abundance and species richness in hypothetical development scenarios representing the housing density/sprawl area trade-off. Our results suggest that clustering development at a high housing density minimizes the impacts of a given human population on carabid beetles. If these results are general across all forest taxa, then planning that favors densification rather than sprawl would minimize urbanization effects on forest biodiversity.

**Key Words:** *development scenario; forest fragmentation; forest taxa; ground beetle; housing density; residential development; urban sprawl*

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### INTRODUCTION

Urbanization generally has negative effects on native biodiversity. An increase in housing density along the rural–urban gradient is accompanied by decreases in the abundance and species richness of native insects, amphibians, lizards, birds, and mammals (reviewed in McKinney 2002 and Hansen et al. 2005), with strong declines for native specialists. Blair (1999) reported the near complete loss of native bird and butterfly species present in a biological preserve in California as housing density increased. Similarly, along a rural–urban gradient in Argentina, native rodent species were only encountered in a natural reserve and parklands with very few buildings (Cavia et al. 2009). Frog and toad populations in Iowan wetlands have also been found to decline with increasing housing density (Pillsbury and Miller 2008).

The implicit conservation implication of these findings is that we should build at low density over the landscape. However, to accommodate a given human population, low-density development must cover a large area, resulting in sprawl and significant negative impacts to native plant and animal

communities (Odell and Knight 2001, Maestas et al. 2003, Hansen et al. 2005). A pertinent question is then, at what housing density are the impacts of a given human population on native biodiversity minimized? For a given human population, it is unclear whether the impacts on native biodiversity are less where housing density is high and sprawl area is small or where housing density is low and sprawl area is large. This question was recently listed as one of the 100 questions that, if answered and acted upon, would have the greatest impact on the conservation of biological diversity worldwide (Sutherland et al. 2009).

We chose to evaluate the housing density/sprawl area trade-off using carabid beetles (Coleoptera: Carabidae). Carabid beetles were particularly appropriate candidates for our study because of their abundance and diversity and the ease with which they can be sampled. The family Carabidae is also well described taxonomically, and individuals can be easily identified to species. In addition, carabid beetles are important prey for many taxa, including salamanders (Andreone et al. 1999), lizards (Hódar et al. 1996), bats (Arletta et al. 1993), and birds (Holland et al. 2006). Finally, the response of

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carabid beetles to urbanization has been quantified. Native forest specialist carabid beetle abundance and species richness in forest fragments have been found to decline with increasing intensity of surrounding urbanization (Sadler et al. 2006, Elek and Lövei 2007, Gaublomme et al. 2008, Magura et al. 2008).

We estimated the impacts of a given human population on carabid beetle abundance and species richness in Ottawa, Ontario and Gatineau, Quebec, Canada. Our methodology can be described in two parts. First, we collected carabid beetles in sites of the same size representing a range of housing densities. We then used these empirical data to estimate the abundance and species richness of carabid beetles in four hypothetical development scenarios representing the trade-off between housing density and sprawl area. Development scenarios were hypothetical forested landscapes of the same size that accommodated a given human population at different housing densities, resulting in dispersed, semi-compact, and compact development patterns (an undeveloped scenario was also created for comparison). We identified the housing density that minimized the impacts of a given human population on carabid beetles by comparing abundance and species richness estimates among scenarios.

## METHODS

### Beetle abundance data collection

#### *Study area*

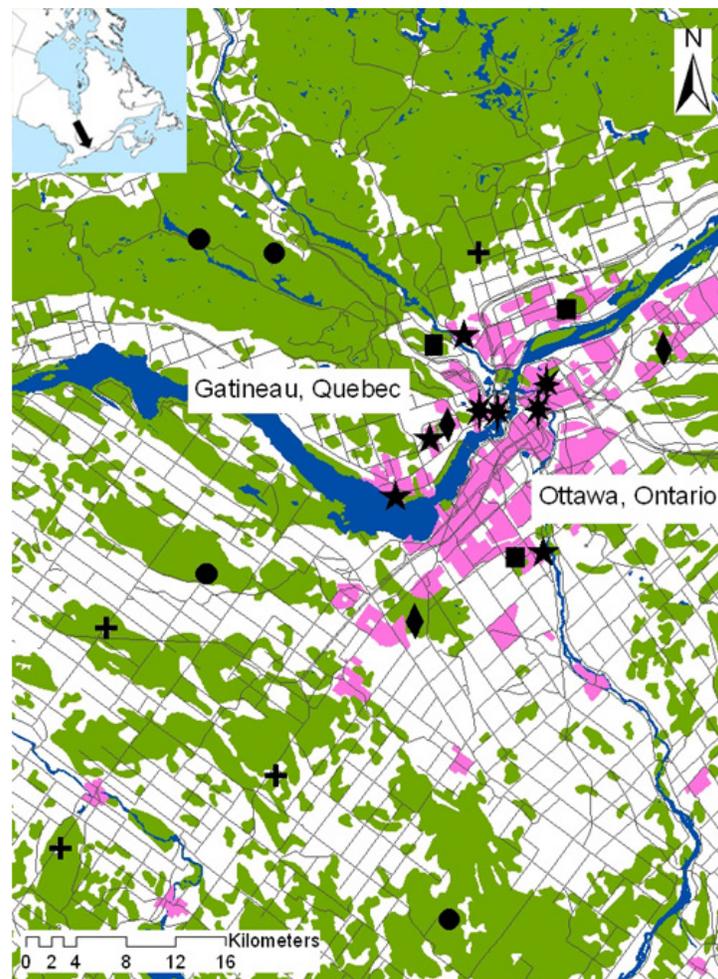
We sampled carabid beetle populations at 22 sites in and around Ottawa, Ontario and Gatineau, Quebec, Canada (Fig. 1). The study area encompassed approximately 4040 km<sup>2</sup> on both sides of the Ottawa River. The northern half of the study area forms part of the Southern Laurentians ecoregion of Quebec and is underlain by the Canadian Shield, composed mainly of massive Precambrian granite and gneiss. Elevation is commonly 300-600 m above sea level. The St. Lawrence Lowlands ecoregion is south of the Ottawa River and is underlain by flat-lying Palaeozoic strata with elevations rarely more than 150 m above sea level. All housing categories (see below) were approximately equally represented in both ecoregions to account for possible differences in forest composition (Fig. 1). In addition, we tested

a posteriori for differences in tree community composition between ecoregions using a redundancy analysis. The single constrained axis was not significant (100 permutations,  $F_{1,2} = 2.37$ ,  $P = 0.29$ ).

#### *Site selection*

We selected four sites in each of four housing density categories: Forested (0 dwellings/km<sup>2</sup>), Exurban (< 56 dwellings/km<sup>2</sup>, mean = 31 ± 9 [SE] dwellings/km<sup>2</sup>), Suburban (140-712 dwellings/km<sup>2</sup>, mean = 555 ± 101 [SE] dwellings/km<sup>2</sup>), and Urban (> 1244 dwellings/km<sup>2</sup>, mean = 3754 ± 492 [SE] dwellings/km<sup>2</sup>) (Fig. 2A). Housing density values for each category were derived from those used by previous authors (Kluza et al. 2000, Marzluff 2001, Odell and Knight 2001, Theobald 2001, Gillham 2002) and reflect the distribution of housing densities in the study area. Each site comprised the area within a 500 × 500 m square (0.25 km<sup>2</sup>). Residential development in Exurban, Suburban, and Urban sites was dominated by traditional land covers, such as pavement and lawns and gardens surrounding homes. In Exurban sites, single-family homes and their associated gardens were separated by natural habitat (forest) within which recreation occurred (e.g., trail use). Suburban and Urban sites were composed exclusively of developed area, consisting of single-family homes and small parks with play structures in Suburban sites and a mix of single-family homes and multi-family complexes (e.g., low-rise and high-rise apartment buildings), small parks, and small shops in Urban sites. Thus, in our hypothetical development scenarios (see below), we compared residential developments composed of similar land covers and land uses (but different densities). In addition to these 16 sites, we selected six forested sites, equal in size to those described above, adjacent to developments of Suburban or Urban housing densities (three sites each) (Fig. 2B). In contrast to Forested sites, which were embedded in a larger forested area, these Neighbor sites were chosen to incorporate the possible effects of adjacent urban development on carabid beetle populations in forest habitat. Forested sites adjacent to undeveloped forest were represented by our Forested site category. We did not select any forested sites adjacent to Exurban-density development because the hypothetical landscapes we used to characterize the housing density/sprawl area gradient (see below) did not contain any forested areas adjacent to Exurban-density development.

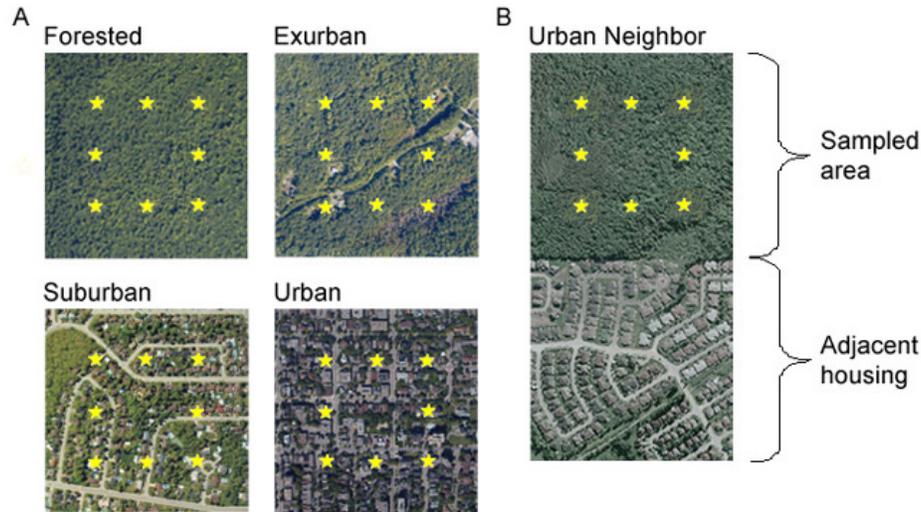
**Fig. 1.** The study area in and around the cities of Ottawa, Ontario and Gatineau, Quebec, Canada. Inset depicts the location of the study area in eastern Canada. Beetle survey sites are 0.25-km<sup>2</sup> areas indicated by symbols representing six housing categories: Forested (circles, 0 dwellings/km<sup>2</sup>), Exurban (crosses, < 56 dwellings/km<sup>2</sup>), Suburban (stars, 140-712 dwellings/km<sup>2</sup>), Urban (asterisks, > 1,244 dwellings/km<sup>2</sup>); and two categories of forested sites adjacent to developments of Suburban or Urban densities: Suburban Neighbor (squares) and Urban Neighbor (diamonds). Dark gray lines indicate roads. Forest cover is in green, large waterbodies are in blue, and urban land cover is in pink.



We searched for sites using a combination of historical topographic maps (~1/50,000, currently produced by the Centre for Topographic Information, Natural Resources Canada, Ottawa, Ontario, Canada) and the most recent aerial photographs available (2002, 1/15,000, produced by the City of Ottawa, Ontario, Canada). Historical topographic maps were derived from aerial photography approximately every 10 years

(depending on the area) and depicted detailed ground relief, drainage, forest cover, populated areas, transportation infrastructure, and individual human-made features (e.g., buildings, dams). Current maps depict wooded areas at least 250 m in diameter, populated areas (excluding parks, cemeteries, and open space at least 0.01 km<sup>2</sup> in area) at least 0.25 km<sup>2</sup> in area, and water bodies at least 50 m in diameter. Contour intervals are at least 10

**Fig. 2.** Typical sites in which carabid beetles were surveyed. All beetle survey sites were  $500 \times 500$  m. The planned locations of pitfall trapping stations are shown as yellow stars (see text for how planned and actual station locations differed). (A) Example sites representing a range of housing densities; we surveyed four replicate sites of each type. (B) Example Urban Neighbor site: the  $500 \times 500$  m forested beetle survey site was adjacent to at least  $500 \times 500$  m of Urban-density development. We surveyed three replicate Neighbor sites adjacent to each of the Suburban and Urban housing density levels.



m. We located areas that were forested prior to development using historical topographic maps. We then checked the present housing density of these areas on aerial photographs to determine whether they could be placed into our predefined categories. In this way, we selected sites that were not subjected to agricultural use for at least as many years as topographic maps have been produced (~ 80 years). No other land use, with the exception of urbanization and recreation, occurred at our sites. We also attempted to standardize development age among sites. Unfortunately, urban sites that were forested prior to development were rare, forcing us to select two sites that were developed in the early 19th century. The remainder of the sites were developed between 1922 and the present, with most development occurring in the 1960s. We minimized edge effects by choosing only sites that were surrounded by  $> 100$  m of development of a similar housing density or forest cover, depending on the category. Due to the scarcity of sites satisfying the above criteria, we were unable to choose sites representing only one forest type. Instead, our sites represented a variety of mature forest types found

in the area, such as *Fagus grandifolia* Ehrh.–*Acer saccharum* Marsh. and *Thuja occidentalis* L.–*Abies balsamea* L.–*Picea mariana* Mill. communities. However, all of our housing categories included a similar representation of forest types. In addition, we did not control for differences in microhabitat among our survey sites. We considered such differences to be the result of differences in housing density among sites, the ultimate driver of changes to beetle community structure in this study. Finally, the number of dwellings at each site and in  $500 \times 500$  m developed areas adjacent to Neighbor forest sites were counted on the ground in August 2006.

#### *Carabid beetle surveys*

We installed pitfall traps for carabid beetles at eight stations in each site in late April and early May 2007, immediately following the spring thaw. The planned locations of traps conformed to a grid pattern at each site, with traps 125 m apart (Fig. 2). If a planned trap location occurred on a rooftop or other impervious surface, the actual trap was installed as close as possible to the planned location.

In most instances, lack of landowner consent was the cause of discrepancies between planned and actual trap locations, resulting in some trap locations being moved 10-20 m (200 m in one case) from planned locations in Urban and Suburban sites, and 50-150 m from planned locations in Exurban sites. Traps consisted of two plastic cups, approximately 8 cm wide at the mouth and 10 cm tall. We buried traps in the ground with the rim of the inner cup flush with the ground surface. The base of the outer cup was punctured to allow for water drainage. We placed a 10 × 10 cm plastic roof, supported by 2.54 cm nails at each corner, above each trap to prevent rain and debris from falling in the trap. We filled traps with 100 mL of propylene glycol and a drop of dish soap. We opened traps May 14 and replaced trap contents weekly until August 3. Thus, we collected beetles continuously over a 12-week period that encompassed the peak in carabid breeding activity in the region (Levesque and Levesque 1986). Carabid beetles were identified to species using Lindroth (1961-1969). Nomenclature followed Bousquet and Larochelle (1993).

The imperfect detectability of individuals during sampling has become a major topic of discussion among empiricists (Johnson 2008). Catches from pitfall traps represent not only carabid beetle abundance, but also the activity level of individuals, trap efficiency, and the sampling design. Detectability is maximized when pitfall trap catches represent the largest possible proportion of the true number of carabid beetles in the environment. We maximized detectability by (1) trapping beetles during the peak activity period of species in our region (see above), thus maximizing the likelihood that individuals would encounter a trap; (2) using a fluid in traps that has been recommended for use in pitfall trapping of carabid beetles due to its low evaporation rate and high preservation of specimens (Lemieux and Lindgren 1999, Isono 2005); (3) using dish soap in traps to prevent escape (H. Goulet, Agriculture and Agri-Food Canada, *personal communication*); (4) using traps with a diameter large enough to capture large-bodied beetle individuals but small enough to minimize the catch of vertebrates (amphibians and small mammals) (Work et al. 2002); (5) installing traps with drainage holes and roofs to ensure their proper functioning throughout the season; (6) collecting trap contents weekly to minimize predation by necrophagous beetles (H. Goulet, *personal communication*); and (7) installing the maximum number of traps per site that we could feasibly operate considering our

weekly collection schedule, site size (0.25 km<sup>2</sup>), and the driving distances between sites. In addition, we used the summed catch of individuals over the entire season as our estimate of the relative abundance of species at sites (see below) because this measure has previously been shown to be significantly positively correlated with true density ( $r \geq 0.91$ ) for two carabid beetle species (Baars 1979).

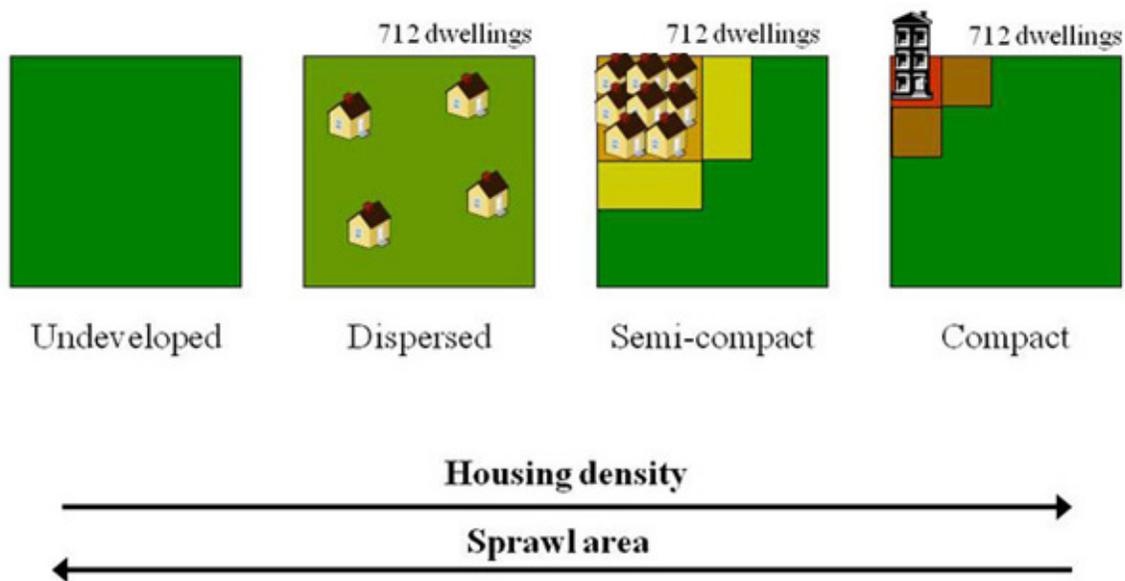
## Comparison of development scenarios

### *Hypothetical development scenarios*

We used the data described above to estimate carabid beetle abundance and species richness along a gradient of increasing housing density and decreasing sprawl area. We represented this gradient with hypothetical development scenarios (Fig. 3). Development scenarios can be envisioned as forested landscapes of the same size, into which the same number of dwellings were placed, but in contrasting patterns. One end of the gradient, where housing density is low and sprawl area is large, was represented by the Dispersed scenario, which was completely covered by Exurban-density development. The other end of the gradient, where housing density is high and sprawl area is small, was represented by the Compact scenario. The Compact scenario was home to the same number of dwellings as the Dispersed scenario, but the dwellings were clustered at an Urban density and the remainder of the Compact scenario was undeveloped forest. We also estimated carabid beetle abundance and species richness for an intermediate development scenario, the Semi-compact scenario. Here, the same number of dwellings as in the other two development scenarios was represented at a Suburban density, with the remainder of the Semi-compact scenario in undeveloped forest. Finally, for comparison, we estimated carabid beetle abundance and species richness for an Undeveloped scenario, that is, the same area as for the developed scenarios but covered entirely in forest.

We defined a development scenario as a 22.96 km<sup>2</sup> square area, or an area equivalent to 91.83 units of the 500 × 500 m (0.25 km<sup>2</sup>) beetle survey sites. We arrived at this development scenario size by calculating the area required to accommodate a given number of dwellings (the mean number of dwellings at our Urban and Urban Neighbor beetle survey sites [712 dwellings]) at the lowest housing density (the Exurban density, mean = 31 dwellings/

**Fig. 3.** Hypothetical development scenarios representing a gradient of increasing housing density and decreasing sprawl area. For a given forested area (the Undeveloped scenario), the same number of dwellings is depicted at three housing densities (Exurban, Suburban, and Urban), resulting in Dispersed, Semi-compact, and Compact development patterns, respectively. Yellow and brown areas represent forest habitat adjacent to development typical of Suburban Neighbor and Urban Neighbor sites, respectively. Drawings, including proportions of each cover type in each scenario, are not to scale. For example, the developed portion of the Semi-compact scenario was 6.18% of the total area of the scenario. Scenarios were 22.96 km<sup>2</sup>.



km<sup>2</sup>). In this way, we created our Dispersed scenario, covered entirely by 712 dwellings at the Exurban housing density or, equivalently, 91.83 Exurban beetle survey sites. In a similar fashion, we determined the size of the developed area (measured in km<sup>2</sup> or in the number of Suburban or Urban beetle survey sites) within the Semi-compact and Compact scenarios. For these, we created square developed areas, positioned in one corner of each development scenario, to represent the area needed to contain 712 dwellings at the mean Urban or Suburban densities (0.25 km<sup>2</sup> and 1.42 km<sup>2</sup>, respectively). For the Semi-compact and Compact scenarios, we assumed that the forest cover adjacent to the developed area had carabid beetle abundances and species richnesses typical of our Neighbor beetle survey sites adjacent to Suburban- and Urban-density development, respectively. We calculated the area of this adjacent forest cover as the number of Neighbor beetle survey sites required to line both edges of the developed area. This pattern matches the spatial

arrangement of our Neighbor beetle survey sites, which shared one complete edge with development (Fig. 2B). Finally, we assumed that the remaining area in the Semi-compact and Compact scenarios was typical of our Forested beetle survey sites. We assumed the Undeveloped scenario was covered entirely in forest cover typical of our Forested beetle survey sites.

#### *Theoretical carabid beetle species abundances*

For each development scenario, we estimated the abundance of each carabid beetle species collected during our surveys. First, we calculated the relative abundance of a species at each beetle survey site by summing the numbers of individuals of the species collected at all eight stations in the site over the entire survey period (Appendix 1). Recall that we measured the area of each development scenario in terms of the numbers of beetle survey sites of each housing category making up the development

scenario (see above). Therefore, to estimate the total abundance of a species for a development scenario, we moved through the scenario, one site area at a time, and randomly selected a relative abundance for the species from one of the three or four beetle survey sites in that housing category (Fig. 4). For areas in the development scenario making up proportions of beetle survey sites, we multiplied the randomly selected abundance value by that proportion. We summed these 91.83 relative abundance values to yield the estimated abundance of a species in the whole development scenario. For example, Fig. 4 depicts the estimation of the abundance of a beetle species in the Semi-compact scenario. The Semi-compact scenario is shown as the equivalent area of many beetle survey sites in three different housing categories: Suburban, Suburban Neighbor, and Forested. For each site area in the Semi-compact scenario, a relative abundance value for the beetle species was randomly selected from among those of the beetle survey sites in that housing category. For instance, the developed portion of the Semi-compact scenario has been "filled in" with randomly selected relative abundance values of the beetle species from the four Suburban beetle survey sites. The randomly selected abundance values for the entire Semi-compact scenario were then summed to yield an estimate of the abundance of the beetle species over the whole area of the Semi-compact scenario. We repeated this estimation procedure 1000 times for each species, resulting in an abundance distribution for each species in each development scenario. In the same manner, we also estimated the total abundance of all carabid beetles in each development scenario and the abundance of beetles belonging to species classified as forest, open-habitat, native, and non-native in each development scenario (Appendix 2).

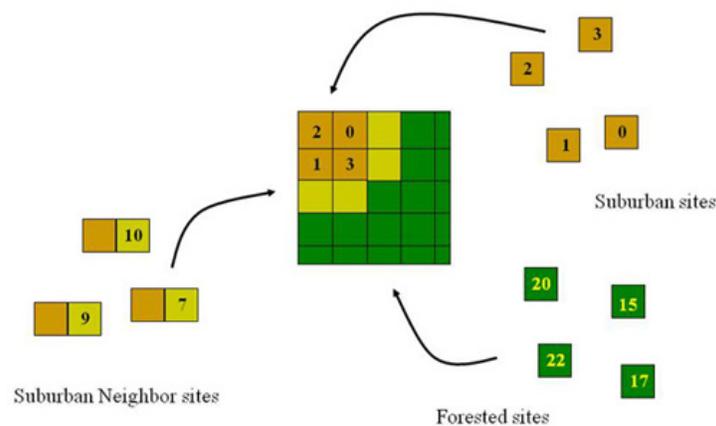
#### *Theoretical carabid beetle species richnesses*

We estimated the species richness of all carabid beetles, forest beetles, and open-habitat beetles in each development scenario. Using species accumulation curves constructed for each housing category and for each beetle group (Colwell and Coddington 1994), we estimated that we collected > 89% of species predicted to be present in each type of site. Therefore, we assumed that we recorded the entire community of beetles present in each housing category. Using this information, we estimated the species richness of each beetle group

in each development scenario with a procedure similar to that described for abundance. For each site area in a development scenario, we randomly selected an actual sampled site from the appropriate housing category and applied the species observed there to the site area in the development scenario. We repeated this procedure for every site area in the development scenario, successively adding any new species to the development scenario's species list. For areas in the development scenario making up fractions of beetle survey site areas, we randomly selected without replacement the observations from two, four, or six of the trapping stations within the beetle survey site, depending on the size of the fraction. The development scenario's final species list once every site area had been "filled" with species was the species richness of that whole development scenario.

Initially, the total number of beetle survey sites available for selection differed among development scenarios (four each in the Undeveloped and Dispersed scenarios and 11 each in the Semi-compact and Compact scenarios). For example, recall that the Dispersed scenario was considered as the equivalent area to 91.83 Exurban beetle survey sites. However, there were only four Exurban beetle survey sites from which species observations could be used to estimate species richness in the Dispersed scenario. The Compact scenario, on the other hand, was made up of areas represented by beetle survey sites in three housing categories: Urban, Urban Neighbor, and Forested. Thus, observations from 11 beetle survey sites (four Urban, three Urban Neighbor, and four Forested) could be used to estimate species richness in the Compact scenario. This represented a difference in sample size among the development scenarios, which could bias the results such that the estimated richnesses in the Undeveloped and Dispersed scenarios would be lower than they should be, relative to the richnesses of the Semi-compact and Compact scenarios. We corrected for this by randomly selecting two Forested beetle survey sites, one Suburban or Urban site, and one Suburban Neighbor or Urban Neighbor site prior to estimating the species richness of each beetle group in the Semi-compact and Compact scenarios. For example, for the Semi-compact scenario, we randomly selected two Forested sites, one Suburban site, and one Suburban Neighbor site. These four beetle survey sites represented the pool from which species observations could be selected according to the procedure described above. Thus, for the Semi-compact and Compact scenarios, the

**Fig. 4.** Illustration of the method for estimating the abundance of a carabid beetle species in a development scenario. Shown is the Semi-compact scenario (see Fig. 3; not to scale). Numbers represent the relative abundance of the species in each beetle survey site, calculated from pitfall trap data. Three types of beetle survey sites make up the Semi-compact scenario: Suburban, Suburban Neighbor, and Forested. For each site area in the scenario, a relative abundance value was randomly chosen from those of the replicate beetle survey sites in the appropriate housing category. To illustrate this, the developed portion of the scenario has been filled in with randomly chosen relative abundance values from the Suburban beetle survey sites. For areas in the development scenario that were smaller than site areas, the relative abundance value was multiplied by the proportion of a site area represented. Finally, the randomly selected values for the entire Semi-compact scenario were summed to yield an estimate of the abundance of the carabid beetle species in the whole development scenario.



initial number of beetle survey sites available for selection was restricted to four to equal the number of beetle survey sites available for the Undeveloped and Dispersed scenarios. Finally, we repeated the entire species richness estimation procedure 1000 times to yield an estimate of the species richness of each beetle group and its associated error in each development scenario. All analyses were carried out using R version 2.6.2 (R Development Core Team 2008).

## RESULTS AND DISCUSSION

We collected 4630 individuals from 90 species during our surveys (Appendix 1). We classified 26 species as forest species, 41 species as open-habitat species, 80 species as native species, and 10 species as non-native species (Appendix 2). We collected 694 individuals of the most abundant species, *Pterostichus mutus*, which occurred at 13 of the 22 survey sites (Appendix 1). The most widespread species, *Carabus nemoralis*, *P. melanarius*, and *P.*

*pensylvanicus*, occurred at 17 survey sites each. We collected only one individual of 16 species during our surveys.

The abundances and species richnesses of forest beetles, open-habitat beetles, and non-native beetles were significantly affected by the housing density of survey sites (Table 1). Forest beetle abundance and species richness were significantly lower in Suburban and Urban survey sites than in sites in the other housing categories. Open-habitat beetles were significantly more abundant in Suburban compared with Forested survey sites, whereas the Suburban and Urban housing categories had significantly more open-habitat beetle species than the Forested or Suburban Neighbor categories. Forested survey sites had significantly fewer non-native beetles than sites in the other housing categories.

The estimates of carabid beetle abundance and species richness in hypothetical development scenarios suggest that clustering development at a Suburban or Urban housing density minimizes the

**Table 1.** Carabid beetle abundance and species richness (mean  $\pm$  SE) at 500  $\times$  500 m beetle survey sites in six housing categories (see *Methods* for category definitions). The species included in each group are given in Appendix 2. Different lowercase letters indicate significant pairwise differences between categories for those response variables for which housing category had a significant effect in single-factor analyses of variance (square-root or log transformations were applied to response variables prior to analyses if the assumptions of normality and homoscedasticity were not met).

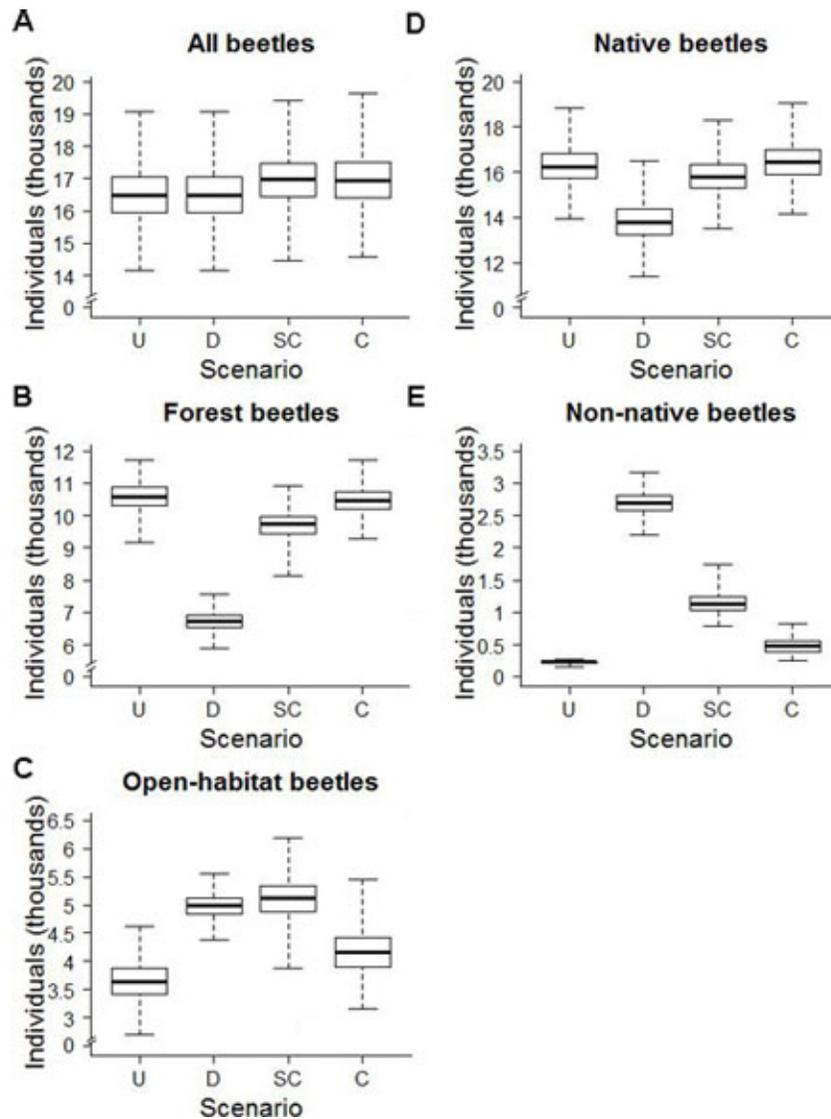
	Forested	Exurban	Suburban	Urban	Suburban Neighbor	Urban Neighbor
<i>n</i>	4	4	4	4	3	3
Housing density (mean dwellings/km <sup>2</sup> $\pm$ SE)	0	31.00 $\pm$ 9.30	555.00 $\pm$ 101.10	3754.00 $\pm$ 491.92	434.68 $\pm$ 159.53	1637.32 $\pm$ 281.98
<u>All beetles</u>						
Abundance	181.75 $\pm$ 49.51	151.50 $\pm$ 28.01	208.50 $\pm$ 56.99	136.25 $\pm$ 38.72	238.00 $\pm$ 81.22	428.67 $\pm$ 114.57
Species richness	18.00 $\pm$ 4.26	25.00 $\pm$ 2.80	21.50 $\pm$ 2.90	18.75 $\pm$ 2.72	14.33 $\pm$ 4.06	23.00 $\pm$ 3.46
<u>Forest beetles</u>						
Abundance	117.00 $\pm$ 30.82 <sup>a</sup>	73.25 $\pm$ 14.42 <sup>a</sup>	6.75 $\pm$ 1.93 <sup>b</sup>	3.50 $\pm$ 1.32 <sup>b</sup>	54.00 $\pm$ 22.81 <sup>a</sup>	97.33 $\pm$ 8.65 <sup>a</sup>
Species richness	9.50 $\pm$ 0.87 <sup>a</sup>	9.25 $\pm$ 0.75 <sup>a</sup>	2.00 $\pm$ 0.41 <sup>b</sup>	1.50 $\pm$ 0.29 <sup>b</sup>	6.00 $\pm$ 1.53 <sup>a</sup>	9.33 $\pm$ 0.88 <sup>a</sup>
<u>Open-habitat beetles</u>						
Abundance	37.50 $\pm$ 32.31 <sup>a</sup>	29.00 $\pm$ 10.19 <sup>ab</sup>	131.25 $\pm$ 49.49 <sup>b</sup>	71.75 $\pm$ 28.29 <sup>ab</sup>	38.33 $\pm$ 17.70 <sup>ab</sup>	158.67 $\pm$ 77.92 <sup>ab</sup>
Species richness	2.25 $\pm$ 0.95 <sup>a</sup>	6.75 $\pm$ 2.59 <sup>ab</sup>	11.75 $\pm$ 1.70 <sup>b</sup>	11.00 $\pm$ 2.27 <sup>b</sup>	2.33 $\pm$ 0.88 <sup>a</sup>	3.00 $\pm$ 1.00 <sup>ab</sup>
Native beetle abundance	179.25 $\pm$ 48.58	121.50 $\pm$ 25.50	142.25 $\pm$ 50.76	76.75 $\pm$ 29.10	114.67 $\pm$ 36.98	321.33 $\pm$ 70.55
Non-native beetle abundance	2.50 $\pm$ 1.04 <sup>a</sup>	30.00 $\pm$ 10.82 <sup>b</sup>	66.25 $\pm$ 19.14 <sup>b</sup>	59.50 $\pm$ 10.02 <sup>b</sup>	123.33 $\pm$ 67.40 <sup>b</sup>	107.33 $\pm$ 64.54 <sup>b</sup>

impacts of a given human population on carabid beetle communities. In particular, we estimated that high-density development over a small area (the Compact scenario) resulted in the highest abundance and species richness of forest beetles when compared with other development patterns (Figs. 5B, 6B). We also estimated the abundance of native beetles and total beetle species richness to be highest in the Compact scenario (Figs. 5D, 6A). The Semi-compact scenario had the highest estimated total beetle abundance (Fig. 5A), likely due to open-habitat beetles having their highest estimated abundance in this scenario (Fig. 5C). Open-habitat beetles were also most speciose in the Semi-compact scenario (Fig. 6C). The Dispersed scenario

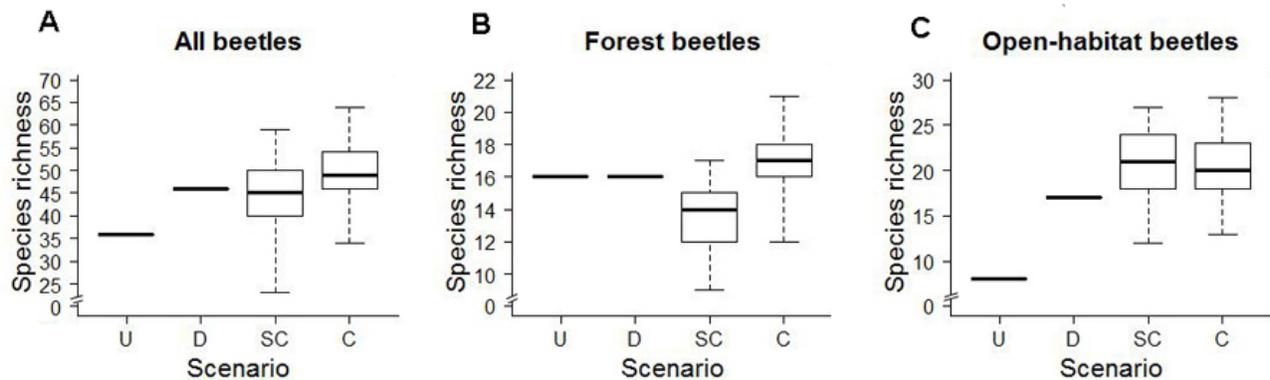
was characterized by the highest estimated abundance of non-native beetles (Fig. 5E).

Very little is presently known about how plants and animals respond to the housing density/sprawl area trade-off. We are aware of only three other studies that have compared plant or animal community structure between clustered or compact development and dispersed development (Kleppel et al. 2004, Lenth et al. 2006, Gagné and Fahrig *in press*). Kleppel et al. (2004) compared the biomasses of emergent vascular plants, phytoplankton, and zooplankton between wetlands situated in watersheds dominated by traditional small town

**Fig. 5.** The estimated abundances of five carabid beetle groups in four hypothetical development scenarios: U, Undeveloped; D, Dispersed; SC, Semi-compact; C, Compact. (A) All beetles. (B) Forest beetles. (C) Open-habitat beetles. (D) Native beetles. (E) Non-native beetles. The species included in each group are given in Appendix 2. The lower edge of each box is the first quartile, the bold center line is the median, and the upper edge is the third quartile of the distribution. Whiskers extend to the minimum and maximum values.



**Fig. 6.** The estimated species richnesses of three carabid beetle groups in four hypothetical development scenarios: U, Undeveloped; D, Dispersed; SC, Semi-compact; C, Compact. (A) All beetles. (B) Forest beetles. (C) Open-habitat beetles. The species included in each group are given in Appendix 2. The lower edge of each box is the first quartile, the bold center line is the median, and the upper edge is the third quartile of the distribution. Whiskers extend to the minimum and maximum values. Species richness estimates for the Undeveloped and Dispersed scenarios had zero variance. This is because every beetle species collected in the four Forested survey sites (for the Undeveloped scenario) and the four Exurban survey sites (for the Dispersed scenario) was always estimated to be in at least one of the large number (91.83) of replicate site areas in these scenarios.



development (high housing density and small sprawl area) or suburban development (low housing density and large sprawl area) in the Hudson River Valley of New York State. Lenth et al. (2006) compared bird, mammal, and plant communities among clustered developments, dispersed developments, and undeveloped prairie in Colorado. Neither study found significant differences in algal or animal communities between development types, although Kleppel et al. (2004) did report increased dominance of the emergent plant community by invasive species and decreased trophic transfer function (the ratio of zooplankton biomass to phytoplankton biomass) in suburban wetlands. In a separate study (Gagné and Fahrig *in press*), we found that estimated forest breeding bird abundance and species richness in the same hypothetical scenarios showed similar trends to those reported here for forest carabid beetles: forest birds, and in particular forest interior birds, were most abundant in the Compact scenario and most speciose in the Semi-compact scenario (not including the Undeveloped scenario). A synthesis of the results described in this paragraph is difficult because Kleppel et al. (2004) and Lenth et al. (2006) did not explicitly control for

landscape size and number of dwellings, whereas Gagné and Fahrig (*in press*) and this study did so (recall that hypothetical development scenarios were 22.96 km<sup>2</sup> and contained 712 dwellings). Thus, the results of Kleppel et al. (2004) and Lenth et al. (2006) are confounded by these variables, obscuring the trade-off between housing density and sprawl area.

We chose to estimate carabid beetle abundances and species richnesses in hypothetical development scenarios of a particular size, yet choice of spatial scale could be expected to change these estimates. Scenario size and structure were determined according to two observed values: the mean number of dwellings in the Urban and Urban Neighbor housing categories and the mean housing density of Exurban survey sites. Variation in these values would change scenario size, as well as the areas covered by development and Neighboring forest cover in the Semi-compact and Compact scenarios. Thus, whereas the Undeveloped and Dispersed scenarios would be covered entirely in forest cover or Exurban-density development regardless of spatial scale, the proportions of the Semi-compact

and Compact scenarios covered by development and neighboring forest cover would change with spatial scale. To illustrate this, we calculated scenario size and the areas covered by Urban-density development and Urban Neighbor forest cover in the Compact scenario for differing numbers of dwellings and housing density values. To accommodate the maximum number of dwellings in Urban and Urban Neighbor survey sites (1167 dwellings) at the minimum Exurban housing density (12 dwellings/km<sup>2</sup>), scenario size would have to be 97.25 km<sup>2</sup>. Urban survey site areas would cover 0.26%, Urban Neighbor survey site areas would cover 0.51%, and Forested survey site areas would cover 99.23% of the Compact scenario. Conversely, if one wished to accommodate the minimum number of dwellings in Urban and Urban Neighbor survey sites (311 dwellings) at the maximum Exurban housing density (56 dwellings/km<sup>2</sup>), scenario size would shrink to 5.55 km<sup>2</sup>, of which 4.50% would be covered by Urban survey site areas, 9.00% would be covered by Urban Neighbor survey site areas, and 86.50% would be covered by Forested survey site areas for the Compact scenario. These calculations exemplify that the Compact scenario will remain largely composed of Forested survey site areas despite an order of magnitude change in spatial scale (recall that the proportions of Urban, Urban Neighbor, and Forested survey site areas for the scenario size used in this paper [22.96 km<sup>2</sup>] were 1.09%, 2.18%, and 96.73%, respectively, in the Compact scenario). The results we report here mainly stem from the Semi-compact and Compact scenarios being largely made up of Forested survey site areas compared with the Dispersed scenario being covered entirely in Exurban-density development. Thus, these results are not likely to change significantly with a change in spatial scale of the magnitude described above. However, the use of numbers of dwellings and housing densities outside of the ranges observed in our survey sites may result in significant changes in the proportions of cover types in the Semi-compact and Compact scenarios, possibly engendering departures from the carabid beetle estimates we calculated here.

The results of Gagné and Fahrig (*in press*) and those presented here indicate that taxa that have previously been found to exhibit strong declines in response to increasing housing density (forest breeding birds [Friesen et al. 1995] and forest carabid beetles [Magura et al. 2008]) have their highest estimated abundances and species richnesses in compact rather than dispersed

development (due to the former being surrounded by a large area of forest cover). Future research on the effects of the housing density/sprawl area trade-off on forest biodiversity should focus on evaluating the responses of taxa other than carabid beetles and breeding birds to determine whether all forest taxa that are negatively affected by increasing housing density reach higher abundances and species richnesses in compact rather than dispersed development. If this is the case, then the conservation implications for forest biodiversity of building compact rather than dispersed development in rapidly urbanizing regions would be significant.

Such work would necessitate the sampling of animal populations at spatial scales matching those at which taxa perceive and interact with the environment. Large-bodied taxa perceive and interact with the environment at larger spatial scales than small-bodied taxa (Holling 1992). Thus, to determine the effect of the housing density/sprawl area trade-off on a large-bodied taxon using the method described in this paper, populations of the taxon would be sampled in survey sites larger than those used here for carabid beetles (0.25 km<sup>2</sup>). Ideally, a preliminary investigation of the survey site size at which a taxon most strongly responds to housing density would be carried out to determine the survey site size to use in constructing hypothetical development scenarios (such an investigation was beyond the scope of the present work). The mean number of dwellings in the Urban and Urban Neighbor housing categories (used to determine scenario size, see above) would be proportional to survey site size. If the mean housing density of Exurban survey sites were fixed at a common value for all taxa, differing survey site sizes would result in hypothetical development scenarios being created at spatial scales relevant to each taxon.

The results presented here have important implications for land use planning in areas experiencing high rates of low-density residential development. At the regional scale, a network of compact developments can result in greenways or large tracts of continuous forest habitat (Arendt 2004). Rather than building outwards from urban centers at low density to accommodate human population growth, as is now the case, we foresee outlying nodal housing developments linked with each other and the urban center by roads and surrounded primarily by forested or other natural habitat. A similar approach to planning is already being considered by some communities (e.g.,

Ingram 2005). Although the roads linking nodal developments would likely have adverse impacts on the biodiversity in greenways, the road density for nodal development would be lower than for typical dispersed housing. Finally, the location of nodal developments would have to be chosen with care to avoid the destruction or alteration of sensitive or rare habitats. For example, although clustering development limits habitat loss in Wisconsin, most clustered developments occur on lakeshores, likely negatively affecting the many sensitive species that rely on these habitats (Gonzalez-Abraham et al. 2007).

## CONCLUSION

We quantified the impacts to carabid beetles of accommodating a given human population in hypothetical landscapes containing housing at different densities. We did so by sampling carabid beetle populations in forested and developed sites representing a gradient in housing density and then using these samples to estimate carabid beetle abundance and species richness in hypothetical scenarios representing the housing density/sprawl area trade-off. Our results suggest that building at a high density over a small area, rather than at a low density over a large area, minimizes the impacts of a given human population on carabid beetles.

These results have important implications for land use planning in urban areas. We suggest that nodal development, rather than typical dispersed development, be implemented in city fringes, particularly in those areas that are dominated by natural land covers, to minimize the impacts of future development on biodiversity. Considering the global scale of urbanization, future work should focus on determining the generality of the conclusions reached here by investigating the responses of forest taxa other than breeding birds and carabid beetles to the housing density/sprawl area trade-off in a variety of biomes.

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**Appendix 1.** Carabid beetle abundances in survey sites and stations.

*[Please click here to download file 'appendix1.xls'.](#)*

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**Appendix 2.** Carabid beetle species collected during pitfall trapping and their estimated abundances in development scenarios. We classified beetles as ‘native’, ‘non-native’, ‘forest’ and ‘open-habitat’ species according to Lindroth (1961-1969). We defined forest species as those that occur primarily in forested or wooded habitat, and in some cases open country. We defined open-habitat species as those occurring in a variety of open-habitat types (e.g., open woods, meadows, fields) including roadsides, gravel pits and cultivated ground. If the habitat affinity of a species was not recorded in Lindroth (1961-1969), we classified the species according to H. Goulet (Agriculture and Agri-Food Canada, *personal communication*) with two exceptions. The habitat affinity of *Cicindela sexguttata* was determined according to Schultz (1998) and the habitat affinity of *Trichotichnus vulpeculus* was determined according to Stanton et al. (2003) and Webster and Bousquet (2008).

	Scientific name	Habitat affinity	Developed scenario with highest abundance	Highest abundance in Undeveloped scenario?
Native beetles	<i>Agonum cupripenne</i>	Open-habitat	Dispersed	
	<i>Agonum gratiosum</i>		Dispersed	
	<i>Agonum melanarium</i>		Compact	
	<i>Agonum palustre</i>		Semi-compact	
	<i>Agonum retractum</i>	Forest	Semi-compact	
	<i>Agonum tenue</i>		Compact	
	<i>Agonum trigeminum</i>		Dispersed	
	<i>Amara angustata</i>	Open-habitat	Semi-compact	
	<i>Amara cupreolata</i>	Open-habitat	Dispersed	

<i>Amara impuncticollis</i>	Open-habitat	Semi-compact	
<i>Amara patruelis</i>	Open-habitat	Semi-compact	
<i>Amara rubrica</i>	Open-habitat	Compact	
<i>Amphasia interstitialis</i>	Forest	Semi-compact	
<i>Anisodactylus harrisii</i>	Open-habitat	Dispersed	
<i>Anisodactylus kirbyi</i>		Compact	
<i>Anisodactylus merula</i>	Open-habitat	Compact	
<i>Anisodactylus rusticus</i>	Open-habitat	Semi-compact	
<i>Anisodactylus verticalis</i>	Forest	Compact	
<i>Badister notatus</i>		Dispersed	
<i>Badister ocellaris</i>		Dispersed	
<i>Bembidion frontale</i>		Compact	Yes
<i>Bembidion inaequale</i>		Semi-compact	
<i>Bembidion praticola</i>	Forest	Compact	Yes
<i>Bembidion quadrimaculatum</i>	Open-habitat	Dispersed	
<i>oppositum</i>			
<i>Bembidion variegatum</i>		Compact	
<i>Bembidion versicolor</i>		Dispersed	
<i>Brachinus medius</i>		Compact	Yes
<i>Bradycellus lugubris</i>	Open-habitat	Compact	Yes
<i>Calathus gregarius</i>	Forest	Dispersed	
<i>Carabus maeander</i>	Open-habitat	Dispersed	
<i>Chlaenius emarginatus</i>	Forest	Dispersed	
<i>Chlaenius impunctifrons</i>		Compact	
<i>Chlaenius lithophilus</i>		Semi-compact	
<i>Chlaenius niger</i>		Dispersed	
<i>Chlaenius tricolor</i>	Open-habitat	Dispersed	

<i>Cicindela sexguttata</i>	Forest	Dispersed	
<i>Cymindis cribricollis</i>	Forest	Compact	
<i>Cymindis neglectus</i>	Forest	Compact	Yes
<i>Diplocheila obtusa</i>	Open-habitat	Dispersed	
<i>Dyschirius globulosus</i>		Dispersed	
<i>Elaphropus granarius</i>	Open-habitat	Compact	
<i>Elaphrus clairvillei</i>	Forest	Dispersed	
<i>Harpalus compar</i>	Open-habitat	Semi-compact	
<i>Harpalus eraticus</i>	Open-habitat	Semi-compact	
<i>Harpalus erythropus</i>	Open-habitat	Semi-compact	
<i>Harpalus faunus</i>	Open-habitat	Semi-compact	
<i>Harpalus fulvilabris</i>	Forest	Compact	
<i>Harpalus herbivagus</i>	Open-habitat	Dispersed	
<i>Harpalus longicollis</i>	Open-habitat	Semi-compact	
<i>Harpalus opacipennis</i>	Open-habitat	Semi-compact	
<i>Harpalus pennsylvanicus</i>	Open-habitat	Semi-compact	
<i>Harpalus providens</i>	Forest	Dispersed	
<i>Harpalus sommulentus</i>	Open-habitat	Dispersed	
<i>Lophoglossus scrutator</i>		Compact	
<i>Loricera pilicornis</i>		Compact	Yes
<i>Loxandrus commutabilis</i>	Open-habitat	Dispersed	
<i>Myas cyanescens</i>	Forest	Compact	Yes
<i>Notiophilus aeneus</i>	Forest	Compact	
<i>Olisthopus micans</i>	Forest	Compact	
<i>Olisthopus parmatus</i>	Forest	Dispersed	
<i>Oxytselaphus pusillus</i>	Open-habitat	Compact	Yes
<i>Patrobus longicornis</i>	Open-habitat	Compact	

	<i>Platynus decentis</i>	Forest	Dispersed	
	<i>Poecilus lucublandus</i>	Open-habitat	Compact	
	<i>lucublandus</i>			
	<i>Pseudamara arenaria</i>	Forest	Compact	Yes
	<i>Pterostichus caudicalis</i>		Compact	
	<i>Pterostichus coracinus</i>	Forest	Compact	Yes
	<i>Pterostichus corvinus</i>		Dispersed	
	<i>Pterostichus luctuosus</i>		Dispersed	
	<i>Pterostichus mutus</i>	Open-habitat	Semi-compact	
	<i>Pterostichus patruelis</i>		Dispersed	
	<i>Pterostichus pensylvanicus</i>	Forest	Dispersed	
	<i>Pterostichus tristis</i>	Forest	Compact	
	<i>Sphaeroderus canadensis</i>	Forest	Compact	Yes
	<i>canadensis</i>			
	<i>Sphaeroderus stenostomus</i>	Forest	Compact	
	<i>lecontei</i>			
	<i>Stenolophus conjunctus</i>	Open-habitat	Semi-compact	
	<i>Syntomus americanus</i>	Open-habitat	Dispersed	
	<i>Synuchus impunctatus</i>	Forest	Compact	Yes
	<i>Trechus apicalis</i>	Forest	Compact	Yes
	<i>Trichotichnus vulpeculus</i>	Forest	Semi-compact	
Non-native beetles	<i>Agonum muelleri</i>	Open-habitat	Semi-compact	
	<i>Amara aenea</i>	Open-habitat	Dispersed	
	<i>Amara apricaria</i>	Open-habitat	Compact	
	<i>Bembidion obtusum</i>	Open-habitat	Compact	
	<i>Bembidion tetracolum</i>	Open-habitat	Semi-compact	
	<i>Carabus granulatus</i>	Open-habitat	Semi-compact	

<i>Carabus nemoralis</i>	Open-habitat	Dispersed
<i>Clivina fossor</i>	Open-habitat	Compact
<i>Harpalus affinis</i>	Open-habitat	Compact
<i>Pterostichus melanarius</i>	Open-habitat	Dispersed

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