Beetles in the city: Ground beetles (Coleoptera: Carabidae) in Coquitlam, British Columbia as indicators of human disturbance

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ABSTRACT

Urban development may cause adverse effects on the ecological integrity of natural areas in cities through habitat loss and fragmentation. Biological communities in habitat fragments may be altered, which may, in turn, negatively impact ecosystem services that contribute to the sustainability of urban areas. As such, methods are required to assess anthropogenic impacts on urban habitats. Here, results are presented of ground beetle (Coleoptera: Carabidae) monitoring in habitat fragments in Coquitlam, British Columbia. Ground beetle diversity in Coquitlam is highest in small, disturbed sites that include both native and introduced European species. Several European carabid species are effective biological indicators of anthropogenic disturbance in urban habitat fragments. Because of the relative ease of collection and identification of carabids, monitoring of carabids by citizen scientists can be used to assess human impacts on urban ecosystems.

Keywords: ground beetles, Carabidae, biological indicators, urban ecology, insect conservation

INTRODUCTION

The development and growth of cities depends on the natural environment and the services it provides to human populations. The quality of human life in cities depends on ecosystem services that are provisioning (*e.g.,* food, water, fibre), regulating (*e.g.*, air-quality regulation, water purification, climate regulation, pollination) and cultural (*e.g.*, spiritual, recreational and aesthetic values) (Ranganathan *et al.* 2008; Montserrat *et al.* 2010). An ecological approach to urban planning should optimize the function of urban ecosystems in order to maintain ecosystem services and the resulting sustainability of cities. This approach presents challenges, because urban development often has negative consequences for ecosystem integrity. For example, urban development causes the fragmentation and elimination of natural habitats, which can have adverse effects on ecological sustainability (Fahrig 2003). In

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addition, urban ecological processes are, and will continue to be, affected by global climate change (Bellard *et al.* 2012).

A rapidly increasing proportion of the world's human population lives in cities. Only 10% of the human population lived in urban areas at the beginning of the 20th century, but since 2008, over 50% of humans live in cities (Grimm *et al.* 2008). As this urbanizing trend continues, an understanding of the ecology of urban areas is essential. Here, we present the results of surveys of urban biodiversity in Coquitlam, a rapidly growing community in the Metro Vancouver area of British Columbia, Canada. Our objectives were (1) to determine the nature of ecological communities in urban habitat fragments, and (2) to identify and develop biological indicator species to monitor ecosystem changes caused by human activities and climate change. In particular, we studied the influence of habitat fragmentation on communities of ground beetles (Coleoptera: Carabidae) in Coquitlam parks.

Ground beetles are members of the family Carabidae, which includes approximately 40,000 species worldwide. More than 3,000 of these species occur in North America (Bland and Jaques 1978; Marshall 2018). Many species exhibit habitat specificity or specificity at least to habitat attributes like moisture, temperature and shade (Rainio and Niemela 2003; Koivula 2011). As such, a strikingly different beetle assemblage can be collected at locations in close proximity if habitat characteristics vary.

Surveys of ground beetles have been widely used to assess the influence of human activities on ecological integrity. Previous studies have investigated the influences of forestry (Lemieux and Lindgren 2004; Latty *et al.* 2005; Pierce and Venier 2006; Work *et al.* 2008; Bergeron *et al*. 2011), agriculture (Raworth *et al.* 1997; Prasad and Snyder 2006; Fusser *et al.* 2018) and urbanization (Magura *et al.* 2004; Hartley *et al.* 2007) on ground beetle abundance and diversity. Ground beetles have been advocated as effective biological indicators of human disturbance (Rainio and Niemela 2003; Pierce and Venier 2006). The beetles are easily collected, and many species can be identified by relatively untrained observers. This allows the participation of municipal staff, students, and members of the general public in monitoring programs.

We have sampled ground beetles in urban habitat fragments in Coquitlam since 2001. Beetle species captured include both native North American carabids and species historically introduced from Europe (Spence and Spence 1988; Klimaszewski *et al.* 2012). We present results of ground beetle surveys in two different habitats that occur in close proximity in Coquitlam—one, a severely human-impacted meadow area, and the other, a fragment of native forest along a riparian corridor. These results indicate that carabid communities vary widely between habitats that have differing levels of anthropogenic influence. Our data suggest that carabid monitoring could be used to assess the level of human disturbance in urban habitats. We also present comparisons of beetle communities from several urban forest fragments in Coquitlam parks that vary both in their level of human disturbance and in their geographic area. Our analysis of these data asks whether particular carabid species can act as effective biological indicators of anthropogenic disturbance. Our data show that monitoring for European carabid species can be used to evaluate human impacts on urban forests. We also discuss the use of biodiversity monitoring in public education—in particular, the potential establishment of a citizen-science (Silvertown 2009) beetle-monitoring network in Metro Vancouver.

MATERIALS AND METHODS

Ground beetle sampling

Pitfall traps were constructed using plastic beverage cups (500 ml). A double-cup system was used where the outer cup had a drainage hole to remove rainwater and the inner cup had a similar hole covered in plastic screening to prevent escape of beetles. Traps were inserted into the soil at sampling locations such that the brim of the trap was level with the surface of the ground. Traps were deployed at field locations for one week, after which captured beetles were returned to the laboratory for counting and identification. Beetles were identified using Lindroth (1961–1969b).

Beetle monitoring, 2001–2005

Surveys were conducted at two sites adjacent to the David Lam campus of Douglas College in Coquitlam, in 2001, 2003, and 2005. One site is dominated by meadow vegetation that has developed on the site of a former gravel mine directly south of the campus (David Lam (DL) Meadow site, 49°17'12.69" N, 122°47'34.63" W). The plant community at this site is dominated by grasses, herbaceous annuals (often introduced weeds), shrubs, and deciduous trees (predominantly red alder (*Alnus rubra* Bong. (Betulaceae)) and black cottonwood (*Populus balsamifera* ssp. *trichocarpa*) (Torr. & A. Gray ex Hook. (Salicaceae)). Native shrubs like hardhack (*Spiraea douglasii* ssp. d*ouglasii* Hook. (Rosaceae)) occur, but introduced species predominate (*e.g.*, Himalayan blackberry (*Rubus discolor* Weihe & Nees (Rosaceae)) and Scotch broom (*Cytisus scoparius* (L.) Link (Fabaceae))). The other site is a fragment of native coniferous forest associated with Hoy Creek, a salmon-bearing stream (Hoy Creek Forest site, 49°17'19.50" N, 122°47'38.39" W). Vegetation at this site is typical of second-growth temperate rain forest in the Vancouver area, where the plant community is dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg. (Pinaceae)) and western red-cedar (*Thuja plicata* Don ex D. Don (Cupressaceae)), with an understorey composed of native plants, including several species of ferns (*Polystichum munitum* (Kaulf.) C. Presl (Dryopteridaceae), *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiacae), *Blechnum spicant* (L.) With. (Blechnaceae), and *Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy (Dryopteridaceae)) and shrubs such as vine maple (*Acer circinatum* Pursh (Sapindaceae)), red huckleberry (*Vaccinium parvifolium* Sm. (Ericaceae)), and salal (*Gaultheria shallon* Pursh (Ericaceae)).

Paired traps were placed at the DL Meadow and Hoy Creek Forest sites for periods of one week in September of 2001 (n=20), 2003 (n=25), and 2005 (n=26) during field exercises of Douglas College Ecology classes (BIOL 2322 and 3305). Beetles were identified and counted for each trap, and trap-catch data for all three years were pooled for analysis (n=71 traps in each habitat).

Beetle monitoring, 2008

Surveys were conducted in 2008 at the DL Meadow and Hoy Creek Forest sites sampled in 2001, 2003, and 2005, and at eight additional forest fragments in Coquitlam parks (Table 1). Park sites were either small (<10 hectares) or large in area (>40 hectares) and were assigned to one of three levels of human disturbance. High-disturbance sites experienced heavy human use (*i.e.,* via trails adjacent to busy residential areas and/or schools), medium-disturbance sites had less use by humans—mostly via hiking on wilderness trails—and low-disturbance sites were undeveloped forest fragments with limited human use. Five pitfall traps were installed at 20-metre intervals along a 100-metre transect arranged from the edge to the interior of each site. Traps were installed at all 10 sites in July 2008 and were emptied once a week at each site on a staggered rotation schedule until early September. Beetles were identified and counted, and beetle-count data were pooled for all collection periods for each trap, producing pooled counts at each site over the two-month period.

Table 1. Ground beetle collection sites in Coquitlam, British Columbia, 2008

Site name	Location	Area (hectares)	Site code	Area code	Disturbance code
DL Meadow	49°17'12.69" N 122°47'34.63" W	2.0	DL	Small	High
Hoy Creek	49°17'19.50" N 122°47'38.39" W	6.7	HO	Small	High
Scott Creek	49°16'44.95" N 122°48'43.79" W	3.0	S	Small	High
Harper	49°18'12.74" N 122°44'54.74" W	7.1	H	Small	Low
Walton Forest	49°17'23.82" N 122°48'19.06" W	4.0	W	Small	Medium
Eagle Mountain	49°18'51.31" N 122°48'08.38" W	42.2	E	Large	Low
Ridge Park	49°18'36.12" N 122°47'39.57" W	59.5	R	Large	Low
Coquitlam River	49°16'45.92" N 122°46'20.91" W	68.1	CR	Large	High
Mundy 1	49°15'00.99" N 122°49'20.28" W	178.3	M1	Large	Medium
Mundy 2	49°15'47.43" N 122°49'28.94" W	178.3	M2	Large	Medium

Data analysis

Abundances of the six most common carabids collected in 2001–2005 (*Carabus granulatus* Linné (CG), *Carabus nemoralis* Müller (CN), *Calathus fuscipes* Goeze (CF), *Pterostichus melanarius* Illiger (PM), *Scaphinotus marginatus* Fischer (SM), and *Scaphinotus angusticollis* Mannerheim (SA)) were compared between the forest and meadow habitats using paired t-tests. Shannon diversity index was calculated for each of the five trap locations at each of the 10 sites sampled in 2008 using PC-ORD (MjM Software, Version 5). Shannon diversity index was compared among sample sites, disturbance levels, and site areas (large vs. small) by single-factor analysis of variance (ANOVA). Means were distinguished in ANOVA using Holm-Sidak tests ($p<0.05$). Analysis of variance and t-tests were conducted using SigmaStat (Version 3.1.1).

Indicator species analysis (Dufrêne and Legendre 1997) was conducted on the 2008 data using PC-ORD (Version 5) to identify carabid species consistently associated with low, medium or high levels of human disturbance. This method calculates the observed indicator value for particular species (IV_{obs}) relative to groups within datasets (*e.g.*, levels of environmental factors of interest). Indicator value varies from no indication of a particular group (0) to perfect indication (100). Statistical significance of IV_{obs} is tested using a Monte Carlo method, where sample units are randomly reassigned to groups and indicator value (IV_{ran}) is recalculated over a set of permutations (in tests presented here, n=4,999 permutations). Significance value (p) is calculated as the proportion of randomized trials, with indicator value equal to or exceeding the observed indicator value (McCune and Grace 2002).

RESULTS

Beetle sampling, 2001–2005

Trap catches from 2001–2005 were dominated by six carabid species: four introduced European species (*C. granulatus*, *C. nemoralis*, *C. fuscipes,* and *P. melanarius*) and two native North American species (*S. marginatus* and *S. angusticollis*). Relative abundances of these six species in the forest and meadow habitats are shown in Figure 1. Although mean abundance of *C. granulatus* did not vary between habitats, mean abundances of the five other species were significantly different between the Hoy Creek Forest and DL Meadow sites. Mean abundances of three European species (*C. nemoralis*, *C. fuscipes*, and *P. melanarius*) were higher at the DL Meadow site than at the Hoy Creek Forest site. Mean abundances of the native species, *S. marginatus* and *S. angusticollis*, were higher at the Hoy Creek Forest site than at the DL Meadow site.

Beetle sampling, 2008

Ground beetles from 17 species were captured in traps at the 10 sites sampled in 2008 (Table 2). The most common species collected was *S. angusticollis*, accounting for 58% of all beetles captured. As in samples from 2001–2005, beetles captured in Coquitlam in 2008 were a mixture of native species and species introduced from Europe.

Shannon diversity index varied significantly among sites, with the highest diversity recorded at the Hoy Creek Forest site (ANOVA: $F=8.51$, $df=9$, $p<0.001$; Figure 2). Traps from the Hoy Creek Forest site yielded 14 of the 17 species collected in Coquitlam in 2008, including all of the

European species and most of the native forest-dwelling species. This site is small in area and has a high level of human disturbance due to its location directly adjacent to a secondary school, apartment residences, and a college campus.

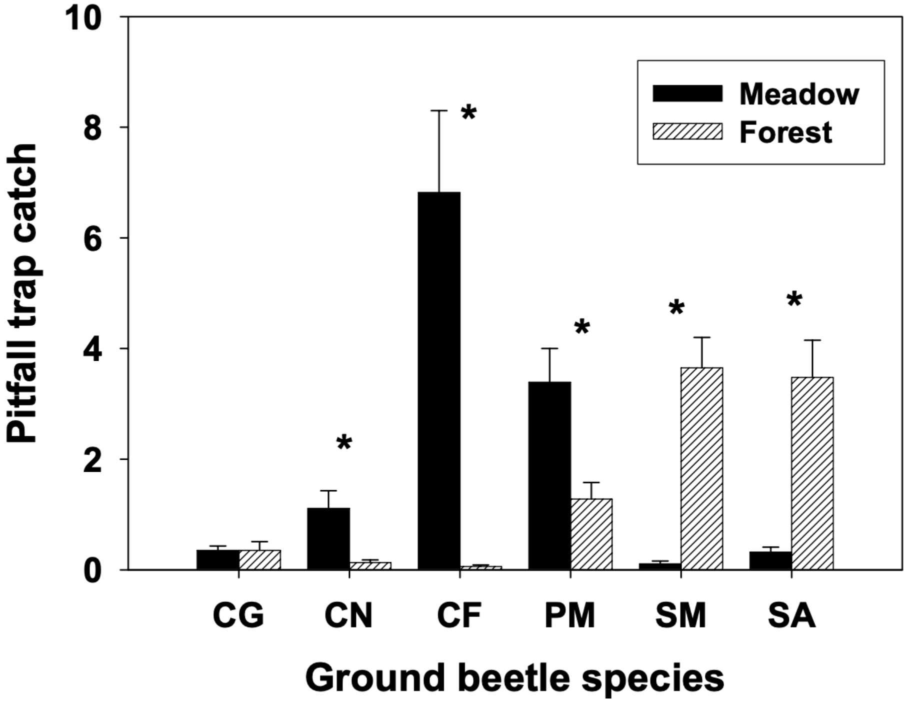

Figure 1. Mean pitfall-trap catches of six ground beetle species in forest and meadow habitats in the 2001–2005 beetle surveys. Trap catches are shown for *Carabus granulatus* (CG), *Carabus nemoralis* (CN), *Calathus fuscipes* (CF), *Pterostichus melanarius* (PM), *Scaphinotus marginatus* (SM), and *Scaphinotus angusticollis* (SA), where black bars are from the meadow habitat and hatched bars are from the forest habitat. Paired bars marked with an asterix are significantly different by t-tests ($p<0.05$).

Shannon diversity index did not vary among levels of human disturbance, but there was a trend to higher diversity at more disturbed sites (ANOVA: $F=2.84$, $df=9$, $p=0.07$). Shannon diversity index was significantly higher in small-area sites than in larger sites (ANOVA: $F=8.56$, $df=1$, $p=0.005$). Higher diversity at small sites and at high-disturbance sites occurred because beetle communities included both native forest–specialist and European species.

Indicator species analysis revealed a significant association of five beetle species with sites at the highest level of human disturbance (Table 3). All five species are European in origin (*C. granulatus*, *C. nemoralis*, *C. fuscipes*, *H. affinis,* and *P. melanarius*). No other beetle species were statistically significant indicators of any of the three disturbance levels.

Table 2. Pooled counts of ground beetles collected at all sites in 2008.

Species	Total abundance
Scaphinotus angusticollis Mannerheim	1,109
Calathus fuscipes Goeze*	176
Pterostichus algidus Leconte	176
Scaphinotus marginatus Fischer	149
Carabus granulatus Linné*	67
Omus dejeanii Reiche	49
Pterostichus herculaneus Mannerheim	49
Pterostichus melanarius Illiger*	47
Carabus nemoralis Müller*	27
Pterostichus pumilis Casey	22
Harpalus affinis Schrank*	9
Leistus ferruginosus Mannerheim	8
Cychrus tuberculatus Harris	6
Scaphinotus angulatus Harris	6
Loricera pilicornis Fabricus	3
Pterostichus lama Ménétries	2
Synuchus impunctatus Say	1
TOTAL	**1,906**

*Species introduced from Europe.

Table 3. Indicator species analysis by disturbance level for 2008 ground beetle survey. Observed indicator values (IV_{obs}) for particular combinations of species and disturbance levels are shown, as are mean randomized indicator values (IV_{ran}) from Monte Carlo simulations (4,999 permutations). p is the proportion of IV_{ran} equal to or exceeding IV_{obs}.

Species	Disturbance	IV_{obs}	Mean IV_{ran}	p
Scaphinotus angusticollis	Medium	38.0	37.7	0.42
Calathus fuscipes *	High	30.0	12.0	<0.01
Pterostichus algidus	High	30.9	39.9	0.89
Scaphinotus marginatus	High	31.4	30.6	0.40
Carabus granulatus *	High	38.8	15.0	<0.01
Omus dejeanii	Medium	20.0	9.4	0.07
Pterostichus herculaneus	Medium	22.2	23.8	0.54
Pterostichus melanarius *	High	29.4	13.1	0.02

Carabus nemoralis *	High	35.6	13.7	<0.01
Pterostichus pumilis	Medium	16.3	13.3	0.25
Harpalus affinis *	High	31.1	12.9	0.01
Leistus ferruginosus	Medium	11.1	12.0	0.46
Cychrus tuberculatus	Low	10.0	10.2	0.53
Scaphinotus angulatus	Medium	8.6	10.3	0.66
Loricera pilicornis	High	10.0	7.0	0.34
Pterostichus lama	High	2.5	6.7	1.00
Synuchus impunctatus	High	5.0	6.0	1.00

*Species introduced from Europe.

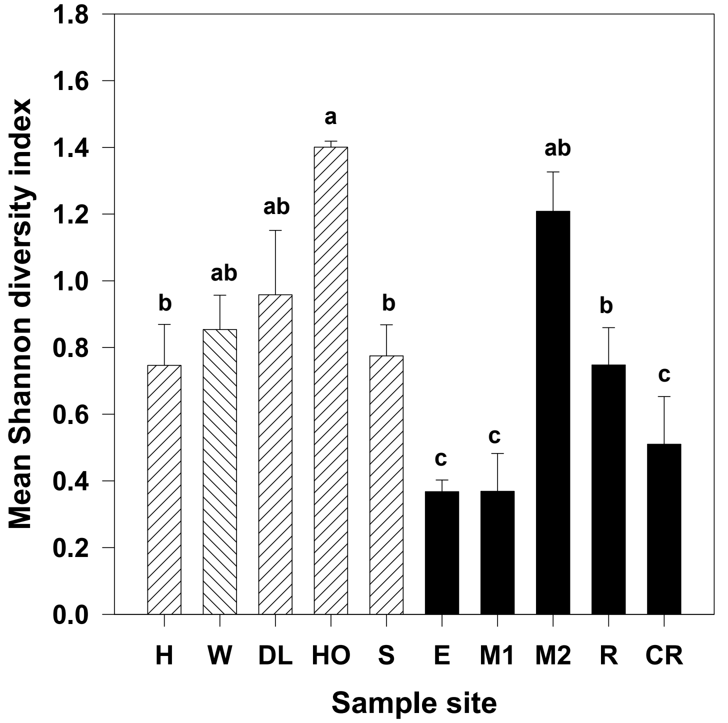

Figure 2. Mean Shannon Diversity Index for 10 sample sites in the 2008 beetle survey. See Table 1 for site codes and descriptions. Hatched bars are for small area sites (<10 hectares) and black bars are for large area sites (>40 hectares). Histogram bars marked with the same letter are not significantly different (Holm-Sidak test $p<0.05$).

DISCUSSION

Ground beetle communities in Coquitlam, British Columbia, vary between human-disturbed areas and fragments of undisturbed native forest. European species dominate the ground beetle community at one highly disturbed meadow site, as they do in local agricultural habitats (Raworth *et al.* 1997). Some forested sites have carabid communities that include most of the common native and European species, whereas others have communities mainly, or exclusively, composed of native forest species. Small, disturbed forest sites have higher beetle diversity than large, undisturbed forest sites do because they have been colonized by European species while retaining native species.

Increased beetle diversity in areas invaded by adventive European species has been frequently observed, arguably because the European species are, for the most part, occupying previously unexploited synanthropic niches in urban environments (Spence and Spence 1988; LaBonte 2011). In a study in southeast Australia, a higher diversity of ants was measured in small habitat fragments compared to large habitat fragments in an urbanizing environment due to the presence of more generalist ant species in small fragments (Gibb and Hochuli 2002). Presumably, diet breadth of carabids should have a similar effect on distributions. For example, mollusc-feeding forest specialists like *S. angusticollis* are primarily restricted to fragments of temperate rain forest where their preferred prey are available (Larochelle and Larivière 2003; Marshall 2018), whereas more generalist European species like *P. melanarius* can penetrate forested habitats in addition to more urbanized environments (Niemelä and Spence 1991).

Indicator species analysis has shown that the presence of European species in Coquitlam carabid communities indicates high levels of human disturbance. This means that urban forest fragments that have undergone more impact by human activity are more susceptible to invasion by European generalist species. This may occur because human contact has altered the forest habitats or because population pressure from European species in adjacent anthropogenic habitats is greater. Regarding habitat alteration, it has been shown that trampling by human traffic in urban forests has a strong influence on carabid community composition (Kotze *et al.* 2012). It is also important to note that our data are derived entirely from pitfall-trap catches and that pitfall traps have been shown to not accurately sample carabid communities. Pitfall catches are often biased towards larger, more active, carnivorous species and deficient in small, phytophagous carabids (Spence and Niemela 1994; Knapp *et al.* 2020). In our study, most carabids that were captured were relatively large in size, and smaller taxa like *Bembidion* Latreille species were not captured. Despite this, our survey method still has utility for assessing human influence on urban forest fragments, because it is relatively inexpensive, it is easy to implement, and it samples a representative proportion of carabid taxa.

It has been argued that the practice of urban planning can be substantially improved by incorporating ecological concepts and recognizing the dynamic nature of urban ecosystems (Flores *et al.* 1998). Given this, carabid beetle monitoring can be used to predict adverse effects of urban development and inform municipal planning decisions when managing for ecosystem services and biodiversity (Angold *et al.* 2006). We predict that the use of European carabids as indicator species will detect ecological effects of urban development with a degree of subtlety higher than simple site assessments of urbanization.

Anthropogenic effects will vary, depending on the nature of both the habitat being developed and the development project itself, and biological monitoring may be the only effective method to assess impacts. Beetle surveys can, therefore, be used to assess the ecological health of natural areas like urban forest fragments and landscape corridors (Li *et al.* 2008), and post-development monitoring can assess negative impacts and, in turn, inform future planning. In addition, carabid monitoring could be used to assess the ecological value of synthetic habitats like green roofs (MacIvor and Lundholm 2010) and "near-natural forests" (Da and Song 2008).

We will expand and continue our ground beetle monitoring program in Coquitlam and other Metro Vancouver municipalities. Long-term monitoring of changes in beetle communities will provide a record of environmental change under the dual influences of urbanization and climate change. We expect that the composition of beetle communities will change in the future, as species ranges expand to the north with warming climate. Novel mechanisms for unexpectedly rapid range expansion have been identified for several insect species in Britain under the influence of climate change (Thomas *et al.* 2001). We also expect that new introductions of beetle species will occur as a consequence of international trade, as has historically been the case through ship ballast material and plant nursery stock (Brown 1940; Spence and Spence 1988). For example, we recently detected the European carabid, *Nebria brevicollis* (Fabricus) in Metro Vancouver, a species previously unrecorded in western Canada (R.R. McGregor, H. Goulet, and J.R. LaBonte, unpublished observations). *Nebria brevicollis* was accidentally introduced into Oregon, where it was first recorded in 2007 and has presumably spread north to British Columbia (Kavanaugh and LaBonte 2008; LaBonte 2011; R.R. McGregor, H. Goulet, and J.R. LaBonte, unpublished observations).

Involvement of citizen scientists in monitoring programs for introduced and invasive species has been advocated to increase the capacity of resource managers to collect data (Silvertown 2009; Crall *et al.* 2010). Because of the relative simplicity of ground beetle trapping and identification, there is a strong potential for public involvement in beetle monitoring programs.

Given that, we plan to establish a beetle-monitoring program for the general public and in Metro Vancouver schools. The program would have the dual purpose of gathering data on local ground beetle communities and educating the general public and local youth about the ecology of urban areas. Such a program would be facilitated by the ease of collection and identification of ground beetles and by our experience in offering environmental education programs. Student-based biodiversity-monitoring programs are part of a recent trend for increased public participation in citizen-science programs (Silvertown 2009). Two examples of similar programs are the Iimbovane Outreach Project in South Africa, where students monitor ant biodiversity (https://www0.sun.ac.za/Iimbovane/) and the Leaf Pack Network in the United

States, where members of the public monitor stream ecology (https://leafpacknetwork.org/).

Our work on beetle diversity in Metro Vancouver forest fragments makes an important contribution to the understanding of ecological communities in urbanizing environments. We have developed a monitoring program that can detect the influence of human activity on ecological health through the presence of alien species. Information from our surveys can be used to predict the consequences of further urban development and, in turn, to inform planning decisions. Participation by students and other citizen scientists in this and other biodiversity monitoring programs educates the public about the importance of natural areas for urban sustainability. Urban habitat fragments provide important ecosystem services and maintain biological diversity in our cities. As such, it is critically important to monitor these areas as development and climate change inevitably proceed.

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REFERENCES

Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K., Small, E., Wood, B., Wadsworth, R., Sanderson, R., and Thompson, K. 2006. Biodiversity in urban habitat patches. Science of the Total Environment, **360**: 196–204.

Bellard, C, Bertelsmeier, C., Leadley, P., Thuiller, W., and Courchamp, F. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters, **15**: 365–377.

Bland, R.G. and Jaques, H.E. 1978. How to know the insects, 3rd edition. W.C. Brown Company, Dubuque, Iowa.

Bergeron, J.A.C., Spence, J.R., and Volney, W.J.A. 2011. Landscape patterns of species-level associations between ground-beetles (Coleoptera: Carabidae) and overstorey trees in boreal forests of western Canada. ZooKeys, **147**: 577–600.

Brown, W.J. 1940. Notes on the American distribution of some species of Coleoptera common to the European and North American continents. Canadian Entomologist, **72**: 65–78.

Crall, A.W., Newman, G.J., Jarnevich, C.S., Stohlgren, T.J., Waller, D.M., and Graham, J. 2010. Improving and integrating data on invasive species collected by citizen scientists. Biological Invasions, **12**: 3419–3428.

Da, L.J. and Song, Y.C. 2008. The construction of near-natural forests in the urban areas of Shanghai. *In* Ecology, planning and management of urban forests: International perspectives. *Edited by* M.M. Carreiro, Y.C. Song and J. Wu. Springer Publishing, New York, USA. Pp. 420–432.

Dufrêne, M. and Legendre, P. 1997. Species assemblages and indicator species definition: the need of an asymmetrical and flexible approach. Ecological Monographs, **67**: 345–366.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution and Systematics, **34**: 487–515.

Flores, A., Pickett, S.T.A., Zipperer, W.C., Pouyat, R.V., and Pirani, R. 1998. Adopting a modern ecological view of the metropolitan landscape: the case of a greenspace system for the New York City region. Landscape and Urban Planning, **39**: 295–308.

Fusser, M.S., Holland, J.M., Jeanneret, P., Pfister, S.C., Entling, M.H., and Schirmel, J. 2018. Interactive effects of local and landscape factors on farmland carabids. Agricultural and Forest Entomology, **20**: 549–557.

Gibb, H. and Hochuli, D.F. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological conservation, **106**: 91–100.

Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., and Briggs, J.M. 2008. Global change and the ecology of cities. Science, **319**: 756–760.

Hartley, D.J., Koivula, M.J., Spence, J.R., Pelletier, R., and Ball, G.E. 2007. Effects of urbanization on ground beetle assemblages (Coleoptera, Carabidae) of grassland habitats in western Canada. Ecography, **30**: 673–684.

Kavanaugh, D.H. and LaBonte, J.R. 2008. Discovery of *Nebria brevicollis* (Fabricius) (Coleoptera: Caribidae: Nebriini), a European Ground Beetle, Established in the Willamette Valley, Oregon. Proceedings of the California Academy of Sciences, **59**: 481–488.

Klimaszewski, J., Langor, D., Batista, R., Duval, J., Majka, C.G., Scudder, G.G.E., and Bousquet, Y. 2012. Synopsis of adventive species of Coleoptera (Insecta) recorded from Canada. Part 1: Carabidae. Pensoft, Sofia, Bulgaria.

Koivula, M.J. 2011. Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. ZooKeys, **100**: 287–317.

Kotze, D.J., Lehvävirta, S., Koivula, M., O'Hara, R.B., and Spence, J.R. 2012. Effects of habitat edges and trampling on the distribution of ground beetles (Coleoptera, Carabidae) in urban forests. Journal of Insect Conservation, **16**: 883–897.

Knapp, M., Knappová, J., Jakubec, P., Vonička, P., and Moravec, P. 2020. Incomplete species lists produced by pitfall trapping: How many carabid species and which functional traits are missing? Biological Conservation, **245**: 108545.

LaBonte, J.R. 2011. *Nebria brevicollis* (Fabricius, 1792) in North America, benign or malign? (Coleoptera, Carabidae, Nebriini). ZooKeys, **147**: 497–543.

Larochelle, A. and Larivière, M.-C. 2003. A Natural History of the Ground-Beetles (Coleoptera: Carabidae) of America north of Mexico. Faunistica, No 27. Pensoft Publishers, Moscow-Sofia.

Latty, E.F., Werner, S.M., Mladenoff, D.J., Raffa, K.F., and Sickley, T.A. 2005. Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood–hemlock forests. Forest Ecology & Management, **222**: 335–347.

Lemieux, J.P. and Lindgren, B.S. 2004. Ground beetle responses to patch retention harvesting in high elevation forests of British Columbia. Ecography, **27**: 557–566.

Li, J., Wang, Y., and Song, Y.C. 2008. Landscape corridors in Shanghai and their importance in urban forest planning. *In* Ecology, planning and management of urban forests: International perspectives. *Edited by* M.M. Carreiro, Y.C. Song and J. Wu. Springer Publishers, New York, USA. Pp. 219–239.

Lindroth, C.H., 1961, 1963, 1966, 1968, 1969a, 1969b. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska, Part 2. Opuscula entomologica Supplements, **20**: 1–200; **24**: 201–408; **29**: 409–648; **33**: 649–944; **34**: 945–1192; **35**: I–XLVIII.

Magura, T., Tóthmérész, B., and Molnár, T. 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecology, **19**: 747–759.

Marshall, S.A. 2018. Beetles: The natural history and diversity of Coleoptera. Firefly Books, Richmond Hill, Ontario.

MacIvor, J.S. and Lundholm, J. 2010. Insect species composition and diversity on intensive green roofs and adjacent level-ground habitats. Urban Ecosystems, **14**: 225–241.

McCune, B. and Grace, J.B. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

Montserrat, V., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E., and DAISIE partners .2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment, **8**: 135–144.

Niemelä, J. and Spence, J.R. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): A test of community impact. Oikos, **62**: 351–359.

Pierce, J.L. and Venier, L.A. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Aranae) as bioindicators of sustainable forest management: A review. Ecological Indicators, **6**: 780–793.

Prasad, R.P. and Snyder, W.E. 2006. Polyphagy complicates conservation biological control that targets generalist predators. Journal of Applied Ecology, **43**: 343–352.

Rainio, J. and Niemela, J. 2003. Ground beetles as bioindicators. Biodiversity and Conservation, **12**: 487–506.

Ranganathan, J., Raudsepp-Hearne, C., Lucas, N., Irwin, F., Zurek, M., Bennett, K., Ash, N., and West, P. 2008. Ecosystem services: A guide for decision makers. World Resources Institute, Washington, D.C.

Raworth, D.A., Clements, S.J., and Cirkony, C. 1997. Carabid beetles in commercial raspberry fields in the Fraser Valley of British Columbia and a sampling protocol for *Pterostichus melanarius* (Coleoptera:

Carabidae). Journal of the Entomological Society of British Columbia, **94**: 51–58.

Silvertown, J. 2009. A new dawn for citizen science. Trends in Ecology & Evolution, **24**: 467–470.

Spence, J.R. and Niemela, J.K. 1994. Sampling carabid beetles with pitfall traps: The madness and the method. The Canadian Entomologist, **126**: 881–894.

Spence, J.R. and Spence, D.H. 1988. Of ground-beetles and men: introduced species and the synanthropic fauna of western Canada. Memoirs of the Entomological Society of Canada, **120**: 151–168.

Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D., Davies, Z.G., Musche, M., and Conradt, L. 2001. Ecological and evolutionary processes at expanding range margins. Nature, **411**: 577–581.

Work, T.T., Koivula, M., Klimaszewski, J., Langor, D., Spence, J., Sweeney, J., and Hébert, C. 2008. Evaluation of carabid beetles as indicators of forest change in Canada. The Canadian Entomologist, **140**: 393–414.