# Bee diversity and abundance in an urban setting

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**Abstract**—We assessed bee diversity and abundance in urban areas of Vancouver, British Columbia, Canada, to determine how urban environments can support bees. Habitats examined were community and botanical gardens, urban wild areas, Naturescape flower beds and backyards, and traditional flower beds and backyards. A total of 56 bee species (Hymenoptera), including species of the genera *Andrena* Fabr. (Andrenidae), *Bombus* Latr. (Apidae), *Osmia* Panzer and *Megachile* Latr. (Megachilidae), and *Halictus* Latr. and *Dialictus* Pauly (Halictidae), were collected. Abundance exhibited strong seasonal variation. Wild bees were most abundant during late spring, whereas honey bees peaked at the end of the summer. The most abundant species seen was the managed honey bee *Apis mellifera* L. (Apidae), followed by wild *Bombus flavifrons* Cresson. Community and botanical gardens, and plants such as cotoneaster (*Cotoneaster* Medik. sp.) and blackberry (*Rubus discolor* Weihe & Nees) (Rosaceae), centaurea (*Centaurea* L. sp.; Asteraceae), buttercup (*Ranunculus* L. sp.; Ranunculaceae), and foxglove (*Digitalis* L. sp.; Scrophulariaceae), had the highest abundance of bees, while bee populations in wild areas were the most diverse. Weeds such as dandelions (*Taraxacum officinale* G.H. Weber *ex* Wiggers; Asteraceae) dominated these wild areas and had one of the highest diversities of bee visitors. Traditional flower beds with tulips (*Tulipa* L. sp.; Liliaceae) and petunias (*Petunia* Juss. sp.; Solanaceae) had relatively poor diversity and abundance of bees throughout the year. Our study suggests that urban areas have the potential to be important pollinator reservoirs, especially if both bloom and habitat heterogeneity are maintained and enhanced through sustainable urban planning.

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**Résumé**—Nous avons estimé la diversité et l'abondance d'abeilles dans différents biotopes urbains de la ville de Vancouver, Colombie-Britannique, Canada, afin de déterminer comment les environnements urbains peuvent supporter les abeilles. Les habitats examinés incluent les jardins potagers et botaniques, les environs urbains sauvages, les parterres et les arrière-cours dits *Naturescape*, et les parterres et les arrière-cours traditionnels. Nous avons ressemblé un total de 56 espèces d'abeilles (Hymenoptera) dont *Andrena* Fabr. (Andrenidae), *Bombus* Latr. (Apidae), *Osmia* Panzer et *Megachile* Latr. (Megachilidae), *Halictus* Latr. et *Dialictus* Pauly (Halictidae). L'abondance a présenté une forte variation saisonnière. Les abeilles féeriques étaient considérablement plus abondantes pendant la dernière moitié du printemps, tandis que les abeilles d'élevage étaient plus abondantes pendant la dernière moitié de l'été. L'espèce la plus abondante était l'abeille d'élevage, *Apis mellifera* L. (Apidae), suivie de l'espèce féerique *Bombus flavifrons* Cresson. Les jardins potagers et botaniques des plantes telles que *Cotoneaster* Medik sp. et *Rubus discolor* Wehie & Ness (Rosaceae), *Centaurea* L. sp. (Asteraceae), *Ranunculus* L. sp. (Ranunculaceae), et *Digitalis* L. sp. (Scrophulariaceae) ont présenté la plus élevée abondance d'abeilles alors que les environs urbains sauvages ont exhibé les plus diverses populations d'abeilles. « Mauvaise herbes », comme les *Taraxacum officinale*

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G.H. Weber *ex* Wiggers (Asteraceae), dominaient ces habitats et présentaient la diversité d'abeilles visiteuses las plus élevée. Les parterres traditionnels, avec fleures telles que les *Tulipa* L. sp. (Liliaceae) et les *Petunia* Juss. sp. (Solanaceae), présentaient une diversité d'abeilles relativement pauvre tout au cour de l'an. Notre étude suggère que les zones urbaines ont du potentiel comme important réservoir de pollinisation, surtout quand et l'hétérogénéité d'habitat et hétérogénéité de fleures sont maintenues et accrues à travers le développement urbain durable.

## Introduction

Bees (Hymenoptera) play an integral role as pollinators in natural and managed ecosystems. Some feral and cultivated plants depend on diverse pollinators, while other species exhibit close coevolutionary relationships with a few or only one specific bee pollinator species (Roubick 1989; O'Toole and Raw 1991). Seed and fruit production of many crops rely on or benefit from bee pollination, a service valued at $20 billion every year in North America (Scott-Dupree *et al.* 1995; Morse and Calderone 2000). Some authors have suggested that pollinators may be in crisis (Buchmann and Nabhan 1996; Allen-Wardell *et al.* 1998), yet hypothesized declines in wild bee populations remain largely undocumented. Surprisingly, few studies have assessed bees in urban settings (Haeseler 1972; Jacob-Remacle 1984; Kratochwil and Klatt 1989; Gayubo and Torres 1991; Risch 1996; Saure 1996; Westrich 1996; Bortoli and Laroca 1997; Frankie *et al.* 1997, 1998; Schick and Sukopp 1998; Goulson *et al.* 2002), and none has surveyed bees in Canadian cities. The lack of substantial data coupled with the significance of wild bees agriculturally and ecologically provides compelling reasons to survey bee species in various habitats in North America.

In urban environments, which tend to be fragmented into small isolated patches of natural areas, habitat features important to bee populations can be detected and bees can thrive in urban settings. For example, 262 bee species were found in the city of Berlin, Germany, with disturbed areas and rural places around the city providing valuable bee habitats that merit protection (Saure 1996). Urban fragments such as road edges, backyard gardens, and flower beds supply habitat for bees in an inhospitable anthropogenic environment (Westrich 1996). They potentially provide a continuous food source for pollinators, and valuable nesting areas in the form of wood fences, bare soil, and cavities in ruderal buildings (Westrich 1996). Some cavity-nesting specialists increase in abundance in fragmented urban areas compared with intact desert shrub areas (Cane 2001). City walls are beneficial nesting sites for a number of bee species in Liège, Belgium, and bees adapted to this nesting substrate are extremely dense in urban centres (Jacob-Remacle 1984). Berlin is a population centre for *Anthidium manicatum* L. (Megachilidae) because hedgenettle (*Stachys* L. sp.; Lamiaceae), a favourite food source of this bee species, is a popular garden plant (Schick and Sukopp 1998). Bumble bee nests placed in suburban gardens in the United Kingdom showed a faster growth rate and bigger size than nests placed in conventional farmland or in farmlands with conservation headlands (Goulson *et al.* 2002). In contrast, Gayubo and Torres (1991) found that urban habitats in Salamanca, Spain, were more homogeneous and hosted fewer species than natural areas outside the city. In their study, ground-nesting bees were especially affected by a lack of nesting habitats because of the increased amount of impervious surfaces in cities. Marginal habitats, when lacking in adequate food sources and nesting areas, can be detrimental to bee populations (Frankie *et al.* 1997, 1998).

Almost half of the 3468 $km^2$ covered by the Greater Vancouver region is urban-industrial land, with the remainder equally divided into productive land (agriculture and forestry) and protected areas (Wynn and Oke 1992). However, this green space is unevenly distributed: 60% of it is found in the northern boundary over the Coast

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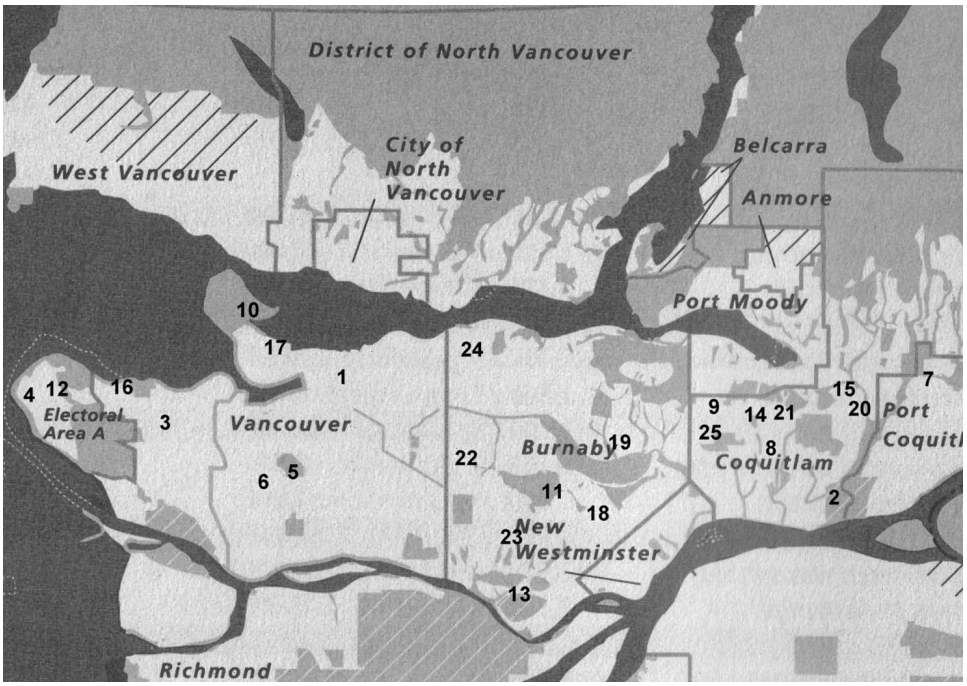



**FIGURE 1. Map of the study area in metropolitan Vancouver, British Columbia, Canada. Numbers represent study sites, which were grouped into four categories: sites 1–6 are city gardens; sites 7–12 are Naturescape sites; sites 13–20 are wild areas; and sites 21–25 are traditional sites (see Table 1). Shaded grey areas correspond to protected green spaces and watersheds.**

Mountains. In the Fraser River lowland, where this study took place, parks constitute only 2.5% of total land use (Wynn and Oke 1992). These 39 urban parks, averaging 1.4 $km^2$ (Wynn and Oke 1992), may maintain a high species diversity in the city environment as fragments of productive and diverse ecosystems (Schaefer 1994). Backyards of low residential dwellings, which constitute almost half of all urban land use in the Greater Vancouver Regional District (Greater Vancouver Regional District 2001), and vacant urban land, which constitutes 2.3% of total urban land use (Greater Vancouver Regional District 2001), may also play an important role in maintaining species diversity in Vancouver by increasing habitat heterogeneity and providing corridors between larger natural areas.

The objectives of our study were to (*i*) survey bee species in the city of Vancouver, British Columbia, Canada, (*ii*) assess and compare bee diversity and abundance in different urban habitats, and (*iii*) define bee-friendly landscape management guidelines for urban areas.

## Methods

### Study area

We conducted a pilot study consisting of informal collections throughout the Vancouver metropolitan area of British Columbia, Canada, (Fig. 1) from April to September 2000. The primary study was then conducted from March to August 2001, divided into

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five seasons: late winter (15 March – 14 April), early spring (15 April – 14 May), late spring (15 May – 14 June), early summer (15 June – 14 July), and late summer (15 July – 15 August).

A total of 25 sites distributed among the following categories were studied (Table 1).

### *City gardens (six sites)*

These sites include botanical and community gardens with a variety of native and non-native plant species, a few weeds, managed honey bee hives, and managed mason bee nests. This category is a mixture of formal, cultivated areas and fragments of old-growth forests with cedar chip trails.

### *Naturescape flower beds and backyards (six sites)*

Naturescape British Columbia is a program that encourages more diverse backyard and metropolitan habitats. These sites consist of multileveled flower beds with a variety of blooms, especially native plant species, surrounded by infrequently mowed fields or grass areas with tall grasses, weeds, and wildflowers.

### *Wild areas (eight sites)*

This category comprises infrequently mowed open spaces such as power line corridors and road edges, mostly colonized by weeds, as well as large, diverse areas including old-growth forests and mowed and unmowed fields.

### *Traditional flower beds and backyards (five sites)*

These sites are formal areas surrounded by extensively mowed fields and grass areas, cultivated mostly with petunias, pansies, tulips, ornamental roses, heathers, and rhododendrons, with few or no weeds present.

## Sampling methods

Two different sampling methods, transect and flower patch, were used to assess bees because of the variation of habitats and their landscapes. The total area of each site, such as the entire acreage of a park or of a backyard, varied among sites and was considered part of the site's characteristics. Using a random number table, a collector chose a random starting point on the edge of the site and then walked along a randomly selected 25 m long × 1 m wide transect for 15 min, sweeping at the bees that were seen on each side of the transect. For the flower patch method, each site was divided into numbered, 5 m × 5 m flower patches. Using a random number table, the collector randomly selected one of the flower patches, stood by it, and collected from it using a sweep net for 15 min. Thus, for each method, 25 $m^2$ were sampled. The flower species from which each bee was collected was recorded, as was the number of flowers of each different plant species present in the transect or patch. In flower beds, backyards, and gardens, we used the flower patch method, whereas the transect method was used in weedy patches and wildlife parks where flowers were more scattered. During each site visit, two collections from two different transects or flower patches were carried out. Thus, each site was assessed for a total of 30 min every 2 weeks, on sunny, warm days either in the morning (1000–1200) or in the afternoon (1200–1600).

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**TABLE 1. Bee collection sites throughout the Greater Vancouver area, grouped in site categories.**

| Site | Site area (ha) | Global positioning system coordinates | Flora | Notes |
|---|---|---|---|---|
| | | | **City gardens** | |
| 1. Strathcona community gardens | 1.46 | 49°16.555′N 123°05.244′W | Mixed fruit, berries, flowers, and vegetables (*i.e.*, *Allium* sp., *Lavandula* sp., *Centaurea* sp., *Vicia* sp., *Solanum tuberosum*, *Rubus discolor*, *Origanum* sp., *Echinacea* sp., *Phaseolus* sp.) | Honey and mason bee hives present; garden plots surrounded by large unmowed patches and shrubby areas |
| 2. Colony Farm community gardens | 2.83 | 49°13.892′N 122°48.445′W | Mixed fruit, berries, flowers, and vegetables (*i.e.*, *Myosotis* sp., *Prunus* sp., *Allium* sp., *Lavandula* sp., *Solanum tuberosum*, *Origanum* sp., *Echinacea* sp., *Lupinus* sp., *Salvia* sp., *Tropeoulum* sp., *Lavatera* sp., *Monarda didyma*) | Honey and mason bee hives present; garden plots surrounded by large unmowed patches and shrubby areas |
| 3. Kitsilano community gardens | 0.05 | 49°16.436′N 123°11.996′W | Mixed fruit, berries, flowers, and vegetables (*i.e.*, *Echinacea* sp., *Allium* sp., *Lavandula* sp., *Solanum tuberosum*, *Origanum* sp., *Lupinus* sp., *Salvia* sp., *Lavatera* sp., *Monarda didym*, *Buddleia* sp.) | Surrounded by mix of low and high residential areas; narrow corridors of unmowed grass along garden plots |
| 4. UBC Botanical Garden | 45 | 49°15.246′N 123°14.954′W | Large variety of native plants, medicinal herbs, and food plants (*i.e.*, *Rhododendron* sp., *Geranium* sp., *Spirea* sp., *Lavandula* sp., *Echinacea* sp., *Mentha* sp., *Althaea* sp., *Magnolia* sp.) | Surrounded by old-growth forest (Pacific Spirit Regional Park); diversity of soil substrates (*i.e.*, cedar chip trails, sandy trails, gravel) |
| 5. Queen Elizabeth Park | 53 | 49°14.366′N 123°06.746′W | Large variety of mixed native and non-native flowering plants (*i.e.*, *Rhododendron* sp., *Rubus spectabilis*, *Myosotis* sp., *Geranium* sp., *Digitalis* sp., *Lavandula* sp., *Echinacea* sp., *Buddleia* sp., *Rudbekia* sp.) | Surrounded by low residential areas |
| 6. VanDusen Botanical Garden | 23 | 49°14.365′N 123°06.744′W | Large variety of mixed native and non-native flowering plants and herbs (*i.e., Rhododendron* sp., *Mentha* sp., *Lavandula* sp., *Origanum* sp., *Ajuga* sp., *Geranium* sp., *Spirea* sp., *Althaea* sp., *Digitalis* sp., *Fragaria* sp.) | Honey bee hives present; surrounded by low residential areas; includes native plant gardens, herbs, and flower gardens |

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TABLE 1 (*continued*).

| Site | Site area (ha) | Global positioning system coordinates | Flora | Notes |
|---|---|---|---|---|
| **Naturescape sites** | | | | |
| 7. Norma's backyard | 0.02 | 49°16.709′N 122°45.809′W | Mix of native plants and herbs (*i.e.*, *Lavandula* sp., *Origanum* sp., *Digitalis* sp., *Lonicera* sp.) | No lawn; surrounded by mix of low residential areas; Coquitlam River Park (old-growth forest) approximately 500 m away |
| 8. Mary's backyard | 0.02 | 49°15.232′N 122°51.313′W | Mix of native plants and herbs (*i.e., Myosotis* sp., *Acer circinatum*, *Centaurea* sp., *Geranium* sp., *Aquilegia* sp., *Origanum* sp.) | Surrounded by low residential areas |
| 9. Desiree's backyard | 0.02 | 49°16.005′N 122°52.112′W | Mix of native and non-native flowers (*i.e.*, *Cotoneaster* sp., *Myosotis* sp., *Ranunculus* sp., *Trifolium* sp., *Rhododendron* sp.) | Infrequently mowed; surrounded by low residential areas |
| 10. Stanley Park flower bed | 0.005 | 49°17.947′N 123°08.066′W | Mix of native and non-native flowers and herbs (*i.e.*, *Rhododendron* sp., *Borago* sp., *Geranium* sp., *Lavandula* sp., *Mentha* sp., *Salvia* sp.) | Size of Stanley Park (*i.e.*, surrounding area) = 405 ha; includes old-growth forests and shrubby areas |
| 11. Deer Lake | 0.07 | 49°14.428′N 122°58.273′W | Mix of native and non-native flowers and herbs (*i.e.*, *Gaultheria* sp., *Rhododendron* sp., *Tulipa* sp., *Smilacina racemosa*, *Geranium* sp., *Lavandula* sp., *Mentha* sp., *Aster* sp.) | Size of Deer Lake Park (*i.e.*, surrounding area) = 300 ha; includes forests and shrubby areas; diversity of solid substrates (*i.e.*, cedar chips, gravel, sand) |
| 12. UBC Main Library | 0.02 | 49°16.016′N 123°15.247′W | Mix of native and non-native flowers (*i.e.*, *Gaultheria* sp., *Salix* sp., *Rhododendron* sp., *Rubus discolor*) | Approximately 4 km from Pacific Spirit Regional Park (old-growth forest); includes large patch of sandy substrate where bee nests were observed |
| **Wild areas** | | | | |
| 13. Queens Park | 1.5 | 49°13.071′N 122°54.577′W | Native flowers and weeds (*i.e.*, *Rubus spectabilis*, *Rubus discolor* sp., *Ranunculus* sp., *Hypochaeris radicata*) | Includes large unmowed patch and a mature native forest; diversity of soil substrates (gravel, sand, logs) surrounded by low residential areas; park = 31 ha |

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**Table 1 (*continued*).**

| Site | Site area (ha) | Global positioning system coordinates | Flora | Notes |
|---|---|---|---|---|
| 14. Como Lake | 0.08 | 49°15.711′N 122°51.492′W | Native flowers and weeds (*i.e.*, *Rhododendron* sp., *Ranunculus* sp., *Epilobium angustifolium*, *Trifolium* sp., *Hypochaeris radicata*) | Includes unmowed patches of recently restored native habitat (area surveyed) surrounded by low residential areas |
| 15. Green Links corridor | 0.08 | 49°15.884′N 122°48.969′W | Native flowers and weeds (*i.e.*, *Ranunculus* sp., *Epilobium angustifolium*, *Trifolium* sp., *Hypochaeris radicata*, *Rosa nutkana*, *Lupinus* sp.) | Surrounded by low residential areas; long corridors of shrubby areas and unmowed patches; diversity of soil substrates (*i.e.*, gravel and sand) |
| 16. Jericho Beach | 0.06 | 49°16.434′N 123°12.000′W | Native flowers and weeds (*i.e.*, *Rubus discolor* sp., *Trifolium* sp., *Vicia* sp., *Hypochaeris radicata*) | Surrounded by low residential areas; numerous wood stumps; diversity of soil substrates (*i.e.*, gravel, sand, cedar chip); park = 47 ha |
| 17. Gastown railroad | 0.01 | 49°17.067′N 123°06.192′W | Native flowers and weeds (*i.e.*, *Trifolium* sp., *Vicia* sp., *Hypochaeris radicata*) | Long unmowed corridor beside railway tracks on roadside; sandy substrate suitable for nesting; surrounded by high-density residential and industrial areas |
| 18. Cariboo Heights roadside | 0.7 | 49°14.079′N 122°54.764′W | Native flowers and weeds (*i.e.*, *Taraxacum officinale*, *Rubus discolor* sp., *Ranunculus* sp., *Hypochaeris radicata*) | Surrounded by low residential areas; large unmowed patch along roadside; shrubby areas |
| 19. Cariboo Avalon roadside | 0.01 | 49°14.883′N 122°55.574′W | Native flowers and weeds (*i.e.*, *Taraxacum officinale*, *Bellis perennis*, *Trifolium* sp., *Rubus discolor*, *Vicia* sp.) | Long unmowed patch along railway tracks; shrubby areas |
| 20. Ranch Park powerline | 0.12 | 49°15.798′N 122°48.525′W | Native flowers and weeds (*i.e.*, *Taraxacum officinale*, *Ranunculus* sp., *Rubus discolor* sp., *Epilobium angustifolium*, *Hypochaeris radicata*) | Surrounded by low residential areas; large unmowed patch; shrubby areas; diversity of soil substrates (*i.e.*, gravel and sand) |

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TABLE 1 (*concluded*).

| Site | Site area (ha) | Global positioning system coordinates | Flora | Notes |
|---|---|---|---|---|
| **Traditional sites** | | | | |
| 21. Jack's | 0.02 | 49°15.485′N 122°50.823′W | Non-native plants (*i.e.*, *Cotoneaster* sp., *Ilex aquifolium*, *Petunia* sp., *Tulipa* sp.) | Extensive lawn, frequently mowed; surrounded by low residential areas |
| 22. Arche's | 0.02 | 49°14.130′N 123°00.305′W | Non-native plants (*i.e.*, *Prunus* sp., *Bellis* sp., *Geranium* sp., *Iris* sp.) | Surrounded by low residential areas |
| 23. Roger's | 0.02 | 49°13.549′N 122°48.235′W | Non-native plants (*i.e.*, *Scilla* sp., *Cotoneaster* sp., *Bellis* sp., *Hydrangea* sp., *Lavatera* sp.) | Surrounded by low residential areas |
| 24. Momiji | 0.16 | 49°16.869′N 123°02.657′W | Ornamental flowering plants (*i.e.*, *Rhododendron* sp., *Hydrangea* sp.) | Surrounded by large parking lot and major road; across from parking lot is Hastings Park |
| 25. Blue Mountain Park | 0.01 | 49°15.102′N 122°52.116′W | Non-native plant species (*i.e.*, *Tulipa* sp., *Narcissus* sp., *Aster* sp., *Petunia* sp.) | Surrounded by low residential areas; recreational park frequently mowed. Only the flower bed was surveyed |

### Bee identification

All *Apis mellifera* L. (Apidae) and most *Osmia lignaria* Say (Megachilidae) and *Bombus* Latr. species (Apidae) were captured, chilled, identified on site, and released. All other species were captured, frozen, and brought to the laboratory for identification. Specimens were keyed to species by the authors and then sent to T Griswold of Utah State University, Logan, Utah, to confirm the identifications. Although most specimens are housed at the Simon Fraser University, Department of Biological Sciences museum in Burnaby, British Columbia, Canada, some have been deposited in the Utah State University collection in Logan, Utah.

### Statistical analysis

Capture rate (number of bees swept/hour) was used as a measure of bee abundance and was calculated by flower type, site, and season. Capture rate data were log-transformed to improve normality and homogeneity of variance. Means were compared using analysis of variance (GLM, SAS 8.01, 1999–2000; SAS Institute Inc. 1990), and Tukey's test was used to detect differences in mean abundance among seasons, sites, and flower types. SAS automatically adjusts alpha levels when performing multiple comparisons to control for the experiment-wise error rate. Species richness was used to assess diversity as recommended by Magurran (1988). The different number of sites per category resulted in variable sampling effort per site category, and thus rarefraction analysis by individual was used to measure species richness. All site categories were rarefied to the minimum number of individuals collected in traditional flower beds and backyards, the site category with the fewest individuals collected, using EcoSim (Gotelli and Entsminger 2001). EcoSim randomly sampled the specified number of individuals, 289, from each site category and also provided simulated confidence intervals for species richness per site category. Statistically significant differences in species richness between site categories were based on these confidence intervals. Species richness was also compared among flower types except petunia (*Petunia* Juss. sp.; Solanaceae) and tulip (*Tulipa* L. sp.; Liliaceae) because we repeatedly observed zero or one individual on these flower species. Species richness was rarefied to the minimum number of individuals, 11, collected on laurel (*Laurus* L. sp.; Lauraceae). Statistically significant differences in species richness between flower types were again based on the confidence intervals provided by EcoSim (Gotelli and Entsminger 2001). Mean species richness was similarly compared across seasons by rarefying to the minimum number of individuals, 38, for late winter and comparing confidence intervals.

## Results

During our pilot study and the primary study, we collected a total of 56 bee species in the Vancouver metropolitan area, including the managed honey bee (*A. mellifera*), 6 *Bombus* species, and 49 other species (Table 2). *Bombus flavifrons* Cresson, a social species, was the most frequently encountered non-*Apis* species of our study (total of 801 individuals), whereas *A. mellifera* was the most commonly encountered bee species overall (911 individuals). The third most common species was *Bombus mixtus* Cresson (547 individuals).

Wild bees were present throughout our study but were most abundant during late spring (15 May – 14 June). Honey bees peaked at the end of the summer (15 July – 15 August, Fig. 2B). We found significant differences in honey bee abundance ($P = 0.0004$) and non-*Apis* bee abundance ($P < 0.0001$) among seasons. At their peak, non-

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**TABLE 2. Bee species captured by sweep netting in urban backyards, gardens, parks, power line corridors, and road edges of the Greater Vancouver Area (March–August 2000, March–August 2001).**

| Species | Total no. of individuals | No. of individuals/hour |
|---|---|---|
| *Andrena angustitarsata* | 16 | 32 |
| *Andrena berberidis* Cockerell* | n/a | n/a |
| *Andrena candida* Smith | 1 | 2 |
| *Andrena cressoni infasciata* Lanham | 7 | 2.8 |
| *Andrena frigida* Smith | 12 | 6 |
| *Andrena hemileuca* Viereck | 10 | 2.8 |
| *Andrena hippotes* Robertson | 6 | 3 |
| *Andrena miserabilis* Cresson | 13 | 5.2 |
| *Andrena prunorum* Cockerell | 4 | 8 |
| *Andrena salicifloris* Cockerell | 4 | 2 |
| *Andrena* sp. 1 | 1 | 2 |
| *Andrena* sp. 2 | 2 | 4 |
| *Andrena* sp. 3 | 1 | 2 |
| *Andrena* sp. 4 | 2 | 4 |
| *Andrena* sp. 5 | 3 | 3 |
| *Andrena vicina* Smith† | 1 | 2 |
| *Anthidium* sp. 1 | 1 | 2 |
| *Apis mellifera* | 911 | 21.7 |
| *Augochlores* sp. 1 | 2 | 4 |
| *Bombus flavifrons*† | 801 | 15.1 |
| *Bombus melanopygus* Nylander† | 194 | 7.2 |
| *Bombus mixtus*† | 547 | 10.8 |
| *Bombus occidentalis*† | 2 | 4 |
| *Bombus* sp. 1 | 16 | 16 |
| *Bombus vosnesenski* Radoszkowski | 38 | 9.5 |
| *Ceratina acantha* Provancher† | 27 | 6 |
| *Dialictus* sp. 1† | 146 | 10.1 |
| *Dialictus* sp. 2† | 29 | 11.6 |
| *Dialictus* sp. 3† | 68 | 9.1 |
| *Dialictus* sp. 4 | 83 | 13.8 |
| *Dialictus* sp. 5 | 16 | 3.2 |
| *Evylaeus* sp. 1† | 9 | 3.6 |
| *Evylaeus* sp. 2† | 35 | 14 |
| *Evylaeus* sp. 3 | 25 | 10 |
| *Halictus confuses* Smith† | 40 | 10 |
| *Halictus rubicundus* Christ† | 31 | 4.1 |
| *Hylaeus* spp.* | n/a | n/a |
| *Lasioglossum pacificum* Cockerell† | 11 | 7.3 |
| *Lasioglossum zonulum* Smith† | 130 | 9 |
| *Megachile frigida* Smith† | 67 | 5.8 |
| *Megachile gemula* Cresson* | n/a | n/a |
| *Megachile melanophnea* Smith† | 40 | 10 |
| *Megachile rotundata* Fabr.† | 18 | 6 |
| *Megachile* sp.1† | 2 | 4 |
| *Megachile* sp. 2 | 8 | 3.2 |
| *Megachile* sp. 3 | 1 | 2 |

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**TABLE 2 (*concluded*).**

| Species | Total no. of individuals | No. of individuals/hour |
|---|---|---|
| *Melissodes* sp. 1* | n/a | n/a |
| *Osmia coerulescens* L. | 32 | 6.4 |
| *Osmia lignaria* | 61 | 6.4 |
| *Osmia* (*Monilosmia*) sp.* | n/a | n/a |
| *Osmia proxima* Cresson | 2 | 2 |
| *Osmia pusilla* Cresson | 6 | 4 |
| *Osmia* sp. 1 | 3 | 6 |
| *Psithyrus fernaldae* Franklin | 6 | 2.4 |
| *Psithyrus insularis* Smith | 2 | 4 |
| *Sphecodes* spp. | 11 | 11 |

*Collected only during summer 2000, as part of a pilot survey.
†Also collected during summer 2000, as part of a pilot survey.

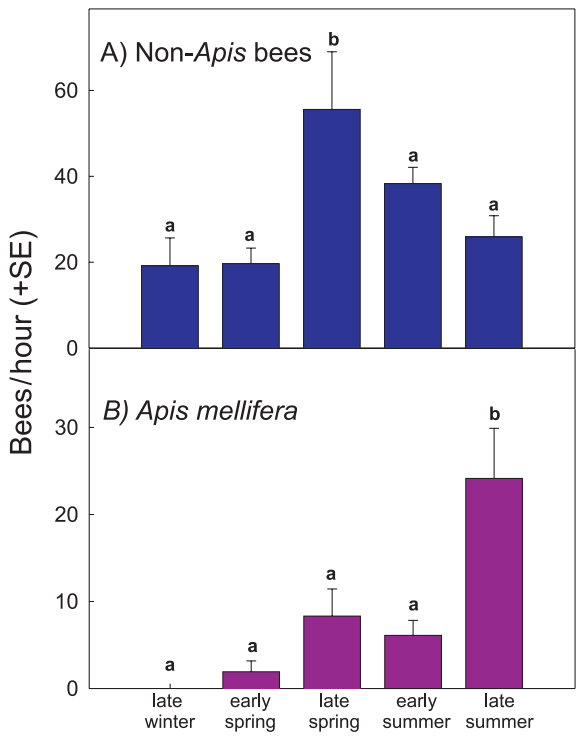



**FIGURE 2. Seasonal abundance (number of bees/hour) of non-*Apis* bees (A) and *Apis mellifera* (B) in Vancouver, 15 March – 15 August 2001. The following seasons were analyzed: late winter (15 March – 14 April), early spring (15 April – 14 May), late spring (15 May – 14 June), early summer (15 June – 14 July), and late summer (15 July – 15 August). Bars topped by different letters are significantly different (non-*Apis* bees, $P < 0.0001$; *A. mellifera*, $P = 0.0004$).**

*Apis* bees were collected at a rate of 56 bees/h (Fig. 2A), whereas honey bees peaked at an abundance of 25 bees/h (Fig. 2B).

Bee species richness remained fairly stable from early spring (15 April – 14 May) until late summer (15 July – 15 August) and was significantly lower during late winter

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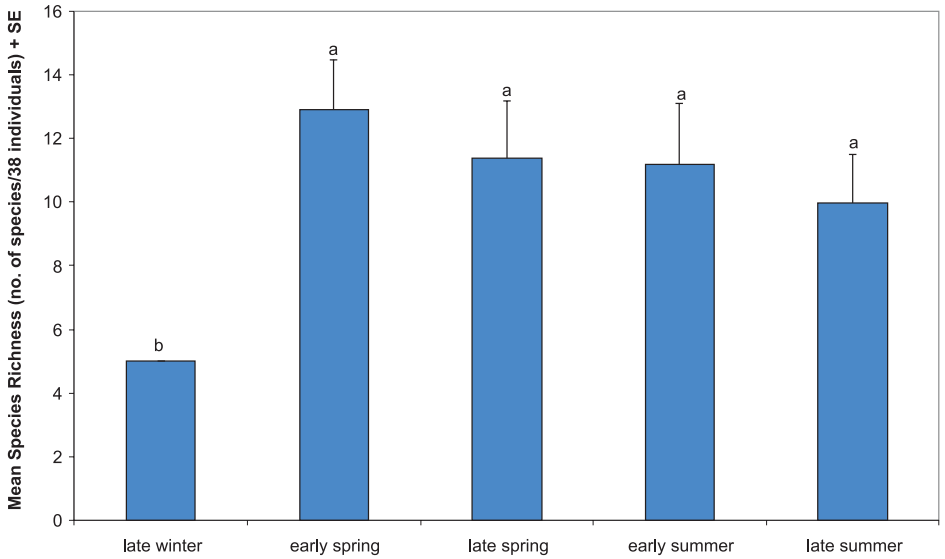



**FIGURE 3. Seasonal mean bee species richness (number of species/38 individuals) in Vancouver, 15 March – 15 August 2001. The following seasons were analyzed: late winter (15 March – 14 April), early spring (15 April – 14 May), late spring (15 May – 14 June), early summer (15 June – 14 July), and late summer (15 July – 15 August). Data were rarefied to the minimum number of individuals (38) for the late winter season. Bars topped by different letters are significantly different.**

(15 March – 14 April; Fig. 3). Bee species richness (Fig. 4) was relatively consistent among sites, whereas abundance (Fig. 5) varied more widely. Wild sites had higher species richness than traditional sites (Fig. 4). Non-*Apis* bee abundance in the traditional site category was the lowest among all categories and was significantly different ($P < 0.0001$) from values in the other three categories (Fig. 5). Significantly more non-*Apis* bees were collected in gardens than in wild sites, and Naturescape sites were intermediate and similar to both of these habitats (Fig. 5). *Apis mellifera* abundance was significantly greater in gardens than in the other three site categories ($P < 0.0001$).

Variation was greater among flowers than among sites. Dandelion (*Taraxacum officinale* G.H. Weber *ex* Wiggers; Asteraceae), salmonberry (*Rubus spectabilis* Pursh; Rosaceae), and cherry laurel (*Prunus laurocerasus* L.; Rosaceae) displayed significantly higher species richness than fireweed (*Epilobium angustifolium* L.; Onagraceae), with all remaining flowers displaying intermediate diversity (Fig. 6).

Blackberry (*Rubus discolor* Weihe & Nees) and cotoneaster (*Cotoneaster* Medik. sp.) (Rosaceae), buttercup (*Ranunculus* L. sp.; Ranunculaceae), centaurea (*Centaurea* L. sp.; Asteraceae), and foxglove (*Digitalis* L. sp.; Scrophulariaceae) had significantly higher non-*Apis* bee abundance than the remaining flower types ($P < 0.0002$, Fig. 7). *Apis mellifera* abundance did not vary significantly among flower types.

## Discussion

In our study, traditionally managed urban landscapes, such as conventional flower beds and backyards, had lower overall bee diversity and abundance than ecosystem-oriented urban landscapes such as Naturescape parks, undisturbed lots, and community gardens. Lancaster and Rees (1979), Collinge (1998), and Melles *et al.* (2003) discussed the significant effects of local-scale factors (*i.e.*, bloom and soil quality) and landscape-scale factors (*i.e.*, corridors, patch size and distribution) on urban avian

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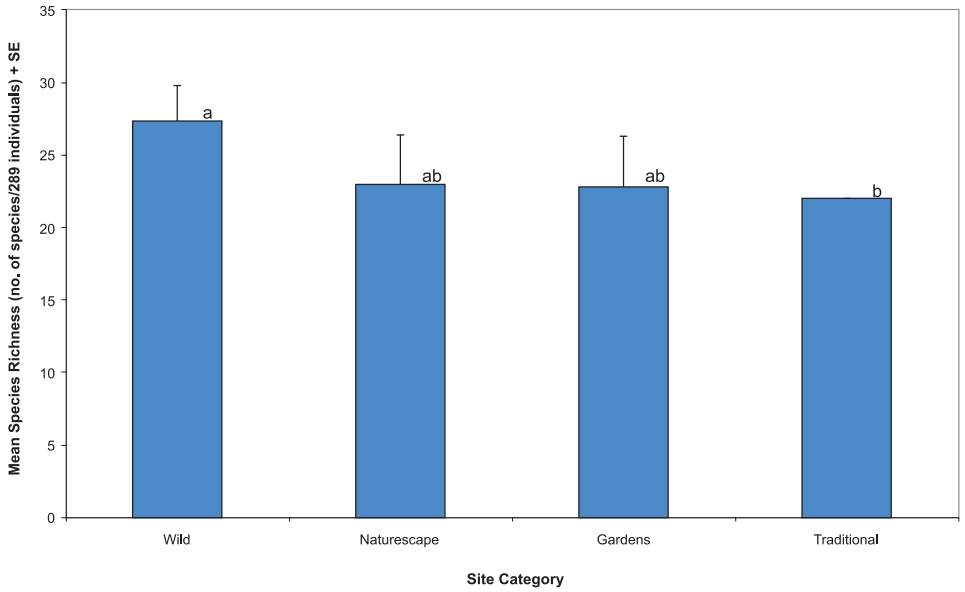



**FIGURE 4. Mean bee species richness (number of species/289 individuals) per site category in Vancouver, 15 March – 15 August 2001. Data were rarefied to the minimum number of individuals (289) for the traditional site category. Bars topped by different letters are significantly different.**

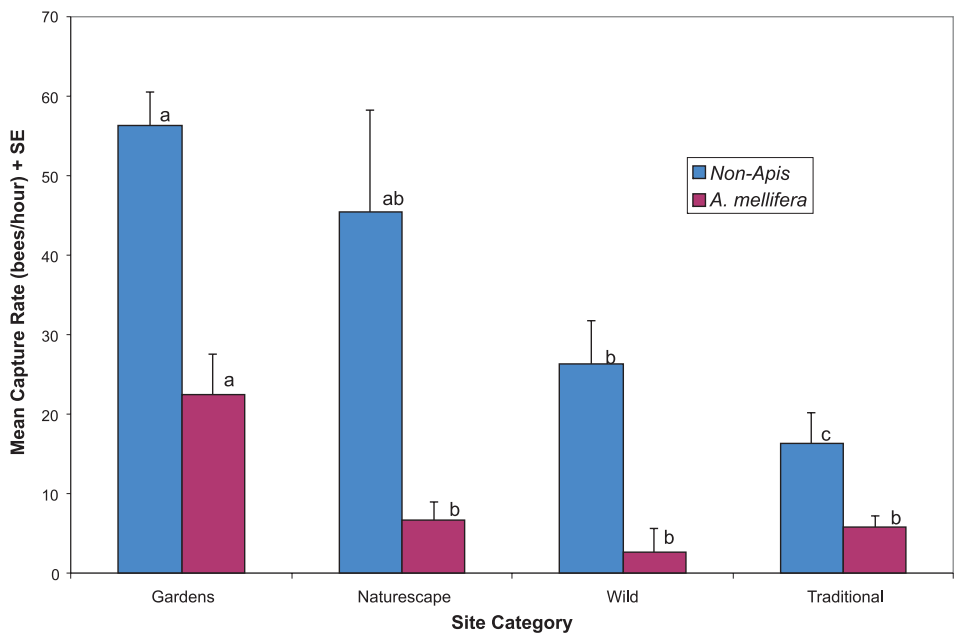



**FIGURE 5. Mean capture rate (number of bees swept/hour) for *Apis mellifera* and non-*Apis* bees per site category in Vancouver, 15 March – 15 August 2001. Bars topped by different letters are significantly different (*Apis mellifera*, $P < 0.0001$; non-*Apis* bees, $P < 0.0001$). Analysis compared non-*Apis* bees at the four site categories and *A. mellifera* at the four site categories; paired bars for each site category (*e.g.*, *A. mellifera* and non-*Apis* bees at garden sites) were not compared for significant differences.**

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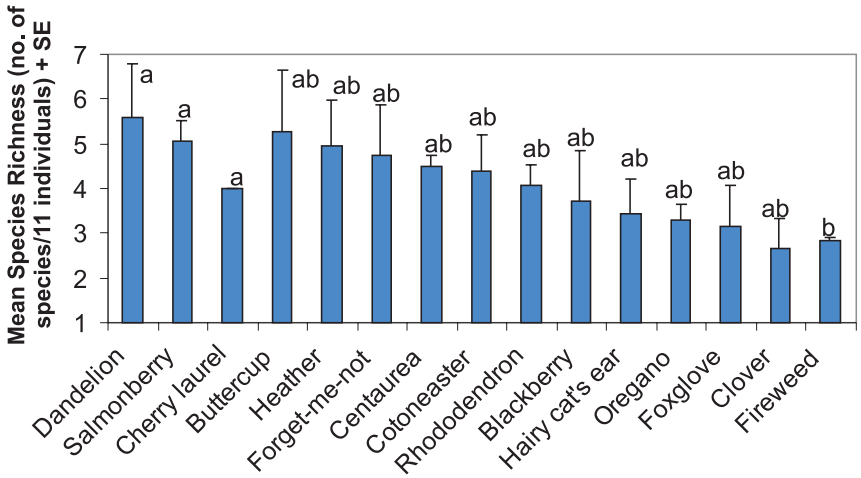



**FIGURE 6. Mean species richness (number of species/11 individuals) per flower in Vancouver, 15 March – 15 August 2001. Data were rarefied to the minimum number of individuals (11) on laurel. Bars topped by different letters are significantly different. Flower species were buttercup (*Ranunculus* sp.), dandelion (*Taraxacum officinale*), hairy cat's ear (*Hypochaeris radicata*), heather (*Gaultheria* sp.), cotoneaster (*Cotoneaster* sp.), blackberry (*Rubus discolor*), forget-me-not (*Myosotis* sp.), rhododendron (*Rhododendron* sp.), foxglove (*Digitalis* sp.), salmonberry (*Rubus spectabilis* Pursh), clover (*Trifolium* sp.), cherry laurel (*Prunus laurocerasus* sp.), oregano (*Origanum* sp.), centaurea (*Centaurea* sp.), and fireweed (*Epilobium angustifolium*).**

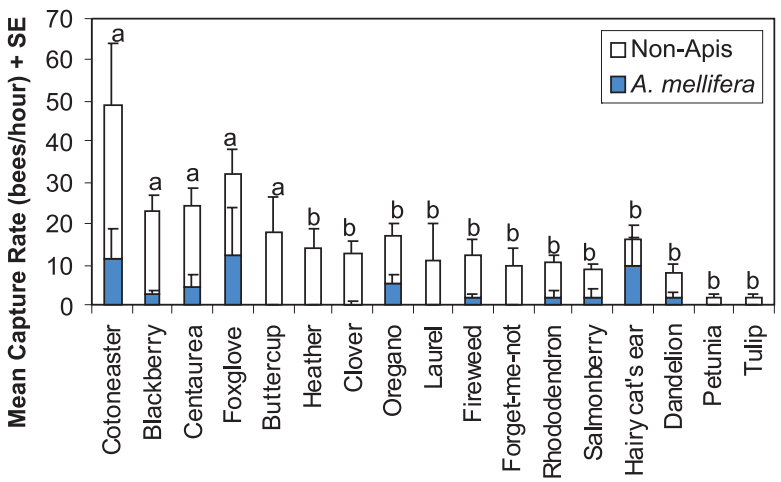



**FIGURE 7. Bee abundance per flower in Vancouver, 15 March – 15 August 2001. Bars topped by different letters are significantly different (non-*Apis* bees, $P < 0.0001$). Analysis compared non-*Apis* bees at different flower types and *A. mellifera* at different flower types; stacked bars for each flower type (*e.g.*, *A. mellifera* and non-*Apis* bees on cotoneaster) were not compared for significant differences. Flower species were buttercup (*Ranunculus* sp.), dandelion (*Taraxacum officinale*), hairy cat's ear (*Hypochaeris radicata*), heather (*Gaultheria* sp.), cotoneaster (*Cotoneaster* sp.), blackberry (*Rubus discolor*), forget-me-not (*Myosotis* sp.), rhododendron (*Rhododendron* sp.), foxglove (*Digitalis* sp.), salmonberry (*Rubus spectabilis* Pursh), clover (*Trifolium* sp.), cherry laurel (*Prunus laurocerasus* sp.), oregano (*Origanum* sp.), centaurea (*Centaurea* sp.), fireweed (*Epilobium angustifolium*), petunia (*Petunia* sp.), and tulip (*Tulipa* sp.).**

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populations. They stressed how urban parks, gardens, backyards, and green corridors can contribute habitat heterogeneity to cities, supporting an abundance and a diversity of beneficial animals.

We found Vancouver to be a similarly complex mosaic of micro- and macrohabitats; pollinator richness and abundance differed significantly between traditionally managed and ecosystem-managed landscapes. Naturescape backyards, botanical gardens, and empty, undisturbed lots constituted important habitats for urban bees. Our finding that traditionally managed landscapes sustain significantly poorer bee populations than ecosystem-managed landscapes suggests that cities can contribute to bee conservation by incorporating more ecosystem-managed habitats in urban design.

Bee abundance and diversity displayed strong seasonal variability in the Vancouver region, consistent with other studies (Jacob-Remacle 1984; Frankie *et al.* 1998; Osborne and Williams 2001). Wild bees peaked in late spring and early summer (Fig. 2A), in synchrony with the natural flowering pattern of the region, where the majority of nectar-producing plants bloom from April to July. Honey bees were most abundant at the end of the summer (Fig. 2B), when colony populations peak, but were less abundant than wild bees both earlier in the season and overall at all sites (Fig. 5), suggesting that wild bees have a more significant role than honey bees as pollinators of native vegetation. However, honey bees may play an important role as pollinators of late-season vegetation.

Non-*Apis* bees displayed patchy spatial and temporal distributions throughout the Vancouver metropolitan area. For example, *Andrena angustitarsata* Viereck (Andrenidae) had the highest hourly abundance (32 bees/h) but one of the lowest overall abundances throughout the study because all 16 individuals were encountered at one site during one collection period. *Bombus flavifrons* was the most abundant wild bee species (801 individuals observed) but, because of its uneven distribution, an average of only 15.1 bees/h was observed. Our survey found bee populations to be highly dispersed and dynamic, consistent with the studies reviewed by Williams *et al.* (2001). Future conservation efforts should consider the importance of specific fragments hosting particular rare bee populations such as *A. angustitarsata* in our study.

Dramatically fewer individuals of the native bee *Bombus occidentalis* Greene were observed in our study than in previous studies, suggesting that the population of this important species may have declined over the last 20 years. *Bombus occidentalis* was one of the most abundant wild bees in Fraser River valley crops in 1981 (Graf and Winston 1982), but during our 2000 and 2001 field seasons we observed only two individuals. These data are consistent with personal observations and informal collections conducted by our laboratory in natural and alpine areas outside Vancouver, where few *B. occidentalis* have been observed. Introduced pests, diseases, and climate change are all potential causes of the possible decline in *B. occidentalis* populations, as suggested by Kerr (2001) as explanations for butterfly decline. Intensive sampling of agricultural, natural, and alpine areas in the lower Fraser River valley of British Columbia would be useful to address this question more quantitatively.

Traditional urban landscapes were the least important sites for non-*Apis* bees, having significantly lower abundance than all other sites ($P < 0.0001$, Fig. 5). Botanical and community gardens, on the other hand, had the highest abundance ($P < 0.0001$, Fig. 5), with a peak capture rate of 56 non-*Apis* bees/h. Also, our wild urban landscape category, with infrequently mowed fields and a diversity of plants and soil substrates (Table 1), showed a significantly higher species richness than the traditional site category (Fig. 4). Frequently disturbed sites can sustain less abundant and less diverse populations of invertebrates such as butterflies, wasps, and bees (De Freitas Barbola and Laroca 1993; Frankie *et al.* 1997; Osborne and Williams 2001; Stork *et al.* 2003). We

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therefore reason that frequent disturbances such as mowing, soil tillage, and regular application of chemicals resulted in our observing lower bee richness at extensively manicured urban sites. Moreover, these frequent manipulations often result in the destruction of important visual cues that direct bees to foraging patches, and in fewer bees (Osborne and Williams 2001). Some sites, such as the Naturescape and garden sites at the University of British Columbia, were close to each other (Table 1) and perhaps shared similar source sites. Thus, because of autocorrelation, differences among sites might have been less evident.

A lack of suitable soil substrates for nesting and (or) hibernation can be a major cause of poor bee diversity and abundance (Jacob-Remacle 1984; Gayubo and Torres 1991; Goulson *et al.* 2002). The traditionally managed urban landscapes we examined were dominated by heavily herbicide-treated and heavily fertilized lawns and (or) asphalt, resulting in a deficiency of bee-friendly soils. A survey of the urban bees of Liège, Belgium, and one of the urban wasps of Salamanca, Spain, showed the importance of earth-and-rock walls in providing nesting cavities to solitary insect species (see Jacob-Remacle 1984 and Gayubo and Torres 1991, respectively). Contrary to the ecosystem-oriented sites we surveyed, traditionally managed areas lacked suitable bee-nesting spaces such as wood fences, log stumps, multileveled earth-and-rock walls, and dense shrubs. The last can provide both nesting sites and significant pollen and (or) nectar sources (Gayubo and Torres 1991). In our study, blackberry and red elderberry (*Sambucus racemosa* L.; Caprifoliaceae) shrubs exemplified this phenomenon, with flowers and stem holes around which we found a remarkable number of *Evylaeus* Robertson, 1902 species (Halictidae). We observed continuous and abundant food sources in ecosystem-oriented habitats, suggesting the importance of abundant, steady food sources to sustain rich bee faunas. Richards and Kevan (2002) argued that a stable, uninterrupted succession of blooms throughout the season is also essential to support bumblebee (*Bombus* spp.) colonies, which tend to store little food.

Bloom heterogeneity likely contributed to the distinct distribution of bees we observed in Vancouver. Dandelion and salmonberry, which dominate weedy patches, presented high bee diversity (Fig. 6) but not the highest bee abundance (Fig. 5). Goulson *et al.* (2002) argued that intensively managed areas often harbour only annuals with lower pollen and nectar contents, and can thus sustain only smaller bumblebee populations. Cotoneaster, which we encountered mostly in traditional backyards, presented high abundance (Fig. 5) and intermediate diversity (Fig. 6). This ornamental plant blooms in late May to early June and is likely to be the most important contributor to the abundance of bees in traditionally managed habitats. Gayubo and Torres (1991) also stressed the importance of recording the plant part on which the pollinator was observed. Although this was not formally done in our study, we did notice a high number of bumblebees collecting wax from the glossy leaves of the cherry laurel shrub, which also attracted a high diversity of bee species. Some of the most attractive plants to bees are non-native (*i.e.*, cotoneaster and cherry laurel), suggesting that in some urban areas mosaics of native plants and nectar-rich introduced plants can promote the "healthiest" bee populations.

The city of Vancouver is a mixture of traditionally managed sites, frequently mowed gardens with non-native ornamental plants, and ecosystem-managed areas where native species dominate in flower beds surrounded by infrequently mowed fields. This habitat mosaic results in patchy and variable diversity and abundance of urban bee populations. Our study highlights how urban areas can contribute to bee-friendly habitats and biodiversity. Cities can display a surprisingly high species diversity compared with intensively cultivated rural areas (Goulson *et al.* 2001; Melles *et al.* 2003), and a number of bee species are well adapted to urban habitats and patchy environments

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(Saure 1996; Bortoli and Laroca 1997; Cane 2001). Thus, future urban bee surveys might focus on systematic comparisons of urban and nearby rural sites. Although bee monitoring is key to assessing the extent of the global decline in pollinators (Buchmann and Nabhan 1996; Allen-Wardell *et al.* 1998; Cane and Tepedino 2001; Frankie *et al.* 2002), published data on pollinator monitoring is still insufficient (Cane and Tepedino 2001; Kevan and Phillips 2001; Frankie *et al.* 2002). Our study presents baseline guild data on bee composition that are necessary to address more complex questions regarding bee population dynamics over more than one season and in urban and agricultural areas (Frankie *et al.* 2002).

We conclude that low-disturbance landscape management and habitat diversity are key components of sustainable urban development for bees. Municipalities and landscape architects should consider these observations when planning residential, recreational, and industrial areas.

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## References

Allen-Wardell G, Bernhardt P, Bitner R, Burquez A, Buchmann S, Cane J, Cox P, Dalton P, Feinsinger P, Ingram M, Inouye D, Jones C, Kennedy K, Kevan P, Koopowitz H, Medellin R, Medellin-Morales S, Nabhan G, Pavlik B, Tepedino V, Torchio P, Walker S. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* **12**: 8–17

Bortoli C, Laroca S. 1997. Relative abundance of wild bees (Apoidea) in an urban biotrope of Guarapuava (PR, Brazil). *Acta Biologica Paranaense* **26**(1–4): 51–8

Buchmann SL, Nabhan GP. 1996. *The forgotten pollinators*. Washington, District of Columbia: Island Press

Cane JH. 2001. Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* [online] **5**(1): 3. Available from http://www.consecol.org/vol5/iss1/art3 [cited 6 January 2003]

Cane JH, Tepedino VJ. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology* [online] **5**(1): 1. Available from http://www.consecol.org/vol5/iss1/art1 [cited 6 January 2003]

Collinge SK. 1998. Spatial arrangement of habitat patches and corridors: clues from ecological field experiments. *Landscape and Urban Planning* **42**: 157–68

De Freitas Barbola I, Laroca S. 1993. The Apoidea (Hymenoptera) community of the Reserva Passa Dois (Lapa, Paraná, Brazil). I. Diversity, relative abundance and seasonal activity. *Acta Biologica Paranaense* **22**(1–4): 91–112

Frankie GW, Vinson SB, Rizzardi MA, Griswold TL, O'Keefe S, Snelling RR. 1997. Diversity and abundance of bees visiting a mass flowering tree species in disturbed seasonal dry forest in Costa Rica. *Journal of the Kansas Entomological Society* **70**(4): 281–96

Frankie GW, Thorp RW, Newstrom-Lloyd LE, Rizzardi MA, Barthell JF, Griswold TL, Kim J, Kappagoda S. 1998. Monitoring wild bees in modified wildland habitats: implications for bee ecology and conservation. *Environmental Entomology* **27**(5): 1137–47

Frankie GW, Vinson BS, Thorp RW, Rizzardi MA, Tomkins M, Newstrom-Lloyd LE. 2002. Monitoring: an essential tool in bee ecology and conservation. pp 187–98 *in* P Kevan, VL Imperatriz Fonseca (Eds), *Pollinating bees — the conservation link between agriculture and nature*. Brasilia, Brasil: Ministry of Environment

https://doi.org/10.4039/n04-010 Published online by Cambridge University Press

Gayubo SF, Torres F. 1991. Urban pressure effect on bees and wasps (Hymenoptera: Aculeata) in Salamanca. IV. *Boletin de la Real Sociedad Espanola de Historia Natural Seccion Biologica* **87**(1–4): 73–92

Gotelli NJ, Entsminger GL. 2001. *EcoSim: null models software for ecology* [online]. Version 7.0 [computer program]. Burlington, Vermont: Acquired Intelligence Inc. and Kesey-Bear. Available from http://homepages.together.net/~gentsmin/ecosim.htm

Goulson D, Hughes WOH, Derwent LC. 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* **130**: 267–73

Graf LH, Winston ML. 1982. Native bee pollinators of berry crops in the Fraser Valley of British Columbia. *Journal of the Entomological Society of British Columbia* **79**: 14–20

Greater Vancouver Regional District. 2001. *GVRD Land Use 2001* [online]. Burnaby, British Columbia: GVRD Policy and Planning Department. Available from http://www.gvrd.bc.ca/publications/file.asp?ID=594 [cited 30 July 2004]

Haeseler V. 1972. Man-made habitats (deforested areas, gravel pits, city gardens and parks) as refuge for insects, exemplified by the Hymenoptera: Aculeata. *Zoologische Jahrbuecher Abteilung fuer Systematik Oekologie und Geographie de Tiere* **99**: 133–212

Jacob-Remacle A. 1984. Ecological study of the aculeate Hymenoptera population living in the most urbanized zone of the city of Liege Belgium. *Bulletin et Annales de la Societe Royale d'Entomologie de Belgique* **120**(7–8): 241–62

Kerr JT. 2001. Butterfly species richness patterns in Canada: energy, heterogeneity, and the potential consequences of climate change. *Conservation Ecology* [online] **5**(1): 10. Available from http://www.consecol.org/vol5/iss1/art10 [cited 6 January 2003]

Kevan PG, Phillips T. 2001. The economic impacts of pollinator declines: an approach to assessing the consequences. *Conservation Ecology* [online] **5**(1): 8. Available from http://www.consecol.org/vol5/iss1/art8 [cited 6 January 2003]

Kratochwil A, Klatt M. 1989. Bee species of ruderal sites in the city of Freiburg in Breisgau, West Germany — submediterranean elements in mosaic habitats with high persistence. *Zoologische Jahrbuecher Abteilung fuer Systematik Oekologie und Geographie der Tiere* **116**(4): 379–89

Lancaster RK, Rees WE. 1979. Bird communities and the structure of urban habitats. *Canadian Journal of Zoology* **57**(12): 2358–68

Magurran AE. 1988. *Ecological diversity and its measurement.* 1st edition. Princeton, New Jersey: Princeton University Press

Melles S, Glenn S, Martin K. 2003. Urban bird diversity and landscape complexity: species–environment associations along a multiscale habitat gradient. *Conservation Ecology* [online] **7**(1): 5. Available from http://www.consecol.org/vol7/iss1/art5 [cited 17 December 2003]

Morse RA, Calderone NW. 2000. The value of honeybees as pollinators of U.S. crops in 2000. *Bee Culture* **March 2000**: 2–15

Osborne JL, Williams IH. 2001. Site constancy of bumble bees in an experimentally patchy habitat. *Agriculture Ecosystems and Environment* **83**: 129–41

O'Toole C, Raw A. 1991. *Bees of the world.* New York: Facts on File

Richards KW, Kevan PG. 2002. Aspects of bee biodiversity, crop pollination, and conservation in Canada. pp 77–94 *in* P Kevan, VL Imperatriz Fonseca (Eds), *Pollinating bees — the conservation link between agriculture and nature*. Brasilia, Brasil: Ministry of Environment

Risch S. 1996. On the bee fauna of Cologne — described on the example of selected city sites. *Decheniana Beihefte* **35**: 273–303

Roubick WD. 1989. *Ecology and natural history of tropical bees*. Cambridge, New York: Cambridge University Press

SAS Institute Inc. 1990. *SAS/STAT user's guide*. Version 6, 4th edition. Cary, North Carolina: SAS Institute Inc

Saure C. 1996. Urban habitats for bees: the example of the city of Berlin. pp 47–54 *in* A Matheson, SL Buchmann, C O'Toole, P Westrich, I Williams (Eds), *The conservation of bees.* Linnean Society Symposium Series 11. London: Academic Press

Schaefer V. 1994. Urban biodiversity. pp 307–18 *in* LE Harding, E McCullum (Eds), *Biodiversity in British Columbia: our changing environment*. Ottawa, Ontario: Canadian Wildlife Service

Scott-Dupree CD, Winston ML, Hergert G, Jay SC, Nelson D, Gates J, Termeer B, Otis G (*Editors*). 1995. *A guide to managing bees for crop pollination*. Winnipeg, Manitoba: Canadian Association of Professional Apiculturists

Schick B, Sukopp H. 1998. Blumen-Bestäuber-Systeme in urbanen Grünflächen: Über Blütenbesuche der Groβen Wollbiene (*Anthidium manicatum* L.) im Botanischen Gaten Berlin-Dahlem. *Zeitschrift fuer Oekologie und Naturschutz* **7**(2): 73–83

Stork NE, Srivastava DS, Watt AD, Larsen TB. 2003. Butterfly diversity and silvicultural practices in lowland rainforests of Cameroon. *Biodiversity and Conservation* **12**: 387–410

https://doi.org/10.4039/n04-010 Published online by Cambridge University Press

Westrich P. 1996. Habitat requirements of Central European bees and the problems of partial habitats. pp 1–16 *in* A Matheson, SL Buchmann, C O'Toole, P Westrich, I Williams (Eds), *The conservation of bees.* Linnean Society Symposium Series 11. London: Academic Press

Williams NM, Minckley RL, Silveira FA. 2001. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology* [online] **5**(1): 7. Available from http://www.ecologyandsociety.org/vol5/iss1/art7 [cited 6 January 2003]

Wynn G, Oke T (*Editors*). 1992. *Vancouver and its region*. Vancouver, British Columbia: University of British Columbia Press

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https://doi.org/10.4039/n04-010 Published online by Cambridge University Press