The Effects of Natural and Anthropogenic Habitats on Pollinator Communities in Oak-Savannah Fragments on Vancouver Island, British Columbia

by

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Abstract

Fragmentation of natural habitat can lead to loss of species but landscapes surrounding habitat fragments may provide resources and so promote species diversity. I examined the role of the surrounding landscape – Douglas-fir forest and urban residential areas – on pollinator communities in oak-savannah fragments. Bees in fragments surrounded by forest were larger, and body size increased with increased availability of early-blooming, native flowering plants. Small-bodied, mid to late-season bees were more abundant in fragments surrounded by urban landscapes. We propose these late-season generalist pollinators were supported by floral resources in the gardens of urban habitats. In contrast, early-flying species were unique to oak-savannah fragments and some bumble bees may rely on nesting resources found only in forested landscapes. Although urban residential lawns and gardens supported a high richness and abundance of pollinator species, conservation of these oak savannah- and forest-associated species will depend on maintaining and restoring oak-savannah habitats.

Keywords: Habitat fragmentation; landscape matrix; pollinators; community composition; species-specific traits; oak-savannah

Every bee is a really cool bee.

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Chapter 1.

Introduction

Understanding biodiversity patterns in increasingly human-dominated landscapes is critical for maintaining our current quality of life. We depend on diverse natural communities for clean air and water, crop pollination, pest control and other economically important and aesthetically pleasing services (Ehrlich and Ehrlich 1992, Daily 1997). These services, in turn, are being affected by the rapid conversion of natural land to urban and agricultural uses (Kaye et al. 2006, Shen et al. 2008). However, fragments of natural land and their unique species are occasionally preserved in human landscapes. How, then, do species respond to their new surroundings?

Traditionally, ecologists have predicted that bigger is better: large fragments are able to support increasingly diverse communities. This prediction originated from the theory of island biogeography (MacArthur and Wilson 1967), a mathematical model that attempts to predict species richness on oceanic islands of varying size. Islands that are large are predicted to have higher habitat heterogeneity with a greater number of exploitable niches. The predictor variables in the theory of island biogeography, island size and isolation, have been extrapolated to study the effects of fragmentation in terrestrial ecosystems (e.g. Aizen and Feinsinger 1994, Stouffer and Bierregaard 1995, Steffan-Dewenter et al. 2000, Donaldson et al. 2002). However, terrestrial habitat patches are not embedded in an inhospitable matrix, as true islands are (Wiens 1995). Ecological processes in remnant habitats are affected by direct interactions with the surrounding landscape, whereas oceanic islands do not experience the same processes (Brotons et al. 2003).

Structural features of the surrounding landscape and biological traits can influence how species respond to fragmentation (Antongiovanni and Metzger 2005). In an experiment on butterfly movement in natural meadow fragments in Colorado, Ricketts (2001) showed that the surrounding matrix and species traits can significantly influence the effective isolation of habitat patches. For four out of six butterfly taxa studied, coniferous matrix habitat was significantly more resistant to dispersal than willow matrix habitat. Butterflies in the Argynnini taxon, however, had the greatest flight capabilities (longest wing length) and dispersal was not restricted by any matrix habitat. In contrast, Lycaenini had the smallest wing length and both coniferous and willow habitat equally inhibited movement across the landscape. Although this study was not focusing on the effects of anthropogenic fragmentation, it does indicate that responses to matrix habitat differ even among closely related species (Ricketts 2001), and serves to demonstrate that persistence in fragmented habitats may be determined by the quality of the matrix habitat as well as by species characteristics (Ewers and Didham 2006).

Species' traits that create disadvantages in fragmented habitats include having small population size, high degrees of specialization, dependency on mutualists, large body size, low or intermediate dispersal ability, and/or a high trophic position (Davies et al. 2000, Tscharntke et al. 2002, Henle et al. 2004, Ewers and Didham 2006). A few of these traits can even be represented in the same organism: large species tend to be at higher trophic levels, with small, fluctuating populations (Lawton 1994). Small populations have an increased risk of genetic inbreeding and are prone to random extinctions (Pimm et al. 1988, Ellstrand and Elam 1993, Lawton 1994). In addition, large species reproduce more slowly, require higher amounts of resources and high-ranking trophic species are strongly dependent on lower trophic levels (Holt et al. 1999, Tscharntke et al. 2002). Likewise, the survival of specialists and mutualists is dictated by factors that affect their own distribution in addition to spatial processes acting on their required resources or interacting species (Holt et al. 1999). Unlike generalists that can switch to other resources or interact with other species that may occur in matrix habitat, specialists are not able to use the matrix if the landscape doesn't support the resources or species they require. Matrix quality, therefore, is a function of the species in question, and will be particularly important for determining persistence in fragmented habitats.

If traits can predict a species' response to disturbance and differences in matrix quality, we should see shifts in community or guild composition with respect to that quality (Williams et al. 2010). Bees provide a unique system for investigating the relationship between species traits and matrix quality, ranging in size, feeding specialization, nesting preferences and sociality. Their sensitivity to fragmentation and matrix quality should depend on these very traits (Williams et al. 2010). A recent meta-analysis has shown that extreme habitat loss generally results in reduced bee abundance and species richness (Winfree et al. 2009). However, moderate levels of anthropogenic disturbance can be capable of supporting a high diversity of pollinators (e.g. Winfree et al. 2007, Fetridge et al. 2008, Jauker et al. 2009). The goal of my thesis is to determine how the surrounding landscape matrix influences taxonomic and functional diversity of pollinators in remnant fragments of an endangered ecosystem, and determine what qualities of matrix habitat promote diverse pollinator communities. Resources in fragmented habitats and the matrix may influence species differently depending on the resources they require to complete their life cycle, and will vary depending on species-specific traits (e.g. body size, nesting guild, foraging specialisation and foraging phenology).

In this thesis, I examine the influence of the surrounding landscape on plant and pollinator communities in highly fragmented oak-savannah (OS) habitat on Vancouver Island, British Columbia. Specifically, I investigate how pollinator communities differ between habitat fragments surrounded by natural areas – Douglas fir coniferous forest – and fragments surrounded by urban residential development. In Chapter 2, I focus on female bee communities in habitat fragments, and ask how community composition in forest- and urban-associated OS fragments is influenced by both species-specific traits (nesting guild, specialization, and body size) and within-fragment floral resource quality. In Chapter 3, I further explore whether differences in pollinator community composition are due to use of the surrounding matrix habitat (forest or urban) for floral or nesting resources. In addition, I ask whether the assemblage of pollinators in oak-savannah habitat is unique to that ecosystem, relative to urban areas independent of any oak-savannah habitat. This thesis gives insight not only to characteristics of species that are vulnerable to the effects of fragmentation and habitat loss, but also to qualities of urban and natural environments that promote diverse and abundant assemblages of pollinators.

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Chapter 2.

Floral resources, surrounding landscape, and body size influence bee community assemblages in oak-savannah fragments[1]

Introduction

Fragmentation of natural habitats due to urban expansion is occurring at a rapid rate. Although some efforts are made to preserve natural landscapes in urban environments, reserves in urban areas are often not comparable in quality to wild areas, and this may impact biodiversity (Lindenmayer and Fischer 2006). Traditionally, biodiversity in habitat fragments has been examined using the theory of island biogeography, predicting that large island-like fragments should support more species than smaller islands (MacArthur and Wilson 1967). Although the theory has been influential in examining patterns of species richness on oceanic islands, terrestrial habitat patches are not embedded in a truly inhospitable matrix (Wiens 1995; Lindenmayer and Fischer 2006, Prugh et al. 2008, Collinge 2009). Species survival in terrestrial fragments depends on how species interact with their new surroundings, including the quality of the surrounding matrix habitat in addition to fragment habitat quality (Debinski and Holt 2000, Fahrig 2001, Vandermeer and Carvajal 2001). Considering the matrix (the landscape within which habitat fragments are embedded) may be especially important in urban environments, as these environments can differ substantially from the natural condition.

If the matrix provides supplementary or complementary resources for an organism, fragmented habitats can potentially support higher richness and abundance of

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[1] This paper is currently in press: Wray, J. C., L. A. Neame, and E. Elle. *In press* at Ecological Entomology. doi: 10.1111/een.12070

species than contiguous habitats (Dunning et al. 1992, Estades 2001, Ries and Sisk 2004). Persistence of species in fragmented landscapes, then, may be highly dependent on both the quantity and quality of resources in both fragment and matrix, and the degree to which individuals can exploit them (Estades 2001, Antongiovanni and Metzger 2005). The ability of organisms to exploit resources is ultimately determined by species-specific traits and life history strategies related to resource use and acquisition (Andrén 1992, Ricketts 2001, Ewers and Didham 2006), such as foraging ranges, trophic level, and specialization (Davies et al. 2000, Tscharntke et al. 2002, Henle et al., 2004). In fragmented habitats, therefore, we would predict shifts in community composition in fragments embedded in different matrix types, and expect community composition to be related to differences among species in foraging ranges and resource requirements (Bommarco et al. 2010, Williams et al. 2010).

Bees provide an ideal study system for investigating how species-specific traits, such as specialization and foraging range, can influence community assemblages in fragmented habitats. Floral specialists, bees that collect pollen from a restricted number of plant species, are predicted to be more sensitive to the loss of natural habitat because they may be incapable of switching to alternative food resources in the matrix, and anthropogenic disturbance may decrease availability of their required resource in habitat fragments (Tscharntke et al. 2002, Cane and Sipes 2006). Foraging range is related to body size in bees (Greenleaf et al. 2007), and because bees are central place foragers, distances between nest sites and food resources in fragmented habitats will likely affect offspring provisioning and may influence population sizes (Cane 2001, Williams and Kremen 2007). Bees of different body sizes, and so different foraging ranges, can then be expected to respond differently to fragmentation depending on the resources available in the fragment versus the matrix. Large-bodied species, for example, can travel farther distances but also have greater resource requirements (Cresswell et al. 2000). In contrast, small-bodied species are restricted in foraging range and the energy required to find resources further from the nest site may reduce reproductive potential (Peterson and Roitberg 2006, Zurbuchen et al. 2010). For bees, we predict bee communities in fragments surrounded by different matrix types should co-vary not only with resources available in each but also species-specific foraging ranges and degree of floral specialization.

The resources required by bees include both food (floral resources) and nest sites (Westrich 1996). Although increased floral density and diversity in fragmented natural habitats generally has positive effects on pollinator diversity and/or abundance (Hines and Hendrix 2005, Kwaiser and Hendrix 2008), bee diversity is occasionally found to be independent of within-fragment floral resources (Neame et al. 2013). The influence of floral density and diversity on pollinators of different body sizes is variable; some studies report an increase in small-bodied bee abundance with increased floral diversity (Gathmann et al. 1994, Kwaiser and Hendrix 2008), while others show increases in large-bodied bee abundance with increases in floral density (Westphal et al. 2003, Westphal et al. 2006, Williams et al. 2012). Though the relationship between bee diversity and floral resources is variable, floral resources are relatively easy to quantify; in contrast, nesting resource availability is difficult to assess, and few studies attempt to do so (but see Potts et al. 2005). Instead, most studies attribute decreased availability of nest sites to loss of natural habitat, finding that species that require pre-existing cavities for nesting (“renters”) are more sensitive to habitat loss than those that excavate their own nests (“excavators”; Greenleaf and Kremen 2006, Klein et al. 2008, Williams et al. 2010, Burkle et al. 2013). In addition, loss of fragment area results in species loss for particular guilds, such as cavity-nesting bees (Neame et al. 2013). Loss of natural habitat may be associated with loss of specific nest sites (e.g. rodent holes, beetle bores in dead woody substrate), with subsequent negative impacts on the bees that require those resources.

Fragmentation of natural areas for urban development can result in reduced diversity, as well as a shift to generalist and exotic species that increasingly dominate human landscapes (Wania et al. 2006, McKinney 2008, Niinemets and Peñuelas 2008). In order to conserve biodiversity in urban environments, we must understand how species vary in their responses to habitat fragmentation (Koh and Sodhi 2004). I studied bee communities in oak-savannah (OS) habitat fragments on Vancouver Island, British Columbia. These fragments are typically surrounded by one of two matrix types: Douglas-fir coniferous forest, and residential neighbourhoods (MacDougall et al. 2004, Vellend et al. 2008, Lilley and Vellend 2009). I asked whether forest- and urban-associated OS fragments support different communities of bees. Specifically, I asked how forest- vs. urban-associated fragments differ in the richness, diversity, and abundance of i) total bees, ii) nest construction guilds, and iii) abundance of floral specialists. I also analyzed differences in floral and bee community composition with multivariate analyses of species assemblages. I hypothesized that species that require pre-existing cavities as nest sites and floral specialists would be more diverse and/or abundant, or make up more of the community, in forest-associated OS fragments. Finally, I explored potential explanations for observed variation in bee community composition by considering bee body size. Because body size is related to foraging distance and resource requirements, I expected larger bodied bees to be found in greater abundance in larger fragments with more floral resources. In addition, if forest habitat provides nesting resources for large-bodied renting species (e.g. bumble bees), then surrounding forest cover may also have an influence on the composition of the bee community.

Methods

Study area and bee and plant sampling

The study area is within oak-savannah parkland of southwestern British Columbia, an ecosystem characterized by oaks, some shrubs, and an understory dominated by grasses and a diversity of native wildflowers (Fuchs 2001, MacDougall et al. 2004). Non-random habitat loss and fragmentation on Vancouver Island has resulted in less than 5% of the original habitat remaining, with remnants primarily restricted to rocky hilltops (MacDougall et al. 2004, Vellend et al. 2008). Habitat fragments support a diverse community of pollinating insects, including at least 100 species of bees and 37 species of flies (Neame et al. 2013). From April to June of 2007, bees were collected from a randomly selected hectare within each of 19 habitat fragments ranging in size from 0.3 to 31 ha on the Saanich peninsula (detailed methods and map in Neame et al., 2013). Netting surveys were conducted six times throughout the blooming season; two collectors concurrently worked within the designated hectare for a duration of 15 minutes. Two rounds of pan trapping, approximately four weeks apart, were conducted with blue, yellow, and white bowls. I use a subset of these data for analysis, including only female central place foragers and therefore excluding syrphid flies, brood parasites, and all male bees (but see Neame et al. (2013) for more information on how these guilds are influenced by local- and landscape-level variables). Central place foragers have fixed nest sites and focus their foraging to minimize travel back and forth, while other ecological groups are not expected to respond to the landscape in the same way (Kremen et al. 2007). I therefore also excluded the managed honey bee (*Apis mellifera*) from analysis, as this species is expected to respond to management and the location of hives rather than the landscape.

Floral resources were sampled twice in 2007, using 25 random 1-m^2 quadrats at each site. Neame et al. (2013) counted the number of flowering stems by species (excluding wind-pollinated species like grasses) and estimated the proportion of bare rock. Although estimating pollen and nectar resources for each plant species would provide a more accurate estimate of resources available to pollinators, it was not feasible for the 65 plant species in this study. I interpret rockiness within a site as the amount of trampling disturbance, which may eradicate some early-blooming native plant species and decrease availability of pre-existing cavities in mossy substrates. For analysis I considered whether plant species were native or introduced, using “Plants of Coastal British Columbia” (Pojar and MacKinnon 1994) to assign species to the two categories.

Landscape characterization

I used ArcGIS 10.0 (ESRI 2011) and a combination of ground-truthing and high resolution aerial photographs from the Capitol Regional District Natural Areas Atlas (10-cm resolution, © 2010-2012 Capital Regional District) to delineate polygons of coniferous and mixed forest cover in 400-meter buffers surrounding each study site. I chose a 400-meter buffer based on our calculation of the average typical foraging distance of all central place foragers included in our analysis. The foraging range of each species was calculated from Greenleaf et al. (2007), and is based on the inter-tegular distance of bees (see next section). Previous studies have found that the effects of the surrounding landscape on solitary wild bees are strongest at a radius of 250-meters (Steffan-Dewenter et al. 2002, Steffan-Dewenter 2003), and similarly sized buffers are commonly used in research on bee communities (e.g. Brosi et al. 2008, Jauker et al. 2009). The proportion of forest cover in the surrounding landscape ranged from 0 to 62 percent, and I used a natural break in the values to separate oak-savannah sites into predominantly forest- (>24% forest) or urban-associated (<12%). Urban-associated sites were embedded in a matrix of urban and suburban development within the Victoria Census Metropolitan Area (Victoria CMA, population 344 615, density 495.0 per square kilometer; Statistics Canada 2012). Fragment area was previously calculated using the same high-resolution aerial images and ArcGIS 9.2 (ESRI 2009, Neame et al. 2013).

Species-specific traits of bees

I compiled information on nest construction guild for all species from a combination of reference works (e.g. Michener 2000) and published keys (e.g. Gibbs 2010). If published data were unavailable, we inferred trait data based on phylogeny (e.g. all species of *Andrena* excavate nests; Michener 2000). We categorized nest construction type as renting or excavating. Renters included species that construct nests within existing holes or cavities, while excavators dig or bore the nest within existing substrate (Williams et al. 2010).

Bee species were categorized as oligolectic or polylectic based on documented feeding preferences or using data on visit patterns from this ecosystem (G. Gielens, J. Wray, and E. Elle *unpublished data*). Species were defined as oligolectic if they collect pollen from one to a few genera within a single plant family (Cane and Sipes 2006).

For estimates of body size I measured the inter-tegular distance for each species. Inter-tegular distance correlates strongly with other measures of body size and is an accurate predictor of foraging range (Greenleaf et al. 2007). I measured 10 females per species (20 for *Bombus* to account for greater within-species variation) using digital callipers and a dissecting microscope. For five out of the total 75 species fewer specimens from our reference collection were available, so a range of 2-7 bees were measured. I only include *Bombus* workers in analysis, not queens. I used the mean inter-tegular distance for each species to calculate a “weighted-mean inter-tegular distance” for each site with the following equation:

$$\sum_{i=1}^{n} \frac{(IT_i * N_i)}{N_t}$$

Where IT_i is the mean inter-tegular distance of species i, N_i is the number of individuals of species i caught at a site, and N_t is the total abundance of individuals caught at a site.

Statistical analysis

All analyses were conducted in SAS (SAS/STAT® 9.3; SAS Institute 2011) unless indicated otherwise.

Species richness, diversity, and abundance

To determine if different nesting guilds are more abundant or diverse in forest- vs. urban-associated oak-savannah fragments, we tested for differences between site types in species richness, Simpson's diversity, and abundance of i) all bees, ii) excavators, and iii) renters using two sample t-tests. Simpson's diversity was calculated as $D= 1/ [\sum (n_i/N_t)^2]$, where n_i is the number of individuals of species i caught at a site and N_t is the total number of individuals at a site. Because I only collected five species of specialists, I tested for differences in specialization between the communities of urban- and forest-associated OS fragments with measures of abundance of specialists, not richness or diversity.

Plant and bee community composition

I used non-metric multi-dimensional scaling (NMS; PC-ORD v. 5.0; McCune and Mefford 2005) to describe community composition. NMS calculates dissimilarities in species composition between sites to allow a graphical representation of differences among site types (McCune and Grace 2002, Quinn and Keough 2002). I used the Bray-Curtis measure of ecological distance, comparing absolute species' abundances among sites. To enhance the detection of relationships between community composition and habitat type, I removed all bee and plant species for which only a single individual was recorded (McCune and Grace 2002), resulting in the analysis of 60 bee and 55 plant species. Floral abundance data (number of stems) was log-transformed to reduce stress in the final configuration. To interpret the resulting NMS figure, I correlated species' abundances with ordination axis scores to determine if certain species were associated with different axes, and hence different matrix types (forest vs. urban; Quinn and Keough 2002).

I used a non-parametric multivariate analysis of variance (NPMANOVA) in R (R 2.15.3, R Core Team ©2013) to determine if plant and bee community compositions in habitat fragments were significantly different between the two matrix types (vegan tutorial; Oksanen 2011). NPMANOVA follows the framework of ANOVA, applying the partitioning of sums-of squares (SS) and variances directly to dissimilarity measures, such as the Bray-Curtis measure I use in this paper (Quinn and Keough 2002). F-ratios are constructed from the sums of squared distances within and between groups (in our case, our two matrix types), and the test computes permutations of the observations to obtain a distribution of the test statistic under the null hypothesis of no differences between groups (Anderson 2001). I used 5000 permutations, recommended for tests with an alpha-level of 0.01 (Manly 1997).

NPMANOVA allows us to test if there is a significant difference in species composition between groups, however it is also sensitive to dispersion of points (or variability in species' assemblages within a group). To determine if significant results from the NPMANOVA were due to actual group dissimilarities, rather than within-group variability, I also used the betadisper function in R to examine the differences in group homogeneities (vegan tutorial; Oksanen 2011). This test is a multivariate analogue to Levene's test of homogeneity of variances, where deviations from a group mean are represented by Bray-Curtis distances of sites within a group to their group centroid (Anderson 2006).

Floral resources and body size

I assessed whether bee body size (the weighted-mean inter-tegular distance) differed between forest- and urban-associated OS fragments using two sample t-tests. To assess whether detected differences were associated with variation in floral resources, fragment area, or forest cover in the surrounding landscape I performed a series of analyses. To produce a single variable describing floral resource availability at each site, I used principal component analysis (PCA) on the five variables associated with floral resource availability (total richness, total density, proportion of bare rock, proportional richness of introduced species and proportional density of introduced species). Proportion data were transformed using a logistic transformation, recommended for proportion data for improved interpretability (Warton and Hui 2011). The first principal component differentiated among sites with a high density and richness of flowering plants (low values of PC1) and those with a high proportion of bare rock and high richness and density of introduced species (high values of PC1). PC1 accounted for 56.9% of the variation in the data (Table 2.1). I used a two sample t-test to compare floral resource availability (PC1) between forest- and urban-associated sites.

To investigate the role of local and landscape variables on weighted-mean inter-tegular distance (weighted-mean IT) I ran a series of regressions including all possible combinations of predictor variables. I used Akaike's Information Criterion corrected for small sample sizes (AICc) in R (R 2.15.3, R Core Team ©2013) and Akaike weights (w_i) to compare and evaluate the predictive strength of all possible regression models. Predictor variables included PC1, fragment area, and proportion forest cover in a 400-meter radius. I also included bumble bee abundance in these regressions to determine if overall increases in weighted-mean IT could be attributed to a greater abundance of these large-bodied bees, the largest in our dataset. Proportion data and fragment area were transformed using logistic and log transformations, respectively. I examined variance inflation factors to address multi-collinearity between independent variables, however found that all variables met the required assumptions (VIF<4; Quinn and Keough 2002). If more than one model was strongly supported (i.e. delta AICc = 0-2; Burham and Anderson 2002) I examined the relative importance of each predictor variable by calculating the sum of the Akaike weights over all the models in which the predictor variable of interest occurred (MuMIn package; Bartoń 2013). To further explore variation in bumble bee abundance among sites, I performed a multiple linear regression including the following predictor variables: PC1, fragment area, and forest cover. As above, I used AICc to compare models.

Results

Species richness, diversity, and abundance

Surveys collected a total of 2770 female bee central place foragers, with a total of 75 species from 11 genera. There were no differences in species richness, abundance, or abundance of specialists between forest- and urban-associated OS fragments (Table 2.2). Simpson's diversity, however, was higher in urban-associated OS fragments, while forest-associated OS fragments tended to support a higher abundance of bees in the “renting” nesting guild (Table 2.2). The “renting” guild includes both wood-nesting bees such as *Osmia* and *Anthidium* and above- and below-ground nesting bumble bees (*Bombus* spp.), and post-hoc analysis indicated that increased abundance of renters in forest-associated OS fragments was due solely to increased numbers of bumble bees. Wood-nesting renters were actually more abundant in urban-associated OS fragments (Forest = 10.75 ± 1.89, Urban = 18.82 ± 2.07, t_{17}=-2.77, P=0.013), while bumble bee renters were more abundant in forest-associated fragments (Forest = 61.38 ± 9.17, Urban = 24.55 ± 2.12, t_{17}=4.53, P=0.0003).

Plant and bee community composition

I found significant differences in plant and bee community compositions between forest- and urban-associated OS fragments (plants: Final stress=10.75, instability=0.00, $F_{1,18}$=3.50, P<0.001; bees: Final stress=8.98, instability=0.00, $F_{1,18}$=4.65 P<0.001). These differences were not due to within-group variability, as differences in dispersion were not significant (plants: $F_{1,18}$=1.27, P=0.27, bees: $F_{1,18}$=0.41, P=0.53). Correlations between abundances and ordination axis scores demonstrated that bees in forest-associated OS fragments (Fig. 2.1) included early-flying, large-bodied bumble bees (*Bombus* spp.) and mining bees (*Andrena* spp.), as well as some uncommon species of mason bees (*Osmia* spp., Table 2.3). Urban-associated species, on the other hand, were represented by late-flying or small-bodied sweat bees (*Agapostemon, Lasioglossum (Dialictus), Halictus* spp.), as well as commonly observed species of mason bees (e.g. *Osmia odontogaster*, Table 2.3). Differences in plant communities were reflected primarily in plant origin: early-blooming plants native to the oak-savannah system tended to be associated with fragments surrounded by forest (e.g. *Collinsia parviflora, Plectritis congesta, Dodecatheon hendersonii*), while introduced garden exotics (e.g. *Hyacinthoides, Lamium purpureum*) were more prevalent in urban-associated OS fragments (Table 2.3).

Floral resources and body size

Overall body size, measured by the weighted mean inter-tegular distance, was larger in forest- compared to urban-associated OS fragments (t_{17}=2.50, P=0.02; Fig. 2.2a). I also found lower values of PC1 (Table 2.1) in forest- compared to urban-associated OS fragments (t_{17}=-3.56, *P*=0.0024; Fig. 2b), indicating forest-associated OS fragments had a greater density and richness of total floral resources, with a lower proportional richness and density of introduced plants and a lower proportion of bare rock.

The best models predicting increases in mean body size in fragments included a combination of floral resources (PC1) and fragment area (Table 2.4). The relative importance of predictor variables indicates that PC1 was the best predictor of body size: body size increases with an increase in total floral richness and density, and a decrease in the proportion of bare rock and introduced species richness and density (Table 2.4, Figure 2.3a). Increases in bumble bee abundance were best predicted by an increase in the proportion of forest cover in a 400-meter radius around the fragment (Table 2.4, Figure 2.3b).

Discussion

In this study, I set out to determine how different bee species vary in their response to fragmentation, and how species' traits and the surrounding landscape could influence bee community composition. I hypothesized that bees requiring natural habitat for food and/or nesting resources would be found in forest-associated fragments. For mobile individuals like bees, effective isolation of natural landscapes is ultimately determined by the quality of the fragment and matrix habitat, as well as species-specific traits (Estades 2001, Ricketts 2001, Ewers and Didham 2006). Here I provide evidence that differences in bee communities among oak-savannah fragments embedded in different matrix types are related to body size and foraging range, likely due to differences in nesting requirements and within-fragment floral resources.

Species richness, diversity, and abundance

I found no differences in overall richness, overall abundance, or abundance of specialists, but did find higher Simpson's diversity in urban- compared to forest-associated OS fragments. Previous studies have found that fragmented habitats can still support high biodiversity if species are capable of utilizing the surrounding matrix (Gascon et al. 1999, Brotons et al. 2003, Antongiovanni and Metzger 2005). Here, I suggest that urban-associated OS fragments support a high diversity of late-season bees due to the proximity of residential gardens. Generalist bees, in particular, are known to prosper in urban environments (Cane et al. 2006, Winfree et al. 2007, Matteson and Ascher 2008, Fetridge et al. 2008). Conversely, specialists are predicted to be more sensitive to loss of natural habitat (Davies et al. 2000, Tscharntke et al. 2002, Henle et al. 2004). I found no evidence of this being the case, which could be attributed to low numbers of specialist species in our region. Alternatively, flight phenology and dietary restrictions may play a role; early-flying narrowly oligolectic *Andrena* specialists (*Andrena astragali* and *Andrena microchlora*) tended to be found in forest-associated OS fragments, consistent with our predictions. In contrast, two specialists were late-flying broadly oligolectic species (*Megachile perihirta* and *Osmia coloradensis*) that were solely caught in urban-associated OS fragments. If the matrix contains the resource a specialist requires, specialists may persist in fragmented habitats. In our study area, floral resources within fragments are sparse after mid-to-late June (Fuchs 2001, J. Wray personal observation), and surrounding Douglas-fir forest landscapes do not provide late-blooming forage either. Because the broadly oligolectic *M. perihirta* and *O. coloradensis* forage on the Asteraceae (Wilson et al. 2010), they may be found in urban-associated OS fragments because they forage on asters in urban gardens.

I also found a greater abundance of “renting” bees in forest-associated OS fragments, however this trend was due solely to ground-nesting bumble bees. Wood-nesting renters (e.g. *Osmia* spp.) were more abundant in urban-associated OS fragments. Similar results have been seen in desert scrub fragments in the Tucson Basin of Arizona; fragments in urban areas had a higher richness and abundance of renting species than continuous desert habitat (Cane et al. 2006). However, in our study I found increases in abundance alone, and not richness or diversity of renters. Furthermore, previous work in this ecosystem has shown that the diversity of wood-nesting renting species increased with fragment area, indicating that some species may require greater resource heterogeneity found only in natural habitats (Neame et al. 2013). Renters in urban environments, on the other hand, tend to be “nesting generalists”: wood-nesting Megachilidae that can use holes in fence posts and commercially-available nest blocks. Although renters have been shown to be more susceptible to the effects of habitat loss than excavators (Greenleaf and Kremen 2006, Klein et al. 2008, Williams et al. 2010, Burkle et al. 2013), our results suggest that some nesting substrates may be generally available in urban-associated OS fragments.

Plant and bee community composition

I found that early-blooming plant species, native to the oak-savannah ecosystem, tended to be found in forest-associated OS fragments, and a higher density and richness of introduced garden exotics were in urban-associated OS fragments. Native plant species may be eradicated from urban-associated OS fragments due to higher trampling disturbance (represented by increased proportions of bare rock), or from competition with introduced species (Traveset and Richardson 2006, Lilley and Vellend 2009). The increase in introduced species in urban-associated OS fragments, which may include plants that are more resistant to the effects of trampling (McKinney 2002), are most likely due to proximity of residential gardens (Niinemets and Peñuelas 2008). In our study area, flowering plant diversity and density has previously been shown to have little effect on bee diversity and abundance (Neame et al. 2013). However, I found that floral resources do have an influence on the assemblage of bees, and hypothesize residential gardens in the matrix further influence bee community composition in oak-savannah fragments.

Forest-associated OS fragments tended to support early-flying bumble bees and solitary mining bees, while late-flying species and sweat bees were in urban-associated OS fragments (Table 2.3). A post-hoc analysis compared the Julian dates of first capture for forest- and urban-associated species (listed in Table 2.3), using only netted specimens to avoid the confounding influence of collection method. I found that urban-associated species were collected significantly later than forest-associated species (Forest Julian date = 115.5 ± 4.52, Urban Julian date = 135.5 ± 4.35; t_{18}=-2.62, *P*=0.0174). Persistence of late-flying bees in urban-associated fragments could be attributed to the availability of floral resources in matrix habitat during a time when resources are relatively unavailable within habitat fragments. Many late-flying species in our area are small-bodied generalists (e.g. *Lasioglossum (Dialictus) incompletum*, *Lasioglossum (Dialictus) knereri*, Table 2.3), with limited foraging ranges and broad diets. Because forested landscapes do not have a high abundance or richness of pollinator-attractive plant species (J. Wray, *unpublished data*; Winfree et al. 2007), late-flying species may not be as abundant in forest-associated OS fragments due to higher energy costs required to find late-season floral resources outside those fragments (Peterson and Roitberg 2006, Zurbuchen et al. 2010). Similar results have been seen in New Jersey pineland habitat, with the abundance of small bees decreasing with increasing forest cover (Winfree et al. 2007). However, if the urban matrix contains food resources population sizes may increase (Estades 2001). For example, nest density of stingless bees in forest fragments was greater when they were able to feed on crop and mangrove pollen adjacent to fragments (Eltz et al. 2002). Similarly, solitary mason bees that provision offspring with crop pollen have greater offspring production and survival, especially when farms are far from natural habitat (Williams and Kremen 2007). Because the majority of bee-attractive oak-savannah plants are done blooming in mid-June, urban environments may also provide vital floral resources for late season fliers.

Floral resources and body size

I found that increased availability of native floral resources in forest-associated OS fragments supported a greater abundance of larger-bodied bees (Fig. 2.3a). In this ecosystem, early-blooming native plant species that tend to be found within forest-associated OS fragments may be a critical resource for early-flying large-bodied species, such as bumble bees. Early-flowering plant species have been shown to have a greater influence on bumble bee colony production than late-season plants (Williams et al. 2012), possibly due to the importance of floral resources during nest founding by queen bumble bees (Suzuki et al. 2009). Similarly, early-season flower density in alpine meadows had positive effects on the abundance of founding queens, whereas mid- and late-season resources had little impact on the abundance of workers and males (Elliott 2009). Likewise, early-flowering resources may be important for some larger-sized, early-flying solitary bees (e.g. *Andrena transnigra*, Table 2.3) that I found tend to be associated with forested landscapes. Most solitary bee species have short flight periods and limited time to provision offspring with pollen and nectar, and so high abundance and diversity of early-flowering resources may promote high abundances of these species. Finally, it is also possible that early-flying, large-bodied bees, bolstered by the higher abundances of early-flowering resources within fragments, may not be as sensitive as small-bodied bees to late-season floral scarcity due to larger foraging ranges. Because larger bees are capable of travelling further distances to find late-season garden or crop resources in the surrounding landscape, they may be able to persist in forested landscapes while the relative abundance of smaller bees decreases.

Although increases in body size were attributed to increasing richness and density of floral resources in our analysis, bumble bee abundance declined with decreasing proportion of forest cover in the surrounding landscape. Loss of natural habitat has been shown to have negative impacts on native bees (Kremen et al. 2002, Winfree et al. 2009), and bumble bees in particular (Jha and Kremen 2013). As mentioned earlier, flowering phenology may play an important role. Forest-associated OS fragments had a greater availability of early-flowering native species, potentially important for queen bumble bees during colony establishment (Suzuki et al. 2009). Additionally, bumble bees may be responding to the increased availability of “renting” nest sites the forest provides. Some bumble bees use abandoned rodent holes as nest sites (Heinrich 1979; McFrederick and LeBuhn 2006), which may be more abundant at forest edges (Svensson et al. 2000). Many mechanisms have been postulated about the causes of bumble bee declines (Williams 2005, Williams and Osbourne 2009, Cameron et al. 2011), and our results indicate that nesting availability and early-blooming floral resources may play a vital role in the persistence of these important bees in our region.

Conclusions

Although I did not sample the matrix habitat to determine the availability of nest sites or floral resources, our data clearly demonstrate that fragments embedded in forested and urban landscapes support different bee communities. This effect was primarily related to differences among species in body size, which represents requirements for resources as well as the hypothesized ability to access resources in the matrix. More research is required to assess how bees utilize matrix habitat, and to what degree different landscapes support bees with different nesting requirements and dispersal abilities. Although I hypothesize that small bees are more abundant in urban-associated fragments due to use of resources in residential gardens, there may be other explanations. Smaller bees have lower resource requirements, and as such may be sufficiently supported by the lower availability of floral resources in urban-associated fragments (Tscharntke et al. 2002, Cane et al. 2006). In the same fragments, large-bodied species may be forced to divert energy from reproduction to long-distance foraging in order to fulfill their resource requirements.

Our results add to a growing body of literature that highlights the importance of adopting community-based analysis, rather than relying on simple estimates of species richness as indicators of the effects of landscape change on biodiversity (Filippi-Codaccioni et al. 2010, Winfree et al. 2011). Of particular importance is to consider species traits in conjunction with the surrounding landscape in order to determine how communities will respond to habitat fragmentation. I found that oak-savannah fragments in urban environments can still support high diversity of bee species, including those that are predicted to be more vulnerable to the loss of natural habitat (i.e. some specialists, wood-nesting renters). Conversely, some groups like bumble bees and narrow specialists may benefit from the nesting and floral resources only found in natural landscapes. These results provide an important avenue for future research and conservation efforts; sampling the matrix habitat to determine the qualities of urban environments and forested landscapes that drive differences in bee community assemblages.

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Tables

Table 2.1. Eigenvectors for the first principal component, based on an analysis of five within fragment floral resource characteristics for 19 oak-savannah fragments. I used eigenvector sign and magnitude for interpretation of PC1 as negatively related to flowering plant richness and density and positively related to the proportion of bare rock and richness and density of introduced species.

Variable	Principal component 1
Total flowering plant richness	-0.495
Total flowering plant density	-0.491
Proportion bare rock	0.428
Proportional richness of introduced species	0.475
Proportional density of introduced species	0.324
% Variance explained	56.87

Table 2.2. Comparisons of total- and guild-specific species richness, diversity, and abundance of female bees between forest- (N=8) and urban-associated oak-savannah fragments (N=11). Significant differences between means were determined by two sample t-tests

	Nesting guild	Forest mean (SE)	Urban mean (SE)	t_{17}	*P*
Species Richness	Total	27.25 (1.58)	27.18 (1.45)	-0.89	0.39
	Excavators	16.00 (1.38)	17.64 (1.15)	-0.91	0.37
	Renters	9.13 (0.67)	9.09 (0.49)	0.04	0.97
Simpson's Diversity	Total	7.95 (0.60)	10.22 (0.76)	-2.21	0.04
	Excavators	6.11 (0.83)	7.18 (0.72)	-0.96	0.35
	Renters	4.11 (0.35)	4.73 (0.37)	-1.18	0.26
Abundance	Total	135.88 (16.13)	145.82 (18.48)	-0.38	0.71
	Excavators	63.63 (12.43)	101.82 (17.46)	-1.65	0.12
	Renters	72.13 (8.48)	43.36 (2.94)	3.62	0.002
	Specialists	4.75 (2.01)	2.45 (0.74)	1.20	0.25

Table 2.3. List of forest- and urban-associated bee and plant species, based on correlations between species abundance and NMDS site ordination axis 2 scores. Site groupings separate predominantly along axis 2 (Figure 2.1), hence species positively correlated with axis 2 can be considered "forest-associated" while species negatively correlated with axis 2 can be considered "urban-associated". Values in bold indicate that the Pearson correlation coefficient (r) is significant at $P<0.05$, plain text $P<0.10$. Correlations with P-values >0.10 are not shown. ^{a}Indicates introduced plant species. ^{b}Asteraceae floral specialist.

Forest-associated				Urban-associated			
Bee species	r	Plant species	r	Bee species	r	Plant species	r
Andrena nigrocaerulea	0.45	***Cerastium arvense***	**0.46**	*Agapostemon texana*	-0.44	***Barbarea orthocerus***	**-0.60**
Andrena transnigra	**0.66**	***Collinsia parviflora***	**0.55**	***Andrena saccata***	**-0.50**	***Camassia quamash***	**-0.54**
***Andrena* sp. 2**	**0.46**	***Delphinium menziesii***	**0.66**	***Bombus californicus***	**-0.68**	***Erodium circuatum***^{a}	**-0.74**
Bombus bifarius	**0.69**	***Dodecatheon hendersonii***	**0.62**	*Colletes kincadii*	-0.40	*Hyacinthoides* sp.^{a}	-0.39
Bombus flavifrons	**0.74**	***Gallium aparine***	**0.85**	***Lasiglossum(Dialictus) incompletum***	**-0.62**	***Lamium purpureum***^{a}	**-0.58**
Bombus mixtus	**0.58**	***Lithophragma parvifolium***	**0.56**	***Lasioglossum (Dialictus) knereri***	**-0.56**	***Rosa nutkana***	**-0.68**
Osmia cyanella	0.43	***Mimulus alsinoides***	**0.46**	*Halictus rubicundus*	-0.44	***Taraxacum officinale***^{a}	**-0.49**
Osmia tristella	0.42	*Montia parvifolium*	0.44	***Lasioglossum olympiae***	**-0.47**		
		Myosotis discolor	0.40	***Osmia albolateralis***	**-0.55**		
		Plectritus congesta	**0.46**	***Osmia coloradensis***^{b}	**-0.51**		
		Zygadenus venenosus	**0.40**	***Osmia dolerosa***	**-0.48**		
				Osmia odontogaster	**-0.61**		

Table 2.4 Importance of floral resources (PC1), fragment area, and forest cover in predicting body size and bumble bee abundance at 19 oak-savannah fragments (only models with ∆AICc <4 presented). Competing models for best rank indicated in bold (i.e. ∆AICc ≤ 2). RI = relative importance of preceding predictor variable. The variable with the highest relative importance best explains variation in the dependent variable. Log *L* = log transformation of the likelihood (*L*) of the model being the best model, ∆AICc = difference between the most explanatory model and the model of interest, w_i = Akaike weights, indicate probability that the model best explains variation in the dependent variable relative to other candidate models

Mean inter-tegular distance					
Variables included in model (RI)	d.f.	Log *L*	AICc	∆AICc	w_i
PC1 (floral resources) (0.92)	**3**	**-2.04**	**11.69**	**0.00**	**0.37**
PC1, Area (0.37)	**4**	**-1.10**	**13.06**	**1.38**	**0.19**
PC1, Bumble bees (0.32)	4	-1.45	13.76	2.08	0.13
PC1, Area, Bumble bees	5	0.14	14.34	2.65	0.10
PC1, Forest cover (0.17)	4	-2.04	14.94	3.26	0.07
Bumble bee abundance					
Variables included in model (RI)	d.f.	Log *L*	AICc	∆AICc	w_i
Forest cover (0.93)	**3**	**-81.89**	**171.38**	**0.00**	**0.60**
Forest cover, PC1 (0.27)	4	-81.49	173.83	2.42	0.18
Forest cover, Area (0.17)	4	-81.89	174.64	3.26	0.12

Figures

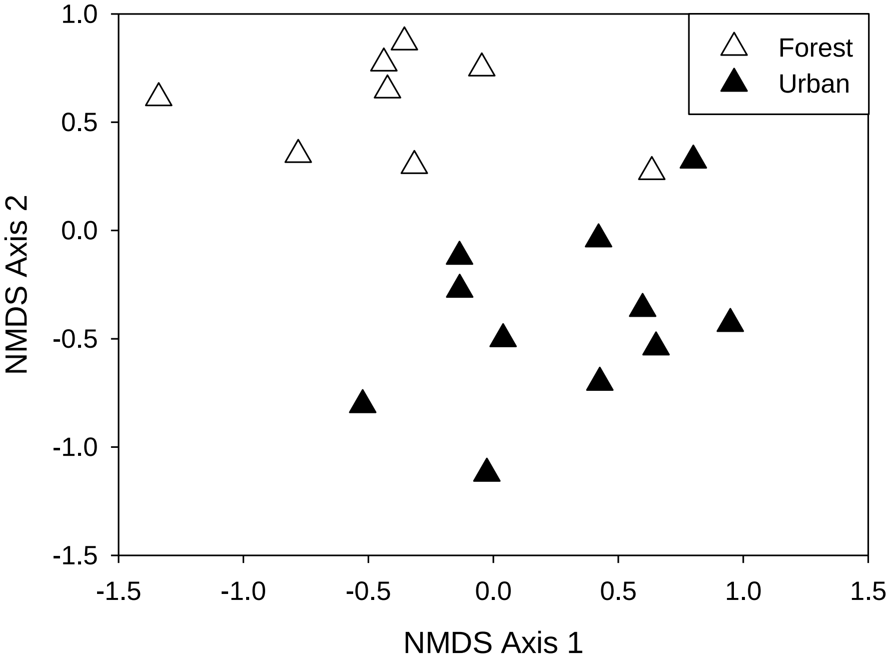

Figure 2.1. NMDS plot showing similarities in female bee community composition between forest- (N=8) and urban-associated OS fragments (N=11) (Final stress = 8.98, instability = 0.00, Non-parametric MANOVA $F_{1,18}$=4.65 *P*<0.001)

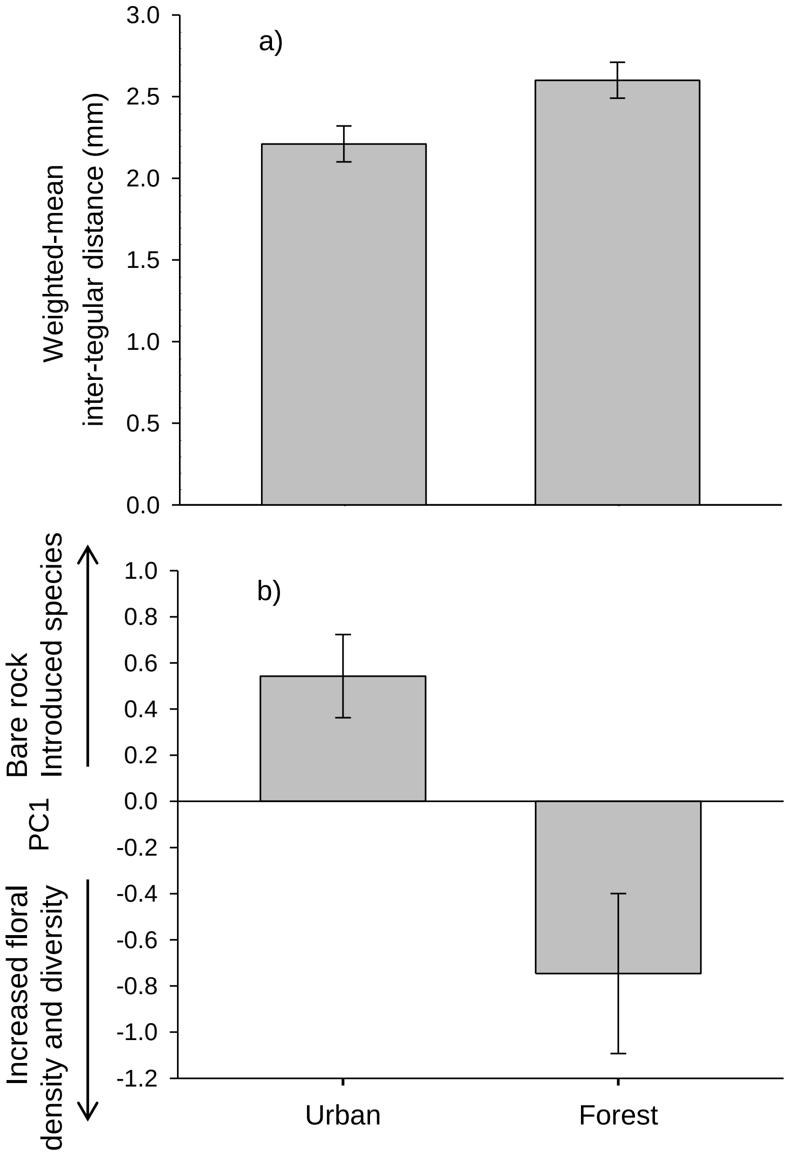

Figure 2.2. Forest-associated OS fragments (N=8) have a) larger bees than urban-associated fragments (N=11; t_{17}=2.50, *P*=0.02), and b) a greater density and richness of total floral resources but reduced density and richness of introduced plants and less bare rock (Table 2.1; t_{17}=-3.56, *P*=0.0024). Bars ± SE

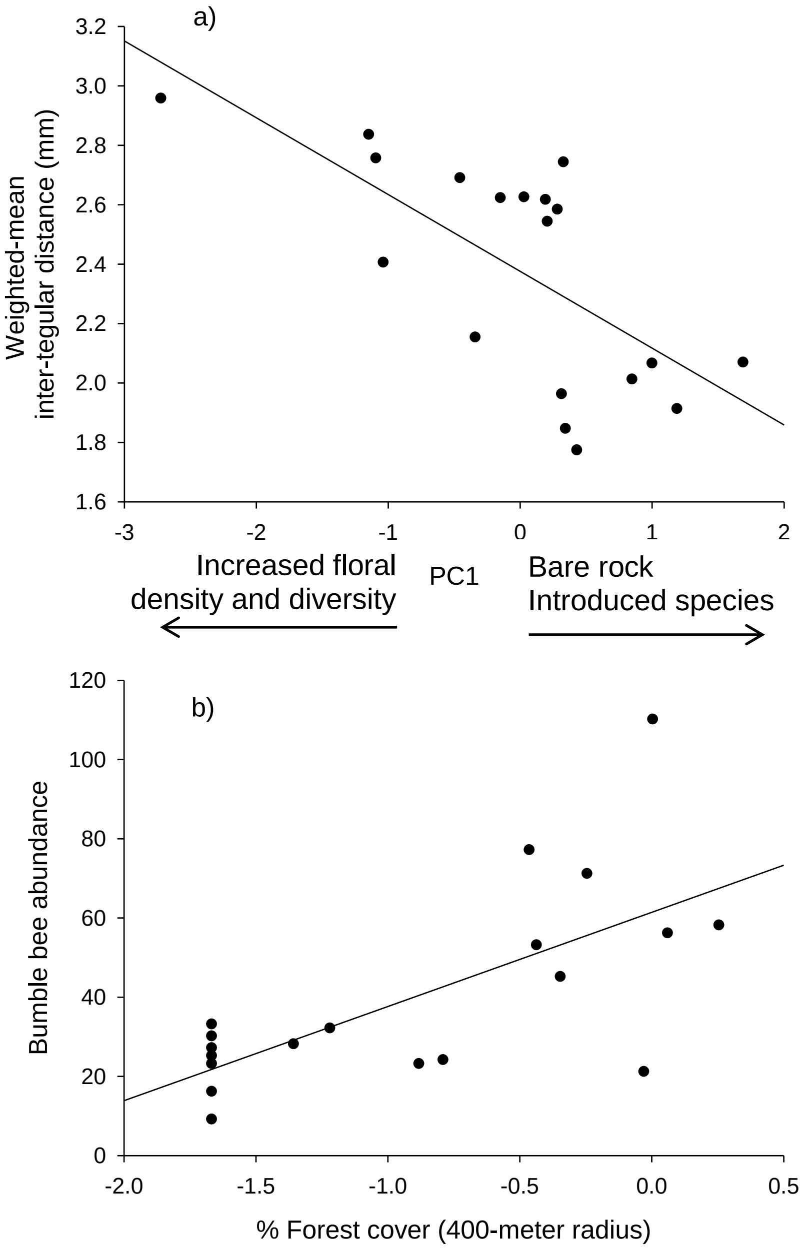

Figure 2.3. A) Body size (as measured by the weighted-mean inter-tegular distance) increases with an increase in floral richness and density and a decrease in proportional richness and density of introduced species and proportion of bare rock (PC1; Adjusted R^2=0.4345, N=19) and b) bumble bee abundance within the habitat fragment increases with increasing forest cover (logit transformed) surrounding the fragment (Adjusted R^2=0.4318, N=19)

Chapter 3.

Flowering phenology and nesting resources influence pollinator community composition in a fragmented ecosystem

Introduction

Conservation of biodiversity within habitat fragments is increasingly focusing on the influence of the surrounding landscape, rather than on measures of simple fragment area (Laurance 2008). Although large habitat fragments are predicted to support a greater heterogeneity of resources and niches for different species, the effects of fragment area on richness, abundance, or diversity are inconsistent (Debinski and Holt 2000). In terrestrial habitat fragments, the quality of the surrounding landscape and species' use of matrix habitat can strongly influence the abundance and composition of species within fragments (Gascon et al. 1999, Perfecto and Vandermeer 2002, Antongiovanni and Metzger 2005, Kennedy et al. 2010). If the surrounding landscape (the non-habitat "matrix") provides resources that augment or complement the availability of resources in fragmented habitat, populations may be buffered from the negative effects of habitat loss and fragmentation (Dunning et al. 1992, Estades 2001, Fahrig 2001, Ries and Sisk 2004).

The effects of habitat loss on wild and managed pollinator populations are facing increasing attention in landscapes modified for human use (Potts et al. 2010, Roulston and Goodell 2011, Winfree et al. 2011). Anthropogenic landscapes are progressively dominating the earth's surface (Ellis et al. 2010), and urbanization in particular is predicted to have negative effects on biodiversity, ecosystem processes, and ecosystem functioning (McKinney 2002, Grimm et al. 2008). However, habitat modification only negatively affects the abundance and species richness of wild bees when losses are severe, and not when changes are moderate (Winfree et al. 2009). Suburban gardens and parks, in particular, are known to support a high richness and abundance of pollinators (e.g. Tommasi et al. 2004, McFrederick and LeBuhn 2006, Winfree et al. 2007, Matteson and Ascher 2008, Fetridge et al. 2008, Wojcik and McBride 2011). Determining the qualities of natural and man-made landscapes that support pollinator diversity, therefore, is a current and relevant avenue for conservation efforts in habitats fragmented by human development.

Pollinators use both natural and anthropogenic areas for food and/or nesting and may increase in abundance or richness when different components of the landscape provide the resources they require (Eltz et al. 2002, Cane et al. 2006, Kim et al. 2006). Floral resources, in particular, can impact bee and hoverfly richness and abundance (e.g. Westphal et al. 2003, Kleijn and van Langevelde 2006, Hatfield and Lebuhn 2007, Meyer et al. 2009, Williams et al. 2012), reproduction (Williams and Kremen 2007, Zurbuchen et al. 2010) and community composition (Potts et al. 2003). Although floral resources in fragmented habitat sometimes do not have an effect on pollinator richness or abundance (Neame et al. 2013), urban gardens in the surrounding landscape may influence the composition of species we find in fragmented habitats (Wray et al. *in press*, Hinners et al. 2012). In landscapes with high variation in temporal and spatial distribution of resources, species may benefit by tracking the availability of resources in different habitats over time (Williams and Kremen 2007, Mandelik et al. 2012). Determining how and when pollinators use different components of human-modified landscapes, therefore, is critical for managing a high quality matrix that supports populations in habitat fragments.

In addition to floral resources, wild bees are influenced by the distribution of nesting substrates and materials across landscapes (Westrich 1996). Female bees are central-place foragers that focus on travelling to and from a nest site for food. Bees exhibit a diverse array of nesting strategies that reflect differences in location (above- or below-ground), nest construction (e.g. species that require holes, “renters”, vs. species that make their own holes, “excavators”), and required nesting materials (e.g. leaves, plant fibres to line nest; Michener 2000). Location of nests, therefore, is highly dependent on species-specific requirements and availability of different nesting substrates across landscapes. Finding these nests, however, is difficult, and as such the materials required for specific species are often unknown (Roulston and Goodell 2011). Previous research has found that the number of ground-nesting bees species increases with the availability of bare soil, while the abundance of cavity-nesting bees increases with the number of large cavities associated with rocks, trees, and rodent holes (Potts et al. 2005). Some bumble bees, in particular, nest underground in abandoned rodent holes or other cavities, and increase in abundance in forested or semi-natural habitats (Svensson et al. 2000, Kells and Goulson 2003, Jha and Kremen 2013, Wray et al. *in press*). Compost bins, abandoned bird houses, and boundary features (e.g. hedges, fences) in urban environments, however, can also provide nesting opportunities and promote high densities of nesting bumble bees (Osborne et al. 2008). Although difficult, determining how nesting resources differ across natural and anthropogenic landscapes is an important aspect of determining how the quality of the surrounding landscapes influences bee community composition in fragmented habitat.

The oak-savannah ecosystem on Vancouver Island has undergone dramatic habitat loss and fragmentation since the early 1800's, with less than 5% of the habitat currently remaining in an unaltered state (MacDougall et al. 2004). Previous research in this ecosystem has found that area of oak-savannah fragments or the amount of surrounding similar habitat does not influence total pollinator species richness or abundance (Neame et al. 2013). Larger fragments, however, support greater abundances of ground-nesters and higher diversity of cavity-nesters (Neame et al. 2013). Differences in bee community composition in these fragments are further hypothesized to be due to supplementary and/or complementary use of the surrounding landscape (Wray et al. *in press*). Natural nesting resources in coniferous forest are predicted to influence the abundance of large-bodied bumble bee renters and rare wood-nesting bees in forest-associated oak-savannah fragments, while floral resources in urban residential gardens may be supporting small-bodied, late-season generalist bees in urban-associated oak-savannah fragments (Wray et al. *in press*).

In this study, I set out to determine how the quality of the surrounding landscape influences pollinator communities in oak-savannah fragments. In addition, I looked at the uniqueness of pollinator assemblages in the oak-savannah ecosystem, in comparison to urban residential areas independent of any oak-savannah habitat. I investigated if differences in pollinator abundance, richness, diversity, or community composition in oak-savannah fragments were due to use of the matrix habitat for floral or nesting resources. Oak-savannah blooming periods are short, and although early-season species may be sufficiently supported by high availability of natural resources, mid- to late-season species may be more abundant or speciose in urban areas (including urban-associated OS fragments) due to supplementary and/or complementary use of urban habitats with longer flowering phenologies. I also predict that coniferous forest would be important for "renting" species restricted by natural nesting resources (e.g. cavities), while urban areas independent of oak-savannah habitat would be dominated by generalist pollinators with broad foraging and nesting requirements.

To answer these questions, I sampled floral resources, nesting resources and pollinators from five different types of habitat from late April through until August, 2012. I selected four oak-savannah (OS) fragments that were predominantly surrounded by Douglas-fir coniferous forest ("forest-associated OS fragment") and four OS fragments that were embedded in an urban landscape, with much of the area dedicated to residential gardens ("urban-associated OS fragment"). I use the term "urban" to define our study sites for clarity, despite the predominance of low-density urban and sub-urban development in our study region (Victoria Census Metropolitan Area; population 344 615, density 495.0 per square kilometer; Statistics Canada 2012). In addition to sampling the OS fragments, I also selected areas in the adjacent landscape – forest-associated OS fragments were paired with "forest matrix" sites, while urban-associated OS fragments were paired with "urban matrix" sites composed of multiple residential properties from willing landowners. Finally, I sampled urban areas independent of oak-savannah habitat ("independent urban"), to determine if pollinator communities in the oak-savannah ecosystem are unique only to that habitat (Figure 3.1).

Methods

Study system and sites

Our study area falls within the Coastal Douglas-fir biogeoclimatic zone on the south-eastern tip of Vancouver Island. Oak-savannah habitat in this region supports a particularly high diversity of native shrubs, wildflowers, and pollinating insects (Fuchs 2001, Neame et al. 2013). Increases in agricultural and residential development on our study region have resulted in a dramatic reduction in the distribution of oak-savannah (MacDougall et al. 2004), and non-random habitat loss has restricted remnants to rocky outcrops that do not reflect historic environmental conditions (Vellend et al. 2008). Less than five percent of the ecosystem currently remains in its original state, with remnants predominantly surrounded by a gradient of natural Douglas-fir coniferous forest to urban residential neighbourhoods (MacDougall et al. 2004). The understory of Douglas-fir forest is sparsely covered by native shrubs (e.g. *Gaultheria shallon, Mahonia nervosa*) with few forbs present relative to oak-savannah, while urban areas vary widely in plantings of native, edible, ornamental and exotic plant species (Figure 3.2).

I sampled eight oak-savannah (OS) fragments previously designated as predominantly urban- or forest-associated, based on analyses of the percentage of forest cover in a 400-meter radius surrounding the fragment (Wray et al. *in press*). Forest-associated OS fragments (N=4) ranged from 34.28 to 51.48 percent surrounding forest cover, while urban-associated OS fragments (N=4) ranged from 0 to 4.0 percent forest cover. Forest- and urban-associated OS fragments were matched in size, in that if I sampled an urban-associated fragment that was 5-hectares, I also sampled a forest-associated fragment that was approximately 5-hectares. However, plant and pollinator sampling occurred within a smaller area (0.7-ha) that was identical across all sites included in the study. This 0.7-ha size was delimited by the smallest urban area available for use (because of the number of homeowner volunteers; see following paragraphs).

I also sampled plants, pollinators, and nesting resources in the adjacent matrix habitats (urban residential or coniferous forest). Because many small bee species are restricted in foraging range (Greenleaf et al. 2007), and are hypothesized to use urban gardens for food resources when floral resources in the oak-savannah habitat are scarce, fragment/matrix pairs were located approximately 100-meters apart. Accessibility to matrix habitat was restricted in two oak-savannah fragments by cliffs and volunteer participation, and as such 1 fragment/forest pair (Mount Douglas Park/forest) and 1 fragment/urban pair (Uplands Park/gardens) were separated by approximately 200 meters.

To assess the uniqueness of the assemblage of pollinators in the oak-savannah ecosystem, I also selected 4 urban sites independent from any oak-savannah habitat (less than 0.01% in a one kilometer radius). Independent urban sites and urban matrix sites were composed of multiple properties of landowners willing to take part in the study. Due to high variation in lot sizes, the number of lots at the different sites was variable but always amounted to a total of 0.7-hectares in size at each site (i.e. average lot size = 0.07-ha, obtained permission from 10 landowners; average lot size = 0.18-ha, obtained permission from 4 landowners). Lot sizes were calculated from high resolution aerial photographs from the Capitol Regional District Natural Areas Atlas (10-cm resolution, © 2010-2012 Capital Regional District). In total I obtained permission from 62 landowners with a wide range in enthusiasm for gardening and our project, so that I was sampling a relatively unbiased representation of urban habitats in Victoria. Due to the highly integrated nature of oak-savannah and coniferous forest habitat, and the limited amount of remaining coniferous forest in the region, it was not possible to find forest habitat that was independent of oak-savannah habitat.

Floral, nest, and pollinator sampling

I surveyed flowering plant resources five times throughout the blooming season, in April, May, June, July and August. I used 20 circular 10-square-meter quadrats, identifying all flowering plants to species (or genera in independent urban and urban matrix sites where exotics and botanical cultivars were common) and estimating the percent cover of each species found in the quadrat. To reduce bias due to differences among observers, the same person conducted all estimations over all sampling periods. If plants in urban sites were easily distinguishable or known to be native to our study region, I identified them to species rather than lumping into genera. In addition, I did not combine garden and weedy invasive varieties into a single genus (e.g. *Geranium* garden spp., *Geranium molle*, *Geranium robertianum* were kept separate).

In oak-savannah fragments and forest matrix sites, I conducted surveys in four parallel transects equally spaced across the width (70-metres) of the sampling hectare unit (= 0.7-ha), with five random sampling plots per transect. Plots and transects in natural areas (oak-savannah fragments, forest matrix) were randomized with each sampling episode. In independent urban and urban matrix sites, I used a 1-cm grid transparency overlaid on high quality aerial orthophotos (10-cm resolution, © 2010-2012 Capital Regional District) to establish 20 random permanent plots in locations that assessed floral resources in garden beds, lawns, and in areas with potted plants (but not on houses or driveways). I adjusted the number of plots per lot dependent on the lot size and how many lots were included in the site. For example, if an independent urban site consisted of 10 lots at 0.07-hectares each, I established two vegetation sampling plots per lot. Similarly, if I sampled four lots at 0.18-hectares each, I established five sampling plots per lot.

In the same quadrats during one floral sampling episode, I surveyed nesting resources hypothesized to be important to female bees and common to all types of habitat. I identified potential nesting requirements based on previous published studies and reference works (e.g. Potts and Willmer 1997, Michener 2000, Potts et al. 2005) and personal observations. Nesting resource categories included the percentage of quadrat covered by sloped ground, bare soil, moss, hollow stems, woody substrate and number of large cavities. I also used impervious ground cover as an example of a substrate unusable by bees (Table 3.1).

Pollinator surveys were conducted a total of 9 times over the blooming season, from late-April to mid-August. Sampling episodes were conducted for 30-minute periods and were rotated among morning (1000-1200h), early afternoon (1200-1400), and late afternoon (1400-1600h) periods. Two collectors concurrently walked the 0.7-hectare unit, collecting only insects observed actively visiting flowers or searching for nests, and keeping specimens separate by plant species (genera in independent urban and urban matrix sites). Pollinators collected nest-searching were restricted to bumble bees which exhibited the following characteristics: ignoring floral resources, flying in random patterns close to the ground, and occasionally inspecting ground surfaces for nest suitability (as in Svensson and Svensson 2000). Surveys were conducted on days with full or part sun, with temperatures above 14° C and non-windy conditions. Oak-savannah fragments and corresponding matrix sites (urban or forest) were sampled on the same day in the same time period, weather permitting. In three cases when the weather changed abruptly the fragment/matrix pair was sampled on two concurrent days in similar conditions, in the same time period. Each site was equally represented in each time period (i.e. each site was sampled 3 times each in the morning, early afternoon, and late afternoon).

Statistical analysis

Preliminary analyses

Due to the paired sampling design and spatial distribution of forest- and urban-associated OS fragments (Fig. 3.3), I first tested for the presence of spatial autocorrelation between sites in terms of pollinator i) richness, ii) abundance, iii) Simpson's diversity and iv) community composition. For the univariate response variables (e.g. i-iii), I used the 'ape' package in R (R 2.15.3, R Core Team © 2013) to calculate Moran's I index, based on an inverse distance matrix generated from geographic latitude and longitude coordinates (UCLA: Statistical Consulting Group 2013). Moran's I index is similar to Pearson's correlation coefficient, and provides a measure of how similar the values of a variable are at different sites based on their geographic location (Legendre and Legendre 1998). Spatial autocorrelation of community composition was assessed with a Mantel test in R (Legendre and Fortin 1989, R 2.15.3, R Core Team ©2013). I compared a geographic distance matrix (calculated using great circle distances with the 'sp' package; Pebesma and Bivand 2013) with a Bray-Curtis/Sorenson dissimilarity matrix of pollinator abundances (calculated with the 'vegdist' function in the 'vegan' package; Oksanen et al. 2013). Univariate measures were not significantly spatially autocorrelated (all $P>0.09$), but sites that were closer together were more likely to have similar pollinator communities (measure iv; Mantel statistic r: 0.2706, $P=0.022$).

Effect of habitat type and sampling period on pollinator abundance, richness, and diversity

I used mixed models in SAS (SAS/STAT® 9.3; SAS Institute 2011) to compare measures of flowering plant and pollinator responses in the five different habitat types (forest-associated OS fragment, forest matrix, urban-associated OS fragment, urban matrix, independent urban) across the entire season. Pollinator abundance and richness were square root transformed and plant abundance and richness were cube root transformed to meet the assumptions of normality and homogeneity of variances. I analysed models with sampling episode, habitat type, and the interaction between sampling episodes and habitat type as fixed factors and site pair as a random blocking effect. I also included site as a random factor, to control for variation and non-independence between consecutive sampling episodes. Mixed models were analysed with an unbalanced block design, with independent urban sites considered as separate random blocks. Models were analysed with an autoregressive covariance structure.

I used similar mixed models to compare measures of Simpson's inverse index of diversity (1/D) between the different habitat types. Because there were sampling episodes in certain habitat types when I did not collect or record any pollinator or plant specimens, calculations of Simpson's diversity were not possible (1/0 = infinity). Thus, sampling episode could not be included in models. Instead, I calculated Simpson's diversity across all sample episodes and analysed models with habitat type as a fixed factor and site pair as a random blocking effect.

For all models I computed degrees of freedom using the Kenwood-Rogers method and report least square (LS) means and standard errors for all fixed effects.

Flowering plant and pollinator community composition

I used non-metric multi-dimensional scaling (NMS; PC-ORD v. 5.0; McCune and Mefford 2005) to visualize the differences in flowering plant and pollinator community composition between the different habitat types. NMS uses measures of ecological distance to ordinate sites in species' space and allows a graphical representation of differences in community composition between site types (McCune and Grace 2002, Quinn and Keough 2002). Flowering plant singletons were removed to reduce stress in the final dimension, but pollinator singletons were left in because removing them did not have an effect on the final stress (McCune and Grace 2002). For pollinators, I used two different measures of ecological distance to ordinate sites; the Bray-Curtis/Sorenson measure, based on absolute species' abundances at sites, and the relative Sorenson measure which considers the relative abundances of species. With the relative Sorenson measure, sites with different abundances but similar species present will be considered more similar to each other than with the absolute Sorenson measure (McCune and Grace 2002). I used Mantel tests in PC-ORD to determine if flowering plant and pollinator communities were significantly related.

I used indicator species analysis in PC-ORD to determine if any pollinator species were associated with specific habitat types and assess the uniqueness of the assemblage of oak-savannah pollinators. First, I combined sites into 3 groupings reflecting similar resource availability – oak-savannah (includes forest- and urban-associated OS fragments), forest matrix, and urban (includes urban matrix and independent urban sites). To determine if there are any species unique to just one type of habitat, I performed the indicator species analysis again with the five original site classifications. Indicator species analysis is based on the abundance and frequency of species in a particular habitat type – a perfect indicator is one that is always present in high abundances in just one habitat type, and not often found in other types of habitat (Dufrêne and Legendre 1997). Indicator values (IV) are calculated by multiplying A_{ij}, the mean abundance of a species (i) in a habitat type (j) adjusted by the mean abundance of that species in all other habitat types, by B_{ij}, the relative frequency of a species in all sites of a particular habitat type.

$A_{ij} = \text{Nindividuals}_{ij} / \text{Nindividuals}_i$
$B_{ij} = \text{Nsites}_{ij} / \text{Nsites}_j$
Indicator value (IV) = $100 \times (A_{ij} \times B_{ij})$
(from Dufrêne and Legendre 1997)

Where Nindividuals_{ij} is the mean number of species i in habitat type j, Nindividuals_i is the mean abundance of species i in all habitat types, Nsites_{ij} is the number of sites in habitat type j where species i is present, and Nsites_j is the total number of sites in that habitat type. The significance of the highest indicator value (IV_{max}) for a given species across habitat types was determined by Monte Carlo permutation tests (4999 iterations) by randomly re-assigning sample units to different groups and re-calculating maximum indicator values. *P*-values were calculated as the proportion of times IV_{max} from the randomized data is equal to or greater than IV_{max} from the actual data (McCune and Grace 2002).

Influence of nesting resources on bee community composition

I used redundancy analysis to determine if differences in community composition could be attributed to variation in nesting resources between the different habitat types (package ‘vegan’ in R; Oksanen 2013). Redundancy analysis (RDA) is a constrained ordination technique which models multivariate response variables as a function of multiple explanatory variables (Legendre and Legendre 1998). RDA is basically a principal component analysis on the fitted values from multiple linear regressions between response and explanatory variables (Legendre and Legendre 1998). As such, the relative position of sites in ordination space is constrained by the relationships between response and explanatory variables (Quinn and Keough 2002). For this analysis, I considered only central place foragers with specific nesting requirements that may be limited by available resources, therefore excluding flies, wasps, brood parasites and all male bees. I also excluded honey bees (*Apis mellifera*) as their distribution is determined by the managed location of hives, rather than natural nesting materials.

Because redundancy analysis is sensitive to rare species (Zuur et al. 2007), I focused specifically on female bees at the genus level, eliminating a genus if there were less than 30 individuals collected (<1% of total 4067 female bees collected). Female bees of a particular genus generally exhibit similar nesting strategies (Michener 2000), and individual species within genera are expected to respond similarly to different environmental cues. Bumble bees (*Bombus* spp.) were caught in disproportionately high abundances and are known to exhibit a variety of nesting preferences (Hobbs 1966, 1967), and were kept as separate species in the analysis, rather than lumped into genus categories. In addition, I based this analysis on the relative, rather than absolute abundances of bees. Similar to analyses of community composition using relative Sorenson dissimilarity measures, sites will be considered more similar to each other if they have similar species composition regardless of how many bees were caught at that site. Relative abundances were transformed with a logit transformation (Warton and Hui 2011). Because explanatory variables were measured on differing scales (i.e. percent cover of quadrat versus number of large cavities), I standardized variables to a mean of zero and standard deviation of one (Legendre and Legendre 1998). I examined variance inflation factors to address multi-collinearity between independent variables, however found that all variables met the required assumptions (VIF<4; Quinn & Keough, 2002).

I tested the significance of the relationship between relative abundances of female and nesting resource variables with a permutation test (Legendre and Legendre 1998). The pseudo F-statistic of the “true” (unpermuted) distribution is calculated by dividing the sum of squares (SS) of variation explained by the canonical axes by the residual sum of squares (RSS) not explained by the canonical axes, standardized by the number of canonical eigenvalues included in the model. Permutation tests then compare the pseudo F-statistic to a reference distribution of F-statistics, obtained from calculations of SS and RSS involving random permutations of response variables. *P*-values are computed as the proportion of permuted values equal to or larger than the true value of the test statistic. I used a similar approach to test for the significance of each canonical axis and explanatory variable included in the model. For our purposes, I was interested in the correlations between relative species abundances and nesting response variables, as well as the approximate Euclidean distances between sites, and present a distance triplot rather than a correlation triplot (Legendre and Legendre 1998).

Results

Surveys collected a total of 5381 flower-visiting animals from 211 species. Bees were the most speciose and abundant (134 species, 4908 individuals), followed by flies (56 species, 384 individuals), wasps (20 species, 80 individuals) and one species of hummingbird (9 individuals). Family Apidae was the most abundant (3133 individuals), with bumble bees (*Bombus* spp., 2127 individuals) and honey bees (*Apis mellifera*, 763 individuals) making up the majority of collected specimens. Apidae also had the highest number of species (39 species (or morphospecies for *Nomada*)), followed closely by Syrphidae (35 spp., 255 individuals), Halictidae (34 spp., 891 individuals), and Megachilidae (31 spp., 498 individuals).

Effect of habitat type and sampling period on pollinator abundance, richness, and diversity

There was a significant effect of sampling period, habitat type, and the interaction between sampling period and habitat type on flowering plant and pollinator richness and abundance (Table 3.2, Fig. 3.4). Flowering plant abundance in all habitat types except the forest matrix peaked in May (sampling episode 2), sharply declining in natural areas and decreasing slightly in urban matrix and independent urban gardens from June to August (Fig. 3.4a). Flowering plant richness in urban areas was significantly higher at all periods than in natural areas, and remained high towards the end of the sampling period. Plant richness in natural areas declined over time (Fig. 3.4c). Pollinator abundance also peaked at the beginning of May, and despite disparity in floral richness was actually highest in urban- and forest-associated OS fragments at that time, rather than in urban areas (Fig. 3.4b). Pollinator abundance in OS fragments gradually declined, with forest-associated OS fragments having significantly lower abundances than urban matrix or independent urban sites starting in June (Fig. 3.4b). Pollinator abundance in urban-associated OS fragments also declined around the same time, but was not statistically different from urban areas until the last sampling episode in August (Fig 3.4b). Pollinator richness, on the other hand, was approximately equal in all habitat types (except forest matrix) until July, when forest-associated OS fragments had significantly lower species richness than urban matrix or independent urban sites (Fig. 3.4d). Similar to pollinator abundance, species richness in urban-associated OS fragments was not significantly different from urban areas until the last sampling period in August (Fig. 3.4d). Forest matrix consistently supported the lowest abundance and richness of pollinating insects across the entire sampling period (Fig 3.4b, d).

Comparing across the entire season, there was a significant effect of habitat type on flowering plant abundance, richness, and diversity (Table 3.2). Floral abundance, species richness, and diversity were all higher in urban matrix and independent urban sites compared to forest- and urban-associated OS fragments and the forest matrix (Fig. 3.5a, c, e). Although natural areas were not significantly different in terms of floral species richness or diversity, abundance was significantly higher in urban matrix and independent urban sites, and urban-associated OS fragments also had more resources than the forest matrix (Fig. 3.5a).

There was also a significant effect of habitat type on pollinator abundance, richness, and diversity (Table 3.2, Fig. 3.5b, d, f). Pollinator abundance and richness were greater in urban sites than in forest-associated OS fragments and forest matrix, however neither was significantly higher compared to urban-associated OS fragments (Fig. 3.5b, d). In addition, urban-associated OS fragments supported slightly higher abundance and richness of pollinators than forest-associated OS fragments, but these results were only marginally significant (abundance: P=0.08; richness: P=0.06; Fig. 3.5b, d). Species richness and abundance were lowest in forest matrix habitat (Fig. 3.5b, d), which also had lower values of diversity compared to urban-associated OS fragments and urban matrix (Fig. 3.5f).

Flowering plant and pollinator community composition

Flowering plant communities were dramatically different between the different habitat types I sampled; despite differences in the surrounding landscape, urban- and forest-associated OS fragments supported similar floral communities that differed from those in forest matrix, urban matrix, and independent urban sites (Fig. 3.6a). Pollinator communities, however, were less distinctly separated between the different habitat types. Urban-associated OS fragments tended to be more similar to urban matrix and independent urban sites than forest-associated OS fragments (Fig. 3.6b). In terms of both absolute and relative pollinator abundances, I found positive relationships between pollinator and flowering plant communities; sites with similar floral resources were also more likely to have similar pollinator community composition (Mantel tests, Absolute abundance: $r = 0.549$, $P<0.001$; Relative abundance: $r=0.492$, $P<0.001$).

Pollinators unique to the oak-savannah ecosystem tended to include early-flying pollinators (e.g. *Andrena* spp., *Volucella bombylans*), while species with long flight periods, generalist foraging strategies, and late emergence times dominated the composition of urban communities (e.g. *Bombus vosensenskii*, *Halictus* spp., *Megachile* spp., *Merodon equestris*; Table 3.3). Of the oak-savannah pollinators, *Bombus bifarius* was the only species that was a significant indicator of forest-associated OS fragments. Urban-associated OS fragments, on the other hand, supported additional sweat bees and small-bodied stem-nesting species with later emergence periods (e.g. *Agapostemon texana, Ceratina acantha*). Of the urban-associated pollinators, independent urban sites had a variety of introduced and native generalist social species with large foraging ranges and greater flight abilities (e.g. *Apis mellifera, Bombus* spp.), solitary cavity nesters (e.g. *Anthidium manicatum, O. lignaria, Megachile* sp.), and small-bodied generalist sweat bees (e.g. *Halictus tripartitus, Lasioglossum (Dialictus)* spp.). Pollinators unique to urban matrix sites included one species of bumble bee, *B. californicus*, as well as some mid- to late-season bees and one species of wasp (*Colletes kincaidii, Osmia pusilla, Polistes gallica*).

Influence of nesting resources on bee community composition

The redundancy analysis based on the relative abundance of female bees indicate there is a significant relationship between bee community composition and nest resource variables (pseudo $F_{7,12}=3.66$, $P=0.005$, variation explained by nesting resources=68.11%). The first and second axis explain 41.67% and 14.38% of this variation, respectively, and all explanatory variables were significant (Bare soil: $F_{1,12}=5.75$, $P=0.005$; slope: $F_{1,12}=4.41$, $P=0.02$; stems: $F_{1,12}=6.48$, $P=0.005$; impervious cover: $F_{1,12}$=3.53, P=0.015; and wood: $F_{1,12}$=3.03, P=0.025) except for the percent cover of moss ($F_{1,12}$=1.57, P=0.18) and the number of large cavities ($F_{1,12}$=0.96, P=0.43). Sites separate along the first canonical axis in terms of the percent cover of woody substrate, which is more abundant in the forest matrix, as well as in the amount of bare soil and impervious ground cover, which are greater in urban matrix and independent urban sites (Fig. 3.7, Table 3.4). Forest- and urban-associated OS fragments were different from all other habitat types in having a greater proportion of hollow stems, while natural areas were all more sloped in profile than urban areas (Fig. 3.7, Table 3.4).

In the redundancy analysis distance triplot, correlations between species (dashed lines) and nesting resources (arrows) are represented by their relative trajectories (Fig. 3.7; Legendre and Legendre 1998). The relative abundance of *Bombus bifarius* increases significantly with the proportion of sloped ground (R^2 =0.60, P<0.001), mossy ground cover (R^2=0.30, P=0.01), and wood (R^2=0.24, P=0.03). Similarly, *B. flavifrons* appeared to be correlated with the abundance of large cavities (Fig. 3.7), but this variable did not contribute significantly to the RDA model and instead relative abundance of *B. flavifrons* increased with the proportion of woody substrate (R^2=0.19, P=0.05). Despite nesting in the ground, the relative abundances of *Andrena* and *Agapostemon* spp. increased with the proportion of stems (*Andrena*: R^2=0.19, P=0.05; *Agapostemon*: R^2=0.30, P=0.01) which were more abundant in urban- and forest-associated OS fragments (Table 4). *Ceratina* species, although classified as nesting in stems, were only marginally related to the proportion of stems (R^2=0.13, P=0.11).

Despite generally nesting in cavities, the relative abundances of *Anthidium manicatum* and *Megachile* spp. were correlated with the proportion of bare soil (*A. manicatum*: R^2=0.42, P=0.002; *Megachile* R^2= 0.35 , P=0.006), which may represent opportunities to locate cavities within soil beds (Fig. 3.7; Michener 2000). The relative abundance of *B. californicus, Halictus*, and *Osmia* species increased with the percentage of impervious ground cover, and as such may not be restricted by the natural nesting materials they are expected require (*B. californicus*: R^2=0.27 , P=0.02; *Halictus*: R^2=0.48 , P<0.001; *Osmia*: R^2=0.32, P=0.009). *B. vosnesenskii* also appeared to be correlated with the amount of impervious ground cover but this relationship was not statistically significant (R^2=0.13, P=0.12).

Discussion

Effect of habitat type and sampling period on pollinator abundance, richness, and diversity

Differences in matrix quality often influence the composition of species in fragmented habitats (Gascon et al. 1999, Antongiovanni and Metzger 2005, Kennedy et al. 2010), and in our study the urban matrix—with a high density of gardens--had a much greater availability of floral resources for pollinating species than the natural areas. These results are consistent with other studies of plant diversity in urban areas; gardens have been shown to exhibit high levels of diversity that far exceed the number of species in natural areas (Thompson et al. 2003, Hope et al. 2003). Flowering plant abundance, on the other hand, peaked in May and was similar in all kinds of habitat except for the forest matrix. Peak bloom of highly attractive oak-savannah plant species (e.g. *Camassia quamash, C. leichtlinii, Plectritis congesta*) coincided with high abundances and richness of pollinators, which were higher (but not significantly so) in forest- and urban-associated OS fragments than in urban sites. Although floral richness in urban sites was much higher than in natural areas, many ornamental varieties I recorded may not be as attractive to pollinators due to trade-offs between breeding for floral display versus pollen and nectar availability (Comba et al. 1999). It wasn’t until bloom of wildflowers in OS fragments declined that pollinator richness and abundance in urban areas increased relative to richness and abundance in natural areas.

If food is available in the surrounding landscape, population densities in habitat fragments may increase (Estades 2001, Ries and Sisk 2004). After May, flowering plant richness and abundance declined significantly in natural areas and remained high in urban areas. Previous studies that examine resource distribution in natural and anthropogenic areas have found similar results; a pulse of floral resources in natural areas in early spring, followed by a switch to greater resources in farmland or urban areas in summer or late summer (e.g. Williams et al. 2012, Mandelik et al. 2012). Pollinators may benefit from these kinds of spatio-temporal dynamics, and track the pulse of resources from natural to managed landscapes. I found that pollinator abundance and richness in forest-associated OS fragments was significantly lower than independent urban and urban matrix sites in June and July, while abundance and richness did not significantly decline in urban-associated OS fragments (compared to urban sites) until our last sampling episode in August. Previous studies have shown that production of offspring can be affected by increased flight distances to forage rewards (Peterson and Roitberg 2006, Zurbuchen et al. 2010). Because there are few resources available in forest-associated OS fragments and the forest matrix from June onwards, pollinators nesting in these areas may be expending more energy on long-distance foraging than on reproduction, influencing population sizes and potentially restricting late-season species from establishing in these areas.

Pollinator abundance, richness and diversity were not significantly different between urban-associated OS fragments, urban matrix or independent urban sites, but abundance and richness was significantly lower in forest-associated OS fragments and the forest matrix compared to urban sites. In addition, pollinator abundance and richness were marginally lower in forest-associated compared to urban-associated OS fragments. Species richness of wild bees has been shown to decline with increasing distance from natural habitat when there are insufficient floral resources in the surrounding landscape, but not when resources are abundant (Jauker et al. 2009). Similarly, the richness and abundance of bees in fallow strips adjacent to crop fields was enhanced by organic agriculture in the surrounding matrix, which had greater availability of floral resources than conventional agriculture (Holzschuh et al. 2008). Differences between habitat types in our study were not due to differences in within-fragment quality of floral resources, as forest- and urban-associated OS fragments did not differ in terms of species richness or abundance of plant species. Instead, I believe that high richness and abundance of pollinators in urban-associated OS fragments was due to supplementary and complementary habitat use of residential gardens in the urban matrix (Dunning et al. 1992).

It is important to note, however, that diversity in forest-associated OS fragments was not significantly different from urban matrix or independent urban sites, and pollinator abundance and richness was only marginally lower in forest-associated than in urban-associated OS fragments. Despite the forest matrix having comparatively little in terms of floral richness and abundance, forest-associated OS fragments are still capable of supporting comparatively high abundance, richness, and diversity of pollinating insects as those surrounded by a high quality matrix with abundant floral resources. In addition, forest-associated OS fragments had a lower abundance of a late-season invasive plant, hairy cat’s ear (*Hypochaeris radicata*), than urban-associated OS fragments. This plant is highly attractive to many late-season pollinators. Although late-season floral resources available in the urban matrix likely affect the composition of pollinators in urban-associated OS fragments, pollinators may also be influenced by specific plant species associated with different types of natural landscapes.

Flowering plant and pollinator community composition

Determining the qualities of the landscape, as well as traits of the species, that influence community composition in fragmented habitats is an increasingly important tool for conservation of wild pollinators (Winfree et al. 2011). I found distinct differences between habitat types in floral resource composition, whereas pollinator community composition was less well defined. Sites separated along a gradient of urbanization, with urban-associated OS fragments similar to communities in urban matrix and independent urban sites, and forest-associated OS fragments similar to pollinator communities in urban-associated OS fragments and the forest matrix. Bees that were indicators of urban-associated OS fragments (e.g. *Agapostemon texana*, *Ceratina acantha*; Table 3.3) were collected off of late-season floral resources in the urban matrix when resources in oak-savannah fragments and forest matrix were scarce. Furthermore, many pollinator species associated with urban habitats that had long flight periods (e.g. *Bombus californicus*, *B. vosnesenskii*, *Halictus* spp.) or late emergence times (e.g. *Melissodes microstricta*) were also found in higher abundances in urban-associated compared to forest-associated OS fragments. Flowering phenology in natural areas and human-modified gardens thus likely influenced the composition of the pollinator community across the different types of habitat.

In addition to availability of resources, differences in pollinator community composition may be attributed (in part) to species-specific emergence periods, foraging generalization, seasonal activity, and nesting requirements. Oak-savannah fragments were unique reservoirs of early-flying species with short life cycles (~6 weeks, e.g. *Andrena* spp.) and were the only sites where I found floral specialists, although these were in low abundance (e.g. *Andrena astragali*, *Zigadenus* floral specialist; 2 individuals caught; *A. microchlora*, *Lomatium* floral specialist, 5 individuals caught). Specialists are predicted to be more sensitive to the effects of fragmentation (Davies et al. 2000, Tscharntke et al. 2002, Henle et al. 2004), because the matrix habitat usually does not contain the specific resource they require. Some generalist bees, in addition, may be limited by distributions of required resources across the landscape. For example, the only indicator of forest-associated OS fragments, an early-flying bumble bee (*Bombus bifarius*) was predominantly observed searching for nests in the forest matrix and was associated with slope, mossy ground cover, and woody substrate in these sites (Fig. 3.7). This species may be an indicator of forest-associated OS habitats because it relies on early-blooming flowering resources as well as the natural nesting materials associated with forested landscapes.

Although urban matrix and independent urban sites support diverse pollinator communities, many of these species are late-season floral (and maybe nesting) generalists. Introduced syrphid flies, in particular, may be more flexible in nesting and foraging requirements (Jauker et al. 2009) and tended to be associated with both independent urban and urban matrix sites (e.g. *Eristalis arbustorum, Merodon equestris, Syritta pipiens*). Independent urban sites further supported high abundances of extreme generalists with long foraging ranges (e.g. *Apis mellifera*, *Bombus mixtus*), as well as small-bodied generalist sweat bees (e.g. *Lasioglossum (Dialictus)* spp.) and common solitary cavity nesters (e.g. *Osmia* spp.). Sweat bees and cavity nesters are often disproportionately abundant in fragmented areas surrounded by urban development (Cane et al. 2006, Matteson et al. 2008, Wojcik and McBridge 2011, Hinners et al. 2012, Wray et al. *in press*), while other species may rely on resource heterogeneity associated with natural habitats (Neame et al. 2013).

Influence of nesting resources on bee community composition

The distribution of nesting resources among the different habitats had a significant effect on the community composition of female bees. Large cavities and mossy ground cover associated with the forest matrix and oak-savannah fragments were hypothesized to influence the distribution of large-bodied bumble bee renters, while high availability of woody substrate and associated small cavities (e.g. beetle bores) in the forest matrix was believed to be important for some rare species of small-bodied solitary renters. Oak-savannah sites were the only habitat type with a high proportion of stems for stem-nesting species, and natural areas differed from urban sites in the amount of sloped ground, which has shown to influence some ground-nesting bees (Potts and Willmer 1997, Potts et al. 2005). Urban areas, on the other hand, were dominated by a high availability of bare soil for ground-nesting excavators (mostly in urban garden beds), but also had increased amounts of impervious ground cover which was expected to restrict most species from nesting in these areas.

The importance of nesting qualities can be hard to separate from the effects of floral resources (Roulston and Goodell 2011), and the influence of floral resources in the different habitat types may influence pollinator communities more than the natural nesting materials we expect bees to require. Despite the prevalence of impervious ground cover (e.g. pavement) in urban areas, this did not have an adverse effect on some bee genera. In addition, pollinators in urban areas may be using nesting materials that were not measured in our study. For example, I counted the number artificial nest sites in commercially available “bee condos” that were in our urban sites, but didn’t fall within our permanent random sampling quadrats. A total of 512 condo holes in 62 urban properties were available to bees, and are likely supporting the high abundance and richness of mason bees (*Osmia* spp.) I found in urban areas. The introduced wool-carder bee (*Anthidium manicatum*) is probably also using these cavities, in addition to lining its nest with plant fibres from the garden plant lamb’s ears (*Stachys byzantia*; Miller et al. 2002). Similarly, *Megachile* spp. are highly variable in their nesting habits (Michener 2000), and their distribution may be dictated more by the plant species they use to line their nest, rather than the proportion of bare soil I found them to be associated with. Finally, soil hardness, slope aspect, and insolation has been shown to impact some ground-nesting bees (Potts and Willmer 1997, Wuellner 1999), and was not measured in our study but may influence the distribution of some ground-nesting species associated with natural habitats (e.g. *Andrena*, *Agapostemon* spp.).

Although the majority of genera and species did not respond in a predictable way to the nesting proxies I measured, some bumble bee species did respond to natural nesting materials associated with forested landscapes. I found the majority of our nest-searching bumble bees (100 out of total 106 nest-searching individuals) in natural areas, with 71 of these 100 bees found in the forest matrix. Nest-searching *Bombus bifarius* and *B. flavifrons* were predominantly caught in the forest matrix, and the relative abundances of these species were correlated with the amount of sloped ground and mossy ground cover in these sites. Previous work on nest-searching bumble bees found that some species tend to be associated with banks and tussocky vegetation associated with forest boundary habitats (Svensson et al. 2000, Kells and Goulson 2003). Bumble bee abundance in this ecosystem and others increases with the percentage of forest cover in the surrounding landscape, and may be related to natural nesting materials (e.g. slope, mossy ground cover), or may also be due to increased availability of early-blooming floral resources associated with natural landscapes (Jha and Kremen 2013, Wray et al. *in press*).

Not all bumble bee species, however, were dependent on nesting resources found in forested landscapes; some late flying-bumble bees (e.g. *Bombus californicus* and *B. vosnesenskii*), were associated with urban environments (Table 3.3). A citizen-science based study in the UK found that nest densities of bumble bees in urban habitat is greater even than in natural areas (Osborne et al. 2008), and may reflect greater plasticity in some species to utilize nesting materials in urban landscapes (e.g. compost bins, abandoned bird houses). *B. californicus* is an above-ground nester that I only observed nest-searching twice, while *B. vosnesenskii* is hypothesized to out-compete other species for nest sites in San Franciscan urban parks (McFrederick and LeBuhn 2006). The range of *B. vosnesenskii* in south-western British Columbia has been expanding since the 1960’s, and may represent a response to climate change or a filling in of the niche emptied by the decline of the western bumble bee (*Bombus occidentalis*; Fraser et al. 2012). Determining how we can protect sensitive species, in addition to maintaining abundances of generalist urban-adapted bees, will be increasingly important in fragmented habitats surrounded by urban development.

Conclusions

Although the impacts of habitat loss and fragmentation on biodiversity are expected to be negative, there are increasing reports of species persistence in areas that have undergone habitat change (e.g. Mayfield and Daily 2005, Tylianakis et al. 2005, Winfree et al. 2007, Williams and Winfree 2013). Pollinators, in particular, may respond more to local habitat structure (e.g. floral resources) than landscape-scale composition (e.g. availability of natural habitat; Gathmann and Tscharntke 2002, Westphal et al. 2003, Winfree et al. 2011). Our study corroborated this, as independent urban sites supported a high richness, abundance, and diversity of pollinator species despite having a lack of natural oak-savannah habitat nearby. Existing reserves of natural land will never cover more than a small fraction of the world, and the importance of managing a high-quality landscape matrix is increasingly relevant for protecting biodiversity in urban areas (Franklin and Lindenmayer 2009). In the oak-savannah ecosystem on Vancouver Island, BC, late-flowering resources in urban gardens provide vital resources and promote diverse and abundant bee populations when floral resources in natural areas are scarce. I even observed the extremely uncommon western bumble bee (*Bombus occidentalis*) a total of nine times throughout the season; four of these observations were in urban areas during our last floral sampling episode in August. *Bombus occidentalis* has been in decline in North America (Cameron et al. 2011), and the fact that I found a sensitive species in urban gardens, in addition to a high diversity of other species, is encouraging.

Furthermore, I found that matrix landscapes do not necessarily need to be structurally similar to natural habitat in order to support abundant and diverse pollinator populations. Flowering plant communities and nesting resources were highly variable between the habitat types and yet I still found similar levels of diversity in all areas (even the forest matrix). Instead, specific qualities of floral and nesting resources in different habitat types support a wide range of pollinators of different sizes, flight periods, and nesting habits. Our results add to a growing body of literature that indicates a combination of natural and anthropogenic landscapes can promote diverse pollinator assemblages (Holzschuh et al. 2008, 2012, Hagen and Kraemer 2010, Kennedy et al. 2013), and provide a future avenue for conservation of native pollinators in urban areas.

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Tables

Table 3.1. Description of measured nesting resources (adapted from Potts et al. 2005)

Resource	**Definition**
Slope	Ground with 30-60º slope
Bare soil	Ground free of vegetation and litter (e.g. trails, garden beds, sand)
Stems	Hollow stems (e.g. grasses, some shrubs)
Impervious	Impervious ground layer (e.g. rock, pavement, deck)
Moss	Ground covered by moss
Wood	Dead and living woody substrate (e.g. downed trees, Douglas-fir bark)
Large cavities	Number of large cavities greater than 2-cm in diameter (e.g. rodent holes, cavities in rock walls)

Table 3.2. Mixed models describing the effects of habitat type, sampling period, and the interaction between habitat type and sampling period on flowering plant and pollinator richness and abundance. All *P*-values are ≤ 0.0001, except for the effect of habitat type on flowering plant and pollinator diversity (plants: *P*=0.0023; pollinators: *P*=0.02).

	Abundance			**Species Richness**			**Simpson's Diversity**		
	num df	den df	F	num df	den df	F	num df	den df	F
Flowering plants									
Habitat type	4	15	87.44	4	15.2	112.16	4	10.2	8.93
Sampling episode	4	44.3	147.33	4	44.6	74.62	x	x	x
Episode*Type	16	47	10.47	16	47.2	13.28	x	x	x
Pollinators									
Habitat type	4	16.1	33.04	4	10.4	29.7	4	10.7	4.57
Sampling episode	8	92.5	8.46	8	96.9	11.48	x	x	x
Episode*Type	32	94.5	5.29	32	97.7	5.71	x	x	x

Table 3.3. List of pollinator species that are indicators of oak-savannah and urban habitats. Letters in brackets indicate that the species is specifically associated with the one type of habitat type within the grouping (FF = forest-associated OS fragment, UF = urban-associated OS fragment, UM = urban matrix, IU = independent urban sites, from indicator species analysis in PC-ORD). IV_{max} is the maximum indicator value for that species across all habitat types, and _P_-values were obtained from permutations. *Denotes introduced species. I excluded species if less than 5 were caught, as the association may be due to rarity rather than habitat preferences (as such there were no significant indicators of forest matrix habitat).

Oak-savannah				**Urban**			
Pollinator species	IV_{max}	Simulated mean IV_{max} (±SD)	_P_	Pollinator species	IV_{max}	Simulated mean IV_{max} (±SD)	_P_
Agapostemon texanus (UF)	66.0	32.0 (13.16)	0.03	_Andrena subtilis_ (IU)	66.7	28 (10.26)	0.004
Andrena angustitarsata	59.7	33.4 (12.19)	0.04	_Anthidium manicatum_* (IU)	55.1	28.7 (10.1)	0.03
Andrena nigrocaerulea	73.9	36.8 (9.57)	0.0014	_Apis mellifera_* (IU)	43.4	30.7 (5.96)	0.02
Andrena salicifloris	74.5	42.6 (10.6)	0.0076	_Bombus californicus_ (UM)	56.9	31.7 (8.66)	0.01
Bombus bifarius (FF)	38.0	28.2 (3.37)	0.01	_Bombus melanopygus_ (IU)	38.5	29.7 (4.0)	0.03
Ceratina acantha (UF)	50.4	32.4 (8.23)	0.04	_Bombus mixtus_ (IU)	38.8	30.4 (4.39)	0.05
Empididae sp. (UF)	60.0	26.7 (11.33)	0.01	_Bombus vosnesenskii_	64.8	14.7 (7.97)	0.0072
Lasioglossum (Dialictus) incompletum	58.8	26.9 (11.95)	0.027	_Colletes kincaidii_ (UM)	54.2	30.9 (12.28)	0.0426
Lasioglossum (Lasioglossum) olympiae	70.0	45.0 (11.79)	0.039	_Eristalis arbustorum_*	50.0	22.3 (11.42)	0.05
Lasioglossum (Evylaeus) sp. 4 (UF)	53.8	29.9 (9.13)	0.03	_Halictus confusus_	71.9	33.5 (11.25)	0.0078
Phorocerus sp. (UF)	77.8	25.4 (11.28)	0.006	_Halictus rubicundus_	68.8	36.5 (9.35)	0.0024
Volucella bombylans	83.5	32.4 (11.7)	0.0012	_Halictus tripartitus_ (IU)	66.2	24.2 (14.08)	0.036
				Lasioglossum (Dialictus) cressonii	54.3	29.4 (11.22)	0.04
				Lasioglossum (Dialictus) laevissimum (IU)	68.9	27.0 (12.38)	0.0072
				Lasioglossum (Dialictus) nevadense	65.0	27 (10.6)	0.009
				Lasioglossum (Dialictus) pacatum (IU)	73.2	28.9 (14.65)	0.04
				Megachile frigida (IU)	62.5	23.0 (12.58)	0.03
				Megahile melanophaea (IU)	50.0	28.5 (9.88)	0.05
				Megachile perihirta	58.3	29.6 (11.39)	0.02
				_Megachile rotundata_*	62.5	24.5 (11.57)	0.02
				_Merodon equestris_*	82.1	38.2 (9.13)	0.0002
				Osmia caerulescens (IU)	75.0	21.0 (13.76)	0.02
				Osmia lignaria (IU)	46.8	30.1 (8.35)	0.05
				Osmia pusila (UM)	47.4	28.4 (8.02)	0.05
				Platycheirus obscurus (UM)	75.0	23.6 (12.61)	0.02
				Polistes gallica (UM)	64.7	25.9 (11.77)	0.01
				Syritta pipiens (IU)*	71.4	26.4 (11.32)	0.0072

Table 3.4. Means (± SE) of nesting resources in different habitat types

Nesting resource	**Forest-associated OS fragment**	**Forest matrix**	**Urban-associated OS fragment**	**Urban matrix**	**Independent urban**
Slope	47.75 ± 4.58	42.31 ± 8.64	30.69 ± 6.61	16.94 ± 6.00	9.69 ± 3.25
Bare soil	4.65 ± 1.64	5.88 ± 1.27	3.40 ± 1.16	13.09 ± 1.88	12.65 ± 2.57
Stems	4.29 ± 1.13	1.74 ± 1.30	8.44 ± 0.52	1.01 ± 0.32	0.64 ± 0.13
Impervious	11.24 ± 6.64	1.69 ± 0.72	13.24 ± 3.40	21.15 ± 7.55	19.22 ± 3.28
Moss	19.33 ± 5.51	28.35 ± 7.56	21.88 ± 4.39	0.56 ± 0.33	0.30 ± 0.18
Wood	3.14 ± 1.23	14.23 ± 2.62	1.03 ± 0.28	0.75 ± 0.23	0.59 ± 0.32
Large cavities	0.39 ± 0.21	1.11 ± 0.42	0.04 ± 0.02	0.96 ± 0.36	0.06 ± 0.04

Table 3.5. Description of nest location and construction characteristics for different genera (species for *Bombus*) included in redundancy analysis. Information on nesting biology was obtained from “The Bees of the World” (Michener, 2000) unless otherwise indicated. *Denotes introduced species.

Genus/Species	**Family**	**Nest location and construction**
Andrena	Andrenidae	Below-ground excavator
Agapostemon	Halictidae	Below-ground excavator
*Anthidium manicatum**	Megachilidae	Above- or below-ground renter; also can excavate cavities in loose soil; uses hairy plants to line nest
Bombus bifarius	Apidae	Below-ground renter (Hobbs 1967)
Bombus californicus	Apidae	Surface or above-ground renter (Hobbs 1966)
Bombus flavifrons	Apidae	Below-ground renter (Hobbs 1967)
Bombus melanopygus	Apidae	Above or below-ground renter (Hobbs 1967; Thorp et al. 1983)
Bombus mixtus	Apidae	Surface or above-ground renter (Hobbs 1967)
Bombus vosnesenskii	Apidae	Below-ground renter (McFrederick and LeBuhn 2006)
Ceratina	Apidae	Above-ground excavator; nests in hollow pithy stems
Halictus	Halictidae	Below-ground excavator
Lasioglossum	Halictidae	Below-ground excavator
Megachile	Megachilidae	Above- or below-ground renter or excavator; uses pieces of leaves to line nest
Osmia	Megachilidae	Above-ground renter; uses mud to separate brood cells

Figures

Figure 3.1. Aerial and landscape photos depicting five different habitat types included in our study: A – forest-associated oak-savannah fragment (FF), B – forest matrix (FM), C – urban-associated oak-savannah fragment (UF), D – urban matrix (UM), E – independent urban (IU)

Figure 3.2. Photographs depicting typical habitat and floral resources available in a) urban- and forest-associated oak-savannah fragments, b) forest matrix, and c) urban matrix and independent urban sites

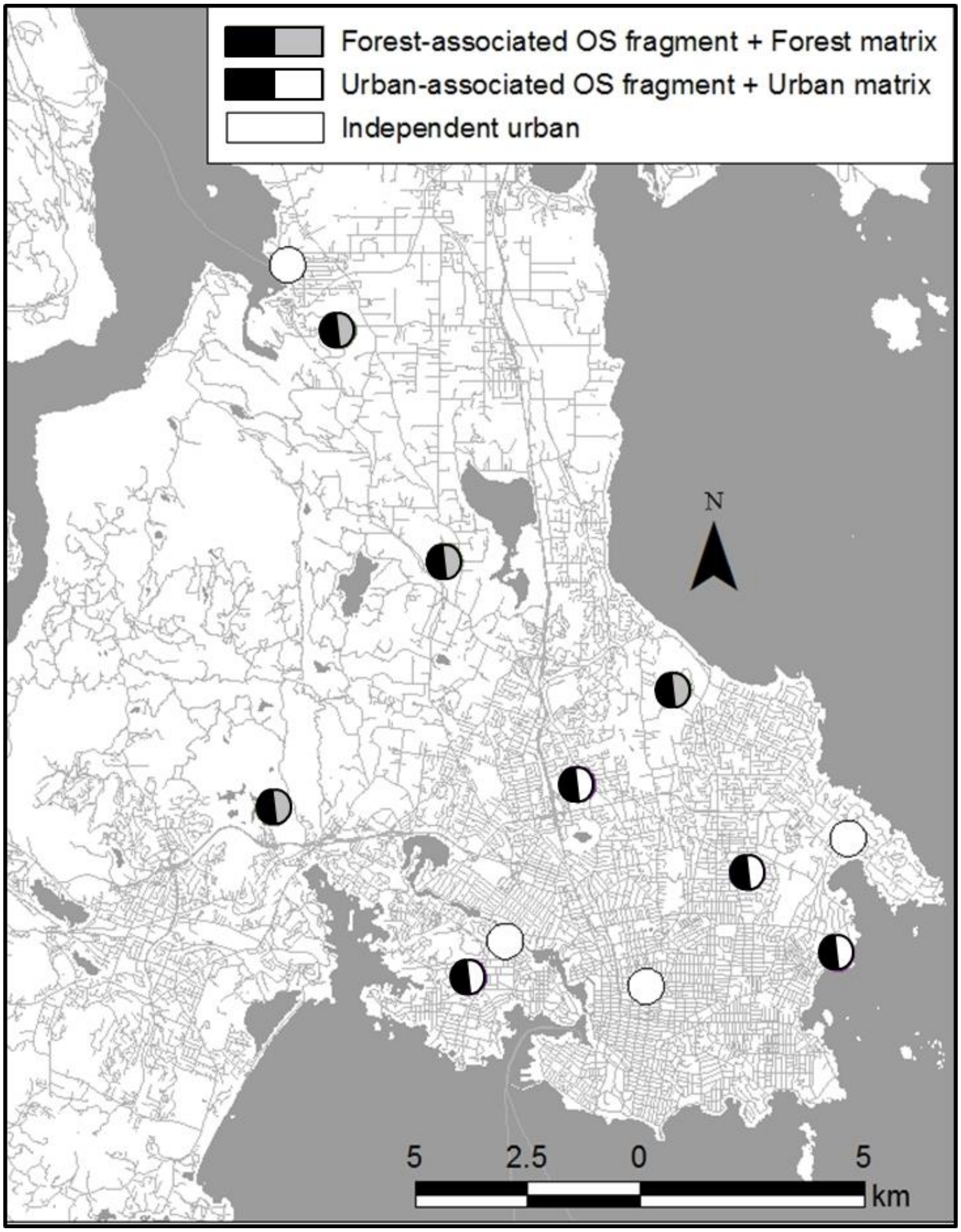

Figure 3.3. Map of study sites on the Saanich Peninsula, British Columbia, Canada. Sites are represented by 400-meter radii surrounding sampling location. Forest-associated OS fragments and corresponding forest matrix are coded in black/grey (respectively), urban-associated OS fragments and urban matrix in black/white (respectively), and independent urban sites are in white. Similar habitat types are represented by like colors, grey lines indicate road density

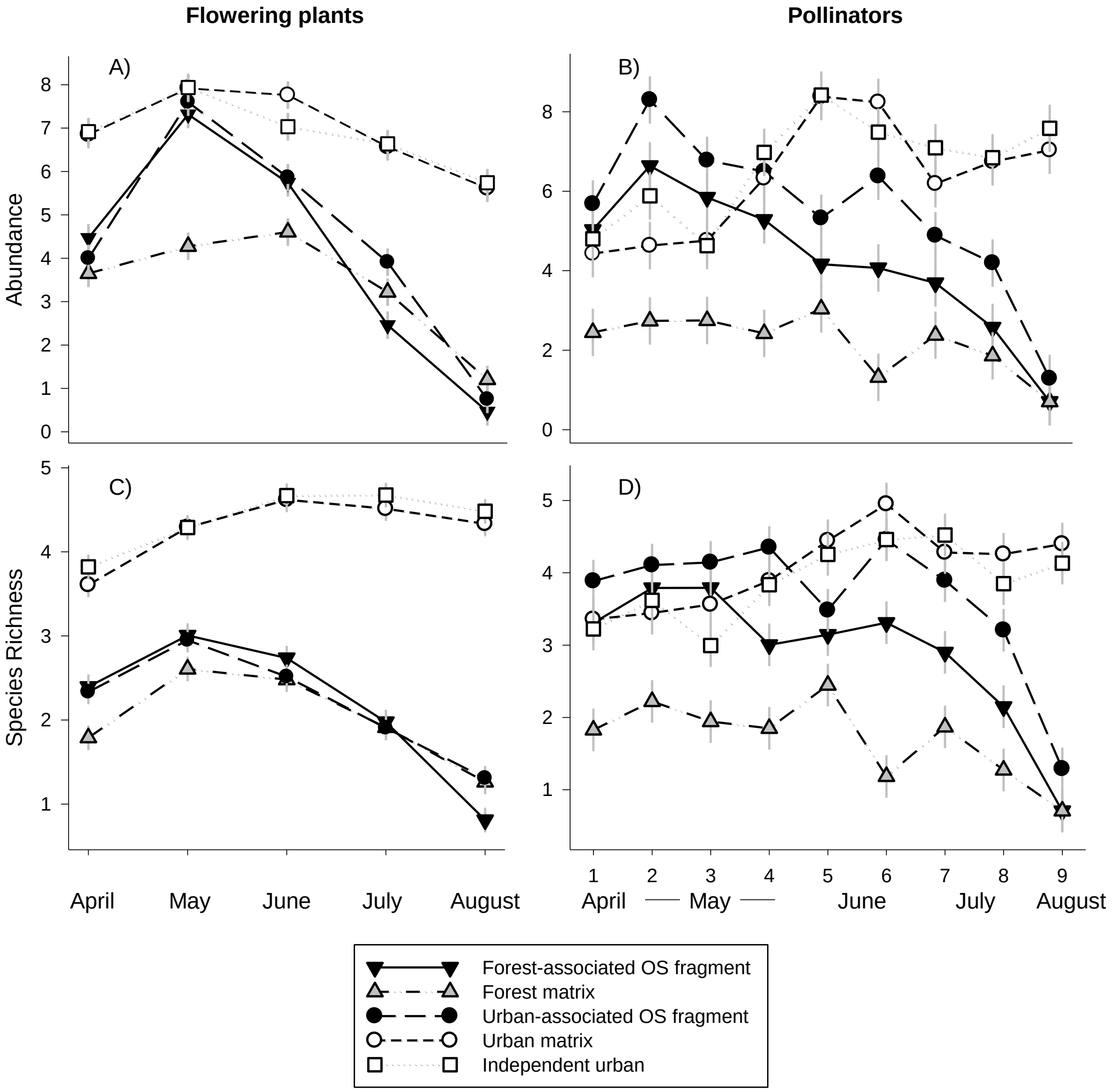

Figure 3.4. Effects of habitat type and sampling period on flowering plant (A, C; cube-root transformed) and pollinator (B, D; square-root transformed) abundance and richness. Bars indicate ± SE (in grey)

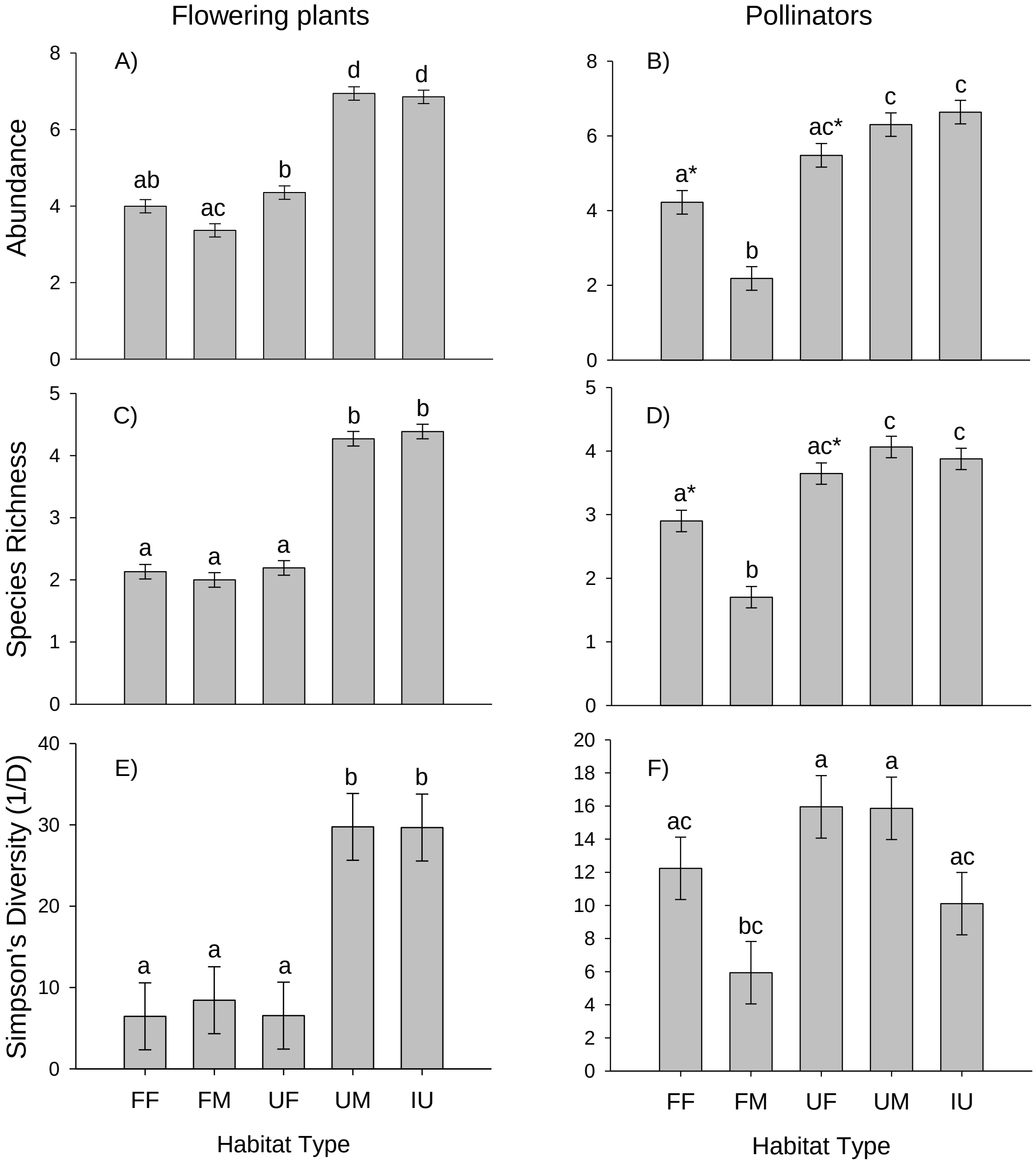

Figure 3.5. Effects of habitat type on abundance, richness, and diversity of flowering plants (A, C, E, respectively; cube-root transformed) and pollinators (B, D, F, respectively; square-root transformed) over the entire blooming season (FF = forest-associated OS fragment, FM = forest matrix, UF = urban-associated OS fragment, UM = Urban matrix, IU = independent urban). Significant differences between least square means are indicated by unique letter combinations. Bars indicate ± SE. *Differences between pollinator abundance and richness in forest- and urban-associated OS fragments approach significance (abundance: *P*=0.08; richness: *P*=0.06)

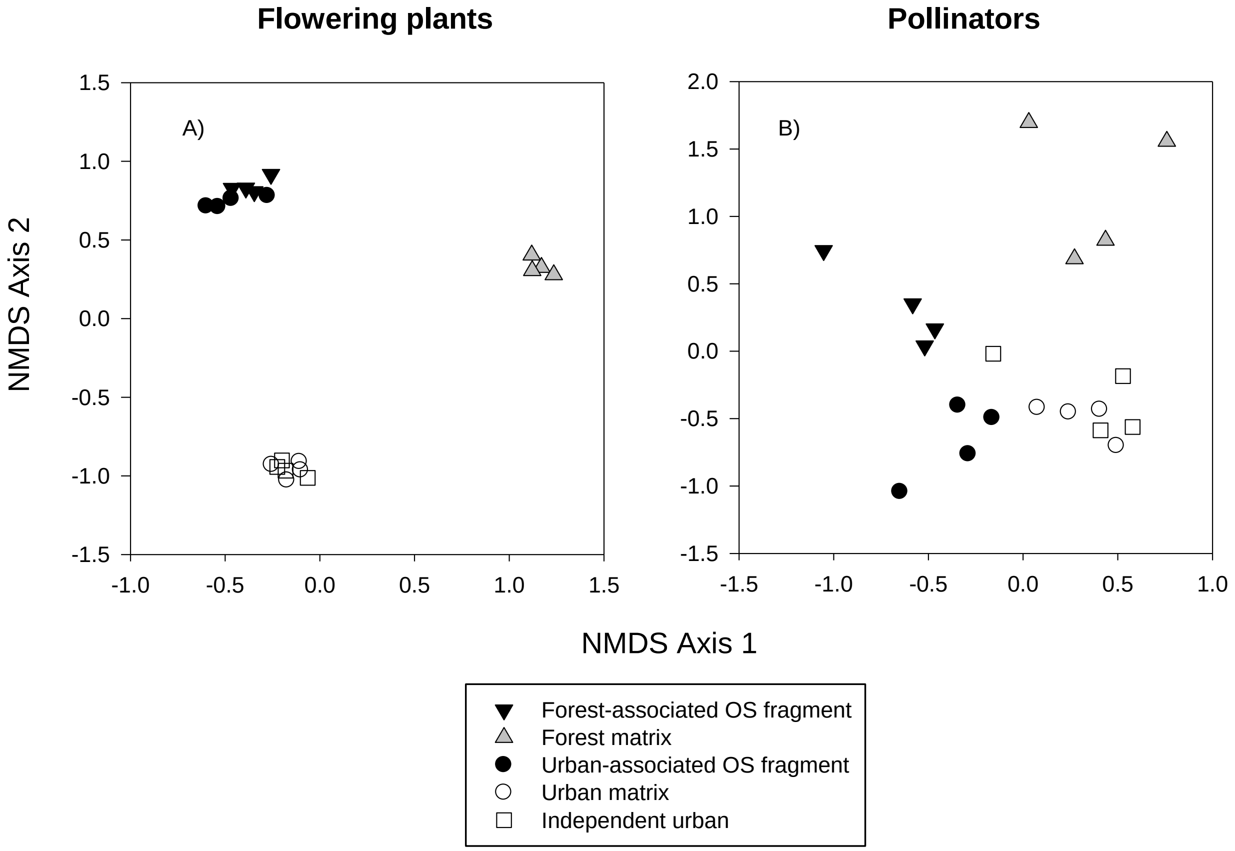

Figure 3.6. NMDS plot showing similarities in A) flowering plant (absolute Sorenson measure, Final stress=5.62) and B) pollinator community composition (relative Sorenson measure, Final stress=8.07) between different habitat types

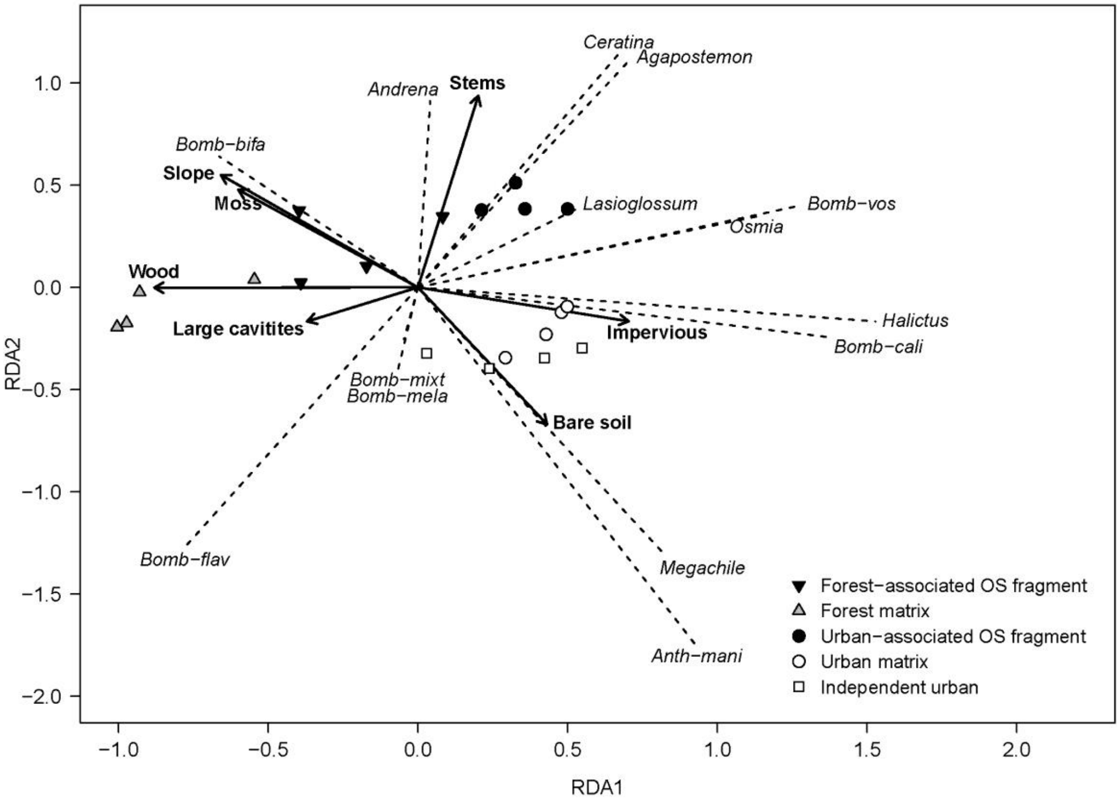

Figure 3.7. Redundancy analysis distance triplot showing correlations between relative female bee abundance (genera and *Bombus* spp.) and nesting resource variables. Angles between species and nesting resource variables represent correlations between them. Explanatory variables are depicted by bold black arrows (as defined in Table 3.1), while dashed lines represent genera/species. Abbreviations for species are: *Anth-mani = Anthidium manicatum*, *Bomb-bifa = Bombus bifarius, Bomb-cali = B. californicus, Bomb-flav = B. flavifrons*, and *Bomb-vos = B. vosnesenskii*. Information on nest location and construction type for different genera/species is presented in Table 3.5.

Chapter 4.

Conclusions

Considering the role of the surrounding landscape matrix for determining species' distributions in habitat fragments is of increasing relevance for conservation biology. Agricultural and anthropogenic settlements now cover approximately 39% of terrestrial surfaces, and the switch from rural to urban living is increasing (Ellis et al. 2010, United Nations 2007). Pollinators may be negatively or positively affected by the process of urbanization, but responses are highly dependent on their ability to use different components of fragmented landscapes (e.g. dependent on species-specific traits). In this thesis, I investigated how the surrounding landscape and species-specific traits (nesting guild, body size, foraging specialization) influenced bee community composition in oak-savannah (OS) fragments (Chapter 2), and determined whether differences in pollinator composition could be due to differential use or quality of floral or nesting resources in the matrix habitat (Chapter 3).

Pollinators, like any organism, require food (pollen, nectar) and a safe nest for sleeping and rearing offspring. Responses to the availability of food and nest sites across the landscape, however, are highly dependent on life-history strategies. For example, large-bodied species require more resources to sustain biological processes, species that fly for long periods need blooming phenology to span the length of their flight period, and those with small foraging ranges require high local availability of resources within close proximity to their nest sites. Although some pollinators have fixed nest sites (e.g. most female bees), and focus foraging to and from the nest, other pollinators (e.g. flies, male bees) do not have a fixed nest sites, and this flexibility may lead to different responses to the surrounding landscape (Kremen et al. 2007). Female bees, especially, differ among species in where they put their nest, how they construct it, and the materials they use to protect brood cells. Pollinator populations, therefore, may be highly influenced by timing in availability of floral resources and distribution of nesting substrates and materials across the landscape.

Although the effects of habitat loss are predicted to be negative, if resources are available in anthropogenic areas, habitat change may support certain levels of biodiversity (e.g. Daily et al. 2001, Fernandez-Juricic 2000, Winfree et al. 2007). In this thesis, I found that solitary cavity nesters and mid to late season generalists were associated with oak-savannah fragments in urban areas (Ch. 2). Late season generalists are likely responding to increased availability of floral resources in the urban matrix; many of these species have modest foraging ranges (e.g. <200-meters), and may not be as abundant in forest-associated OS fragments because the forest matrix does not have a high abundance or richness of attractive flowering plants. Furthermore, although nesting resources for cavity-nesting species were abundant in the forest matrix, the lack of floral resources appears to limit populations more than the nest sites we expect them to require (Ch. 3). Cavity-nesters that emerge late in the season (e.g. *Anthidium manicatum*, *Megachile* spp., *Osmia coloradensis*), especially, likely rely on garden plants in urban areas when native resources in natural areas are scarce. Furthermore, we found a high availability of nest cavities in artificial nests (“bee condos”) in urban sites, in addition to plant materials that some species may use for protecting brood cells (e.g. *A. manicatum* uses hairs from the garden plant lamb’s ears [*Stachys bizantia*] to line nests; Ch. 3). Although previous work in this ecosystem found that the diversity of cavity-nesters increases with increasing fragment area (Neame et al. 2013), not all species necessarily rely on the natural nesting or floral heterogeneity of natural landscapes.

Even though abundance and richness of flowering plants in urban sites was high, I found that oak-savannah areas were unique reservoirs of early-flying species. This pattern could be attributed to a variety of reasons, including flight phenology, foraging specialisation, or disruption of nest sites. For example, some mining bee and syrphid fly foraging periods have a direct overlap with peak bloom in oak-savannah fragments. Because they are not foraging past the bloom of resources in oak-savannah, they may not be found in urban areas because they have already finished provisioning offspring or foraging for the season. Our data also indicate that some species of mining bees (e.g. *Andrena auricoma*, *A. angustitarsata*) were predominantly collected off plants in the carrot family in oak-savannah fragments, and may represent increased floral specialisation in this ecosystem that has not yet been documented. Determining levels of floral specialisation would require additional examination of pollen loads that is beyond the scope of this study, but may be of interest for future conservation efforts of specialist species. Finally, residential development may have extirpated some species from urban areas (e.g. *Andrena nigrocaerulea*, *Volucella bombylans*) and because foraging phenology overlaps with peak bloom of resources in oak-savannah, they are unlikely to disperse to new urban environments.

Sampling over a longer time frame, in addition to sampling the surrounding landscape, gave insight into broader patterns of potential factors limiting pollinator populations in this fragmented ecosystem. In Chapter 2, overall body size of bees increased with increasing abundance of early-flowering native resources, bumble bees were more abundant in forest-associated OS sites, and bumble bee abundance increased with increasing proportion of forest cover in the surrounding landscape. I hypothesized that bumble bees were responding to increased nesting heterogeneity associated with forested landscapes; however, in Chapter 3 I found that only two species of early-flying bumble bees (*Bombus bifarus, B. flavifrons*) were associated with moss, slope, and woody substrate in the forest matrix and *B. bifarius* was the only significant indicator of forest-associated OS fragments. Other bumble bee species were indicators of independent urban (e.g. *B. mixtus*) or urban matrix sites (*B. californicus*). The reasons for the discrepancy between the two chapters could be due to longer sampling periods in the Chapter 3 data, and sampling the matrix habitat – bumble bee colonies with long foraging periods, especially, rely on bloom phenology that lasts from April to October. Decreased abundance of bumble bees in urban-associated OS sites in Chapter 2 may have been due to export to the surrounding urban landscape; floral resources in urban residential gardens may be drawing pollinators away from less abundant resources in urban-associated OS fragments. Such dynamics could have important implications for plant reproduction in oak-savannah fragments in urban areas, and may provide an interesting and relevant avenue of research for future conservation efforts.

Caveats and future directions

This thesis provides some encouraging results for biological persistence in urban environments, but there are some important caveats to consider. First, using species richness as an indicator of biodiversity can ignore specialist responses and may mask homogenization of biological communities (Filippi-Codaccioni et al. 2010). Many of the pollinator species associated with urban areas were generalists (and in some cases introduced), and overall I caught a very low abundance of floral specialists. Although some broadly oligolectic species were more abundant in urban habitats (Ch. 2), narrowly oligolectic species were found only in oak-savannah habitats. In addition, our data indicate that there may be more than 2 species of narrowly oligolectic mining bees associated with oak-savannah habitat, but would require additional examination of pollen loads that is beyond the scope of this study. Conservation of specialists, in addition to a broad range of generalists, will depend on maintaining diverse resources in both natural and anthropogenic habitats.

Second, our sampling in urban habitats was dependent on homeowner participation, and may represent some bias in availability of floral and nesting resources. In many urban sites, at least one homeowner was an avid gardener and volunteered for the project without hesitation. I attempted to alleviate these issues by including properties in a similar neighbourhood regardless of interest in gardening and dividing pollinator sampling evenly time-wise between properties. However, all urban habitats represented a similar demographic – suburban development with flowering plant and potential nesting resources available in lawns, potted plants, and garden beds. I did not sample any extremely urban habitats, where buildings and concrete dominate the landscape. Although most bees were not affected by local scale values of impervious ground cover in urban habitats (Ch. 3), previous research has shown that impervious cover associated with urban development on a landscape scale can have negative effects on bumble bees abundance and genetic diversity (Jha and Kremen 2013a, b). Pollinator populations in more developed urban areas may be influenced on a different level (e.g. genetic) and by a larger scale than examined in this thesis, with potential implications for species' persistence in extreme urban habitats.

There are many avenues of public outreach and future research opportunities for pollinator conservation in this study system. Oak-savannah sites are becoming increasingly dominated by introduced grasses and flowering herbs (Fuchs 2001, MacDougall et al. 2004). Scotch broom (*Cytisus scoparius*), in particular, is a large woody flowering shrub that over-shadows native flowering herbs (J. Wray, personal observation). Although removal of invasive species is ideal for ecosystem integrity, removal without subsequent replacement of native flowering plants may have negative effects on pollinator populations. For example, mid- to late-season pollinators seem to rely heavily on hairy cat's ear (*Hypochaeris radicata*), and before removal restoration managers should consider replacement with native flowering plants (e.g. *Grindelia integrifolia, Holodiscus discolor*). Previous research has shown that invasive species in this ecosystem are becoming highly integrated into pollination networks, but the effects of invasive species on native flowering plants' reproduction are unclear (Gielens 2012).

Finally, pollinators in urban-associated OS fragments are being supported by floral resources in the urban matrix, but the export of pollinating species to urban areas may have negative consequences for wildflower reproduction in oak-savannah. Flowering native species that bloom towards the end of peak bloom, in particular, may suffer from competition with floral resources in urban gardens. In addition, pollination of wildflowers may be influenced by high pollen loads of non-native residential garden flowering plants. Extending bloom periods in urban areas with non-native, non-invasive plants, however, seems to support a high richness, abundance, and diversity of pollinator species, including a species of conservation concern believed to be in decline across North America (*Bombus occidentalis*; Cameron et al. 2011). Continued conservation and restoration of natural areas (e.g. oak-savannah, coniferous forest), in addition to encouraging the public to plant non-invasive species with wide ranges in bloom phenology, may serve to promote temporal and spatial diversity of pollinators across the landscape.

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