TITLE: The conservation value of urban green space habitats for Australian native bee communities

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ABSTRACT

Networks of urban green space can provide critical resources for wild bees, however it is unclear which attributes of green spaces provide these resources, or how their management can be improved to benefit a diversity of bee species. We examined bee communities in three dominant urban green space habitats: 1) golf courses, 2) public parks and 3) front gardens and streetscapes in residential neighbourhoods in Melbourne, Australia and assessed which local and landscape attributes influenced bee communities. There was a greater abundance and richness of bee species in public parks compared to golf courses and residential neighbourhoods, where the latter habitat was dominated by European Honeybees (*Apis mellifera)*. The occurrence of *A. mellifera* was positively associated with increases in flowering and native plants. Ground-nesting *Homalictus* species occurred more frequently in older golf courses and public parks surrounded by low impervious surface cover, and with a low diversity of flowering plants. Cavity nesting, floral specialists within the Colletidae family occurred more often in green space habitats with greater native vegetation, and occurred infrequently in residential neighbourhoods. The lack of appropriate nesting habitat and dominance of exotic flowering plants in residential neighbourhoods appeared to positively impact upon the generalist *A. mellifera*, but negatively affected cavity and ground nesting floral specialist bee species (e.g. Halictidae and Colletidae). Our results highlight the need to include urban areas in pollinator conservation initiatives, as providing resources critical to diverse bee communities can assist in maintaining these key pollinators in urban landscapes.

Keywords: Bees; pollinators; urban ecology; urban landscapes

1. INTRODUCTION

Wild and managed bees are the most economically important pollinators in natural and managed landscapes (Garibaldi et al. 2013; Klein et al. 2007), contributing to the pollination of up to 87% of the world's flowering plants (Ollerton et al. 2011). Consequently, reports of bee declines due to increasing land use change, spread of parasites and pathogens, increased use of pesticides, and climate change are of concern (Potts et al. 2010). Much of our understanding of the impacts of land use change and habitat loss on bee communities has come from studies in forested and agricultural environments (Winfree et al. 2009), whereas the impacts of urbanisation are less well understood. Because the extent of urbanised areas is increasing rapidly (Seto et al. 2013), management of urban bee assemblages will become increasingly important as they play a vital role in the persistence of wild and managed plants in urban areas (Cane et al. 2006; Williams and Winfree 2013). Many native plant species have gone locally extinct in cities worldwide (Hahs et al. 2009) and altered biotic interactions are one of the proposed drivers of these extinctions (Hahs et al. 2009; Williams et al. 2009). This was highlighted by Pauw et al (2007; 2011), who documented the parallel declines of insect pollinators and associated insect pollinated plants in urban conservation reserves in South Africa. Taken together these studies highlight the importance of understanding the persistence of insect pollinators in cities and the potential consequences of pollinator loss on other components of the urban ecosystem.

Most studies of bees in urban landscapes have focussed on bee communities within discrete land uses such as home gardens or remnant habitats (Cane 2005; Hinners et al. 2012; Matteson and Langellotto 2010; Matteson et al. 2008; Matteson et al. 2012; McIntyre and Hostetler 2001; Pardee and Philpott 2014). They suggest that traits, including flight ability, floral specialisation and nest location shape urban bee communities (Cane et al. 2006; Hinners et al. 2012; Pardee and Philpott 2014). However, there is little consensus regarding how urban bee communities are shaped by habitat attributes, or what management actions could promote urban bee diversity. Some authors report that urban intensity has a negative impact upon bee species richness and abundance (Bates et al. 2011; Fortel et al. 2014), whereas Matteson (2012) found no direct influence of urban development intensity on bee and other insect pollinator communities. Many types of urban habitats appear to support abundant and diverse bee communities, especially residential gardens (Banaszak-Cibicka and Żmihorski 2012; Fetridge et al. 2008; Matteson et al. 2008). However, the value of residential gardens and other recreational green spaces (e.g. parks and golf courses) for bees is likely to be dependent upon the quality of foraging and nesting habitat (Cane, 2005). While some studies have found that increases in the cover of green spaces such as golf courses and parks are positively associated with bee abundance (Pardee and Philpott 2014), others show a negative relationship (Tonietto et al. 2011), most likely due to differences in floral quality across different green space types (Matteson et al. 2012) and the floral specialisation of certain bee genera (Cane et al. 2006; McIntyre and Hostetler 2001).

A common strategy used to conserve bees in agricultural landscapes is the preservation of networks of remnant or 'wild' habitat (Ricketts et al. 2008; Steffan-Dewenter et al. 2002). However, in most urban landscapes, few patches of remnant habitat remain, and they are often small and fragmented. As an alternative, networks of urban green spaces could be managed to provide bee habitat in otherwise resource-poor environments. These networks may include natural, planted and managed vegetation in public and private spaces such as residential gardens and recreation fields (Tzoulas et al. 2007).

There is currently a lack of consensus about which attributes of green spaces support bee communities, or whether patterns observed to date are consistent in different parts of the world. To assess the potential contribution of networks of green spaces to urban bee conservation efforts, we examined 1) bee community composition in a range of urban green space habitats and 2) how local and landscape variables influenced bees with differing floral and nesting requirements, in Melbourne, Australia.

2. MATERIALS AND METHODS

2.1 Study Area and Experimental Design

Melbourne is Australia's second most populated city with approximately 4 million human inhabitants. Melbourne spans several bioregions, so to minimise soil type, rainfall and vegetation variation we restricted the study to the south-eastern suburbs within the Gippsland Plain bioregion. This area is characterised by sandy soils, dominated by grassy woodland and heathland vegetation communities. Urbanisation began in the early 1900's, but this region continues to experience rapid urban expansion as 85,000 new houses are to be built between 2005 and 2030 (Victorian Department of Sustainability and Environment 2005). Suburbs built in the early 1900's, closer to Melbourne's city centre, contain more trees and are characterised by larger residential gardens (Hall 2010) than those in the outer suburbs. In recent decades, urban development styles have changed to smaller single detached dwelling residential blocks with larger building footprints, and much less garden area (Hall 2010). Hence, the arrangement and extent of urban green spaces vary considerably between suburbs.

We sampled 130 20 m x 30 m (600 m^2) plots across 39 green space sites located in 13 suburbs of different development age (1890s to 2000s), which varied in the cover of woody vegetation and impervious surfaces (Fig 1). The decade each suburb was established was determined by examining historical aerial imagery, and consulting municipal land release and construction records. We sampled bees in three dominant green space habitats: 1) golf courses (13 golf courses: 52 plots), 2) public parks (13 public parks: 26 plots) and 3) residential neighbourhoods (13 neighbourhoods: 52 plots comprised of front gardens and streetscapes). We did not sample remnant or agricultural habitats as these land covers are not dominant in the study area, and remnant habitat cannot be re-instated in urban landscapes. In addition, the diversity of vegetation communities present in different remnants made it difficult to establish a consistent reference bee community. Instead, we sampled the dominant urban green space habitats in our study area, as these have significant opportunities for habitat improvement through changes to vegetation management. Within each suburb, the selected suite of three green space habitats (residential neighbourhoods, public park and golf course) were on average greater than one km apart.

Within golf courses and public parks, we established 78 plots randomly (52 and 26 plots respectively) within the 'out of play', wooded areas. In residential neighbourhoods, we established the remaining 52 plots by randomly selecting four streets within each residential neighbourhood, and mailing invitations to households on those streets to take part in the study. Plots were usually greater than 100 m apart within each green space (residential neighbourhood, public park and golf course). To adequately represent residential neighbourhoods these plots consisted of the front garden, the pavement and road verge (if present) out to a midway point of the road directly in front of the property. The width and depth of each front garden primarily dictated the size of each plot in the residential neighbourhoods as we could only sample properties for which we had permission.

2.2 Bee Sampling

Within each plot we used two standard methods to sample the bee species present, both of which have been recognised for their ability to representatively sample bee species across varied habitats (Westphal et al. 2008). We placed six coloured pan traps (two yellow, two blue and two white; 15 cm diameter) randomly on the ground throughout each plot for a 24 hr period, leading to the deployment of 1560 coloured pan traps throughout the study. Pan traps were 1/3 filled with water containing a few drops of detergent to break the surface tension and cause trapped insects to sink to the bottom. On the same day, we collected bees from flowers within each plot through 200 sweeps of a sweep net allocated evenly across all vegetation present within the plot boundary to a height of 2 m, leading to a total of 390 hours of sweep net sampling. We limited our bee surveys to warm sunny days (average temperature 24.7°C) with low wind speeds and little to no rain. We sampled all plots twice in austral spring and twice in summer during 2012, totalling four bee data collection periods over two seasons. Bees were stored in 70% ethanol, and returned to the laboratory for sorting and subsequent identification to species where possible, and otherwise to morphospecies. We air-dried and pinned representative specimens from each species for taxonomic verification.

For golf course and public park plots, we calculated the number of individuals per plot for 600 m^2 (20 m x 30 m plot). To account for the smaller and variable plot sizes within residential neighbourhoods, we scaled the abundance of individual bees within these plots to an area of “available and suitable” green space habitat within a 600 m^2 area of residential matrix, to be able to compare these plots to those containing available habitat in golf courses and public parks. As the residential matrix is characterised by impervious building structures, it would be inappropriate to scale up each residential plot to an equivalent 600 m^2 area, as much of this area would comprise the interior of single or double storey buildings, unsuitable as bee habitat. We scaled up each residential plot after accounting for the percentage area of unsuitable impervious building roof surface within that residential area. We used i-Tree canopy (i-Tree, 2013; USDA Forest service, USA) to estimate impervious building roof area from Google Earth imagery. We classified 200 randomly selected points as roof, grass, pavement, roads, soil or trees. As residential neighbourhoods ranged in age from 5 to 110 years old, the ratio of building roof to other land surfaces varied considerably. The percentage area of building roof per site varied between 25% and 41%, and was used to estimate the area of available and suitable bee habitat within the equivalent of 600 m^2 area of a residential neighbourhood. As an example, if a residential plot was 400 m^2 and situated in a residential neighbourhood with an average of 25% roof cover, instead of scaling up the number of individual bees caught within the plot to a 600 m^2 equivalent, we scaled it up to 75% of 600 m^2 (i.e. 450 m^2) to account for the 25% of building space unavailable to bees.

2.3 Environmental Variables

We measured several variables in the field to describe the floral resources and nesting habitat available to bees (Table 1). We identified all plants within each plot to species where possible, noting which species were flowering during bee sampling, and whether it was native to Australia or exotic. We then calculated the proportion of native plants per plot as a function of all species recorded. We also calculated the number of plant species in flower per square metre, by dividing the number of recorded flowering plants by the area (m^2) of the plot. We removed plant families dominated by wind-pollinated species (e.g. grasses) from this metric, as these do not provide foraging resources for bees. Nesting habitat was characterised by recording the presence or absence of bare ground and tree hollows using the intercept method outlined below, and health of all trees within each plot (category ranging 1 to 8 from healthy tree with no dead limbs to dead stump less than 5 m high).

To measure vegetation structure within a plot, we established four parallel 30 m transects at five metre intervals, and measured the vegetation at 0, 5, 10, 15, 20, 25 and 30 m point locations along four of the transects (i.e. 4 transects x 7 locations = 28 points sampled). At each sampling point, we recorded: 1) the nature of ground cover (presence of bare ground, pavement, litter, rock, gravel, mulch, vegetation) and 2) the growth form of any vegetation (i.e. tree, shrub, grass, forb etc) that intercepted a vertical measurement pole at five height intervals: 0.0-0.2 m; 0.2-0.5 m; 0.5-1.0 m; 1.0-2.0 m; and > 2.0 m. The sum of vegetation intercepts in each height interval was used to calculate vegetation volume (Eq. 1):

$$V_{VEG}H_X = ((P_{NI}H_X / P_TH_X) \times V_SH_X) \qquad \text{[Equation 1]}$$

where $V_{VEG}H_X$ is estimated vegetation volume occupying a specific height interval, $P_{NI}H_X$ is the actual number of times vegetation intercepted the pole for that height interval, P_TH_X is the number of pole point locations surveyed (usually 28 for a 600 m^2 plot), and V_SH_X is the total volume for that height interval based on the area of the plot multiplied by the height interval. To estimate total vegetation volume, the $V_{VEG}H_X$ for each height interval were summed together. To account for irregular plot sizes, we divided the sum of the estimated volumes by the total available volume (area sampled multiplied by total height) to produce a percentage estimate of vegetation volume in that plot.

To quantify the urban landscape surrounding each site, we calculated the percent impervious surface cover within a 1 km radius buffer around the centre point of the site using Arc Map (ESRI, Redlands, California, USA, version 10.1) and a ‘Directly Connected Imperviousness’ GIS data layer obtained from Melbourne Water. We chose one kilometre as it complemented our site selection methodology, as associated residential neighbourhoods, public parks and golf courses were located 1 km or more away from one another, and to reflect a distance bees are capable of flying. Impervious surface cover ranged from 3 – 63 %.

2.4 Data Analysis

2.4.1 Bee community composition in urban green space habitats

We first calculated sample completeness by comparing sample coverage within each green space habitat, following Chao and Jost (2012). Using the software iNEXT (version 1.0) we plotted sample completeness (as measured by sample coverage) with respect to sample size (Hsieh et al. 2013).

To examine the distribution of the bee community amongst green space habitats, we used generalized linear mixed models (GLMMs), an approach that allowed us to account for the nested nature of the experimental design. We specifically examined differences across green space habitats for six measures of the bee community: 1) bee species richness; 2) total bee abundance; and the occurrence of 3) *Apis mellifera*; 4) *Homalictus* species; 5) *Lasioglossum* species and 6) bees within the Colletidae. The latter four taxonomic groupings reflect species that share ecological traits (Appendix A1), and are predicted to respond in a similar manner to the environment. Indeed, trait based RLQ and clustering analyses (results not presented here) indicate the bee community separated into these four groups. We fitted the species richness model with a Poisson error distribution, the abundance model with a normal distribution, and the occurrence models with a binomial distribution. In all models, 'Site' was specified as a random effect, to account for multiple plots within each of the 39 green spaces sampled.

Non-metric multidimensional scaling (NMDS) was performed to explore how similar the bee community was between the different green space habitats, using a Bray-Curtis similarity index, including only the bee species present in more than one site. We tested for differences between green space habitats using a one-way analysis of similarities test (ANOSIM).

2.4.2 The effect of local and landscape variables on bees in urban green space habitats

To understand what specific attributes of green spaces provide important habitat for bees, we examined the four groups of bees identified above, as these groups represent sets of species that share similar responses to the environment based on shared traits. To evaluate the best predictors of the presence of each of the four groups we again used generalized linear mixed models (GLMMs), using the same structure as stated above. In these models, environmental variables listed in Table 1 were specified as fixed effects. To avoid over parameterization, the number of predictor variables was restricted based on the number of presence sites, with one variable added per 10 presence sites per functional group (Wintle et al. 2005). To reduce the number of variables used in each model, we created sets of predictor variables based on the scale at which they occurred, and their possible impact on bee distributions (Rhodes et al. 2009). Predictor variables described 1) sampling conditions (the diversity of plants in flower at the time of sampling), 2) floral resources (the composition and volume of vegetation present), 3) nesting resources, 4) age since establishment and 5) per cent impervious surface cover within 1 km radius. The environmental variables were not strongly co-linear (Pearson correlation coefficient < 0.5), and therefore were included together in regression models. Skewed explanatory variables were log-transformed prior to analysis, and all continuous variables were standardised to have a mean of zero and standard deviation of one. Initial exploratory analyses revealed that average daily temperature, average daily humidity, calendar date of sampling and the area of each site (ha) had no significant correlation with bee responses (Pearson correlation coefficient < 0.1, p-values > 0.2 in all cases), and hence these variables were not considered further.

We constructed our GLMMs using all combinations of the five variable groups (e.g. sampling conditions, floral resources, etc.) resulting in a maximum of 31 possible alternate models, including a null model made up of random effects only. We assessed the fit of each model using an information theoretic approach by calculating the Akaike Information Criterion corrected for small sample size (AICc), using package 'AICcmodavg' (Mazerolle 2013). For each bee response group, a 95 % confidence set of models was constructed listing all models that have a summed Akaike weights (w_i) >0.95 (Burnham and Anderson 2002). The "relative importance" of each variable group was then calculated by summing the weight for all of the models incorporating that predictor set (Burnham and Anderson 2002). We selected our final model based on the lowest AICc and the highest model w_i (Burnham and Anderson 2002). Model residuals were also checked for spatial autocorrelation using Moran's I (Moran 1950).

All statistical analyses were conducted in 'R', version 3.0.1 (http://www.r-project.org/). GLMMs were fitted using the 'glmer' function in package 'lme4' (Bates et al. 2008).

3. RESULTS

We collected 736 individual bees representing 19 species or morphospecies of Apidae, Colletidae, Halictidae and Megachilidae (Appendix A1). Most individuals were sampled by sweep net, followed by white and yellow pan traps, with few individuals being sampled by blue pan traps. The sweep net caught a broad range of bee species and families, whereas the majority of species caught by pan traps were exclusively in Halictidae and Apidae. The most abundant native Australian bee species or groups were the short-tongued ground-nesting bees including *Homalictus (Homalictus) sphecodoides, Homalictus (Homalictus) punctatus* complex, and *Lasioglossum (Chilalictus) brunnesetum* (Appendix A1). The European Honeybee *Apis mellifera* was also abundant, although it is unknown whether these individuals came from feral or managed colonies (Appendix A1). Six of the 19 morphospecies found were represented by a single individual (31%), and an additional three species were found at only one site. An assessment of sample completeness for each of the three green space habitats was comparable after collection of 100 individuals, indicating sufficient sampling effort within each land use (Appendix A2).

3.1 Bee community composition in urban green space habitats

We recorded totals of 13 bee species in public parks, 12 in golf courses and nine in residential neighbourhoods. On average public parks had significantly higher bee species richness in comparison to golf courses ($z = 2.01$, $p = 0.038$) and residential neighbourhoods ($z = 2.20$, $p = 0.028$), which did not differ from each other ($z = 0.14$, $p = 0.89$) (Table 2). Bee abundance was twice as great in public parks in comparison to golf courses ($t = 3.01$, $p = 0.003$) and residential neighbourhoods ($t = 3.78$, $p = 0.0002$), which again did not differ from each other ($t = 0.82$, $p = 0.41$) (Table 2).

Apis mellifera was significantly more likely to occur in residential neighbourhoods and public parks in comparison to golf courses (RG vs GC $z = 3.4$, $p <0.001$; UP vs GC $z = 2.0$, $p = 0.045$), and equally likely to occur in the former two green spaces ($z = 0.96$, $p = 0.34$) (Table 2). *Homalictus* spp. were significantly more likely to occur in golf courses and public parks in comparison to residential neighbourhoods (GC vs RG $z = 2.6$, $p = 0.009$; UP vs RG $z = 2.84$, $p = 0.004$), and equally likely to occur in the former two green spaces ($z = 1.26$, $p = 0.21$). *Lasioglossum* spp. were equally likely to occur in all three green spaces ($p>0.05$ all comparisons). Bees within the Colletidae were least likely to occur in residential neighbourhoods in comparison to public parks ($z = 2.71$, $p = 0.007$), and were also more prevalent within golf courses (Table 2), however no other significant pairwise differences occurred ($p>0.05$).

Bee community composition significantly differed amongst green space habitats (Fig 2). ANOSIM analysis revealed that the bee community present within residential neighbourhoods was significantly different to the community present within golf courses ($p = 0.01$) and public parks ($p = 0.01$). However the latter two green space habitats contained a similar bee community ($p = 0.11$).

3.2 The effect of local and landscape variables on bees in urban green space habitats

Floral resources were the highest-ranking predictor variable for three of the bee functional groups (Table 3; Appendix A3). Plots with more native vegetation had higher occurrence of *A. mellifera*, *Lasioglossum* spp. and bees within the Colletidae (Fig 3a, c and d), whereas plots with a greater volume of understorey vegetation had a negative impact on the occurrence of these three groups of bees (Fig 3a, c and d). The diversity of plants in flower was also ranked as a good predictor of *A. mellifera* and *Homalictus* spp. (Table 3), where increasing floral diversity was positively associated with greater occurrence of these two groups (Fig 3a and b). Age and impervious surface cover were also ranked as good predictors of *Homalictus* spp. where this group was more likely to occur in older plots with lower impervious surface cover (Table 3, Fig 3b). The large number of models included in the 95% confidence table for *A. mellifera* and *Lasioglossum* spp. (Appendix A4), which included the 'null model' in the case of *Lasioglossum* spp., indicated that there was a very high degree of uncertainty in predicting occurrence of these two groups of bees. There was no evidence of spatial autocorrelation in the residuals for any final model for either of the three bee response groups ($p \geq 0.1$ in all cases).

4. DISCUSSION

Given the severe ecological impact of urban land transformation, reported plant extinctions in cities, and the possible causal connection between declining plant populations and their pollinators, it is imperative to understand the biodiversity value of different urban land uses for pollinator conservation. The results of our study not only inform local conservation efforts to help develop management strategies to improve habitat for a range of bee species, they also point to the opportunity for landscape-scale pollinator conservation in cities worldwide. Our results suggest that established green spaces that contain native flowering plants (planted or remnant), which are situated in relatively green landscapes with lower surrounding impervious surface cover, support greater bee abundance and a greater richness of bee species, especially ground nesting and floral specialist bees. We found that residential neighbourhoods supported a distinctly different community of bees, dominated by the European Honeybee *Apis mellifera.* This was likely due to the floral resources in this land use, which were dominated by exotic flowering plants, leading to greater occurrence of this generalist bee species.

We found that ground nesting native Australian bee taxa, such as *Homalictus* spp., had a significantly higher probability of occurrence in older green space habitats with less surrounding impervious surface cover, including golf courses and parks that contained a lower diversity of plants in flower. However, we found that large bodied generalist *Lasioglossum* spp. were not significantly likely to occur in one green space habitat over another, and that these bees were not strongly correlated with any of our site or landscape variables. Public parks and 'out of play' areas in some golf courses had a reduced presence of exotic plant species, and appeared to experience less intensive management than that found in many residential gardens (C. Threlfall personal observation). The combination of appropriate floral resources and less intense management may provide suitable habitat for ground nesting *Homalictus* species, particularly as they require areas of undisturbed soil to build nests (Michener 1965). The availability of suitable nesting habitat in urban green spaces may help explain why this group occurred significantly less in residential neighbourhoods, where the ground has a high frequency of management and disturbance compared to parks and golf courses which have areas that are less intensively managed. Indeed, nesting resource availability has been shown to significantly influence the composition of bee communities in

Mediterranean landscapes (Potts et al. 2005). Our findings are consistent with Tonietto *et al* (2011) who suggest that compacted soils can discourage ground nesting bees, highlighting the importance of unmanaged, little managed or 'wild' patches within urban green spaces to ground nesting bee species. Creating refuge areas of undisturbed soil such as field margins, untilled areas and semi-natural habitat has helped to conserve bees in highly modified agricultural landscapes (Kremen et al. 2002; Lentini et al. 2012) and similar management strategies could be promoted to conserve bee diversity in urban landscapes.

We found that the highly endemic bees within the Colletidae were almost absent from residential landscapes, instead being significantly more likely to occur in public parks and green spaces with greater proportions of native vegetation, including planted native vegetation. These Australian bee species have co-evolved with Australian plants over long periods (Michener 1965), are short tongued and considered floral specialists. These bees are especially dependent upon accessing nectar from shallow flower cups, such as those found within the Myrtaceae (Michener 1965) a dominant family in the Australian flora. Hence, it is not surprising that the occurrence of Colletid bees significantly increased in those green spaces with more than 50% cover of native Australian plant species.

These Colletid bees are also cavity-nesting, and their reliance on existing holes in reeds, stems and dead wood may further explain their low occurrence in residential neighbourhoods. The nesting success of taxa that nest in wood and pith cavities has been reported to decline in urban areas where vegetation is highly maintained and woody debris is often frequently removed (Matteson et al. 2008). Although, some studies have reported a greater abundance of cavity nesting species in more urban habitats (Fortel et al. 2014), this is likely dependent upon the substrate in which each cavity is located and the ability of species to utilise man-made materials.

The occurrence of *A. mellifera* was significantly higher in residential neighbourhoods, where it was positively associated with increases in the diversity of plants in flower, and negatively associated with increasing vegetation structure. This is of conservation concern, as insect-dependant native plants in urban landscapes may suffer from limited pollination if the functional diversity of bee communities is reduced. Our findings agree with previous studies that found *A. mellifera* is common in many urban habitats (Bates et al. 2011; Matteson et al. 2008; Smith et al. 2006), due to the dominance of non-native vegetation and the ability of *A. mellifera* to forage widely on many types of flowers. Residential neighbourhoods in our study area did not contain any more managed or unmanaged hives of *A. mellifera* than observed in other green spaces (the authors, personal observation), and instead we believe our results suggest that residential neighbourhoods provide adequate foraging grounds for this species, particularly if dominated by flower beds, as our's were. The dominance of *A. mellifera* in residential neighbourhoods may actually present a risk to pollination services in this habitat type should the bee parasite *Varroa destructor* enter Australia and lead to the dramatic reductions in bee populations and pollination services observed elsewhere (Le Conte et al. 2010). Communities of native bee pollinators may offer insurance for the retention of adequate pollination services in urban landscapes, and should be encouraged by introducing more suitable green space management regimes.

While a recent study found a similar richness and abundance of bees between nearby remnant heathland patches and the golf course and public park plots we sampled (Baumann 2014), our study only recorded around 15% of the diversity of bee species that have been historically recorded in the region (Walker 2009). The reduced diversity may be partly explained by seasonal variation and spatial variability in bee species occurrences, as well as potentially due to declines associated with urbanisation. In our study, the number of individual bees collected was similar to that reported for many other urban bee studies (Ksiazek et al. 2012; Matteson et al. 2012; Pardee and Philpott 2014; Tonietto et al. 2011), and agrees with recent findings that urban areas can support similar bee abundance and richness to surrounding farmland and nature reserves (Baldock et al. 2015). To account for the expectation that bee abundance may be lower in urban green space habitats as compared to more natural landscapes, we implemented a sampling regime that far exceeded that of previous urban bee studies (e.g. McIntyre and Hostetler 2001). Regardless, we did not collect as many individual bees as studies in regions dominated by social bees, such as bumblebees (e.g. McFrederick and LeBuhn 2006). Our results may reflect 1) that the majority of bee species in our study region are solitary, 2) that the green space habitats present do not provide all the resources required for certain bee species of this bioregion, or 3) that toxins and pesticides detrimantal to bees may be present. As such, our findings appear to contradict those of recent northern hemisphere studies that suggest urban areas may harbour rich communities of wild bees (Fortel et al. 2014). Whilst remnant habitats in cities have been suggested to support diverse pollinator communities (Cane et al. 2006; Hinners et al. 2012), our study suggests that the far more dominant forms of urban green space habitat in our cities (gardens within residential neigbourhoods, parks, golf courses) also provide opportunities for urban bee conservation. Remnant vegetation is likely to be very important to urban bee communities, so remnant areas should be conserved where possible. However, in areas where remnant vegetation has all but gone, alternative green space habitat must be prioritised. Further research is required on urban bees in remnant habitats within urban landscapes, including an examination of the movement of bees between habitat patches, to elucidate foraging and nesting habitat requirements and to more fully understand the importance of different urban habitats for urban bee conservation.

4.1 Considerations for the conservation of bees in urban green spaces

If the decline in bee diversity seen in agricultural landscapes (Potts et al. 2010) is mirrored in urban landscapes, it could have far reaching consequences for the continued reliable pollination of urban remnant vegetation, horticultural plantings and urban food production, threatening the viability of some plant populations in the urban landscape. Furthermore, pollination services provided by *A. mellifera* supplement, rather than substitute, pollination services provided by native bees (Garibaldi et al. 2013). Considering the high occurence of plant extinctions reported globally (Hahs et al. 2009), and potential link between declining pollinators and their associated insect dependant plant species (Biesmeijer et al. 2006; Pauw 2007), it is imperitive that alternative management strategies be considered to improve the suitability of habitat for a wider range of bee species than is currently being supported.

Internationally, current strategies to conserve and restore pollinator communities are mostly focussed on agricultural landscapes, however our data supports recent suggestions that pollinator conservation programmes need to include initiatives in urban areas (Baldock et al. 2015). This is especially important considering the rapidly increaing urban population, and the increasing extent of urban areas worldwide (Seto et al. 2013). Pollinator conservation initiatives could include actively designing habitats to be more beneficial to a variety of bee species (Hernandez et al. 2009), and enormous potential exists for such programmes to be implemented in a range of urban green space habitats. Due to the diversity of bees recorded utilising urban areas and their various nesting and foraging requirements, we recommend any pollinator conservation programme incorporate actions to create or maintain a wide variety of nesting and native plant forage resources. For example to create bee nesting habitat, undisturbed or unmanaged vegetation can be created by removing mowing or reducing its frequency. Less managed, uncompacted patches of bare soil should be encouraged through restricting public access to some areas or encouraging vegetation types which lack a continuous ground cover e.g. tussock rather than rhizomatous grasses. Dead or dying vegetation, such as logs and reeds should be retained for cavity-nesting bees, in addition to installing articifical habitat where nesting resources are lacking, such as bee nesting boxes, although the utility of bee hotels for native bee conservation needs further research attention (MacIvor and Packer 2015). Bee foraging habitat could be created by encouraging native plantings in residential neighbourhoods. This will not only provide foraging resources for a greater number of endemic bee species, it will also assist the conservation of many other fauna groups, such as birds and butterflies which are known to respond positively to native vegetation in urban residential landscapes (Burghardt et al. 2009; Ikin et al. 2013). Ensuring our cities continue to support diverse and abundant bee communities is a critical step towards building the resilience of urban ecoystsems and the essential network of plant-pollinator interactions. Simple, low cost changes in urban green space management will improve habitat suitability for bees, helping to strengthen the ability of green space networks to provide critical pollination services, which ultimately will contribute to national efforts to conserve pollinator communities.

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667 **Table 1:** Environmental variables used generalised linear mixed models (GLMMs).

Variable	**Scale**	**Description**	**Variable group**
Floral diversity	Plot	The number of animal pollinated plant species in flower divided by plot area (m^2): flowering plants/m^2 per sampling event	Sampling conditions
Vegetation volume	Plot	Vegetation volume intercepted (per cent) using the structure pole	Floral resources
Proportion Native Plants	Plot	Proportion of plants native to Australia per plot (no. native species/total number of species)	Floral resources
Tree Health	Plot	Median tree health (median tree senescence score for all trees per plot)	Nesting opportunities
Bare Ground	Plot	Proportion of structure pole intercepts classified as containing bare ground per plot	Nesting opportunities
Age	Site	Age since establishment (nearest decade, in years)	Age
Impervious Cover	Landscape	Per cent impervious surface cover within a 1 km buffer of each site	Impervious Cover

Table 2: Mean (± standard error) values for each bee response variable, recorded in 600m^2 plots within the three focal green space habitats.

Land Use	**Golf Courses**	**Residential Neighbourhoods**	**Public parks**
Bee Species Richness	1.88 ± 0.18	1.85 ± 0.19	2.62 ± 0.22
Bee Abundance	4.83 ± 0.66	3.94 ± 0.63	10.96 ± 2.53
% plots with *Apis mellifera*	17.0	50.0	38.5
% plots with *Homalictus* spp.	80.8	55.8	92.3
% plots with *Lasioglossum* spp.	32.7	28.8	42.3
% plots with Colletidae	15.4	5.8	30.8

Table 3: Model parameters for the final generalised linear mixed models (GLMMs) analyses of the occurence of bee functional groups. For each model, we present the variable groups included in models, the coefficient, standard error (SE) and p-value. Bold values denote significant difference at α = 0.05.

Bee Response Group	Variable Group	Term	Estimate	SE	p-value
Apis mellifera		Intercept	-0.69	0.20	**<0.001**
	Sampling conditions	Floral diversity	0.33	0.22	0.125
	Floral Resources	Prop Native Plants	0.34	0.23	0.142
		Vegetation Volume	-0.58	0.22	**0.007**
Homalictus spp.		Intercept	1.32	0.27	**<0.001**
	Sampling conditions	Floral diversity	-0.50	0.23	**0.033**
	Age	Age	1.14	0.34	**0.001**
	Impervious Cover	Impervious Cover	-0.49	0.32	0.131
**Lasioglossum* spp.		Intercept	-0.80	0.22	**<0.001**
	Floral Resources	Prop Native Plants	0.12	0.22	0.583
		Vegetation Volume	-0.45	0.23	0.053
Colletidae		Intercept	-1.89	0.27	**<0.001**
	Floral Resources	Prop Native Plants	0.63	0.26	**0.015**
		Vegetation Volume	-0.15	0.26	0.562

* Listed is the model which contained variables with the greatest relative importance to this bee group, however, there was a high degree of uncertainty surrounding estimating relationships for *Lasioglossum* spp.

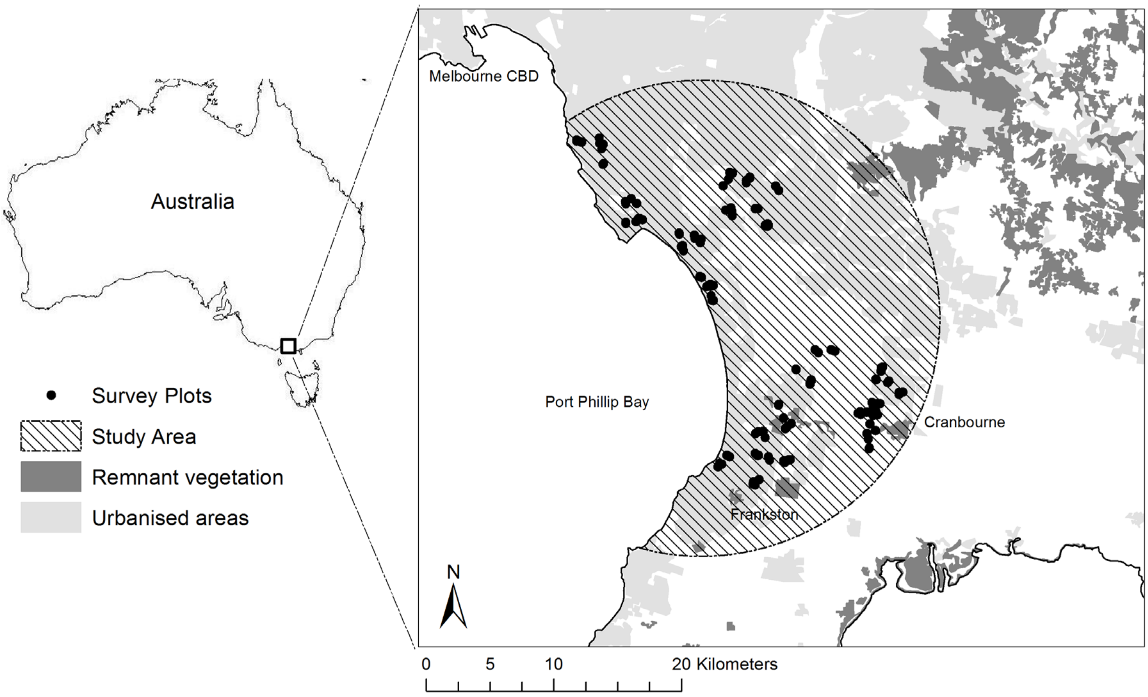


Figure 1: Location of study area and the 39 sites containing the 130 plots where bees were surveyed in Melbourne, Australia.

Figure 2: Non-metric multidimensional scaling (NMDS) of the bee community sampled in plots within golf courses, public parks and residential neighbourhoods, using a Bray-Curtis similarity index, including only the bee species present in more than one site.

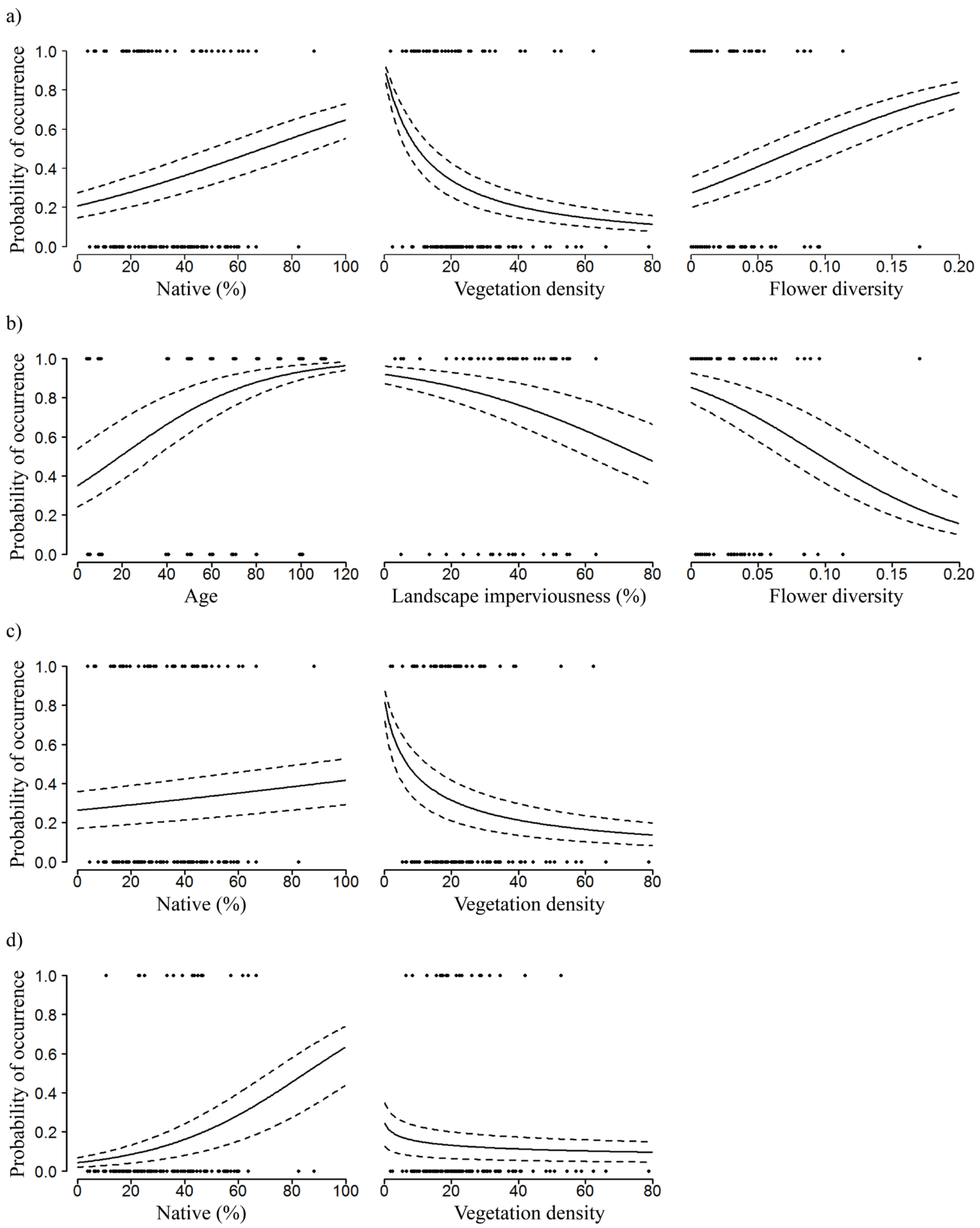


Figure 3: Predicted relationships between bee functional groups: a) *Apis mellifera*; b) *Homalictus* spp.; c) *Lasioglossum* spp.; and d) Colletidae and explanatory variables in the final 'best' model. Refer to Table 3 for model parameters. Solid lines represent the mean response and dashed lines the associated 95% confidence interval. Solid circles represent the data points.

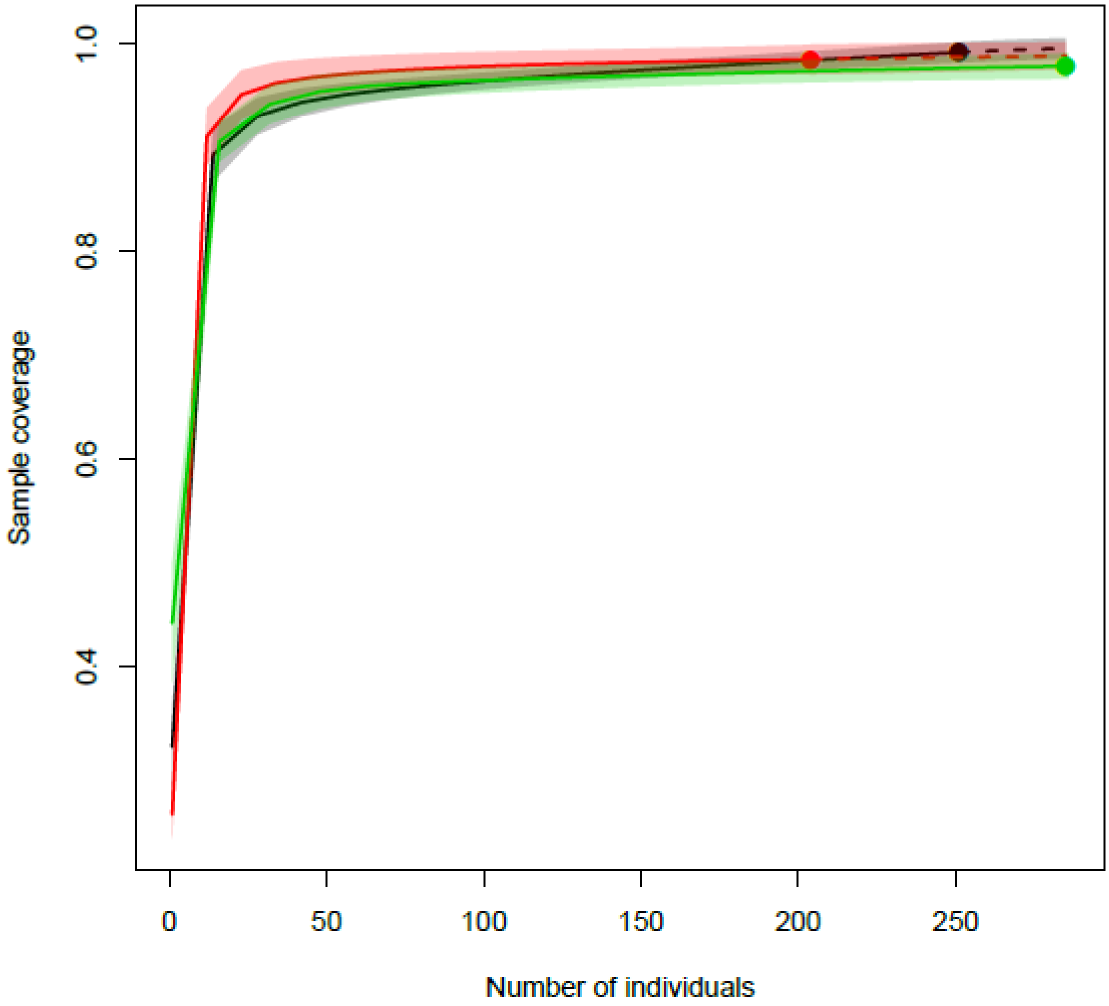
Supplementary Material:

Appendix A1: Number of each bee species collected in this study and their traits. We compiled data on bee traits from our knowledge of bee biology, published literature, and a database of bee records from Victoria (PaDIL database, Walker 2009). Number of plant families is the number of plant families each species has been recorded foraging on, as detailed on the PaDIL (Walker 2009). Body size was measured as the inter-tergular distance (ITD) between wing bases (Cane 1987).

	Individuals	**Plant Families**	**Floral specificity**	**Nesting Substrate**	**Nest Construction**	**Sociality**	**Tongue Length**	**Body Size (mm)**
Apidae								
Apis mellifera	91	13	Generalist	Above ground	Renter	Eusocial	Long	3.25
Exoneura angophorae	2	3	Generalist	Above ground	Excavator	Social	Short	1.1
Amegilla asserta	1	1	Specialist	Below Ground	Excavator	Semi-social	Long	4
Colletidae								
Euhesma fasciatella	5	1	Specialist	Above ground	Renter	Solitary	Short	1
Euryglossina sp1	1	1	Specialist	Above ground	Renter	Solitary	Short	0.8
Euryglossina sp2	2	1	Specialist	Above ground	Renter	Solitary	Short	0.8
Euryglossina adelaidae	1	1	Specialist	Above ground	Renter	Solitary	Short	1.75
Euryglossina fuscesens	3	1	Specialist	Above ground	Renter	Solitary	Short	0.75
Hylaeus sp1	4	1	Specialist	Above ground	Renter	Solitary	Short	1
Hylaeus sp2	3	1	Specialist	Above ground	Renter	Solitary	Short	0.8

Hylaeus sp3	5	1	Specialist	Above ground	Renter	Solitary	Short	1.13
Hylaeus honestus	1	1	Specialist	Above ground	Renter	Solitary	Short	2
Pachyprosopis kelleyi	7	1	Specialist	Above ground	Renter	Solitary	Short	1.35
Megachilidae								
Megachile heriadiformis	1	5	Specialist	Below Ground	Excavator	Solitary	Long	2.2
Halictidae								
Homalictus (Homalictus) dotatus	1	13	Generalist	Below Ground	Excavator	Semi-social	Short	1
Homalictus (Homalictus) complex: punctatus, brisbanensis and megastigmus	342	12	Generalist	Below Ground	Excavator	Semi-social	Short	1.16
Homalictus (Homalictus) sphecodoides	195	11	Generalist	Below Ground	Excavator	Semi-social	Short	1.5
Lasioglossum (Chilalictus) brunnesetum	69	8	Generalist	Below Ground	Excavator	Semi-social	Short	1.5
Lasioglossum (Parasphecodes) hilactum	2	5	Generalist	Below Ground	Excavator	Semi-social	Short	2.5

Appendix A2: Sample completeness curves and 95% confidence intervals for bees sampled within three green space habitats: golf courses (black), public parks (green), and residential neighbourhoods (red), produced using iNEXT (Hsieh et al. 2013), following Chao and Jost (2012).



Appendix A3: Relative importance indices, following Burnham and Anderson (2002), calculated from AICc values of the 95 % confidence set of the GLMMs for bee functional groups. The response variable modelled was the likelihood of occurrence of each functional group. See Table 1 for a description of variable groups, and Appendix S4 for further details of each model. The highest values for each functional group is highlighted in bold.

Response	***Apis mellifera***	***Homalictus* spp.**	***Lasioglossum* spp.**	***Colletidae* spp.**
Sampling conditions	**0.41**	**0.79**	0.25	0.11
Floral resources	**0.67**	0.09	**0.37**	**0.45**
Nesting opportunities	0.4	0.35	0.17	0.00
Historic context	0.34	**0.92**	0.29	0.14
Urban context	**0.52**	**0.51**	0.29	0.07

Appendix A4: Summary from generalised linear mixed model (GLMM) analysis of bee response groups. Summary shows the 95% confidence set of models, variable groups included in models, corrected Akaike's Information Criteria (AICc), corrected model weights (W_i), and the relative importance of each variable group, calculated using the AICc weights from each model as per Burnham and Anderson (2002). The response variable modelled was the likelihood of occurrence of each functional group. 'Season' = sampling conditions (the diversity of plants in flower at the time of sampling); 'Floral' = floral resources that related to the composition and structure of the vegetation present; 'Nesting' = nesting resources for below ground and above ground nesting species; 'Historic' = historic context (age since establishment); 'Landscape' = urban context (impervious surface cover in the area).

Response	**Model**	**Season**	**Floral**	**Nesting**	**Historic**	**Landscape**	**AICc**	**W_i**
***Apis mellifera* occurrence**	mod8	x	x				166.62	0.1
	mod4		x				166.84	0.09
	mod14		x			x	166.96	0.09
	mod17				x	x	167.39	0.07
	mod20	x	x			x	167.76	0.06
	mod22		x	x		x	167.91	0.05
	mod30	x	x		x	x	168	0.05
	mod23			x	x	x	168.39	0.04
	mod12		x	x			168.44	0.04
	mod19	x	x		x		168.7	0.04
	mod16			x		x	168.71	0.04
	mod5			x			168.74	0.04
	mod18	x	x	x			168.88	0.03
	mod26	x			x	x	168.9	0.03
	mod13		x		x		169.01	0.03
	mod31		x	x	x	x	169.23	0.03
	mod28	x	x	x		x	169.36	0.03
	mod9	x		x			170.09	0.02
	mod29	x		x	x	x	170.48	0.01
	mod21		x	x	x		170.53	0.01

	mod1	x	x	x	x	x	170.65	0.01
	mod25	x		x		x	170.7	0.01
	mod15			x	x		170.82	0.01
	mod3	x					171.13	0.01
	mod27	x	x	x	x		171.15	0.01
***Homalictus* spp. occurrence**	mod26	x			x	x	138.99	0.23
	mod10	x			x		139.07	0.22
	mod29	x		x	x	x	140.47	0.11
	mod24	x		x	x		140.51	0.11
	mod17				x	x	141.27	0.07
	mod23			x	x	x	141.83	0.05
	mod30	x	x		x	x	142.55	0.04
	mod9	x		x			143.3	0.03
	mod19	x	x		x		143.35	0.03
	mod15			x	x		143.81	0.02
	mod6				x		144.2	0.02
	mod1	x	x	x	x	x	144.45	0.01
	mod27	x	x	x	x		144.93	0.01
	mod5			x			145.26	0.01
***Lasioglossum* spp. occurrence**	mod2						166.11	0.14
	mod6				x		166.74	0.1
	mod4		x				166.87	0.09
	mod7					x	167.17	0.08
	mod14		x			x	167.83	0.06
	mod3	x					168	0.05
	mod12		x	x			168.09	0.05
	mod13		x		x		168.58	0.04

	mod10	x			x		168.67	0.04
	mod11	x				x	168.74	0.04
	mod17				x	x	168.77	0.04
	mod8	x	x				169	0.03
	mod5						169.47	0.03
	mod22		x	x		x	169.52	0.02
	mod20	x	x			x	169.8	0.02
	mod15			x	x		169.9	0.02
	mod21		x	x	x		169.97	0.02
	mod18	x	x	x			170.2	0.02
	mod26	x			x	x	170.57	0.01
	mod19	x	x		x		170.7	0.01
	mod16			x		x	170.86	0.01
	mod9	x		x			171.21	0.01
	mod28	x	x	x		x	171.37	0.01
	mod24	x		x	x		171.56	0.01
***Colletidae* spp. occurrence**	mod3		x				110.36	0.45
	mod1						112	0.2
	mod5				x		112.74	0.14
	mod2	x					113.21	0.11
	mod6					x	114.07	0.07