# Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens

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**Authors' contributions:** KSP designed the study, conducted the fieldwork, collated the data, performed the data analysis, and drafted the manuscript. JO edited the manuscript, advised on analyses, and provided critical feedback and supervision.

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## Abstract

Urbanisation is a prominent and increasing form of land-use change, with the potential to disrupt the interactions between pollinators such as bees and the flowering plants that they visit. This in turn may cause cascading local extinctions and have consequences for pollination services. Network approaches go beyond simple metrics of abundance and species richness, enabling understanding of how the structure of plant-pollinator communities are affected by urbanisation. Here we compared pollination networks between native vegetation (bushland) remnants and residential gardens in the urbanised region of the southwest Australian biodiversity hotspot. Across fourteen sites, seven per habitat, plant-bee visitor networks were created from surveys conducted monthly during the spring-summer period over two years. Extinction slope (a measure of how extinctions cascade through the network), and network robustness and nestedness were higher for bushland remnants, suggesting that networks in bushland remnants had greater functional integrity, but if disrupted, more cascading extinctions could occur. In contrast, niche overlap between pollinators was higher in residential gardens, suggesting greater competition for resources. Most species-level properties did not differ between habitats, except for normalised degree, which was higher in bushland remnants. In conclusion, it appears that pollination networks in managed residential gardens are not structurally equivalent with those in bushland remnants. This has implications for conservation of wild bee assemblages in this biodiversity hotspot, and suggests removal of remnant native vegetation for residential development could disrupt the integrity of plant-pollinator assemblages.

**Keywords: bees; bipartite; honeybees; plant-pollinator networks; flower-visitors; urbanisation.**

## INTRODUCTION

Ecosystems that function well involve robust mutualistic networks. However, if there are losses of key interactions, this can cause declines in network functioning (Kearns et al. 1998). Conserving networks of species interactions is vital for conservation and maintenance of ecosystem functions such as animal-mediated pollination (Tylianakis et al. 2010). Analyses of plant-pollinator communities using interaction networks have enhanced understandings of ecological patterns and processes, and the structure and functioning of these ecological assemblages (Burkle and Alarcón 2011; Thébault and Fontaine 2010; Vázquez et al. 2009). Wild bees are integral to many ecosystems due to their roles as pollinators (Garibaldi et al. 2013; Ollerton 2017), however there are recorded declines and extinctions of bees across the globe, with concomitant declines in pollination services (Biesmeijer et al. 2006), jeopardising plant populations (Pauw 2007). Pollinators appear to be particularly susceptible to habitat loss (Taki and Kevan 2007), suggesting that habitat loss can lead to declines in flower-visitor network integrity.

Urbanisation is a major and ongoing cause of habitat loss (Güneralp et al. 2013). The effect of urbanisation on wild bees and pollination services however is inconsistent, varying according to the habitat type being surveyed (Dylewski et al. 2019), and ecological traits such as specialisation (Hernandez et al. 2009). Despite the importance of looking at bees and plants using a network-level approach (Ings et al. 2009), and the increased sophistication of analytical tools to do so, plant-pollinator networks have rarely been analysed in urban areas. This is a major knowledge gap, given that urbanisation is an increasing and significant form of land-use modification (Faeth et al. 2011), causing changes in the composition of both plants and pollinators (Bartomeus et al. 2017; Harrison and Winfree 2015).

Urbanisation results in loss, degradation and fragmentation of the original native vegetation, to be replaced by builtspace and managed greenspaces, such as residential gardens (Niinemets & Peñuelas 2008). These vegetation changes often result in increased numbers of flowering plant species, most of which are exotic, often horticulturally-modified, varieties (Niinemets & Peñuelas 2008). Such changes are expected to disrupt co-evolved plant-pollinator networks (Kearns, Inouye & Waser 1998). Namely, it can be expected that in more modified urban greenspaces, networks will involve a greater number of nodes due to the increased plant species richness, but a loss of specialisation, which may be observed in terms of greater generalisation of the network and interacting taxa. Depending on the foraging flexibility of pollinators, they may expand their niche breadth, and increase overlap, dividing up the resources, resulting in greater functional complementarity. Conversely, if pollinator taxa are restricted in their foraging preferences, the loss of native flora may mean they must concentrate their foraging on a narrower subset of native flora that persist. Urbanisation, by causing loss of specialised mutualisms, could lead to loss in the robustness of pollination networks, and cascading extinctions (Kaiser-Bunbury et al. 2010).

Previous studies in urban habitats have looked at number of interactions (essentially visitation frequency) rather than networks *per se* (Buchholz and Kowarik 2019; Geslin et al. 2013) or compared urban habitats with those outside the urban context (Theodorou et al. 2017). Likewise, in the recent large-scale study by Baldock et al. (2019), the properties and structure of pollinator networks was not compared among habitat types. Our knowledge of the effects of urbanisation on plant-pollinator networks is still limited, particularly in the context of how different habitat types within urban areas such as remnant natural areas compare with managed greenspaces, and the influence of exotic species on the structure of these networks. Few studies have compared plant-pollinator networks between natural vegetated habitats and anthropogenic garden habitats in the same urban setting, and thus this study is a major advance in understanding how plant-pollinator networks are structured in different habitat types within urban areas.

This study assessed the structure of urban flower-visitor networks, with the aim of investigating how flower-visitor networks in bushland remnants of natural vegetation embedded within the urban matrix compare with those of residential gardens, in terms of network- and species-level properties. We hypothesised that bushland remnants were not comparable habitats to residential gardens, and due to divergent plant and pollinator assemblages and ecological conditions in these two urban greenspaces, plant-pollinator networks would differ in both network- and species-level properties.

## METHODS

Flower visitation networks were constructed from data on visits by both native Australian bees and the introduced European honeybee to flowers during surveys of fourteen sites in the region of Perth, Western Australia, located in the southwest Western Australian (SWWA) biodiversity hotspot (Myers et al. 2000). Seven of these were bushland remnants – fragments of the original native vegetation that persisted on the Swan Coastal Plain (Hopper & Burbidge 1989); the other seven sites were residential gardens. To prevent selection bias, and with the aim of sampling a representative sample of residential gardens in the region, residential gardens were not visited prior to selection, and were chosen blindly from a pool of citizens offering to allow their property to be surveyed on a first to offer basis. The only constraint was that they were interspersed among bushland sites, and that each site was at least 2 km away from the closest site to ensure independence, as this is beyond the flight range of the majority of bee species (Greenleaf et al. 2007). A map of the sites and the surrounding landscape can be found in Prendergast et al. (2020), Fig. 1. The two urban habitats differed significantly in plant community, with bushland remnants having fewer total plant species, but a higher proportion of native flora (Prendergast ~~et al., in prep~~2020b).

**Flower visitor surveys**

Sites were surveyed once a month between 1045h-1345h over the austral spring/summer from November to February 2016/2017 and October to March 2017/2018. Surveys were conducted over an approximately 100 m x 100 m area of greenspace. As bushland remnants were larger than 100 x 100 m, this encompassed part of a bushland remnant, such that bushland remnant sites surveyed consisted only of the remnant native vegetation ecosystem. For residential gardens, only one property was surveyed, however as the 100 x 100 m often was larger than the garden of property, the area surveyed comprisedthe front and backyard, and often road verges. For the entire three-hour duration a single researcher (KSP) walked haphazardly between flowering patches, with a minimum of 5 min spent at each patch, recording the visitations of all native bees and honeybees to flowers. Plant species were photographed and identified using Barrett and Tay (2016) and in consultation with botanists for native flora; Hussey et al. (1997) for weeds; and web-based searches and garden community forums for exotic species. Patterns of visitation were constructed from visual observations, as well as from specimens collected by targeted sweep-net collection to confirm the taxonomic identity. Networks were not constructed from collected specimens alone due to the bias in collecting specimens by sweep-netting, whereby some taxa are relatively more difficult to capture due to their body size and flight characteristics, and how abundant taxa foraging in trees were outside the reach of the sweep-net (Prendergast et al. 2020). Due to difficulties in species-level classification from observations of bees on the wing, they were assigned into the following meaningful taxonomic groups which correspond to both level of identification possible in the field, and similarities in body-size, flight behaviour, nesting, and often flower preferences: honeybees, *Amegilla, Coelyoxis,* Euryglossinae*, Exoneura, Homalictus,* Hylaeinae*, Lasioglossum, Leioproctus, Lipotriches, Megachile, Trichocolletes, Thyreus* (Online Resource 1). Such classifications into phylogenetic and (assuming phylogenetic conservatism) similar functional groups represent “functional taxonomic groups of flower visitors” (*sensu* Fenster et al. 2004; Ollerton et al. 2007). We also felt this was also a more appropriate level due to the many singletons and doubletons, and species occurring only in one survey (Prendergast 2020a), limiting our~~t~~ ability to make generalisations. The use of higher-level categorisations such as generic level like in the present study, as well as coarser levels, are often used in pollination network studies (e.g. Ballantyne et al. 2017; Watts et al. 2016). Specimens were also collected with an entomological sweep net (Prendergast 2020a), which verified these assignments. Although we acknowledge there are biases in all methods, we did not constrain our analyses to only specimens that were collected due to disparities in the ease of collecting different taxa (Prendergast *et al.* 2020).

**Construction of flower-visitation networks**

Flower-visitor networks were constructed using the package *bipartite* (Dormann et al. 2008) in R (version 3.6.2) (R Core Team 2014). Individual flower-visitor networks were constructed for each survey (N = 140).

Network and species-level indices commonly used in plant-pollinator networks, and which are considered to provide ecologically-relevant information about the structure and functioning of these networks, were calculated using *bipartite*.

The following network-level indices were calculated for each plant-pollinator network (for more comprehensive descriptions, refer to Online Resource 2):

- $H_2$': network generalisation
- weighted connectance: realised proportion of possible links weighted by network size
- nestedness based on overlap and decreasing fill (NODF): the extent to which specialists interact with a subset of species that also interact with generalists
- niche overlap of bees: mean similarity in interaction patterns between flower visitors
- extinction slope at both the bee and plant level: simulated secondary loss of species with extinctions of species in the other level
- robustness at both the bee and plant level: the “fragility” of a level to losses in the other level
- functional complementarity of bees: the extent of sharing of interactions between bees

At the level of the participants – the bee taxa and plants visited - in the interaction networks (“species-level”, following the terminology for describing theses metrics in bipartite analyses (Dormann et al. 2008)), the following parameters were calculated, using the function ‘specieslevel’ in *bipartite* (for more comprehensive descriptions, refer to Online Resource 1):

- normalised degree: links per species, scaled by the number of possible partners
- species strength: sum of the dependencies for each plants species for a given visitor, and is co-determined by the specialisation of other pollinators in the network

- interaction push-pull (IPP): asymmetry in dependencies between flower visitors and the flowers they visit
- species specificity: coefficient of variability in interactions
- pollination service index (PSI): an index measuring the importance of a flower-visitor taxon for all plant species in the network
- Bluthgen's d (d'): a measure of specialisation of a flower visitor taxon in terms of its discrimination from a random sampling of plant partners

Modularity is an important feature of plant-pollinator networks (Olesen et al. 2007). Above a given size, networks often exhibit modularity, whereby within the network there are link-dense regions and link-sparse regions. These link-dense regions are known as modules, and species within a module are more tightly linked to each other than to species in other modules (Olesen et al. 2007). The number of modules was calculated using the "computemodules" function in *bipartite*. Modularity was calculated using the function DIRT_LPA_wb_plus, which is based on Beckett (2016)'s DIRTLPAwb+ algorithm, which aggregates modules until no further improvement of modularity can be achieved. Modularity calculations used combined networks including all surveys per habitat type for each month of surveys, since networks conducted from each survey were too small for modularity to be calculated.

## Statistical analysis

Comparison of flower-visitor network metrics and species-level metrics between urban gardens and bushland remnants were made using mixed effects models (lme4, lmer function) in R (Bates et al. 2015). Site was included as a random factor in the models to account for multiple surveys per site. The significance of habitat-type was determined by performing an ANOVA between a model with and without habitat type (Kuznetsova et al. 2017); a significant difference between habitat types was considered when the ANOVA produced a value of $p<0.05$, and lower AICc of greater than two for the model containing habitat. Differences in modularity between habitat types was tested with linear models (lm function) as data were pooled across sites for each habitat type. Model fit was checked visually using diagnostic plots (quantile plots) and the data natural log-transformed if model assumptions were violated.

Analyses were performed for each year separately due to the different number of months over which surveys were conducted in each year, and how pollination networks can vary inter-annually (Alarcón et al. 2008; Dupont et al. 2009; Santamaría et al. 2018). Results of network metrics are presented as the means across the seven sites per habitat ± standard error.

### Pollinator and plant community structure

In addition to analysing the plant-pollinator networks between habitat types, we visually depicted the species composition between the bushland remnants and residential gardens for both the pollinators and flowering plants by constructing NMDS (non-metric multi-dimensional scaling) plots for each year of surveys. For the plant NMDS plots, only flowering plants visited during a survey were included. NMDS plots were constructed using the multivariate statistical software PRIMER v7 and the PERMANOVA+ add-on package (PRIMER-E Ltd, Plymouth,  UK). NMDS plots (100 restarts) were based on Bray-Curtis species x site matrices. Abundances were fourth-root transformed and log+1 transformed for the bee assemblage and plant matrixes, respectively, to reduce the influence of dominant taxa. Each point in the plot represents the taxonomic composition (taxa and their relative abundances) of each survey, with distances between points representing the similarity/dissimilarity between surveys, and surveys in each habitat type being assigned a different colour and symbol. In addition, for the bee assemblages, we performed a DISTLM (distance-based redundancy analysis, dbRDA and DISTLM, routines, available in the suite of programs for multivariate ecological data in the PERMANOVA+ add-ons to PRIMER v7 (Anderson et al., 2008)). DISTLM analysis used an AICc (Akaike Information Criterion adjusted for small sample size) selection procedure run with 9999 permutations (Anderson et al. 2008). Here, vectors of each bee taxon were overlaid on the plot of the sites, with the length of the vector representing the strength of the association. A PERMANOVA (9999 permutations, unrestricted permutation of raw data), with habitat type and month as factors, was performed for the bee and plant assemblage in each year to determine if community composition differed between bushland remnants and residential gardens.

## RESULTS

### Bee and plant communities in urban bushland remnant and residential gardens

In both years of surveys the bee and plant community composition differed significantly between habitat type ($p=0.0001$, Table 1), with assemblages clearing clustering in NMDS space (Fig. 1a-d), with differences being particularly pronounced for the plant communities (Fig. 1c-d). Average similarity of assemblages within each habitat were similar for both bushland remnants and residential gardens (Table 1). Honeybees ~~were associated with residential gardens,~~ and to a lesser extent, the native bee taxa *Amegilla, Exoneura, Lasioglossum,* and *Homalictus*, were associated with residential gardens. In contrast, the native bee taxa Euryglossinae, *Leioproctus,* and especially *Megachile*, were associated with bushland remnants (Fig. 1a, b). These differences in the association of bee taxa to bushland remnants and residential gardens were reflected in variation in the relative proportion of each taxonomic group (Fig. 2a, b).

## Network summary

Across all surveys network size ranged from 3 – 27 (where network size = bee taxa + plant taxa), with the number of interactions ranging from 10 – 6165 (Online Resource 3). Mean network size in the first year was 9.6 ± 0.4, with a mean number of interactions of 339.8 ± 66.9, whereas in year two mean network size was 13.8 ± 0.5, with an average of 633.1 ± 93.9 interactions. Across all surveys residential gardens had larger network sizes than bushland remnants on average (residential gardens: 13.8 ± 0.9, bushland remnants: 10.4 ± 0.5), as well as a greater number of interactions (residential gardens: 651.5 ± 109.1, bushland remnants: 380.1 ± 61.2) (Table 2). Differences in network size by habitat were significant in the second year, and trending towards significance in the first year; however, there was no significant difference between habitats in number of interactions for either year (Table 2). Examples of a network in each habitat type in each year are visualised in Fig. 3 a-d.

## Network properties

### *$H_2$': network generalisation*

Across all surveys in year one, average $H_2$' was 0.7 ± 0.04. No difference between bushland vs. residential habitats in the generalisation of their plant-pollinator networks was observed ($p=0.210$, Table 2). In year two, average $H_2$' score across all surveys was 0.6 ± 0.03. There was a trend for plant-pollinator networks in bushland remnants to be more generalised (based on their $H_2$' score) than those in residential gardens ($p=0.057$, Table 2).

### *Weighted connectance*

Average weighted connectedness of plant-pollinator networks was 0.2 ± 0.01 in year one and 0.2 ± 0.005 in year two. There was no significant difference in plant-pollinator networks between urban and residential sites with respect to weighted connectance in year one (p=0.320), whereas in year two here was a trend (p=0.059) for connectance to be higher in bushland remnants than residential gardens (p=0.059) (Table 2)

*Nestedness (NODF)*

Average NODF in year one was 35.7 ± 3.5, and was 42.4 ± 1.7 in year two. NODF did not differ by habitat in year one (p=0.489, Table 2), but trended towards being high in in bushland remnants than residential gardens (p=0.067, Table 2).

*Extinction slope (pollinators)*

Extinction slope for pollinators was significantly higher in bushland sites in year one (p=0.006, Table 2), suggesting that pollinators were more prone to secondary extinctions if plant taxa are eliminated from bushlands sites. Extinction slopes of the pollinators, however, did not differ between habitats in year two (p=0.44),

*Extinction slope (plants)*

There was no significant difference in extinction slopes for the plant network on which bees were recorded foraging in year one (p=0.411, Table 2), whereas extinction slope at the plant level was significantly higher in bushland remnants than residential gardens in year two (p=0.001, Table 2).

*Robustness to extinction*

In the first year of surveys pollinator-level network robustness was significantly higher in bushland sites than residential (p=0.003), whereas robustness at the level of the visited plants did not differ between habitats (p=0.594, Table 2). Robustness of plant-pollinator networks in both habitats in the first year was >0.5, with a mean robustness value of 0.6 ± 0.01, indicating that few secondary extinctions of native bees will occur if some plants are lost from the network (Table 2). Plant networks were also robust to secondary extinctions, with a mean robustness of 0.6 ± 0.01. In the second year, robustness at the level of pollinators did not differ between habitats (p=0.593), whereas robustness was significantly higher for the plant level in bushland remnants (p=0.001, Table 2).

*Niche overlap*

Overall niche overlap between all bees across all sites and months was 0.4 ± 0.03 in year one and 0.5 ± 0.03 in year two. Niche overlap did not vary by habitat type in year one (p=0.34), however niche overlap was significantly higher in residential areas in year two (p=0.011, Table 2).

### *Functional complementarity*

Functional complementarity between pollinators did not differ between habitat types (year one: p=0.410, year two; p=0.194, Table 2).

### *Normalised degree*

Normalised degree was the only index to differ significantly between habitats, where species in networks in bushland remnants had a significantl~~lt~~y higher normalised degree than those in residential garden networks in both year one (mean bushland remnants: 0.5 ± 0.02 vs. mean residential: 0.4 ± 0.03, p=0.005, Table 3), and in year two (mean bushland: 0.4 ± 0.02 vs. mean residential: 0.3 ± 0.02, p=0.0003).

### *Species strength*

There was no difference in strength bewteen habitats in year one or year two (Table 3).

### *Species specificity*

Specificity did not differ between bushland remnants and residential gardens in both year one and year two (Table 3).

### *Pollination Service Index (PSI)*

There was a trend for IPP to differ between habitats in year one (p=0.077), being higher in residential areas, suggesting bees are more reliant on plants than vice versa in residential gardens, but in both habitat types on average bees were more reliant on the plant level than plants on the pollinator level (bushland: -0.3 ± 0.05, residential: -0.1 ± 0.06, Table 3).

### *Blüthgen's d'*

The degree of interaction specialisation at the species level, d', did not vary between habitats in either year (Table 3). d' did not differ between habitats (Table 3).

**Modularity**

In year one all networks had 4 or 5 modules, with an average of 4.3 ± 0.2, and modularity was low, averaging 0.3 ± 03. In year two, networks contained 3-5 modules, with an average of 4.2 ± 0.2, and mean modularity was 0.3 ± 0.02. Modularity and number of modules did not differ between habitats in either year (Table 3).

## DISCUSSION

Consistent with our hypothesis of how plant-pollinator networks would differ in their structure between managed residential gardens and natural remnant native vegetation, we found that there were significant differences ~~in~~ for a number of properties between these two urban habitat types. Extinction slopes, robustness and nestedness were often higher for bushland remnants, whereas niche overlap was higher in residential gardens (Fig. 4a). Species-level properties did not differ between habitat types, except normalised degree, which was higher in residential gardens, and in year two species specificity index was higher in bushland remnants, whilst there was a trend for interaction push-pull to be higher in residential gardens in year one (Fig. 4b). Modularity and number of modules was unaffected by habitat type (Fig. 4c). These differences in network structure likely were due to differences in the assemblage composition of bees and plants in these habitat types, which exhibited clear difference at both the bee (Fig. 1a,b, Fig. 2) and plant levels in both years (Fig. 1c, d).

A previous network analysis was performed comparing ornamental garden networks with networks in a natural habitat outside of urban settlements (Gotlieb et al. 2011). Unlike in our study where $H_2$' (generalisation) did not differ between garden and natural network, Gotlieb et al. (2011) found that network-level generalisation was significantly higher in gardens. The difference may stem from how Gotlieb et al. (2011)'s study was undertaken in a desert where differences between the habitat types are more extreme and there was almost no overlap in plant species. Another non-mutually-exclusive explanation is that, because in our study plots of the different habitat types were interspersed within the same urbanised region differences were dampened out. However, as with our study, Gotlieb et al. (2011) also did not find differences in community or species-level generalisation. It thus appears the difference in network-level generalisation is largely due to the plant species in the gardens.

A recent study compared network complexity, specialisation, and flower visitor generality of plant-pollinator networks across an agricultural to urban gradient (Theodorou et al. 2017), where it was found that the degree of urbanisation was positively associated with network and flower-visitor specialisation. These findings align with the present study where the more urbanised residential sites had lower network generalisation than the urban bushland sites (at least in year two). This pattern can be considered to arise from how in more urbanised areas the majority of flowering plants are exotic and are not preferred by native bees, such that the native bees concentrate their foraging efforts on the few native, preferred plants available.

## Network properties

The average value of $H_2$’ across all networks in both years revealed that that plant-pollinator networks in the urbanised SWWA biodiversity hotspot are composed of specialised species. Moreover, it should be emphasised that this value considerably underestimates the true selectivity given that bee taxa were not resolved to species-level for these analyses.

$H_2$’ was higher in bushland remnant networks than in networks in residential gardens, which reflects how bushland remnants provided habitat for more specialised species, with a greater number of oligolectic bee species being dependent upon such habitats (Prendergast~~,~~ 2020a). In particular, there was a greater representation of Euryglossinae – an Australian endemic subfamily that are almost all oligoleges (Houston 2018), in the bushland remnants, whereas the social polylectic *Exoneura* (Allodapini) (Houston 2018), were associated with residential gardens. This pattern therefore reveals how bushland remnants are important for the preservation of specialised species’ interactions. The average level of $H_2$’ across all surveys in both habitats however indicated that plant-pollinator networks observed here are highly specialised. The reason for this high degree of specialisation remains to be elucidated, but it may reflect the long period of isolation and relative climate stability in the southwest Western Australian biodiversity hotspot, allowing co-evolution between native bees and flora (Hopper 2009). Further studies in similar habitat types in other countries, and studies in different habitat types in the southwest Western Australian biodiversity hotspot (i.e. agricultural and natural landscapes) may help identify an explanation. Further studies looking at the fidelity of bee-plant associations across years will shed light on the extent of specialisation (Alarcón et al. 2008; Prendergast & Ollerton, in prep.).

Nestedness is proposed to enhance community stability (Bastolla et al. 2009; Saavedra et al. 2013), and therefore it appears that our bushland networks, with generally higher nestedness values than residential networks, have greater stability. Analyses outside of urban areas have found most plant-visitor networks are highly nested in structure (Bastolla et al. 2009). The levels of nestedness (as NODF) reported here are comparatively high for plant-visitor networks, compared with a dataset of 54 community-wide pollination networks (4.0-63.6, mean 20.9, median 28.8) (Trøjelsgaard and Olesen 2013). Comparing NODF values of other urban flower visitor networks, the NODF values here are exceptionally higher than those of (Jędrzejewska-Szmek and Zych 2013), however making direct comparisons is difficult since they included non-bee taxa at the pollinator-level, whilst limiting observation to ruderal communities at the plant-level. In contrast, those reported by Zotarelli et al. (2014) were higher than those of the NODF values reported here, but again direct comparisons are difficult to make since only corbiculate bees were included in their study.  Further studies are required to determine whether these differences reflect differences in the assemblage, environment, taxonomic resolution, or taxonomic range of pollinators.

Values of weighted connectance averaged across sites were comparatively high compared with those typically reported across networks in the literature (Traveset et al. 2016), which don't exceed values of about 0.16; this contrasts with values reported here of 0.205 ± 0.012 for the bushland remnant networks, and 0.189 ± 0.010 for the residential garden networks. Therefore, a high number of links were realised, and networks were highly connected. This high level of connectance can also be taken to indicate a high level of stability in these networks (Thébault and Fontaine 2010), which counters the assumption that urbanised habitats, as 'disturbed' habitats, are unstable (Ferreira et al. 2013; Garibaldi et al. 2011). It should be noted however that, in comparison to networks resolved at the species-level, those resolved at lower taxonomic resolution tend to have higher absolute values of connectance (Renaud et al. 2020). Additionally, the interpretation of connectance as being an indicator of stability has been called into question (Heleno et al. 2012). Moreover, it should be noted that, as is typical for most bipartite networks, only realised interactions were included – plants that were not visited were not included in the construction of the networks. Field observations revealed that, especially for the residential gardens, the majority of plants were in fact not visited (Prendergast 2020b~~& Mason, in review~~). Thus, common to bipartite networks as a whole, our results only apply to the subset of flora that were involved in interactions with bees in the system.

The lower niche overlap of plant-pollinator networks in bushland sites in year two can be considered to reflect how bee taxa were better able to partition resources, and there was lower competition among pollinators in this habitat. This result may at first seem counter-intuitive, given that residential gardens tend to be characterised by a high floral diversity (McKinney 2008). However, they are in accordance of the higher network specialisation values in bushland, such that specialised species could partition resources in bushlands that hosted high number and proportions of native flora (Prendergast 2020b~~& Mason, in review~~), whereas the relatively lower proportion of native flowers of the total flower diversity in residential gardens meant that native bees were constrained to forage on the same restricted set of resources in residential gardens. As niche overlap is often considered to be a proxy for competition (Pianka 1974), this suggests competition for resources may be more intense in residential gardens, and is in accordance with greater potential for competition in more disturbed habitats (Aizen & Feinsinger 1994). These patterns do not reflect differences in relative abundance of flora, since we previously found that not only did floral abundance not influence pollinator visitation patterns (Prendergast & Mason, in review), but a greater number of plants were visited in bushland remnants than residential gardens, despite the lower species diversity (Prendergast & Mason, in review).

Measures of niche overlap were unusually high compared with the 52 networks analysed by Traveset et al. (2016), despite urban areas having an exceptionally high diversity of flowering plants. It may be that the native bee fauna of Australia has co-evolved to forage on a restricted range of endemic flora, resulting in high overlap in the resources used. Due to many singletons in the system (Prendergast 2020a), this limited calculating niche overlap between bees at species-level, however it may be that values of niche overlap would be reduced if they were calculated at a species-level taxonomic resolution.

We found opposite patterns between habitats comparing extinction slope and robustness: extinction slope of bushlands was higher than that of residential gardens for pollinators (year one) and plants (year two), whereas robustness was of bushlands was higher than that of residential gardens for pollinators (year one) and plants (year two). This suggests that although bushland remnants are less fragile to losses of one level causing losses at another level, if losses do occur, the severity of cascading extinctions is greater.

## Species-level properties

In year one and two, normalised degree at the species level across taxa was significantly higher in bushland remnants than in residential gardens. This finding is unexpected, given that residential gardens had a significantly higher number of plant taxa potentially available for bees to intereact with (Prendergast 2020b~~& Mason, under review~~), and studies in other systems have found plant species richness tends to promote bee species richness and visitation frequency (Ebeling et al. 2008). Our results suggests that there are larger number of *preferred* plant species in bushland remnants, providing a greater range of plants that bees will visit, and shows the value of using a network approach to reveal unexpected patterns that are not apparent when considering observed numbers of flowering plants present. A previous pollinator network approach likewise found that increases in the number of plant species available to pollinators does not necessarily translate into increased numbers of flora visited for specialists – which represented the majority of bees in our system, who are "choosy" in the flowers they visit (Vamosi et al. 2014). In year two, species specificity index was higher in bushland remnants, again emphasising the greater number of specialised species in this habitat type.

Values of interaction push-pull revealed that in both habitats, bees tended to be more reliant on plants than vice versa. This dependence asymmetry of pollinators being more reliant on plants may be a reflection of the urbanised environment, whereby only native flora that are visited by many pollinators can persist, and exotic flora are necessarily visited by generalist bees. It may also relate to our study system, as Myrtaceae, which represents the dominant plant family in Australia, relies on a generalist pollination strategy, and is visited by a great many native bees, including a large number of specialists (Brown 1997; Houston 2000). Our results underscore the importance of planting native flowering species that cater to native bees in urban areas, especially in light of a recent study revealing the vulnerability of pollinators to habitat disturbance, exotic species, and loss of host plants (Mathiassen & Rehan 2020). Average values of d' fall within that measured from other habitat types (Weiner et al. 2011) suggesting that bees as a taxonomic group have a general range of d' values across habitat and landscape types.

### Modularity of networks

The modularity scores calculated here were comparatively low compared with those calculated for 23 plant-pollinator networks by Beckett (2016). Although this may be influenced by the pollinator-level networks being resolved at genus, rather than species-level (Renaud et al. 2020); the low modularity scores may be a positive sign of the intactness of plant- flower visitor networks in this biodiversity hotspot. This is despite habitat loss due to urbanisation, since increased modularity has been associated with habitat loss and a corresponding potential to result in extinction debts for ~~e~~ assemblages already suffering from habitat loss (Spiesman and Inouye 2013). Increases in network modularity have also been proposed to reflect the loss of many links across modules when core nodes  are lost (such as when generalist connector species are lost and disconnected from modules), rendering networks less cohesive and more vulnerable (Olesen et al. 2007; Thébault and Fontaine

2010). On the other hand, low modularity has been proposed to be an indicator of disruptions of specialised co-evolutionary plant-pollinator units, as can be expected to occur under recent disturbance (Dalsgaard et al. 2013). It should be noted that modularity could only be calculated from networks at the larger scales, created from surveys across multiple sites. As such, whether these modularity results (as well as modules calculated from other studies that have likewise pooled networks across sites or months), are "real" modules is questionable: they may be an artefact of lumping.

### Biological implications for urban plant-pollinator networks

Our results suggest that replacement of natural vegetation with home gardens, despite both being "urban greenspaces" causes major alterations of plant-pollinator interactions. Even with a greater number of interactions occuring in residential gardens, these interactions were less robust, and nesteded, whereas bushland remnants appears to be more vulnerbale to cascading extinctions, and contain more specialised interactions. Together these differences suggest that residential networks that are of lower conservation value. We can see that this altered structural appears to arise from the greater dominance of the introduced European honeybee, which can monopolise interactions, and occupy interactions with exotic plants that are unsuitable for native bees (Aizen, Morales & Morales, 2008). Our study has also suggests that differences assemblage composition in terms of relative abundances of different taxa translate to differences in the emergent structure of networks. Consequently, to preserve biodiversity as a whole across urban environments (Tylianakis et al. 2020), preservation of native bushland remnants is required to prevent loss of mutual interactions and co-evolved relationships (Pauw 2007).

### Caveats and considerations

This study involved constructing and comparing network properties across two years. By doing so it was revealed that values of network and species-level properties, as well as the significance or lack thereof of differences between habitats or species, at times differed between the networks constructed in the first and second years. This raises questions about the interpretation of conclusions of previous studies where networks are created by merging data gathered over multiple years, or just based on a single year of data collection. Indeed, in this study, and in plant-pollinator networks in general, it is known that plants and bees both display strong temporal dynamics (Alarcón et al. 2008; Burkle and Irwin 2009; Lázaro et al. 2010; Olesen et al. 2008; Trøjelsgaard and Olesen 2016).

In our analyses, the pollinator-level was represented by bee genera (or in the case of Euryglossinae, subfamily). It remains to be determined whether taxonomic resolution would alter the qualitative conlusions observed here (Renaud et al. 2020). Whilst networks could be constructed at the species-level, the ease at which different taxa can be collected, and their observed:sweepnetted ratio varies, resulting in taxonomic biases (Prendergast et al. 2020). The ability to calculate various metrics would also be hampered by the numerous singletons in this system. Moreover, by using functional taxonomic groupings, this provides an eco-evolutionary context. Differences between the current study and some studies cited above which involved finer (or coarser) levels of taxonomic resolution however may limit such cross-study comparisons, in terms of absolute values of network properties except for network robustness (Renaud et al. 2020); nevertheless, relative values of indices appear to be robust to taxonomic resolution (Renaud et al. 2020).

## Conclusion

For the first time comparing urban plant-pollinator networks between patches of remnant native vegetation with residential garden greenspaces, we have revealed that plant-flower-visitor networks differ in numerous network-level properties. Bushland remnants had lower niche overlap, higher robustness and nestedness, but higher extinction slopes. This suggests that they had greater environmental integrity, and represented higher environmental quality, than pollination networks in residential gardens (Ferriera, Boscolo & Viana 2013); however, if disrupted, they would be more prone to cascading extinctions. We conclude that conversion of native vegetation remnants to residential gardens under urbanisation has major impacts on plant-pollinator network properties.

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## TABLES

**Table 1.** Percentage similarity between bushland remnants and residential gardens in the bee and floral taxonomic community composition, and the test statistics associated with a PERMANOVA comparing community composition between habitat types.

| **Year** | **Assemblage** | **Average similarity (%)** | | | **df** | **t** | **p** | **unique perms** |
|---|---|---|---|---|---|---|---|---|
| | | **Bushland - Bushland** | **Residential garden - Residential garden** | **Bushland - Residential Garden** | | | | |
| One | Bees | 51.8 | 51 | 45.3 | 48 | 3.08 | 0.0001 | 9950 |
| | Plants | 14.1 | 12 | 4.4 | 48 | 2.57 | 0.0001 | 9896 |
| Two | Bees | 55.6 | 55 | 52.2 | 72 | 2.81 | 0.0001 | 9948 |
| | Plants | 17.5 | 17 | 4.7 | 72 | 3.85 | 0.0001 | 9893 |

**Table 2.** Network-level properties of urban plant-pollinator networks constructed from bushland remnants (7 sites) and residential gardens (7 sites). For each year of surveys, average values are provided for each metric across all surveys, as well as that for each habitat type. Generalised linear mixed effect model outputs comparing metrics between habitats are presented; significant differences ($p<0.05$) are in bold, and trends towards significance ($p=0.05-0.1$) are italicised.

| | **Year one** | | | | | | **Year two** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Network property** | **Overall (n=56)** | **Bushland (n=28)** | **Residential (n=28)** | **Δ AICc** | **$X^2$** | **p** | **Overall (n=56)** | **Bushland (n=28)** | **Residential (n=28)** | **Δ AICc** | **$X^2$** | **p** |
| **Network size** | 9.61± 0.44 | *8.36 ± 0.42* | *10.86 ± 0.71* | *1.1* | *3.60* | *0.080* | 13.76 ± 0.511 | **11.76 ± 0.62** | **15.76 ± 0.694** | **18.3** | **20.27** | **<0.001** |
| **No. of interactions** | 339.8 ± 66.8 | 220.40 ± 48.5 | 513.1 ± 65.6 | 0.1 | 2.05 | 0.152 | 633.1 ± 93.9 | 486.5 ± 93.6 | 743.8 ± 175.9 | 1.4 | 0.60 | 0.435 |
| **$H_2'$** | 0.63 ± 0.04 | 0.67 ± 0.06 | 0.59 ± 0.06 | 0.4 | 1.58 | 0.209 | 0.593 ± 0.032 | *0.65 ± 0.04* | *0.53 ± 0.04* | *1.6* | *3.62* | *0.057* |
| **weighted connectance** | 0.20± 0.01 | 0.21 ± 0.01 | 0.19 ± 0.01 | 1.0 | 1.01 | 0.316 | 0.150 ± 0.005 | *0.16 ± 0.01* | *0.14 ± 0.001* | *1.5* | *3.57* | *0.059* |
| **nestedness (NODF)** | 35.73 ± 3.45 | 38.32 ± 5.77 | 33.14 ± 3.82 | 1.4 | 0.57 | 0.449 | 42.36 ± 1.69 | 42.38 ± 2.34 | 42.33 ± 2.46 | 1.9 | 0.13 | 0.723 |
| **extinction slope bee visitors (higher level)** | 1.74 ± 0.01 | **2.07 ± 0.15** | **1.42 ± 0.09** | **4.5** | **7.47** | **0.006** | 2.03 ± 0.08 | 1.97 ± 0.12 | 2.11 ± 0.11 | 1.4 | 0.60 | 0.440 |
| **extinction slope plants visited (lower level)** | 1.80 ± 0.09 | 1.73 ± 0.10 | 1.88 ± 0.14 | 1.2 | 0.82 | 0.367 | 1.65 ± 0.07 | **1.89 ± 0.12** | **1.43 ± 0.05** | **8.8** | **10.80** | **0.001** |
| **robustness bee visitors (higher level)** | 0.61 ± 0.01 | **0.65 ± 0.01** | **0.58 ± 0.01** | **6.8** | **8.87** | **0.003** | 0.67 ± 0.01 | 0.68 ± 0.12 | 0.66 ± 0.01 | 1.7 | 0.29 | 0.593 |
| **robustness plants visited (lower level)** | 0.63 ± 0.01 | 0.63 ± 0.01 | 0.63 ± 0.01 | 2.0 | 0.03 | 0.858 | 0.61 ± 0.01 | **0.65 ± 0.01** | **0.60 ± 0.01** | **8.9** | **10.90** | **0.001** |
| **niche overlap** | 0.38 ± 0.03 | 0.42 ± 0.04 | 0.33 ± 0.04 | 1.1 | 0.90 | 0.344 | 0.50 ± 0.03 | **0.39 ± 0.03** | **0.60 ± 0.04** | **4.5** | **6.51** | **0.011** |
| **functional complementarity** | 505.31 ± 119.35 | 595.49 ± 221.73 | 415.13 ± 90.02 | 0.6 | 2.55 | 0.110 | 992.19 ± 204.06 | 1404.09 ± 389.75 | 570.23 ± 67.18 | 0.3 | 1.68 | 0.194 |

**Table 3.** Species-level properties of urban plant-pollinator networks constructed from bushland remnants (7 sites) and residential gardens (7 sites). For each year of surveys, average values are provided for each metric across all surveys, as well as that for each habitat type. Generalised linear mixed effect model outputs comparing metrics between habitats are presented; significant differences ($p<0.05$) are in bold, and trends towards significance ($p=0.05$-$0.1$) are italicised.

| **Species-level network property** | **Year one** | | | | | | **Year two** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Overall (n=219)** | **Bushland (n=114)** | **Residential (n=105)** | **Δ AICc** | **$X^2$** | **p** | **Overall (n=389)** | **Bushland (n=209)** | **Residential (n=180)** | **Δ AICc** | **$X^2$** | **p** |
| **normalised degree** | 0.43 ± 0.02 | **0.47 ± 0.02** | **0.39 ± 0.030** | **6.1** | **8.06** | 0.005 | 0.36 ± 0.01 | **0.39 ± 0.02** | **0.33 ± 0.02** | **10.9** | **12.9** | **<0.001** |
| **species strength** | 1.29 ± 0.13 | 0.87 ± 0.09 | 1.74 ± 0.24 | 0.2 | 1.86 | 0.170 | 1.81 ± 0.14 | 1.33 ± 0.14 | 2.36 ± 0.18 | 0.2 | 1.86 | 0.172 |
| **interaction push-pull** | -0.21 ± 0.04 | *-0.27 ± 0.05* | *-0.15 ± 0.06* | *1.1* | *3.12* | *0.080* | -0.13 ± 0.03 | -0.17 ± 0.04 | -0.10 ± 0.03 | 0.6 | 1.42 | 0.234 |
| **species specificity index** | 0.85 ± 0.01 | 0.85 ± 0.02 | 0.84 ± 0.02 | 1.9 | 0.10 | 0.755 | 1.89 ± 1.06 | **2.81 ± 1.97** | **0.82 ± 0.01** | **290.6** | **292.6** | **<0.001** |
| **PSI** | 0.71 ± 0.03 | 0.69 ± 0.04 | 0.72 ± 0.04 | 1.8 | 0.21 | 0.649 | 0.48 ± 0.02 | 0.46 ± 0.02 | 0.51 ± 0.02 | 0.1 | 1.92 | 0.166 |
| **d'** | 0.44 ± 0.02 | 0.42 ± 0.03 | 0.47 ± 0.04 | 0.6 | 1.45 | 0.230 | 0.46 ± 0.02 | 0.44 ± 0.02 | 0.47 ± 0.02 | 1.4 | 0.63 | 0.426 |

**Table 3.** Modularity and number of modules of urban plant-pollinator networks in bushland remnant and residential gardens, calculated from networks constructed pooling all surveys conducted in each habitat in a given month.

| **Modularity** | **Year one** | | | | | | **Year two** | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **Overall (n=8)** | **Bushland (n=4)** | **Residential (n=4)** | **SS** | **F** | **p** | **Overall (n=12)** | **Bushland (n=6)** | **Residential (n=6)** | **SS** | **F** | **p** |
| **Modularity** | 0.25 ± 0.03 | 0.297 ± 0.03 | 0.22 ± 0.04 | -0.002 | 0.27 | 0.621 | 0.300 ± 0.028 | 0.345 ± 0.05 | 0.27 ± 0.02 | -0.014 | 1.66 | 0.227 |
| **Module N** | 4.25 ± 0.16 | 4.25 ± 0.25 | 4.25 ± 0.25 | -1.000 | 0.00 | 1.000 | 4.167 ± 0.207 | 3.83 ± 0.17 | 4.50 ± 0.34 | -1.333 | 3.08 | 0.11 |

## FIGURES

**Fig. 1. NMDS plots of the bee taxonomic composition in year one (a) and year two (b) and plant community composition in year one (c) and year two (d).** Each point represents a survey, with surveys in bushland remnants and residential gardens symbolised by different colours and symbols. Vectors of each bee taxon are overlain on a and b, with the length of the vector approximating the strength of the association.

**Fig. 2. Relative proportion of each bee taxonomic group in year one (a) and year two (b).**

**Fig. 3. Illustrative examples of bipartite plant-pollinator networks:** a) bushland remnant (Wireless Hill, January 2017), year one; b) residential garden (Gosnells, January 2017), year one; c) bushland remnant (Piney Lakes, January 2018), year two; d) residential garden (Bibra Lake, January 2018), year two. Pollinators are the upper level, plants the lower level. Honeybees are depicted in red, native bees in gold, exotic flora in dark green, and native flora in light green. The width of bars indicate the number of visits to a plant species by a bee taxon.

**Fig. 4. Summary of how network parameters compare between plant-pollinator networks in bushland remnants and residential gardens.** Up arrows indicate higher in that habitat and conversely down arrows indicate that parameter is lower in that habitat; equal sign means that parameter does not differ significantly between habitat types.

## Electronic Supplementary Information

**Online Resource 1 Table S1 Taxonomic categories**

**Online Resource 2 Definitions of network and species-level indices**

**Online Resource 3 Table S1 Network sizes.** Network size was calculated as animals + plants (following Albrecht et al. 2010; Chacoff et al. 2012; Santamaría and Rodríguez-Gironés 2007).