A global review of determinants of native bee assemblages in urbanised landscapes

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Abstract

1. Loss of natural habitat through land-use change threatens bees. Urbanisation is a major, increasing form, of habitat loss, and a novel, pervasive form of disturbance known to impact bee diversity and abundance in a variety of often inconsistent ways.

2. We conducted a comprehensive, semi-quantitative review, involving 215 studies, on responses of bees to urban landscapes, and local and landscape variables proposed to influence bee abundance and diversity.

3. Urban areas tend to be favourable habitat for bees compared with agricultural ones, but compared with natural areas, urban areas often host more abundant populations yet fewer species.

4. Factors associated with urban landscapes, including changes in foraging resources and nesting substrate types and availability, contribute to changes in abundance, species richness, and composition of native bee assemblages. However, the conclusions of studies vary greatly because of the difference in the ecological traits of bees, habitats surveyed, and geographic region, as well as noise in the data resulting from inconsistencies in sampling methodology, and definitions of ‘urban’ and ‘natural’.

5. Identifying what biotic and abiotic features of cityscapes promote or threaten the persistence of urban bee diversity is critical. We provide a comprehensive evaluation of how bees (both in aggregate and according to their ecological guild) have responded to the urban environment, identify gaps in knowledge in urban bee ecology, and make recommendations to advance our understanding of bees in urban environments to promote conservation of diverse bee communities.

KEYWORDS

cities, conservation, ecological traits, knowledge gaps, pollinators, urban ecology

INTRODUCTION

Bees are the most important pollinating group globally (Willmer et al., 2017) and the pollination services they perform are essential for stable, functioning ecosystems, both natural and anthropogenic (Potts et al., 2016). Although the domesticated European honey bee Apis mellifera L. is the most familiar and widely managed pollinator, wild bees, with an estimated global diversity of over 20,000 species (Ascher & Pickering, 2020), are critical to healthy ecosystems and are an essential component of biodiversity (Garibaldi et al., 2013; Potts et al., 2016).
There have been documented declines of bees across Europe, America, and China, particularly over the last 50 years (Bartomeus et al., 2013; Biesmeijer et al., 2006; Williams et al., 2009). But while there are concerns that bee declines are a global phenomenon (Potts et al., 2010), the conservation status of most bees is unknown (Nieto et al., 2014; Potts et al., 2016). The cause(s) of these declines include habitat loss, fragmentation and degradation, poor nutrition, disease, toxins, climate change, inappropriate disturbance regimes, and exotic species (Brown & Paxton, 2009; Goulson & Nicholls, 2016). Urbanisation can involve all of these threatening processes.

Urbanisation is considered a leading form of ecologically destructive global change (Elmqvist et al., 2016). Urbanised environments – landscapes of human settlement that are created specifically for human occupation (Adler & Tanner, 2013; McIntyre et al., 2008) – are the most heavily modified and rapidly expanding forms of anthropogenic land-use modification (Seto et al., 2011). By 2030, global urban expansion is predicted to increase by 285% over 2000 levels (Seto et al., 2012) and is occurring in regions known to harbour rare, endemic fauna (e.g. Ives et al., 2016; Phillips et al., 2010). Urbanisation is now a major driver of fragmentation and loss of natural habitat (Winfree et al., 2007), and a key cause of biodiversity loss worldwide (Brown & Paxton, 2009), with bees predicted to be especially susceptible (Winfree et al., 2011). However, depending on patch quality and connectivity, and the surrounding matrix, urban areas have the potential to support a high diversity and abundance of native bees (Hinners et al., 2012) (Supplementary Materials S1). This may especially be the case when comparing urban with agricultural assemblages, which contrasts highly complex landscapes typical of urban areas, with low-complexity landscapes typical of agricultural monocultures. Although urban and agricultural lands are both anthropogenic habitats, they differ abiotically and biotically (Table 1), reflected in distinctive bee assemblages (e.g. De Palma et al., 2015, 2016; Sattler et al., 2011). Generalisations from bee responses to agricultural landscape modification should not, therefore, be extrapolated to urban landscapes.

Urbanisation can be predicted to influence native bee populations by altering the amount, quality, diversity, and distribution in space and time of the two most important resources for bees: flowers and nest sites. Urbanisation also alters the plant community composition, whereby native vegetation is often replaced by exotic plants. Urbanisation can be considered as a selective force filtering out species that are maladapted to urban conditions and selecting for ‘synanthropic’ species, which may reach high abundances (McKinney, 2006). Traits such as resource specialisation, body size, sociality, nesting substrate, and kleptoparasitism can be expected to determine the success of bee taxa in urban landscapes (Table 2) and influence species richness, abundance, evenness, community composition and functional and phylogenetic diversity of bee communities. These in turn can have implications for pollination; for example, functional trait diversity has been shown to maximise pollination (e.g. Fründ et al., 2013; Woodcock et al., 2019).

Evidence-based recommendations for bee-friendly management in cities are rare (notable exceptions include Bee City USA®; Bee City USA, 2021; Bee City Canada; Bee City Canada, 2021; and the European Commission’s ‘A Guide for pollinator-friendly cities’; Wilk et al., 2019). Moreover, planting guides are often focussed on the domesticated, often introduced and non-threatened European honey bee (e.g. Edmansun, 2021), giving honey bees a competitive edge and favouring this introduced species to the detriment of native bees (Prendergast et al., 2021). There are, however, promising opportunities to harmonise bee conservation with activities that promote ecosystem services and human welfare in cities. For improved management plans to be developed, there is a need to understand the current state of the science and where the knowledge gaps remain.

Here, we review publications on the responses of wild bees to urbanisation throughout the world. Although there have been reviews on, or that include, bees in urban areas (Cane et al., 2005; De Palma et al., 2015; Hall et al., 2017; Hernandez et al., 2009; Wenzel et al., 2019; Winfree et al., 2009; Winfree et al., 2011; Wojcik, 2009; Wojcik & Buchmann, 2012), ours is the most comprehensive to date with 215 studies reviewed in total. Moreover, our review is the first to conduct semi-quantitative analyses, investigating how abundance and species richness vary according to landscape type, local and landscape variables, and how responses vary among bee taxa with different functional traits. We also identify key knowledge gaps in understanding the determinants of urban bee abundance and diversity.

METHODS

From August 2016 to December 2019 searches were performed in Google Scholar using combinations of the terms: ‘bees, pollinators, insects, arthropods, native bees, wild bees’ combined with ‘urbanisation, cities, urban, land-use change, suburban, metropolis’.

Google Scholar was chosen as it has less barriers than many other search engines (Martin-Martin, 2018, 2021): it is not restricted to users affiliated with a research institution and does not suffer from constrained coverage. Thus, our search included theses, books, reports, conference proceedings and articles, which may not be in mainstream English science journals (e.g. especially those published in developing countries) (e.g. Haddaway et al., 2015; Haddaway & Bayliss, 2015; Meneghini & Packer, 2007). This approach allowed us to achieve our objective of providing a comprehensive review on bees in urban areas.

Each text was incorporated if it included a measure of bee(s) abundance, reproduction or species richness in an urbanised landscape or response to urbanisation (however defined by the authors of the paper – see results below and Supplementary Materials S2). Papers included in this review therefore were either conducted in urban landscapes or in non-urban habitats that considered the influence of surrounding urban land use on bees.

Our search of the literature yielded a total of 215 studies from 198 publications (disparities result from unpublished studies cited in published ones, or multiple studies published in one text)
| Characteristic                          | Urban         | Agricultural | Natural                  | Characteristic's potential effects on bees in an urban situation | Examples                                      |
|----------------------------------------|---------------|--------------|--------------------------|-----------------------------------------------------------------|-----------------------------------------------|
| Habitat heterogeneity                  | High          | Low          | Low to intermediate      | +: ↑ diversity of habitats = resources for ↑ species of bees; ↓ fragmentation and reduced patch size = ↓ patch colonisation and ↓ area suitable for foraging/nesting | +: Kaluza et al. (2016); ←: Theodorou et al. (2021) |
| Habitat fragmentation                  | High          | High         | Low                      | +: ↑ range of habitat types; ←: reduces (re) colonisation of suitable habitat patches; ↓ demographic and genetic connectivity; ↓ habitat size | +: Cane (2001); Everaars et al. (2018); Yates and Ladd (2005) ←: (Davis et al. 2010); Didham et al. (1996) |
| Patch size                             | Small         | Small to moderate | Large                 | +: concentrate resources = ↑ bee density (but ↓ abundance at landscape scales); ←: smaller patches = ↓ bees and species Alter competitive dynamics: refuge from competition? or intensify competition? | +: Steffan-Dewenter et al., 2006 ←: Howell et al., 2017 |
| Impervious surfaces                    | High          | Low/absent   | Low/absent               | +: fences and buildings can provide nesting substrates for cavity-nesting bees ←: unsuitable for nesting, foraging | +: Sivakoff et al. (2018); ←: Makinson et al., 2016 |
| Roads                                  | Numerous      | Few          | Few/none                 | +: linear landmarks = navigation and foraging efficiency; vegetated roadsides = nesting and foraging resources ←: ↓ isolation; vehicle collision mortality; impediments to movement ↓ foraging, nesting, population connectivity, geneflow; pollutant exposure; adverse roadside management practices; poor vegetation (weedy grasses). | +: Hopwood et al. (2015) ←: Baxter-Gilbert et al. (2015) |
| Climate                                | Hotter, more stable Less water-stress when municipalities and | Hotter? (less tree cover in non-tree crops) | Natural                  | ±: smaller, warm-adapted species in temperate areas | ±: Hamblin et al. (2017) +: Petanidou et al. (1999) |

(Continues)
| Characteristic          | Urban                                    | Agricultural                     | Natural                                      | Characteristic’s potential effects on bees in an urban situation                                                                                   | Examples                                                                 |
|------------------------|------------------------------------------|----------------------------------|----------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------|
|                       | home-owners water greenspaces            | Less water-stress (watered)      |                                              | —: large-bodied, cool-adapted species?: / / a species realised niche; alters species composition                                                     |                                                                          |
| Flower abundance       | High depending on site type              | High during crop bloom, low otherwise | Depends on natural habitat type             | +: food = bee N and R ?: alter species composition and competitive conditions                                                                            | +: Smith, Gaston, et al. (2006); Smith, Warren, et al. (2006) —: Plascencia and Philpott (2017) |
| Angiosperm species richness | High                                    | Low                              | Depends on natural habitat type             | +: resource diversity = +: nutrition (polyleges), ↑ chance of host (oligoleges) = ↑ bee species richness. —: within an area, ↓ proportion of preferred plant species; favour polyleges over oligoleges | +: Ebeling et al. (2012); Hennig and Ghazoul (2012); Steffan-Dewenter et al. (2006) —: Prendergast et al. (2022) |
| Native flora           | Low                                      | Almost absent                    | High                                         | +: ↑ exotic pollinators —: maladapted to local bees; ↓ oligoleges Alters assemblage composition                                                                 | ±: Garbuzov and Ratnieks (2014b); Pardee and Philpott (2014)           |
| Floral spatial distribution (clumped vs. dispersed) | High (discrete clumped patches) | Low (large monocultures)          | Low (dispersed)                              | +: clumped, concentrated patches = ↓ time and energy costs; single species of flora in clumps more attractive than dispersed —: dispersed patches allow co-existence between competing bees | +: Cresswell and Osborne (2004) —: Johnson and Hubbell (1975) |
| Environmental contaminants (excluding pesticides) | High (city centres and industrial areas) | Low                              | Low                                          | —: direct and indirect mortality; exhaust fume chemicals interfere with bee foraging                                                                            | —: Lusebrink et al. (2015); Moroń et al. (2012)                           |
| Weeds (exotic, non-managed flora) | High                                      | Low                              | Low                                          | +: abundance of flowers —: weeds = ↓ preferred forage plants; herbicides/pesticides applied to weeds = ↓ bees                                                                                             | ±: Bretagnolle and Gaba (2015)                                        |
| Herbicides             | Moderate                                 | High                              | Low                                          | +: eliminate competitively dominant unsuitable plants —: remove valuable foraging resources;                                                                 | +: Hopwood et al. (2016) —: Le Féon et al. (2010)                             |

(Continues)
Landscape and habitat types were assigned according to categories provided by original authors. For single-species publications, we excluded those on honey bees, as their numbers are largely impacted by husbandry (Champetier et al., 2015).

We could not attempt a formal meta-analysis due to the extreme variability in survey duration and number of sites surveyed, area surveyed, survey methods, sampling intensity, range of flora assessed (single plant species, experimental plants, whole floral communities), and taxonomic resolution (Supplementary Materials S3, S4, Figure 1). Instead, we conducted a semi-quantitative review, an approach that enables quantification of suggestive trends and patterns across the many studies included which varied too widely for a meta-analysis to be appropriate (for examples of the success of semi-quantitative approaches, see: Malinger et al., 2017; Mitchell et al., 2013; Nicholson & Egan, 2020).

We extracted the following information from each publication: the main findings; the type of study (whether it was of an entire community, a subset of the bee community, or focused on just one or a few species); details about the study design (geographic region, city, climatic zone); the number of sites surveyed; duration of the study (number of months per year, number of years), the sampling area, the sampling intensity, and the sampling method used; the landscape type (natural/rural/urban), and the urban habitat type(s) surveyed (see Figure 2b) (Supplementary Materials S1). For studies providing data on bees in urban landscapes as well as those in agricultural and/or natural landscapes, we recorded whether bee abundance and/or species richness was significantly different between these landscapes as

| Characteristic | Urban | Agricultural | Natural | Characteristic’s potential effects on bees in an urban situation | Examples |
|---------------|-------|--------------|---------|---------------------------------------------------------------|----------|
| Pesticides    | Low to Intermediate | High (conventional) | Absent – low (i.e. due to drift) | can cause harm/mortality | −: Arena and Sgolastra (2014) 
|               | Low (Integrated Pest Management or Organic) | Low (Integrated Pest Management or Organic) | | | |
| Ground cover  | Low to high depending on habitat type | Low to high depending on crop and management | Low to high depending on ecosystem | +: open sandy areas in vacant lots, landfills, construction sites and roadsides = ↑ ground-nesting bees −: lawns, turf, mulch = ↓ ground-nesting bees | +: Wesseler and Tscharntke (1995) −: Quistberg et al. (2016) |
| Canopy cover  | Low to intermediate | Low to high (depending on crop growth form) | Low to high depending on ecosystem type | +: ↑ solar radiation = bee activity, and can ↑ herbaceous flowers −: ↑ trees = ↓ foraging and nesting resources | ±: Jha and Vandermeer (2009) +: Winfree et al. (2007) −: Prendergast (2018) |
| Tillage       | Low | High | Absent | −: ↓ food resources; destroys eggs, larvae, pupae and overwintering adults nesting in soil | −: Hopwood (2008); Julier and Tai (2009); Roulston and Goodell (2011) |
| Mowing/grazing| High (mowing) | High (mowing and grazing) | Low to moderate (mowing and grazing) | +: ↑ floral resources (at appropriate scales and frequencies) −: ↓ flowering resources; altered vegetation structure; grazing animals compete with bees | ±: Lerman et al. (2018) +: Hudewenz et al. (2012) −: Del Toro and Ribbons (2020) |
| Exotic bees   | Low to high (especially honey bees) | High | Low to Intermediate | +: ↑ pollination −: outcompete native bees | +: Russo (2016) −: Prendergast and Ollerton (2021a, 2021b); Prendergast et al. (2021) |
### TABLE 2 Predictions on how bee functional traits will influence how bees respond (at a relative advantage or disadvantage) to urbanisation

| Functional trait Categories | Advantages                                                                 | Disadvantages                                                                 | References |
|-----------------------------|----------------------------------------------------------------------------|------------------------------------------------------------------------------|------------|
| **Body size**               |                                                                           |                                                                              |            |
| Larger                      | Greater mobility in fragmented landscapes, maintain higher effective population sizes over larger areas | Higher energy demands                                                        | Cane et al. (2006), Harrison and Winfree (2015), Martins et al. (2013), Müller et al. (2006), and Wright et al. (2015) |
| Smaller                     | Lower energy requirements, can maintain high effective population sizes in small areas | Reduced mobility                                                              | Banaszak-Cibicka and Zmihorski (2012), Harrison et al. (2017); Torné-Noguera et al. (2014), Tscharntke et al. (1998), and Wray et al. (2014) |
| **Sociality**               |                                                                           |                                                                              |            |
| Social                      | Numerically dominant, Highly efficient foraging, Polylectic Store food      | Smaller effective population size Found to be negatively affected by anthropogenic disturbance | Banaszak-Cibicka and Zmihorski (2012), Chapman and Bourke (2001), Roubik (2001), Williams et al. (2010), Winfree et al. (2009), and Zanette et al. (2005) |
| Solitary                    | Found to be more resilient to anthropogenic disturbances                   | Smaller demographic population sizes Lower reproductive rates Do not store food | Roubik (2001), Williams et al. (2010), and Winfree et al. (2009) |
| Host/ kleptoparasites       | If kleptoparasites are disadvantaged, lowered rates of parasitism-induced mortality | Depending on body size, search capacities and host-specificity, kleptoparastic species may be less sensitive to features of urban landscapes than a host, exacerbating pressures on host populations | Archer (2013), Egerer et al. (2017), Holzschuh et al. (2010), Roland and Taylor (1997), and Tylianakis et al. (2007) |
| Kleptoparasite              | Parasitic bees increase with increasing landscape diversity                | Specialisation and species occupying higher-trophic levels associated with greater sensitivity to disturbance Fate dependent upon hosts Low population sizes | Albrecht et al. (2007), Cane et al. (2005), Fortel et al. (2014), Holzschuh et al. (2010), Loyola and Martins (2006), Steffan-Dewenter and Schiele (2008), Tscharntke et al. (1998), and Tscharntke et al. (2002) |
| Nesting substrate Below-ground | More open habitat Sand-pits, roadides, vacant lots, building sites provide nesting habitat Soils are not tilled | Turf, pavement, fake grass unsuitable Regular mowing, weeding, irrigation, mulching, and weed-barrier fabrics prevent establishment and disturb ground-nesting bees High surface run-off and erosion from storm drains and ditching | Benjamin et al. (2014), Cane (2005), Cane et al. (2005), Linsley (1958), and Matteson et al. (2008) |
| Above-ground                | Installation of bee hotels Cavities in brick mortar, adobe walls, cavities and nail holes in wooden telephone poles, fences and other wooden man-made structures, bamboo stakes in gardens | Removal of dead trees and wood Few large, old trees Removal of lantana and blackberry weeds | Alves-dos-Santos (2003), Boyle and Pitts-Singer (2017), Rolón and Cilla (2012), and Roulston and Goodell (2011) |

Note: Note for sociality these traits may not apply for all species in a sociality category.
determined by the authors of these studies. We also extracted information on environmental variables that might influence bee communities and how these related to bee abundance and/or diversity. These related to both food and nesting resources, and landscape composition (Supplementary Information S1 and S5). We coded each variable in each study in terms of it having a positive, negative, or non-significant impact on bees (Supplementary Material S1). Some potentially important variables (pesticides, mowing and grazing, ‘wildlife-friendly’ gardening, human activity, landscape diversity, socio-economics, housing density, human density, road traffic) were investigated in too few studies to be included but are summarised in Supplementary Information S5.

We also tabulated abundance and species richness responses (positive, negative, non-significant) by the following ecological traits of bees: nesting substrate, kleptoparasite/host, sociality, body-size, lecty, origin (native/exotic), or higher-level bee taxonomic categories (family or genus). (Supplementary Materials S2 and S3). We note that there is a continuum of sociality but for ease of analysis, we categorised species as: solitary – one female per nest or social: any form of communal nesting or sociality with a reproductive division of labour (Wcislo & Fewell, 2017). We also investigated the community composition of bees in urban areas. We extracted information from each study in terms of the number of individuals recorded, the number of species, and number of genera. We also averaged the proportion of bee individuals and species in the different ecological trait categories listed above across urban bee studies.

RESULTS

Overview of urban bee studies

Of the 215 publications reviewed (Supplementary Materials S1) (Figure 1a), 154 involved entire bee communities. Of the 61 studies looking at a subset of bees, 18 involved Bombus, 2 Meliponini, 3 Euglossini, and 6 cavity-nesting bees (Figure 1b). Thirty-two studies focused on particular species (typically from one to three species, sometimes in different genera), and of these, there was a clear taxonomic bias: 76% were apids, of which 66% were Bombus (Figure 1c). Therefore, both guild-based and species-level studies were over-represented by apids.

Methods to survey bees varied (Figure 2b); most (64%) used only one method (Supplementary Material S1). There was also a large variation in study duration and sampling intensity (Supplementary...
Material S1). Most studies (53%) were restricted to a single season or year (Figure 1a).

There was an extreme geographic, and therefore associated climatic and phylogenetic, bias in urban bee studies (Figure 3): Approximately 40% were conducted each in North America (the United States of America and Canada) and Europe. Despite having a large proportion of the global human population living in urban areas (Ritchie & Roser, 2020), Africa and Asia were particularly under-represented. The fewest studies were conducted in the Middle East. Of the 26 countries where bee studies have been conducted, approximately 35% were undertaken in the United States, 15% in the United Kingdom, 9% in Germany, and 7% in Brazil; over two-thirds of the total are from just four countries. Across all types of studies there was a diversity of urban habitat types in which bee surveys were conducted; residential gardens were over-represented compared with all other urban greenspace types (see Figure 2b for a detailed breakdown).

Many studies (47%) did not define explicitly what constituted an ‘urban area’. For those that did, definitions varied widely (Supplementary Materials S2). How intensity of urbanisation was determined also

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**Figure 2** Breakdown of urban bee studies in terms of (a) survey methods; (b) urban habitat types surveyed. Note that some studies included more than one topic/habitat type or did not mention the habitat type other than just classifying it as ‘urban’; hence, total numbers may not be the same as the total number of studies. Categories of habitat types in which native bee surveys and studies have been conducted (f): campus: university or college campus; residential garden: residential/home gardens; Industrial: industrial, commercial or business district; park: public green area, often recreational; urban ag: vegetable garden, urban orchard; native remnant: native vegetation fragment or remnant vegetation within the urban matrix; green linear element: linear vegetation element including roadsides, rights-of-way, railways; Uni: university campus; cemetery: cemetery, churchyard or temple; wasteland: derelict site, landfill, vacant lot; greenspace: public lawn, sometimes ill-defined in papers.
varied, as did the scale and resolution at which urbanisation intensity was measured (Supplementary Materials S2). The most frequent criteria were either that some component of impervious surfaces or built space was present or the authors simply stated that the study site took place in a named city (Figure 4, Supplementary Materials S2).
Bees in urban versus natural and agricultural landscapes

There were 51 studies that compared bee communities between urban and rural/agricultural and/or ‘natural’ landscapes (as defined by the authors). The rest compared a variety of urban habitat types (Supporting Information S1, S5 and Figure S5). For urban and agricultural landscape comparisons, urban bee abundance was higher in 38% of cases, lower in 19%, and did not differ in 43% (Figure 5). Likewise, for comparisons of urban and natural landscapes, urban bee abundance was higher in 32%, lower in 22%, but similar in 47% (Figure 5). For bee species richness comparisons between landscape types, urban areas had more species than agricultural landscapes (44% of cases) or did not differ (33%), with 22% of cases having fewer (Figure 5). In contrast, species richness in natural areas was higher than in urban sites in almost half of the comparisons (48%), while urban areas had more species in 26%, and in 26% of cases, there was no significant difference (Figure 5).

Determinants of native bee diversity and abundance in urban areas

While local and landscape factors are important determinants of wild bee abundance and diversity, no single factor consistently influenced either variable; however, some general patterns are evident (Figure 6, see also Supplementary Materials S5, including for sample sizes).

Diversity, and especially abundance, of floral resources more often had a positive than negative effect on bee abundance (flower diversity: 43% positive associations vs. 12% negative associations; flower abundance: 52% positive associations vs. 3% negative) and species richness (flower diversity: 31% positive associations vs. 14% negative associations; flower abundance: 51% positive associations vs 4% negative) (Figure 6a,b). Approximately half of the studies, however, found no effect of flower abundance and richness on bee abundance (flower abundance: 45%, flower richness: 45%) or bee species richness (flower abundance: 56%, flower richness: 46%) (Figure 6a,b). When authors considered how native versus introduced plant species influence bees in terms of proportion of flowers or flower species that were native, native flora were generally beneficial, with 50% of cases finding positive associations with bee abundance and richness (Figure 6), and most of the remaining associations were non-significant (bee abundance: 42%, bee species richness: 46%). There were therefore almost no negative associations (bee abundance: 8%, bee species richness: 5%).

Our data indicate that less groundcover (i.e. greater amounts of open, natural substrate) tends to be associated with increased bee abundance in urban habitats (38% of cases, compared with 6% of negative associations), and especially bee species richness (100% of cases) (Figure 6). The proportion of area covered by trees had mainly positive (36%) or neutral (57%) associations with bee abundance (Figure 6a). Greater openness (i.e. the reciprocal of canopy cover, and an indicator of how much solar radiation a site receives) also tends to promote bee abundance (positive associations in 35% of cases vs. 12% negative associations) (Figure 6a). Increase in the area sampled (Figure 6) had inconsistent effects on both bee abundance (36% positive, 22% negative and 44% non-significant associations) (Figure 6a) and species richness (30% positive, 13% negative, 57% non-significant associations) (Figure 6b).

Although built space at landscape scales was more often negatively than positively correlated with bee abundance (negative associations in 40% of cases vs. 13% of positive associations) and richness...
(negative associations in 27% of cases vs. 17% of positive associations), in approximately 50% of cases, there was no significant impact (47% for abundance and 56% for species richness) (Figure 6). Proportion of the urban area that was greenspace had more positive than negative impacts on bee abundance (31% positive and 12% negative) and species richness (40% positive and 24% negative). Isolation from natural areas was often negatively and never positively associated with bee abundance (37% negative vs. 0% positive) and especially species richness (56% negative vs. 0% positive). Distance from city centres tended to have a positive association with bee abundance (67% positive, 33% neutral, 0% negative) and species richness (57% positive, 29% neutral); however, a small proportion of negative associations (14%) were recorded for species richness (Supplementary Materials S5 and Figure S5).

There were few strong patterns found for particular bee guilds and environmental variables, conceivably due to small sample sizes. The raw data are tabulated in Supplementary Materials S3 and S4). With more studies providing data on *Apis mellifera* and *Bombus* (either...
focussed on these species or as a category within bee assemblage studies), clear favourable associations between their abundance and flower abundance were evident: for Apis, 10 positive, one negative and two non-significant associations and for Bombus 11 positive, one negative and five non-significant associations. These data can be contrasted with a predominance of neutral associations between flower abundance and that of all other (i.e. non-Apis and non-Bombus) bee taxa combined: six non-significant and four positive associations. Therefore, it appears that general positive associations between flower abundance and bee abundance are more apparent for Apis and Bombus, whereas neutral associations feature to a greater extent for other bee taxa.

Ecological traits of urban bee assemblages

Oligolectic bees averaged 17% of species (n = 27 studies) and 16% of individuals (n = 12 studies) (Supplementary Materials S1) and large-bodied bees dominated in 54% of studies (n = 35 studies). Solitary bees comprised 29% of individuals (n = 30 studies) and 48% of species (n = 29 studies) in urban environments. Kleptoparasites averaged 10% of species (n = 54 studies) but only 2% of individuals (n = 28) in cities. Only one study provided data on parasitism rates (32.35%; Archer, 2013). On average, ground-nesting bees were more common than cavity-nesting bees, representing 63% (n = 28 studies) of individuals, and 62% (n = 34 studies) of species.

DISCUSSION

Bees in urban versus natural and agricultural landscapes

A key finding of our review was the importance of assessing abundance and species richness separately, as these metrics exhibited different patterns. While abundance was often higher in urban than natural landscapes, urban landscapes had fewer species. This suggests that a subset of species are benefitting in urban areas, while others are lost when natural areas are replaced with urban landscapes. However, urban areas tended to be better for bees than agricultural landscapes. This may be attributed to higher pesticide and herbicide use, homogenisation of the landscape, lack of suitable resources and floral monocultures (often of cereal-dominated wind-pollinated crops) in most agricultural contexts (Calatayud-Vernich et al., 2018; Goulson et al., 2015; Roulston & Goodell, 2011), which contrasts with the highly heterogeneous landscape and diversity of flora that can be found in some urban areas (Table 1).

Although some cities are deficient in regionally rare bees (Harrison et al., 2017), others harbour regionally rare endemics (Banaszak et al., 2018; Hausmann et al., 2015; Vereecken et al., 2021). Even in the last decade, new species have been discovered in urban areas, for example, Leioproctus (Ottocolletes) muelleri (Houston & Maynard, 2012), which has not been found outside of urban areas (ALA, 2021).

Even though wild bees can be adversely affected by some facets of the urban environment (Table 1), some features of cities can be beneficial (Figure 7). For example, we found that most studies found positive rather than negative associations between bees and openness, and both flower abundance and richness. Thus, in comparison with dense, floristically poor wind-pollinated deciduous forest, flower-rich urban habitats (e.g. roadides, waste-lands, and urban gardens) can be favourable for bees (Hall et al., 2017; Sirohi et al., 2015). By comparison, in natural habitats that have a diverse bee-friendly flora, native bees may respond less favourably to replacement of natural vegetation by urbanised landscapes (Martins et al., 2013).

Determinants of native bee diversity and abundance in urban areas and their composition

Although flower numbers had more often positive than negative associations with bees, most studies failed to find flower abundance, species richness, or even the proportion of flora that is native, to be associated with significantly greater abundance and/or species richness of bees in urban areas (Figure 6 and Results above). It is also notable that over 13% of cases found a significant negative association between flower species richness and bee species richness (Figure 6b). The lack of positive relationships may be because bees are more strongly correlated with the abundance of a few particularly attractive plant species than with plant diversity per se (Haaland et al., 2011; Lazaro & Totland, 2010; Prendergast et al., 2022; Rundlöf et al., 2014). Even generalists may benefit from single-species pollen diets if these have high protein, sterol and essential amino acid content (Di Pasquale et al., 2016; Moerman et al., 2017). Oligolectic bees are inevitably dependent on the limited plant taxa they forage on (Praz et al., 2008), so with native flora being replaced by exotic flora in urban areas, oligoleges may be expected to be less resilient to urbanisation. Lower effective population sizes of oligoleges also renders them at higher risk of extinction from stochastic and genetic events, reduced adaptability, and increased metapopulation extinction (Frankham et al., 2002; Zayed, 2009). Nevertheless, there is evidence that some oligolectic species can persist or even benefit under urbanisation, depending on how urbanisation alters their host plant availability (Cane et al., 2006). For example, a survey in Brazil assessing urbanisation impacts at a single site over 40 years recorded a small increase in the proportion of oligolectic species, even as bee richness and abundance declined overall (Martins et al., 2013).

Social bees require food over a greater proportion of the year than do solitary bees (Ogilvie & Forrest, 2017), so it is not surprising that abundances of social honey bees and Bombus, but not abundance of solitary bee taxa, were positively associated with floral abundance and diversity.

Bees of different nesting guilds might be expected to show different responses to urbanisation, due to how urbanisation impacts substrates for ground-nesting versus cavity-nesting taxa (Table 2, Supplementary Materials S3, S4) (Krombein, 1967). Although some studies have found that species nesting in small cavities are more
abundant in urban than nearby natural areas (Cane et al., 2005),
ground-nesting bees are generally more abundant and species rich
than cavity-nesting species in urban areas (Supplementary Materials
S1), although slightly less than the estimated global level of 83%
(Harmon-Threatt, 2020). This difference may indicate cavity-nesting
bees can capitalise on the novel substrates present in urban areas
(Gess & Roosenschoon, 2017; MacIvor & Moore, 2013;
Prendergast, 2019) (Figure 6).

Body size has also been predicted to influence the ability of a spe-
cies to persist in urban habitats, but predictions vary regarding direc-
tionality of the response (Table 2). We found larger bodied bees were
favoured relative to small-bodied bees both in proportion of individ-
uals and species. Presumably, the ability to traverse the urban matrix
to find rewarding patches favours larger species with greater foraging
ranges (Merckx et al., 2018; Theodorou et al., 2021).

Predictions about how sociality influences bees in relation to
urbanisation also vary (Table 2). We found the average proportion of
solitary species in urban areas was lower than the 75% of species
globally (Danforth et al., 2019). However, it should be noted that
authors varied in their categorisation of sociality especially in halictids,
which exhibit variation in sociality, even within a species (e.g.
Yanega, 1997). For example, Arena and Sgolastra (2014) considered
Halictidae to be solitary, whereas most were classified as eusocial by
Fetridge et al. (2008).

Kleptoparasite species appear to be relatively underrepresented
in urban areas, comprising approximately 10% of species, less than
worldwide estimates of 15% according to Wcislo (1996), and 13%
according to Danforth et al. (2019). However, the abundance of
kleptoparasitic individuals was similar to their relative abundances in
natural habitats (e.g. Minckley, 2008). Kleptoparasites are predicted to
be vulnerable to urbanisation, with complex consequences on hosts
(Table 2). We found, however, that urban environments can still repre-
sent supportive habitats for this guild as has been found by others
(Tschamktsche et al., 1998; Sheffield et al., 2013).

KNOWLEDGE GAPS AND FUTURE RESEARCH
DIRECTIONS FOR BEES IN THE URBAN
CONTEXT

We identify seven broad knowledge gaps that should be fruitful areas
for future research:

1. Under-represented regions: Urban bee biodiversity studies have
been geographically biased (Figure 3), so caution is needed when
making generalisations. Further studies in under-represented
biomes and continents (Figure 3) are required to determine
whether trends reported in this review are valid across these
poorly represented biogeographic regions.

2. Conducting detailed studies on specialist, solitary bees in
urban areas: Single-species studies can provide in-depth informa-
tion about mechanisms of responses to urbanisation such as
foraging behaviour, genetic and demographic responses and
metapopulation dynamics (Lindenmayer et al., 2007). However,
single-species studies on bees in urban areas were dominated by
Bombus; more studies on solitary and oligolectic taxa are required,
as well as on halictids (with their diverse sociality and cavity-
nesting megachilids – large components of bee faunas in urban
areas (Supplementary Materials S1).
3. Investigating how historical land-use influences the current composition of the bee fauna: Historical land use and the age of a city are likely to have a major influence on the composition of contemporary urban bee communities (Cusser et al., 2015), although there is also evidence that bees respond rapidly to landscape alterations both negatively and positively (Bommarco et al., 2014; Onufreko et al., 2018). Older cities may have a bee fauna adapted to the city environment, whereas in recently urbanised areas, bees may have had insufficient time to adapt, while sensitive species may not yet have been eliminated due to lag effects (Ramalho et al., 2014; Ramalho & Hobbs, 2012). Such historical or legacy effects have not been sufficiently investigated when evaluating bee responses to urbanisation. What makes this a particularly attractive line of research is the detailed maps that are often available for cities for much of their history. Although ongoing monitoring using systematic methods is optimal (Marlin & LaBerge, 2001; Prendergast & Hogendoorn, 2021), in the absence of repeated surveys, museum collections represent a means of assessing changes in bee composition with ongoing urbanisation over time (e.g. Vaudo et al., 2018). Extinction debt under urban expansion has been considered for other pollinators (Soga & Koike, 2013), and future work on bees requires addressing the predictions that ongoing losses may occur in recently urbanised landscapes, whereas in landscapes with long histories of anthropogenic modification, we may now detect little effects of urbanisation.

4. Investigating in long-term ongoing monitoring of bees in urban areas: Studies involving long-term (>5 years) bee community changes under urbanisation have no clear consistent findings (Archer, 2013; Frankie et al., 2009; Martins et al., 2013) (Supplementary Materials S1). Moreover, these suffer from being comparisons in two points in time; ongoing systematic monitoring over time is required (Cane, 2001; Lebuhn et al., 2013; Packer & Darla-West, 2021). The limited duration of surveys also raises concerns over the reliability of conclusions given high variability in bee populations [Roubik, 2001; Williams et al., 2001; see Cane & Tepedino, 2001 for pitfalls associated with documenting declines over time and potential solutions for them]. As cities expand, how to best develop cities in harmony with biodiversity is a challenge. There is some evidence that to optimise ecosystem services, land sparing (leaving aside large areas of land to nature i.e. in protected areas) is superior to land sharing (integrating ‘wildlife friendly’ practices into coupled human-nature landscapes) in urban ecosystems (Stott et al., 2015), and recent research indicates urban native vegetation remnants are crucial for conserving native bees (Prendergast & Ollerton, 2021a). That species richness is naturally high in areas undergoing rapid urban expansion underscores the importance of identifying how best to manage urban growth to preserve local bee biodiversity (Luck, 2007), and monitor bees under future urbanisation using an adaptive management approach.

5. Investigating how definitions of urban and the scale of analysis influences results: Urban landscapes can differ markedly in impervious and ‘greenspace’ cover, design and configuration (Fuller & Gaston, 2009). Part of the lack of consistency of the impacts of urbanisation on bees that we have found likely stems from differences among authors as to how ‘urban’ or ‘urbanisation’ were defined (McIntyre et al., 2008) (Supplementary Materials S4). For example, using the definition of ‘>50% impervious cover’ (Glaum et al., 2017), ‘village’ habitats considered urban in the study by Samuelson et al. (2018) would be considered to fall outside this category, having on average less than 14% impervious cover. Equally, the ‘urban’ sites in Nakamura and Kudo (2019) would fail to be considered urban with the >50% impervious definition as they comprised 66.9% forest, 4.1% open grassland, 5.5% green-rich residential district, 9.7% pasture, 4.8% abandoned crop field, and only 8.3% developed land. These urban sites were, however, clearly distinct from their ‘natural’ counterparts, which had negligible (<0.2%) developed land, no agricultural/cropland, only 2.8% managed grassland, and were predominantly forest (95.2%). Variation also occurred in what constituted ‘natural’ habitat: in some studies, grazed grasslands were considered ‘natural’, whereas in others natural landscapes referred to legally conserved areas with minimal anthropogenic influence. Our review emphasises that not all greenspaces are equally suitable for bees.

6. Produce evidence-based lists of preferred flora and nesting substrates catering to the local assemblages of native bees in a given city: Rather than floral abundance or diversity, floral composition may be of overriding importance for healthy bee populations (Picanço et al., 2017). Indeed, the fact that most studies found no association between flower abundance or diversity with bee abundance or species richness suggests that treating all flowers as equal misses the point. Consequently, strategies should target plant species proven to be preferred by many bee species (e.g. Bukovinszky et al., 2017; Filipiak, 2019; Nichols et al., 2019). There should also be a focus on targeting oligolectic species’ floral hosts, especially if they are of conservation interest. There is no shortage of lists of ‘pollinator-friendly’ plants, but few are supported by empirical data, are often anecdotal and may focus on generalists such as honey bees and bumble bees and bee of little value to solitary bees (Garbuzov & Ratnieks, 2014a; Prendergast & Ollerton, 2021a). They may even favour exotic generalists to the detriment of native bees (Prendergast et al., 2021). Because plant species can vary in attractiveness to pollinators depending on the landscape-type (Frankie et al., 2013; O’Neill et al., 2004) preference tests should be conducted specifically in urban environments that target conservation priority bee species. However, public education may be important to promote bee-friendly plants among urban residents, considering that the flowers useful to wild bees may be considered weeds (e.g. Frankie et al., 2013; Lowenstein et al., 2019).

In addition to flower resources, bees also require nesting resources. Greater investigation into the importance of large, old trees as nesting resources for bees in urban areas is required to prevent potentially important nesting habitats from being removed. Research into how well artificial ‘bee hotels’ can compensate for losses of natural nesting resources for cavity-nesting
Conserving wild bees in the urban jungle

From our review of the literature on bees in urban areas, the following recommendations can be made on how to improve urban areas to support native bee assemblages:

- Retain, restore, revegetate and reconnect patches of remnant natural habitat throughout the urban matrix.
- Encourage homeowners, gardeners, landscape managers, and nurseries to focus on flowers that have been demonstrated to be visited by wild bees in the region. Flowers should be primarily native species and ensure oligolectic bee preferences are represented. Key exotic flowers that have low risk of becoming invasive and offer quality and large volumes of nectar and pollen, especially outside the main flowering period of native flora, can also be included.
- Retain entomophilous street trees, as well as maintain open habitat.
- Leave patches of bare ground in greenspaces, and avoid plastic turf and large-scale mulching of gardens.
- Leave flowers and weeds on lawns, or even better, opt for flowering groundcover as a replacement for lawns.

CONCLUSIONS

Despite global bee declines (Tylianakis, 2013), cities retain remarkably intact, diverse and abundant bee assemblages (Figure 1a, Figure 7, Supplementary Materials S1). Responses of bees to urbanisation differ considerably from their responses to agriculture, despite both causing fragmentation and destruction of natural habitat. Moreover, in some cases, cities can be bee-beneficial landscapes, certainly in comparison to agricultural ones and perhaps even compared with natural landscapes. Strategies to manage urban areas for bees therefore cannot be extrapolated from recommendations based upon agricultural habitats. Responses of bees to urbanisation differ widely according to life-history strategy of the bee taxa involved.

Our identification of knowledge gaps aided in development of meaningful recommendations for future research efforts. If we are to mitigate global decline of bees, a greater understanding of how bees respond to urbanisation is required so that effective management strategies and restoration/landscaping strategies can be designed and implemented. Most importantly, it is evident that urban areas have the potential to successfully harbour native bees, with their attendant pollination services, provided the ecological needs of the species are understood.

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CONFLICT OF INTEREST

None to declare.

DATA AVAILABILITY STATEMENT

All data is available in the Supplementary Materials

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SUPPORTING INFORMATION
Additional supporting information may be found in the online version of the article at the publisher’s website.

Supplementary Materials S1 Table S1. A global assessment of determinants of native bee assemblages in urbanised landscapes: literature reviewed (215 studies). Also available at: Prendergast, K. (2021) Supporting data for a global review of determinants of native bee assemblages in urbanised landscapes. Curtin University. DOI: 10.25917/0qnd-j961.

Supplementary Materials S2 Definitions of urban/urbanisation used by authors in urban bee publications.

Supplementary Materials S3 Table S3. Responses of bee abundance (positive, negative or non-significant) in relation to various local & landscape potential explanatory variables according to guild & taxonomic categories. Table S4. Urban/urbanisation definitions and presence/absence of a land-use map in urban bee publications. Also available at: Prendergast, K. (2021) Supporting data for a global review of determinants of native bee assemblages in urbanised landscapes. Curtin University. DOI: 10.25917/0qnd-j961.

Supplementary Materials S4 Table S4. Responses of bee abundance (positive, negative or non-significant) in relation to various local & landscape potential explanatory variables according to guild & taxonomic categories. Also available at: Prendergast, K. (2021) Supporting data for a global review of determinants of native bee assemblages in urbanised landscapes. Curtin University. DOI: 10.25917/0qnd-j961.

Supplementary Materials S5 Figure S5. Response of bee abundance and species richness to variables measured in urban bee studies.

Supplementary Materials S6 References for Figure 6 Aspects of the urban environment that can be beneficial for bees

Table S2 Urban/urbanisation definitions and presence/absence of a land-use map in urban bee publications reviewed

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