







The relative performance of sampling methods for native bees: an empirical test and review of the literature

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Abstract. Many bee species are declining globally, but to detect trends and monitor bee assemblages, robust sampling methods are required. Numerous sampling methods are used, but a critical review of their relative effectiveness is lacking. Moreover, evidence suggests the relative effectiveness of sampling methods depends on habitat, yet efficacy in urban areas has yet to be evaluated. This study compared the bee community documented using observational records, targeted netting, mobile gardens, pan traps (blue and yellow), vane traps (blue and yellow), and trap-nests. The comparative surveys of native bees and honeybees were undertaken in an urbanized region of the southwest Australian biodiversity hot spot. The outcomes of the study were then compared to a synthesis based on a comprehensive literature review of studies where two or more bee sampling methods were conducted. Observational records far exceeded all other methods in terms of abundance of bees recorded, but were unable to distinguish finer taxonomic levels. Of methods that captured individuals, thereby permitting taxonomic identification, targeted sweep netting vastly outperformed the passive sampling methods, yielding a total of 1324 individuals, representing 131 taxonomic units—even when deployed over a shorter duration. The relative effectiveness of each method differed according to taxon. From the analysis of the literature, there was high variability in relative effectiveness of methods, but targeted sweep netting and blue vane traps tended to be most effective, in accordance with results from this study. However, results from the present study differed from most previous studies in the extremely low catch rates in pan traps. Species using trap-nests represented only a subset of all potential cavity-nesters, and their relative abundances in the trap-nests differed from those in the field. Mobile gardens were relatively ineffective at attracting bees. For urbanized habitat within this biodiversity hot spot, targeted sweep netting is indispensable for obtaining a comprehensive indication of native bee assemblages; passive sampling methods alone recorded only a small fraction of the native bee community. Overall, a combination of methods should be used for sampling bee communities, as each has their own biases, and certain taxa were well represented in some methods, but poorly represented in others.

Key words: bee assemblages; biodiversity; honeybees; monitoring; native bees; sampling; surveys; urbanization.

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INTRODUCTION

In many regions, bees are important pollinators of a large number of native and agricultural plant species (Tepedino 1979, Klein et al. 2007, Potts et al. 2016). However, bees are declining across the globe due to a number of often interacting threats, including habitat loss, degradation, and fragmentation due to agricultural and urban expansion, disease, pesticides, and climate change (Goulson et al. 2015, Potts et al. 2016). Indeed, declines in pollinator populations are among the most pressing environmental issues of the 21st century due to the threat to food security and ecosystem functioning (Brown et al. 2016).

A reliable, robust methodology for surveying bees is required to make valid assessments of the status of bee populations, understand the ecology of species, and to track whether management actions have had their desired outcomes (Cane 2001, Cane and Tepedino 2001). A number of methods for sampling bees have been developed, each with their own benefits and limitations, including sampling effort, skill required, taxonomic and functional group biases, and cost of implementation (Table 1). However, as yet, there is no consensus on which method is superior, with the optimal method likely to differ depending on the study system and research aim. Using a range of methods has been previously recommended to reduce biases in any one method and because methods often are complementary in the bee fauna they collect (Krug and Alves-dos-Santos 2008, Wilson et al. 2008). There is growing evidence that phylogenetic group and bee functional traits (e.g., body size, lecty, and sociality) influence various variables of interest, such as response to land-use change (Williams et al. 2010, Banaszak-Cibicka and Zmihorski 2012, Rader et al. 2014) and pollination services (Brittain and Potts 2011, Munyuli 2014). However, the sampling method used may be biased toward bees of a particular lineage or functional group, meaning that the appropriate sampling method varies depending on the taxonomic group or question at hand (Gonzalez et al. 2016, Sircom et al. 2018, McCravy et al. 2019).

A recent review of the efficacy of different sampling methods was focused on tropical forest agroecosystems (Prado et al. 2017), and almost

all other empirical studies explicitly comparing sampling methods have been restricted to natural or agricultural ecosystems in the Northern Hemisphere (Wilson et al. 2008, Grundel et al. 2011; see also Appendix S1: Table S1). No reviews that explicitly compare bee monitoring or surveying methods have so far considered urban habitats. Urban habitats may differ from natural and agricultural ones in having higher plant species richness and habitat complexity (McKinney 2008, Faeth et al. 2011), which may alter the relative efficacy of different sampling methods (Templ et al. 2019). Urban areas often have a high diversity of plant associations across the region, which contrasts with often large monocultural fields in agricultural areas, and fairly uniform habitat types even in natural areas, which, however, differ from urban areas in having large, contiguous patches of native vegetation (Kaluza et al. 2017).

Urbanization is a significant form of land-use change and is set to increase (United Nations 2015), with the potential for adverse consequences to bee abundance and diversity and through the associated loss of natural habitat and other aspects of the built environment (Martins et al. 2013, Potts et al. 2016). Alternatively, urbanization may provide benefits to bees, depending on type of urban habitat, the regional context, and local and landscape conditions (Hall et al. 2017). For example, in cold, temperate regions with low floral diversity, and dominated by closed-canopy conifer forests, the urban heat island effect and preponderance of flowering plant species may allow a longer foraging season with a greater abundance and diversity of flowering resources (Baldock et al. 2015, Luder et al. 2018). Similarly, in arid regions, management of urban flora can extend plant bloom, with benefits to pollinators (Neil et al. 2014).

The urbanized region on the Swan Coastal Plain of Perth, southwest Western Australia (SWWA), is within a globally recognized biodiversity hot spot that has been severely affected by historical and ongoing land-clearing for urbanization (Hopper and Gioia 2004, Lambers 2014). With a high diversity of endemic flora, this region has the potential to harbor a high diversity of native bees. Indeed, Western Australia is known to host a diversity of bees (estimated at 800 species; Houston 2011), yet no systematic

Table 1. Advantages and disadvantages of common methods used for sampling bee communities.

	Sweep net	Pan traps/ bowl traps/ bee bowls/ Moericke traps	Vane traps	Baits	Vacuum/ Aspirator	Malaise	Trap-nests
Advantages	<ul style="list-style-type: none"> • Can match bees with floral hosts • Can identify diel activity patterns • Active search-and-net collecting can target specialist bees • Low cost • Easily transportable • No setup time • Opportunity for catch and release • Specimens collected in good condition 	<ul style="list-style-type: none"> • Easy to deploy • Cost-effective • No experience required • Can sample from hours to days • Samples bees active over entire day (and night) 	<ul style="list-style-type: none"> • Can sample for extended durations • Easy to deploy • Samples bees active over entire day (and night) 	<ul style="list-style-type: none"> • Targets specific taxa of interest (mainly orchid bees, Tribe: Euglossini), including those that have rapid flight • Targets males so that females are not depleted, limiting potential to reduce population reproductive capacity • Samples bees active over entire day (and night) 	<ul style="list-style-type: none"> • Can match bees with floral hosts • Can collect bees from flowers without damaging vegetation • Can identify diel activity patterns • Easily transportable • No setup time • Opportunity for catch and release 	<ul style="list-style-type: none"> • Can sample for extended durations • Easy to deploy • Samples bees active over entire day (and night) • Can be hoisted into canopies • No experience required 	<ul style="list-style-type: none"> • Can sample for extended durations • Measures demographic parameters: sex ratios, reproductive output, individual fitness • Assesses mortality from predators and parasites/parasitoids of brood • Can target particular species based on hole diameter • Can uniquely associate males with females • Can match bees with floral hosts (by analysis of food provisions) • Easy to replicate
Disadvantages	<ul style="list-style-type: none"> • Height limited by handle length • Requires skill • Limited duration • No standard protocol/difficult to standardize • Biased toward slower-flying, visually or audibly conspicuous bees • Catch rates vary with environmental conditions (wind, temperature, time of day) • Catch rates vary with vegetation type • Labor-intensive 	<ul style="list-style-type: none"> • Only catch low-flying bees • High bycatch • Limited height sampled • Potential to deplete populations of some species • Success varies with color • Success can vary with color • Success can vary with bowl size • Bias against large bees • Contents can evaporate if left out for long durations • Contents can spill over if rain occurs • Subject to disturbance from wind/animals • Cannot match bees with host flowers† • Specimens can be degraded‡ 	<ul style="list-style-type: none"> • High bycatch • Potential to deplete populations of some species • Success varies with color • Cannot match bees with host flowers† • Specimens can be degraded 	<ul style="list-style-type: none"> • Targets only limited range of taxa • Dependent on bait used • No standardized method for comparison • Cannot match bees with host flowers† 	<ul style="list-style-type: none"> • Limited to slow, low-flying, conspicuous, smaller bees • Requires skill • Limited height sampled • Limited duration • Catch rates vary with environmental conditions (wind, temperature, time of day) • Catch rates vary with vegetation type • Labor-intensive 	<ul style="list-style-type: none"> • High bycatch • Success varies with color • Success highly dependent on placement, that is, within flight path such as corridors • Cannot match bees with host flowers† • Specimens can be degraded • Can be vulnerable to damage from vandalism, animals, wind • Limited height sampled 	<ul style="list-style-type: none"> • Limited to cavity-nesting bees, and of those, a subset that use trap-nests • Success varies with hole diameter, trap-nest material, orientation • Requires facilities to rear offspring • Utilization in relation to natural nesting resources in the landscape unknown • Mortality in trap-nests compared with natural nests unknown • Labor-intensive: requires obtaining material to construct trap-nests, making the nests (potentially drilling through hardwood), installing nests, periodically checking them, and then rearing offspring

(Table 1. Continued.)

	Sweep net	Pan traps/ bowl traps/ bee bowls/ Moericke traps	Vane traps	Baits	Vacuum/ Aspirator	Malaise	Trap-nests
Suitable habitat	Flowering shrubs in open habitat	Open habitat	All	All	Flowering shrubs in open habitat	Most (preferred method in tropical habitat)	Most
Non-suitable habitat	Dense vegetation Thorny vegetation	Sites with rich and abundant flora Shaded habitat High vegetation			Dense vegetation, plants flowering in inaccessible locations	Exposed, windy habitats	Limited colonization in closed-canopy forest

Note: Specific examples are presented in Appendix S1: Table S1.

† Analyses of pollen on body or in gut can aid matching bees to foraging resources but requires time, money, skill, and equipment.

‡ Although traps can be filled with preservative (e.g., propylene glycol), specimens can nevertheless degrade, and while protocols for washing specimens to retain quality exist, this is time-consuming and specimens can nevertheless be damaged, compromising species-level identification.

surveys of native bees in the urbanized parts of this region have been conducted. Consequently, there has been little research into the response of native bee communities in this region to land-use change. Many bee species remain undescribed, and only two of the estimated 800 species in the state have been adequately assessed to be given legislative protection and recognized as threatened (Department of Sustainability 2016).

We used a range of methods to characterize the bee community in an urbanized area of SWWA: observations (randomized bee walks); targeted sweep netting; baiting in the form of mobile gardens; blue and yellow pan traps; blue and yellow vane traps; and trap-nests (bee hotels). The first two methods are active sampling methods, and the latter four are passive. Furthermore, we compared their relative efficiency to determine the most effective method(s) for sampling the community and identified any biases in monitoring of native bee assemblages, as well as providing comparative data on the advantages and disadvantages of each method. Finally, to place the results in the context of the wider literature, a review was conducted to identify articles that compare sampling methods or were surveys of bee communities that included two or more sampling methodologies. Articles were sourced through Google Scholar using the search terms “sampling bees method* technique pan bowl trap* sweep net* pollinator bait vane” and through references in the articles thus found. Articles included were those published prior to 28 November 2019.

METHODS

Study region and sites

Perth is Australia’s fourth largest city, with a population of 2.14 million people and a density of 317.7 people/km², and is also Australia’s fastest-growing city (Population Australia 2017). The region has a Mediterranean climate and is characterized by a high incidence of nutrient-deficient landscapes with highly weathered surface soils (Hopper and Gioia 2004). The metropolitan region on the Swan Coastal Plain is renowned for a high concentration of endemic flora (Hopper and Gioia 2004). The region has also undergone extensive clearing, with over 80% of the original vegetation being removed, and ongoing clearing for development being a continuing threat (Hopper and Burbidge 1989, Witham 2012).

Bees were surveyed at seven sites each of bushland remnants and residential gardens within the same geographic, geological, and climatic region (Newman et al. 2013; Fig. 1). To ensure independence and minimize spatial autocorrelation, sites were greater than 1 km apart, which exceeds the average flight range of most bee species (Gathmann and Tschamtkke 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010). Site area ranged from 835 to 4,370,000 m², but the area surveyed was standardized to a 100 × 100 m area.

Sampling methods

Each site was surveyed once per month over the Southern Hemisphere spring/summer period

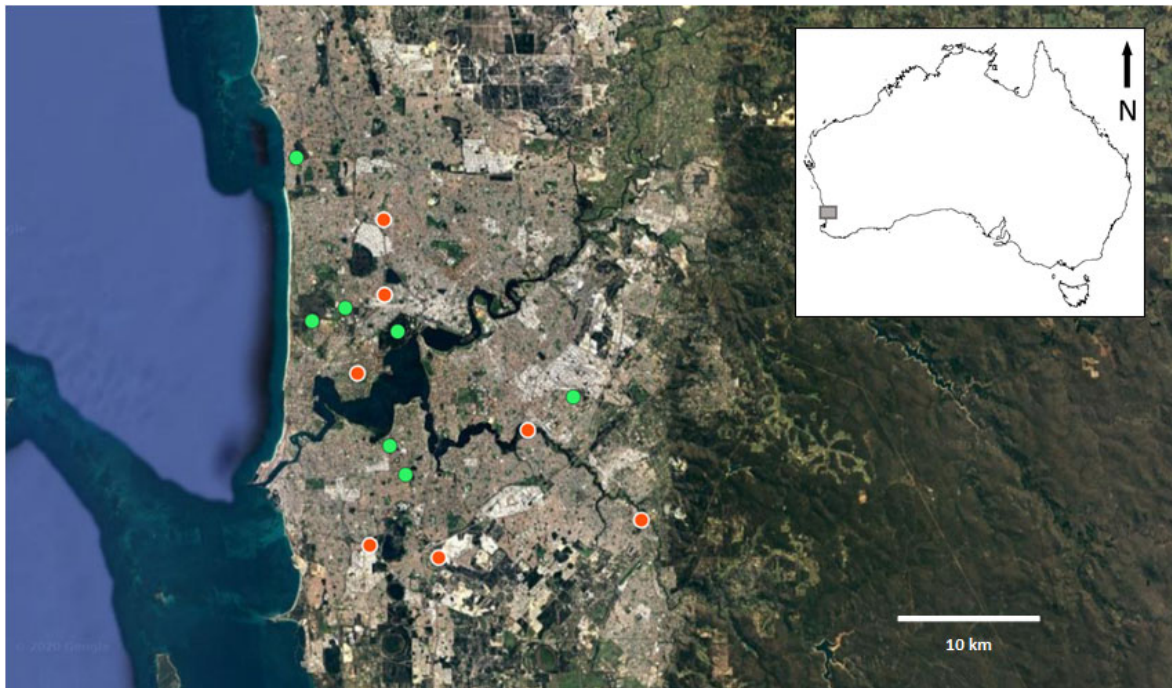


Fig. 1. Map of the 14 sites surveyed for native bees in the urbanized region of the southwest Western Australian biodiversity hot spot. Bushland sites (green): Star Swamp, Bold Park, Kings Park, Maniana Reserve, Wireless Hill, and Piney Lakes; and residential sites (red): Osborne Park, Wembley, Nedlands, Wilson, Jandakot, Bibra Lake, and Gosnells.

(November–February) in 2016/2017. Surveys were conducted during conditions conducive to bee activity (clear skies, wind speed <30 km/h, and temperatures >17°C). All specimens collected were identified by KSP to the lowest taxonomic resolution possible using published keys, the Australian Pests and Diseases Image Library (PaDIL) website (<http://www.padil.gov.au/>), and with reference to the collection at the Western Australian Museum. Separate taxonomic units were used for each male and female of a species due to limitations in the taxonomy of Australian bee fauna (Batley and Hogendoorn 2009) and because there can be sex-specific differences in catch rates (Leong and Thorp 1999).

Observations and targeted sweep netting.—Targeted sweep netting and observations (randomized bee walks) were conducted for three hours, from 10:45 until 13:45 hours, the time of peak bee activity (Yates et al. 2005). Targeted sweep netting was performed using an entomological net (119-cm aluminum handle, 38 cm diameter hoop, and 74 cm long white net with

0.9 × 0.3 mm mesh). Targeted sweep netting and timed observations were conducted by a single collector (KSP) using an active search-and-net approach, walking randomly around a 100 × 100 m area of the site observing flowering plants. Areas with flowering resources were observed for 5 min before moving on to another if no bees were observed. Each bee captured was transferred into an individual labeled vial for later identification. The European honeybee (*Apis mellifera*) was counted but was not captured. For bushland remnants, the 100 × 100 m area was at least 100 m away from roads to avoid edge effects. As residential gardens were mostly <100 m², surrounding vegetation on the verge and adjacent front yards was also surveyed.

Mobile gardens.—A mobile garden of potted plants was taken to each site to measure bee visitation. A number of studies have conducted observations and/or targeted sweep netting of bees at mobile gardens—standardized arrays of bee-attractive potted plants that are placed at each site (Lowenstein et al. 2015). These gardens allow

patch size and floral species to be standardized, and control for edaphic and genetic variables that can alter attractiveness of flora between sites. Four Australian plant species—*Eutaxia myrtifolia* (syn. *obovata*; Fabaceae, flowers in November, plant size 0.4×0.5 m), *Dianella revoluta* (Hemerocallidaceae, flowers in November–December, 0.4×0.4 m), *Leptospermum* “Pink Cascade” (Myrtaceae, flowers in November, 0.4×0.6 m), and *Scaevola aemula* (Goodeniaceae, flowers in November–February, 0.4×0.2 m)—were selected for use in the mobile garden experiment. These species were selected as the genera represent common elements of the Australian flora, and they are also commercially available and often planted in garden beds. Five plants per species were purchased from a commercial native flower nursery and kept in a shade house. During each survey, two to four plants were placed in an open location approximately 10 m apart from each other for the duration of the survey (3 h) of each site, and monitored for 5 min/h, as well as opportunistically observed for bee visitation when in view. Plant species visited, and the species of the bee visiting, were recorded.

Pan traps.—Prior to commencing targeted sweep netting surveys, nine large (350 mL) yellow pan traps and 20 small (96 mL) pan traps painted UV-fluorescent yellow and UV-fluorescent blue (New Horizons Support Services, Upper Marlboro, Maryland, USA) were deployed. These were two-thirds filled with water and surfactant (Tween-80). Size and color of the pan traps were selected based on pilot trials published in Droege (2006). The large pan traps were placed on the ground. The smaller pan traps were mounted 20 cm above the ground on bamboo stakes, as elevating pan traps has been reported to increase capture success (Tuell and Isaacs 2009, McCravy and Ruhoff 2017). Pan traps were placed randomly around the site away from vegetation in open, sunny areas, and spaced 5 m apart as this has been found to maximize capture success (Carboni and LeBuhn 2003). Pan traps were collected at the end of each targeted sweep netting survey (after 3 h). Captured bees were transferred into vials containing 75% ethanol.

Vane traps.—At each site, two blue vane and two yellow vane traps (Springstar, Woodinville, Washington, USA) were installed at 1–2 m above the ground on branches, or, in residential areas,

under eaves, and half-filled with water and propylene glycol (Droege and Guldin 2011). Vane traps were installed the month prior to the start of the survey period and remained there until the survey season ended. Captured specimens were transferred to vials containing 75% ethanol during each monthly visit. Rainfall was low during the sampling period, and at no point did the vane traps overflow.

Trap-nests

Trap-nests were used to sample cavity-nesting bees. Trap-nests were made from untreated jarrah (*Eucalyptus marginata*, a local Myrtaceae endemic to SWWA) blocks 100 mm tall \times 100 mm wide \times 150 mm deep. Fifteen 120 mm deep holes were drilled into each block, and five cardboard bee tubes (Jonesville Paper Tube) of each size, 4, 7, and 10 mm diameters, were inserted into the holes. Trap-nests were installed on tree branches, or, in residential areas, under eaves or on fences and windowsills 1–2 m above the ground in locations that were minimally obscured and received sunlight. A total of eight trap-nests were installed at each site, representing a total of 120 potential nesting cavities (40 per diameter) across all trap-nests at each site. Trap-nests were installed during the first survey in November 2016 and removed after the last survey in February 2017. During each monthly survey, completed tubes (nests capped with material) were collected and replaced with new tubes. The capped tubes were stored individually in plastic containers with perforated lids and kept in the laboratory at ambient temperatures to complete development. At the end of October, bee tubes were moved from the laboratory into a greenhouse. Tubes were checked every two days for emergence.

Data analysis.—Linear mixed-effects models were used to compare the relative effectiveness of sampling methods in terms of individuals and taxonomic units collected, using the package lme4 (Bates et al. 2015) in R (R Core Team 2014). The non-native *A. mellifera* was analyzed separately. A generalized linear mixed-effects model with a Poisson error distribution was used to model the effect of method and a method \times habitat interaction on the number of taxonomic units recorded, and a glmer with a binomial error distribution was used to investigate the effect of habitat type (urban and bushland) on the proportion of native bee

individuals observed or collected by sweep net. Site was included as a random factor in all models. Models were tested for overdispersion using the `dispersion_glm` function in the package `blemco` (Korner-Nievergelt et al. 2015); response variables were transformed in order to improve model fit with the particular transformation (e.g., \ln , $\ln + 0.1$, \log_{10}) depending on the fit of residuals. Significance of the explanatory variable (sampling method) or interactions (sampling method \times habitat, and sampling method \times sex) was obtained by comparing models with and without the variable/interaction using ANOVA. Differences between levels were analyzed using Tukey's post hoc tests in the package `lsmeans` (Lenth 2016).

Due to differences in duration in which the blue vane traps were deployed compared to the other sampling methods, we also performed analyses by standardizing the sampling time to 3 h, which involved dividing the results for vane traps by 90 (assuming that the traps could potentially collect bee for a period of 9 h, which encompasses the activity period of bees from 08:00 to 17:00 hours, hence approximately 270 h per monthly survey). However, due to the overall difficulty in determining comparative sampling effort, we retained the actual capture data in our presentation of the results, but also discuss the standardized results. Model outputs using the standardized vane trap data are presented in Appendix S5.

Variation in the composition of bee communities (taxonomic units) between sampling methods (excluding trap-nests) was analyzed using Primer/Permanova 7 (<http://www.primer-e.com/>). Data were \log_{10} -transformed to remove the influence of extremes, given that the data were non-

normal and included many zeros, singletons, and doubletons, as well as some species having >100 individuals. A Bray–Curtis similarity matrix was then calculated to quantify the percentage similarity between sampling methods. Results were visualized using non-metric multidimensional scaling (NMDS).

An estimate of the completeness of each sampling method was assessed by creating rarefaction curves and calculating Chao 1 estimates in EstimateS (Colwell 2013). Biased correction was applied when calculating the Chao 1 estimates. However, for yellow pans, yellow vanes, and blue vanes, the Chao 1 classic estimate was calculated as recommended for when the coefficient of variation in the abundance distribution is >0.5, under which the bias-corrected formula becomes imprecise (Colwell 2013).

RESULTS

Comparison of collection methods for native bees

Both the number of specimens collected and their taxonomic richness differed among the collection methods (Table 2). Targeted sweep netting was by far the most effective method for sampling bees with respect to both abundance and taxonomic unit richness, and blue vane traps were the next most effective in terms of absolute numbers (Table 2; Appendix S2: Table S1). However, when standardized to approximate an equal sampling duration to the other methods (3 h), blue vane traps caught a comparable number of bees to pan (Table 2).

Blue vane traps caught more individuals and taxonomic units than yellow vane traps, whereas yellow pan traps were more effective than blue

Table 2. Total number of native bee individuals and taxonomic diversity caught by the different collection methods.

Method	Targeted sweep netting	Blue vane	Yellow vane	Blue pan trap	Yellow pan trap	Large yellow pan trap
Individuals caught	1324	347 (3.86)‡	15 (0.17)‡	8	15	6
Taxonomic units caught†	134	31 (0.34)‡	10 (0.11)‡	7	6	5
Genera caught	20	11	7	4	3	2
Families caught	4	4	4	3	3	2

† Given variation in body size between sexes (K. S. Prendergast, *unpublished data*), and known differences in color preferences between sexes (Heneberg and Bogusch 2015), for species where both sexes were collected, these were treated as distinct taxonomic units.

‡ Numbers in parentheses are divided by 90 to standardize results to 3 h in order to quantitatively compare results with the other methods.

pan traps. Large (non-UV) yellow pan traps were the least effective (Table 2).

There were significant differences in number of individual native bees caught between the different methods ($P < 0.0001$; Appendix S2: Table S1). All pairwise comparisons between targeted sweep netting and all passive methods were significantly different ($P < 0.0001$). All pairwise comparisons between blue vane traps and other methods were significantly different ($P < 0.0001$; Appendix S2: Table S2), but were not once vane trap data were standardized ($P > 0.05$; Appendix S5: Table S2). There was a significant method \times habitat interaction ($P < 0.0001$; Appendix S2: Table S1), but the main findings of the superiority of targeted sweep netting were consistent across habitats (Fig. 2).

Taxonomic unit richness also differed between sampling methods ($P < 0.0001$, Appendix S2: Table S3, Appendix S3: Table S1), following a similar pattern to that for abundances (Appendix S2: Table S4). Targeted sweep netting caught over 90% of all taxonomic units (Table 2). Blue pan traps caught slightly more taxonomic units than yellow pan traps, but the difference was nonsignificant (Table 2; Appendix S2: Table S4). As with abundance, blue vane traps caught more taxonomic units overall than the other passive methods (Table 2; Appendix S2: Table S4), but not when catch rates were standardized to three hours (Table 2; Appendix S5: Table S4). There was no method \times habitat interaction ($P = 0.376$; Appendix S2: Table S3).

Of the 145 taxonomic units (separate for each sex), of those with $n \geq 10$, all 43 were collected at

higher frequencies by targeted sweep netting except for four: *Amegilla chlorocyanea* (female; 196 blue vane, 17 targeted sweep netting, 2 yellow vane, and 1 blue pan trap); *A. chlorocyanea* (male; 68 blue vane and 9 targeted sweep netting); the kleptoparasite of *Amegilla*, *Thyreus waroonensis* (female; 11 blue vane and 2 targeted sweep netting); and *Lasioglossum (Chilalictus) castor* (female; 14 blue vane, 12 targeted sweep netting, 9 yellow pan trap, 4 yellow vane, and 2 blue pan trap; Appendix S3: Table S1).

No species were exclusive to large yellow pan traps or UV-blue or UV-yellow pan traps. Only two species, *Lasioglossum (Chilalictus) sp.12* (female) and *Braunsapis nitida* (female), both singletons, were exclusive to yellow vane traps. Five taxonomic units were exclusive to blue vane traps (*Lasioglossum (Chilalictus) lanarium* [male], *Lasioglossum (Chilalictus) inflatum* [female], *Homalictus (Homalictus) sphecoides* [female], all singletons, *Euryglossula fultoni* [male, $n = 3$], and *L. (Chilalictus) lanarium* [female, $n = 4$]). By contrast, 98 taxonomic units were captured exclusively by targeted sweep netting (Appendix S3: Table S1).

There was a significant sex \times method interaction ($P = 0.0002$), indicating that the sexes were sampled differently depending on the method used (Appendix S2: Table S5).

Rarefaction curves and Chao estimates followed the same general pattern based on the observed numbers of taxonomic units by sampling method (Table 3; Appendix S4: Fig. S1).

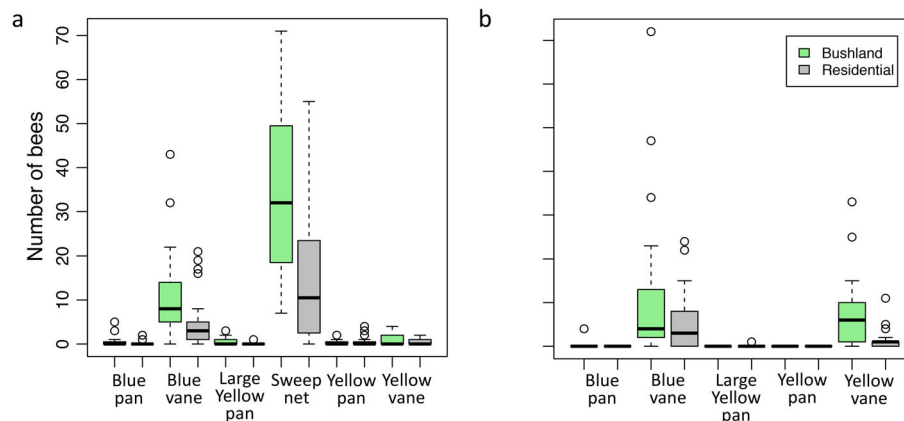


Fig. 2. Abundance (\pm standard error) of native bees (a) and honeybees (b) sampled by all collection methods in bushland remnants and residential gardens. Circles represent outliers.

Table 3. Chao 1 estimates of the number of taxonomic units collected by the different sampling methods, compared with the number observed to have been collected.

Method	Observed	Chao 1 mean	95% CI lower bound	95% CI upper bound	Chao 1 SD	%obs of Chao 1
Large yellow pans	4	5.2	4.12	16.5	2.14	76.9
Yellow pans	6	13.5	6.92	66.7	10.9	44.5
Blue pans	9	12.4	9.58	29.4	3.9	72.3
Yellow vanes	10	21.4	12.1	73.8	12.3	46.7
Blue vanes	32	57.5	39.4	119.9	17.9	55.6
Targeted sweep netting	134	181.5	154.6	243.5	21.2	73.8

Notes: CI, confidence intervals; SD, standard deviation; %obs, percentage of the observed number of taxonomic units is of that calculated by the Chao 1 analysis.

While the passive sampling methods followed a shallow incline with increasing sampling effort (Appendix S4: Fig. S1), the netting followed a curvilinear pattern and had still yet to plateau (Appendix S4: Fig. S1), indicating that despite high sampling effort, more taxonomic units were likely with increased sampling effort. Considering the taxonomic units captured as a percentage of the Chao 1 estimate, netting, large yellow pans, and blue pans had values above 70%, whereas the number collected in the blue vanes was only 55.6% of the estimated value, and for the yellow vane and yellow pan traps, taxonomic unit richness was only 46.7% and 44.5%, respectively, of the estimated value (Table 3). It should be noted that the confidence intervals of the Chao 1 estimates were relatively wide (Table 3).

A Bray–Curtis similarity matrix of species composition revealed that of the five collection methods, pan traps of different colors were the most similar. Both blue and yellow vanes were more similar to blue pan traps than yellow pan traps. The most successful method—targeted sweep netting—had a species composition most similar to blue vane traps, but low similarity to the other methods (Table 4). An NMDS analysis comparing taxonomic composition between the methods had low stress (0.01), indicating a good fit to the data, and depicted that the two small UV-reflective pan traps were most similar to each other (Fig. 3). Taxonomic composition of the bees caught in large yellow pan traps was most dissimilar to all other methods. Targeted sweep netting was also dissimilar to all other methods, but most similar to blue vanes.

Native bees observed vs. targeted sweep netting

Due to being inaccessible (out of reach of the entomological sweep net) or to the difficulty in

catching rapid-flying taxa, not all bees that were observed were netted. Out of a total 5299 native bees recorded by active sampling, 1324 were netted and 4366 were observed: a ratio of observed to netted bees of 1:3. Across all surveys, a mean of 6.32 ± 1.07 (standard error) bees were netted vs. 17.16 ± 4.01 observed. The proportion of netted bees to observed bees did not differ according to habitat ($P = 0.147$; Appendix S2: Table S2). There were, however, significant differences between taxa in the proportion of bees netted relative to that of bees observed (<0.001 ; Table 5; Appendix S2: Table S6), with differences in most pairwise comparisons between taxa (Tukey's post hoc test; Appendix S2: Table S7). The greatest differences in netted:observed catch rates were for the genus *Amegilla*, which included only a single, large-bodied species (*A. chlorocynea*), and for *Exoneura*, a genus of small social bee. For *Amegilla*, the larger numbers observed relative to netted related to their extremely fast, erratic flight and short duration alighting at flower. For *Exoneura*, the high observed:netted ratio was likely due to the large numbers that often forage simultaneously on bushes, making netting some individuals easy yet impossible to catch all that were foraging. Excluding the rarely encountered taxa, most taxa were observed more frequently than netted, except for *Meroglossa*, represented by a single species (*M. rubricata*) that was often observed in trap-nests but seldom foraging, and *Lipotriches*, mainly represented by *L. flavoviridis*, a common species present at most sites and foraging on a wide range of flora.

Observed vs. passive collections

Both native bees and honeybees were surveyed using observational recording and passive collections. For both, observational counts vastly

Table 4. Percentage similarity in species composition of native bees collected by different sampling methods.

Method	Targeted sweep netting	Blue vane	Yellow vane	Blue pan trap	Yellow pan trap	Large yellow pan trap
Targeted sweep netting						
Blue vane	23.75					
Yellow vane	5.68	15.77				
Blue pan trap	4.15	21.36	24.53			
Yellow pan trap	4.01	15.04	22.31	30.58		
Large yellow pan trap	2.53	5.88	0.00	14.11	0.00	

Note: The species \times method Bray–Curtis matrix was log + 1-transformed for the analysis.

exceeded numbers recorded by all passive sampling methods combined. A total of 572 honeybees were collected across all passive sampling methods, whereas 19,825 were observed, amounting to numbers observed being 34.7 times greater than numbers caught by the passive traps. Numbers of native bees observed were 11-fold greater than those caught passively (391 native bee individuals caught by passive traps, compared with 4366 being observed), despite there being more passive than active methods employed.

Trap-nests

Only a small subset of the potential cavity-nesting bee species used the trap-nests. Of the 34 cavity-nesting megachilids (including the kleptoparasitic *Coelioxys*) caught, only 10 species used the trap-nests, and of the 17 hylaeine bees, only four species used the trap-nests (Table 6). However, the value of the trap-nests was in being able to confirm males and females belonging to the same species; namely, no males of *Megachile (Eutricharaea) chrysopyga*, *Megachile (Mitchellapis) fabricator*, and *Hylaeus (Euprosopis) violaceus* were collected in the field, but they emerged from bee tubes. Not only did the composition of trap-nesting species represent only a fraction of the diversity of cavity-nest species, but also the relative abundances did not mirror those caught in the field (Table 6).

Mobile gardens

The mobile gardens were unsuccessful, despite the plants having a high density of blooms. Throughout the four months (56 sampling days), only *S. aemula* was visited, and on only five days at three sites. It should be noted that *S. aemula* was the only plant that flowered throughout the

survey season; the other three were restricted to the first month (only *D. revoluta* had some flowers still present in December). A total of 15 bees visited the mobile garden plants, but only one of these was native (*L. (Chilalictus) castor*, female)—the remainder were honeybees.

Comparison of different passive sampling methods for honeybees and native bees and the influence of habitat type

There was a significant difference in catch rates of native bee individuals by different methods ($P < 0.001$; Appendix S2: Table S8). Significantly more individuals were caught in blue vane traps than all other methods ($P < 0.001$); no other comparisons were significantly different ($P > 0.05$). There was no significant interaction between method and habitat ($P = 0.115$; Appendix S2: Table S8), although vane traps caught more bees in bushland than residential areas, where the other methods were comparable between habitats, but the sample size was too small for any valid conclusions (Fig. 2a).

Honeybee catch rates differed significantly by method ($P < 0.001$; Appendix S2: Table S6). Pairwise comparisons between both colored vane traps and all pan traps were highly significant ($P < 0.001$). Blue vanes also caught significantly higher numbers of honeybees than yellow vanes ($P = 0.001$). Comparisons between the pan traps were nonsignificant. There was also a significant method \times habitat interaction ($P < 0.001$; Appendix S2: Table S8), where vane traps, which caught more bees overall, had higher catch rates in bushland remnants than residential habitats, whereas for the other methods, these caught no honeybees in most cases except for a few outliers, in both habitat types (Fig. 2b).

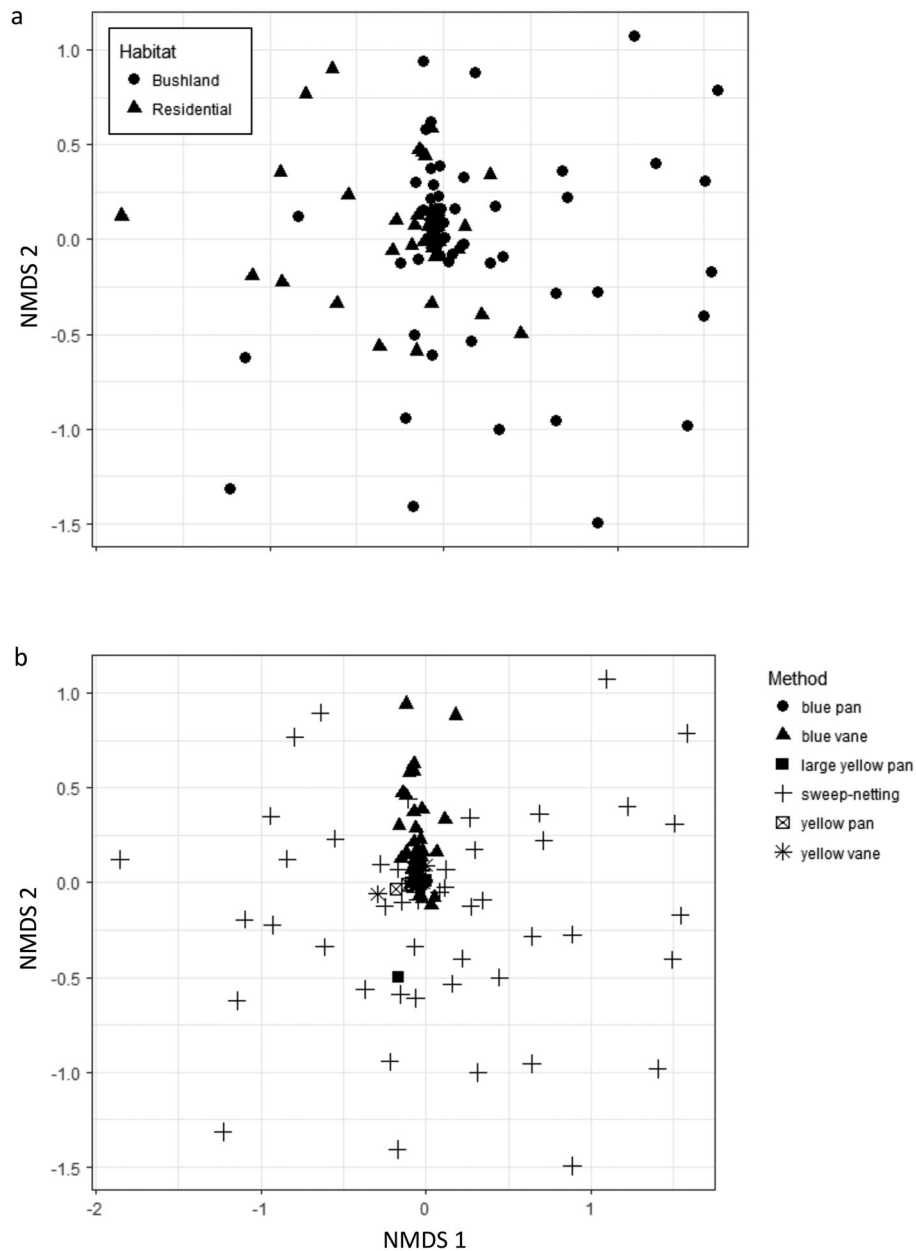


Fig. 3. Non-metric multi-dimensional scaling (NMDS) plot showing the similarity in species composition of native bee assemblages in 2D space according to (a) habitat type and (b) method collection. Greater distance between points corresponds to greater dissimilarity.

Assessing each method regarding whether there were differences in abundance of native bees and honeybees, it was found that the relative differences in abundance of honeybees vs. native bees differed between methods (Appendix S2: Table S9). Abundances of native bees and honeybees

were similar for blue vane traps (mean native bees 8.26 ± 1.45 vs. mean honeybees 9.14 ± 1.27 , $P = 0.171$), whereas there was a trend for honeybees to be recorded at higher abundances based on observational counts (mean native bees 94.3 ± 11.0 vs. mean honeybees 360.3 ± 97.1 , $P = 0.077$;

Table 5. Total number of individuals netted and observed, and the ratio of netted to observed individuals for each major bee taxon, and body size and flight characteristics that could influence catchability.

Taxon	Total netted	Total observed	Netted:observed	Body size	Flight characteristics
<i>Amegilla</i>	26	214	1:8.23	Large	Very rapid, zipping flight, seldom alights long on flowers In reach of sweep nets, often foraging on vegetation that can be sweep netted
<i>Coelioxys</i>	2	0	2:0	Large	Rapid, rare bee
Euryglossinae	162	423	1:2.6	Small	Seldom encountered singly Flying rapidly around inflorescences often in a cloud Never on ground-level flora; prefer branches of flowering trees but if within reach are relatively easy to capture by sweeping through cloud
<i>Exoneura</i>	46	373	1:8.1	Small	Intermediate flight speed Seldom encountered singly Prefer shrubs and trees to forage on, never at ground level
<i>Homalictus</i>	31	54	1:1.7	Small	Intermediate flight speed Prefer shrubs and trees to forage on, never at ground level
<i>Hylaeus</i>	136	234	1:1.7	Predominantly small	Seldom encountered singly Flying rapidly around inflorescences often in a cloud Never on ground-level flora; prefer branches of flowering trees but if within reach are relatively easy to capture by sweeping through cloud Males may be territorial around flowers
<i>Lasioglossum</i>	46	65	1:1.4	Small–medium	Intermediate flight speed Forage at multiple heights, including low-lying flora
<i>Leioproctus</i>	70	153	1:2.2	Medium	Intermediate flight speed Often forage on low-lying flora
<i>Lipotriches</i>	88	77	1:0.88	Predominantly medium	Intermediate flight speed Buzz pollinators—stay on flowers for a longer period of time Forage at various heights, including ground level
<i>Megachile</i>	586	1648	1:2.8	Small–medium	Fast flight Alight only briefly on flowers Forage at various heights, including ground level
<i>Meroglossa</i>	18	15	1:0.83	Medium	Intermediate flight speed Longer foraging duration Frequently observed just resting inside entrances of trap-nests
<i>Thyreus</i>	3	1	1:0.33	Large	Rarely encountered
<i>Trichocolletes</i>	1	3	1:3	Large	Intermediate flight speed Prefer shrubs and trees to forage on, never at ground level

Notes: Body size categories: small, 0.48–1.78 mm ITD; medium, 1.79–3.10 mm; large, 3.11–4.41 mm. Categories were based on subtracting the minimum body size, as measured by intertegular distance (ITD), from the maximum and dividing by three.

Appendix S2: Table S7). Both types of yellow pan traps caught significantly more native bees than honeybees (UV-fluorescent pan traps, mean native bees 0.392 ± 0.116 vs. mean honeybees 0 ± 0 , $P < 0.001$; and large yellow, mean native bees 0.303 ± 0.119 vs. mean honeybees 0.024 ± 0.024 , $P = 0.001$), but the trend was reversed for yellow vanes, which caught sixfold more honeybees than native bees (mean native bees 0.722 ± 0.172 vs. mean honeybees 9.14 ± 2.17 , $P < 0.001$; Appendix S2: Table S9).

LITERATURE REVIEW

The literature review yielded 70 articles, of which 12 were conducted in urban areas (Appendix S1: Table S1). Sixty studies involved two or more methods; the remaining studies compared variables within a method, for example, pan or vane traps differing in color, height, or size. There was high variability in the number of studies comparing different methods, and so conclusions are tentative, but targeted sweep netting

Table 6. Species utilizing trap-nests.

Taxon	Species	No. of tubes	No. of bees emerged	Proportion of tubes	Proportion of bees emerged	No. of cavity-nesting bees collected during surveys	Proportion of cavity-nesting bees collected during surveys
Hylaeinae	<i>Hylaeus (Euprosopis) violaceus</i>	15	68	0.093	0.133	3	0.004
	<i>Hylaeus (Gnathoprosopis) amicus</i>	1	1	0.006	0.002	7	0.009
	<i>Hylaeus (Gnathoprosopis) euxanthus</i>	1	1	0.006	0.002	14	0.018
	<i>Meroglossa rubricata</i>	4	8	0.025	0.016	19	0.024
Megachilidae	<i>Megachile (Eutricharaeae) obtusa</i>	3	14	0.019	0.028	27	0.035
	<i>Megachile (Mitchellapis) fabricator</i>	39	145	0.24	0.285	3	0.004
	<i>Megachile apicata</i>	1	1	0.006	0.002	10	0.013
	<i>Megachile aurifrons</i>	6	37	0.037	0.070	25	0.032
	<i>Megachile erythropyga</i>	85	227	0.525	0.446	6	0.008
	<i>Megachile fultoni</i>	1	1	0.006	0.002	24	0.031
	<i>Megachile "houstoni" M306/F367†</i>	1	1	0.006	0.002	151	0.195
	<i>Megachile ignita</i>	3	3	0.019	0.006	20	0.026
	<i>Megachile (Hackeriapis) tosticauda</i>	2	2	0.012	0.004	6	0.008
	Totals		162	509			

Notes: Number of tubes occupied, the number of bees to emerge, proportion of all tubes occupied by a given species, proportion of all cavity-nesting bees are presented. To compare with survey results, number of a given species collected during the bee surveys and the proportion of all cavity-nesting bees collected during surveys (i.e., No. of sp. collected/No. of all cavity-nesting bees collected) are provided.

† Undescribed species, lodged in the WA Museum as M306/F367.

emerged as both one of the most common methods and the method that is relatively more effective than alternative methods (Fig. 4a; Appendix S1: Table S1). Vane traps, only if they are blue, are also relatively effective, but have been less commonly employed (Fig. 4a). Compared with pan traps—the second most frequently used method and often used in conjunction with targeted sweep netting—it appears that targeted sweep netting tends to be more effective (Fig. 4a; Appendix S1: Table S1). However, there was considerable variation in the relative effectiveness of methods between studies (Fig. 4a). This may be explained by the different duration a method is used; for example, targeted sweep netting has been used for anywhere between 10 min per sampling period and a number of hours throughout the day, whereas pan traps are typically deployed for 24–48 h, leading to unequal sampling effort (Appendix S1: Table S1). The effect of sampling effort on relative performance between methods in species capture rates can be seen in analyses that used rarified species richness (Nardone 2013). The pattern of relative effectiveness was similar when

including studies conducted in urban landscapes only (Fig. 4b). Vane traps had yet to be used prior to this study.

Almost all studies found that trap color influenced catch rates, as well as species composition (Appendix S1: Table S1). In all vane trap studies, blue vanes outperformed yellow vanes (Fig. 4a). Of studies comparing pan traps of different colors, most studies compared blue, yellow, and white (Appendix S1: Table S1). Of these, no color emerged as consistently being superior, but white pan traps were the least frequent in having the highest catch rates: Blue and yellow pan traps had the highest catch rates in 13 studies each, white in five studies, and no significant differences between colors in seven studies (Appendix S1: Table S1).

DISCUSSION

Active vs. passive sampling methods

Observational counts yielded the highest numbers of individual bees. However, this method must be supplemented with those that catch

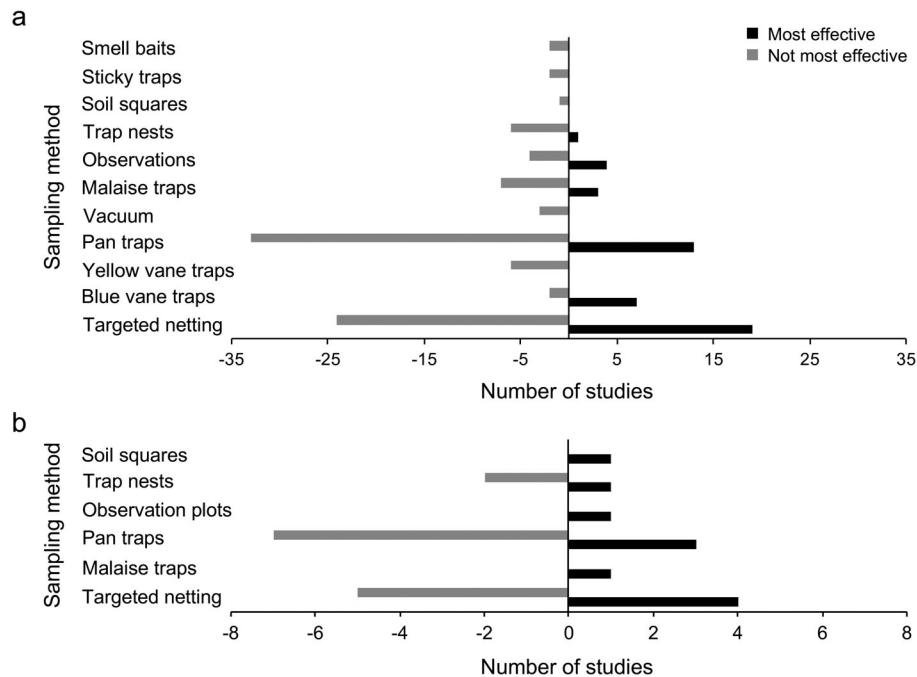


Fig. 4. Number of studies where a given method was reported to be relatively more effective than other methods employed to sample bees: (a) all studies ($n = 71$) and (b) subset of studies in urban landscapes ($n = 12$). See also Appendix S1: Table S1.

specimens to provide finer taxonomic level classification. Of the methods where bees were captured, targeted sweep netting was by far superior, which is in agreement with the literature (Appendix S1: Table S1). Blue vane traps were the next most effective method in catching bees, especially large-bodied species (i.e., *Amegilla*), when deployed for their standard month-long duration, whereas yellow vanes performed poorly, consistent with results of our literature review (Rhoades et al. 2017, Hall 2018).

Although targeted sweep netting was the most effective method of bee collection in terms of both individuals and taxonomic units, it still only caught about one-quarter of all bees in terms of abundance. The relative number of individuals observed-to-netted differed significantly among the higher taxonomic categories. This finding strongly suggests that although species-level identification cannot be obtained via observations, including observational counts is important for recording abundances. While it is often believed that smaller-bodied taxa are more likely to be missed from targeted sweep netting (Prado

et al. 2017, Templ et al. 2019), this was not the case in the present study. In fact, the largest-bodied taxon had the lowest number of bees netted relative to that of bees observed. The discrepancy may relate to the behavior of particular taxa, whereas large-bodied *Bombus* are generally both easy to detect visually and are slow fliers, making them relatively easy to catch. In contrast, *Amegilla* are rapid flyers (K. S. Prendergast, *personal observation*), and their large body size likely contributes to these bees being relatively harder to catch.

In this study, sweep netting caught more taxonomic units and individuals than pan traps. The two previous Australian studies that compared targeted sweep netting with pan traps found that targeted sweep netting outperformed pan traps (Popic et al. 2013, Threlfall et al. 2015). Studies outside of Australia have had mixed results: 20 studies comparing sweep netting with pan trapping found targeted sweep netting was more effective, 14 found pan trapping was more effective, and three found that while targeted sweep netting caught more species, pan trapping

caught more individuals (Appendix S1: Table S1). In the present study, pan traps were deployed for the same duration as the active sampling methods (3 h). While this was shorter than the typical duration over which pan traps are deployed (24–48 h; see Appendix S1: Table S1), it ensured an equal duration of time employed as sweep netting—something other studies have often not controlled for. However, even if catch rates in pan traps are multiplied 16 times to extrapolate to 48 h, numbers still fall short of those caught by targeted sweep netting. This further underscores the utility of targeted sweep netting as an effective sampling method for native bees, a finding that not only was clear from our study, but also emerged from our review of the literature (Appendix S1: Table S1). One caveat is that people may vary in their collection efficiency in using an entomological net.

Pan and vane traps

No previous published studies using pan traps to study native bee communities have been conducted in SWWA, but of those conducted in Australia, Threlfall et al. (2015) found yellow and white pans traps had higher catches than blue, whereas Gollan et al. (2011) found yellow pan traps had higher catch rates than white, and Saunders and Luck (2013) found that yellow pans traps had higher catch rates of both native bees and honeybees compared with white pans traps, with blue pans traps having the lowest catch rates.

In the present study, there were no differences in the mean number of individuals or taxonomic units captured among the colors of pan traps. Based on the literature review, it was apparent that no single color emerged as being superior, with the relative effect of colors in capturing bees being highly variable to nonexistent. We also found no significant differences between the UV-fluorescent and non-UV-fluorescent pan traps, and the blue vane traps caught more bees than the UV-fluorescent pan traps. The importance of UV fluorescence in attracting bees has recently been challenged, with bees having no significant difference in their preference for fluorescent or non-fluorescent pan traps (Shrestha et al. 2019).

The relatively low success of pan traps in the present study may be due to the flight characteristics of native bees in the region. Even elevated,

the traps were only ~25 cm above ground level. If most bees have flight trajectories higher up, and typically forage in canopies, pan traps may not attract these species due to their behavioral patterns. Indeed, the preferred foraging height of bees in Western Australia is poorly known and could result in underestimation of bee abundance and diversity. Although various species were netted in abundance on low-lying vegetation such as *Jacksonia*, *Scholtzia*, and *Scaevola*, many species, in particular the species-rich but tiny hylaeine and euryglossine bees, were also observed to be highly attracted to mass-flowering Myrtaceae such as *E. marginata* and *Corymbia calophylla*—large trees that produce masses of blossom in the canopy, out of reach of sweep nets and even visual observation. There is evidence from some habitats in other countries that bees are more frequent in canopies than near the ground (Ramalho 2004, Ulyshen et al. 2010). Future studies investigating the vertical stratification of bees foraging on such flora (e.g., using a cherry picker at different heights) would be very informative and allow future surveys to ensure that surveys take into account foraging preferences of bees and are not biased toward lower-flying species.

This urban bee study corroborates results from studies conducted in non-urban habitats that blue vane traps tended to have higher catch rates compared with yellow vane traps (Appendix S1: Table S1). The comparatively high catch rates of *A. chlorocyanea* in blue vane traps corroborate other studies that have found that blue vane traps are highly attractive to larger-bodied bees (often represented by *Bombus* in the Northern Hemisphere), whereas such bees are often underrepresented in pan traps (Stephen and Rao 2007, Wilson et al. 2008, Geroff et al. 2014, Buchanan et al. 2017, Rhoades et al. 2017). The relatively high catch rates of large-bodied bees found here (up to 45 *A. chlorocyanea* in one month), as well as reported in several other studies, caution against leaving these traps out for extended durations due to concerns over over-sampling (Tepedino et al. 2015).

The differences in captures in blue vane traps compared to yellow vane traps as found in our study, as well as in the broader literature (refer to Appendix S1: Table S1), compared with no clear color preference when it comes to pan traps,

remain to be elucidated. Future studies could measure the spectral properties of the blue vanes and replicate their spectral properties with pan traps, as well as place the blue vane traps at ground level, to test whether the difference is due to the spectral properties of the blue vanes, or a combination of the blue color and the relatively more elevated trap placement.

Blue vane traps had higher absolute catch rates compared to the pan traps, whereas yellow vane traps were comparable to the pan traps. However, the vane traps were deployed for a longer duration, and when standardized to three hours, the vane traps had the lowest catch rates (Table 2; see also Appendix S5). Attempting to standardize sampling of different methods is a challenge; however, we presented our results here based on the standard entomological practice whereby vane traps are typically deployed for longer durations. This is one of the practical advantages of vane traps as a sampling method whereby they can be left to sample for insects in the field for a month or more. In contrast, pan traps can often only be deployed for a more limited duration: In hot weather (as occurred in the present study), the water evaporates, and in rainy weather, they soon fill up and overflow (Prado et al. 2017). Pan traps can also be knocked over by wind or animals, or vandalized (Droege et al. 2017; K. S. Prendergast, *personal observation*). There are also animal welfare concerns: In hot weather, vertebrate animals may drink out of the pan traps and potentially fall ill from ingesting soapy water. Consequently, when considering how these passive methods are deployed in practice, we recommend including blue vane traps when sampling bee communities, based on their detection of large-bodied bees that were seldom caught by the other methods. From our own surveys, and considering the literature, it is evident that it is hard to achieve a level playing field when comparing different sampling methods, given that each has their own standard usage.

Trap-nests

Trap-nests have advantages over other monitoring methods in that they enable studying trophic relations (bee–pollen relationships and bee–parasitoid relationships; e.g., Roubik and Villanueva-Gutiérrez 2009) and enable bee demographic and fitness parameters to be quantified (Paini 2004,

Hudewenz and Klein 2013). However, occupancy of nests may be influenced not only by the abundance of bees in the environment but also by nesting resources already present in the wider environment, and the design of the trap-nests themselves (MacIvor 2016). And while trap-nests enable monitoring of bee populations, this is limited to aboveground cavity-nesting bees, which may comprise only a minor component of the overall bee assemblage (Twerd and Banaszak-Cibicka 2019) and may differ in their response to environmental variables (Neame et al. 2013).

A key finding of our research, which to our knowledge has yet to be explicitly investigated in previous trap-nesting studies, was our comparison of the representation of cavity-nesting bees collected during surveys vs. those using the trap-nests. Trap-nests were only occupied by a subset of the potential diversity of cavity-nesting species present at a site, and even for species both observed in the field and utilizing the bee hotels, the relative representation of species differed markedly. We nevertheless recorded a substantial diversity of cavity-nesting bees using a trap-nests, and in some cases, species, or individuals of both sexes, that were not observed in the field. A previous study in urban community gardens in Australia found only an exotic bee species occupied the trap-nests (Makinson et al. 2016); the reasons for this are unclear but it may have been poor trap-nest design or location, or that better nesting resources were present in the wider environment. Other Australian studies outside of urban areas (Murphy 2015), as well as urban bee studies overseas, have, however, had more success (Fortel et al. 2016). We conclude that trap-nests provide a complimentary means of monitoring native bee populations, with a number of advantages over other methods, but are inadequate for evaluating the composition of native bee assemblages.

Mobile gardens for surveying bees

Of all methods, the mobile gardens were the least effective. Few bees were attracted to the mobile gardens, despite selecting flora known to be visited by bees in the region. This may be due to foraging behavior of bees in a known environment, in that they previously learned where the flora hot spots are at a site and so avoid these new plants. Studies on *Bombus* and euglossine

bees have often reported site constancy (at least temporarily) where individuals establish home ranges or foraging routes (e.g., trap-lines) such that they remember, and repeatedly return to, rewarding resource patches (Amaya-Márquez 2009). Three other studies have used mobile gardens in urban areas with far greater success (Williams and Winfree 2013, Lowenstein et al. 2014, 2015). Observations per survey went for a longer duration than the current study, yet the greater visitation success was disproportionately higher (Table 7). The reason for the discrepancy can only be speculated, but may be due to different foraging strategies of bees in Australia compared to other countries or the relatively high proportion of specialized pollination systems that occur

in Australia (Phillips et al. 2010). Due to the uncertainty of bees actually visiting mobile gardens, recording visitation to plants in situ is more effective for monitoring native bee communities.

The effect of habitat

Habitat can impact the suitability and success of different sampling methods (Rhoades et al. 2017, O'Connor et al. 2019; Table 1), and this was supported by our data. As with Saunders and Luck (2013), we found evidence that relative attractiveness of pan trap colors varies according to habitat type. While vane traps caught a higher number of individuals in bushland sites, pan traps had higher relative percentages of bees of the total catch when placed in residential areas,

Table 7. Comparison of results from surveys recording bee visitation to mobile gardens.

Publication	Plant species used	Plants/site	Flowers (<i>n</i>)	Bees visiting (<i>n</i>)	Average visits/survey (range)	Average R per survey (range)	Sites (<i>n</i>)	No. of times visited/site	Duration (min)	Country, city	Habitat
This study	<i>Scaevola aemula</i>	2	Approximately 10–40	15	0.286 (range 0–8)	0.036 (range 0–1)	14	4	15	Australia, Perth	Urban (bushland remnants and residential gardens)
Lowenstein et al. (2007)	<i>Leptospermum</i> “Pink Cascade”	1	Approximately 5–20	0	0	0	14	4	15	USA, Chicago	Urban (residential gardens)
	<i>Dianella revoluta</i>	1	Approximately 2–6	0	0	0	14	4	15		
	<i>Eutaxia myrtilifolia</i>	1	Approximately 5–20	0	0	0	14	4	15		
Lowenstein et al. (2017)	Purple coneflower (<i>Echinacea purpurea</i> , var. “Magnus”)	...	20–30	...	7.8 (range 0–31)	4 (range 0–11)	25	3	60	USA, Chicago	Urban (residential gardens)
Williams and Winfree (2007)	Cucumber (<i>Cucumis sativus</i> , var. “Picklebush”)	3	6–9 female flowers (2:1 ratio)	...	9 (median, all visitors, not restricted to bees)	1.5 (median, all visitors, not restricted to bees)	30	2	30	USA, Chicago	Urban (residential gardens)
	Eggplant plants (<i>Solanum melongena</i> , var. “Black Beauty”)	3	5–9 flowers	...	1 (median, all visitors, not restricted to bees)	1.0 (median, all visitors, not restricted to bees)	30	2	30		
	Purple coneflower plants (<i>Echinacea purpurea</i> , var. “Magnus”)	3	6–9 flowers	...	10 (median, all visitors, not restricted to bees)	3.0 (median, all visitors, not restricted to bees)	30	2	30		
Williams and Winfree (2007)	<i>Claytonia virginica</i>	5–7 per pot (10 × 8 L pots)	40–70	<0.001–1.6 visits-flower ⁻¹ . h ⁻¹	1–5 spp/h		21	1	60	USA, Chicago	Urban (residential gardens)
	<i>Polemonium reptans</i>	1 per pot (10 × 8 L pots)	160–200	0.05–1.8 visits-flower ⁻¹ . h ⁻¹	1–8 spp/h		19	1	60	USA, Philadelphia	Urban (forest remnants)

Note: Names in ellipses refer to the plant cultivar.

despite native bees being more abundant in bushland remnants (pooled across all sampling methods). Relatively lower catch rates of native bees in pan traps located in bushland habitat may be due to bushland having more bee suitable flowers, whereas in residential areas, the wide array of unsuitable flowers may mean that bees are more likely to be attracted to colored pan traps, akin to suggestions that pan traps are more effective in resource-poor habitats (Potts et al. 2005, Roulston et al. 2007, Baum and Wallen 2011). Furthermore, bee communities in residential areas tend to be dominated by generalist species (Cane et al. 2005), which may make them more likely to respond to pan traps.

Native bees vs. honeybees

Comparing all methods where both native bees and honeybees were sampled, different methods were not uniform in whether native bees or honeybees were caught at significantly higher abundances. For example, we found catch rates of honeybees were significantly greater in yellow vane traps relative to native bees, but not for blue vane traps. This has implications for assessing competition between native bees and honeybees (Wojcik et al. 2018), because relative abundance of honeybees to native bees recorded will vary depending on the survey method used.

CONCLUSIONS

Although pan traps are widely used, are easy to deploy, and can collect large numbers of specimens in certain habitats in the Northern Hemisphere, they were found to be insufficient at sampling native bee communities in this study in an urbanized region of the southwest Western Australian biodiversity hot spot. Targeted sweep netting was shown to be the most effective method for collecting a representative, comprehensive sample of native bee assemblages. Blue vane traps are recommended to accompany targeted sweep netting, as they can be effective at collecting a subset of taxa that may be underrepresented in other methods.

Although there have been a number of studies employing different sampling methods to survey bees, no synthesis of these methods across landscapes, countries, and habitat types has been undertaken. Our literature review

therefore contributes to the global goal of monitoring native bee populations and emphasizes that a number of methods should be employed in order to sample the bee community as well as possible.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3076/full>

Appendix S1: Literature review

Appendix S2: Generalized linear mixed effect models

Appendix S3: Taxonomic units by sampling method

Appendix S4: Species accumulation curves of taxonomic units for each of the sampling methods

Appendix S5: Generalized linear mixed effect models with vane traps standardized to 3 h