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RESEARCH ARTICLE

Rapid responses of bees and butterflies but not birds to targeted urban road verge habitat enhancements

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Abstract

1. Cities provide opportunities for biodiversity conservation through the design of urban greenspaces as wildlife habitat. A significant proportion of urban public land is narrow linear road verges, though their small size and harsh environmental conditions (e.g. high soil temperatures) may limit their ability to support plants and animals.
2. We worked with a municipal government in a highly urbanised area to test whether conversion of standard road verges (e.g. lawn) to predominantly native understorey plants (forbs, grasses and shrubs) selected for their abilities to tolerate harsh growing conditions and provide habitat increased the abundance and richness of bees, butterflies and birds. We used a before-after-control-impact experiment and characterised temporal dynamics of biodiversity responses 1 year prior to planting and 4 years post-planting. We also tested whether traits known to influence species responses to urbanisation (body size and feeding specialisation) mediated responses to road verge plantings.
3. Bee species richness and abundance increased at experimental plantings in the first post-planting year and remained stable thereafter despite fluctuations at control sites. Butterfly abundance but not richness increased, and there was no evidence of bird responses to plantings.
4. Larger bee species, which are known to be most negatively impacted by urbanisation, benefited more from the road verge plantings, while there was no effect of feeding specialisation. Bird and butterfly traits did not mediate responses to plantings.
5. *Synthesis and applications*. Road verges comprise a significant proportion of urban green spaces, and our results suggest that despite their small sizes and harsh environmental conditions they can provide habitat for bees and to a lesser extent butterflies. We demonstrated that habitat value can be rapidly enhanced by converting standard road verges to native understorey plants and that these benefits may be greatest for the bee species most negatively impacted by urbanisation. Modifications such as additional plant species or wider verges may be required

for urban road verges to provide habitat for a greater range of taxa including birds and butterflies.

KEYWORDS
community, ecology with the city, experimental co-design, pollinator, urban ecology, urban greening

1 | INTRODUCTION

Urban expansion and intensification are drivers of global biodiversity decline. Cities can mitigate and reverse these declines through increasing habitat quality, area and connectivity (Aronson et al., 2014, 2017). Road verges collectively comprise a significant proportion of urban public land (e.g. Marshall et al., 2019) that is currently under-utilised for biodiversity conservation (Soanes & Lentini, 2019). Street trees are well-known to provide ecosystem services such as climate regulation and pollution control, while fewer studies have looked at other growth forms (e.g. herbs) and services such as the provision of habitat for native animal species (Säumel et al., 2016).

The small size of road verges is thought to limit their capacity to provide habitat because extinction rates are higher in small patches (Aronson et al., 2017). However, the traditional view that small habitat patches are less valuable for conservation has been overturned by empirical evidence revealing their disproportionately high conservation value, due to the more rapid spatial accumulation of species across small compared to large patches and historical patterns of habitat clearing leading to small patches being the last remaining habitats for rare or specialist species (Fahrig, 2020; Riva & Fahrig, 2022; Wintle et al., 2019). If individual small areas of vegetation created in verges can provide habitat, the challenge of coordinating actions at large scales across neighbourhoods and cities (Aronson et al., 2017) is mitigated using many but smaller patches.

The limited amount of previous research on urban road verges as wildlife habitat suggests they can provide habitat for some species, particularly insects, although this varies with road verge characteristics (e.g. lawn vs bioswale) (e.g. Baldock et al., 2019; Kazemi et al., 2011; White et al., 2005). This research highlights the need to investigate designs with relatively high value for biodiversity conservation. Lawns are ubiquitous in urban areas, including along road verges, but are thought to provide low-quality habitat (Aronson et al., 2017). While street trees can provide additional habitat elements, understorey plants have recently been shown to be particularly important habitat in larger urban greenspaces (Mata et al., 2021; Threlfall et al., 2016) and so might similarly enhance the biodiversity value of road verges. It may also be important to select indigenous plant species as they often support more native animal species compared to exotic plants (Berthon et al., 2021). However, due to their proximity to concrete paths and asphalt roads which increase soil temperatures, soil compaction and nutrient inputs (Calfapietra et al., 2015), the range of plants capable of growth and survival in the harsh environment of road verges is limited. The challenge therefore requires the selection of plants that will tolerate these conditions while providing habitat for fauna.

It is also important to understand which animal species benefit from road verge habitat plantings and the mechanisms that might underly these responses. It has been argued that while small-scale restoration plantings in highly modified landscapes often contain higher numbers of species and individuals (compared to the modified matrix), it is typically only the resilient and common species that benefit (Kleijn et al., 2006). However, recent research from agricultural landscapes suggests that small-scale restoration is more beneficial for uncommon species with traits sometimes associated with vulnerability to agriculture (e.g. specialised feeding or nesting habits), indicating that small-scale restoration can reverse some of the negative impacts of converting natural habitat to agriculture (Kremen & M'Gonigle, 2015; Nicholson et al., 2020). Less is known about the effects of small-scale restoration in urban environments, but a growing body of trait-based studies makes it possible to identify traits associated with vulnerability to urbanisation (e.g. Hahs et al., 2023), providing a basis for determining whether small-scale road verge habitat improvements can reverse the effects of converting natural habitat to urban environments.

We describe a unique 'ecology with the city' (Pickett et al., 2022) co-designed experiment. University researchers and urban land managers collaboratively designed and planted a palette of predominantly native forbs, grasses and shrubs specifically selected to tolerate harsh urban environments while providing resources to target fauna (hereon referred to as the 'road verge biodiversity planting/palette'). We compared the biodiversity value of the road verge biodiversity palette to standard urban road verges (e.g. mowed lawn or pavement with street trees) by surveying bee, butterfly and bird communities over 5 years using a before-after-control-impact (BACI) design. BACI designs are better able to detect biodiversity responses to human impacts, particularly over short-medium time scales in highly disturbed systems (França et al., 2016), and are the most appropriate but least used method for evaluating ecological restoration (Hale et al., 2019). We also tested whether road verge plantings were more likely to be used by animals with traits that make them more vulnerable to urbanisation compared to control sites.

2 | MATERIALS AND METHODS

2.1 | Site selection

This research was conducted in partnership with the City of Melbourne local government in Melbourne, Australia. Prior to European colonisation in 1835, the area that is now the City of Melbourne was dominated by grassy woodlands with sparse tree cover and an understorey of predominantly forbs and grasses (Bull & Sinclair, 2014). While today it has comparatively high levels of open space and biodiversity, much of this comprises exotic species (Ives et al., 2013). Four impact sites on road verges and medians (areas separating traffic lanes) within the highly urbanised municipality were selected from streets that the City had scheduled for planting upgrades. In 2018 these were planted with species from the Urban Nature Planting Guide (https://www.melbourne.vic.gov.au/community/greening-the-city/urban-nature/Pages/urban-nature-planting-guide.aspx), a plant palette of predominantly native flora designed by University of Melbourne researchers specifically to increase urban vegetation complexity and provide food, shelter and reproduction resources needed by local bees, butterfly and bird species (e.g. nectar for insects and insectivorous birds, shrubs for bird nests; see Tan et al. (2022) for more detail). We selected three control sites for each impact site (giving a total of 16 sites) that had no road verge understorey plantings but similar surrounding land use and overstorey street trees to the impact site using satellite imagery (NearMap). The control sites were selected to be between 500 m and ~1 km from its paired impact site, and a similar distance from nearby parks. Within each control site, control plots with approximately the same area as the impact plots were established on road verges or medians.

Plots were surveyed for bees, butterflies and birds before and after planting (impacts) occurred. Before surveys occurred twice in March 2017 (late summer season) at all impact sites and four control sites, and twice in November/December 2017 (late spring/early summer season) at all 16 sites. After surveys occurred twice in late summer (February to March) and twice in spring/early summer (October–December) in 2018–2019, 2019–2020 and 2021–2022 at all 16 sites. Permission for field work and ethics approval were not required.

2.2 | Survey methods

2.2.1 | Bees and butterflies

Bees and butterflies were sampled within plots using an area-based survey method and a variable transect walk, which are methods successfully employed in previous pollinator surveys in urban garden plots (Makinson et al., 2017) and are effective for both bees and butterflies (Kadlec et al., 2012; Westphal et al., 2008). We placed 1 m × 1 m quadrats on the largest flower patches in each plot and recorded bees and butterflies within quadrats for 10 min each. Following the quadrat surveys, the entire plot was surveyed for bees and butterflies for an additional 10 min. If no flower resources were present in the plot no quadrat surveys were made, however, the plot was still surveyed for the additional plot level time period to record butterflies or bees utilising non-flowering plants or moving through the plot. This was done using a variable transect method, walking at a steady pace within the plot, and targeting understorey plants while covering the whole area of the plot. Given the various sizes of the impact and paired control sites in this project, which ranged from ~200 to 1000 m^2, we scaled time spent surveying per plot (i.e. the number of quadrats and time spent doing plot-level surveys) according to area.

The flowering plant that each bee and butterfly specimen was recorded on was also recorded or photographed for later identification. To gain a measure of forage availability, the number of floral units, i.e., raceme, umbel, capitulum, etc., on each flowering plant species within each quadrat were recorded in seven categories (<25, 25–50, 51–100, 101–200, 201–500, 501–2000 and 2001–4000 floral units).

Bees were collected off flowers with a sweep net and placed in vials. If they could be identified in the field they were released after the survey time to avoid double counting, and if not, were frozen and pinned for later taxonomic verification (Ken Walker, Melbourne Museum). Butterflies were identified on the wing or collected with a sweep net to confirm identification (Field, 2013). The time taken to catch and identify a specimen was not included in the survey time.

Following the plot surveys, an additional 10 min was also spent surveying floral resources within ~25 m of the edge of the plots. Bees and butterflies observed in these areas were also recorded to determine species presence and to construct interaction networks but were not included in the plot level species diversity and abundance data.

Surveys only took place under suitable weather conditions for bee and butterfly activity: between 09:00 and 17:30, when the temperature was between 20 and 35°C, with at least partial sun and wind speed less than 4 m/s.

2.2.2 | Birds

To survey birds we used the ‘standardised search’ bird survey method (Watson, 2003). Using this technique each site was searched visually (by two experienced observers familiar with Melbourne bird species) until no new species were detected for a period of 20 min. Walking at a steady pace around the study site, birds were counted if they were seen on the ground or on plants. Each time a new species was observed the 20-min count would start again, until no new species were recorded. This technique is designed to achieve a more complete bird species list for habitat patches that differ greatly in size and the number of species present. Surveys only took place between 06:00 and 11:00 on days with no rain and wind speed less than 6 m/s.

2.3 | Analyses

2.3.1 | Abundance and species richness

The impact of understorey road verge biodiversity plantings on bee, butterfly and bird abundance and species richness were tested using generalised linear mixed models (GLMMs), using site-by-year combinations as samples (i.e. $n=16$ sites × 4 years = 64). GLMMs allow for a statistical test of impact via a treatment × time interaction (i.e. test of whether the difference between impact and control sites differs between before compared to after the impact occurs) while accounting for the non-independence between repeat observations at each site using a random effect for site, as follows:

$$R_{ij} = a + \beta_1 \mathit{treatment}_j \times \beta_2 \mathit{time}_i + \mu_1 \mathit{site}_j + \varepsilon_{ij},$$

where R_{ij} is the species richness at site j in time period (year of sampling) i, $\mathit{treatment}_j$ is the treatment applied at site j, time_i is the year of sampling, site_j is the site identity, β_1 and β_2 are fixed effect parameters, and μ_1 is the random effect parameter.

Bee, butterfly and bird abundance (i.e. the sum of all individuals recorded across all surveys within each site-by-year combination, excluding outside plot observations), species richness (i.e. the sum of all species recorded across all surveys within each site-by-year combination, excluding outside plot observations) and estimated species richness (Chao1 calculated using 'estimateR' function in 'vegan' package; Oksanen et al., 2015) were modelled (separately for bees, butterflies and birds) as functions of: (1) treatment; (2) survey year; (3) treatment × survey year interaction; (4) site (as a random effect); (5) the total number of survey hours in each site-by-year combination (bee and butterflies only, to account for the fact that only plot-level surveys occurred when there was nothing flowering, and eight of the control sites were only surveyed twice in the first survey year), or the total number of surveys in each site-by-year combination (birds only, to account for the fact that eight of the control sites were only surveyed twice in the first survey year); (6) number of hours since 5 am (for birds only) and (7) the proportion of impervious surface within 200 m of each site (this measure of landscape context has previously been shown to influence bee, butterfly and bird communities in urban Melbourne (Kurylo et al., 2020; Threlfall et al., 2015, 2016) and so its inclusion was expected to reduce unexplained variation). Total number of survey hours was included as a second-order polynomial when appropriate (i.e. when abundance or species richness plateaued at higher level of survey effort). Likelihood-ratio tests were used to test the statistical significance of the interaction between treatment and time for each model. Poisson models were used to account for heteroskedasticity, and negative binomial models were used when Poisson models were over-dispersed.

We used network diagrams to aid the interpretation of bee and butterfly responses to road verge biodiversity plantings, and to inform future selection of plant species for road verge plantings. Six bipartite plant-pollinator interaction meta-networks (i.e. network including multiple sites) were also produced using observations of bees and butterflies visiting flowers inside and outside plots across all sites or across sites belonging to the four BACI categories (i.e. before-control, before-impact, after-control and after-impact) (Figures S4–S6).

2.3.2 | Trait analysis

We tested the effects of species traits on responses to restoration using Hierarchical Modelling of Species Communities (HMSC) implemented in the R package 'Hmsc' (Tikhonov et al., 2019). HMSC is a Bayesian joint species distribution modelling approach with Markov chain Monte Carlo sampling that uses a hierarchical structure to model species environmental responses as functions of traits and phylogenetic relationships (Ovaskainen & Abrego, 2020). We excluded the first year of data (i.e. before restoration plantings) and combined the 3 years of post-restoration data (i.e. after data) to produce for each taxonomic group a site-by-species matrix with 16 rows (one for each site). This allowed us to model species presence/absence in the years after restoration (separately for birds, bees and butterflies) as a function of site type (control vs impact) and total survey hours at each site using a probit error distribution, and test whether between-species variation in responses to site type were explained by species traits and phylogenetic relatedness.

All species occurring at less than two sites were removed to reduce the influence of extremely rare species. Exotic species (i.e. not present in Australia prior to the arrival of European people) were not included. This left 18 bee species, 17 bird species and 6 butterfly species. Since the number of species determines the sample size for testing trait effects on species responses, and trait models include an intercept term and phylogenetic relatedness, we only included a single trait in each model and so ran separate models to test the effects of different traits. There were too few butterfly species to perform trait analysis.

We selected traits that previous research suggests mediate responses to urbanisation. Specialisation in feeding or nesting requirements, and mobility/body size are among the strongest predictors of bird and bee responses to urbanisation, with more specialised and larger/more mobile species being more negatively impacted, particularly at high levels of urbanisation (Hahs et al., 2023). We therefore tested whether feeding specialisation, body size and commonness (to test whether only already common species benefit) mediated bird and bee responses to road verge biodiversity plantings.

Trait values were obtained from a number of sources. For birds and bees the commonness of each species was defined as the number of sites it was detected in during the first year of surveys (i.e. before plantings). For bees, inter-tegular distance (ITD, range = 0.90–2.69 mm) and diet specialisation (oligolectic vs. polylectic) were taken from Threlfall et al. (2015). For birds, body mass (range = 14–720 g) and feeding guild defined as an omnivore (generalist), insectivore, nectarivore or herbivore according to were obtained from Pigot et al. (2020).

Phylogenetic relatedness was obtained from a number of sources. A species-level phylogeny for birds was obtained from the global phylogeny of birds website (https://birdtree.org/downloads/), pruned for the species present in our data. In the absence of a species-level phylogeny for the bee species we collected, we assembled a phylogenetic tree with genus-level soft polytomies modified from Brown and Cunningham (2022).

We obtained posterior parameter estimates with 95% credible intervals for species responses to road verge biodiversity plantings, and the effects of traits and phylogeny on these species' responses. Herein we refer to parameter estimates with 95% credible intervals not overlapping zero as providing strong support for an effect of the associated variable. We also report overall area under the receiver operator curve (AUC) values (where AUC = 1 when a model perfectly discriminates presences and absences, and 0.5 when discrimination is as good as random) by averaging AUC across all species (Ovaskainen & Abrego, 2020). Four independent chains of 1000 samples each, with a thinning interval of 100 and burn-in of 500 samples, was sufficient to obtain satisfactory model convergence for all parameters estimated in all models, which was assessed with the potential scale reduction factor (which was close to one, indicating the four independent chains produced similar results and the posterior was well sampled) and the effective number of samples (which was close to the actual number of samples, indicating independence between consecutive recorded samples) (Ovaskainen & Abrego, 2020).

3 | RESULTS

Over the four monitoring years, we recorded 1362 bees belonging to 25 species/morphospecies (23 native, 2 exotic), 656 butterflies belonging to 8 species (7 native, 1 exotic) and 3785 birds belonging to 37 species (30 native, 7 exotic species). Here we report the results for native species only, as these are the target of management for enhancing biodiversity. Responses to road verge biodiversity plantings varied between bees, butterflies and birds (Figure 1) and results for species richness were similar whether based on raw richness or estimated (Chao1) species richness (Figure S7).

3.1 | Bees

We detected positive effects of the road verge biodiversity plantings on native bee abundance and species richness. The treatment × year interaction was statistically significant (alpha = 0.05) for bee abundance ($p = 0.001$) and richness ($p = 0.004$), with bee abundance and richness both being higher at impact sites after, but not before, planting works (Figure 1a,b). Bee diversity and abundance increased significantly in impact compared to control sites in the first year post-planting increased further in the second year (less so for richness), and then by the final survey year (fourth year post-planting) had not increased further. The temporal patterns of bee diversity and abundance varied between impact and control sites, with impact sites initially increasing and then plateauing while control sites decreased and then returned to their initial levels. There were also significant negative relationships between impervious surface cover and bee richness (estimate = −0.018, $p < 0.001$) and abundance (estimate = −0.025, $p < 0.001$).

In the HMSC analysis 12 of 18 bee species exhibited strongly supported (i.e. 95% credible intervals did not overlap zero) positive associations with the road verge biodiversity plantings (Figure 2). There was a strongly supported effect of bee body size (ITD) on species responses, with larger bees exhibiting stronger positive responses to restoration (Gamma = 2.202, lower credible interval = 0.721, upper credible interval = 3.816). There was no strong evidence of phylogenetic signal in responses to restoration, and it was not only the large-bodied Megachilidae species that responded positively to restoration but also the larger Halictidae and Colletidae species (Figure 2). Average AUC for this model was 0.88. There was no strong support for an effect of commonness or floral specialisation on bee species responses to road verge biodiversity plantings.

The bee-plant interaction network revealed the importance of plant species in our road verge biodiversity plantings as floral resources for bees. The plants from our palette received more bee visits compared to other understorey plants and trees, and the three most visited species (*Wahlenbergia communis*, *Brachyscome multifida*, and *Myoporum parvifolium*) were all part of our road verge biodiversity planting palette (see Figure S2).

3.2 | Butterflies

We detected a positive effect of road verge biodiversity plantings on native butterfly abundance, but no effect on species richness. The treatment × year interaction was statistically significant for butterfly abundance ($p = 0.002$), with butterfly abundance being higher in impact sites after but not before road verge biodiversity plantings (Figure 1c,d). The interaction was not statistically significant for butterfly richness ($p = 0.234$). As with bees, the increase in abundance was sustained over the four post-treatment years, though the magnitude of this increase was less. Butterfly richness and abundance were both negatively associated with increasing impervious surface cover (richness estimate = −0.014, $p = 0.007$; abundance estimate = −0.020, $p = 0.001$). In the HMSC analysis, none of the six butterfly species exhibited strongly supported responses to the road verge biodiversity plantings.

The butterfly-plant interaction network revealed that plant species in our road verge planting palette were less important for butterflies compared to bees (Figure S4 vs. S5). The three most visited plant species included one from the planting palette (*Brachsycome multifida*) and two weeds (*Trifolium repens* and *Galenia pubescens*) (Figure S3).

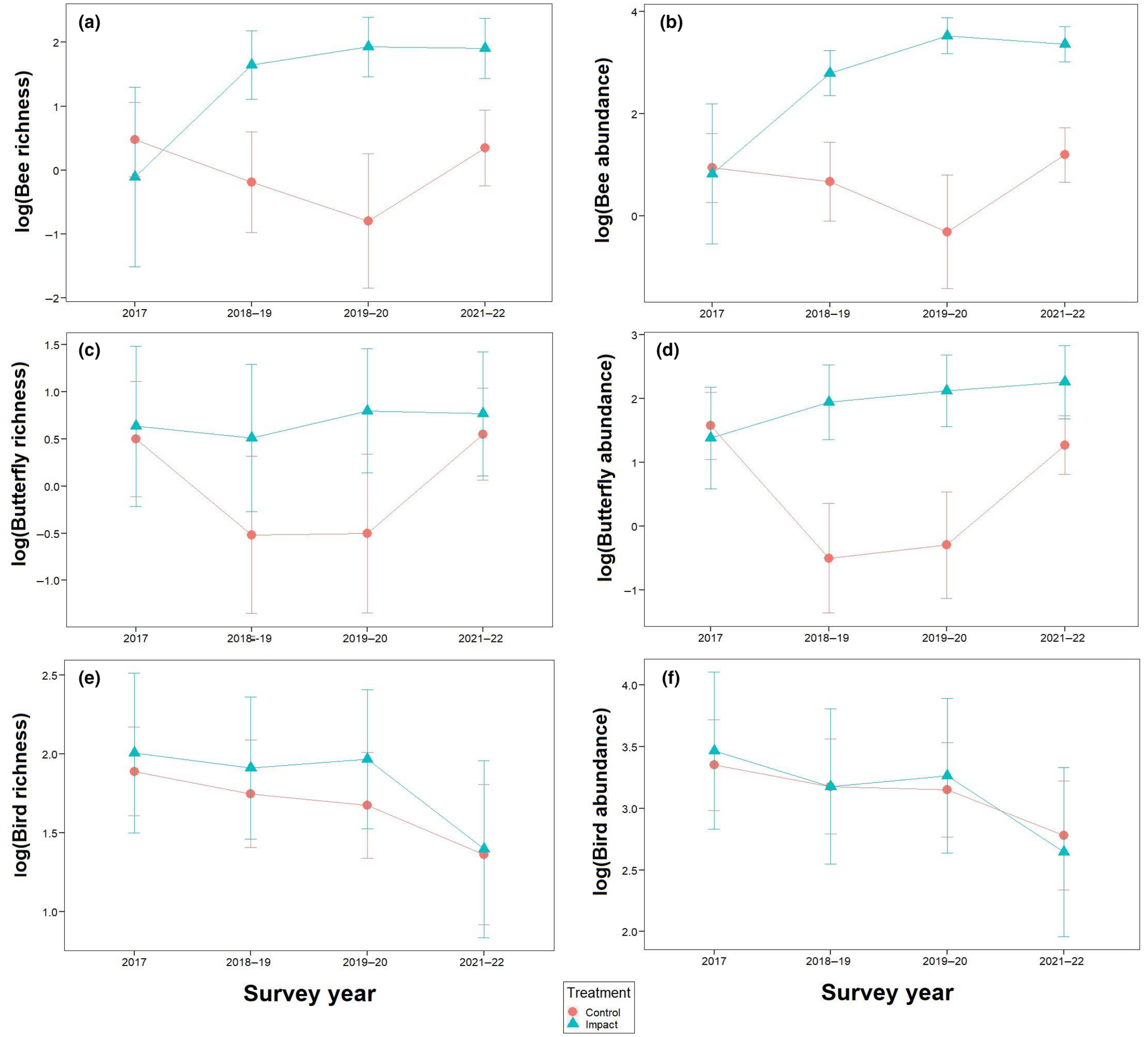

FIGURE 1 Bee, butterfly and bird responses to road verge biodiversity plantings through time. Interaction plots show the average (with 95% confidence intervals) richness (a, c, e) and abundance (b, d, f) of bees (a and b), butterflies (c and d) and birds (e and f) recorded at control (red circles) and impact (blue triangles) sites in each survey year. Note that 2017 is prior to planting.

3.3 | Birds

We did not detect any effect of our road verge biodiversity plantings on native birds. The treatment × year interaction was not statistically significant for bird abundance ($p = 0.650$) or species richness ($p = 0.864$), meaning that differences in bird abundance and species richness between control and impact sites did not change following planting (Figure 1e,f). There was no significant effect of impervious surface cover on bird richness (estimate = −0.003, $p = 0.334$) or abundance (estimate = −0.005, $p = 0.483$). In the HMSC analysis, only two of 17 bird species (white-plumed honeyeater and pied currawong) exhibited strongly supported (positive) responses to restoration, and there was no strong support for an effect on any trait on bird species responses to road verge plantings.

4 | DISCUSSION

Biodiversity conservation in urban environments is important but faces many challenges including limits on the size of habitat patches. We investigated whether small-scale plantings of predominantly native species deliberately selected for their ability to tolerate harsh urban environmental conditions and provide resources for target fauna increased the value of urban road verges as habitat for birds, bees and butterflies. The plantings provided floral resources for the

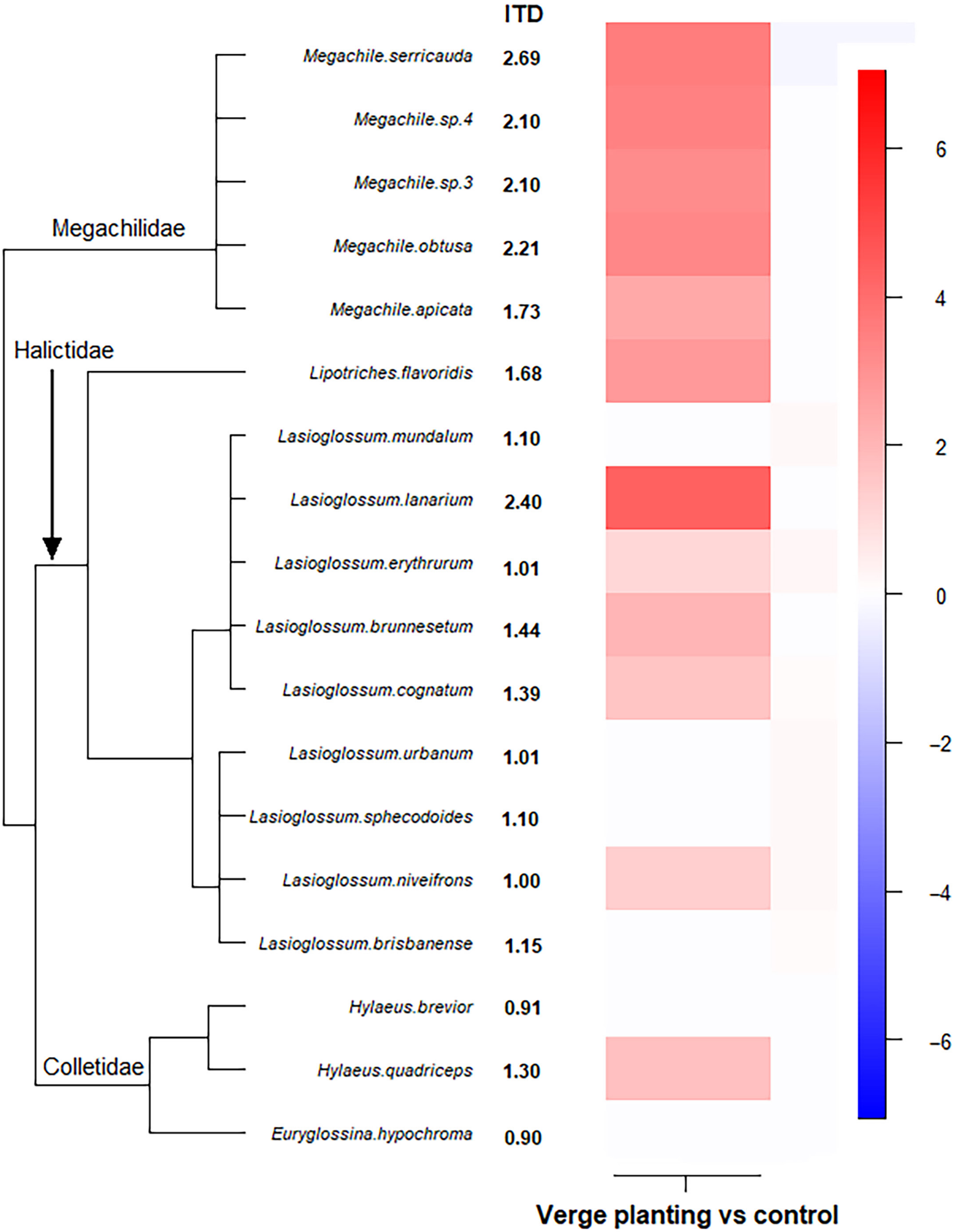

FIGURE 2 Bee community responses to road verge biodiversity plantings. A colour rectangle next to a species indicates a strongly supported response (95% credible intervals did not include zero), the colour indicates direction of response (red = positive, blue = negative), and darker shades indicate stronger relationships (i.e. larger parameter estimate) shown on temperature bar on right-hand side. Inter-tegular distance for each species is shown next to its name. Phylogenetic relationships between species are shown on the left side of the figure, with family indicated.

duration of the study (see Figure S1), demonstrating their ability to survive in urban road verges at least in the short-medium term, and bees (and to a lesser extent butterflies) responded positively to these plantings. We did not detect significant bird responses to the plantings, suggesting that modifications are required to the habitat enhancement program to improve their habitat value for birds.

4.1 | Urban road verges as habitat

Recent reviews of rights-of-way, including road verges, railways, and power line corridors in rural and urban landscapes have found that these habitats can support biodiversity comparable to nearby (semi) natural habitats and that management interventions can increase local biodiversity (Gardiner et al., 2018; Morelli et al., 2014; Phillips et al., 2020; Villemey et al., 2018). Bee abundance and species richness increased in response to our road verge plantings, and the plant species we planted included those most frequently visited by bees. Our findings thus provide further evidence that enhancing floral resources on road verges benefits bees (see also Hopwood, 2008), including in heavily urbanised areas.

Butterflies did not appear to benefit as much from the road verge plantings, increasing in abundance (temporarily) but not species richness. The butterfly community was dominated by *Zizinia labradus* whose caterpillars feed on the introduced lawn species White Clover (*Trifolium repens*) and other Fabaceae species (Field, 2013) that were not included in our planting palette. There were Poaceae and Asteraceae specialists (*Heteronympha merope*, *Ocybadistes walker*, *Vanessa kershawi*) that surprisingly did not appear to benefit from road verge plantings containing plants from both families, possibly because of the ability of their caterpillars to feed on exotic lawn species found on standard road verges and other urban greenspaces (Field, 2013; Kurylo et al., 2020). Compared to bees, a lower proportion of butterfly visits were made to plants from our understorey palette, and exotic weeds were among the most frequently visited (note that we did not distinguish between visits for nectar or oviposition). Butterflies may also be more sensitive to road verge width than are bees (Hopwood, 2008; Phillips et al., 2020), and so less likely to be attracted to our narrow road verge plantings.

Bird abundance and richness did not respond to road verge plantings, though two species (white-plumed honeyeater *Lichenostomus penicillatus*, and pied currawong *Strepera graculina*) were more likely to occur at these plantings. Previous studies in Melbourne have found that large urban greenspaces with more understorey and *Eucalyptus* trees support more bird species, particularly small insectivorous or nectarivore species, compared to other large urban greenspaces and residential areas (road verges and front yards) (Threlfall et al., 2016; White et al., 2005). This is thought to be because understorey provides shelter, nesting and foraging opportunities for these smaller species, and *Eucalyptus* trees support higher insect prey numbers and nectar volumes (Threlfall et al., 2016; White et al., 2005). Small insectivorous species were rare or absent across our study sites, including experimental plantings, possibly because these plantings were too small (relative to habitat area requirements of birds), immature (i.e. shrub cover not fully developed) and/or isolated from large green spaces. There were eight nectivore species observed across our study sites, though only one (white-plumed honeyeater) was positively associated with impact sites, suggesting that other factors such as street tree species composition were driving variation in these bird species.

4.2 | Temporal dynamics

The temporal patterns of bee responses to road verge plantings are consistent with rapid population increase, though other explanations cannot be ruled out. Increases in bee richness at impact sites plateaued sooner (in first post-planting year) than increases in abundance (in second post-planting year), possibly because additional bee species and individuals rapidly detected the new plantings, but there was a lag in population increase as subsequent generations benefited from the locally enhanced floral resource (Crone, 2013; Inari et al., 2012). The increases in bee abundance and richness at impact compared to control sites were sustained over 4 years, despite substantial annual variability at the control sites (i.e. background ecological variation). This suggests a stabilising influence of the road verge biodiversity palette on local bee communities. It is possible that increased species richness and abundance at planting sites resulted from dilution-concentration effects, whereby forager numbers increased at road verge biodiversity plantings and decreased in other parts of the landscape, without an overall population increase (Tscharntke et al., 2012). We cannot rule this out as we did not survey bees in the surrounding landscape. However, bee abundance continued to increase for 2 years post-planting despite floral resource levels plateauing in the first post-planting year (Figure S1), which is more consistent with lagged population increase over multiple years than concentration-dilution effects as the latter are short-term foraging responses to altered resource levels (Tscharntke et al., 2012).

The weaker responses of birds and butterflies, compared to bees, to our road verge plantings might have arisen from differences in life history traits mediating temporal lags, though different traits predict different outcomes. For instance, bees are expected to respond more rapidly to habitat creation compared to birds because their faster life histories (i.e. earlier maturation and higher reproductive output) allow for a more rapid population response, while birds are expected to respond more rapidly than bees because of their generally greater dispersal abilities (though dispersal may be inhibited for some species in urban environments) (Lira et al., 2019; Watts et al., 2020). Disentangling these contrasting effects was beyond the scope of our study.

4.3 | Traits

Analysis of bee traits was consistent with the notion that road verge plantings supported species that had been most negatively impacted by urbanisation. Larger-bodied bees were more positively associated with impact sites after planting. Previous reviews of traits mediating bee responses to urbanisation found that larger bees were more negatively impacted, particularly at high levels of urbanisation, possibly due to their greater resource requirements (Buchholz & Egerer, 2020; Gathof et al., 2022; Hahs et al., 2023). Larger bees might also have a greater ability to find restored sites due to their greater mobility (Greenleaf et al., 2007). Our findings thus suggest that road verge plantings did not just benefit the resilient and common bee species (we did not detect an effect of commonness on bee responses to plantings) but may have partly reversed the negative impacts of urbanisation by benefiting species that may have experienced the greatest historical declines.

We did not detect an effect of floral specialisation on bee responses to plantings. Previous studies investigating whether this trait mediates bee responses to urbanisation have found mixed results (Buchholz & Egerer, 2020; Gathof et al., 2022). Specialist bees in Australia mostly belong to the Colletidae family and tend to specialise on Gondwanan plant lineages such as Myrtaceae and Proteaceae species (Brown & Cunningham, 2022; Michener, 1965; Slattery et al., 2023). Most Colletid species we detected were visiting street trees belonging to the Myrtaceae family (*Eucalyptus*, *Angophora*, *Corymbia*, *Callistemon*, *Melaleuca*, *Lophostemon* and *Tristaniopsis* species, see Figure S4), and rarely visited species from our plant palette which belonged predominantly to recently arrived lineages (e.g. all Asteraceae tribes; Crisp & Cook, 2013).

There was no evidence of butterfly or bird traits mediating responses to plantings. No butterfly species, and only two bird species, exhibited strong responses to plantings so there was probably insufficient between-species variation in responses for traits to explain.

4.4 | Management

Opportunities for habitat creation in urban landscapes are limited by the availability of and competition for space, and by harsh growing conditions. However, our results suggest that even small plantings comprising stress-tolerant native species can have conservation benefits relative to standard road verges.

The benefits of our plantings were largely confined to generalist bees, possibly due to the combination of traits including fast life histories, high mobility and generalist feeding. Therefore, taxon-specific refinement of the planting palette may increase its value as a wildlife habitat. Modifying the plant palette to include more species that are hosts for specialist bees and butterflies (i.e. Myrtaceae, Proteaceae and other Gondwanan lineages that Colletid bees specialise on) may increase the number of species road verge plantings support. Additionally, butterfly and bird species may benefit from wider road verge plantings or a greater total area of verges planted within landscapes, potentially requiring greater coordination between land managers.

Our study demonstrates that collaborations between university researchers and urban land managers can result in fruitful coproductions of place and knowledge (Pickett et al., 2022). Designing and empirically evaluating the biodiversity benefits of the road verge planting palette required university expertise. Obtaining council support, resources (financial and project management) and the technical expertise required to convert standard road verges into relatively complex vegetation communities in highly urbanised social-ecological settings required collaboration with experienced urban land managers. The outcome was enhanced habitat for bees within the harsh urban growing environment, and a basis for further co-design aimed at extending the benefits to a broader range of taxa in line with the City of Melbourne biodiversity conservation policy.

AUTHOR CONTRIBUTIONS

Nicholas S. G. Williams, Caragh G. Threlfall and Lee Harrison conceived the study and designed the methodology and contributed to subsequent drafts. Jess Baumann and Julian Brown collected the data. Julian Brown analysed the data and wrote the first draft.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.7m0cfxq33 (Brown et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Site locations within Melbourne.

Figure S2: Qualitative (binary) site-plant interaction network.

Figure S3: Average floral score across impact sites in each survey year.

Figure S4: Quantitative plant-bee interaction meta-network (i.e. pooling across all 16 sites).

Figure S5: Quantitative plant-butterfly interaction meta-network (i.e. pooling across all 16 sites).

Figure S6: Quantitative plant-bee and butterfly meta-networks for each treatment-by-time category.

Figure S7: Bee, butterfly, and bird responses to road verge biodiversity plantings through time.

Table S1: Site information.

Table S2: Outputs from GLMM models of bee, butterfly, and bird abundance, richness, and estimated richness (Chao1).

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