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Indigenous plants promote insect biodiversity in urban greenspaces

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Abstract

The contribution of urban greenspaces to support biodiversity and provide benefits for people is increasingly recognised. However, ongoing management practices favour vegetation oversimplification – often limiting greenspaces to lawns and tree canopy rather than multi-layered vegetation that includes under- and midstorey – and the use of nonnative species. These practices hinder the potential of greenspaces to sustain indigenous biodiversity, particularly for taxa like insects, that rely on plants for food and habitat. Yet, little is known about which plant species may maximise positive outcomes for taxonomically and functionally diverse insect communities in greenspaces. Additionally, while cities are expected to experience high rates of introductions, quantitative assessments of the relative occupancy of indigenous vs. introduced insect species in greenspace are rare – hindering understanding of how management may promote indigenous biodiversity while limiting the establishment of introduced insects. Using a hierarchically replicated study design across 15 public

66 parks, we recorded occurrence data from 552 insect species on 133 plant species –
67 differing in planting design element (lawn, midstorey and tree canopy), midstorey
68 growth form (forbs, lilioids, graminoids and shrubs) and origin (nonnative, native and
69 indigenous) – to assess: (1) the relative contributions of indigenous and introduced
70 insect species; and (2) which plant species sustained the highest number of indigenous
71 insects. We found that the insect community was overwhelmingly composed of
72 indigenous rather than introduced species. Our findings further highlight the core role
73 of multi-layered vegetation in sustaining high insect biodiversity in urban areas, with
74 indigenous midstorey and canopy representing key elements to maintain rich and
75 functionally diverse indigenous insect communities. Intriguingly, graminoids
76 supported the highest indigenous insect richness across all studied growth forms by
77 plant origin groups. Our work highlights the opportunity presented by indigenous
78 understory and midstorey plants – particularly indigenous graminoids – in our study
79 area to promote indigenous insect biodiversity in urban greenspaces. Our study
80 provides a blueprint and stimulus for architects, engineers, developers, designers, and
81 planners to incorporate into their practice plant species palettes that foster a larger
82 presence of indigenous over regionally native or nonnative plant species, whilst
83 incorporating a broader mixture of midstorey growth forms.

84 **Key words:** Bayesian inference, Greenspace design and management, Invertebrates,
85 Nature in cities, Plant-insect metanetwork, Species-specific responses, Urban ecology

86 **Introduction**

87 Urban greenspaces provide well-documented benefits for biodiversity and people.
88 Remnant bushland, parks, gardens, golf courses, greenroofs, pop-up parks and other
89 types of greenspace support a great diversity of microbial, fungal, plant and animal
90 species (Madre et al. 2013, Aronson et al. 2014, Baldock et al. 2015, Beninde et al.
91 2015, McGregor-Fors et al. 2016, Mata et al. 2017, Threlfall et al. 2017, Baldock et
92 al. 2019, Mata et al. 2019), and provide a diverse array of health, mental, cognitive,
93 social, cultural and spiritual benefits for people who interact with them (Keniger et al.
94 2013, Dadvand et al. 2015, Hartig and Kahn 2016, Flies et al. 2017, Maller et al.
95 2018, Lai et al. 2019, Mata et al. 2020). Hence, researchers, practitioners, built-
96 environment professionals (e.g., architects, engineers, transport experts, developers,
97 and other urban design and planning professionals) and policymakers are increasingly
98 working together to promote the positive socio-ecological outcomes of greenspaces
99 (Aronson et al. 2017, Lepczyk et al. 2017, Nilon et al. 2017, Parris et al. 2018, Soanes

et al. 2019). Further, the importance of greenspaces has been recently highlighted at an international policy level with the United Nations' New Urban Agenda committing to "promoting the creation and maintenance of well-connected and well-distributed networks of open, multipurpose, safe, inclusive, accessible, green and quality public spaces" (United Nations 2017).

An ubiquitous practice that can hinder the potential of greenspaces to support biodiversity is the oversimplification of vegetation structure (Le Roux et al. 2014, Threlfall et al. 2016), which has led many greenspaces to be vegetated by only two planting design elements: lawn and tree canopy (Ignatieva et al. 2015, Aronson et al. 2017). In contrast, greenspaces with a more complex, multi-layered vertical structure – those including understorey and midstorey vegetation (henceforth midstorey for brevity) – provide positive outcomes for a taxonomically and functionally diverse range of taxa (Burkman and Gardiner 2014, Mata et al. 2017, Threlfall et al. 2017, Aguilera et al. 2019, Majewska and Altizer 2020). Unlike the lawn and tree canopy, the midstorey is a heterogeneous mix of different plant growth forms, including forbs, graminoids, lilioids and shrubs. Yet, at present, the combination of plant species and growth forms that maximise positive outcomes for non-plant species in the midstorey remains poorly understood.

An additional issue that limits biodiversity in urban areas is that most non-remnant greenspaces, particularly intensively manicured ones such as residential gardens and public parks, are composed predominately of nonnative plant species (Threlfall et al. 2016). Nonnative plants are rarely well-suited to provide resources for indigenous primary consumers (e.g., herbivorous insects and frugivorous birds), nor to indigenous secondary and apex consumers (e.g., predatory and parasitoid insects and insectivorous birds and bats) that depend on primary consumers as food resources (Ballard et al. 2013, Burghardt and Tallamy 2013, Ikin et al. 2013, Salisbury et al. 2015, Threlfall et al. 2017). Management practices that promote the use of nonnative plants are, therefore, likely to reduce the capacity of greenspaces to sustain diverse communities of indigenous biodiversity.

In most studies in urban environments to date, plant origin has been treated as an aggregate plot-level explanatory variable (e.g., treatment plot as either nonnative or native; plot nativeness as percentage cover of native vegetation; Ballard et al. 2013, Salisbury et al. 2015, Threlfall et al. 2017; but see Russo et al. 2013 and M'Gonigle et al. 2017 for network- and optimisation-based approaches in the context of agricultural

habitat restoration). A focus on plant species rather than plot as the unit of analysis allows for a more nuanced understanding of how plant origin may influence the capacity of plants to provide resources for associated consumer species. Moreover, focusing on the plant species level may advance understanding of how plant origin interacts with other plant-level attributes — such as planting design element and growth form — to produce positive outcomes for consumer species. This is particularly the case for taxa such as insects that rely extensively on plants for food and habitat resources.

Insects are a particularly important component of urban biodiversity (Sattler et al. 2011, New 2015) and the ecological functions they perform provide numerous benefits to urban residents (Prather et al. 2013, Benett and Lovell 2014, Baldock et al. 2015), along with some disbenefits (Dunn 2010, Rust and Su 2012). Plants and insects have often coevolved in close association with each other, with many insect species showing high levels of specialisation (Forister et al. 2012). Plants also provide food, foraging, nesting, oviposition, shelter and overwintering resources to generalist insect detritivores, predators and parasitoids; indeed, practices that promote these resources in agroecosystems by fostering plant diversity and structural complexity are key components of pest management strategies (Landis et al. 2000). The availability of suitable host plants within greenspaces is therefore a key determinant of insect diversity in urban environments (Aronson et al. 2016). However, as far as we are aware no study has sought to identify how origin and growth form relates to the value of individual plant species for sustaining taxonomically and functionally diverse insect communities in urban greenspaces.

Urban environments are central nodes of human-mediated dispersal networks (Bullock et al. 2018) and hotspots of novel resource utilisation (Valentine et al. 2020), such that introduced species are often prominent (Cadotte et al. 2017, Paap et al. 2017). The number of introduced insect species can be relatively low (Uno et al. 2010, Madre et al. 2013, Mata et al. 2017), but they often occur in high abundance and this is especially the case for generalist ants, bees and butterflies (Connor et al. 202, Matteson & Langellotto 2010, Uno et al. 2010, Threlfall et al. 2015). However, as far as we are aware, quantitative analyses of the relative contributions of indigenous and introduced species in greenspace insect communities have not been previously reported in the literature. This paucity of data hinders understanding of

how greenspaces may be managed to promote indigenous insect biodiversity while limiting the establishment of introduced species.

Here we use a plant-insect metanetwork dataset collected across 15 greenspaces within a densely urbanised inner-city municipality (Melbourne, Australia) to assess: (1) the relative contributions of indigenous and introduced species in insect communities of urban environments, and (2) which plant species should be planted to support indigenous insect species. We are motivated to understand the degree by which urban greenspaces may be contributing positive outcomes for indigenous as opposed to introduced biodiversity (Cadotte et al. 2017, Lepczyk et al. 2017, Parris et al. 2018, Soanes et al. 2019) and to provide new primary evidence of the extent to which plant growth form and origin may be linked to the value of individual plant species for promoting indigenous insect biodiversity in urban greenspaces. The project followed the science-government partnerships model (Ives and Lynch 2014) – an approach that advocates for industry professionals and researchers to work in close association to guarantee that theoretically interesting and practically important questions are identified. This ensured that the implications of our research findings could be applied as practical on-ground actions that were embedded into a new business as usual at the City of Melbourne. We began by determining what proportion of insect species occurring in the greenspaces are indigenous, and whether indigenous insect species are more common than introduced species. We then examined how the richness of indigenous insect species varies with planting design element (lawn, midstorey and tree canopy), midstorey growth form (forbs, lilioids, graminoids and shrubs) and plant origin groups (nonnative, native and indigenous). Finally, we grouped plants species according to a combination of planting design element by plant origin (Fig. 1a), and midstorey growth form by plant origin (Fig. 1b) to assess how the richness of indigenous insect species vary amongst these groups. We do this assessment for the whole insect community and for five key functional groups: pollinators and other flower-visiting taxa, herbivores, predators, parasitoids and detritivores. We also examined variation amongst the plant groups in insect species composition and number of unique species.

Methods

Study design

The study was conducted in the City of Melbourne, Australia. This is one of 31 municipalities within Greater Melbourne, a large metropolitan area spanning

approximately 10,000 km² within the Urban Growth Boundary and home to over five million people (Victorian State Revenue Office: <https://www.sro.vic.gov.au/greater-melbourne-map-and-urban-zones>). The City of Melbourne covers 37.7 km² and incorporates a central business district along with transport and distribution hubs. Approximately 13% of the land area is covered by vegetated open space, including grassy woodlands, wetlands, estuaries and a greenspace network of parks, gardens and streetscapes. The municipality is home to approximately 180,000 residents and receives approximately 800,000 daily visitors (City of Melbourne: <https://www.melbourne.vic.gov.au/>).

Our study was conducted across 15 public parks, which varied in size across four orders of magnitude (1.1 x 10³ m² – 1.3 x 10⁶ m²; Appendix S1: Table S1; Appendix S1: Fig. S1a). We established a total of 130 plots across the 15 parks, with the number of plots in each park (2-36), and their size (84-148 m²), varying according to the park's area (Appendix S1: Eq. S1-S3) and planting design elements and midstorey growth forms present (Appendix S1: Table S1; Appendix S1: Fig. S1b). Within each plot we identified all plants, totalling 133 species, genera or species complexes; and representing the main monocot and eudicot phylogenetic clades across the angiosperm tree of life (Appendix S2: Table S2; Appendix S2: Table S7).

We classified plant species by origin as indigenous (30), regionally native (9) and nonnative (94). We define indigenous plant species – also referred to in the literature as locally native – as those that are native to the local bioregions. For this study, indigenous plant species are those that occurred before European settlement in the Volcanic Victorian Plain and Gippsland Plain bioregions (State of Victoria: <https://www.environment.vic.gov.au>). Regionally native (henceforth native) are species that are native to Australia but not to the local bioregions and have been anthropogenically introduced. Nonnative species are those that have been introduced to Australia.

We also classified plant species by planting design element (henceforth design element) as lawn complex (41), midstorey (67) and tree canopy (25) (Fig. 1a). Midstorey taxa were further stratified by growth form as forb (8), lilioid (13), graminoid (8) and shrub (38) (Fig. 1b). We define lawn complexes (henceforth lawns) as patches dominated by turf-forming grasses (Poaceae) intermixed with one or more small, ruderal herbaceous species. Midstorey species included broad-leaved perennial and annual herbaceous plants (forbs); petaloid monocots in orders Liliales and

Asparagales (lilioids); grasses, sedges and rushes of typically vertical habit with linear foliage and inconspicuous wind-pollinated flowers (graminoids); and woody perennials with multiple stems and < 5 m in height (shrubs). Tree canopy species included single-stemmed woody plants > 5 m in height.

Insect survey

We sampled plant species for 12 insect groups known to dominate insect communities on above-ground vegetation: ants, bees, beetles, cicadas, flies, heteropteran bugs, jumping plant lice, leaf- and treehoppers, parasitoid wasps, planthoppers, sawflies and stinging wasps. Samples were taken by direct observation and by sweeping with an entomological net. Observation time and sweeps per plant species were standardised as a proportion of the plant species' volume within the plot (Appendix S1: Eq. S4-S5), with each plant species in each plot sampled three times from January (summer) to late March (autumn) 2015. Sampled insect specimens were processed in the laboratory and identified to species/morphospecies. We assigned these as (1) either indigenous to the studied bioregions and/or native to Australia (henceforth indigenous) or introduced to Australia, and (2) one or more of the following functional groups: pollinators and other flower-visiting taxa (henceforth pollinators), herbivores, predators, parasitoids and detritivores (Appendix S2: Table S1).

Data analysis

Estimating insect occupancy and species richness per plant species

To assess the proportion of indigenous insect species occurring in the greenspaces, whether they were more common than introduced ones, and how their species richness varied amongst the studied single and combined plant groups, we analysed our data with a three-level hierarchical metacommunity occupancy model (Kéry and Royle 2016). Plant species was our unit of analysis for drawing inferences on insect species occupancy, and each repeated spatial (individuals of the same plant species sampled in different plots) and temporal (same individual of a given plant species sampled at different times) samplings constituted the unit of detection replication. We estimated model parameters under Bayesian inference, using Markov Chain Monte Carlo (MCMC) simulations to draw samples from the parameters' posterior distributions. As the species richness calculations were conducted within this modelling framework, we were able to derive the insect species per plant species estimates with their full associated uncertainties. This allowed us to average the species richness estimates of plant species belonging to the same group, and therefore

obtain posterior distributions for each group that we could statistically compare. We structured the model around three levels: one for species occupancy; a second for species detectability; and a third to treat the occupancy and detection parameters for each species as random effects (Kéry and Royle 2016). Specifically, we used a variation of the model described by Mata et al. (2017), in which we specified the occupancy level model as:

$$Z_{ij} \sim \text{Bernoulli}(\Psi_{ij})$$

where Ψ_{ij} is the probability that insect species i occurs at plant species j , and the detection level model as:

$$y_{i,j,k} \sim \text{Bernoulli}(\Phi_{i,j,k} \cdot Z_{ij})$$

where $\Phi_{i,j,k}$ is the detection probability of insect species i at plant species j at spatiotemporal replicate k .

The occupancy and detection level linear predictors were specified on the logit-probability scale as:

$$\text{logit}(\Psi_{ij}) = \text{occ}_i$$

$$\text{logit}(\Phi_{i,j,k}) = \text{det}_i$$

where occ_i and det_i are the species-specific random effects, which were specified as:

$$\text{occ}_i \sim \text{Normal}(\mu.\text{occ}_{Int...Ind}, \tau.\text{occ})$$

$$\text{det}_i \sim \text{Normal}(\mu.\text{det}, \tau.\text{det})$$

where the metacommunity mean occupancy hyperpriors for introduced and indigenous insect species, $\mu.\text{occ}_{Int}$ and $\mu.\text{occ}_{Ind}$, respectively, and the metacommunity mean detection hyperprior $\mu.\text{det}$, were specified as Uniform (0, 1); and the metacommunity precision occupancy and detection hyperpriors, $\tau.\text{occ}$ and $\tau.\text{det}$, respectively, were specified as Gamma (0.1, 0.1).

We then use the latent occurrence matrix Z_{ij} to estimate the insect species richness associated with each plant species SR_j through the summation:

$$SR_j = \sum_{i=S_{ij}} Z_{ij}$$

where S_{ij} is a ‘specificity’ vector indexing the insect species to be included in each plant species’ estimate. SR_j is then an estimate that accounts for plant-insect specificity, in which, for each plant species, the observed insect species are included with probability of occurrence = 1 and a limited random sub-sample of other insect species occurring in the study area are included with their $0 < Z < 1$ estimated

probabilities of occurrence. This allowed us to work within the reasonable ecological assumption that across the study area not every insect species will be associated with every co-occurring plant species. We conducted these estimations for the insect community as a whole but also independently for introduced and indigenous species. Our model was implemented in JAGS (Plummer 2003) and accessed through the R package *jagsUI* (Kellner 2016). We used three chains of 5,000 iterations, discarding the first 500 in each chain as burn-in. We visually inspected the MCMC chains and the values of the Gelman-Rubin statistic to verify acceptable convergence levels of $\hat{R} < 1.1$ (Gelman & Hill 2007).

Community dissimilarity

To determine whether the composition of insect species varied amongst the design elements/growth form by plant origin groups, we reorganised the data into insect-by-plant species matrices – cell values summarising the number of times a given insect species was sampled on a given plant species across its spatiotemporal replicates – and used these to calculate amongst-group community dissimilarity. Specifically, we used 1 - Jaccard similarity index as implemented in the R package *vegan* (Oksanen et al. 2016). We further used the data to create insect species lists for each group, which we partitioned into their corresponding Venn sets with the R package *VennDiagram* (Chen 2016). This allowed us to calculate the number of unique insect species – species found exclusively at a given plant group and not shared with any of the other groups – belonging to each group.

Results

Our survey recorded 552 insect species, with the richest taxa being beetles (125 species), parasitoid wasps (121), flies (101), heteropteran bugs (61), leaf- and treehoppers (40) and jumping plant lice (31) (Appendix S2: Table S1). These represented 154 pollinator, 299 herbivore, 231 predator, 150 parasitoid and 231 detritivore species. The most commonly occurring species was the minute brown scavenger beetle *Cortinicara* sp. 1 (Latridiidae), an indigenous detritivore species that accounted for 12% of all insect records. The Argentine ant *Linepithema humile* was the most frequently occurring introduced species, accounting for approximately 3% of all records. Four previously unknown species were also discovered: one ant, one heteropteran bug and two jumping plant lice (Mata et al. 2015, 2016).

Indigenous vs introduced insect species

There were approximately 30 times more indigenous (534) than introduced (18) insect species across the study area, with our model estimates indicating that any particular plant species was associated with 19 times more indigenous than introduced insect species (Fig. 2a; Appendix S2: Table S2). The mean number of introduced insect species per plant species varied from zero to four; whereas the mean number of indigenous insect species varied from one to 109, with most plant species being associated with more than ten indigenous insect species (Fig. 2b; Appendix S2: Table S3; Appendix S2: Figure S1). The probability of occurrence of any particular insect species at a given plant across the study area was similarly low for introduced and indigenous species (Fig. 2c; Appendix S2: Table S4). The introduced insect fauna was represented by species showing moderate to very low ($0.6 > P_{occ} > 0$) species-specific probabilities of occurrence (Fig. 2d; Appendix S2: Table S1); whereas the species-specific probabilities of occurrence of indigenous insect species varied widely, with a few species showing very high occupancy levels ($P_{occ} > 0.8$) and most species showing low occupancy levels ($P_{occ} < 0.4$) (Fig. 2d; Appendix S2: Table S1). The probability of detecting any particular insect species at a given plant across the study area was similarly very low for introduced and indigenous species ($P_{det} < 0.03$; Appendix S2: Table S4), and the species-specific probabilities of detection were consistently low for the large majority of insect species (Appendix S2: Table S1).

Effect of design element, growth form and plant origin

We found that the midstorey and tree canopy species supported an estimated 2.5 times more insect species than the lawn complex (Fig. 3a; Appendix S2: Table S5). The species richness of indigenous insects per plant species varied amongst midstorey growth forms, with the average graminoid species showing 2.9 times more insect species than the average lilioid, 2.4 times more than the average forb and 1.8 times more than the average shrub (Fig. 3b; Appendix S2: Table S5). We also found marked statistical differences with plant origin in the number of indigenous insect species per plant species (Appendix S2: Figure S1), with the average indigenous plant species showing 2.9 and 1.6 times more insect species than the average nonnative and native plant, respectively; and the average native plant showing 1.9 times more insect species than the average nonnative plant (Fig. 3c; Appendix S2: Table S5).

Combined effect of design element and plant origin

All design element by plant origin groups had different levels of indigenous insect species richness per plant species. In general, indigenous groups were associated with

higher species richness per plant species than native and these with higher richness than nonnative. The single exception was native midstorey and nonnative tree canopy, which showed richness levels per plant species that were not statistically different from each other (Fig. 4a; Appendix S2: Table S6). Overall, the indigenous midstorey was associated with the highest level of indigenous insect species richness per plant species, with the average plant species in this group showing 2.6 and 1.6 times more insect species than the average nonnative and native midstorey plant species, respectively (Fig. 4a; Appendix S2: Table S6). The indigenous tree canopy was associated with the second highest level of insect species richness per plant species, with the average plant species in this group showing 1.8 and 1.4 times more insect species than the average nonnative and native tree canopy plant species, respectively (Fig. 4a; Appendix S2: Table S6).

Across insect functional groups, lawns showed the lowest insect species richness per plant species (Fig. 5a,c,e,g,i; Appendix S2: Table S6). The indigenous midstorey showed the highest number of indigenous insect species; however, for predators and detritivores the indigenous midstorey was not statistically different to the indigenous tree canopy (Fig. 5e,i; Appendix S2: Table S6). Other departures from the general pattern were observed for each functional group. The indigenous and native tree canopy groups did not show different levels of indigenous pollinators or parasitoid species (Fig. 5a,g; Appendix S2: Table S6), and the native tree canopy and midstorey groups did not show different levels of indigenous herbivore species (Fig. 5c; Appendix S2: Table S6). For predators, parasitoids and detritivores, the nonnative tree canopy group had a higher species richness than the native midstorey and was not statistically different than the native tree canopy – the native and nonnative midstorey groups in turn did not show different levels of associated species (Fig. 5e,g,i; Appendix S2: Table S6).

Combined effect of growth form and plant origin

We found that indigenous groups had higher insect species richness than did native and these had higher insect richness than nonnative (Fig. 4b; Appendix S2: Table S6). The group with the highest insect species richness per plant species was indigenous graminoids, with the average plant species in this group showing nearly five times more species than the average nonnative graminoid (Fig. 4b; Appendix S2: Table S6) – a pattern that was consistent across all insect functional groups (Fig. 5b,d,f,h,j; Appendix S2: Table S6). Indigenous shrubs were associated with the second highest

level of insect species richness per plant species, with the average indigenous shrub showing 2.1 and 1.6 times more insect species than average nonnative and native shrubs, respectively (Fig. 4b; Appendix S2: Table S6). The group with the third highest insect species richness was indigenous lilioids, with the average indigenous lilioid showing 2.5 times more insect species than the average nonnative lilioid (Fig. 4b; Appendix S2: Table S6). In general, the indigenous growth form groups were associated with the highest number of indigenous insect species across all insect functional groups (Fig. 5b,d,f,h,j; Appendix S2: Table S6). An alternative ‘Combined effect of phylogenetic clade by plant origin’ analysis revealed that – in all clades, with the exception of basal eudicots – indigenous groups had higher insect species richness than did native plants, and the latter had higher insect richness than nonnative plants (Appendix S2: Table S8).

Community composition and unique species

The highest dissimilarity in insect species composition between indigenous and nonnative groups across the design elements by plant origin and growth forms by plant origin groups was found between the midstoreys (Fig. 6a) and shrubs (Fig. 6b), respectively. Within the design element by plant origin group, 33% and 30% of all indigenous insect species were unique to the indigenous and midstorey groups, respectively (Fig. 6a). From the growth form by plant origin perspective, 29% and 24% of all indigenous insect species recorded in the midstorey were unique to the indigenous and shrub groups, respectively (Fig. 6b).

Discussion

Our findings demonstrate that taxonomically and functionally diverse indigenous insect communities occur in greenspaces in a densely urbanised inner-city municipality, with the potential to boost ecosystem multifunctionality (Soliveres et al. 2016) and biotic resistance against the establishment of introduced insects (Kennedy et al. 2002). Our study further highlights that multi-layered, structurally complex indigenous vegetation plays a core role in sustaining high insect biodiversity in urban areas, with the indigenous midstorey and canopy key to maintaining a rich and functionally diverse indigenous insect community within this system. Within the indigenous midstorey, graminoids surprisingly support the highest indigenous insect species richness per plant species across all functional groups – particularly for herbivores, predators and detritivores – followed by indigenous shrubs and lilioids. The indigenous midstorey also hosts the largest percentage of unique species. Taken

together our findings emphasise the opportunity presented by indigenous understory and midstorey plants, particularly indigenous graminoids in our study area, to promote indigenous insect biodiversity in urban greenspaces.

Greenspace insect communities are dominated by indigenous insect species

Our results indicate that insect communities in Melbourne greenspaces are overwhelmingly composed of indigenous rather than introduced species. This finding aligns with previous studies of insect richness in cities across other continents (Goertzen and Suhling 2014, Sing et al. 2016, Brown and Hartop 2017). Despite the expectation that urban environments act as hotspots for biological invasions (Cadotte et al. 2017), particularly of nonnative plants and insects (Pysek et al 2010), we found a relatively low number of introduced insect species. Not surprisingly, however, some of these introduced species, for example the Argentine ant *Linepithema humile* and the European honeybee *Apis mellifera*, were relatively common and widespread, which is consistent with previous studies (Connor et al. 2020, Matteson & Langellotto 2010, Uno et al. 2010, Threlfall et al. 2015). In the case of the European honeybee this pattern could be symptomatic of the growing trend of urban beekeeping, which may have unintended detrimental effects on indigenous bees (Egerer & Kowarik In press).

Indigenous plant species promote indigenous insect diversity

We found multiple threads of evidence to suggest that indigenous plant species sustain the highest numbers of indigenous insect species and host the largest percentage of unique species. It is generally accepted in restoration ecology that the presence of indigenous plant species promotes recolonisation by indigenous insect species (Moir et al. 2005, Nemec and Bragg 2008). In most cases, phytophagous taxa drive this trend (Procheş et al. 2008, Woodcock et al. 2009) and it is a function of the host-specificity of the insect species, provided that other factors are accounted for, such as the insect's power of dispersal and suitable micro-climate conditions (Moir et al. 2005).

It follows, therefore, that indigenous plants should encourage the occurrence of indigenous insects, especially for herbivores, but also for other insect functional groups. Indeed, our findings clearly show that pollinators, herbivores, predators, parasitoids and detritivores all reach higher levels of species richness in association with indigenous plant species. Experimental studies also support this assumption (Ballard et al. 2013, Burghardt and Tallamy 2013, Salisbury et al. 2015, 2017). For

example, using experimental plantings of tree and shrub species, Burghardt and Tallamy (2013) showed that nonnative plants supported less diverse herbivorous insect communities than indigenous plants. Similarly, in an early successional experiment the biomass, abundance and species richness of herbivorous, predatory and parasitoid insects was lower on nonnative forbs than on indigenous forbs (Ballard et al. 2013). Working specifically in an urban setting, Salisbury and colleagues (2015, 2017) experimented with the origin of flowering plants in garden borders, demonstrating that insects across a diverse range of functional groups were less abundant on nonnative than indigenous plant species. These experimental findings have been substantiated by observational approaches, particularly by studies conducted within urban environments. For instance, a study that included the species-specific responses of bees, beetles and heteropteran bugs to vegetation attributes of gardens, parks and golf courses revealed how occurrence probabilities for most insect species decreased as a function of the amount of nonnative plants present in the studied greenspaces (Threlfall et al. 2017).

Midstorey as a key planting design element

Our results have shown that the midstorey is a highly valuable ecological asset in urban landscapes in terms of promoting insect diversity. Midstorey vegetation – which in our study also included plants species associated with the understorey – harboured nearly as many indigenous insect species as canopy vegetation. Indigenous midstorey plant species in particular promoted higher levels of overall insect richness, a pattern that was consistent across all insect functional groups. The midstorey also sustained the highest number of unique indigenous insect species. Taken together, our results indicate that the under- and midstorey are underappreciated strata with great potential for supporting insect biodiversity across urban environments.

Our findings go beyond the accepted understanding that the greater structural complexity of experimental, restored or managed sites, the higher the taxonomical and functional diversity of insects and other invertebrates (Murdoch et al. 1972, Brown 1984, Majer et al. 2007, Woodcock et al. 2009, Gibb and Cunningham 2010, Mata et al. 2017, Threlfall et al. 2017, Schuldt et al. 2019). We show that within the midstorey it is the indigenous species – particularly indigenous graminoids and shrubs – that distinctly outperform their native and nonnative counterparts. Our results are also consistent with previous studies that have documented how insect and other arthropod communities are highly stratified across forest strata (Basset et al. 2003,

Ulyshen 2011). It is likely that greenspace midstorey vegetation supports different insect taxa due to differences in habitat structure (e.g., foliage complexity or plant surface textures), microclimate (e.g., light, temperature, wind or humidity differences), unique food resources or particular inter-specific interactions, as has been discussed for temperate deciduous forest (Ulyshen 2011). Unpacking the causal mechanisms for our results would require experimental manipulations that fell beyond the scope of this study.

Graminoids as a key midstorey growth form

A striking result to emerge from our study is that graminoids sustain the highest number of indigenous insect species per plant species across all growth forms and indigenous graminoids show the highest species richness of indigenous insects across all growth form by plant origin groups. Three indigenous tussock grass species made particularly important contributions to supporting indigenous insect biodiversity in our study area: common tussock-grass *Poa labillardierei*, wallaby grass *Rytidosperma* sp. and kangaroo grass *Themeda triandra*. Indeed, *P. labillardierei* had the highest number of indigenous insect species across the study, with any particular tussock grass patch supporting as much as 5.4 times more indigenous insect species than the most speciose lawn complex and 1.7 times more indigenous insect species than the spotted gum *Corymbia maculata*, which was the tree species sustaining the highest number of indigenous insect species across the study. These results substantiate previous findings stressing the relevance of indigenous tussock grasses and other structurally complex graminoids in providing a diversity of habitat and food resources for the immature and adult life stage of insects and other invertebrates (Tscharrntke and Greiler 1995, Morris 2000, Barratt et al. 2005).

Remarkably, the capacity of indigenous graminoids to support the highest levels of indigenous insect species per plant species across all studied plant groups was true for all insect functional groups. This finding extends previous studies reporting on the positive effects of tussocks and other graminoids on specific insect functional groups – predominantly on herbivores, predators and parasitoids (Dennis et al. 1998, Woodcock et al. 2007, Haaland et al. 2011), but also for pollinators (Saarinen et al. 2005, Potts et al. 2009). Our finding that graminoids, which are predominantly pollinated by wind, support more pollinators and other flower-visiting insect species than do lilioids or shrubs, which are predominantly pollinated by insects, is highly noteworthy and provides insight into function and value of non-floral resources for

insect pollinators (Roulston and Goodell 2011, Requier and Leonhardt 2020). We hope that our research will serve as a base for future studies on the capacity of graminoids to provide habitat and food resources for insects in urban greenspaces, particularly of non-floral resources for pollinators and other flower-visiting species. Beyond graminoids, our data further emphasise the contributions of other midstorey growth forms. For instance, indigenous shrubs and lilioids sustained the second and third highest number of indigenous insect species per plant species across the growth from by plant origin groups. Indeed, our findings indicate that any particular indigenous shrub or lilioid species supports the same number of indigenous insect species as any particular indigenous tree species; and substantially more insect species than any particular native or nonnative tree species. However, we found that the number of unique indigenous insect species varied markedly between these two plant groups, with indigenous shrubs showing as much as 7.4 times more unique insect species than their lilioid counterparts. In general, shrubs outperformed all other midstorey growth forms, with approximately one out of every four indigenous insect species across the study being exclusively associated with shrub species. Taken together, our findings point to the critical role that midstorey growth forms – particularly indigenous plant species – play in supporting taxonomically and functionally diverse indigenous insect communities in urban greenspaces. This is not only critical for insect conservation in urban environments but of direct, immediate relevance for a wide range of animals such as reptiles, birds and mammals that rely on them as food sources. Our findings therefore underscore the potential of a diverse, primarily indigenous understorey and midstorey strata to increase the positive biodiversity outcomes provided by structurally complex vegetation. As such, they support ideas that move beyond the traditional approach of designing urban greenspaces predominantly or often exclusively with nonnative short turfgrass lawn and tall trees (Ikin et al. 2015, Smith et al. 2015, Parris et al. 2018, Norton et al. 2019).

Limitations and future research

We are aware of some features of our study context and design that might have influenced our results. Firstly, the small proportion of introduced insects found in this study may be the result of recent introductions that have not yet had enough time to develop into established, large populations – a pattern that is common to both the Northern (Roques et al. 2009) and Southern Hemispheres (Ward and Edney-Browne

2015). It is therefore not inconceivable that some introduced species occurring in our study area in small, isolated populations might have gone undetected. Indeed, a recent related study in one of the study sites revealed the occurrence of the European firebug *Pyrrhocoris apterus* – a Palaearctic species not previously recorded in Australia (LM unpublished data). As with any observational study, our study design may have introduced unintended bias because our data collection period was purposely designed to coincide with the peak activity season for insects in our study area (i.e., the summer months). We believe however that this effect is negligible as far fewer insect species are more active over the colder periods. Finally, we are also aware that our study was conducted at a single scale, focusing exclusively at the plant level. Although beyond the scope of this paper, to fully understand the mechanisms structuring insect communities in urban environments it would be necessary to analyse the patterns driving their diversity and distribution across multiple spatial and temporal scales (Estes et al. 2018, Fournier et al. 2020, Piano et al. 2020). For example, in a follow-up study, we are using a multi-scale occupancy model (Kéry and Royle 2016, Szewczyk & McCain 2019) to assess the species-specific responses of insects at the site, plot, plant and detection levels. This will allow the effect of greenspace size, plot spatial configuration, and any potential observation-process covariates such as temperature and wind speed to be identified.

This research has revealed many questions in need of further investigation. While we believe that our finding, that indigenous plants sustain substantially more indigenous insect species than their regionally native and nonnative counterparts, are transferable to other urban environments worldwide, the strong relationships we found between indigenous graminoids and indigenous insects might be less transferable. While graminoids, particularly tussock forming species, were a dominant growth form in our study area before colonial settlement other growth forms might have been more representative in other bioregions. A global study across many bioregions is needed to shed light on this question.

While we have emphasised the critical role of indigenous plants, we have also shown that indigenous insects are being found in association with a wide array of regionally native and nonnative plants. Thus, our study supports the idea that urban environments facilitate novel resource utilisation by indigenous insects (Padovani et al. 2020, Valentine et al. 2020). Future experimental work on this topic is needed to clarify to what extent these associations reflect host shifting patterns unique to urban

environments and to fully understand the opportunities and risks provided by novel urban resources. On a wider level, research is also needed to determine to what extent the increases in insect biodiversity provided by complementing lawns and trees with a diverse palette of midstorey growth forms, particularly indigenous species, can boost ecosystem multifunctionality in urban greenspaces – as recently demonstrated for meso- and macrofauna influencing soil multifunctionality (Tresch et al. 2019). The prospect of being able to understand the mechanistic links between, and to quantify the contributions of, increased biodiversity due to greenspace management actions and greenspace multifunctionality serves as a continuous incentive to future research.

Applications to greenspace design and management

As our research was conducted following the science-government partnerships model (Ives and Lynch 2014), our findings have now been used by the City of Melbourne to provide practical guidance for designing greenspaces that meet the needs of both people and nature. We share these examples of applied ecological knowledge here as a demonstration of how this ecological research can inform practical actions.

In the first instance, our study provides a blueprint and stimulus for built-environment professionals, including architects, engineers, planners and designers, to conceptualise and incorporate into their practice palettes of plant species that foster a larger presence of indigenous plants over regionally native or nonnative species, whilst incorporating a broader mixture of midstorey growth forms. These features are expected to promote taxonomically and functionally diverse indigenous insect communities – even when increasing the amount of greenspace is not feasible due to other pressures (Beninde et al 2015). Integrating these plant palettes into practice may further allow built-environment professionals to plan and design complex plant communities that support and boost indigenous biodiversity in greenspaces and that will likely contribute to bring locally extinct or rare species back into urban environments (Baruch et al. 2020, Mata et al. 2020). Optimisation-based tools may aid in the identification of these plant palettes (M’Gonigle et al. 2017). Importantly, our study suggests that indigenous plants can be used to promote indigenous insects without concerns of unintentionally promoting introduced insects. Indeed, no indigenous plant species in our study was associated with more than three introduced insect species, and the strongest association between an indigenous plant and an introduced insect accounted for less than 0.3% of all records (Appendix S2: Table S9).

Another promising pathway that can be explored by greenspace professionals includes identifying locations where lawns can be converted to more complex vegetation that includes indigenous plants, and in the bioregional context of our study, graminoids, shrubs and lilioids. Simple strategies for incorporating more complex vegetation without compromising access to lawn areas include placing the plantings around the greenspace boundaries or under the canopy areas of larger trees where they can also act as a subtle exclusion zone and reduce the risk of injury due to falling limbs or branches. Placing the taller midstorey plantings away from footpaths and other infrastructure can also help meet ‘Crime Prevention Through Environmental Design’ principles by maintaining a line of sight (Piroozfar et al. 2019).

Making a difference – implications for policy and beyond

Through our study we have gained considerable insights that advance knowledge of plant-insect relationships in urban greenspaces. However, to bring about beneficial outcomes for urban landscapes, this scientific evidence must be embedded into policy and, ultimately, operationalised into practice. Indeed, our research was conducted as part of ‘The Little Things that Run the City’ (Mata et al. 2015, 2016), and two of our co-authors were working for the City of Melbourne during the formation and early analysis of this research. Not unexpectedly, project findings have been contributing to inform City of Melbourne decision-making and policy, including the Council’s ‘Nature in the City Strategy’ (City of Melbourne 2017), which includes goals to increase indigenous biodiversity and specific targets to increase plant-related midstorey habitat for insects and other taxa. Project findings have also been applied to develop an insect biodiversity educational portal (<http://biodiversity.melbourne.vic.gov.au/insects/>) and a children’s book (Cranney et al. 2017). These non-academic outcomes highlight the value of our work and provide encouragement for future partnerships between industry professionals and researchers advocating for and evidencing the value of urban biodiversity.

Another significant approach that could be used by local governments to advance practice aimed at promoting insect biodiversity in urban environments is to incentivise the translation of research findings into landscape design guidelines. These non-mandatory documents, which have traditionally focused on aesthetic outcomes at the expense of biodiversity, can distinctly influence outcomes on the ground.

Ultimately however, contractors and consultants responsible for delivering capital works projects will overlook these if the required plants are not readily available

when needed. Therefore, the crucial role played by plant nurseries should not be overlooked – an industry where supply tends to influence demand, with growers often limiting production to reliable, profitable and easy to grow plants. Influencing plant supply will require a dedicated engagement with the nursery industry to broaden production to include a wider range of plant species known to support insect biodiversity as those provided evidence for in this study, while maintaining the genetic diversity of local floras (Vander Mijnsbrugge et al. 2010, Breed et al. 2013).

A further benefit of promoting locally grown indigenous plants is that it can reduce the long-distance transport of plants, which is one of the main pathways for the spread of invasive nonnative plants (Bullock et al. 2018, Seebens et al. 2018).

Finally, while government officers may apply research findings to design greenspaces capable of supporting diverse insect communities, they must synergistically encourage operational and maintenance programs that can enable these communities to thrive. On ground teams responsible for the day to day management of greenspaces have the potential to be involved in identifying opportunities and challenges for supporting insects – and the plants they are more closely associated with – which may expand beyond the obvious choices available to or envisaged by office-based decision-makers. They are, for example, uniquely positioned to readily transfer knowledge on where the optimal soil and microhabitat conditions required for focal plant species within a given greenspace are met – a necessary prerequisite for these to be able to deliver the resources needed by insects to become established and thrive.

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Supporting Information

Additional supporting information may be found online at: [link to be added in production]

Data Availability

Data are available on Zenodo (Mata et al. 2020):

<http://doi.org/10.5281/zenodo.4127119>

Literature cited

- Aguilera, G., J. Ekroos, A.S. Persson, L.B. Pettersson, and E. Öckinger. 2019. Intensive management reduces butterfly diversity over time in urban green spaces. *Urban Ecosystems* 22:335–344.
- Aronson, M. F. J., C. A. Lepczyk, K. L. Evans, M. A. Goddard, S. B. Lerman, J. S. MacIvor, C. H. Nilon, and T. Vargo. 2017. Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment* 15:189–196.
- Aronson, M. F. J., et al. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B* 281:20133330.
- Aronson, M. F. J., et al. 2014. Hierarchical filters determine community assembly of urban species pools. *Ecological Applications* 97:2952–2963.
- Baldock, K., et al. 2015. Where is the UK’s pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society of London B* 282: 20142849.
- Baldock, K., et al. 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology and Evolution* 3:363–373.
- Ballard, M., J. Hough-Goldstein, and D. Tallamy. 2013. Arthropod communities on native and nonnative early successional plants. *Environmental Entomology* 5: 851–859.
- Barratt, B.I.P, C.M. Ferguson, R.A.S. Logan, D. Barton, N.L. Bell, S.U. Sarathchandra, and R.J. Townsend. 2005. Biodiversity of indigenous tussock

grassland sites in Otago, Canterbury and the central North Island of New Zealand I. The macro-invertebrate fauna. *Journal of the Royal Society of New Zealand* 35:287–301.

Baruch, Z., C. Liddicoat, M. Laws, L.K. Marker, H. Morelli, D. Yan, J.M. Young, and M.F. Breed. 2020. Characterising the soil fungal microbiome in metropolitan green spaces across a vegetation biodiversity gradient. *Fungal Ecology* 47: 100939.

Basset, Y., P.M. Hammond, H. Barrios, J.D. Holloway, and S.E. Miller. 2003. Vertical stratification of arthropod assemblages. Pages 17–27 in Y. Basset, V. Novotny, S.E. Miller, and R.L. Kitching, editors. *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, UK.

Benett, A.B., and S.T. Lovell. 2014. A comparison of arthropod abundance and arthropod mediated predation services in urban green spaces. *Insect Conservation and Diversity* 7:405–412.

Beninde, J., M. Veith, and A. Hochkirch. 2015. Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters* 18:581–592.

Breed, M.F., M.G. Stead, K.M. Ottewell, M.G. Gardner, and A.J. Lowe. 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics* 14:1–10.

Brown, V.K. 1984. Secondary succession: insect-plant relationships. *BioScience* 34: 710–716.

Brown, B.V., and E.A. Hartop. 2017. Big data from tiny flies: patterns revealed from over 42,000 phorid flies (Insecta: Diptera: Phoridae) collected over one year in Los Angeles, California, USA. *Urban Ecosystems* 20:521–534.

Bullock, J.M., D. Bonte, G. Pufal, C. da Silva Carvalho, D.S. Chapman, C. García, D. García, E. Matthysen, and M.M Delgado. 2018. Human-mediated dispersal and the rewiring of spatial networks. *Trend in Ecology and Evolution* 33:958–970.

Burghardt, K.T., and D.W. Tallamy. 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. *Diversity and Distributions* 19:1553–1565.

Burkman, C.E., and M.M. Gardiner. 2014. Urban greenspace composition and landscape context influence natural enemy community composition and function. *Biological Control* 75:58–67

774 Cadotte, M.W., S.L.E Yasui, S. Livingstone, and J.S. MacIvor. 2017. Are urban
 775 systems beneficial, detrimental, or indifferent for biological invasion? *Biological*
 776 *Invasions* 19:3489–3503.

777 Chen, H. 2016. VennDiagram: generate high-resolution Venn and Euler plots. R
 778 package version 1.6.17. <https://CRAN.R-project.org/package=VennDiagram>

779 City of Melbourne. 2017. Nature in the City – Thriving biodiversity and healthy
 780 ecosystems. City of Melbourne, Melbourne, Australia.

781 Connor, E.F., J. Hafernik, J. Levy, V.L. Moore, and J.K. Rickman. 2002. Insect
 782 conservation in an urban biodiversity hotspot: The San Francisco Bay Area. *Journal*
 783 *of Insect Conservation* 6: 247–259.

784 Cranney, K., S. Bekessy, and L. Mata. 2017. The Little Things that Run the City - 30
 785 amazing insect that live in Melbourne! City of Melbourne, Melbourne, Australia.

786 Dadvand, P., et al. 2015. Green spaces and cognitive development in primary
 787 schoolchildren. *Proceedings of the National Academy of Science* 112:7937–7942.

788 Dennis, P., M.R. Young, and I.J. Gordon. 1998. Distribution and abundance of small
 789 insects and arachnids in relation to structural heterogeneity of grazed, indigenous
 790 grasslands. *Ecological Entomology* 23:253–264

791 Dunn, R.R. 2010. Global mapping of ecosystem disservices: the unspoken reality that
 792 nature sometimes kills us. *Biotropica* 42:555–557.

793 Egerer, M., and I. Kowarik. In press. Confronting the modern gordian knot of urban
 794 beekeeping. *Trends in Ecology and Evolution*.

795 Estes, L., P.R. Elsen, T. Treuer, L. Ahmed, K. Caylor, J. Chang, J.J. Choi, and E.C.
 796 Ellis. 2018. The spatial and temporal domains of modern ecology. *Nature Ecology*
 797 *and Evolution* 2:819–826.

798 Flies, E.J., C. Skelly, S.S. Negi, P. Prabhakaran, Q. Liu, K. Liu, F.C. Goldizen, C.
 799 Lease C, and P. Weinstein. 2017. Biodiverse green spaces: a prescription for global
 800 urban health. *Frontiers in Ecology and the Environment* 15:510–516.

801 Forister, M.L., L.A. Dyer, M.S. Singer, J.O. Stireman, and J.T. Lill. 2012. Revisiting
 802 the evolution of ecological specialization, with emphasis on insect–plant interactions.
 803 *Ecology* 93:981–991.

804 Fournier, B., D. Frey, and M. Moretti. 2020. The origin of urban communities: From
 805 the regional species pool to community assemblages in city. *Journal of Biogeography*
 806 47:615–629.

807 Gelman, A. and J. Hill. 2007. Data analysis using regression and
 808 multilevel/hierarchical models. Cambridge University Press, Cambridge, UK.

809 Gibb H., and S.A Cunningham. 2010. Revegetation of farmland restores function and
 810 composition of epigaeic beetle assemblages. *Biological Conservation* 143:677–687.

811 Goertzen, D., and F. Suhling. 2014. Central European cities maintain substantial
 812 dragonfly species richness – a chance for biodiversity conservation? *Insect*
 813 *conservation and diversity* 8:238–246.

814 Haaland, C., R.E. Naisbit, and L. Bersier. 2011. Sown wildflower strips for insect
 815 conservation: a review. *Insect Conservation and Diversity* 4:60–80.

816 Hartig, T., and P.H. Kahn. 2016. Living in cities, naturally. *Science* 352:938–940.

817 Kellner, K. 2016. jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses.
 818 Version 1.4.2. <https://CRAN.R-project.org/package=jagsUI>

819 Kennedy T.A., S. Naeem, K.M. Howe, J.M.H. Knops, D. Tilman, and P. Reich. 2002.
 820 Biodiversity as a barrier to ecological invasion. *Nature* 417:636–638.

821 Keniger, L., K.J. Gaston, K. Irvine, and R.A. Fuller. 2013. What are the benefits of
 822 interacting with nature? *International Journal of Environmental Research and Public*
 823 *Health* 10:913–935.

824 Kéry, M., and J.A. Royle. 2016. Applied hierarchical modeling in Ecology: analysis
 825 of distribution, abundance and species richness in R and BUGS Volume 1: prelude
 826 and static models. Academic Press, London, UK.

827 Ignatieva, M., et al. 2015. Lawn as cultural and ecological phenomenon: a conceptual
 828 framework for transdisciplinary research. *Urban Forestry and Urban Greening*
 829 14:383–387.

830 Ikin, K., E. Knight, D.B. Lindenmayer, J. Fischer, and A.D. Manning. 2013. The
 831 influence of native versus exotic streetscape vegetation on the spatial distribution of
 832 birds in suburbs and reserves. *Diversity and Distributions* 19:294–306.

833 Ikin, K., D.S. Le Roux, L. Rayner, N.R. Villaseñor, K. Eyles, P. Gibbons, A.D.
 834 Manning, and D.B. Lindenmayer. 2015. Key lessons for achieving biodiversity-
 835 sensitive cities and towns. *Ecological Management and Restoration* 16:206–214.

836 Ives, C.D., and Y. Lynch. 2014. Untapping the potential of science-government
 837 partnerships to benefit urban nature. *The Nature of Cities*, August 2014.

838 Lai, H., E.J. Flies, P. Weinstein, and A. Woodward. 2019. The impact of green space
 839 and biodiversity on health. *Frontiers in Ecology and the Environment* 17:383–390.

840 Landis, D.A., S.D. Wratten, and G.M. Gurr. 2000. Habitat management to conserve

841 natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*
842 45:175–201.

843 Le Roux, D.S., K. Ikin, D.B. Lindenmayer, W. Blanchard, A.D. Manning, and P.
844 Gibbons. 2014. Reduced availability of habitat structures in urban landscapes:
845 implications for policy and practice. *Landscape and Urban Planning*, 125:57–64.

846 Lepczyk, C.A., M.F.J. Aronson, K.L. Evans, M.A. Goddard, S.B. Lerman, J.S.
847 MacIvor. 2017. Biodiversity in the city: fundamental questions for understanding the
848 ecology of urban green spaces for biodiversity conservation. *BioScience* 67:799–807.

849 M’Gonigle, L.K., N.M. Williams, E. Lonsdorf, and C. Kremen. 2017. A tool for
850 selecting plants when restoring habitat for pollinators. *Conservation Letters* 10:105–
851 111.

852 Madre, F., A. Vergnes, N. Machon, and P. Clergeau. 2013. A comparison of 3 types
853 of green roof as habitats for arthropods. *Ecological Engineering* 57:109 –117.

854 Majer, J.D., K.E.C. Brennan, and M.L. Moir. 2007. Invertebrates and the restoration
855 of a forest ecosystem: 30 years of research following bauxite mining in Western
856 Australia. *Restoration Ecology* 15:S104–S115.

857 Majewska, A.A., and S. Altizer. 2020. Planting gardens to support insect pollinators.
858 *Conservation Biology* 34:15–25.

859 Maller, C., L. Mumaw, and B. Cooke. 2018. Health and social benefits of living with
860 ‘wild’ nature. Pages in N. Pettorelli, S.M Durant, and J.T. Du Toit, editors.
861 *Rewilding*. Cambridge University Press, Cambridge, UK.

862 Mata, L., G. Garrard, F. Fidler, C.D Ives, C. Maller, J. Wilson, F. Thomas, and S.
863 Bekessy. (2019) Punching above their weight: the ecological and social benefits of
864 pop-up parks. *Frontiers in Ecology and the Environment* 17:341–347.

865 Mata, L., C.E. Ramalho, J. Kennedy, K.M. Parris, L. Valentine, M. Miller, S.
866 Bekessy, S. Hurley, and Z. Cumpston (2020) Bringing nature back into cities. *People*
867 *and Nature* 2:350–368.

868 Mata, L., C.G. Threlfall, N.S.G. Williams, A.K. Hahs, M. Malipatil, S.E. Stork and
869 S.J. Livesley. 2017. Conserving herbivorous and predatory insects in urban green
870 spaces. *Scientific Reports* 7:40970.

871 Mata, L., et al. 2015. The Little Things that Run the City: how do Melbourne’s green
872 spaces support insect biodiversity and ecosystem health? City of Melbourne,
873 Melbourne, Australia.

874 Mata, L., et al. 2016. The Little Things that Run the City – Insect ecology,
875 biodiversity and conservation in the City of Melbourne. City of Melbourne,
876 Melbourne, Australia.

877 Mata, L., et al. 2020. The Little Things that Run the City dataset (Version v1
878 rhapsodyingreen). Zenodo, data set. <http://doi.org/10.5281/zenodo.4127119>

879 Matteson, K.C., and G.A. Langellotto. 2010. Determinates of inner city butterfly and
880 bee species richness. *Urban Ecosystems* 13:333–347.

881 McGregor-Fors, I., et al. 2016. City “green” contributions: the role of urban
882 greenspaces as reservoirs for biodiversity. *Forests* 7:146.

883 Moir, M.M., K.E.C. Brennan, J.M. Koch, J.D. Majer, and M.J. Fletcher. 2005.
884 Restoration of a forest ecosystem: The effects of vegetation and dispersal capabilities
885 on the reassembly of plant-dwelling arthropods. *Forest Ecology and Management*
886 217:294–306.

887 Morris, M.G. 2000. The effect of structure and its dynamics on the ecology and
888 conservation of arthropods in British grasslands. *Biological Conservation* 95:129–
889 142.

890 Murdoch, W.W, F.C. Evans, and C.H. Peterson. 1972. Diversity and pattern in plants
891 Nemec, K.T., and T.B. Bragg. 2008. Plant-feeding hemiptera and orthoptera
892 communities in native and restored mesic tallgrass prairies. *Restoration Ecology* 16:
893 324–335.

894 New, T.R. 2015. Insect conservation and urban environments. Springer.

895 Nilon, C.H., et al. 2017. Planning for the future of urban biodiversity: a global review
896 of city-scale initiatives. *BioScience* 67:332–342.

897 Norton, B.A., et al. 2019. Urban meadows as an alternative to short mown grassland:
898 effects of composition and height on biodiversity. *Ecological Applications* 29:e01946.

899 Oksanen, J., et al. 2016. vegan: community ecology package. R package version 2.3-
900 4. <https://CRAN.R-project.org/package=vegan>

901 Paap, T., T.I. Burgess, and M.J. Wingfield. 2017. Urban trees: bridge-heads for forest
902 pest invasions and sentinels for early detection. *Biological Invasions* 19:3515–3526.

903 Padovani, R.J., A. Salisbury, H. Bostock, D.B. Roy, and C.D. Thomas. 2020.
904 Introduced plants as novel Anthropocene habitats for insects. *Global Change Biology*
905 26:971–988.

906 Parris, K.M., et al. 2018. The seven lamps of planning for biodiversity in the city.
907 *Cities* 83:44–53.

908 Piano, E., et al. 2020. Urbanization drives cross-taxon declines in abundance and
 909 diversity at multiple spatial scales. *Global Change Biology* 26:1196–1211.

910 Piroozfar, P., E.R.P Farr, E. Aboagye-Nimo, and J. Osei-Berchie. 2019. Crime
 911 prevention in urban spaces through environmental design: a critical UK perspective.
 912 *Cities* 95:102411.

913 Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using
 914 Gibbs sampling. *In* K. Hornik, et al., editors. *Proceedings of the 3rd International*
 915 *Workshop on Distributed Statistical Computing*.

916 Potts, S.G., B.A. Woodcock, S.P.M. Roberts, T. Tscheulin, E.S. Pilgrim, V.K. Brown,
 917 and J.R. Tallowin. 2009. Enhancing pollinator biodiversity in intensive grasslands.
 918 *Journal of Applied Ecology* 46:369–379.

919 Prather, C.M., et al. 2013. Invertebrates, ecosystem services and climate change.
 920 *Biological Reviews* 88:327–348.

921 Procheş, S., J.R.U Wilson, D.M Richardson, and S.L. Chown. 2008. Herbivores, but
 922 not other insects, are scarce on alien plants. *Austral Ecology* 33:691–700.

923 Pysek, P., et al. 2010. Contrasting patterns in the invasions of European terrestrial and
 924 freshwater habitats by alien plants, insects and vertebrates. *Global Ecology and*
 925 *Biogeography* 19:317–331.

926 Requier, F., and S.D. Leonhardt. 2020. Beyond flowers: including non-floral
 927 resources in bee conservation schemes. *Journal of Insect Conservation* 24:5–16.

928 Roques, A., W. Rabitsch, J. Rasplus, C. Lopez-Vaamonde, W. Nentwig, and M.
 929 Kenis. 2009. Alien terrestrial invertebrates of Europe. Pages 63–79 in DAISIE,
 930 editors. *Handbook of alien species in Europe*. Springer, Dordrecht, The Netherlands.

931 Roulston, T.H., and K. Goodell. 2011. The role of resources and risks in regulating
 932 wild bee populations. *Annual Review of Entomology* 56:293–312.

933 Russo, L., N. DeBarros, S. Yang, K Shea, and D. Mortensen. 2013. Supporting crop
 934 pollinators with floral resources: network-based phenological matching. *Ecology and*
 935 *Evolution* 3: 3125–3140.

936 Rust, M.K., and N.Y. Su. 2012. Managing social insects of urban importance. *Annual*
 937 *Review of Entomology* 57:355–375.

938 Saarinen, K., A. Valtonen, J. Jantunen, and S. Saarnio. 2005. Butterflies and diurnal
 939 moths along road verges: Does road type affect diversity and abundance? *Biological*
 940 *Conservation* 123:403–412.

941 Salisbury, A., J. Armitage, H. Bostock, J. Perry, M. Tatchell, and K. Thompson. 2015.
 942 Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should
 943 we plant native or exotic species? *Journal of Applied Ecology* 52:1156–1164.

944 Salisbury, A., S. Al-Beidh, J. Armitage, S. Bird, H. Bostock, A. Platoni, M. Tatchell,
 945 K. Thompson, and J. Perry. 2017. Enhancing gardens as habitats for plant-associated
 946 invertebrates: should we plant native or exotic species? *Biodiversity Conservation*
 947 26:2657–2673.

948 Sattler, T., M. Obrist, P. Duelli, and M. Moretti. 2011. Urban arthropod communities:
 949 added value or just a blend of surrounding biodiversity? *Landscape and Urban*
 950 *Planning* 103:347–361.

951 Schuldt, A., et al. 2019. Multiple plant diversity components drive consumer
 952 communities across ecosystems. *Nature Communications* 10:1460.

953 Seebens, H., et al. 2018. Global rise in emerging alien species results from increased
 954 accessibility of new source pools. *Proceedings of the National Academy of Science*
 955 115: E2264-E2273.

956 Sing, K., W.F.A. Jusoh, N.R. Hashim, and J. Wilson. 2016. Urban parks: refuges for
 957 tropical butterflies in Southeast Asia? *Urban Ecosystems* 19:1131–1147.

958 Smith, L.S., M.E.J. Broyles, H.K. Larzleer, and M.D.E. Fellowes. 2015. Adding
 959 ecological value to the urban lawnscape. Insect abundance and diversity in grass-free
 960 lawns. *Biodiversity Conservation* 24:47–62.

961 Soanes, K., M. Sievers, Y.E. Chee, N.S.G. Williams, M. Bhardwaj, A.J. Marshall, and
 962 K.M. 2019. Correcting common misconceptions to inspire conservation action in
 963 urban environments. *Conservation Biology* 33:300–306.

964 Soliveres, S., et al. 2016 Biodiversity at multiple trophic levels is needed for
 965 ecosystem multifunctionality. *Nature* 536:456–459.

966 Szewczyk, T.M., and C.M. McCain. 2019. Disentangling elevational richness: A
 967 multi-scale hierarchical Bayesian occupancy model of Colorado ant communities.
 968 *Ecography* 42:977–988.

969 Threlfall, C.G., K. Walker, N.S.G. Williams, A.K. Hahs, L. Mata, N. Stork, and S.J.
 970 Livesley. 2015. The conservation value of urban green space habitats for Australian
 971 native bee communities. *Biological Conservation* 187:240–248.

972 Threlfall, C.G., A. Ossola, A.K. Hahs, N.S.G Williams, L. Wilson, and S.J. Livesley.
 973 2016. Variation in vegetation structure and composition across urban green space
 974 types. *Frontiers in Ecology and Evolution* 4:66.

- Threlfall, C.G., L. Mata, J. Mackie, A.H. Hahs, N. Stork, N.S.G. Williams, S.J. Livesley. 2017. Increasing biodiversity in urban green spaces through simple vegetation interventions. *Journal of Applied Ecology* 54:1874–1883.
- Tresch, S., D. Frey, R. Le Bayon, P. Mäder, B. Stehle, A. Fliessbach, and M. Moretti. 2019. Direct and indirect effects of urban gardening on aboveground and belowground diversity influencing soil multifunctionality. *Scientific Reports* 9:9769.
- Tscharntke, T., and H. Greiler. 1995. Insect communities, grasses and grasslands. *Annual Review of Entomology* 40:535–558.
- Uno, S., J. Cotton, and S.M. Philpott. 2010. Diversity, abundance, and species composition of ants in urban green spaces. *Urban Ecosystems* 13:425–441.
- Ulyshen, M.D. 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management* 261:1479–1489.
- United Nations. 2017. The new urban agenda. United Nations, New York, USA.
- Valentine, L.E., C.E. Ramalho, L. Mata, M.D. Craig, P.L. Kennedy, and R.J. Hobbs. 2020. Opportunities and risks of novel resources for species conservation. *Frontiers in Ecology and the Environment*: doi.org/10.1002/fee.2255.
- Vander Mijnsbrugge, K., A. Bischoff, and B. Smith. 2010. A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology* 11:300–311.
- Ward, D., and E. Edney-Browne. 2015. Poles apart: comparing trends of alien Hymenoptera in New Zealand with Europe (DAISIE). *PlosOne* 10:e0132264.
- Woodcock, B.A., et al. 2007. The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. *Journal of Applied Ecology* 44:60–69.
- Woodcock, B.A., S.G. Potts, T. Tscheulin, E. Pilgrim, A.J. Ramsey, J. Harrison-Cripps, V.K. Brown, and J.R. Tallwin. 2009. Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins. *Journal of Applied Ecology* 46:920–929.

Figure legends

Figure 1 Visual representation of the planting design element by plant origin (a) and midstorey growth form by plant origin (b) groups that were part of the theoretical and empirical dimensions of this study. Dimmed boxes in (b) indicate theoretical

combinations of midstorey growth form by plant origin groups that did/may not occur in the study area or that occur but not at surveyable densities within the study's plots.

Figure 2 Estimated species richness per plant species of introduced and indigenous insect species at the plant community (a) and individual plant species (b) levels. Estimated probabilities of occurrence of introduced and indigenous insect species at the plant community (c) and individual plant species (d) levels. In all figures the black lines represent mean responses; the grey boxes in (a) and (c) represent the associated statistical uncertainty (95% Credible Intervals). Y-axis in (b) drawn in the log10 scale.

Figure 3 Estimated species richness of indigenous insects by planting design element (a), midstorey growth form (b) and plant origin (c). Black lines represent mean responses and grey boxes the associated statistical uncertainty (95% Credible Intervals).

Figure 4 Estimated species richness of indigenous insect by planting design element by plant origin (a) and midstorey growth form by plant origin (b). Black lines represent mean responses and coloured boxes the associated statistical uncertainty (95% Credible Intervals). For ease of interpretation plant origin has been colour coded as yellow (nonnative), orange (native) or blue (indigenous).

Figure 5 Estimated species richness of indigenous insects by planting design element by plant origin (a,c,e,g,i) and midstorey growth form by plant origin (b,d,f,h,j) for pollinators (a,b), herbivores (c,d), predators (e,f), parasitoids (g,h) and detritivores (i,j). Black lines represent mean responses and coloured boxes the associated statistical uncertainty (95% Credible Intervals). For ease of interpretation plant origin has been colour coded as yellow (nonnative), orange (native) or blue (indigenous).

Figure 6 Indigenous insect community dissimilarity matrices for the planting design element by plant origin (a) and midstorey growth form by plant origin (b) groups. Percentages in the white cells were calculated using the Jaccard dissimilarity index, where 0 and 1 represents minimum and maximum dissimilarity, respectively. Values in the adjacent left columns represent the percentage of unique species observed in each group.

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