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17 **Indigenous plants promote insect biodiversity in urban greenspaces**

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51

52 **Abstract**

53 The contribution of urban greenspaces to support biodiversity and provide benefits for
54 people is increasingly recognised. However, ongoing management practices favour
55 vegetation oversimplification – often limiting greenspaces to lawns and tree canopy
56 rather than multi-layered vegetation that includes under- and midstorey – and the use
57 of nonnative species. These practices hinder the potential of greenspaces to sustain
58 indigenous biodiversity, particularly for taxa like insects, that rely on plants for food
59 and habitat. Yet, little is known about which plant species may maximise positive
60 outcomes for taxonomically and functionally diverse insect communities in
61 greenspaces. Additionally, while cities are expected to experience high rates of
62 introductions, quantitative assessments of the relative occupancy of indigenous vs.
63 introduced insect species in greenspace are rare – hindering understanding of how
64 management may promote indigenous biodiversity while limiting the establishment of
65 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

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

105 An ubiquitous practice that can hinder the potential of greenspaces to support
106 biodiversity is the oversimplification of vegetation structure (Le Roux et al. 2014,
107 Threlfall et al. 2016), which has led many greenspaces to be vegetated by only two
108 planting design elements: lawn and tree canopy (Ignatieva et al. 2015, Aronson et al.
109 2017). In contrast, greenspaces with a more complex, multi-layered vertical structure
110 – those including understorey and midstorey vegetation (henceforth midstorey for
111 brevity) – provide positive outcomes for a taxonomically and functionally diverse
112 range of taxa (Burkman and Gardiner 2014, Mata et al. 2017, Threlfall et al. 2017,
113 Aguilera et al. 2019, Majewska and Altizer 2020). Unlike the lawn and tree canopy,
114 the midstorey is a heterogenous mix of different plant growth forms, including forbs,
115 graminoids, lilioids and shrubs. Yet, at present, the combination of plant species and
116 growth forms that maximise positive outcomes for non-plant species in the midstorey
117 remains poorly understood.

118 An additional issue that limits biodiversity in urban areas is that most non-remnant
119 greenspaces, particularly intensively manicured ones such as residential gardens and
120 public parks, are composed predominately of nonnative plant species (Threlfall et al.
121 2016). Nonnative plants are rarely well-suited to provide resources for indigenous
122 primary consumers (e.g., herbivorous insects and frugivorous birds), nor to
123 indigenous secondary and apex consumers (e.g., predatory and parasitoid insects and
124 insectivorous birds and bats) that depend on primary consumers as food resources
125 (Ballard et al. 2013, Burghardt and Tallamy 2013, Ikin et al. 2013, Salisbury et al.
126 2015, Threlfall et al. 2017). Management practices that promote the use of nonnative
127 plants are, therefore, likely to reduce the capacity of greenspaces to sustain diverse
128 communities of indigenous biodiversity.

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

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

142 Insects are a particularly important component of urban biodiversity (Sattler et al.
143 2011, New 2015) and the ecological functions they perform provide numerous
144 benefits to urban residents (Prather et al. 2013, Benett and Lovell 2014, Baldock et al.
145 2015), along with some disbenefits (Dunn 2010, Rust and Su 2012). Plants and
146 insects have often coevolved in close association with each other, with many insect
147 species showing high levels of specialisation (Forister et al. 2012). Plants also provide
148 food, foraging, nesting, oviposition, shelter and overwintering resources to generalist
149 insect detritivores, predators and parasitoids; indeed, practices that promote these
150 resources in agroecosystems by fostering plant diversity and structural complexity are
151 key components of pest management strategies (Landis et al. 2000). The availability
152 of suitable host plants within greenspaces is therefore a key determinant of insect
153 diversity in urban environments (Aronson et al. 2016). However, as far as we are
154 aware no study has sought to identify how origin and growth form relates to the value
155 of individual plant species for sustaining taxonomically and functionally diverse
156 insect communities in urban greenspaces.

157 Urban environments are central nodes of human-mediated dispersal networks
158 (Bullock et al. 2018) and hotspots of novel resource utilisation (Valentine et al. 2020),
159 such that introduced species are often prominent (Cadotte et al. 2017, Paap et al.
160 2017). The number of introduced insect species can be relatively low (Uno et al.
161 2010, Madre et al. 2013, Mata et al. 2017), but they often occur in high abundance
162 and this is especially the case for generalist ants, bees and butterflies (Connor et al.
163 202, Matteson & Langellotto 2010, Uno et al. 2010, Threlfall et al. 2015). However,
164 as far as we are aware, quantitative analyses of the relative contributions of
165 indigenous and introduced species in greenspace insect communities have not been
166 previously reported in the literature. This paucity of data hinders understanding of

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

197 **Methods**

198 Study design

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

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

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

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

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

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

239 Insect survey

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

253 Data analysis

254 *Estimating insect occupancy and species richness per plant species*

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

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

$$275 Z_{ij} \sim \text{Bernoulli}(\Psi_{ij})$$

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

$$278 y_{i,j,k} \sim \text{Bernoulli}(\Phi_{i,j,k} \cdot Z_{ij})$$

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

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

$$283 \text{logit}(\Psi_{ij}) = \text{occ}_i$$

$$284 \text{logit}(\Phi_{i,j,k}) = \text{det}_i$$

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

$$286 \text{occ}_i \sim \text{Normal}(\mu.\text{occ}_{Int...Inds}, \tau.\text{occ})$$

$$287 \text{det}_i \sim \text{Normal}(\mu.\text{det}, \tau.\text{det})$$

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

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

$$295 SR_j = \sum_{i=S_{ij}} Z_{ij}$$

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

301 probabilities of occurrence. This allowed us to work within the reasonable ecological
302 assumption that across the study area not every insect species will be associated with
303 every co-occurring plant species. We conducted these estimations for the insect
304 community as a whole but also independently for introduced and indigenous species.
305 Our model was implemented in JAGS (Plummer 2003) and accessed through the R
306 package *jagsUI* (Kellner 2016). We used three chains of 5,000 iterations, discarding
307 the first 500 in each chain as burn-in. We visually inspected the MCMC chains and
308 the values of the Gelman-Rubin statistic to verify acceptable convergence levels of \hat{R} -
309 $\hat{r} < 1.1$ (Gelman & Hill 2007).

310 *Community dissimilarity*

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

322 **Results**

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

333 *Indigenous vs introduced insect species*

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

353 *Effect of design element, growth form and plant origin*

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

365 *Combined effect of design element and plant origin*

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

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

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

394 *Combined effect of growth form and plant origin*

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

402 level of insect species richness per plant species, with the average indigenous shrub
403 showing 2.1 and 1.6 times more insect species than average nonnative and native
404 shrubs, respectively (Fig. 4b; Appendix S2: Table S6). The group with the third
405 highest insect species richness was indigenous lilioids, with the average indigenous
406 lilioid showing 2.5 times more insect species than the average nonnative lilioid (Fig.
407 4b; Appendix S2: Table S6). In general, the indigenous growth form groups were
408 associated with the highest number of indigenous insect species across all insect
409 functional groups (Fig. 5b,d,f,h,j; Appendix S2: Table S6). An alternative ‘Combined
410 effect of phylogenetic clade by plant origin’ analysis revealed that – in all clades, with
411 the exception of basal eudicots – indigenous groups had higher insect species richness
412 than did native plants, and the latter had higher insect richness than nonnative plants
413 (Appendix S2: Table S8).

414 *Community composition and unique species*

415 The highest dissimilarity in insect species composition between indigenous and
416 nonnative groups across the design elements by plant origin and growth forms by
417 plant origin groups was found between the midstoreys (Fig. 6a) and shrubs (Fig. 6b),
418 respectively. Within the design element by plant origin group, 33% and 30% of all
419 indigenous insect species were unique to the indigenous and midstorey groups,
420 respectively (Fig. 6a). From the growth form by plant origin perspective, 29% and
421 24% of all indigenous insect species recorded in the midstorey were unique to the
422 indigenous and shrub groups, respectively (Fig. 6b).

423 **Discussion**

424 Our findings demonstrate that taxonomically and functionally diverse indigenous
425 insect communities occur in greenspaces in a densely urbanised inner-city
426 municipality, with the potential to boost ecosystem multifunctionality (Soliveres et al.
427 2016) and biotic resistance against the establishment of introduced insects (Kennedy
428 et al. 2002). Our study further highlights that multi-layered, structurally complex
429 indigenous vegetation plays a core role in sustaining high insect biodiversity in urban
430 areas, with the indigenous midstorey and canopy key to maintaining a rich and
431 functionally diverse indigenous insect community within this system. Within the
432 indigenous midstorey, graminoids surprisingly support the highest indigenous insect
433 species richness per plant species across all functional groups – particularly for
434 herbivores, predators and detritivores – followed by indigenous shrubs and lilioids.
435 The indigenous midstorey also hosts the largest percentage of unique species. Taken

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

439 *Greenspace insect communities are dominated by indigenous insect species*

440 Our results indicate that insect communities in Melbourne greenspaces are
441 overwhelmingly composed of indigenous rather than introduced species. This finding
442 aligns with previous studies of insect richness in cities across other continents
443 (Goertzen and Suhling 2014, Sing et al. 2016, Brown and Hartop 2017). Despite the
444 expectation that urban environments act as hotspots for biological invasions (Cadotte
445 et al. 2017), particularly of nonnative plants and insects (Pysek et al 2010), we found
446 a relatively low number of introduced insect species. Not surprisingly, however, some
447 of these introduced species, for example the Argentine ant *Linepithema humile* and
448 the European honeybee *Apis mellifera*, were relatively common and widespread,
449 which is consistent with previous studies (Connor et al. 2020, Matteson & Langellotto
450 2010, Uno et al. 2010, Threlfall et al. 2015). In the case of the European honeybee
451 this pattern could be symptomatic of the growing trend of urban beekeeping, which
452 may have unintended detrimental effects on indigenous bees (Egerer & Kowarik In
453 press).

454 *Indigenous plant species promote indigenous insect diversity*

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

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

470 example, using experimental plantings of tree and shrub species, Burghardt and
471 Tallamy (2013) showed that nonnative plants supported less diverse herbivorous
472 insect communities than indigenous plants. Similarly, in an early successional
473 experiment the biomass, abundance and species richness of herbivorous, predatory
474 and parasitoid insects was lower on nonnative forbs than on indigenous forbs (Ballard
475 et al. 2013). Working specifically in an urban setting, Salisbury and colleagues (2015,
476 2017) experimented with the origin of flowering plants in garden borders,
477 demonstrating that insects across a diverse range of functional groups were less
478 abundant on nonnative than indigenous plant species. These experimental findings
479 have been substantiated by observational approaches, particularly by studies
480 conducted within urban environments. For instance, a study that included the species-
481 specific responses of bees, beetles and heteropteran bugs to vegetation attributes of
482 gardens, parks and golf courses revealed how occurrence probabilities for most insect
483 species decreased as a function of the amount of nonnative plants present in the
484 studied greenspaces (Threlfall et al. 2017).

485 *Midstorey as a key planting design element*

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

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

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

511 *Graminoids as a key midstorey growth form*

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

528 Remarkably, the capacity of indigenous graminoids to support the highest levels of
529 indigenous insect species per plant species across all studied plant groups was true for
530 all insect functional groups. This finding extends previous studies reporting on the
531 positive effects of tussocks and other graminoids on specific insect functional groups
532 – predominantly on herbivores, predators and parasitoids (Dennis et al. 1998,
533 Woodcock et al. 2007, Haaland et al. 2011), but also for pollinators (Saarinen et al.
534 2005, Potts et al. 2009). Our finding that graminoids, which are predominantly
535 pollinated by wind, support more pollinators and other flower-visiting insect species
536 than do lilioids or shrubs, which are predominantly pollinated by insects, is highly
537 noteworthy and provides insight into function and value of non-floral resources for

538 insect pollinators (Roulston and Goodell 2011, Requier and Leonhardt 2020). We
539 hope that our research will serve as a base for future studies on the capacity of
540 graminoids to provide habitat and food resources for insects in urban greenspaces,
541 particularly of non-floral resources for pollinators and other flower-visiting species.
542 Beyond graminoids, our data further emphasise the contributions of other midstorey
543 growth forms. For instance, indigenous shrubs and lilioids sustained the second and
544 third highest number of indigenous insect species per plant species across the growth
545 form by plant origin groups. Indeed, our findings indicate that any particular
546 indigenous shrub or lilioid species supports the same number of indigenous insect
547 species as any particular indigenous tree species; and substantially more insect species
548 than any particular native or nonnative tree species. However, we found that the
549 number of unique indigenous insect species varied markedly between these two plant
550 groups, with indigenous shrubs showing as much as 7.4 times more unique insect
551 species than their lilioid counterparts. In general, shrubs outperformed all other
552 midstorey growth forms, with approximately one out of every four indigenous insect
553 species across the study being exclusively associated with shrub species.
554 Taken together, our findings point to the critical role that midstorey growth forms –
555 particularly indigenous plant species – play in supporting taxonomically and
556 functionally diverse indigenous insect communities in urban greenspaces. This is not
557 only critical for insect conservation in urban environments but of direct, immediate
558 relevance for a wide range of animals such as reptiles, birds and mammals that rely on
559 them as food sources. Our findings therefore underscore the potential of a diverse,
560 primarily indigenous understorey and midstorey strata to increase the positive
561 biodiversity outcomes provided by structurally complex vegetation. As such, they
562 support ideas that move beyond the traditional approach of designing urban
563 greenspaces predominantly or often exclusively with nonnative short turfgrass lawn
564 and tall trees (Ikin et al. 2015, Smith et al. 2015, Parris et al. 2018, Norton et al.
565 2019).

566 *Limitations and future research*

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

572 2015). It is therefore not inconceivable that some introduced species occurring in our
573 study area in small, isolated populations might have gone undetected. Indeed, a recent
574 related study in one of the study sites revealed the occurrence of the European firebug
575 *Pyrrhocoris apterus* – a Palaearctic species not previously recorded in Australia (LM
576 unpublished data). As with any observational study, our study design may have
577 introduced unintended bias because our data collection period was purposely designed
578 to coincide with the peak activity season for insects in our study area (i.e., the summer
579 months). We believe however that this effect is negligible as far fewer insect species
580 are more active over the colder periods. Finally, we are also aware that our study was
581 conducted at a single scale, focusing exclusively at the plant level. Although beyond
582 the scope of this paper, to fully understand the mechanisms structuring insect
583 communities in urban environments it would be necessary to analyse the patterns
584 driving their diversity and distribution across multiple spatial and temporal scales
585 (Estes et al. 2018, Fournier et al. 2020, Piano et al. 2020). For example, in a follow-up
586 study, we are using a multi-scale occupancy model (Kéry and Royle 2016, Szewczyk
587 & McCain 2019) to assess the species-specific responses of insects at the site, plot,
588 plant and detection levels. This will allow the effect of greenspace size, plot spatial
589 configuration, and any potential observation-process covariates such as temperature
590 and wind speed to be identified.

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

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

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

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

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

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

650 *Making a difference – implications for policy and beyond*

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

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

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

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

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

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

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711 **Supporting Information**

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

714 **Data Availability**

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

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1004 1005 **Figure legends**

1006 Figure 1 Visual representation of the planting design element by plant origin (a) and
1007 midstorey growth form by plant origin (b) groups that were part of the theoretical and
1008 empirical dimensions of this study. Dimmed boxes in (b) indicate theoretical

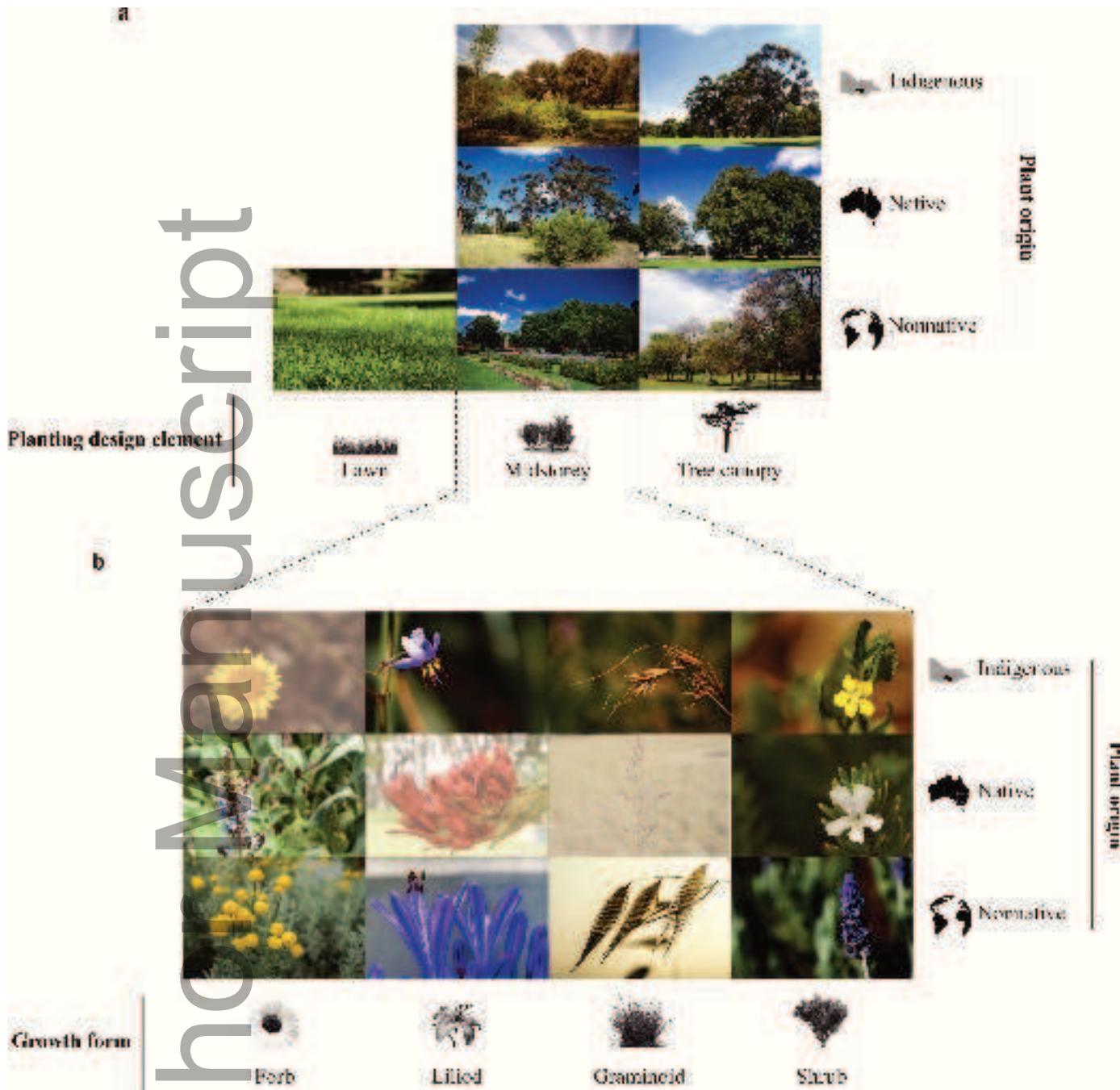
1009 combinations of midstorey growth form by plant origin groups that did/may not occur
1010 in the study area or that occur but not at surveyable densities within the study's plots.
1011 Figure 2 Estimated species richness per plant species of introduced and indigenous
1012 insect species at the plant community (a) and individual plant species (b) levels.
1013 Estimated probabilities of occurrence of introduced and indigenous insect species at
1014 the plant community (c) and individual plant species (d) levels. In all figures the black
1015 lines represent mean responses; the grey boxes in (a) and (c) represent the associated
1016 statistical uncertainty (95% Credible Intervals). Y-axis in (b) drawn in the log₁₀
1017 scale.

1018 Figure 3 Estimated species richness of indigenous insects by planting design element
1019 (a), midstorey growth form (b) and plant origin (c). Black lines represent mean
1020 responses and grey boxes the associated statistical uncertainty (95% Credible
1021 Intervals).

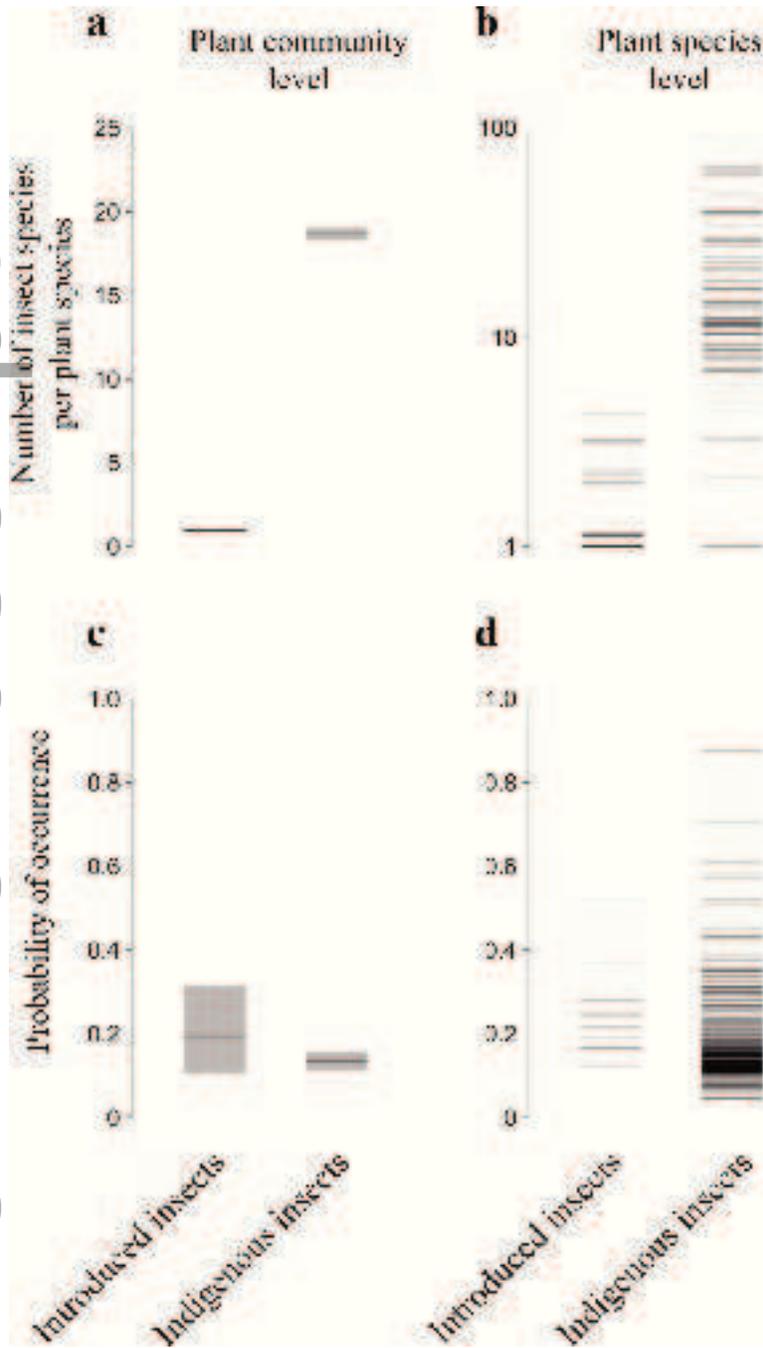
1022 Figure 4 Estimated species richness of indigenous insect by planting design element
1023 by plant origin (a) and midstorey growth form by plant origin (b). Black lines
1024 represent mean responses and coloured boxes the associated statistical uncertainty
1025 (95% Credible Intervals). For ease of interpretation plant origin has been colour coded
1026 as yellow (nonnative), orange (native) or blue (indigenous).

1027 Figure 5 Estimated species richness of indigenous insects by planting design element
1028 by plant origin (a,c,e,g,i) and midstorey growth form by plant origin (b,d,f,h,j) for
1029 pollinators (a,b), herbivores (c,d), predators (e,f), parasitoids (g,h) and detritivores
1030 (i,j). Black lines represent mean responses and coloured boxes the associated
1031 statistical uncertainty (95% Credible Intervals). For ease of interpretation plant origin
1032 has been colour coded as yellow (nonnative), orange (native) or blue (indigenous).

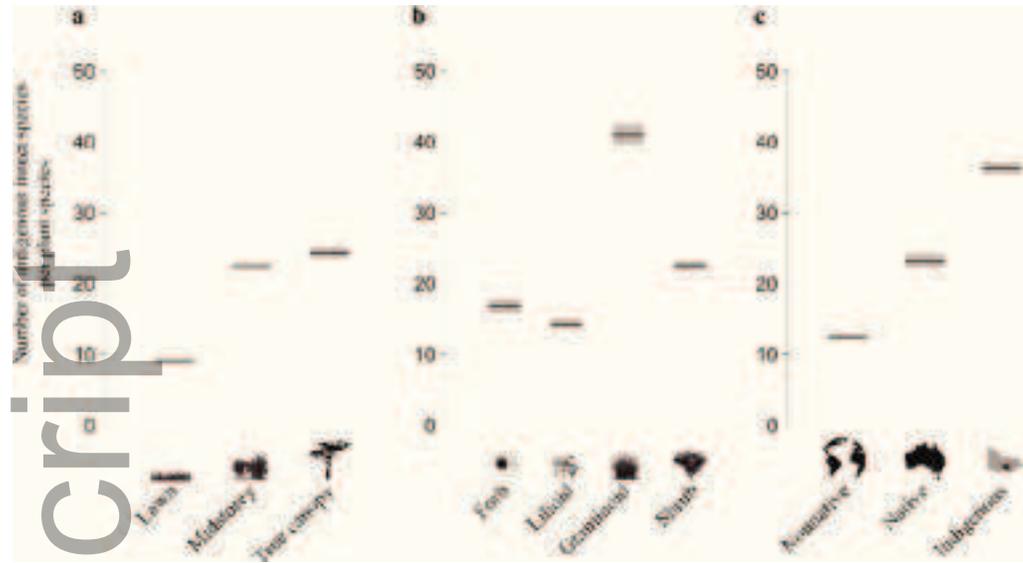
1033 Figure 6 Indigenous insect community dissimilarity matrices for the planting design
1034 element by plant origin (a) and midstorey growth form by plant origin (b) groups.
1035 Percentages in the white cells were calculated using the Jaccard dissimilarity index,
1036 where 0 and 1 represents minimum and maximum dissimilarity, respectively. Values
1037 in the adjacent left columns represent the percentage of unique species observed in
1038 each group.



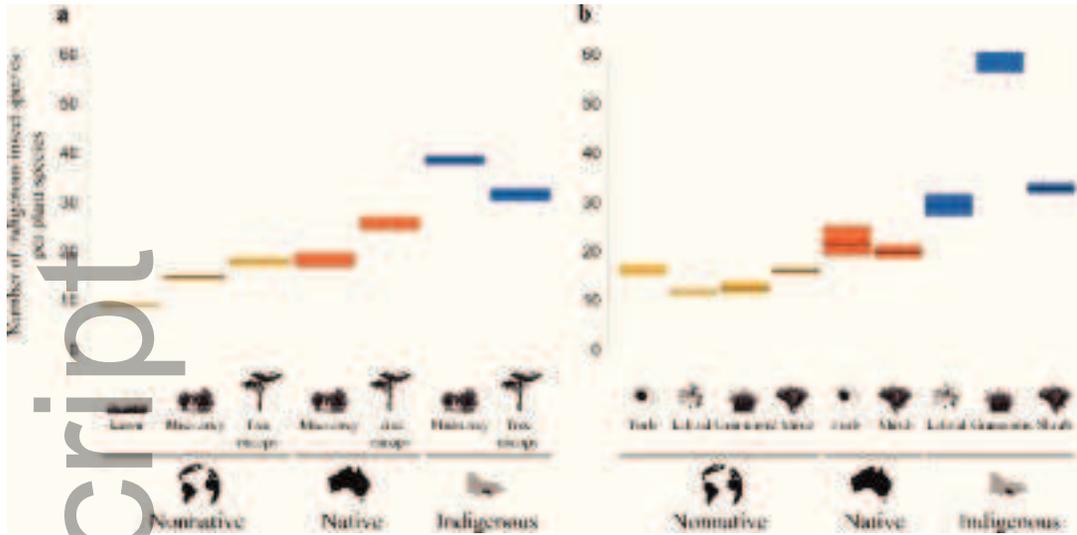
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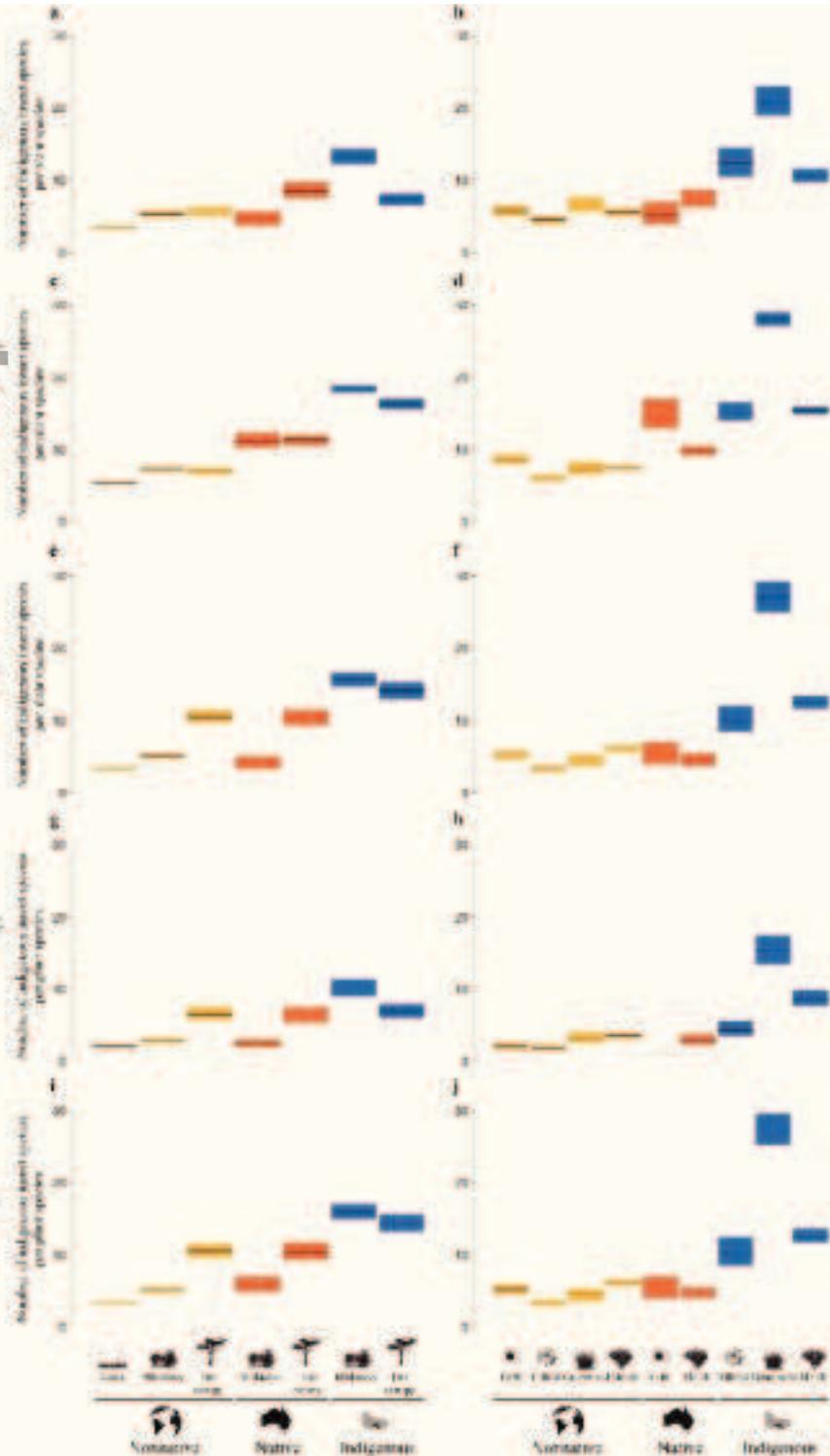
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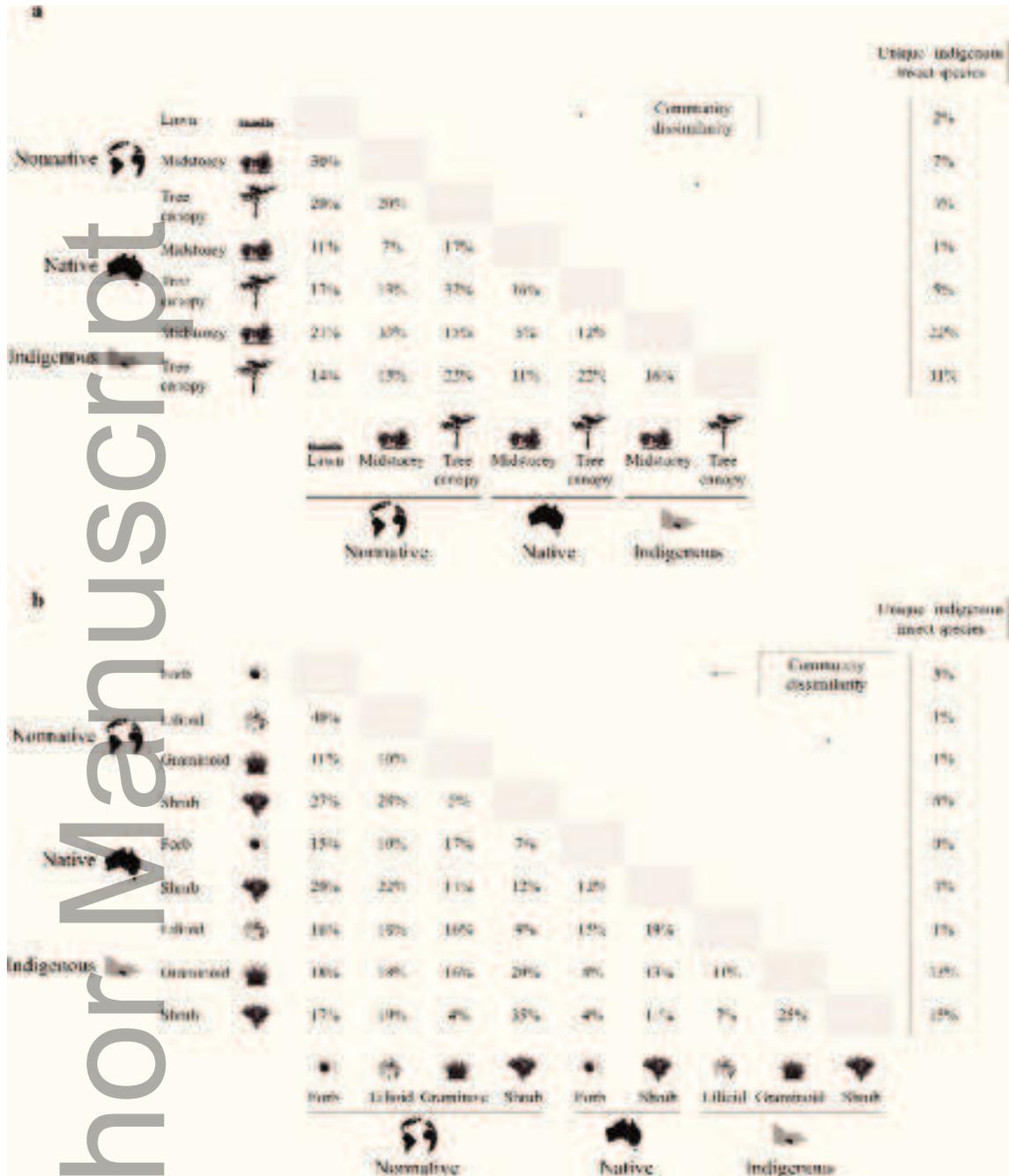
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