

1 **Running head: Indigenous plants promote urban insect diversity**

2 **Title: Indigenous plants promote insect biodiversity in urban greenspaces**

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34 **Abstract** (max 350 words)

35 The contribution of urban greenspaces to support biodiversity and provide benefits for
36 people is increasingly recognised. However, ongoing management practices still
37 favour (1) vegetation oversimplification, often limiting greenspaces to lawns and tree
38 canopy rather than multi-layered vegetation that includes under and midstorey; and
39 (2) the use of nonnative plant species. These practices likely hinder the potential of
40 greenspaces to sustain indigenous biodiversity, particularly for taxa like insects, that
41 rely on plants for food and habitat. Yet, little is known about which plant species may
42 maximise positive outcomes for taxonomically and functionally diverse insect
43 communities in urban greenspaces. Additionally, while urban environments are
44 expected to experience high rates of introductions, quantitative assessments of the
45 relative occupancy of indigenous vs. introduced insect species in greenspace are rare
46 – hindering understanding of how greenspace management may promote indigenous
47 biodiversity while limiting the establishment of introduced insects. Using a
48 hierarchically replicated study design across 15 public parks, we recorded occurrence
49 data from 552 insect species on 133 plant species – differing in planting design

50 element (lawn, midstorey and tree canopy), midstorey growth form (forbs, lilioids,
51 graminoids and shrubs) and origin (nonnative, native and indigenous) – to assess: (1)
52 the relative contributions of indigenous and introduced insect species and (2) which
53 plant species sustained the highest number of indigenous insects. Our data indicates
54 that the insect community was predominately composed of indigenous rather than
55 introduced species. Our findings further highlight the core role of multi-layered
56 vegetation in sustaining high insect biodiversity in urban areas, with indigenous
57 midstorey and canopy representing key elements to maintain rich and functionally
58 diverse indigenous insect communities. Intriguingly, graminoids supported the
59 highest indigenous insect richness across all studied growth forms by plant origin
60 groups. Taken together, our study emphasise the opportunity posed by indigenous
61 understory and midstorey plants, particularly indigenous graminoids in our study area,
62 to promote indigenous insect biodiversity in urban greenspaces. Our work provides a
63 blueprint and stimulus for built-environment professionals to incorporate into their
64 practice plant species palettes that foster a larger presence of indigenous over
65 regionally native or nonnative plant species, whilst incorporating a broader mixture of
66 midstorey growth forms.

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

69 **Introduction**

70 Urban greenspaces provide well-documented benefits for biodiversity and people.
71 Remnant bushland, parks, gardens, golf courses, greenroofs, pop-up parks and other
72 types of greenspace support a great diversity of microbial, fungal, plant and animal
73 species (Madre et al. 2013, Aronson et al. 2014, Baldock et al. 2015, Beninde et al.
74 2015, McGregor-Fors et al. 2016, Mata et al. 2017, Threlfall et al. 2017, Baldock et

75 al. 2019, Mata et al. 2019), and provide a diverse array of health, mental, cognitive,
76 social, cultural and spiritual benefits for people who interact with them (Keniger et al.
77 2013, Dadvand et al. 2015, Hartig and Kahn 2016, Flies et al. 2017, Maller et al.
78 2018, Lai et al. 2019, Mata et al. 2020). Hence, researchers, practitioners, built-
79 environment professionals and policymakers are increasingly working together to
80 promote the positive socio-ecological outcomes of greenspaces (Aronson et al. 2017,
81 Lepczyk et al. 2017, Nilon et al. 2017, Parris et al. 2018, Soanes et al. 2019). Further,
82 the importance of greenspaces has been recently highlighted at an international policy
83 level with the United Nations' New Urban Agenda committing to "promoting the
84 creation and maintenance of well-connected and well-distributed networks of open,
85 multipurpose, safe, inclusive, accessible, green and quality public spaces" (United
86 Nations 2017).

87 An ubiquitous practice that can hinder the potential of greenspaces to support
88 biodiversity is the oversimplification of vegetation structure (Le Roux et al. 2014,
89 Threlfall et al. 2016), which has led many greenspaces to be vegetated by only two
90 planting design elements: lawn and tree canopy (Ignatieva et al. 2015, Aronson et al.
91 2017). In contrast, greenspaces with a more complex, multi-layered vertical structure
92 – those including understorey and midstorey vegetation (henceforth midstorey for
93 brevity) – provide positive outcomes for a taxonomically and functionally diverse
94 range of taxa (Beninde et al. 2015, Mata et al. 2017, Threlfall et al. 2017, Majewska
95 and Altizer 2020). Unlike the lawn and tree canopy, the midstorey is a heterogenous
96 mix of different plant growth forms, including forbs, graminoids, lilioids and shrubs
97 amongst others. Yet, at present, the combination of plant species and growth forms
98 that maximise positive outcomes for non-plant species in the midstorey remains
99 poorly understood.

100 An additional issue that limits biodiversity in urban areas is that most non-remnant
101 greenspaces, particularly intensively manicured ones such as residential gardens and
102 public parks, are composed predominately of nonnative plant species (Threlfall et al.
103 2016). Nonnative plants are rarely well-suited to provide resources for indigenous
104 primary consumers (e.g. herbivorous insects and frugivorous birds), nor to indigenous
105 secondary and apex consumers (e.g. predatory and parasitoid insects and
106 insectivorous birds and bats) that depend on primary consumers as food resources
107 (Ballard et al. 2013, Burghardt and Tallamy 2013, Ikin et al. 2013, Salisbury et al.
108 2015, Threlfall et al. 2017). These studies highlight how management practices that
109 promote the use of nonnative plants are likely to reduce the capacity of greenspaces to
110 sustain diverse communities of indigenous biodiversity.

111 In most of the studies to date, plant origin has been treated as an aggregate plot-level
112 explanatory variable (e.g. treatment plot as either nonnative or native; plot nativeness
113 as percentage cover of native vegetation). A focus on plant species rather than plot as
114 the unit of analysis allows for a more nuanced understanding of how plant origin may
115 influence the capacity of plants to provide resources for associated consumer species.
116 Moreover, focusing on the plant species level may advance understanding of how
117 plant origin interacts with other plant-level attributes — such as planting design
118 element and growth form — to produce positive outcomes for consumer species,
119 particularly of taxa that rely extensively on plants for food and habitat resources, such
120 as insects.

121 Insects are a particularly important component of urban biodiversity (Sattler et al.
122 2011, New 2015) and the ecological functions they perform provide numerous
123 benefits to urban residents (Prather et al. 2013, Benett and Lovell 2014, Baldock et al.
124 2015), along with some disbenefits (Dunn 2010, Rust and Su 2012). Plants and

125 insects have often coevolved in close association with each other, with many insect
126 species showing high levels of specialisation (Forister et al. 2012). Plants also provide
127 food, foraging, nesting, oviposition, shelter and overwintering resources to insect
128 detritivores, predators and parasitoids; indeed, practices that promote these resources
129 in agroecosystems by fostering plant diversity and structural complexity are key
130 components of pest management strategies (Landis et al. 2000). The availability of
131 suitable host plants within greenspaces is therefore a key determinant of insect
132 diversity in urban environments (Aronson et al. 2016). However, as far as we are
133 aware no study has sought to identify specific plant species of differing origins and
134 growth forms that promote taxonomically and functionally diverse insect
135 communities in urban greenspaces.

136 Urban environments are central nodes of human-mediated dispersal networks
137 (Bullock et al. 2018) and hotspots of novel resource utilisation (Valentine et al. 2020),
138 and introduced species are therefore often prominent (Cadotte et al. 2017, Paap et al.
139 2017). The number of introduced insect species can be relatively low (Madre et al.
140 2013, Mata et al. 2017), but they often occur in high abundance and this is especially
141 the case for generalist bees and butterflies (Matteson & Langellotto 2010, Threlfall et
142 al. 2015). However, as far as we are aware, no quantitative assessments of the relative
143 contributions of indigenous and introduced species in greenspace insect communities
144 have been reported in the literature. This paucity of data hinders understanding of
145 how greenspaces may be managed to promote indigenous insect biodiversity while
146 limiting the establishment of introduced species.

147 Here we use a plant-insect metanetwork dataset collected across 15 greenspaces
148 within a densely urbanised inner-city municipality to assess: (1) the relative
149 contributions of indigenous and introduced species in insect communities of urban

150 environments, and (2) which plant species should be planted to support indigenous
151 insect species. The project followed the science-government partnerships model (Ives
152 and Lynch 2014) – an approach that advocates for industry professionals and
153 researchers to work in close association to guarantee that theoretically interesting and
154 practically important questions are identified. This ensured that the implications of
155 our research findings could be applied as practical on-ground actions that were
156 embedded into a new business as usual at the City of Melbourne. We began by
157 determining what proportion of insect species occurring in the greenspaces are
158 indigenous, and whether indigenous insect species are more common than introduced
159 species. We then examined how the richness of indigenous insect species varies with
160 planting design element (lawn, midstorey and tree canopy), midstorey growth form
161 (forbs, lilioids, graminoids and shrubs) and plant origin groups (nonnative, native and
162 indigenous). Finally, we grouped plants species according to a combination of
163 planting design element by plant origin (Fig. 1a), and midstorey growth form by plant
164 origin (Fig. 1b) to assess how the richness of indigenous insect species vary amongst
165 these groups. We do this assessment for the whole insect community and for five key
166 functional groups: pollinators and other flower-visiting taxa, herbivores, predators,
167 parasitoids and detritivores. We also examined variation amongst the plant groups in
168 insect species composition and number of unique species.

169 **Methods**

170 **Study design**

171 The study was conducted in the City of Melbourne, Australia. This is one of 31
172 municipalities within Greater Melbourne, a large metropolitan area spanning
173 approximately 10,000 km² within the Urban Growth Boundary and home to over five
174 million people (Victorian State Revenue Office: [7](https://www.sro.vic.gov.au/greater-</p></div><div data-bbox=)

175 melbourne-map-and-urban-zones). The City of Melbourne covers 37.7 km² and
176 incorporates a central business district, transport and distribution hubs. Approximately
177 13% of the land area is covered by vegetated open space, including grassy woodlands,
178 wetlands, estuaries and a greenspace network of parks, gardens and streetscapes. The
179 municipality is home to approximately 180,000 residents and receives approximately
180 900,000 daily visitors (City of Melbourne: <https://www.melbourne.vic.gov.au/>).

181 Our study was conducted across 15 public parks, which varied in size across four
182 orders of magnitude (1.1 x 10³ m² – 1.3 x 10⁶ m²; Appendix 1: Table S1; Appendix 1:
183 Fig. S1a). We established a total of 130 plots across the 15 parks, with the number of
184 plots in each park (2-36), and their size (84-148 m²), varying according to the park's
185 area (Appendix S1: Eq. S1-S3) and planting design elements and midstorey growth
186 forms present (Appendix 1: Table S1; Appendix 1: Fig. S1b). Within each plot we
187 identified all plants, totalling 133 species, genera or species complexes across the
188 study area (Appendix S2: Table S2).

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

198 We also classified plant species by planting design element (henceforth design
199 element) as lawn complex (n=41), midstorey (n=67) and tree canopy (n=25) (Fig. 1a).

200 Midstorey taxa were further stratified by growth form as forb (n=8), lilioid (n=13),
201 graminoid (n=8) and shrub (n=38) (Fig. 1b). We define lawn complexes (henceforth
202 lawns) as patches dominated by turf forming grasses (Poaceae) intermixed with one
203 or more small, ruderal herbaceous species. Midstorey species included broad-leaved
204 perennial and annual herbaceous plants (forbs); petaloid monocots in orders Liliales
205 and Asparagales (lilioids); grasses, sedges and rushes of typically vertical habit with
206 linear foliage and inconspicuous wind pollinated flowers (graminoids); and woody
207 perennials with multiple stems and < 5 m in height (shrubs). Tree canopy species
208 included single-stemmed woody plants > 5 m in height.

209 Insect survey

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

223 Data analysis

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

225 To assess the proportion of indigenous insect species occurring in the greenspaces,
226 whether they were more common than introduced ones, and how their species
227 richness varied amongst the studied single and combined plant groups, we analysed
228 our data with a three-level hierarchical metacommunity occupancy model (Kéry and
229 Royle 2016). Plant species was our unit of analysis for drawing inferences on insect
230 species occupancy, and each repeated spatial (individuals of the same plant species
231 sampled in different plots) and temporal (same individual of a given plant species
232 sampled at different times) samplings constituted the unit of detection replication. We
233 structured the model around three levels: one for species occupancy; a second for
234 species detectability; and a third to treat the occupancy and detection parameters for
235 each species as random effects (Kéry and Royle 2016). Specifically, we used a
236 variation of the model described by Mata et al. (2017), in which we specified the
237 occupancy level model as:

$$238 \quad Z_{i,j} \sim \text{Bernoulli}(\Psi_{i,j})$$

239 where $\Psi_{i,j}$ is the probability that insect species i occurs at plant species j , and the
240 detection level model as:

$$241 \quad y_{i,j,k} \sim \text{Bernoulli}(\Phi_{i,j,k} \cdot Z_{i,j})$$

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

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

$$246 \quad \text{logit}(\Psi_{i,j}) = \text{occ}_i$$

$$247 \quad \text{logit}(\Phi_{i,j,k}) = \text{det}_i$$

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

$$249 \quad \text{occ}_i \sim \text{Normal}(\mu.\text{occ}_{\text{Int...Ind}}, \tau.\text{occ})$$

250 $\text{det}_i \sim \text{Normal}(\mu.\text{det}, \tau.\text{det})$

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

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

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

258 where S_{ij} is a ‘specificity’ vector indexing the insect species to be included in each
259 plant species’ estimate. SR_j is then an estimate that accounts for plant-insect
260 specificity, in which, for each plant species, the observed insect species are included
261 with probability of occurrence = 1 and a limited random sub-sample of other insect
262 species occurring in the study area are included with their $0 < Z < 1$ estimated
263 probabilities of occurrence. This allowed us to work within the reasonable ecological
264 assumption that across the study area not every insect species will be associated with
265 every co-occurring plant species. We conducted these estimations for the insect
266 community as a whole but also independently for introduced and indigenous species.
267 We estimated model parameters under Bayesian inference, using Markov Chain
268 Monte Carlo (MCMC) simulations to draw samples from the parameters’ posterior
269 distributions. As the species richness calculations were conducted within this
270 modelling framework, we were able to derive the insect species per plant species
271 estimates with their full associated uncertainties. This allowed us to average the

272 species richness estimates of plant species belonging to the same group, and therefore
273 obtain posterior distributions for each group that we could statistically compare.
274 Our model was implemented in JAGS (Plummer 2003) and accessed through the R
275 package *jagsUI* (Kellner 2016). We used three chains of 5,000 iterations, discarding
276 the first 500 in each chain as burn-in. We visually inspected the MCMC chains and
277 the values of the Gelman-Rubin statistic to verify acceptable convergence levels of \hat{R} -
278 $\hat{R} < 1.1$ (Gelman & Hill 2007).

279 *Community dissimilarity*

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

291 **Results**

292 Our survey recorded 552 insect species, with the richest taxa being beetles (125
293 species), parasitoid wasps (121), flies (101), heteropteran bugs (61), leaf- and
294 treehoppers (40) and jumping plant lice (31) (Appendix S2: Table S1). These
295 represented 154 pollinator, 299 herbivore, 231 predator, 150 parasitoid and 231
296 detritivore species. The most commonly occurring species was the minute brown

297 scavenger beetle *Corticicara* sp. 1 (Latridiidae), an indigenous detritivore species that
298 accounted for 12% of all records. The Argentine ant *Linepithema humile* was the most
299 frequently occurring introduced species, accounting for approximately 3% of all
300 records. Four new species were also discovered: one ant, one heteropteran bug and
301 two jumping plant lice (Mata et al. 2015, 2016).

302 *Indigenous vs introduced insect species*

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

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

323 Our model estimates indicate that all three design elements had different levels of
324 indigenous insect species richness, with the average midstorey or tree canopy species
325 showing approximately 2.5 times more insect species than the average lawn complex
326 (Fig. 3a; Appendix S2: Table S5). Likewise, we found that the species richness of
327 indigenous insects varied amongst midstorey growth forms, with the average
328 graminoid species showing 2.9 times more insect species than the average lilioid, 2.4
329 times more than the average forb and 1.8 times more than the average shrub (Fig. 3b;
330 Appendix S2: Table S5). Our estimates further indicate marked statistical differences
331 with plant origin in the number of indigenous insect species (Appendix 2: Figure S1),
332 with the average indigenous plant species showing 2.9 and 1.6 times more insect
333 species than the average nonnative and native plant, respectively; and the average
334 native plant showing 1.9 times more insect species than the average nonnative plant
335 (Fig. 3c; Appendix S2: Table S5).

336 *Combined effect of design element and plant origin*

337 Our model estimates indicate that all design element by plant origin groups had
338 different levels of indigenous insect species richness. In general, indigenous groups
339 were associated with higher species richness than native and these with higher
340 richness than nonnative. The single exception was native midstorey and nonnative
341 tree canopy, which showed insect species richness levels that were not statistically
342 different from each other (Fig. 4a; Appendix S2: Table S6). Overall, the indigenous
343 midstorey was associated with the highest level of indigenous insect species richness,
344 with the average plant species in this group showing 2.6 and 1.6 times more insect
345 species than the average nonnative and native midstorey plant species, respectively
346 (Fig. 4a; Appendix S2: Table S6). The indigenous tree canopy was associated with the

347 second highest level of insect species richness, with the average plant species in this
348 group showing 1.8 and 1.4 times more insect species than the average nonnative and
349 native tree canopy plant species, respectively (Fig. 4a; Appendix S2: Table S6).

350 Across insect functional groups, lawns showed the lowest insect species richness (Fig.
351 5a,c,e,g,i; Appendix S2: Table S6). The indigenous midstorey showed the highest
352 number of indigenous insect species; however, for predators and detritivores the
353 indigenous midstorey was not statistically different to the indigenous tree canopy
354 (Fig. 5e,i; Appendix S2: Table S6). Other departures from the general pattern were
355 observed for each functional group. The indigenous and native tree canopy groups did
356 not show different levels of indigenous pollinators or parasitoid species (Fig. 5a,g;
357 Appendix S2: Table S6), and the native tree canopy and midstorey groups did not
358 show different levels of indigenous herbivore species (Fig. 5c; Appendix S2: Table
359 S6). For predators, parasitoids and detritivores, the nonnative tree canopy group has a
360 higher species richness than the native midstorey and was not statistically different
361 than the native tree canopy – the native and nonnative midstorey groups in turn did
362 not show different levels of associated species (Fig. 5e,g,i; Appendix S2: Table S6).

363 *Combined effect of growth form and plant origin*

364 Our model estimates indicate that the species richness of indigenous insects varied
365 amongst the growth form by plant origin groups. In general, indigenous groups had
366 higher insect species richness than did native and these had higher insect richness than
367 nonnative (Fig. 4b; Appendix S2: Table S6). The group with the highest insect species
368 richness was indigenous graminoids, with the average plant species in this group
369 showing nearly five times more species than the average nonnative graminoid (Fig.
370 4b; Appendix S2: Table S6). Indigenous shrubs were associated with the second
371 highest level of insect species richness, with the average indigenous shrub showing

372 2.1 and 1.6 times more insect species than average nonnative and native shrubs,
373 respectively (Fig. 4b; Appendix S2: Table S6). The group with the third highest insect
374 species richness was indigenous lilioids, with the average indigenous lilioid showing
375 2.5 times more insect species than the average nonnative lilioid (Fig. 4b; Appendix
376 S2: Table S6).

377 Indigenous graminoids showed the highest number of indigenous insect species
378 across all insect functional groups (Fig. 5b,d,f,h,j; Appendix S2: Table S6). In
379 general, the indigenous growth form groups were associated with the highest number
380 of indigenous insect species across all insect functional groups (Fig. 5b,d,f,h,j;
381 Appendix S2: Table S6).

382 *Community composition and unique species*

383 Indigenous insect community composition varied markedly across the design
384 elements by plant origin (Fig. 6a) and growth forms by plant origin (Fig. 6b) groups.
385 The insect composition of a few group pairs was markedly similar such as between
386 indigenous and native midstorey (5%; Fig. 6a) and between nonnative graminoids and
387 shrubs (5%; Fig. 6b). However, most group pairs showed moderate to high
388 dissimilarity (> 20%) in species composition, for example, between native and
389 nonnative tree canopy (32%; Fig. 6a) and between nonnative forbs and lilioids (40%;
390 Fig. 6b).

391 The number of unique insect species also varied substantially across groups (Fig. 6).
392 Within the design element by plant origin group, up to 33% of all indigenous insect
393 species recorded in the study were unique to the indigenous groups followed by their
394 nonnative and native counterparts, with 12% and 6% unique species, respectively
395 (Fig. 6a). From the design element perspective, 30% of all indigenous insect species
396 recorded in the study were unique to the midstorey groups, followed by their tree

397 canopy and lawn counterparts, with 19% and 2% unique species, respectively (Fig.
398 6a). Similarly, within the growth form by plant origin group, as much as 29% of all
399 indigenous insect species recorded in the midstorey were unique to the three
400 indigenous groups, followed by their nonnative and native counterparts, with 11% and
401 3% unique species, respectively (Fig. 6b). From the growth form perspective, 24% of
402 all indigenous insect species recorded in the midstorey were unique to the shrub
403 groups, followed by the graminoid, forb and lilioid groups, with 14%, 3% and 2%
404 unique species, respectively (Fig. 6b).

405 **Discussion**

406 Our findings demonstrate that taxonomically and functionally diverse indigenous
407 insect communities occur in greenspaces in densely urbanised inner-city
408 municipalities such as the City of Melbourne, with the potential to boost ecosystem
409 multifunctionality (Soliveres et al. 2016) and biotic resistance against the
410 establishment of introduced insects (Kennedy et al. 2002). We have shown that insect
411 communities in Melbourne greenspaces are predominately composed of indigenous
412 rather than introduced species. Our study further highlights that multi-layered,
413 structurally complex indigenous vegetation plays a core role in sustaining high insect
414 biodiversity in urban areas, with the indigenous midstorey and canopy key to
415 maintaining a rich and functionally diverse indigenous insect community within this
416 system. Within the indigenous midstorey, graminoids surprisingly support the highest
417 indigenous insect species richness across all functional groups – particularly for
418 herbivores, predators and detritivores – followed by indigenous shrubs and lilioids.
419 The indigenous midstorey also hosts the largest percentage of unique species. Taken
420 together our findings emphasise the opportunity presented by indigenous understory

421 and midstorey plants, particularly indigenous graminoids in our study area, to
422 promote indigenous insect biodiversity in urban greenspaces.

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

424 Our results indicate that the insect community in our study area was composed
425 predominately of indigenous species. This finding aligns with previous studies of
426 insect richness in cities across other continents (Goertzen and Suhling 2014, Sing et
427 al. 2016, Brown and Hartop 2017). Despite the expectation that urban environments
428 act as hotspots for biological invasions (Cadotte et al. 2017), particularly of nonnative
429 plants and insects (Pysek et al 2010), we found a relatively low number of introduced
430 insect species. Interestingly however, some of these introduced species, for example
431 the European honeybee *Apis mellifera*, were common in and widespread across the
432 studied greenspaces. Consequently, the probability of occurrence of introduced insect
433 species on any particular plant across the study area is similar than that of indigenous
434 species.

435 *Indigenous plant species promote indigenous insect diversity*

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

445 It follows, therefore, that indigenous plants should encourage the occurrence of
446 indigenous insects, especially for herbivores, but also for other insect functional
447 groups. Indeed, our findings distinctly show that pollinators, herbivores, predators,
448 parasitoid and detritivores reach higher levels of species richness in association with
449 indigenous plant species. Experimental studies also support this assumption (Ballard
450 et al. 2013, Burghardt and Tallamy 2013, Salisbury et al. 2015, 2017). For example,
451 using experimental plantings of tree and shrub species, Burghardt and Tallamy (2013)
452 showed that nonnative plants supported less diverse herbivorous insect communities
453 than indigenous plants. Similarly, in an early successional experiment the biomass,
454 abundance and species richness of herbivorous, predatory and parasitoid insects was
455 lower on nonnative forbs than on indigenous forbs (Ballard et al. 2013). Working
456 specifically in an urban setting, Salisbury and colleagues (2015, 2017) experimented
457 with the origin of flowering plants in garden borders, demonstrating that insects
458 across a diverse range of functional groups were less abundant on nonnative than
459 indigenous plant species. These experimental findings have been substantiated by
460 observational approaches, particularly by studies conducted within urban
461 environments. For instance, a study that included the species-specific responses of
462 bees, beetles and heteropteran bugs to vegetation attributes of gardens, parks and golf
463 courses revealed how occurrence probabilities for most insect species decreased as a
464 function of the amount of nonnative plants present in the studied greenspaces
465 (Threlfall et al. 2017).

466 *Midstorey as a key planting design element*

467 Our results have shown that the midstorey is a highly valuable ecological asset in
468 urban landscapes in terms of promoting insect diversity. Midstorey vegetation –
469 which in our study also included plants species associated with the understorey –

470 harboured nearly as many indigenous insect species as canopy vegetation. Indigenous
471 midstorey plant species in particular promoted higher levels of overall insect richness,
472 a pattern that was consistent across all insect functional groups. The midstorey also
473 sustained the highest number of unique indigenous insect species. Taken together, our
474 results indicate that the under- and midstorey are underappreciated strata with great
475 potential for supporting insect biodiversity across urban environments.

476 Our findings go beyond the accepted understanding that the greater structural
477 complexity of experimental, restored or managed sites, the higher the taxonomical
478 and functional diversity of insects and other invertebrates (Murdoch et al. 1972,
479 Brown 1984, Majer et al. 2007, Woodcock et al. 2009, Gibb and Cunningham 2010,
480 Mata et al. 2017, Threlfall et al. 2017, Schuldt et al. 2019). We show that within the
481 midstorey it is the indigenous species – particularly indigenous graminoids and shrubs
482 – that distinctly outperform their native and nonnative counterparts. Our results are
483 also consistent with previous studies that have documented how insect and other
484 arthropod communities are highly stratified across forest strata (Basset et al. 2003,
485 Ulyshen 2011). It is likely that greenspace midstorey vegetation supports different
486 insect taxa due to differences in habitat structure (e.g. foliage complexity or plant
487 surface textures), microclimate (e.g. light, temperature, wind or humidity differences),
488 unique food resources or particular inter-specific interactions, as has been discussed
489 for temperate deciduous forest (Ulyshen 2011). Unpacking the causal mechanisms for
490 our results would require experimental manipulations that fell beyond the scope of
491 this study.

492 *Graminoids as a key midstorey growth form*

493 A striking result to emerge from the data is that graminoids sustain the highest
494 number of indigenous insect species across all growth forms and indigenous

495 graminoids show the highest species richness of indigenous insects across all growth
496 form by plant origin groups. Three indigenous tussock grass species made particularly
497 important contributions to supporting indigenous insect biodiversity in our study area:
498 common tussock-grass *Poa labillardierei*, wallaby grass *Rytidosperma sp.* and
499 kangaroo grass *Themeda triandra*. Indeed, *P. labillardierei* had the highest number of
500 indigenous insect species across the study, with any particular tussock grass patch
501 supporting as much as 5.4 times more indigenous insect species than the most
502 speciose lawn complex and 1.7 times more indigenous insect species than the spotted
503 gum *Corymbia maculata*, which was the tree species sustaining the highest number of
504 indigenous insect species across the study. These results substantiate previous
505 findings stressing the relevance of indigenous tussocks and other structurally complex
506 graminoids in providing a diversity of habitat and food resources for the immature
507 and adult life stage of insects and other invertebrates (Tschardt and Greiler 1995,
508 Morris 2000, Barratt et al. 2005).

509 Remarkably, the capacity of indigenous graminoids to support the highest levels of
510 indigenous insect species across all studied plant groups was true for all insect
511 functional groups. This finding extends previous studies reporting on the positive
512 effects of tussocks and other graminoids on specific insect functional groups –
513 predominantly on herbivores, predators and parasitoids (Dennis et al. 1998,
514 Woodcock et al. 2007, Haaland et al. 2011), but also for pollinators (Saarinen et al.
515 2005, Potts et al. 2009). Our finding that graminoids, which are predominantly
516 pollinated by wind, support more pollinators and other flower-visiting insect species
517 than do lilioids or shrubs, which are predominantly pollinated by insects, is highly
518 noteworthy and provides insight into function and value of non-floral resources for
519 insect pollinators (Roulston and Goodell 2011, Requier and Leonhardt 2020). We

520 hope that our research will serve as a base for future studies on the capacity of
521 graminoids to provide habitat and food resources for insects in urban greenspaces,
522 particularly of non-floral resources for pollinators and other flower-visiting species.
523 Beyond graminoids, our data further emphasises the contributions of other midstorey
524 growth forms. For instance, indigenous shrubs and lilioids sustained the second and
525 third highest number of indigenous insect species across the growth form by plant
526 origin groups. Indeed, our findings indicate that any particular indigenous shrub or
527 lilioid species supports the same number of indigenous insect species as any particular
528 indigenous tree species; and substantially more insect species than any particular
529 native or nonnative tree species. However, we found that the number of unique
530 indigenous insect species varied markedly between these two plant groups, with
531 indigenous shrubs showing as much as 7.4 times more unique insect species than their
532 lilioid counterparts. In general, shrubs outperformed all other midstorey growth
533 forms, with approximately one out of every four indigenous insect species across the
534 study being exclusively associated with shrub species.

535 As underlined by an increasing body of literature (Mata et al. 2017, Threlfall et al.
536 2017, Aguilera et al. 2019, Norton et al. 2019, Majewska and Altizer 2020), including
537 recent reviews (Burkman and Gardiner 2014, Aronson et al. 2017), and meta-analyses
538 (Beninde et al. 2015), the evidence we found points to the critical role that midstorey
539 growth forms – particularly indigenous plant species – play in supporting
540 taxonomically and functionally diverse indigenous insect communities in urban
541 greenspaces. This finding is not only critical for insect conservation in urban
542 environments but of direct, immediate relevance for a wide range of animals such as
543 reptiles, birds and mammals that rely on them as a primary or complementary food
544 source. Our findings therefore underscore the potential of a diverse, primarily

545 indigenous understorey and midstorey strata to increase the positive biodiversity
546 outcomes provided by structurally complex vegetation. As such, they support ideas
547 that move beyond the stagnant approach of designing urban greenspaces
548 predominantly or often exclusively with nonnative short turfgrass lawn and tall trees
549 (Ikin et al. 2015, Smith et al. 2015, Parris et al. 2018, Norton et al. 2019).

550 *Limitations and future research*

551 We are aware of some features of our study context and design that might have
552 influenced our results. Firstly, the small proportion of introduced insects found in this
553 study may be the result of recent introductions that have not yet had enough time to
554 develop into established, large populations – a pattern that is common to both the
555 Northern (Roques et al. 2009) and Southern Hemispheres (Ward and Edney-Browne
556 2015). It is therefore not inconceivable that some introduced species occurring in our
557 study area in small, isolated populations might have gone undetected. Indeed, a recent
558 follow up study in one of the study sites revealed the occurrence of the European
559 firebug *Pyrrhocoris apterus* – a Palaearctic species not previously recorded in
560 Australia (LM unpublished data). As with any observational study, our study design
561 may have introduced unintended bias because our data collection period was
562 purposely designed to coincide with the peak activity season for insects in our study
563 area (i.e., the summer months). We believe however that this effect is negligible as far
564 fewer insect species are more active over the colder periods.

565 This research has revealed many questions in need of further investigation. While we
566 believe that our finding, that indigenous plants sustain substantially more indigenous
567 insect species than their regionally native and nonnative counterparts, are transferable
568 to other urban environments worldwide, the strong relationships we found between
569 indigenous graminoids and indigenous insects might be less transferable. While

570 graminoids, particularly tussock forming species, were a dominant growth form in our
571 study area before colonial settlement other growth forms might have been more
572 representative in other bioregions. A global study across many bioregions is needed to
573 shed light on this question.

574 While we have emphasised the critical role of indigenous plants, we have also shown
575 that indigenous insects are being found in association with a wide array of regionally
576 native and nonnative plants. Thus, our study provides considerable insights in support
577 of the idea that urban environments may facilitate novel resource utilisation
578 (Valentine et al. 2020). We recommend future experimental work on this topic to
579 clarify to what extent these associations reflect host shifting patterns unique to urban
580 environments and to fully understand the opportunities and risks provided by novel
581 urban resources. On a wider level, research is also needed to determine to what extent
582 the increases in insect biodiversity provided by complementing lawns and trees with a
583 diverse palette of midstorey growth forms, particularly indigenous species, can boost
584 ecosystem multifunctionality in urban greenspaces – as recently demonstrated for
585 meso- and macrofauna influencing soil multifunctionality (Tresch et al. 2019). The
586 prospect of being able to understand the mechanistic links between, and to quantify
587 the contributions of, increased biodiversity due to greenspace management actions
588 and greenspace multifunctionality serves as a continuous incentive to future research.

589 *Implications for greenspace design and management*

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

595 In the first instance, our study provides a blueprint and stimulus for built-environment
596 professionals, including architects, engineers, planners and designers, to conceptualise
597 and incorporate into their practice palettes of plant species that foster a larger
598 presence of indigenous plants over regionally native or nonnative species, whilst
599 incorporating a broader mixture of midstorey growth forms. These features are
600 expected to promote taxonomically and functionally diverse indigenous insect
601 communities – even when increasing the amount of greenspace is not feasible due to
602 other pressures (Beninde et al 2015). Integrating these plant palettes into practice may
603 further allow built-environment professionals to plan and design complex plant
604 communities that support and boost indigenous biodiversity in greenspaces and that
605 will likely contribute to bring locally extinct or rare species back into urban
606 environments (Baruch et al. 2020, Mata et al. 2020).

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

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

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

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

640 Ultimately however, contractors and consultants responsible for delivering capital
641 works projects will overlook these if the required plants are not readily available
642 when needed. Therefore, the crucial role played by plant nurseries should not be
643 overlooked – an industry where supply tends to influence demand, with growers often

644 limiting production to reliable, profitable and easy to grow plants. Influencing plant
645 supply will require a dedicated engagement with the nursery industry to broaden
646 production to include a wider range of plant species known to support insect
647 biodiversity as those provided evidence for in this study.
648 Finally, while government officers may apply research findings to design greenspaces
649 capable of supporting diverse insect communities, they must synergistically
650 encourage operational and maintenance programs that can enable these communities
651 to thrive. On ground operational and maintenance teams, that practice greenspace
652 management on a regular basis, have the potential to be involved in identifying
653 opportunities and challenges for supporting insects – and the plants they are more
654 closely associated with – which may expand beyond the obvious choices available to
655 or envisaged by office-based decision-makers. They are, for example, uniquely
656 positioned to readily transfer knowledge on where the optimal soil and microhabitat
657 conditions required for focal plant species within a given greenspace are met – a
658 necessary prerequisite for these to be able to deliver the resources needed by insects
659 to become established and thrive.

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917 field margins. *Journal of Applied Ecology* 46:920–929.

918 **Figure legends**

919 Figure 1 Visual representation of the planting design element by plant origin (a) and
920 midstorey growth form by plant origin (b) groups that were part of the theoretical and
921 empirical dimensions of this study. Dimmed boxes in (b) indicate theoretical
922 combinations of midstorey growth form by plant origin groups that did/may not occur
923 in the study area or that occur but not at surveyable densities within the study's plots.

924 Figure 2 Estimated species richness of introduced and indigenous insect species at the
925 average plant species across the study (a) and at each surveyed plant species (b).

926 Estimated probabilities of occurrence of introduced and indigenous insect species at
927 the average plant species across the study (c) and at each surveyed plant species (d).

928 In all figures the black lines represent mean responses; the grey boxes in (a) and (c)
929 represent the associated statistical uncertainty (95% Credible Intervals). Y-axis in (b)
930 drawn in the log₁₀ scale.

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

935 Figure 4 Estimated species richness of indigenous insect by planting design element
936 by plant origin (a) and midstorey growth form by plant origin (b). Black lines

937 represent mean responses and coloured boxes the associated statistical uncertainty
938 (95% Credible Intervals). For ease of interpretation plant origin has been colour coded
939 as yellow (nonnative), orange (native) or blue (indigenous).

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

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

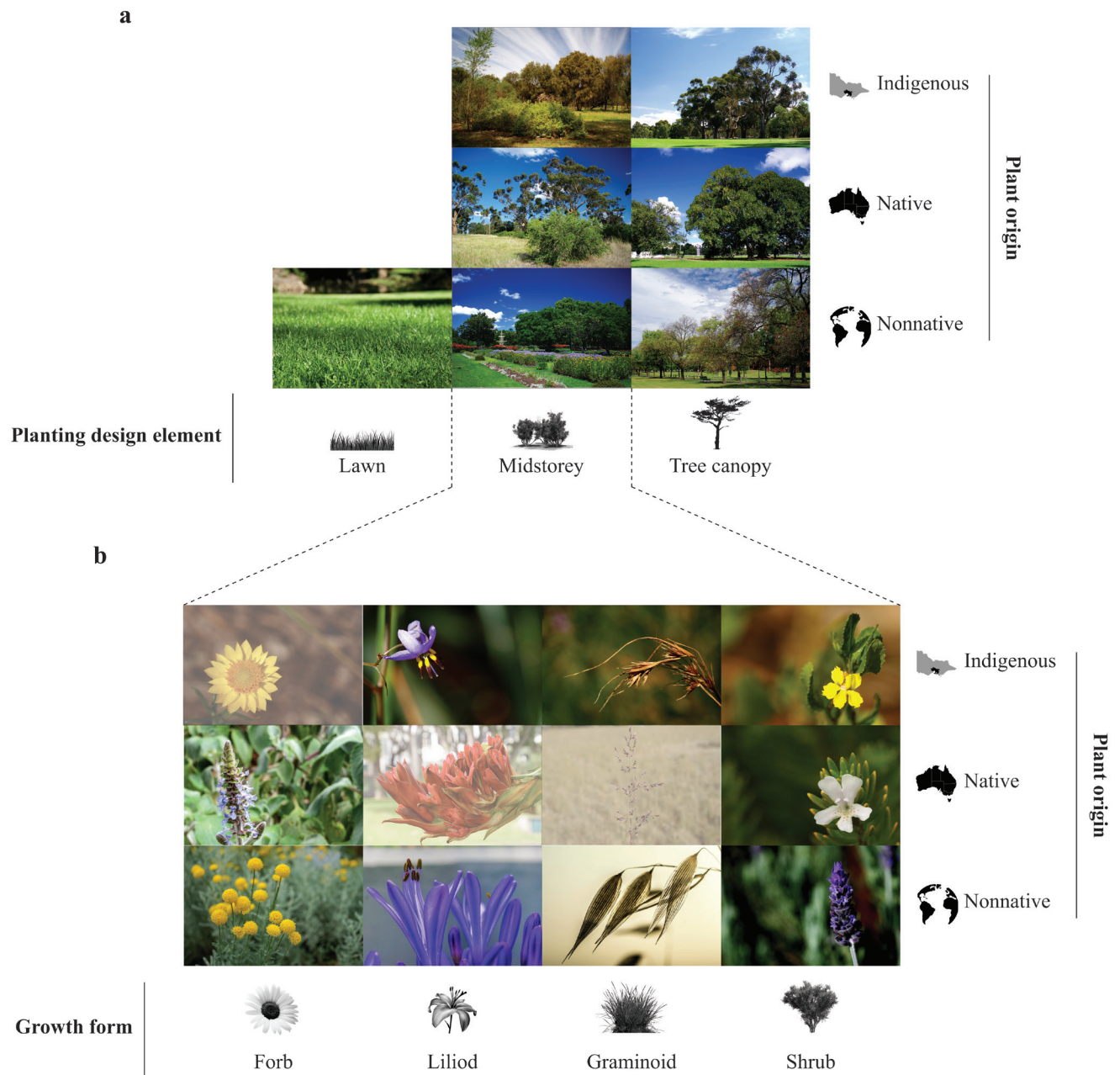


Figure 1. Visual representation of the planting design element by plant origin (a) and midstorey growth form by plant origin (b) groups that were part of the theoretical and empirical dimensions of this study. Dimmed boxes in (b) indicate theoretical combinations of midstorey growth form by plant origin groups that did/may not occur in the study area or that occur but not at surveyable densities within the study's plots.

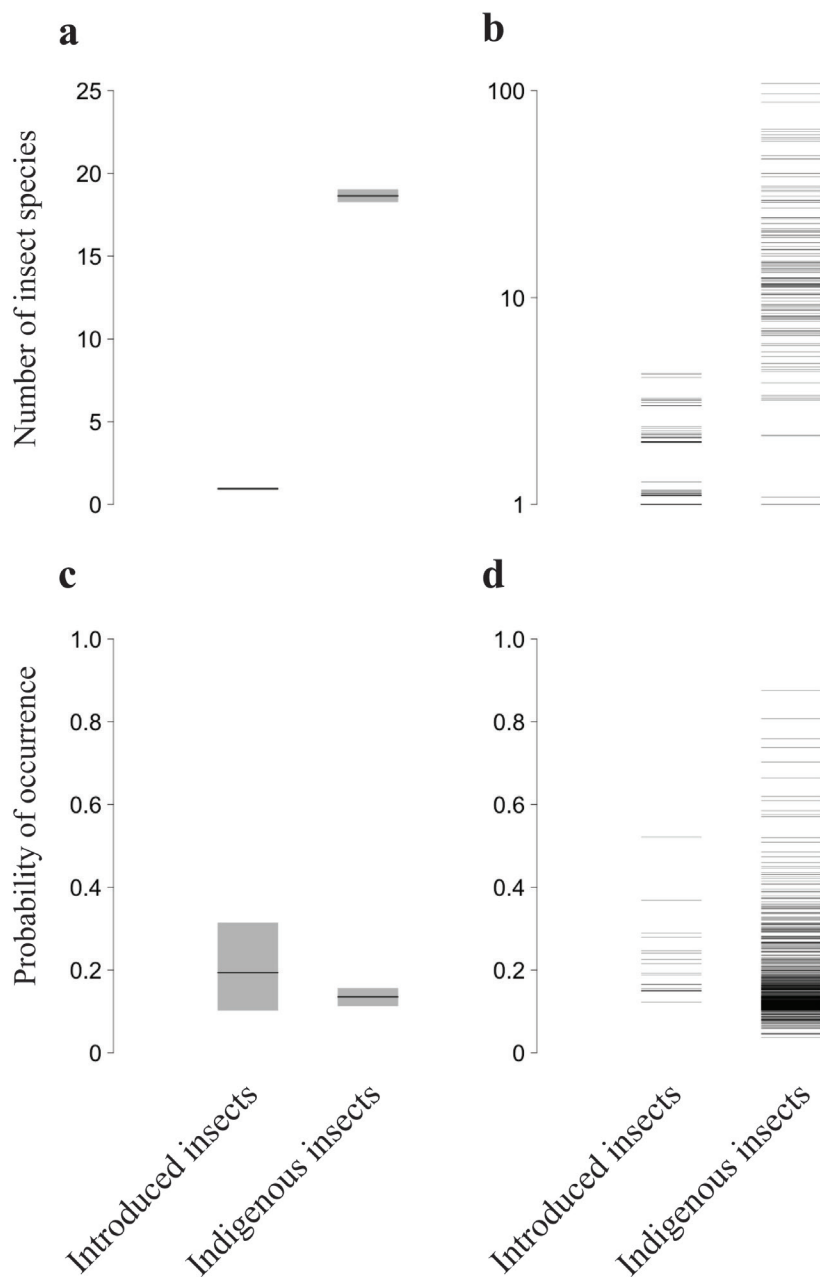


Figure 2. Estimated species richness of introduced and indigenous insect species at the average plant species across the study (a) and at each surveyed plant species (b). Estimated probabilities of occurrence of introduced and indigenous insect species at the average plant species across the study (c) and at each surveyed plant species (d). 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.

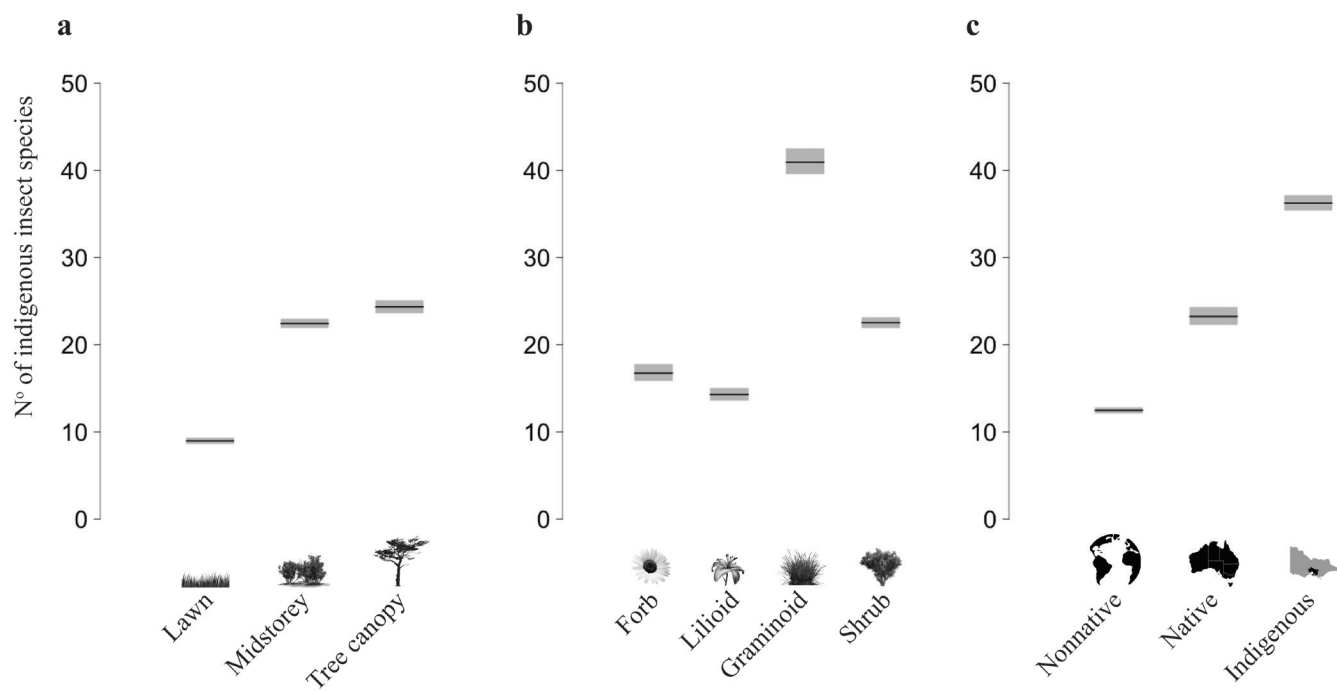


Figure 3. Estimated species richness of indigenous insects by planting design element (a), midstorey growth form (b) and plant origin (c). Black lines represent mean responses and grey boxes the associated statistical uncertainty (95% Credible Intervals).

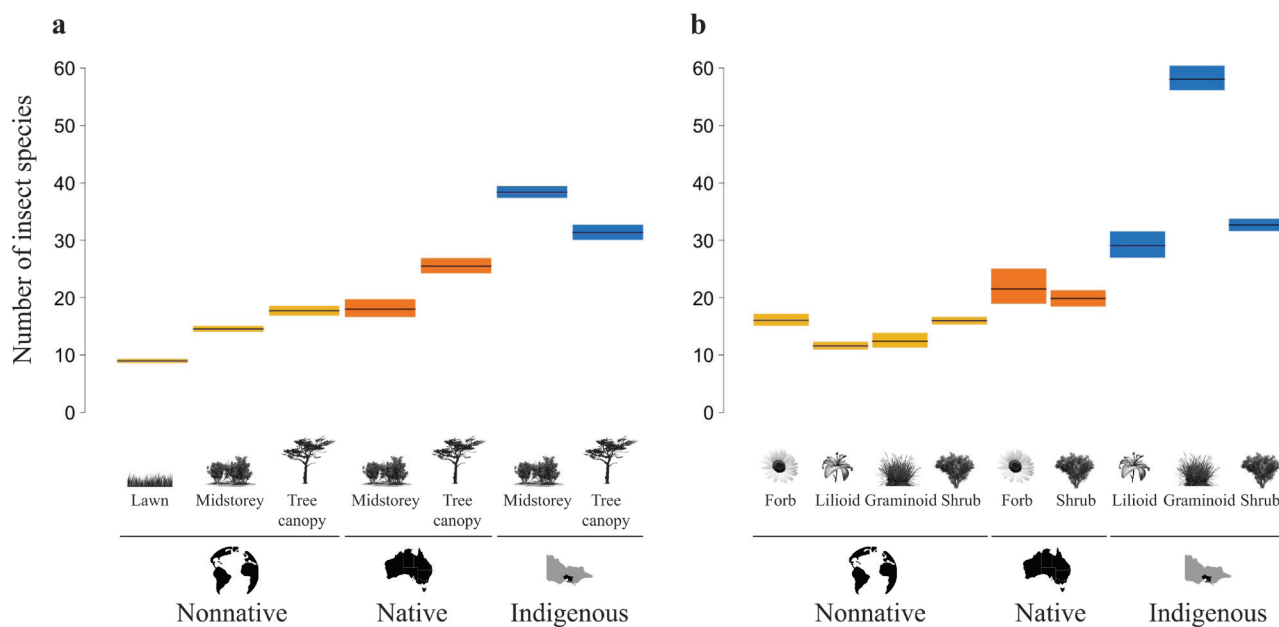


Figure 4. Estimated species richness of indigenous insect by planting design element by plant origin (a) and midstorey growth form by plant origin (b). Black lines represent mean responses and coloured boxes the associated statistical uncertainty (95% Credible Intervals). For ease of interpretation plant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

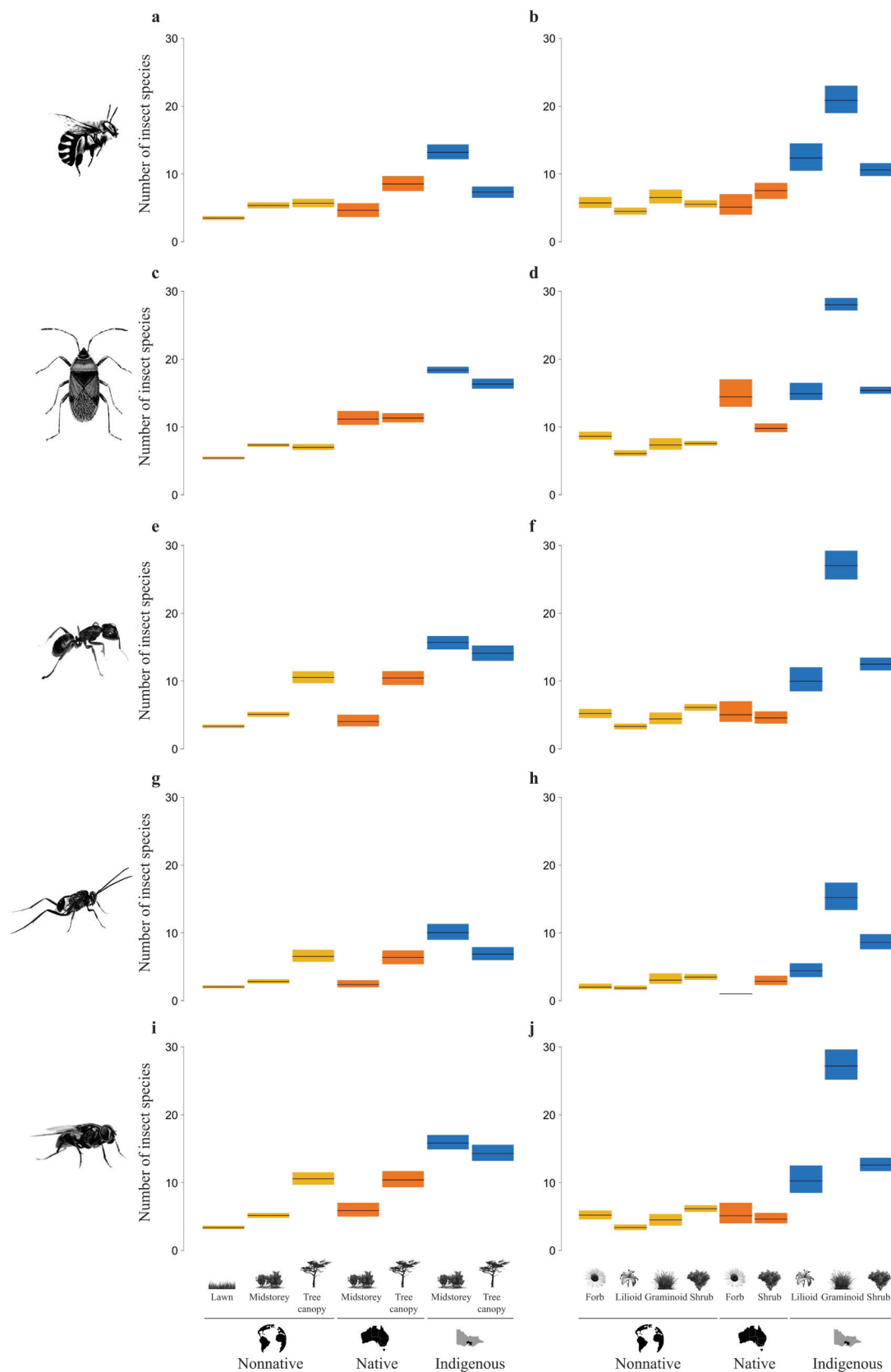


Figure 5. Estimated species richness of indigenous insects by planting design element by plant origin (a,c,e,g,i) and midstorey growth form by plant origin (b,d,f,h,j) for pollinators (a,b), herbivores (c,d), predators (e,f), parasitoids (g,h) and detritivores (i,j). Black lines represent mean responses 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).

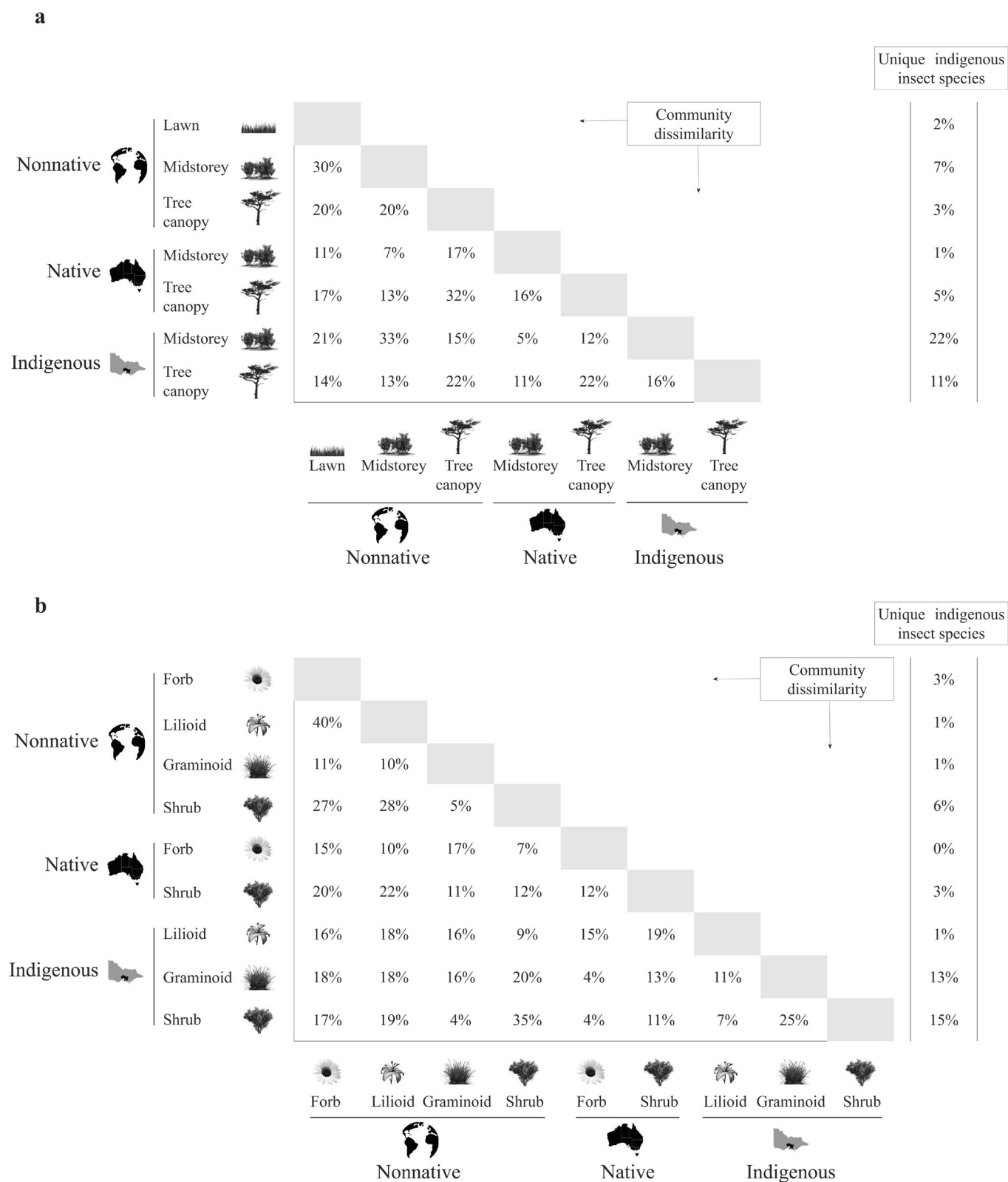


Figure 6. Indigenous insect community dissimilarity matrices for the planting design element by plant origin (a) and midstorey growth form by plant origin (b) groups. Percentages in the white cells were calculated using the Jaccard dissimilarity index, where 0 and 1 represents minimum and maximum dissimilarity,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