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

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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

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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.

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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

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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

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150 environments, and (2) which plant species should be planted to support indigenous

151 insect species. Th 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 km^2 within the Urban Growth Boundary and home to over five

174 million people (Victorian State Revenue Office: https://www.sro.vic.gov.au/greater-

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175   melbourne-map-and-urban-zones). The City of Melbourne covers 37.7 km^2 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 10^3 m^2 – 1.3 x 10^6 m^2; 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 m^2), 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*

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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     $Z_{i,j} \sim$ 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     $y_{i,j,k} \sim$ Bernoulli $(\Phi_{i,j,k} \bullet Z_{i,j})$

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   logit $(\Psi_{i,j}) = occ_i$

247   logit $(\Phi_{i,j,k}) = det_i$

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

249     $occ_i \sim$ Normal $(\mu.occ_{Int...Ind}, \tau.occ)$

250      $det_i \sim$ Normal (μ.det, τ.det)

251   where the metacommunity mean occupancy hyperpriors for introduced and

252   indigenous insect species, $\mu.occ_{Int}$ and $\mu.occ_{Ind}$, respectively, and the metacommunity

253   mean detection hyperprior μ.det, were specified as Uniform (0, 1); and the

254   metacommunity precision occupancy and detection hyperpriors, τ.occ and τ.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

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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 R-

278   hat < 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

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297   scavenger beetle *Cortinicara* 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 > Pocc > 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 (Pocc > 0.8) and most

317   species showing low occupancy levels (Pocc < 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 (Pdet < 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).

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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

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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

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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

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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

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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, Nemec 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).

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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 –

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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

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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 (Tscharntke 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

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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 from 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

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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

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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.

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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*

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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

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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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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

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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).
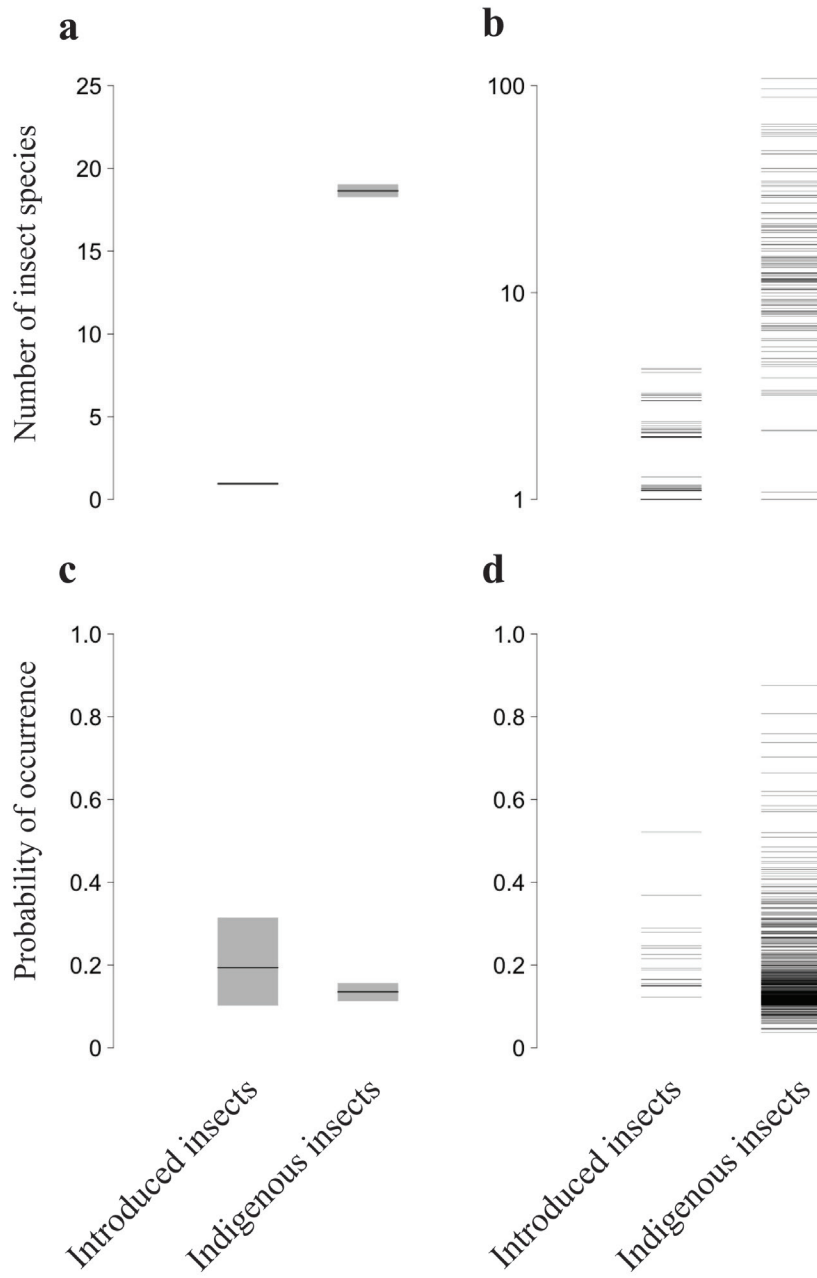
940   Figure 5 Estimated species richness of indigenous insects by planting design element

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 dissimilarly, respectively. Values

950   in the adjacent left columns represent the percentage of unique species observed in

951   each group.
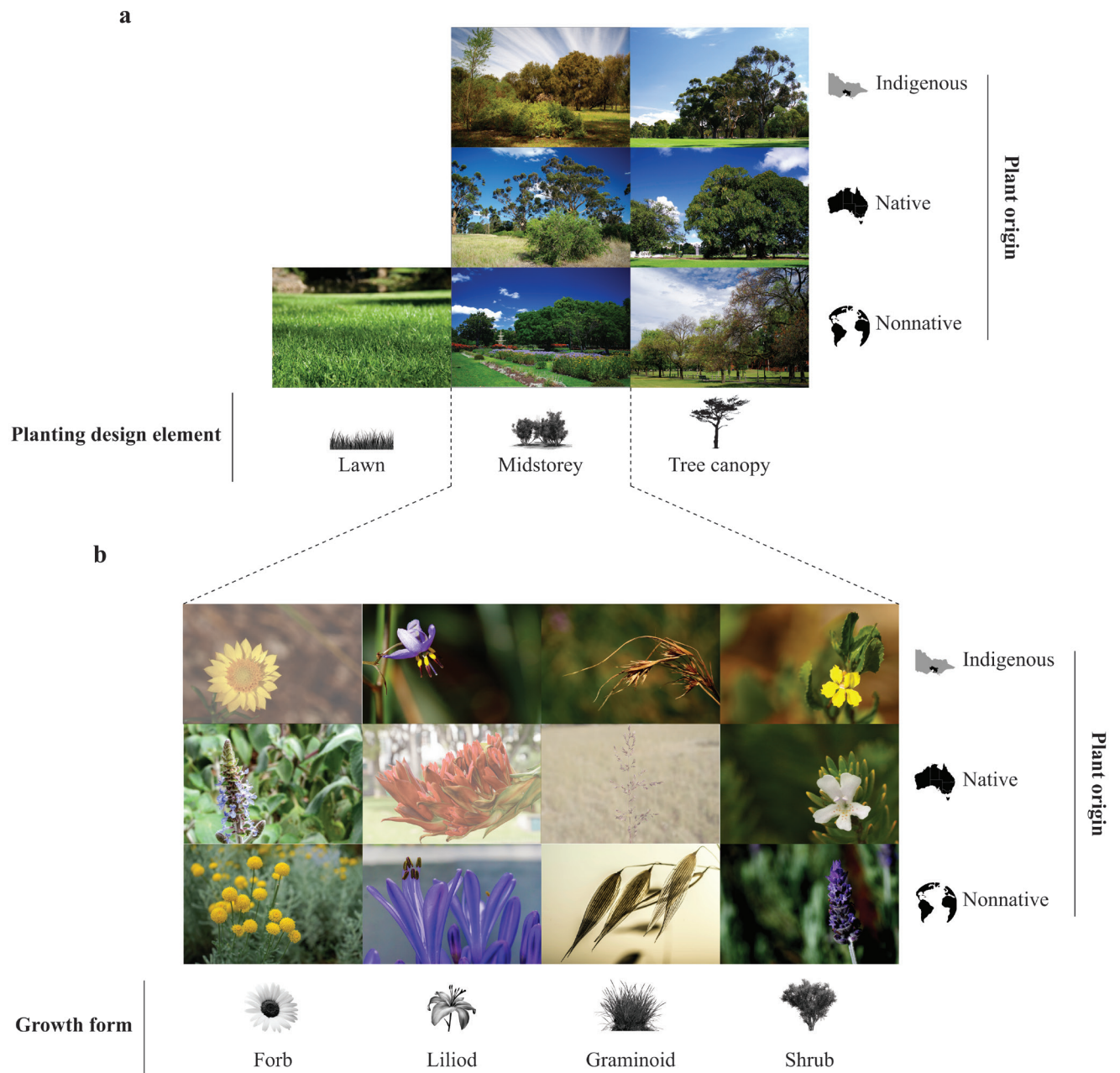
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Figure 1. Visual representation of the planting design element by plant origin (a) and midstorey growth form by plant origin (b) groups that were part of the theoretical and empirical dimensions of this study. Dimmed boxes in (b) indicate theoretical 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.
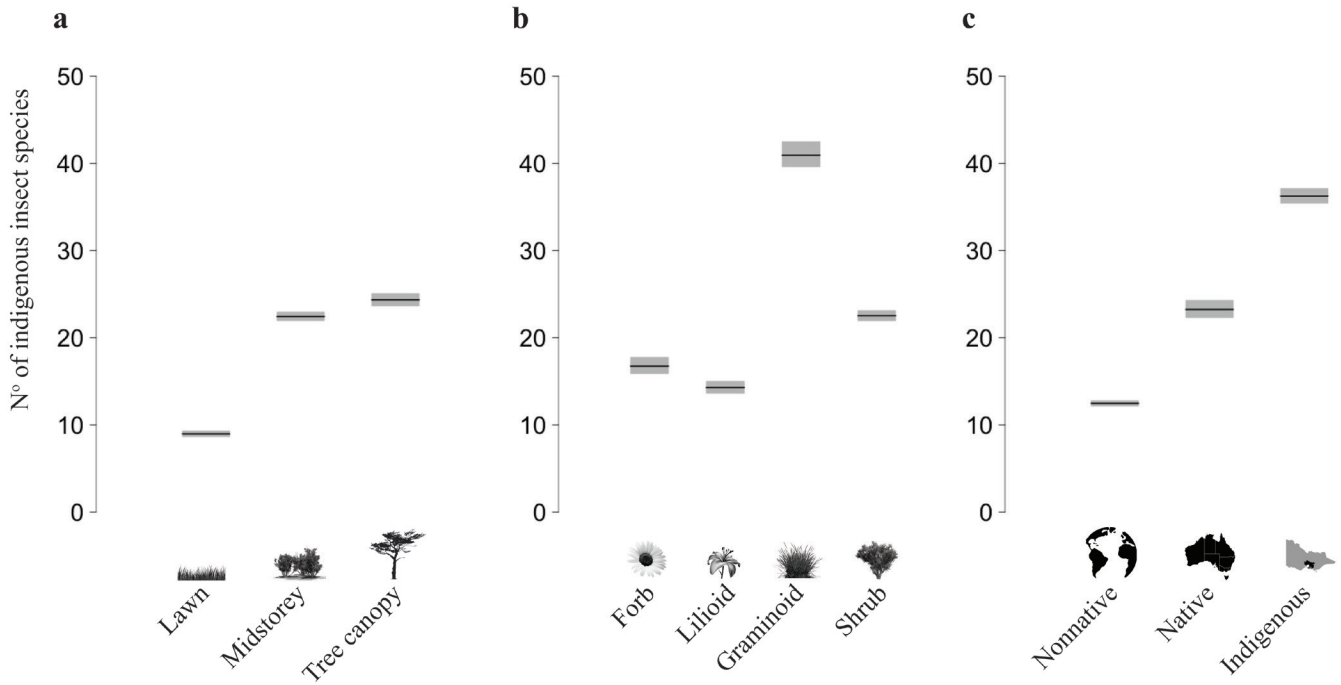
Figure 3. Estimated species richness of indigenous insects by planting design element (a), midstorey growth form (b) and plant origin (c). Black lines represent mean responses and grey boxes the associated statistical uncertainty (95% Credible Intervals).
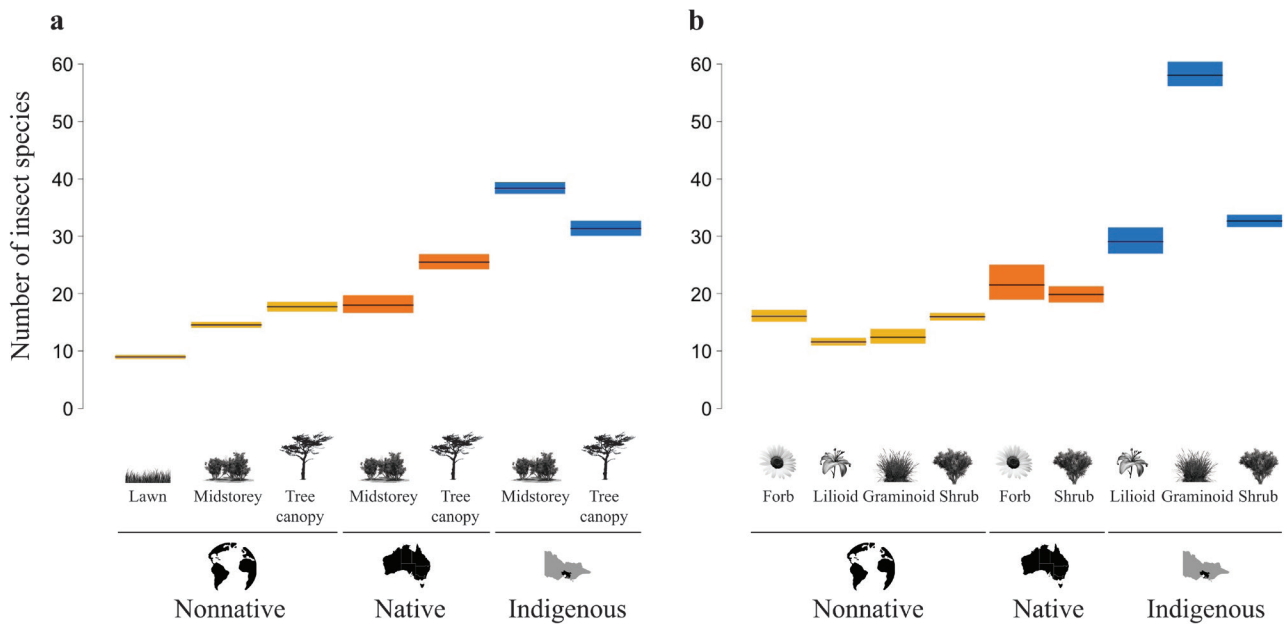
Figure 4. Estimated species richness of indigenous insect by planting design element by plant origin (a) and midstorey growth form by plant origin (b). Black lines represent mean responses and coloured boxes the associated statistical uncertainty (95% Credible Intervals). For ease of interpretation plant origin has been colour coded as yellow (nonnative), orange (native) or blue (indigenous).
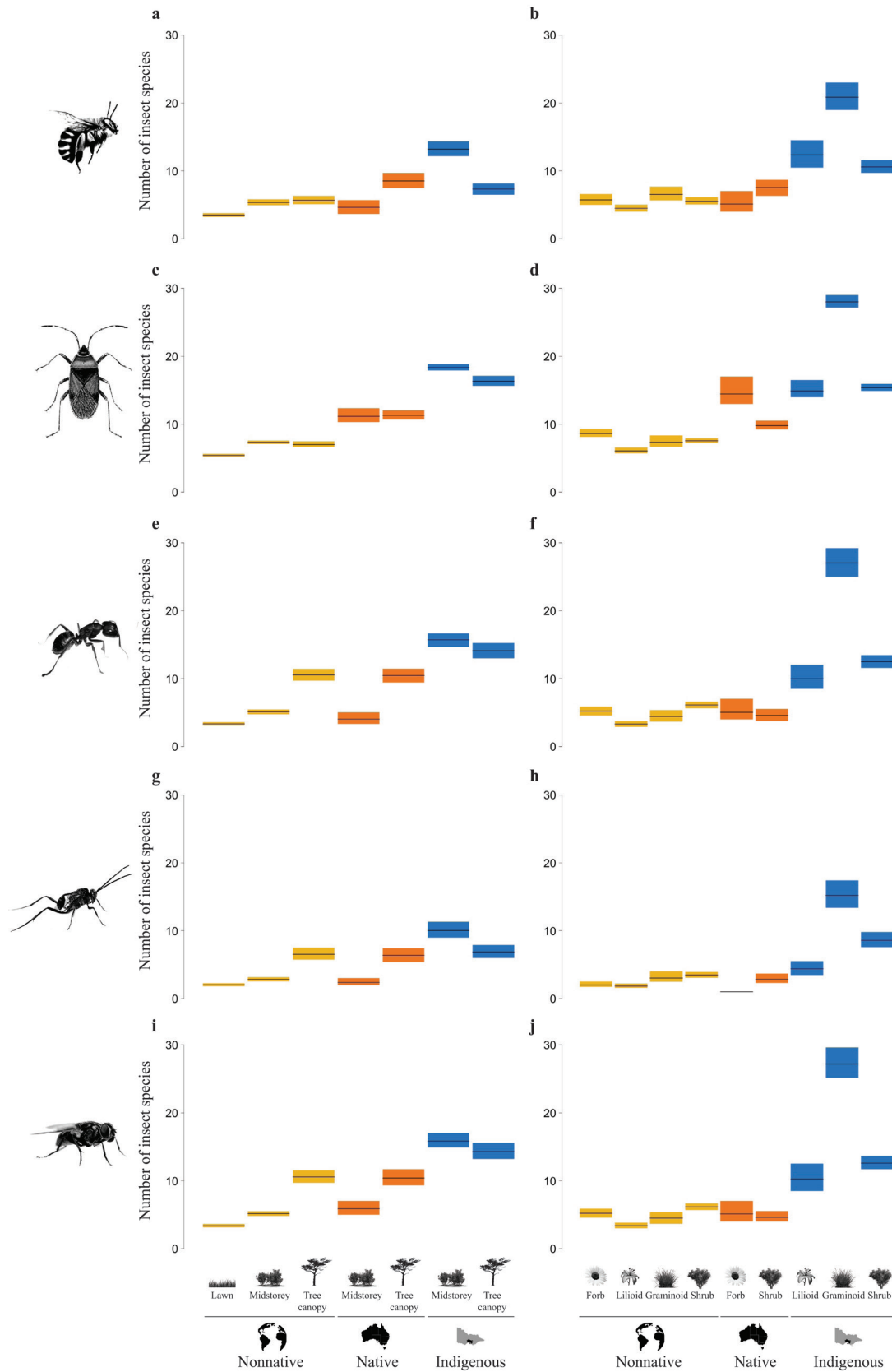
Figure 5. Estimated species richness of indigenous insects by planting design element by plant origin (a,c,e,g,i) and midstorey growth form by plant origin (b,d,f,h,j) for pollinators (a,b), herbivores (c,d), predators (e,f), parasitoids (g,h) and detritivores (i,j). Black lines represent mean responses 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).

a

	Unique indigenous insect species
Nonnative — Lawn	2%
Nonnative — Midstorey	7%
Nonnative — Tree canopy	3%
Native — Midstorey	1%
Native — Tree canopy	5%
Indigenous — Midstorey	22%
Indigenous — Tree canopy	11%

Community dissimilarity (Jaccard %):

	Lawn	Midstorey (Nonnative)	Tree canopy (Nonnative)	Midstorey (Native)	Tree canopy (Native)	Midstorey (Indigenous)
Midstorey (Nonnative)	30%					
Tree canopy (Nonnative)	20%	20%				
Midstorey (Native)	11%	7%	17%			
Tree canopy (Native)	17%	13%	32%	16%		
Midstorey (Indigenous)	21%	33%	15%	5%	12%	
Tree canopy (Indigenous)	14%	13%	22%	11%	22%	16%

b

	Unique indigenous insect species
Nonnative — Forb	3%
Nonnative — Lilioid	1%
Nonnative — Graminoid	1%
Nonnative — Shrub	6%
Native — Forb	0%
Native — Shrub	3%
Indigenous — Lilioid	1%
Indigenous — Graminoid	13%
Indigenous — Shrub	15%

Community dissimilarity (Jaccard %):

	Forb	Lilioid (Nonnative)	Graminoid (Nonnative)	Shrub (Nonnative)	Forb (Native)	Shrub (Native)	Lilioid (Indigenous)	Graminoid (Indigenous)
Lilioid (Nonnative)	40%							
Graminoid (Nonnative)	11%	10%						
Shrub (Nonnative)	27%	28%	5%					
Forb (Native)	15%	10%	17%	7%				
Shrub (Native)	20%	22%	11%	12%	12%			
Lilioid (Indigenous)	16%	18%	16%	9%	15%	19%		
Graminoid (Indigenous)	18%	18%	16%	20%	4%	13%	11%	
Shrub (Indigenous)	17%	19%	4%	35%	4%	11%	7%	25%

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 dissimilarly, respectively. Values in the adjacent left columns represent the percentage of unique species observed in each group.