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Measuring competitive impact: joint-species modelling of invaded plant communities

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1   **Abstract**

2   1.   Non-native species can dominate plant communities by competitively displacing native

3   species, or because environmental change creates conditions favourable to non-native species

4   but unfavourable to native species. We need to disentangle these mechanisms so that

5   management can target competitively dominant species and reduce their impacts.

6   2.   Joint-species distribution models (JSDMs) can potentially quantify competitive impacts

7   by simultaneously modelling how species respond to environmental variation and to changes in

8   community composition. We describe a JSDM to model variation in plant cover and show how

9   this can be applied to compositional data to detect dominant competitors that cause other

10   species to decline in abundance.

11   *3.*   We applied the model to an experiment in an invaded grassy-woodland community in

12   Australia where we manipulated biomass removal (through slashing and fencing to prevent

13   grazing by kangaroos) along a fertility gradient. Non-native species dominated plant cover at

14   high fertility sites in the absence of biomass removal. Results from the JSDM identified three of

15   the 72 non-native plant species (*Bromus diandrus*, *Acetosella vulgaris* and especially *Avena*

16   *fatua*) as having a strong competitive impact on the community, driving changes in composition

17   and reducing the cover of both native and non-native species, particularly in the absence of

18   grazing. The dominant non-native grasses *Bromus diandrus* and *Avena fatua* were among the

19   tallest species in the community and had the greatest impact on shorter-statured species, most

20   likely through competition for light under conditions of high fertility and low grazing.

21   *4.*   Synthesis. We demonstrate a method to measure competitive impact using a JSDM,

22   which allowed us to identify the species driving compositional change through competitive

23   displacement, and where on the landscape competitive impacts were greatest. This information

24   is central to managing plant invasions: by targeting dominant non-native species with large

25   competitive impacts, management can reduce impacts where they are greatest. We provide

26   details of the modelling procedure and reproducible code to encourage further application.

Introduction

28   Dominance by non-native plant species is frequently associated with declines in the

29   abundance and diversity of native species (Vilà et al., 2011). These changes can occur if non-

30   native species are superior competitors, such that increasing abundance of non-natives directly

31   drives declines in native species through competitive displacement (Levine et al., 2003;

32   MacDougall, Gilbert, & Levine, 2009). Alternatively, increasing dominance by non-native species

33   could be a consequence of changing environmental conditions that favour non-natives over

34   natives due to species in each group having different environmental tolerances

35   (HilleRisLambers, Yelenik, Colman, & Levine, 2010; Shea & Chesson, 2002). As plant invasions

36   are frequently accompanied by environmental perturbations (Pysek et al., 2010; Vellend et al.,

37   2017), it can be difficult to determine when non-native dominance is driven by competitive

38   impact (Godsoe, Franklin, & Blanchet, 2017; Soberón, 2010). In fact, many non-native species

39   appear to have little impact on the communities they invade (Lai, Mayfield, Gay-des-combes,

40   Spiegelberger, & Dwyer, 2015; Williamson & Fitter, 1996). In order to manage non-native

41   species appropriately, we need ways to identify which non-native species, if any, are having

42   strong competitive impacts, and where those impacts are greatest (Gallien, Münkemüller,

43   Albert, Boulangeat, & Thuiller, 2010; Ricciardi, Hoopes, Marchetti, & Lockwood, 2013).

44

45   Joint species distribution models (JSDM) are extensions of standard species distribution

46   models that have the potential to measure both competitive impact and species responses to

47   environmental conditions using community composition data from sites along known

48   environmental gradients (Kissling et al., 2012; Nieto-Lugilde, Maguire, Blois, Williams, &

49   Fitzpatrick, 2018). JSDMs use data on species composition across multiple sites to jointly model

50   individual species responses to environmental variation, interpreting residual among-species

51   covariation as potentially resulting from interactions such as competition (Latimer, Banerjee,

52   Sang, Mosher, & Silander, 2009; Ovaskainen, Hottola, & Shtonen, 2010; Pollock et al., 2014;

53   Warton et al., 2015). To date, JSDMs have mostly been used to model presence-absence data,

54   where large negative residual covariance between two species could be interpreted as the

55   competitive displacement of one species from sites that both could occupy. However, presence-

56   absence data can only detect competitive impacts that result in complete exclusion from a site,

57   yet dominance without exclusion is an important component of species impact (Levine et al.,

58   2003; Seabloom et al., 2013). Here we use a method proposed by Clark et al. (2017) to model

59   cover data in a JSDM that overcomes the problem of zero-inflation that is typically inherent in

60   these data (see: *Joint-species tobit modelling in Methods*; Fig. 1). With this approach, we can

61   detect declines in species abundance associated with the presence of competitors, which should

62   provide greater resolution in quantifying competitive impacts.

63

64   Even with these improvements to JSDMs, separating environmental responses from

65   competitive impacts is challenging (Adler et al., 2018), suggesting we should apply JSDMs to

66   systems where the primary environmental drivers of species abundances are well understood

67   (Giannini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013; Wisz et al., 2013; Zurell,

68   Pollock, & Thuiller, 2018). In grasslands around the world, non-native plant species often

69   increase in dominance at higher fertility sites and when grazing is excluded (Seabloom et al.,

70   2015). This shift in dominance has been attributed to the competitive displacement of native

71   species by non-native species that are competitively superior under conditions of high resource

72   availability and low grazing. This competitive superiority arises because, relative to native

73   species, many non-native grassland species have traits associated with rapid growth and high

74   biomass (Ordonez, Wright, & Olff, 2010; Van Kleunen, Weber, & Fischer, 2010), traits that are

75   likely beneficial when there is little above ground disturbance and competition for light is

76   intense (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009). These trait differences between

77   native and non-native species should be less important under herbivory where biomass

78   removal may reduce any competitive advantage of fast growth (Lind et al., 2013).

79

80   We aim to test these ideas using data from a 7-year experiment that tracked changes in plant

81   cover over time following herbivore exclusion (Driscoll, 2017). Sites were arrayed along a

82   fertility gradient and we predicted that non-native species would dominate under high fertility

83   and would increase in dominance following herbivore exclusion. We used JSDMs to model how

84   species cover varied with fertility, grazing and rainfall, and identified species with strong

85   negative residual covariances, suggestive of strong competitive impacts on the community. We

86   predicted that: 1) competitive impacts, and hence the magnitude of negative residual

87   covariances, would increase in the absence of grazing where competition for light would be

88   most intense; and 2) if competition for light caused competitive displacement, the strength of

89   negative covariances between species (reflecting the strength of competitive interactions)

90   should correlate with trait differences associated with growth and light capture.

91

92   **Methods**

93   _Study system_

94   This study was carried out in a box-gum grassy woodland reserve in south-eastern Australia

95   (Pinnacle Reserve, ACT. 35° 15' S, 149° 02' E; 620 - 708 m a.s.l.). The vegetation of the reserve

96   comprised a scattered overstorey of trees, predominantly _Eucalyptus blakelyi_ and _E. melliodora_,

97   with a dense understorey of grasses and forbs. The vegetation has been extensively modified

98   over the last 150 years, primarily by tree clearance and livestock grazing. Livestock grazing

99   ceased in the reserve in 1993 and the dominant herbivore is now the native eastern grey

100   kangaroo (_Macropus giganteus_), which was at moderately high density over the course of the

101   study ($1.8 – 2.2$ ha^{-1}; Driscoll 2017). The understorey vegetation was dominated by a mix of

102   native and non-native species, with many non-native species introduced for pasture

103   improvement (e.g. _Dactylis glomerata_ and _Trifolium subterraneum_) or as pasture contaminants

104   (e.g. _Avena fatua_ and _Bromus diandrus_). Mean annual precipitation in the area was ~660 mm

105   year^{-1} and daily maximum temperatures range from 9 °C to 33 °C during the spring growing

106   period and as low as 4 °C in the preceding winter months (Australian Government Bureau of

107   Meteorology, 2017). Soils are typically of relatively low fertility, shallow and rocky, although

108   some deeper soils occur on slopes and in depressions.

109

110   *Data collection*

111   We used data from an experiment that tested whether different management interventions

112   can increase native grassland species richness (Driscoll, 2017). In 2010, ten sites were

113   established in open, unshaded areas along a natural fertility gradient (see below). Sites ranged

114   from relatively uninvaded communities to communities dominated by non-native species. Each

115   site contained 10 permanently marked 5 m x 5 m plots separated by at least 1 m. One of 10

116   different experimental treatments was applied to each plot, but we use only a subset of the

117   treatments in this study (see Appendix 1, Fig S1). From 2011, five plots at each site were fenced

118   in a single enclosure to exclude mammalian herbivores (predominantly kangaroos but also

119   rabbits). One plot inside and one plot outside the fence had its above-ground biomass removed

120   each year by slashing, and one plot inside and one plot outside the fence was left unmanipulated

121   (unslashed). We analysed these four treatments at each site (grazed, unslashed; grazed, slashed;

122   fenced, unslashed; and fenced, slashed), allowing us to test whether the competitive impact of

123   non-native species was stronger in the absence of biomass removal by grazing and/or slashing,

124   and to assess whether uniform biomass removal by slashing had similar effects to herbivore

125   grazing.

126

127   Vegetation surveys were conducted every year from 2010 to 2016, except for 2014. In late

128   spring (October) of each year, the percent cover of all vascular plant species was visually

129   estimated in four 1 m x 1 m quadrats placed in the corners of each plot (only three quadrats per

130   plot were surveyed in 2013 due to time constraints). We use plant cover as a proxy for

131   abundance. Our dataset thus comprised six years of vegetation cover data from 160 quadrats

132   across 40 plots. In total, we had 920 quadrat level vegetation measurements, comprising 10,780

133   cover estimates for 142 species (70 native and 72 non-natives; see Appendix 1, Fig. S2 for more

134   detail). In 2015 and 2016, we measured the traits of abundant species, defined as those

135   comprising the first 80% of total recorded cover at each site. At each site, we measured traits

136   associated with growth rate and light capture on 5-10 adult individuals in each of the unslashed

137   plots following standard protocols (Pérez-Harguindeguy et al., 2013). These traits included

138   canopy height (m), maximum height (m), canopy width (m), leaf length and width (cm) and

139   specific leaf area (mm^2 mg^{-1}; SLA). To avoid the influence of outliers, we used 90th quantile

140   values from all measured plants to estimate species maximum potential for each trait.

141

142   Total extractable nitrogen at sites along the fertility gradient ranged from 615 ppm to 2420

143   ppm (Driscoll & Strong, 2017). Total soil carbon, nitrogen and phosphorus levels, as well as

144   extractable nitrogen and phosphorus, all covaried strongly across the 10 sites (Appendix 1), and

145   we used total extractable nitrogen as a proxy for overall soil fertility. Grasslands in this region

146   also respond strongly to variation in annual rainfall (Prober, Thiele, & Speijers, 2013; Fig. S3).

147   We obtained data on total rainfall for the four months prior to each survey (August –

148   November) from the Australian Bureau of Meteorology (BOM, Appendix 1) as a proxy for water

149   availability. Total rainfall during these four months ranged from 185 – 414 mm over the seven

150   years of the study. Both total nitrogen and spring rainfall were centred and scaled prior to

151   model fitting.

152

153   *Analyses*

154   1) *Relative dominance of non-native species.*

155   We examined how the dominance of non-native species changed over time, in relation to soil

156   fertility and rainfall, and in response to the experimental treatments (fencing and slashing). Our

157   response variable was the proportion of non-native species cover in each plot in each year. This

158   was calculated by taking the average cover of each species across quadrats in each plot in each

159   year, summing these averages to get the total average cover of all species in each plot in each

160   year, and calculating the proportion of total cover comprising non-native species. We logit-

161   transformed this proportion and modelled it as a linear function of soil fertility, fitting a

162   separate intercept and slope for each experimental treatment (grazed/fenced and

163   slashed/unslashed) and for each year. We included rainfall by specifying a single coefficient for

164   the effect of inter-annual rainfall variation on the proportion of non-native cover. The model

165   structure is described in detail in Appendix 2.

166

167   2) *Joint-species tobit modelling*

168   In order to test if dominance by non-native species was a consequence of environmental

169   responses or competitive displacement, we specified a JSDM that modelled the cover of each

170   species in response to variation in soil fertility, rainfall and experimental treatment (JSDM1).

171   This model included a single covariance matrix to capture unexplained residual variation, with

172   negative residual covariances potentially indicating competitive impacts. We fitted a second

173   model (JSDM2) to test whether competitive impacts varied with grazing and slashing

174   treatments. JSDM2 had the same structure as JSDM1, but we fitted separate residual covariance

175   matrices for each experimental treatment, which allowed us to test if the magnitude of negative

176   residual covariances were greater in the absence of biomass removal where light competition

177   should be most intense. We analysed data for the years 2013-2016, which were the years during

178   which the experimental treatments showed clear effects (see: Figs 2 & S4b), and restricted our

179   analyses to species present in >20% of plots measured between 2013 and 2016 (N = 30, 14

180   native and 16 non-native species; Fig S2.) These species were present at >50% of sites in each

181   year and were thus sufficiently widespread that absences were more likely due to unsuitable

182   environmental conditions or competitive displacement rather than dispersal limitation. We

183   analysed cover data at the quadrat level because we expected species interactions to be most

184   evident at this scale. Zero cover was recorded when a species was absent from a quadrat. Even

185   after restricting our analysis to the 30 most common species, most of our data comprised zero

186   values (~69%; 4,396 cover estimates, 10,004 absences).

187   We used tobit regression to accommodate zero inflation by treating absences as censored

188   data (Clark et al., 2017; Tobin, 1958). Censored data occur when it is not possible to observe a

189   value beyond some limit. In this case, we assume there is an unobserved latent variable that

190   measures the 'suitability' of each quadrat for each species, where suitability encompasses all

191   biotic and abiotic factors that might influence species cover. When a species is present in a

192   quadrat we equate the latent suitability with cover, assuming that higher cover indicates higher

193   suitability (Fig. 1). Quadrats where species are absent can be thought of as sufficiently low

194   suitability that a species cannot persist but quadrats with zero cover can still vary in their

195   underlying suitability. We model observations of zero cover as censored data arising from this

196   latent suitability distribution, which can take values less than zero:

197

198    $$y = \begin{cases} y^*, & \text{if } y^* > 0 \\ 0, & \text{if } y^* \leq 0 \end{cases}$$

199

200   where y is the observed cover and y^* is the corresponding latent suitability value. To complete

201   the model, we need to specify a distribution for the underlying latent variable. We specified the

202   underlying distribution as multivariate normal with 30 dimensions, one for each species.

203

204   We regressed latent suitability (y^*) against the environmental variables soil fertility and

205   rainfall, with residual variation captured in a single covariance matrix (JSDM1). We specified

206   different regression coefficients for each experimental treatment, modelled hierarchically, and

207   included normally distributed random effects to account for repeated measurements of plots

208   nested within sites. The structure of JSDM1 was:

209

210   JSDM 1:

211    $$\boldsymbol{y}^*_{[ijkl]} \sim MultiNormal\left(\boldsymbol{\mu}_{[ijkl]}, \boldsymbol{\Sigma}\right)$$

212
$$\boldsymbol{\mu}_{[ijkl]} = \begin{pmatrix} \mu_{1_{[ijkl]}} \\ \mu_{2_{[ijkl]}} \\ \vdots \\ \mu_{N_{[ijkl]}} \end{pmatrix}$$

213
$$\mu_{s_{[ijkl]}} = \beta_{intercept_{S[j]}} + \beta_{slope_{S[j]}} \cdot fertility_{[jk]} + \beta_{rain_{S[j]}} \cdot rainfall_{[i]} + \beta_{plot_{[jk]}}$$

214
$$\beta_{plot_{[jk]}} \sim Normal\left(\beta_{site_{[k]}}, \sigma^2_{plot}\right)$$

215
$$\beta_{site_{[k]}} \sim Normal\left(0, \sigma^2_{site}\right)$$

216   where $\boldsymbol{y}^*_{[ijkl]}$ is an N-length vector of latent suitability values in year i (1-3), under treatment j

217   (1-4), at site k (1-10) in quadrat l (1-4). s indexes species ($s = 1 \dots N$) with intercept terms

218   measuring average site suitability for each species in each treatment, and slope and rain terms

219   measuring how site suitability varied with soil fertility and rainfall for each species in each

220   treatment. $\boldsymbol{\Sigma}$ is an N x N covariance matrix with the diagonal containing the residual variances in

221   suitability for each species, $\boldsymbol{\sigma^2}$, and the off-diagonals containing the residual covariances

222   between each species pair, conditional on the value of $\boldsymbol{\mu}_{[ijkl]}$. This matrix has $N * (N - 1) / 2 =$

223   435 unique elements, with the covariance between two species defined as: $\boldsymbol{\Sigma}_{12} = \sigma_1 \sigma_2 \rho_{12} = \boldsymbol{\Sigma}_{21}$.

224   The covariances describe how residual variation in the cover of one species is related to

225   residual variation in the cover of a second species. If, having accounted for environmental

226   effects, the cover of one species declined in quadrats when the cover of a second species

227   increased, the residuals of the two species would covary negatively. We interpreted negative

228   covariances as due to competition on the grounds that we had modelled species responses to

229   the major environmental gradients in these grasslands (fertility and water availability)

230   (Leishman & Thomson, 2005; Morgan et al., 2016; Prober, Thiele, & Speijers, 2016). Large

231   negative covariances imply potentially strong competitive impacts, while species with low

232   cover, or where cover is well explained by environment variables, will have smaller covariances

233   because there is less residual variation that could be associated with co-occurring species.

234   Moreover, if a dominant species caused several species to decline in cover, resulting in strong

235   negative covariances, this is likely to induce a pattern of positive covariances among the

236   impacted species because they would all tend to have lower cover at sites where the dominant

237   species was present and higher cover at sites where it was absent.

238

239   3) *Change in species covariances by treatment*

240   Specifying a single covariance matrix in JSDM1 meant the covariances were estimated from

241   the data in all treatments. In JSDM2, we specified a separate covariance matrix for each of the

242   four treatments:

243   JSDM2:

244
$$\boldsymbol{y}^*_{[ijkl]} \sim MultiNormal\big(\boldsymbol{\mu}_{[ijkl]}, \boldsymbol{\Sigma}_{[j]}\big)$$

245
$$\mu_{s_{[ijkl]}} = \beta_{intercept_{s[j]}} + \beta_{slope_{s[j]}} \cdot fertility_{[jk]} + \beta_{rain_{s[j]}} \cdot rainfall_{[i]} + \beta_{quadrat_{[jkl]}}$$

246   where both the coefficients for species *s* and the covariances $\boldsymbol{\Sigma}$ varied with treatment *j* (1-4).

247   Comparing the covariance matrices for different treatments in JSDM2 allowed us to evaluate

248   whether competitive interactions were stronger in plots without slashing or grazing.

249

250   4) *Predicting competitive impact from functional traits*

251   We predicted that competitive impacts, measured as the magnitude of negative covariance

252   between species, should be linked to differences in traits associated with growth and light

253   capture. To test this, we regressed the posterior mean of the negative covariance parameters

254   estimated in JSDM2 against the absolute difference in measured trait values for each species

255   pair. Trait values were normalised prior to analysis so that traits measured using different units

256   could be compared directly. For the regression models, we specified separate intercept and

257   slope coefficients for the covariance-trait relationships in each experimental treatment, with the

258   slopes and intercepts modelled as drawn from normal distributions for each trait.

259

260   All models were fitted to the data in a Bayesian framework using adaptive Hamiltonian

261   Monte Carlo with the probabilistic programming language Stan (Carpenter et al., 2017) and the

262   rstan interface (Guo et al., 2016) in R, version 3.4 (R Core Team, 2016). Details of model fitting

263   and prior specification are in Appendix 2 and online at https://github.com/aornugent/impact2.

264   We took a conservative approach to identifying interactions in the data by specifying that we *a*

265   *priori* expected covariances to be weak (see prior specification in Appendix 2), meaning that

266   strong residual covariances required strong support from the data.

267

268   **Results**

269   1)   *Relative dominance of non-native species*

270   Overall, the proportion of total cover that comprised non-native species increased with

271   increasing soil fertility (Figs 2, S4a). Prior to and immediately after fencing (2010 & 2011), the

272   relationship between fertility and proportion of non-native cover was similar in the fenced and

273   grazed, and in the slashed and unslashed treatments. However, from 2012 onwards the

274   proportion of non-native cover increased substantially at higher fertility sites in the fenced,

275   unslashed plots (i.e., in the absence of biomass removal). There was no clear change over time in

276   the proportion of non-native cover along the fertility gradient in plots that were grazed, slashed

277   or both (Figs 2, S4b). The proportion of non-native cover was higher in years with higher spring

278   rainfall (Fig. S3a)

279

280   2)   *Joint species tobit modelling*

281   Species responded differently to changes in soil fertility, with latent site suitability increasing

282   strongly with higher soil fertility (i.e. total extractable nitrogen) for two native and five non-

283   native species (95% credible intervals above zero in at least one treatment; Fig. 3). The

284   remaining species, both native and non-native, declined in cover with increasing fertility.

285   Relationships between cover and fertility did not vary much between experimental treatments

286   with three exceptions: relative to other species, the cover of the non-native species *Avena fatua,*

287 *Bromus diandrus* and *Acetosella vulgaris* increased more strongly with fertility in the fenced,

288 unslashed treatment. At high fertility, several fenced, unslashed plots were completely

289 dominated by one or more these species. For most species, cover was positively related to

290 rainfall across years (Fig. S3b).

291

292   Figure 4 shows species' residual covariances from JSDM1 as a pairwise covariance matrix

293 (Fig. 4a) along with the median covariance for each species across all pairwise interactions (Fig.

294 4b). We report the median covariance because covariance values could be highly skewed. One

295 species, *Avena fatua*, stood out as having strong negative covariances, with high cover of *A. fatua*

296 often associated with reduced cover of other species. Median covariance for the native grass

297 *Themeda triandra* was the second most negative but of much smaller magnitude than *A. fatua*.

298 Moreover, *T. triandra* covaried negatively with *A. fatua* (Fig. 4a), such that high cover of *A. fatua*

299 was associated with low cover *T. triandra* and vice versa. Small-statured species, such as those

300 in the genera *Aira*, *Vulpia* and *Hypochaeris*, tended to covary positively.

301

302 3)   *Change in species covariances by treatment*

303   JSDM2 revealed that species' residual covariances varied by grazing and slashing treatment

304 (Fig. 5), suggesting that competitive interactions were altered by biomass removal. Covariances

305 were weakest in the grazed, slashed treatment with the median close to zero for most species

306 (mean median covariance with 95% confidence intervals = -0.4, CI -2.2 to 1.3), implying weak

307 interactions. Covariances were larger but still relatively weak in the fenced, slashed treatment

308 (mean = 0.2, CI -1.5 to 2). Median covariances were most negative in the grazed, unslashed

309 treatment (mean = -1.3, CI -3 to 0.5) and especially the fenced, unslashed treatment (mean = -

310 3.2, CI = -4.9 to -1.5), suggesting stronger competitive interactions in the absence of slashing,

311 and especially in the absence of both grazing and slashing. Relative to the natural situation in

312 these grasslands (the grazed, unslashed treatment), the three species whose cover increased

313 most strongly with fertility in the fenced, unslashed plots (*Avena fatua, Bromus diandrus* and

314   *Acetosella vulgaris*) showed a marked shift to more negative covariances in the same treatment,

315   especially *A. fatua* (Fig. 5). This implies these species had a greater competitive impact on other

316   species in the absence of biomass removal.

317

318   4)   *Predicting impact from functional traits*

319   In the fenced, unslashed treatment, stronger negative covariances between species were

320   associated with greater differences in plant height (Fig. 6). This relationship was evident,

321   though weaker, in the grazed, unslashed treatment but largely absent in both slashed

322   treatments. Covariances were less negative between species that had greater differences in SLA

323   in all treatments, but the strength of this relationship was much weaker than for height. None of

324   the remaining trait differences (canopy width and leaf dimensions) showed strong relationships

325   with covariances.

326

327   **Discussion**

328   Measuring the strength of species interactions when these are confounded with

329   environmental variation remains a major obstacle to studying the impact of non-native species

330   in plant communities (HilleRisLambers et al., 2010; Levine et al., 2003; MacDougall &

331   Turkington, 2005). We have shown how a joint-species-distribution model can be adapted to

332   model plant cover and, when applied to our case study, could identify the non-native species

333   having large competitive impacts on the community, along with the conditions under which

334   those impacts were greatest. Globally, non-native species frequently dominate grasslands under

335   conditions of high fertility in the absence of grazing (Seabloom et al., 2013, 2015). Our findings

336   show this can result from displacement of native species by one or more competitively

337   dominant non-native species. In our study, greater cover of three non-native species (*Bromus*

338   *diandrus*, *Acetosella vulgaris* and especially the annual grass *Avena fatua*) was associated with

339   strong declines in the cover of native species after accounting for differences in environmental

340   responses. This outcome is consistent with previous studies that have measured the impact of

341   non-native species in Australian temperate grasslands (Driscoll & Strong, 2017; Prober, Thiele,

342   Lunt, & Koen, 2005) and in grasslands globally (Chang & Smith, 2014; Flores-Moreno et al.,

343   2016; Harpole et al., 2016).

344

345   Our results support the predictions outlined in the Introduction. First, competitive impacts,

346   as revealed by the strength of negative covariances, were much stronger in the absence of

347   biomass removal (Fig. 5). Second, under low or no biomass removal, the strength of negative

348   covariances were linked to differences in plant height: in unslashed plots, taller species had

349   greater impact on shorter species, implying a strong competitive advantage associated with

350   plant height under these conditions (Fig. 6). This outcome most likely results from competition

351   for light, which should favour taller, higher biomass species (Borer et al., 2014; Hautier et al.,

352   2009). While negative covariances were linked most strongly to height differences, negative

353   covariances were smaller among species with greater differences in specific leaf area (Fig. 6).

354   This implies that, while competitive dominance was due primarily to a trait advantage in height,

355   this was partly offset by trait dissimilarity in SLA, potentially indicative of reduced competitive

356   impact through niche differentiation (Gross, Börger, Duncan, & Hulme, 2013).

357

358   Results from the JSDMs provide additional insights into interactions in these grasslands. For

359   example, negative covariances, and hence competitive interactions, were weaker in the slashing

360   treatments (Fig. 5). Annual biomass removal by slashing may prevent species from attaining

361   cover sufficient to have a strong competitive impact (Mortensen et al., 2018). Grazing may also

362   prevent competitive dominance, although interactions were stronger under grazing alone than

363   when plots were slashed (Fig. 5), suggesting grazing removes less biomass than slashing, or

364   selectively removes certain species allowing others to attain cover sufficient to have measurable

365   impact (Evju, Austrheim, Halvorsen, & Mysterud, 2009). The most dominant species, *Avena*

366   *fatua* had the greatest competitive impact, but also covaried negatively with two other species

367   that had relatively high impact overall: the native grass *Themeda triandra* and non-native forb

368   *Acetosella vulgaris* (Fig. 4). *Avena fatua* and *A. vulgaris* both increased in cover at higher fertility

369   in the absence of biomass removal, suggesting these species competed for site occupancy under

370   those conditions. The ability of *A. vulgaris* to form dense rhizomatous mats may have excluded

371   *A. fatua* from some sites (Fan & Harris, 1996). *Themeda triandra*, in contrast, had higher cover at

372   lower fertility. *Themeda triandra* is known to dominate more intact native grasslands (Prober &

373   Lunt, 2009), suggesting that *A. fatua* may be displacing an otherwise competitively dominant

374   native grass at higher fertility sites.

375

376   Other non-native species were abundant in these grasslands but had little or no competitive

377   impact. Short-statured annual grasses in the genera *Aira* and *Vulpia*, for example, were

378   widespread (Fig. S2) and had high average cover where they occurred (15% and 24% for *Aira*

379   and *Vulpia*, respectively, compared with 30% for *Avena fatua*). Both *Aira* and *Vulpia* strongly

380   negatively covaried with *A. fatua* and *B. diandrus*, and both covaried positively with other,

381   typically short-statured, species that were also impacted by the competitive dominants. Hence,

382   in addition to identifying the drivers of change in this community, we can identify non-native

383   species that achieve moderate to large cover without impacting the community, most likely

384   because they are ruderal-like species that exploit more marginal habitats.

385

386   We have demonstrated how a JSDM can be applied to field data to measure impact and

387   identify the species driving compositional change in a plant community. We emphasise that

388   interpreting negative residual covariation as due to species interactions relies on having

389   measured and correctly modelled the major environmental variables, fertility and rainfall in our

390   case, that control species abundances (Hui, Taskinen, Pledger, Foster, & Warton, 2015). Our

391   approach of crossing a natural fertility gradient with manipulation of biomass removal no doubt

392   helped to disentangle competitive from environmental effects in this system, as it meant

393   differences between the biomass treatments at each site were not confounded with

394   environmental variation. Nevertheless, the model appeared successful in identifying species

395   having impact in the unmanipulated treatment alone (grazed, unslashed; Fig. 5), suggesting

396   JSDMs can detect interactions in systems without experimental manipulation where the

397   environmental drivers are well understood.

398

399   **Conclusion**

400   Quantifying the importance of competitive interactions is difficult when species abundance is

401   confounded with environmental variation (Adler et al., 2018). We approached the problem by

402   using a JSDM to model changes in the cover of Australian temperate grassland species in

403   response to gradients of fertility and rainfall, biomass removal treatments, and variation in

404   community composition. This identified the dominant non-native species driving compositional

405   change through competitive displacement in this community, highlighting the utility of JSDMs in

406   studies of plant invasion where it is often unclear which non-native species, if any, are directly

407   impacting invaded communities (HilleRisLambers et al., 2010; Lai et al., 2015; MacDougall &

408   Turkington, 2005). By experimentally altering grazing we were able to show that the

409   competitive impact of the dominant non-native species increased in the absence of grazing and

410   that species responses were mediated by trait-differences in height, consistent with the

411   outcome we would expect due to competition for light (Borer et al., 2014). Hence, the modelling

412   approach provided insights into the mechanisms underlying impact, paving the way for general

413   tests of the drivers of community structure in other communities (Mortensen et al., 2018). We

414   have provided the data and code in an R package (https://github.com/aornugent/impact2) to

415   reproduce our analyses and encourage further application of the approach.

416

417   **Acknowledgements**

424

425   **Author contributions**

426   AO, EW and RD conceived the study. DD designed and established the experiment. AO and DD

427   collected data. AO developed the JSDM models. AO, EW and RD analysed data and model output.

428   AO wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

429

430   **Data accessibility**

431   Data and code used in this manuscript are freely available at

432   https://github.com/aornugent/impact2

433

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600

601

Figures:

Figure 1. A simulated example of tobit regression. Black circles show observed cover for a species measured at points along an environmental gradient. Cover declines as environmental suitability decreases, eventually reaching a point where the environment is unsuitable for the species and cover is zero. Beyond that point, environmental suitability continues to decline but cover remains at zero. These zero values are censored in that zero cover provides partial information about the latent suitability (open circles): it tells us a site is unsuitable but, beyond that, does not measure how unsuitable. Tobit regression aims to estimate latent suitability (the open circles, which are uncensored) by fitting a regression line (red) to the cover data, treating the zero values as censored.

Figure 2. Proportional cover of non-native species (logit-transformed) as a function of soil fertility at 10 sites measured over 7 years (2010-2016 with no measurement in 2014). There were four treatments at each site, which are plotted separately. Slashed plots are shown on the top line and unslashed plots on the lower line, with filled circles and solid lines for fenced plots, and open circles and dashed lines for grazed plots. Fertility is scaled and standardized as described in Appendix 1.

Figure 3. Latent suitability with respect to soil fertility for 30 species estimated using a joint-species-distribution model and tobit regression (see text). Separate relationships were fitted for each species in each of four treatments, shown as different panels. Native species are drawn with dashed lines (n = 14) and non-native species with solid lines (n = 16). Lines are coloured from dark blue to light yellow corresponding to a shift from negative to positive slopes, respectively.

627   Figure 4. a) The full residual covariance matrix for JSDM1 and b) the median residual

628   covariance from all pairwise interactions for each species, with negative covariances indicative

629   of competitive displacement (see text). The full matrix shows mean covariances from the

630   posterior distributions shaded by magnitude and direction, ranging from large negative

631   covariances (deep red) to large positive covariances (blue). A black dot indicates the 95%

632   credible intervals for a covariance did not include zero. Non-native species are marked with

633   asterisks.

634

635   Figure 5. The median residual covariance from all pairwise interactions for each species from

636   JSDM2, where a separate covariance matrix was fitted for each treatment (shown as separate

637   panels). The median covariance summarises the magnitude of competitive displacement

638   between a single species and the rest of the community. Names of non-native species are shown

639   in black and native species in grey. Non-native species are marked with asterisks.

640

641   Figure 6. Mean (circles) and 95% credible intervals for the slope of the relationship between

642   covariance and trait differences among species. Negative values indicate that competitive

643   displacement is associated with greater difference in trait values between species. The

644   relationships are plotted separately for the four treatments, with filled circles for fenced plots,

645   open circles for grazed plots, and slashed and unslashed plots in different panels. Trait

646   differences were normalized before analysis to allow direct comparison of slope estimates for

647   traits measured in different units.
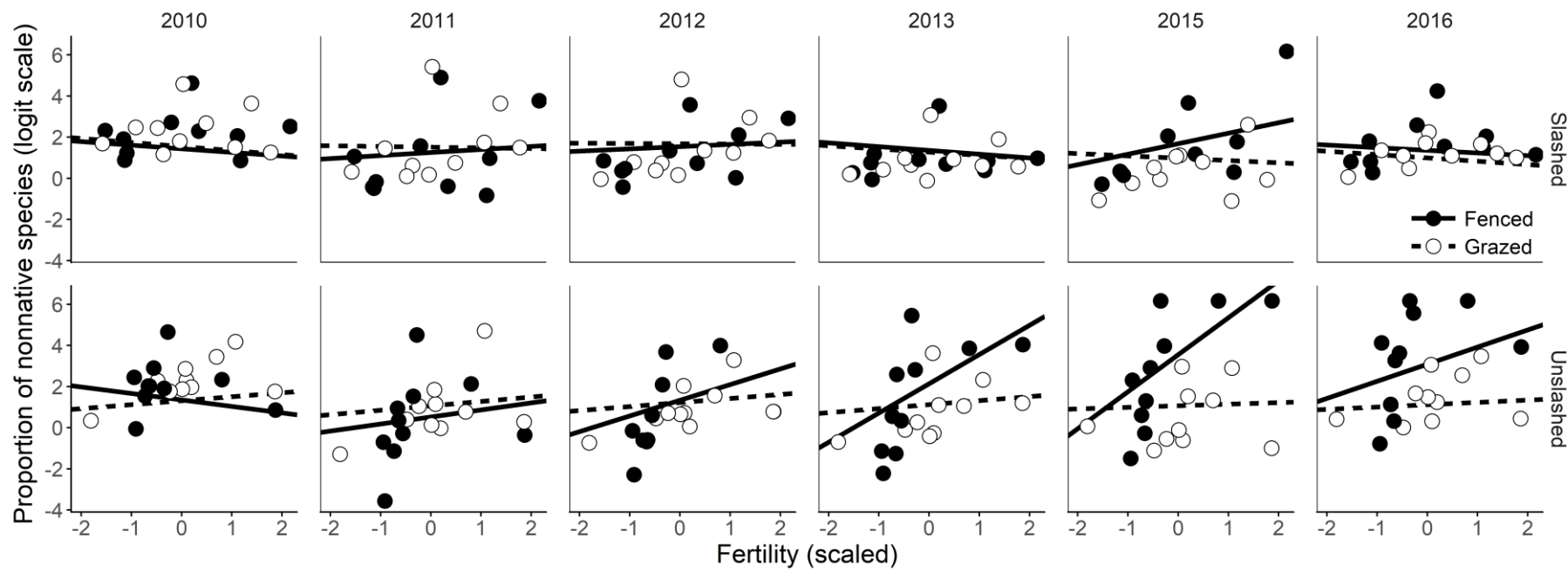
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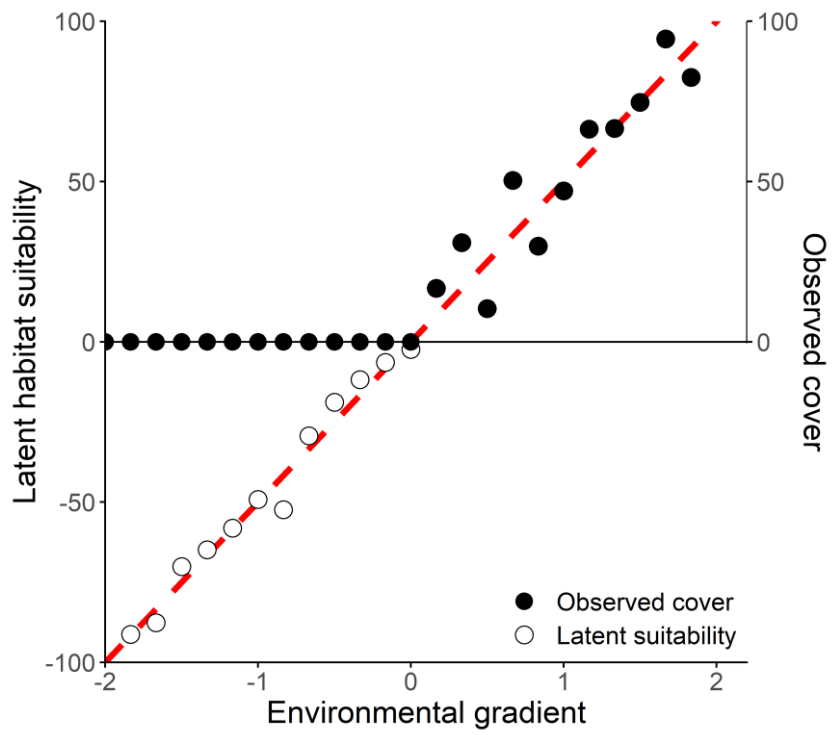
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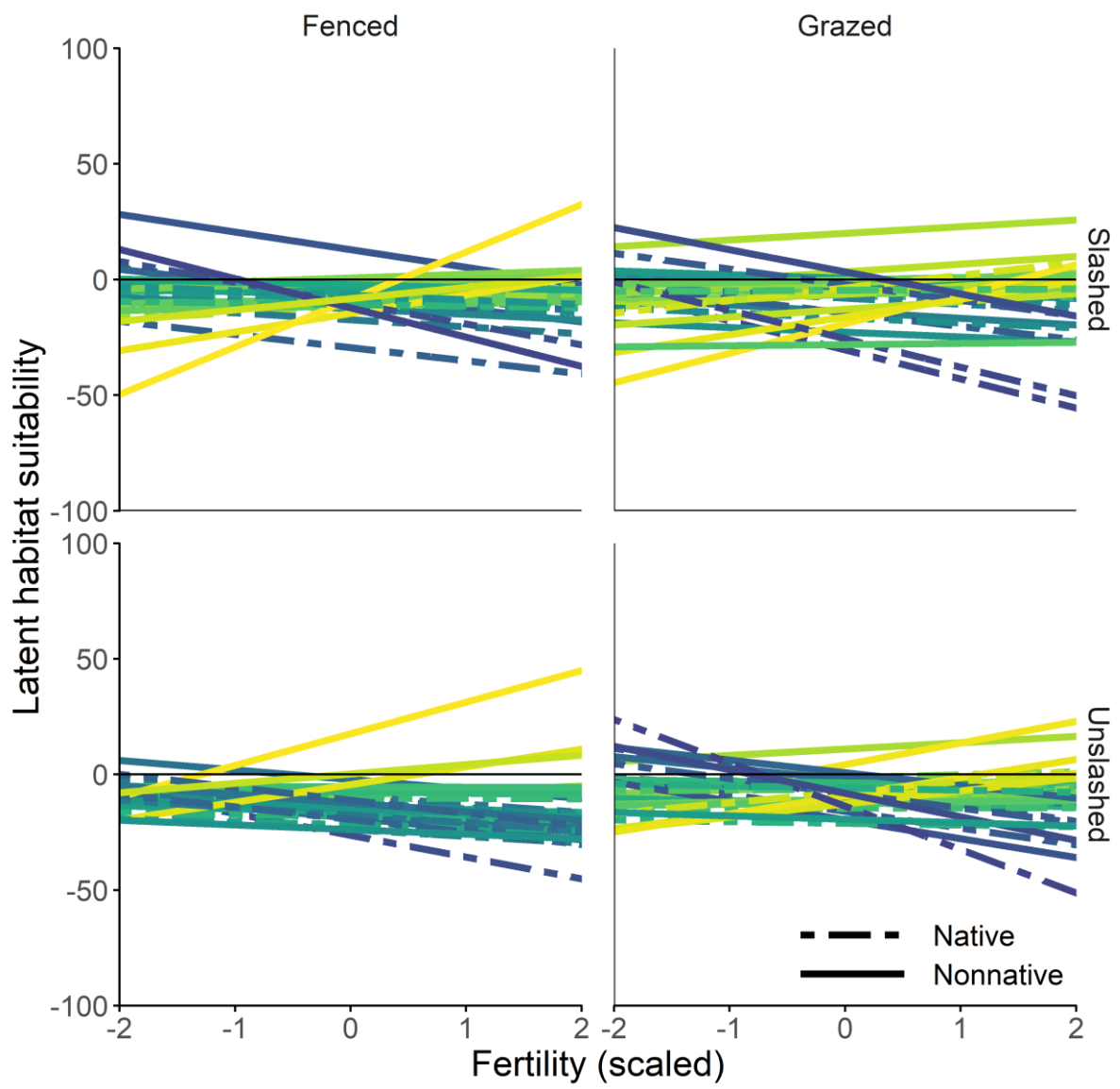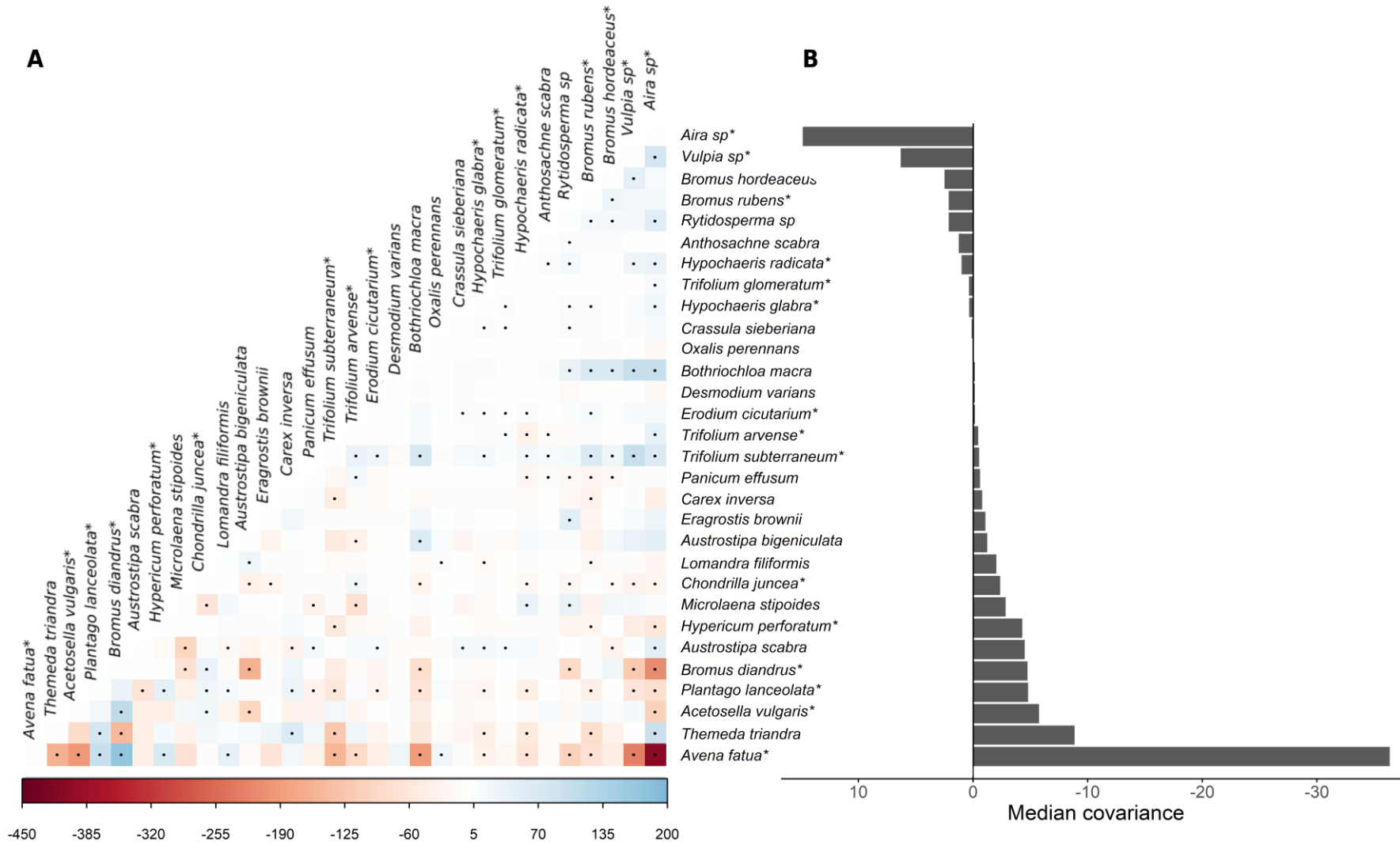
650   **Figure 1.**

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.