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1 **Species roles in plant-pollinator communities are conserved across native**

2 **and alien ranges**

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4 Carine Emer[1,2], Jane Memmott[1], Ian P. Vaughan[3], Daniel Montoya[1,4,5] & Jason M.

5 Tylianakis[6,7]

6

7 [1]Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol UK BS81TQ

8 [2] Departamento de Ecologia, Universidade Estadual Paulista (UNESP), 13506-900 Rio Claro,

9 São Paulo, Brazil

10 [3]Cardiff School of Biosciences, Cardiff University, Museum Avenue, Cardiff UK CF103AX

11 [4]*Center for Biodiversity Theory and Modeling, Station d'Ecologie Theorique et Experimentale,*

12 *Centre National de la Reserche Cientifique, 09200 Moulis, France*

13 [5]*INRA, UMR 1347 Agroecologie, Dijon cedex 21065, France*

14 [6]Centre for Integrative Ecology, School of Biological Sciences, University of Canterbury,

15 Private bag 4800, Christchurch 8140, New Zealand

16 [7]Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst

17 Road, Ascot, Berkshire UK SL5 7PY

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19 **Running title:** Native-alien species roles in pollination networks

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21   **ABSTRACT**

22   *Aim.* Alien species alter interaction networks by disrupting existing interactions, for example

23   between plants and pollinators, and by engaging in new interactions. Predicting the effects

24   of an incoming invader can be difficult, although recent work suggests species roles in

25   interaction networks may be conserved across locations. We test whether species roles in

26   plant-pollinator networks differ between their native and alien ranges, and whether the

27   former can be used to predict the latter.

28   *Location*: worldwide.

29   *Methods*. We used 64 plant-pollinator networks to search for species occurring in at

30   least one network in its native range and one network in its alien range. We found 17

31   species meeting these criteria, distributed in 48 plant-pollinator networks. We characterized

32   each species' role by estimating species-level network indices: normalised degree, closeness

33   centrality, betweenness centrality, and two measures of contribution to modularity (c and z

34   scores). Linear Mixed Models and Linear Regression Models were used to test for

35   differences in species role between native and alien ranges and to predict those roles from

36   the native to the alien range, respectively.

37   *Results.* Species roles varied considerably across species. Nevertheless, although species

38   lost their native mutualists and gained novel interactions in the alien community, their role

39   did not differ significantly between ranges. Consequently, closeness centrality and

40   normalised degree in the alien range were highly predictable from the native range

41   networks.

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42 *Main conclusions.* Species with high degree and centrality define the core of nested

43 networks. Our results suggest that core species are likely to establish interactions and be

44 core species in the alien range, whilst species with few interactions in their native range will

45 behave similarly in their alien range. Our results provide new insights into species role

46 conservatism, and could help ecologists to predict alien species impact at the community

47 level.

INTRODUCTION

51 Predicting novel species interactions is a crucial challenge in today's rapidly changing world.

52 Alien species are an important driver of novel ecosystems (Hobbs *et al.*, 2006) due to their

53 ability to outcompete native species (Chittka & Schurkens, 2001; Madjidian *et al.*, 2008; Roy

54 *et al.*, 2012), change the community structure (Albrecht & Gotelli, 2001; Memmott & Waser,

55 2002; Carpintero *et al.*, 2005) and disrupt species interactions (Aizen et *al.*, 2008; Traveset &

56 Richardson, 2006; Tylianakis *et al.*, 2008). Studies on alien species mostly focus on species

57 considered to be invasive, which means that rather little is known about those alien species

58 that remain at low population size or have fewer interactions with (and hence, impact on)

59 the recipient community.

60 While many studies have tried to identify key features that predict which species will

61 become invasive and which communities are more likely to be invaded (Thuiller *et al.*, 2005;

62 Richardson & Pysek, 2006; Pysek & Richardson, 2007) these remain of limited practical

63 value. For example it remains difficult to predict whether a mutualistic interaction will

64 facilitate the establishment and dispersal of an alien species (Hulme, 2012). The limited

65 practical value of current work is partially due to the need for detailed information on each

66 species involved in the potential novel interactions, which is usually very time consuming to

67 gather. Therefore, new methods to simplify predictions are required. An alternative could

68 be to assess the role a given species plays in the topology of interaction networks (e.g.

69 Stouffer et al. 2012; Martin Gonzalez *et al.*, 2010; Albrecht et al. 2014). Species roles

70 summarize their ability to interact with, and potentially affect, other species in the

71 community in a way that is relatively easy to sample compared with measures of multiple

72   species and community traits. The application of species roles in ecological networks to

73   predict invasion currently remains untested.

74   Ecological networks have been of considerable use when trying to understand how

75   alien species integrate into local communities (Memmott & Waser, 2002; Garcia *et al.*, 2014,

76   Maruyama *et al.*, 2016) and how they affect the overall mutualistic network structure

77   (Olesen *et al.*, 2002a; Santos *et al.*, 2012; Albrecht *et al.*, 2014). In general, alien species are

78   generalists, i.e. they interact with many species in the community in which they occur (Aizen

79   *et al.*, 2008; Santos *et al.*, 2012). Generalist species tend to occupy central positions in

80   ecological networks, and by interacting with other generalists and specialists (Memmott &

81   Waser, 2002; Aizen *et al.*, 2008) they contribute to the pattern of nestedness that

82   characterises many mutualistic networks (Bascompte, 2003; Bascompte & Jordano, 2007).

83   In addition to its number of direct interaction partners (termed 'degree'), a species' position

84   allows it to connect different parts of the network and maintain network cohesiveness. This

85   helps to define its role in structuring the overall network topology (Martin Gonzalez *et al.*,

86   2010), including elements of network structure such as clustering or modularity (Olesen *et*

87   *al.*, 2007). Thus, the species' position in the network, i.e. its network role, captures key

88   information on its interactions with, and potential effects on, other species in the

89   community.

90   Recent work suggests that species roles are conserved across different locations.

91   Species interactions, either generalist or specialist, have been shown to be phylogenetically

92   conserved across space and time (Jordano *et al.*, 2003; Rezende *et al.*, 2007; Gómez *et al.*,

93   2010), because intrinsic (inherited) characteristics of species can constrain who can interact

94   with whom (Eklöf *et al.*, 2013) and can be related to native and alien species roles in

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95   network topology (Maruyama *et al.*, 2016). If these traits show low intraspecific variability

96   across locations, this indicates that species roles in networks should also be conserved. For

97   example, species roles in predator-prey networks can be conserved from an evolutionary

98   perspective, such that dynamically-important species in one network will be important in

99   the other networks in which it occurs (Stouffer *et al.*, 2012). Similarly, species roles in host-

100   parasitoid networks were found to be intrinsic characteristics conserved over different

101   temporal and spatial scales (Baker *et al.*, 2015).

102   Despite evidence of an intrinsic component of species network roles, species

103   interactions and network roles may also be affected by local environmental and biotic

104   conditions (Tylianakis *et al.*, 2008; Trøjelsgaard *et al.*, 2015). Moreover, the number and

105   type of interactions a species has increase with that species' abundance (e.g., Trøjelsgaard

106   *et al.*, 2015), and species abundance and interactions may change during different stages of

107   invasion (Aizen *et al.*, 2008). Finally, patterns of non-random association among species

108   based on their phylogenetic relatedness (Rezende *et al.*, 2007) suggest that coevolved

109   interactions may be important for structuring mutualistic networks. Therefore, it is currently

110   not clear whether species roles can be extrapolated from one location to another that

111   differs in its evolutionary history and local community traits.

112   Here we aim to understand whether species roles differ and can be predicted from

113   the native to the alien range of their distribution. Specifically, we use measures of plant and

114   insect species roles in plant-pollinator networks (normalised degree, closeness and

115   betweenness centrality, and c and z scores) recorded in both their native and alien ranges to

116   test whether they differ consistently or can be predicted between ranges. Based on the

117   findings that species roles and ecological interactions can be temporally, spatially and

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118 phylogenetically conserved (Rezende *et al.*, 2007; Gómez *et al.*, 2010; Stouffer *et al.*, 2012;

119 Baker *et al.*, 2015) we predict that a species' network role will be similar in its native and

120 alien ranges, such that the former can be used to predict the latter. By including both

121 specialist and generalist species we can draw conclusions about both rare and common

122 alien species.

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124

125 **METHODS**

126 We searched for plant-pollinator networks where we could potentially find species recorded

127 in both their native and alien range. We found 48 plant-pollinator networks of which 42

128 were downloaded from the "Web of Life" database (Ortega, 2014), three are our own data

129 sampled in New Zealand and three are unpublished data from Lopezaraiza-Mikel and

130 Memmott in Hawaii; Table S1). Our criteria of species/network inclusion in the dataset was

131 to have a target species occurring in at least one network as native and one network as

132 alien. Thus each network can contain more than one target species, each of which may be

133 either in its native or its alien range. As some of these networks contain only the

134 presence/absence of interactions and the sampling effort of these networks is mostly

135 unknown, we analysed all networks as binary matrices. In addition, here a flower visitor was

136 considered to be a pollinator, irrespective of whether effective pollination was

137 demonstrated. To define species range as native or alien, we used the following online

138 information: Global Invasive Species Database (http://www.issg.org/database/welcome/),

139 Global Invasive Species Information Network (http://www.gisin.org), Delivering Alien

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140 Invasive Species Inventories for Europe (http://www.europe-aliens.org/), GB Non-Native

141 Species Secretariat Website (http://www.nonnativespecies.org), Plant Pest Information

142 Network of New Zealand (http://archive.mpi.govt.nz/applications/ppin), Centre for Invasive

143 Species and Ecosystem Health (http://www.bugwood.org/), Weeds in Australia

144 (http://www.environment.gov.au/biodiversity/invasive/weeds/), and Invasive Species of

145 Japan (https://www.nies.go.jp).

146

147 **Species roles**

148 Species roles in networks can be described by a variety of different, yet often correlated

149 metrics. Our intent here was not to provide an exhaustive comparison of different potential

150 measures of species roles, or to determine which metrics were best conserved and why.

151 Rather, we focused on testing a 'proof of concept' that roles could be conserved, so we

152 focused on five complementary metrics that could potentially capture different aspects of

153 species ecology:

154   1) Normalised degree – the number of interactions per species (i.e. degree) divided

155 by the number of possible interacting partners, which controls for differences in network

156 size. Normalised degree is the most local centrality index that characterizes a species'

157 network position, such that species with high degree are core in the network structure and

158 enhance robustness (Solé & Montoya, 2001; Dunne *et al.*, 2002). Additionally, normalised

159 degree estimates how generalist/specialist a species is relative to other species in the same

160 trophic level of the community in which it occurs.

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161   2) Closeness centrality (hereafter, closeness) – the average distance (path length) to

162   all other species in the network. Closeness incorporates the number of immediate

163   connections to adjacent nodes and the connections of those nodes, so is a more global

164   measure of location than degree. In bipartite networks, closeness and betweenness are

165   measured for the unipartite projection of each trophic level based on shared interaction

166   partners, such that higher closeness indicates a greater number of interaction partners

167   shared with other species in the same trophic level that also share partners with many other

168   species (Freeman, 1979; Martín Gonzalez *et al.*, 2010). Thus, closeness is a measure of niche

169   overlap with other species at the same trophic level via shared pollinators and the potential

170   for either positive or negative indirect effects via short path lengths (Morales & Traveset,

171   2008; Carvalheiro *et al.*, 2014).

172   3) Betweenness centrality (hereafter, betweenness) – the proportion of the shortest

173   paths linking any pair of species in the network that cross through a given species. It

174   estimates species importance for network cohesiveness (Freeman, 1979; Martín Gonzalez *et*

175   *al.*, 2010). Species with high betweenness can potentially connect different parts of the

176   network that could be otherwise sparsely linked or even isolated; thus alien species that

177   tend to be highly generalist may be linking previously isolated species in plant-pollinator

178   networks and affect the overall network structure.

179   4) and 5) *c* and *z* scores: the combination of these two metrics describes a species'

180   role in the topology of the network as a hub, peripheral or connector within and among

181   modules (Olesen *et al.*, 2007) based on the modularity of the network (Guimera & Amaral,

182   2005). The *z*–score calculates the standardized number of links a species has within a

183   module, and the *c*–score calculates the among module connectivity, which is the number of

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184 links a given species establishes among different modules. Therefore, high values of c and z

185 are related to generalist species that have many interactions throughout the whole

186 network, either as hubs connecting species within modules, or as connectors linking

187 different modules. On the other hand, low values of c and z describe peripheral species that

188 tend to be specialists. Alien plant species that invade a new range may act as network hubs

189 by attracting many different pollinator species through providing high amounts of nectar,

190 for example, Himalayan balsam (*Impatiens glandulifera* Royle) acts as a "magnet species" in

191 its alien range (Chittka & Schurkens, 2001, Lopezaraiza-Mikel et al. 2007), whilst alien

192 pollinator species may act as network connectors while searching for floral resources in

193 different modules.

194   To allow comparisons across networks with different size, closeness and

195 betweenness were each scaled to sum to 1. Species role metrics were calculated using

196 bipartite (Dormann *et al.*, 2009) and rnetcarto packages (Doulcier, 2015) for R; correlations

197 among these metrics are shown in Table S5.

198

199 **Statistical analysis**

200 **Are there differences in species roles in their native vs. alien range?**

201 To answer whether species roles differed from native to alien ranges we used Linear Mixed-

202 Effects Models (LMMs) in the lme4 package (Bates *et al.*, 2014). Individual models were

203 fitted for normalised degree, closeness, betweenness, and c- and z-scores. The first four

204 metrics were logit transformed to solve the issue of being bounded from zero to one

205 (Warton & Hui, 2011). Range (native vs. alien) was modelled as a fixed factor, whilst

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206 network and species were fitted as random effects to account for multiple observations

207 from the same network and to group native and alien measures from the same species.

208 Residual plots were used to check model adherence to assumptions. The overall variance

209 explained by the model, and the proportion that could be attributed to the fixed factor

210 (range) and the random factors were estimated by calculating: i) conditional Pseudo R-

211 squared ($R^2GLMM_{(fix+rand)}$), to estimate total variance explained by the fixed and random

212 effects combined, ii) marginal Pseudo R-squared ($R^2GLMM_{(fix)}$), to estimate the variance

213 explained by range, and iii) the difference between the two ($R^2GLMM_{(fix+rand)} – R^2GLMM_{(fix)}$)

214 to estimate the contribution of the random effects only ($R^2GLMM_{(rand)}$) (Nakagawa &

215 Schielzeth, 2013), using the MuMIm package (Barton, 2013). Then, to determine if any

216 difference in species roles between native and exotic range could have occurred due to

217 biogeographical patterns from tropical to temperate zones (Olesen & Jordano, 2002;

218 Schleuning *et al.*, 2012), we re-ran the above models including the absolute latitude as a

219 fixed effect interacting with range. Likewise, we re-ran the models with trophic level (plant

220 or pollinator) and its interaction with range to determine whether any differences between

221 native and alien range only applied to one trophic level.

222

223 **Does a species' role in the native range predict its role in the alien range?**

224 To test whether a species' role in the native range can predict its role in the alien range, we

225 fitted five linear regressions relating species' mean normalised degree, closeness,

226 betweenness, and the *c-* and *z*-scores in the alien range to the mean values in their native

227 range. Normalised degree was strongly influenced by an outlier, which was removed and

228 consequently improved model fit (Appendix S1). Model validation to check for

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229   homoscedasticity and normality of the residuals was performed following Crawley (2013)

230   and Zuur et al. (2009). As previously, we re-ran these regressions including, separately,

231   absolute latitude and trophic level and their interactions with species' role in the native

232   range to determine whether the predictive power depended on these variables. Latitude

233   was determined for each species as the absolute difference between latitudinal mean in the

234   native range and the latitudinal mean in the alien range. The latitudinal mean was obtained

235   by averaging the absolute latitude of all occurrences each species has in its native and alien

236   ranges.

237   Subsequently, we jack-knifed the linear regression models to provide an unbiased

238   assessment of how accurately species roles could be predicted in alien networks based on

239   their mean role in the native networks (Efron, 1983). Each species was removed from the

240   linear regression in turn, the regression re-fitted, and predictions of the role metrics were

241   generated for that species in the alien networks based on its mean value across its native

242   networks. The observed mean values in the alien range were then compared against the

243   predicted values using Pearson`s correlations. Individual species roles and mean species

244   roles were tested for correlation (presented as the Spearman coefficient in Table S5) and a

245   Bonferroni correction was used in both LMMs and LMs. All statistical and network analyses

246   were run in R v. 2.15.3 and v. 3.1.1 (R Core Team, 2014).

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248

249   **RESULTS**

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250　We compiled information on 12 plant species and five pollinator species that occurred in at

251　least one network in a native range and one network in an alien range (Table 1). These 17

252　species, from 19 different countries, were distributed in all continents except Antarctica

253　(Fig. 1, Table S1); this translates into a large range of different habitats, climatic conditions

254　and species richness. In total, we worked with 167 occurrences of the 17 target species (i.e.

255　one occurrence corresponds to the occurrence of a species in either its native or alien

256　range; note that multiple target species can occur in the same network) (Table S2).

257

258　Are there differences in species roles in their native and alien range?

259　There was no significant difference between native and alien ranges in any of the measures

260　of species' role (Table 2). In other words we found no evidence that, for example, species

261　consistently interact in a more generalist way in their exotic vs. native range. Rather, the

262　variance explained by the models was primarily attributable to the random factors

263　(R^2GLMM$_{(rand)}$ was 94%, 40%, and 20% in the closeness, normalised degree and

264　betweenness models respectively), which were the network and the species identity, whilst

265　range, the fixed term, was not statistically significant for any of the metrics tested (Table 2).

266　Similarly, the random structure explained around one third of the variance in the *z*-score

267　(29%) and the *c*-score models (37%). The large variance retained by the random structure

268　suggests that species differ considerably in their network roles and that, unsurprisingly,

269　species roles depend on the local network (e.g., network size constrains the range of

270　possible roles), and this large variance within native or exotic ranges of a species blurred any

271　significant differences between them.

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272   Even though network architecture can change across regions (Olesen & Jordano,

273   2002), we found no systematic change in species roles with latitude, neither significant

274   range x latitude interaction (Table S3). However, a significant range x trophic level

275   interaction for closeness (Table S3) revealed that the native range had lower closeness for

276   pollinators but not for plants. This indicates that pollinators may move into a more central

277   role in their alien range by pollinating generalist plants that are also pollinated by many

278   other species and share those pollinators with many other plants. Given that in our analyses

279   there were more plant species than pollinator species, this interaction effect captured the

280   difference between ranges for pollinators that was otherwise masked by the lack of

281   difference on plant species. Moreover, pollinator species had higher c-scores than plant

282   species independently of range, suggesting that the pollinators included in our analyses may

283   be better network connectors (Table S3). In fact, most plant and pollinator species played

284   peripheral roles in our networks (73%) but pollinators were the main connectors (88%),

285   module hubs (75%) and the only network hubs (100%) (Table S4).

286

287   **Does a species' role in the native range predict its role in the alien range?**

288   Two measures of species roles, closeness and normalised degree, in the alien range could be

289   predicted from the native range data ($F_{1,15}$ = 27.32, p = 0.0001, r^2 = 0.62 and $F_{1,14}$ = 13.56, p

290   = 0.0025, r^2 = 0.46, respectively; Fig. 2). The coefficients for closeness and normalised

291   degree were 0.98 (SE ± 0.187) and 0.71 (SE ± 0.192), respectively, and both had intercepts

292   that did not differ significantly from zero (closeness: t = 0.25, p = 0.809; normalised degree: t

293   = 0.67, p = 0.512), suggesting that a species' role in the native range is associated to that in

294   the alien range. In contrast, the positive trend in the relationship between native and alien

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295   range when estimating betweenness (slope = 0.208 SE ± 0.109) and the z-score (slope =

296   0.412 ± 0.204) was marginally non-significant ($F_{1,15}$ = 3.63, p = 0.076, r^2 = 0.14 and $F_{1,15}$ =

297   4.07, p = 0.062, r^2 = 0.16, respectively; Fig. 2) and lacked any significance for the c-score

298   model ($F_{1,15}$ = 0.22, p = 0.649). Although the testing of correlated variables (Table S5)

299   increases the probability of type I error, the effects for closeness and normalised degree

300   remained significant when a Bonferroni correction was applied (corrected alpha = 0.01).

301   Moreover, out of five variables tested, the probability of finding two significant at an alpha

302   below 0.0025 is extremely low (6.2×10^{-5}, calculated using the Bernoulli process described in

303   Moran 2003), indicating that overall the suite of species roles in the exotic range could be

304   predicted better from roles in the native range than would be expected by chance.

305   The predictive effects of closeness and normalised degree were consistent when

306   latitude and trophic level were included in the models (Table S4). Neither latitude

307   (normalised degree: $F_{3,13}$ = 0.355, p = 0.787; closeness: $F_{3,13}$ = 1.61, p = 0.235; betweenness:

308    $F_{3,13}$ = 0.938, p = 0.450; c-score: $F_{3,14}$ = 2.00, p = 0.173; z-score: $F_{3,14}$ = 0.56, p = 0.652) or

309   trophic level (normalised degree: $F_{3,13}$ = 0.262, p = 0.851; closeness: $F_{3,13}$ = 1.708, p = 0.214;

310   betweenness: $F_{3,13}$ = 1.044, p = 0.406; c-score: $F_{3,14}$ = 2.00, p = 0.173; z-score: $F_{3,14}$ = 0.56, p =

311   0.652) showed any significant interaction with range when tested for predictive effects of

312   species roles from the native to the alien range of a species distribution (Table S4).

313   Congruent with the LMM results, after model selection we detected that the mean c-score

314   was also higher for pollinators than for plants independently of range ($F_{2,14}$ = 12.02, p =

315   0.0009).

316   In the jack-knife validation of our predictions, predicted values of closeness in the

317   alien range were highly correlated with the corresponding observed values (t = 15.339, p <

        15

318   0.0001, r = 0.777), suggesting that the species closeness in the native range is a good

319   predictor of the species closeness in the alien range. The predictive power of native range

320   was lower but still a good predictor for more than half of the species when estimating

321   normalised degree (t = 9.040, p < 0.0001, r = 0.583), z-score (t = 8.0445 p = < 0.0001, r=

322   0.53), and c-score (t = 8.587, p < 0.001, r = 0.56), though not as good for betweenness (t =

323   5.621, p < 0.0001, r = 0.401).

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325

326   **DISCUSSION**

327   Two consistent patterns emerged from our analyses of the 48 datasets: 1) although species

328   differed considerably in their roles, the roles of species generally did not differ consistently

329   between their alien and native ranges, and 2) two metrics of species roles, closeness and

330   normalised degree, in the alien range could be predicted from the native range.

331   Betweenness and z-score predictions from the native to the alien range were marginally

332   non-significant, but showed a trend toward positive correlation, which was unsurprising in

333   the case of betweenness, given its high correlation with normalised degree and closeness

334   (Table S5b). Despite this overall predictive ability, we found that pollinators (but not plants)

335   had a higher closeness in their alien range, probably due to their ability to exploit a wide

336   range of resources and thus interact with generalist plants. Still, trophic level (pollinator vs.

337   plants) did not interact significantly with range, except for c-score, which showed higher

338   values for pollinators, suggesting they may play a better role in connecting the whole

339   networks than did plants. Our results suggest that species role conservatism may occur,

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340 such that species that are generalists or play a central role in their native network are likely

341 to play a similar role in their alien range.

342

343 **Limitations**

344 In an ideal situation, the networks studied would have been collected using the same

345 methods, aiming for quantitative data collected over similar periods of time. The dataset

346 used comes from different sources that used different sampling methodologies, spatial and

347 temporal scales. Moreover, it contains only species that successfully established in the alien

348 range thus it lacks information for those species that failed to establish in the alien range.

349 Moreover, our models do not consider species abundance, which is known to drive some

350 network patterns (Blüthgen *et al.*, 2007; Dorado *et al.*, 2011; Staniczenko *et al.*, 2013; Fort *et*

351 *al.*, 2016) as well as the effects of invasive species (Dostal *et al.*, 2013; Carvalheiro *et al.*,

352 2014; Traveset & Richardson, 2014). Furthermore, the conservation status of the areas from

353 which the networks were sampled is mostly unknown. Thus, the native range should not be

354 necessarily interpreted as a pristine environment given that we are likely working with

355 altered environments in both ranges. This high heterogeneity in the dataset generated high

356 variance across different networks (even within a species' native or alien range), which

357 would have reduced the probability of detecting differences across 'treatments'. In that

358 sense, the absence of evidence for differences in species roles in native vs. alien range

359 cannot be viewed as evidence of absence. That said, the positive correlations we observed

360 between native- and alien-range values of closeness and normalised degree were robust

361 enough to be seen despite the data being averaged across these heterogeneous replicate

362 networks and spanning species with a range of roles from specialists to generalists.

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363

The intrinsic roles of alien species in pollination networks

The correlation between species roles in their native and alien range in the five network statistics concurs with other authors who report that species have intrinsic properties in ecological networks that persist over temporal and spatial scales (Jordano *et al.*, 2003; Gómez *et al.*, 2010; Stouffer *et al.*, 2012; Baker *et al.*, 2015). From the roles estimated here, high degree and high closeness define the core of the nested network (i.e. those generalists that interact with both specialists and generalists), and our results suggest that core species will tend to maintain this role even when they enter novel communities. Species with high degree, i.e. generalists, are expected to be good invaders because they can increase their chance to establish and spread through the population by interacting with many of the "available" species. Conversely, specialist species with few interactions in the native range will also have only few interactions in the alien range, and this may lower their chance of establishing into the novel community if, for example, the resource is scarce and competition strong (Aizen *et al.*, 2008; Aizen *et al.*, 2012), as shown in previous work that simulated invasion of food webs (Romanuk *et al.*, 2009). In turn, high closeness can be seen in species that interact with other central species in the community, even if the focal species is not a generalist itself. In fact, in our dataset the average normalised degree and average closeness were not significantly correlated (r = 0.24, Table S5b), such that a species could occupy a consistently central position in networks by interacting with central species, rather than by being a generalist itself. Therefore, the combination of degree and closeness can potentially be good indicators of species with high risk of introduction success in terms of invasion. On the other hand, the poor prediction of betweenness and the *c*- and *z*-score,

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386 which indicate the role a species plays as connecting different parts of the network,

387 suggests that the role of species as connectors may depend on the distribution of species

388 into modules.

389   Most plant species depend on animal species for pollination (Waser & Ollerton,

390 2006; Ollerton *et al.*, 2011), thereby any characteristic that enhances interactions with

391 pollinators would likely be favourable when colonizing a new area. Central alien plants may

392 have an advantage in the new range in terms of gene flow if local pollinators show high

393 fidelity. A greater number of pollinator species constantly visiting different conspecific

394 flowers may promote greater deposition of conspecific pollen grains, therefore increasing

395 pollination (Brosi & Briggs 2013; Huang *et al.,* 2015). Nevertheless, the benefits of this

396 increased visitation frequency may be partly offset by an increase in heterospecfic pollen

397 transport (Fang & Huang 2013) if, instead, the alien plant interacts with a generalist

398 pollinator that visits different plant species therefore increasing heterospecific pollen

399 transfer, potentially reducing seed set (Ashman & Arceo-Gómez, 2013). Still, heterospecific

400 pollen transfer has been shown to be generally low and have none, low or species-specific

401 effect on plant reproduction (Bartomeus *et al.*, 2008; Montgomery & Rathcke, 2012; Fang &

402 Huang, 2013; Emer *et al.*, 2015). Moreover, central pollinator species may have an

403 advantage over less connected species when arriving in an alien community due to their

404 ability to visit different flower species, thereby obtaining different food resources (Traveset

405 et al, 2013). Pollinators were the main connectors in our networks and that was more

406 frequent in their alien range. Given that the main pollinator connectors in our network were

407 social insects (i.e *Apis mellifera* and *Bombus* spp.), which are usually highly abundant in

408 invaded areas (e.g. Aizen *et al*., 2008; Santos *et al*., 2012), and whose foraging individuals

19

409   reflect the colony needs (Willmer & Finlayson 2014 and references therein), it may be that

410   these species' roles vary according to their population density and foraging behaviour. Yet,

411   central pollinator species may face high competition with the local pollinators with which

412   they share interactions, a constraint that may make it difficult for pollinators to establish in

413   a novel community with low nectar/pollen resources, for example.

414   Our findings also have implications for network persistence. Rewiring, i.e. the

415   reshuffling of interaction links among species, can enhance network resilience and

416   robustness to disturbance (Staniczenko *et al.*, 2010; Kaiser-Bunbury *et al.*, 2011; Olesen *et

417   al.*, 2011). Given that both plant and pollinator links can be transferred from native

418   generalist to alien generalist species (Aizen *et al.*, 2008), and that the probability of a native

419   pollinator interacting with an alien plant increases with its degree and nestedness

420   contribution (Stouffer *et al.*, 2014), the introduction of a highly generalist alien species may

421   affect not only the local generalist species but also the more specialized ones that connect

422   to it via interaction rewiring (Aizen *et al.*, 2008). The consequences of this will depend on

423   the centrality of the introduced species in combination with that of the native species, e.g.

424   highly-connected alien species will likely promote local species rewiring, whilst the arrival of

425   a poorly-connected species (i.e. a specialist) may have a mild or even neutral effect on local

426   species interactions. Moreover, a species that remains in its home range in which the

427   community has changed due to local extinctions and alien species invasion will find itself in

428   a novel network of interactions. Given that species roles are conserved, rewiring of

429   interactions will be needed for the local species to fit into the novel community (Gilljam et

430   *al*., 2015).

431

20

Conclusions

In summary, there seems to be an intrinsic component of species roles in plant-pollinator networks that is conserved across species native and alien ranges. Our results suggest that the core network position that a species occupies when introduced in a novel community will resemble how generalist or specialist it is in its native community. Our results provide new insights into the recent literature about interactions and species role conservatism, and have implications regarding the potential links that alien species may be able to create or disrupt once introduced into novel communities. Further studies incorporating community traits and the phylogenetic relationship between species with species network roles will advance our understanding of how alien species interact with, and potentially drive the formation of, novel communities.

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676

677 **SUPPORTING INFORMATION**

678 Additional Supporting Information can be found in the online version of this article:

679

680 **APPENDIX S1.** Outlier detection analyses.

31

681   **TABLE S1** – Description of the networks used for the analyses of the species' roles of plants

682   and pollinators in the alien and native range.

683   **TABLE S2**. List of the target species and the networks in which they were recorded. Network

684   ID follows Figure 1 and Table S1 in which details of each network are provided.

685   **TABLE S3.** Results of the Linear Mixed-Effect Models (LMMs) and the Linear Regression

686   Models (LMs) testing whether latitude and trophic level interact with species range to

687   determine species' roles.

688   **TABLE S4.** Species roles on pollination networks following Olesen et al. (2007): Peripheral $z \leq$

689   2.5, $c \leq 0.62$; Connector $z \leq 2.5$, $c > 0.62$; Module hub $z > 2.5$, $c \leq 0.62$; Network hub $z > 2.5$, c

690   > 0.62. The first number is the number of occurrences in networks in the species native

691   range, and the second number is the species occurrences in networks in its alien range.

692   **TABLE S5.** Correlation between normalised degree, closeness, betweenness, c and z scores

693   measured with (a) individual entries, i.e. the value of the role of each species in each

694   network is taking into account, as used in the Linear Mixed Models, and (b) when the

695   averages for each species are considered, as used in the Linear Regressions of the

696   manuscript. Values correspond to the Spearman correlation coefficient ρ.

697

698

699   **BIOSKETCHES**

700   **Carine Emer** is a community ecologist interested on understanding how anthropogenic

701   disturbance affect animal-plant interactions. Her research includes both mutualistic and

32

702 antagonistic processes in tropical and temperate habitats. Recently she has studied the

703 effects of invasive species, habitat loss and fragmentation on ecological networks. She is

704 currently a postdoctoral researcher at the Universidade Estadual Paulista (UNESP) in Brazil.

705 The authors are part of a collaboration established during her doctorate at the University of

706 Bristol, UK.

707 **Authors contributions:** CE and JMT developed the study framework. CE gathered the data,

708 ran the analyses, and wrote the manuscript. IPV provided statistical advice. DM contributed

709 with the study design and discussion. JM advised on the collection of the field data, and JM

710 and JMT commented and edited the versions of the manuscript.

711

33

TABLES AND FIGURES LEGEND

713

714 **Table 1**. The 17 plant and pollinator species analysed in this study (see Table S1 for further

715 information about each network).

716 **Table 2.** Results of the Linear Mixed-Effects Models (LMMs) testing whether species roles

717 differ from the native to the alien range. Pseudo R-squared values were calculated to

718 estimate the variance explained by the fixed and random structure of each model: $R^2_{fix+rand}$ -

719 estimates total variance explained by the fixed and random effects combined; R^2_{fix} -

720 estimates the variance explained by range; R^2_{rand} estimates the contribution of the random

721 effects only.

722 **Figure 1.** The location of the 48 plant-pollinator networks. Panels A-G show the location of

723 those networks that overlap in the full map. Numbers are the individual codes of each

724 network identity (see Supplementary Material).

725 **Figure 2**. Results of the linear regression models testing whether a species' role in the native

726 range predicts its role in the alien range. (a) Normalised degree; (b) Closeness; (c)

727 Betweenness; (d) c-score; and (e) z-score. Results of normalised degree are shown after the

728 removal of an outlier.

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Table 1

Plant species	Family	Number of networks present	
		Native networks	Alien networks
Achillea millefolium L.	Asteraceae	4	5
Cirsium arvense (L.) Scop	Asteraceae	3	6
Cytisus scoparius (L.) Link	Fabaceae	1	1
Eupatorium cannabinum L.	Asteraceae	1	2
Hieracium pillosela L.	Asteraceae	2	4
Hypochaeris radicata L.	Asteraceae	5	6
Leucanthemum vulgare Lam.	Asteraceae	2	4
Lotus corniculatus L.	Fabaceae	3	1
Taraxacum officinale F.H. Wigg	Asteraceae	4	1
Trifolium pratense L.	Fabaceae	2	4
Trifolium repens L.	Fabaceae	3	10
Verbascum thapsus L.	Scrophulariaceae	2	3
Total plants` occurrences		31	47
Insect species	**Order**		
Apis mellifera L.	Hymenoptera	9	28
Bombus hortorum L.	Hymenoptera	7	4
Bombus terrestris L.	Hymenoptera	9	6
Eristalis tenax L.	Diptera	5	11
Pieris rapae L.	Lepidoptera	3	6
Total insects` occurrences		33	46
Total		64	102

730 **Table 2**

	Linear Mixed-Effects Models					
	Est	t	p	$R^2_{\text{fix-rand}}$	R^2_{fix}	R^2_{rand}
Normalised degree	0.305	1.227	0.226	0.408	0.011	0.397
Closeness	-0.108	-1.188	0.237	0.939	0.003	0.936
Betweenness	0.116	0.326	0.747	0.201	0.000	0.201
z – score	-0.029	-0.158	0.875	0.285	0.000	0.285
c - score	0.028	1.076	0.285	0.378	0.010	0.377

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(a) Normalized degree, p = 0.002, r^2 = 0.49

(b) Closeness, p = 0.0001, r^2 = 0.65

(c) Betweenness, p = 0.076, r^2 = 0.19

(d) c−score, p = 0.644, r^2 = 0.01

(e) z−score, p = 0.062, r^2 = 0.21

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