Local and regional specialization in plant-pollinator networks

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Abstract

Specialization of species is often studied in ecology but its quantification and meaning is disputed. More recently, ecological network analysis has been widely used as a tool to quantify specialization, but here its true meaning is also debated. However, irrespective of the tool used, the geographic scale at which specialization is measured remains central. Consequently, we use data sets of plant-pollinator networks from Brazil and the Canary Islands to explore specialization at local and regional scales. We ask how local specialization of a species is related to its regional specialization, and whether or not species tend to interact with a non-random set of partners in local communities. Local and regional specialization were strongly correlated around the 1:1 line, indicating that species conserve their specialization levels across spatial scales. Furthermore, most plants and pollinators also showed link conservatism repeatedly across local communities, and thus seem to be constrained in their fundamental niche. However, some species are more constrained than others, indicating true specialists. We argue that several geographically separated populations should be evaluated in order to provide a robust evaluation of species specialization.

Introduction

The Earth's biodiversity is shaped by a plethora of interactions between species that may range from being relatively specialized to relatively generalized, and the exact nature of these interactions depend upon a variety of ecological and evolutionary factors. Many of these types of interactions are common and ecologically vital; pollination by animals for example is the norm for an estimated 87.5% of the c. 352,000 species of flowering plants (Ollerton et al. 2011). Extensive work based on visitation data between plants and pollinators indicate that such interactions tend to be more generalized than previously thought, even for tropical systems (Ollerton and Cranmer 2002, Schleuning et al. 2012, Waser et al. 1996). However, recent studies, considering visitation frequency and service effectiveness, suggest stronger fidelity between interaction partners and that binary visitation data might overestimate generalization levels (King et al. 2013, Rosas-Guerrero et al. 2014 – though see Ollerton et al. 2015). Furthermore, several studies indicate that species can appear as generalists while actually being composed of specialist populations, or even generalist populations composed of specialist individuals (Araujo et al. 2008, Bolnick et al. 2002, Devictor et al. 2010, Dupont et al. 2011, Fox and Morrow 1981, Tur et al. 2014). Such studies suggest that phylogenetic and geographic scale are highly relevant when studying specialization, and sampling of multiple populations is necessary to reliably determine the niche breath of a species to account for cross-community variation (Carstensen et al. 2014, Fox and Morrow 1981, Ollerton et al. 2007, Ollerton et al. 2009, Poisot et al. 2015, Trøjelsgaard et al. 2015).

The fundamental taxonomic niche of a species describes the set of potential interaction partners as determined by functional traits (Junker et al. 2013). Conversely, the realized taxonomic niche is the subset of species within a given community with which the focal species interacts. Thus, while functional traits do not necessarily enable us to predict the occurrence of a given interaction, they do partly define the set of possible interactions (Morales-Castilla et al. 2015) and

55 trait complementarity does seem to consistently govern general interaction patterns within

56 communities (Carstensen et al. 2016). The fundamental and realized niche concepts are related to

57 specialization at the level of species and populations respectively, and the fundamental niche is

58 seldom fully realized in any single local community because of differences in relative abundances,

59 species composition and other biotic and abiotic factors (Burkle et al. 2016, Carstensen et al. 2014,

60 Trøjelsgaard et al. 2015).

61   Here, we explore species specialization across interacting plants and pollinators within two

62 contrasting regions: Brazilian *campo rupestre*, or rupestrian grasslands, and the Canary Islands.

63 Both datasets consist of seven spatially separated community-level plant-pollinator networks,

64 sampled in a standardized way within their regions. Using these data we explore the relationship

65 between local and regional specialization, and investigate whether this relationship differ between

66 these two contrasting study regions, assuming the ecological specialization framework (Armbruster

67 2017). Specifically we ask: 1) Are local and regional measures of specialization correlated? 2) Do

68 species interact locally with a non-random subset of the available species in the community?

69   We expect that the specialization level of a species is conserved across populations, but that

70 the identity of interaction partners might change. If so, species would appear more generalized at

71 the regional level compared to the local level.

72

73 **Methods**

74 *Study sites and field observations*

75   Data were collected in October-December 2012 from seven sites of rupestrian grasslands, or

76 *campo rupestre*, in the National Park of Serra do Cipó, SE Brazil (Carstensen et al. 2014, 2016).

77 *Campo rupestre* is a species-rich vegetation of mostly shrubs and herbs associated with rocky

78 outcrops surrounded by sandy and stony grasslands (Silveira et al. 2016). Sites were 1.4-8.5 km

apart within an altitudinal range of 1073-1260 m a.s.l. One site was sampled per day with a weekly

rotation among sites. Attempting to observe all flowering plant species in each site, plant

individuals were observed in 15 min intervals (totalling 252 hours of observation), recording all

visitors touching the reproductive floral parts (for more details see Carstensen et al. 2014). For each

15-min interval randomly selected plant individuals were observed, and if individuals of the same

species were in close proximity of each other they were often surveyed simultaneously. Flower

visitors were collected for taxonomic identifications by experts. For each site, the data were

summarized in a quantitative interaction matrix expressing the frequency of interactions between

pairs of plants and pollinators. This resulted in seven spatially separated networks with a total of

101 plant species and 201 pollinator species.

Data were also collected from five islands within the Canarian archipelago (El Hierro, La

Gomera, Tenerife (two sites), Gran Canaria and Fuerteventura) and a single site in Western Sahara

located at the West African coast close to the Canary Islands (Trøjelsgaard et al. 2013). In total this

gave us seven spatially separated pollination networks from habitats characterized as semi-arid and

dominated by shrubs. The Canary Island networks were 53-455 km from each other and separated

by ocean, except the two sampling sites at Tenerife, which, conversely, were separated by El Pico

del Teide (3718 m a.s.l.). All flowering perennial plant species were surveyed for flower visitors in

intervals of 15 min (totalling 296 hours of observation) in January-March 2010 through flower-

based focal observations in a similar way as for the Brazilian data set (for more details see

Trøjelsgaard et al. 2013). Most plant species were observed in 15-min intervals approximately 8

times (mean = 7.0, Std. dev. = 1.8). Randomly selected individuals were preferably chosen for each

of the individual 15-min surveys, although low abundance of some species precluded this practice.

Sometimes multiple individuals of the same species were surveyed simultaneously depending on

their spatial aggregations, and also depending on the total number of flowers per individual.

103 Approximately 1300 flower visitors were collected for taxonomic verifications by entomological

104 experts, allowing species identification of many pollinators, while some were grouped as

105 morphospecies. Overall we scored interactions between 39 plant species and 249 pollinator species

106 and, similar to the Brazilian dataset, all seven networks from the Canary Islands were quantitative

107 interaction matrices expressing the frequency of interactions between plants and pollinators.

108

109 *Specialization and interaction richness*

110 For each plant and pollinator species observed in more than one site, we defined a metaweb of

111 species s (Dunne 2006) as the network consisting of all species occurring in the sites in which s

112 occurs, as well as all the interactions between them. In other words, it is the regional network of

113 interactions for species s and its co-occurring species. We quantified specialization using the index

114 d'_s, which describes the deviation of interactions from what would be expected under neutral

115 conditions. Instead of counting the number of interaction partners, d'_s measures the exclusiveness of

116 a species' interactions and is insensitive to variation in observation frequencies across species

117 (Blüthgen et al. 2006). Specialization, d'_s, was calculated using the *dfun* function in the package

118 'Bipartite' in R (Dormann 2011); and for all species we calculated both a regional specialization

119 level using the metaweb of species s ($d'_{s,meta}$) as well as an average local specialization level using

120 the local networks in which species s occurred ($d'_{s,local}$).

121   We tested the correlation between local and regional specialization using the Pearson

122 correlation coefficient. Through simple linear regression, we further tested whether the regional

123 specialization was affected by the number of sites in which a species occurred, or rather, the number

124 of potential interaction partners with which it co-occurred across the region.

125   To quantify if regional interaction richness of a species differed from what could be

126 expected if species interacted randomly with the available set of partners, we first calculated the

127 regional degree for each species, γ_s, which is the total number of different interaction partners

128 across all sites in which the species was observed (i.e. the degree in the metaweb for species s). We

129 then compared the empirical γ_s with a null model where the identity of partners in the local

130 networks was randomized while conserving the local number of interactions for each species. New

131 interaction partners were drawn with a probability proportional to their abundance (measured as

132 total number of interactions, i.e. the marginal sums in the quantitative interaction matrix) among all

133 potential partner species in a local community, and random partners were drawn with replacement

134 until the empirical number of interactions was reached. In this way, the total number of local

135 interactions (i.e. the marginal sum) was retained, but the regional degree was allowed to change as

136 species were allocated new interaction partners among all potential partners at a local site. This

137 procedure was repeated 1000 times for each species, which allowed us to calculate a mean ($\gamma_{s,random}$)

138 and standard deviation (SD_{random}) for each species. Subsequently we compared empirical regional

139 species degrees (γ_s) with the randomized regional degrees ($\gamma_{s,random}$) by using z-scores [(γ_s -

140 $\gamma_{s,random}$)/SD_{random}]. If the z-score was less than -1.96, or larger than 1.96, the difference between the

141 empirical and random regional degree was deemed statistically significant. Moreover, negative

142 values suggest that a species is more constrained in its choice of interaction partners than if partner

143 identities were determined solely by availability (abundance) (we call this 'link conservatism'),

144 while positive values suggest that the species is more opportunistic than expected (we call this 'link

145 opportunism'). By incorporating species abundance as a way of selecting partners in the null-model,

146 the procedure leans towards the neutral perspective which assumes that interactions between species

147 is largely determined by species abundance (see e.g. Canard et al. 2014, Poisot et al. 2015). It is

148 important to note that the null-model ignores phenological or morphological constraints (e.g. Olesen

149 et al. 2011), and therefore may overestimate the availability of potential partners.

150   Finally, we tested for a correlation between the z-scores (link conservatism) and $d'_{s,meta}$ (the

151   regional specialization, or exclusiveness) in order to examine how the two measurements coincide.

152   While $d'_{s,meta}$ measures the deviation of interactions from neutrality based on the availability of

153   partners in the metaweb, the z-scores measure the deviation of the interactions in the metaweb from

154   a null model were each local network is randomized before aggregating the metaweb. These two

155   measures thus quantify specialization, or conservatism, from slightly different approaches and

156   should be negatively correlated. All analyses were done in R, version 3.2.0 (R Development Core

157   Team 2008).

158

159   **Results**

160   Regional ($d'_{s,meta}$) and local ($d'_{s,local}$) specialization were significantly and strongly correlated in

161   the Brazilian networks for both plants and pollinators (Pearson correlation, r = 0.76 and 0.83

162   respectively, p < 0.001, Fig. 1A) as well as in the Canary Islands networks (Pearson correlation, r =

163   0.76 and 0.89 respectively, p < 0.001, Fig. 1B). In Brazil, the number of co-occurring species (i.e.

164   the number of potential interaction partners in the metaweb) had no effect on regional specialization

165   values for plants (p > 0.7, R^2 < 0.01), but correlated significantly with regional specialization of

166   pollinators, albeit with a very poor fit (p < 0.05, R^2 = 0.05, indicated by size of data points in Fig.

167   1A). In the Canary Islands the number of co-occurring species had no effect on regional

168   specialization for neither pollinators nor plants (p > 0.2, R^2 < 0.01).

169   The null model analysis showed similar results for the Brazilian and Canary Islands networks (Fig.

170   2). In both systems, the majority of the plant species showed link conservatism because 81%

171   (Brazil) and 57% (Canary Islands) of the plants had significantly fewer regional interaction partners

172   than expected if partner identity were determined solely by availability (abundance). That is, these

173   species tend to conserve their interaction partners across sites. The majority of the pollinators also

8

174 showed link conservatism in Brazil but not in the Canary Islands as 58% and 46% of the

175 pollinators, respectively, had significantly fewer regional interaction partners. Finally, the

176 pollinators deviation from randomness (i.e. the z-scores, with negative and positive values being

177 suggestive of link conservatism and opportunism, respectively) correlated significantly and

178 negatively with regional specialization in both Brazil (Pearson correlation, r = -0.34, p < 0.001) and

179 the Canary Islands (Pearson correlation, r = -0.30, p = 0.009), while the relationship where non-

180 significant for plants in both Brazil (Pearson correlation, r = -0.25, p = 0.14) and the Canary Islands

181 (Pearson correlation, r = 0.16, p = 0.50) (Fig. 3).

182

183 **Discussion**

184 The results from the two regions were surprisingly similar. Local and regional specialization were

185 strongly correlated in both regions. Plants were generally more specialized than pollinators (Fig. 1)

186 despite a general trend of having more interaction partners (Fig. 2). A correlation between local and

187 regional specialization was expected, however, a strong correlation close to 1:1 indicates that local

188 and regional specialization, in terms of d'_s, is largely interchangeable, and that species in plant-

189 pollinator networks are consistent in their specialization level across scales. By aggregating the

190 specialization level across geographically separated sampling sites, the current procedure attempted

191 to capture the differences in interactions that can be found between populations and individuals (see

192 e.g. Araujo et al. 2008, Tur et al. 2014). In the Canary Islands the geographical distance between

193 sites varied from 52 to 456 km, while the distance in Brazil varied between 1.4 and 8.5 km. Yet, the

194 rocky outcrops found in the *campo rupestre*, within which the surveys were done in Brazil, can to

195 some extent be seen as isolated habitat patches within a matrix of grassland, and the actual isolation

196 between the populations is likely larger than the geographical distances dictates. However, we

197 cannot preclude that increasing the geographical extent so that we covered even more distant

198 populations, especially in Brazil, would lead to different results. Nevertheless, it seems encouraging

199 that the relationship between local and regional specialization were almost identical when

200 comparing the Brazilian and Canarian communities, which suggest that this pattern might actually

201 be a general trend. More studies from different communities are needed, however, to explore the

202 generality of this finding.

203 Larger distances and increased isolation between sites could result in local population-

204 specific adaptations within species, and thus translate into a larger inter-island variability in

205 interaction partners, which ultimately would result in higher opportunism at the regional scale

206 (Thompson 2005, Trøjelsgaard et al. 2015). Indeed, this could potentially partly explain why a

207 lower percentage of plants and animals showed link conservatism in the Canary Island compared

208 with the networks in Brazil. In fact, it is important to note that the Brazilian and Canarian

209 communities also differ in a number of other aspects. For example, across the sampling sites the

210 ratio of pollinators:plants were on average 4.4 ± 1.0 (mean±SD) in the Canary Islands, and 2.6 ± 0.4

211 in Brazil. A lower diversity of plants in the Canarian communities may hamper the pollinators

212 potential to show a strong fidelity across sites when compared with a null model. However, if

213 partner diversity was the sole explanation, we would expect the Canarian plants to show a stronger

214 fidelity as they have more partners to choose from and, therefore, a larger potential to deviate from

215 the null model. Nonetheless, as mentioned, both Canarian plants and pollinators had a lower

216 percentage of link conservative species compared with the species found in Brazil. Thus, partner

217 diversity (i.e. the pollinators:plants ratio) is likely not the sole explanation. Another important

218 aspect could be species turnover (see also Carstensen et al 2014, Trøjelsgaard et al. 2015). That is,

219 if there is a strong turnover in partners from site to site (or island to island) the potential for link

220 conservatism diminishes. The plant communities were on average more similar across the Canary

221 Islands (average Sorensen similarity across sites ± SD, Canary Islands = 0.44 ± 0.13; Brazil = 0.33

222   ± 0.14), while the pollinator communities on average were more similar in Brazil (average Sorensen

223   similarity across sites ± SD, Canary Islands = 0.24 ± 0.12; Brazil = 0.43 ± 0.06). Thus, while the

224   high turnover of pollinators at the Canary Island might explain why a lower percentage of the plants

225   show significant link conservatism, this does not explain the patterns observed for the pollinators.

226   Finally, the studied communities also differ in e.g. species composition, climate conditions, and

227   other biotic and abiotic aspects, which makes it difficult to isolate a single common mechanism as

228   responsible for the difference in link conservatism between the Canarian and Brazilian

229   communities.

230   Overall, for specialist species the foraging and interaction choices are most likely a

231   consequence of trait complementarities, while generalists could be expected to forage or interact

232   mainly according to relative abundances of potential partners. Link conservatism should therefore

233   be higher for specialist species, as we have confirmed (Fig. 3). Indeed, as we argue below, link

234   conservatism and d_s' should be evaluated together to reliably indicate true specialists.

235   Our results show that most species have significantly fewer regional interactions than

236   expected based on our null model. Thus, at the local scale species are constrained in their

237   fundamental niche, indicating innate restrictions in their interaction partners, likely because of trait

238   complementarity (Olesen et al. 2011, Santamaria and Rodríguez-Girones 2007). Species with the

239   largest negative z-values tend to interact repeatedly with the same species across sites, and they

240   therefore show high link conservatism (see also Trøjelsgaard et al. 2015). This indicates stronger

241   constraints on the fundamental niche. Even within the species that show significant link

242   conservatism (z-score < -1.96) some species show much stronger constraints, indicating true

243   specialists. Interestingly, the level of conservatism seems unrelated to regional interaction richness

244   (γ_s) (Fig. 2). We argue that labeling a species as specialist is not necessarily dependent only upon it

245   having few interaction partners, but that interactions are repeatedly formed with the same subset of

246   species, and thus showing a strong signal of link conservatism. This might add another dimension to

247   the discussion about species specialization vs. generalization (Ollerton et al. 2007, Rosas-Guerrero

248   et al. 2014, Schleuning et al. 2012, Waser 2006), as the categorization as specialist or generalist

249   might be strongly dependent upon the spatial scale at which species are investigated. For pollinators

250   there was a significant correlation between z-scores and the measurement of regional specialization

251   ($d'_{s,meta}$) in both Brazil and the Canary Island, which further supports the designation of true

252   specialists. It is here important to re-emphasize that our null model was framed around the neutral

253   theory suggesting that biotic interaction to a large extent is governed by species abundance (Canard

254   et al. 2014, Poisot et al. 2015). By ignoring any phenological and morphological constraints we may

255   overestimate the availability of potential partners, and some species may appear more conservative

256   than if such constraints were also taken into account. Importantly, however, large deviation form

257   randomness also occurred among species having many regional interaction partners, where there is

258   little evidence of phenological and morphological constraints, as they interact with a large

259   proportion of the available partners. Therefore, incorporating such constraints would probably have

260   minimal impact for at least some of the species. Still, with good phenological resolution and

261   detailed morphological trait data the impact of these constraints could be explored further. Also, our

262   approach could be further applied to investigate the role of floral traits in defining visitation fidelity,

263   revisiting the discussion on the generalization in pollination system towards the tropics (Ollerton et

264   al. 2009, Rosas-Guerrero et al. 2014, Schleuning et al. 2012), with consequences for plant

265   reproductive success and adaptation to environmental changes.

266   The interaction richness of a species is ultimately limited by the availability of

267   potential partners at a given site, which, in turn, is determined by functional traits (Ibanez et al.

268   2016). However, according to our results, it would be sensible to distinguish between niche breath

269   and specialization, because link conservatism (z-scores) and niche breath (regional interaction

270   richness) were not correlated (Fig. 2). In some cases, species with wider niches might repeatedly

271   choose the same partners across populations while species with narrower niches exert a random

272   pattern, indicating specialists and generalists, respectively. Thus, we argue that measures of local

273   and regional specialization, together with a null model approach, can provide a robust evaluation of

274   species specialization by including information on whether the identity of interaction partners

275   change across local populations.

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286

287   **Author contributions**

288   The first and second author contributed equally to this paper.

289

290 Figure 1. Mean local specialization ($d'_{s,local}$) and regional specialization ($d'_{s,meta}$) are strongly

291 positively correlated in both Brazil and the Canary islands. Plants and pollinators are represented by

292 blue and red points, respectively. The size of the data points indicate the number of co-occurring

293 species (i.e. the number of potential interaction partners in the metaweb). Note that plants are

294 generally more specialized than pollinators.

295

296 Figure 2. Null model analysis on expected regional interaction richness vs. observed regional

297 interaction richness (γ_s). A z-score below -1.96 means that the species has significantly fewer

298 regional interaction partners than expected from random (link conservatism), and colored data

299 points fall below this threshold. Density curves indicate the distribution of points across the spectra.

300 Note that plants generally have more interaction partners (higher interaction richness) than

301 pollinators. Plants and pollinators are represented by blue and red points, respectively.

302

303 Figure 3. Z-scores and regional specialization ($d'_{s,meta}$) show significantly negative correlations for

304 pollinators in both Brazil (r = -0.34, p < 0.001) and the Canary Islands (r = -0.30, p = 0.009). These

305 are highlighted with trend lines. For the plant species, however, the relationships were non-

306 significant in both Brazil and the Canary Islands and trend lines have been omitted. Plants and

307 pollinators are represented by blue and red points, respectively.

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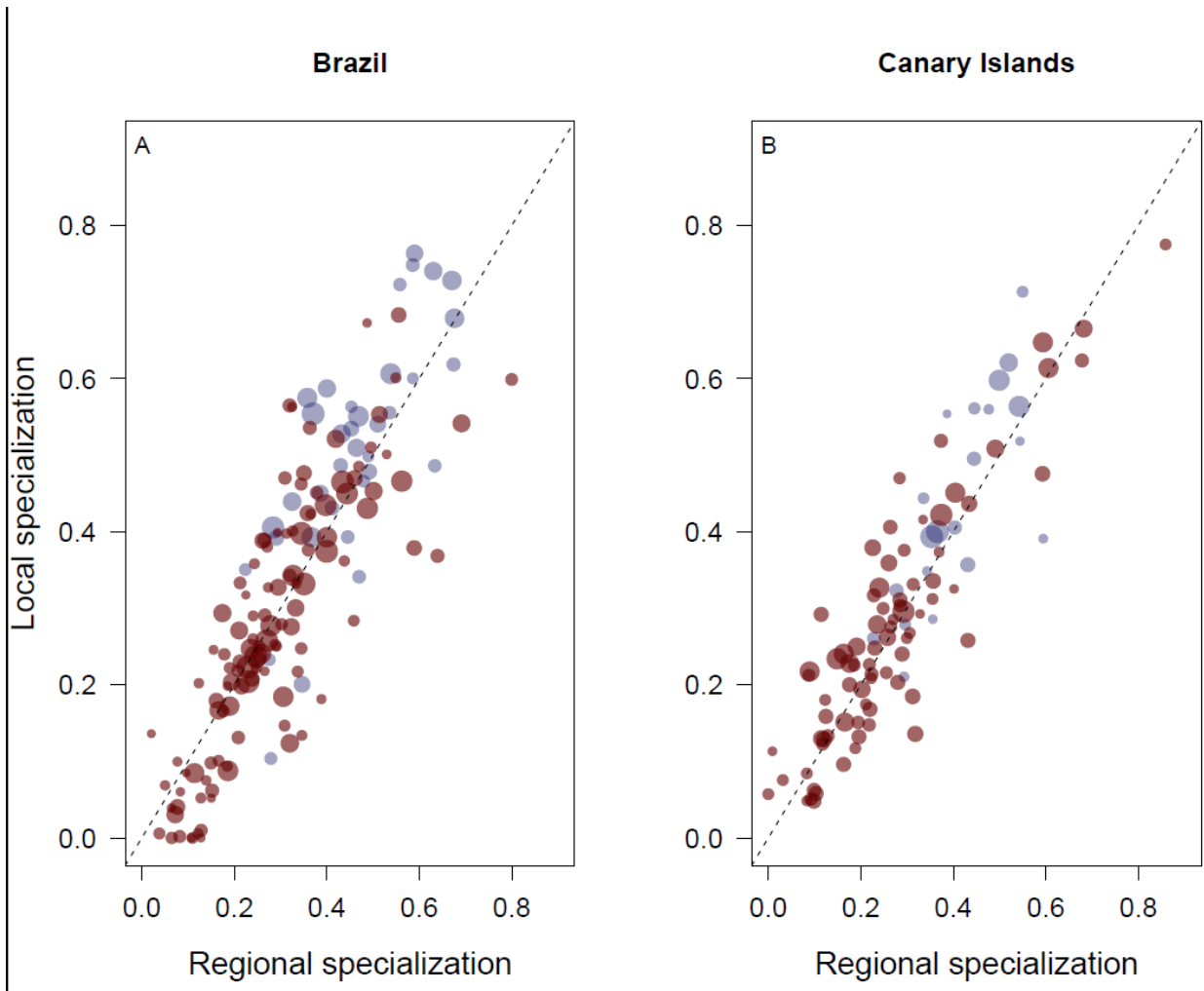386 1043-1060.

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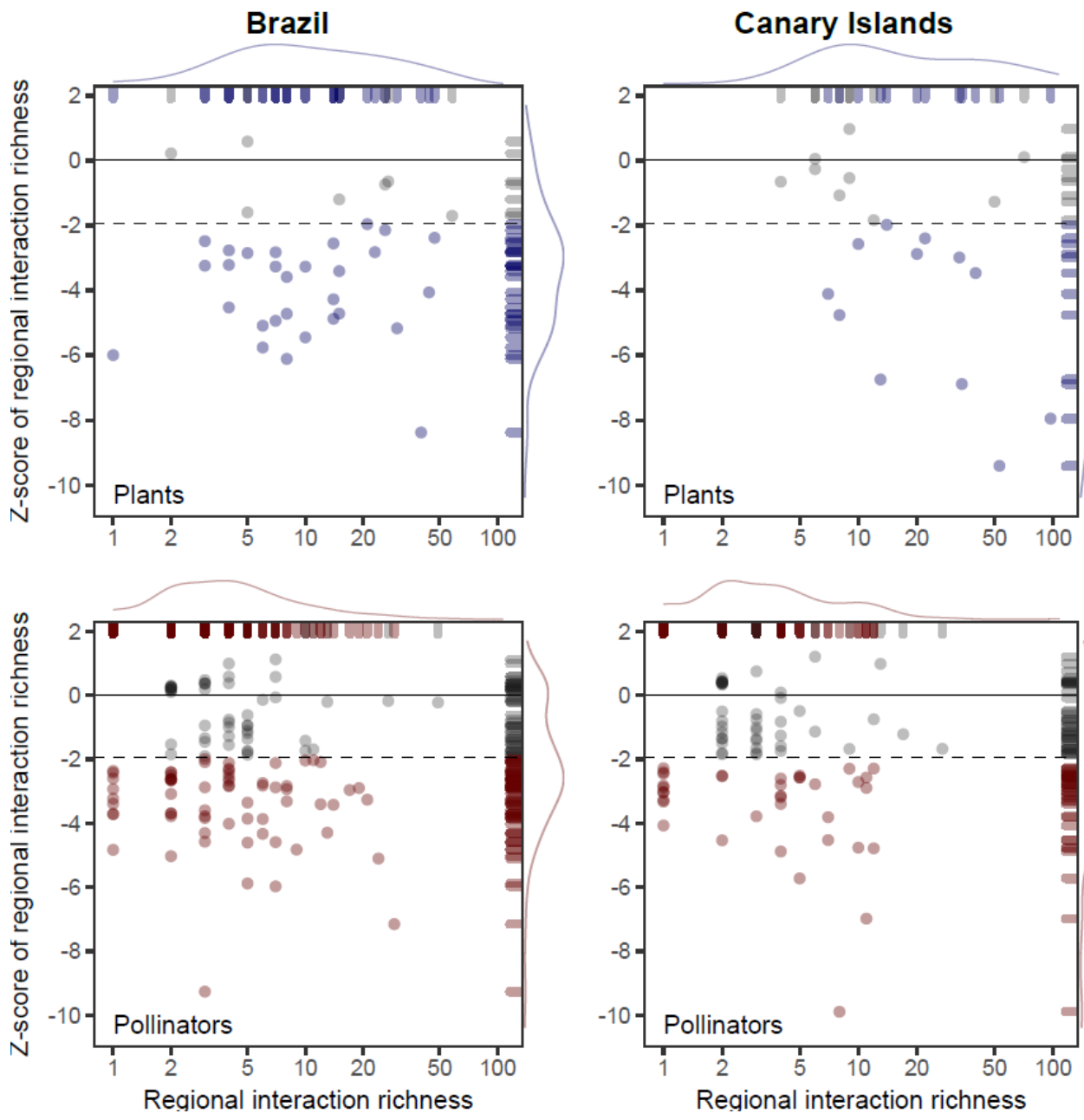
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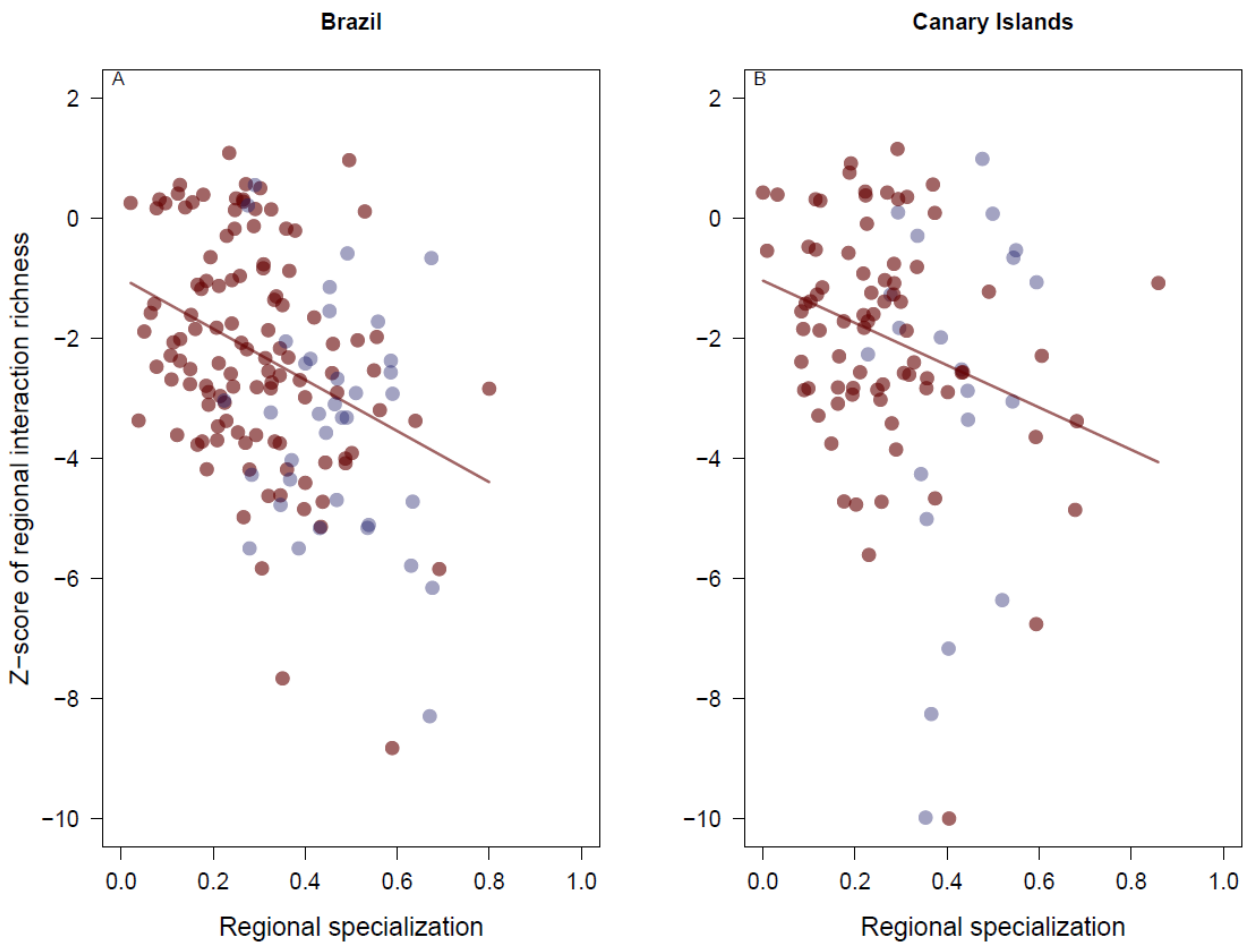**Brazil**

Canary Islands

402

403   Fig 1

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405

406   Fig 2

407

Fig 3