

1 The influence of biotic and abiotic drivers on arthropod co-occurrence 2 network topology in native forest remnants in the Azores

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16

17 Abstract

18 Island biota are in imminent threat from anthropogenic impacts. Of these impacts the negative effects
19 of exotic species on the taxonomic and functional diversity of the local fauna are of particularly major
20 concern. Aside from their impact on the diversity of native fauna, exotics may also have a detrimental
21 effect on native interactions which, in turn, can destabilise ecological networks. Species co-occurrence

22 networks are used to predict ecological interaction networks and utilised as tools to assess
23 environmental impacts on community structure. Here, we investigate the topological differences of the
24 arthropod co-occurrence networks among native forest fragments from seven Azorean islands and
25 reveal the influence of the abiotic environment and exotic species on these networks. We found that co-
26 occurrence networks were sensitive to environmental and community dissimilarities, showing a clear
27 separation between islands and pinpointed differences between indigenous and exotic networks. Most
28 exotics are little connected and exotic networks have a large proportion of unconnected species. The
29 resulting decreased connectance and the increased modularity with the increase of the proportions of
30 exotics in the networks suggests that most exotics have too low prevalence to show associations with
31 other species, and only a few dominants drive co-occurrences. Moreover, the proportion of negative
32 links, as indicators of competition, did not increase with the increase of exotics in the habitats,
33 suggesting that exotics occupied empty niches when they colonised native forest remnants. However,
34 when the theoretical networks consisting of only indigenous species were investigated both the number
35 of negative associations and modularity increased with the increase of exotics, suggesting obscure
36 competition and processes of network degradation. Since our study provides ample evidence for the
37 usefulness of co-occurrence network analysis in studying island ecosystems, we recommend the use of
38 this tool for ecosystem assessments, early warning systems and decision making in island biodiversity
39 conservation.

40 Significance statement

41 Global anthropogenic biodiversity decline affects islands to a disproportionately greater extent than
42 other ecosystems. One major cause of declining island biodiversity is the spread of exotic species which
43 may overcompete and replace native biota. In this study, we show, by using arthropod species co-
44 occurrence networks from the Azorean archipelago, that species association patterns reflect both

45 abiotic and biotic impacts and that the increasing proportion of exotics in an ecosystem seemingly has
46 little impact on association networks at large. However, when the effects on the association network of
47 solely indigenous species were scrutinised, signs of network degradation were observed, suggesting an
48 obscure, and most likely slow, negative impact of exotics on native arthropod assemblages. This
49 disintegration of the co-occurrence networks can be the first sign of disappearing interaction links
50 which, in turn, may jeopardise ecosystem function and can lead to regime shifts. In this work, we used a
51 unique long-term dataset collected across the islands of the Azorean archipelago with standardised
52 methodology. We built on the deep knowledge gathered over two decades on the ecology of species, as
53 well as on the ongoing processes shaping the islands' arthropod fauna, yet took a novel methodological
54 approach and disentangled hidden ecological processes of great ecological and conservation concern.

55 **Keywords**

56 exotic species, network complexity, modularity, island introductions, native fauna

57

58 Introduction

59 Plant and animal biodiversity are declining worldwide due to human-induced stresses and insects, as the
60 most diverse animal taxon, are critically impacted (Seibold et al. 2019, Wagner 2020, Cardoso et al.
61 2020, Hallmann et al. 2021). Current changes in insect species abundances with numerous extinctions
62 are caused in different degree by habitat loss (including for agriculture), pollution (including pesticides),
63 invasive species, climate change, direct exploitation and co-extinction of dependent species (Wagner
64 2020, Cardoso et al. 2020). Due to their isolated nature and fragile ecosystems, with a high number of
65 endemic species, islands are particularly threatened by these anthropogenic stressors and thus their
66 native species decline at an unprecedented pace (Gillespie and Roderick 2002, Fernández-Palacios et al.
67 2021). Whilst worldwide species declines can stem from a broad range of causes, the majority of threats
68 to native flora and fauna on islands originates from two major sources: disappearing natural habitats
69 due to changes in land use and the introduction of exotic species (Cardoso et al. 2010, Triantis et al.
70 2010, Borges et al. 2019, Pyšek et al. 2020, Fernández-Palacios et al. 2021). Whereas habitat destruction
71 most commonly results in direct loss of species, and is relatively easy to quantify and test its effects, the
72 consequences of spreading exotics are more difficult to study as it requires data on species interactions
73 (Sax et al. 2002, Borges et al. 2020). These processes are thus more complex to measure, and the subtle
74 changes can often only be unveiled by detailed community analysis. One of the first signs of such
75 community changes is the altered network structure of species associations and interactions (Delmas et
76 al. 2019). Indeed, interactions between species tend to break up on environmental stress sooner than
77 species get extinct or communities change substantially (Valiente-Banuet et al. 2015). Conventional
78 species richness or diversity-based studies may therefore be less effective in detecting changes than
79 those scrutinizing interspecific relationships, such as associations between species pairs (Kay et al.
80 2018).

81 Undeniably, species do not live in isolation, they form ecological associations and from these
82 associations ecological interactions emerge. These interactions underpin ecological functions, most of
83 which are crucial in delivering the ecosystem services humans vitally depend on (e.g. Albrecht et al.
84 2014, Hines et al. 2015). Since biodiversity decline and homogenisation unfolds in degrading interaction
85 networks (Laliberté and Tylianakis 2010, Burkle et al. 2013), which, in turn, decreases the stability and
86 resilience of ecosystems and results in loss of biodiversity function (Valiente-Banuet et al. 2015), the
87 importance of the protection of healthy ecological networks has been increasingly recognised (Tylianakis
88 et al. 2010, Heleno et al. 2020). Hence, there is an urgent need to understand how anthropogenic
89 impacts drive changes in interaction networks in order to precisely assess the effect of these altered
90 networks on ecosystem functions. However, despite the considerable amount of research to investigate
91 the anthropogenic impact on island biodiversity (Fernández-Palacios et al. 2021), little is known how
92 anthropogenic influence impacts the interactions of species within insular communities. Different
93 examples on how introduced exotic species can encroach indigenous network and sometimes even
94 replace native species have been documented (García et al. 2014) though.

95 Since interaction networks are notoriously difficult to discover, a simple mapping of species associations
96 based on their co-occurrence is often used as a proxy to predict interactions (e.g. Bohan et al. 2011,
97 2017). Although links in association networks not necessarily reflect biotic interactions (Blanchet et al.
98 2020), these networks nevertheless proved to be sensitive to environmental differences (Araújo et al.
99 2011, Lima-Mendez et al. 2015, Pozsgai et al. 2016) and to reflect anthropogenic impacts (e.g. Veech
100 2006, Kay et al. 2018, Elo et al. 2020). Thus, investigating relatively well-documented island faunas
101 through co-occurrence networks offers an evident way to study how environmental factors shape local
102 community assemblage structure and to predict the impact these factors can have on interaction
103 networks. Analysing the structure (topology) of these co-occurrence networks can both facilitate the
104 early detection of degrading effects and pinpointing the most vulnerable species and the most

105 threatening exotics which, in turn, has the potential to inform stakeholders and decision-makers to
106 maximize the success of conservation management (Delmas et al. 2019).

107 The Azores archipelago has been under intensive anthropogenic influence for nearly 600 years, with
108 most of its native habitat areas being converted to agricultural landscapes (Triantis et al. 2010) and a
109 high number of exotic species introduced (Borges et al. 2010). Taxonomic, functional and phylogenetic
110 diversity patterns and community structures of Azorean arthropods have been widely studied (Borges et
111 al. 2005, 2016, Rigal et al. 2018), but little attention focused on ecological networks of interspecific
112 associations (Rego et al. 2019, Valido and Olesen 2022). Yet, the availability of this unique dataset on the
113 arthropods of the Azores provides an opportunity to map detailed co-occurrence networks and compare
114 them among islands and relate them to biotic and abiotic environmental factors.

115 We hypothesize that although species pools among the Azorean islands are highly similar, due to the
116 presence of single island endemics the co-occurrence networks differ between islands (**H1**). We predict
117 that island association network structure will depend on the size of habitat remnants and their
118 proportion in the landscape as well as on the size of the island (**P1**). Moreover, island association
119 network topologies are also likely to be driven by abiotic factors, such as temperature, precipitation, or
120 altitude range (**P2**).

121 The other important factor potentially influencing the topology of co-occurrence networks is the
122 number and the proportion of non-native species in the community. Exotics in the Azores spread rapidly
123 (Borges et al. 2020) and although they have the potential to decrease the functional diversity of
124 assemblages (Boyer and Jetz 2014), exotics were found to increase the functional space of native
125 arthropod fauna in the Azorean ecosystems (Whittaker et al. 2014). The role they play in ecological
126 networks, and how their ratio compared to native fauna influences network structure is yet to be
127 determined. Thus, we hypothesized that association assembly between exotics and natives follows non-

128 random organisation rules (**H2**) and that exotic species influence the structure of co-occurrence
129 networks (**H3**). We predict that native and exotic species will not have the same role in the network,
130 thus their node properties will differ, (**P3**) and that the topology of the theoretical networks consisting
131 of exotic species only will have structural peculiarities (e.g. differing degree distribution) (**P4**).
132 Biotic stress (i.e. increased competition) can cause species to become rare, which results in these
133 species sharing fewer sites with others and thus having fewer co-occurrence links. Ultimately, these
134 species will not reach the detection threshold in samples and will be exempted from the networks (Kay
135 et al. 2018). This leads to a significant decline in the number of nodes but not so much in the number of
136 edges because of the low number of links to other species of the exempted species. Furthermore, the
137 introduction of exotics increases the number of species (nodes) but, since they are most commonly
138 habitat generalists, they are likely to co-occur with many other species, thus increasing the number of
139 interspecific associations (edges) at a greater pace than that of nodes (Fridley et al. 2007). Since both
140 processes increase the realised associations to all potential associations ratio (connectance), we
141 predicted that the connectance will increase, and the modularity decline, with the increasing number of
142 exotics (**P5**). We also anticipated that, if competitive exclusion is a major factor driving associations, the
143 proportion of negative edges among all edges will increase with the increasing number of exotics (**P6**).

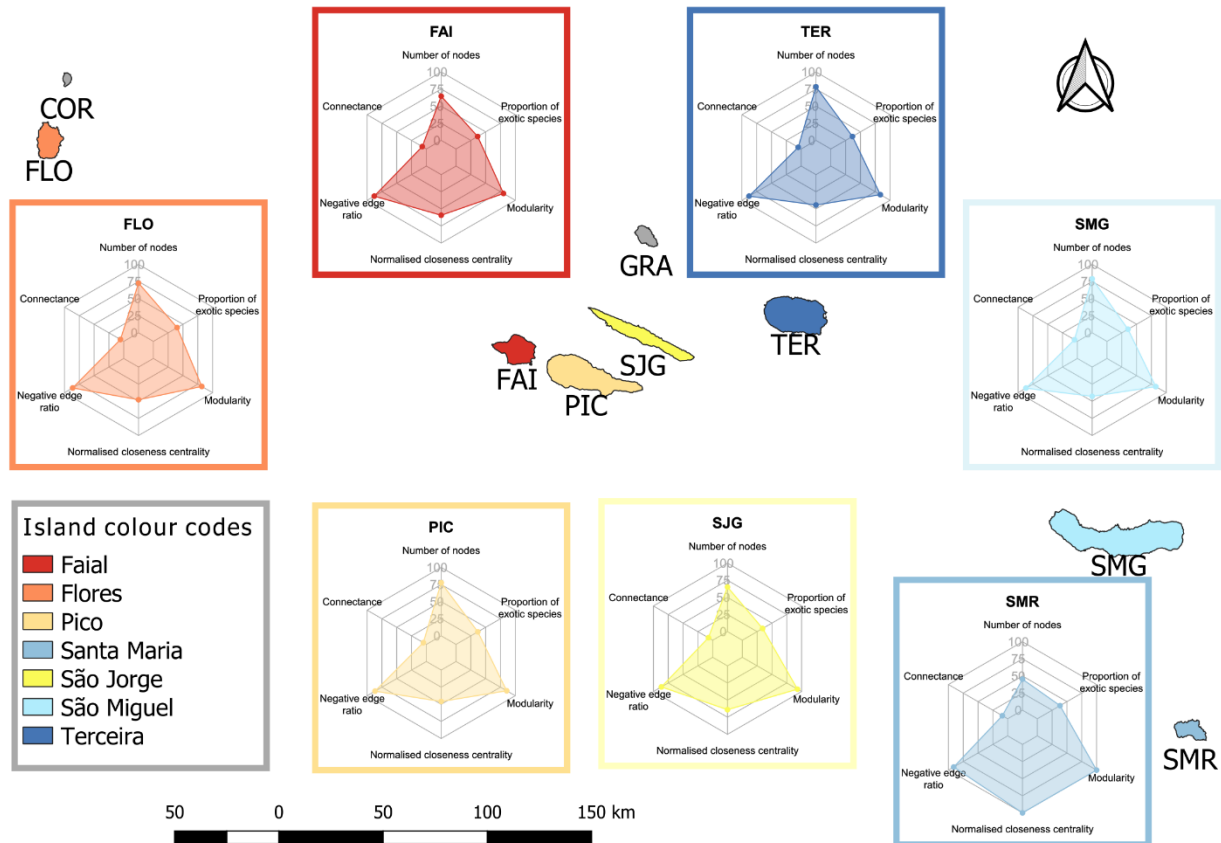
144 Materials and Methods

145 Arthropod sampling followed the 'Biodiversity of Arthropods from the Laurisilva of the Azores' (BALA)
146 protocol (Borges et al. 2005, 2006, 2016, Gaspar et al. 2008). Arthropods were collected in native
147 Laurisilva forest remnants on seven islands of the Azores archipelago (Faial, Flores, Pico, Santa Maria,
148 São Jorge, São Miguel, Terceira, Figure 1) from 1999 to 2002 (BALA I) (Borges et al. 2005) and in 2010
149 and 2011 (BALA II) (Borges et al. 2016). Altogether unique 91 transects were sampled, at 116 sampling
150 occasions, 81 in BALA I and 35 in BALA II. Twenty-five sites from BALA I were repeatedly sampled in

151 BALA II. In order to maximise the coverage of sampled diversity, two complementary methods were
152 applied: pitfall trapping was used to sample ground-dwelling arthropods and vegetation beating was
153 used to collect canopy-dwelling arthropods. In each forest patch, 30 pitfall traps were placed along a
154 150-meter long transect. Of the 30 traps, 15 were filled with Turquin (a mixture of dark beer, chloral
155 hydrate, formalin and glacial acetic acid) and the other 15 with ethylene-glycol. In each transect, ten
156 beating samples were taken from the three most common native woody plant species. The most
157 common trees and shrubs sampled were *Juniperus brevifolia* (Cupressaceae), *Erica azorica* (Ericaceae),
158 *Ilex azorica* (Aquifoliaceae), *Laurus azorica* (Lauraceae) and *Vaccinium cylindraceum* (Ericaceae) (Ribeiro
159 et al. 2005, Gaspar et al. 2008).

160 *Environmental variables*

161 The environmental variables were obtained from the CIELO model (Azevedo et al. 1999). This is a
162 physical model based on the transformations experienced by an air mass crossing over a mountain, and
163 simulates the evolution of an air parcel's physical properties starting from the sea level up to the
164 mountain. The model has been developed in order to produce high-resolution fields of the elemental
165 climatic variables (pressure, temperature, rainfall, relative humidity, etc.) using a grid resolution of 100
166 by 100 m cell size (for more detail see also Borges et al., 2006).



167
 168 **Figure 1. Map of the Azorean archipelago and the basic characteristics of the island co-occurrence**
 169 **networks. Islands are colour coded and squares with borders of corresponding colours contain radar**
 170 **charts showing (clockwise from the top) 1) the percentage of island species richness to the species**
 171 **richness in the meta-network, 2) the percentage of exotic species to the island species richness, 3) the**
 172 **island modularity as a percentage of the maximum modularity of all islands, .4) the normalised**
 173 **closeness centrality of the island as a percentage of the maximum normalised closeness centrality of**
 174 **all islands, 5) the percentage of negative edges of all edges in an island, 6) connectance of a network.**
 175 **Island abbreviations: FAI – Faial, FLO – Flores, PIC – Pico, SJG – São Jorge, SMG – São Miguel, SMR –**
 176 **Santa Maria, TER – Terceira.**

177

178 *Network estimation and statistical analysis*

179 A species-site matrix was used as a baseline dataset to generate a large meta-network, containing all

180 species abundance data collected from all islands and sampling sites with the two sampling periods

181 separated. When the ecological functions of adults and juvenile stages were substantially different,

182 adults and juveniles of the same species were recorded separately (e.g. Lepidoptera). Based on Borges

183 et al (2016), each species was categorised as either endemic, non-endemic but native (termed as native
184 henceforth), or exotic species, and higher taxonomic levels, such as family, order, and class, were also
185 assigned to them. Natives and endemics were sometimes merged and referred together as 'indigenous'
186 species. Species whose nativity status was unknown remained included in the overall species numbers
187 but they were not categorised into either indigenous or exotics and thus they did not inflate the number
188 of any of those groups. Species with less than ten individuals in overall abundance and those occurring
189 at less than three sampling sites were removed and excluded from the further analysis.

190 Due to methodological constrains, abundances were converted to binary (i.e. presence-absence) data
191 and were used in the co-occurrence analysis. Two co-occurrence networks, one for the years of BALA I
192 and one for those of BALA II, were generated using the *cooccur* package (Griffith et al. 2016) in an R
193 programming environment (R Core Team 2012). The union of the two networks (i.e. merging all nodes
194 and edges from both networks), a meta-network, consisting of species (represented as nodes) and their
195 predicted associations (represented as links or edges) served as a base of our further analysis.

196 The association detecting method provided by the R package uses a probabilistic model based on
197 hypergeometric distribution to assess if species co-occur more or less frequently than expected by
198 mathematical chance. If a species pair occurs more often than random choice would predict, the
199 association between them is considered as positive. On contrary, if the observed co-occurrence
200 frequencies are lower than expected from random associations, they are considered as negatively
201 associated. A network of positive and negative links between species nodes is thus formed by iterating
202 through all potential species combinations. The probability for the species pair occurring together, as
203 well as the p-values for the association being negative or positive, are given. Species and corresponding
204 species pairs, which were expected to have less than one co-occurrence were removed prior to analysis.
205 Species pairs with completely random association (i.e. p-value > 0.05) and those with less than 25%
206 probability of co-occurring were removed from the generated network.

207 A series of 999 Erdős-Rényi random graphs with the same node number as our meta-network were
208 generated, their degree distributions were calculated and compared to the empirical degree distribution
209 of our meta-network to estimate the probability that our co-occurrence network is a random graph.

210 The meta-network was first split into seven subnetworks (henceforth island subnetworks). For each
211 island, only species occurring on that particular island were selected to the subnetwork as nodes, and
212 edges linking those species were retained from the meta-network. Subnetworks for each sampling site
213 (termed as site subnetworks hereafter) were also generated, using the same method. These sub-
214 networks were used when island networks, indigenous and exotic networks, and the node properties of
215 native and exotic species were compared (see below).

216 Commonly used measures to characterise network topological properties, such as the number of nodes
217 and edges, connectance, proportion of negative links, the proportion of isolated nodes, mean closeness
218 and betweenness centralities, and modularity (based on the ‘fast and greedy’ community detection
219 algorithm) were calculated. Similarly, node characteristics, such as the number of edges connecting
220 other nodes (degree), the proportion of degree to the number of all nodes (relative degree); the number
221 of negative edges (vulnerability) and the proportion of those to the relative degree (relative
222 vulnerability); betweenness, closeness centralities were also computed, with the help of the igraph
223 package (Csárdi and Nepusz 2006). Since most of these measures strongly depend on the number of
224 nodes (i.e. show high correlation), a z-score normalised version of each centrality measure was also
225 calculated. During the process of excluding highly correlating variables (Spearman’s $p < 0.05$, Spearman’s
226 $Rho > 0.6$ or Spearman’s $Rho < -0.6$) non-normalised versions of these variables were discarded and only
227 normalised values were included in the analysis. The process of network generation and the description
228 of all calculated network measures, the way how they were calculated, and their correlations are given
229 in Supplementary Material 1.

230 All network properties were calculated for each subnetwork, and node properties were calculated in
231 each subnetwork separately to all species, indigenous and introduced.

232 Site networks were used to compare island networks and to investigate their relationship to the island
233 area, the total native forest area, and the native forest to island area ratio, as well as to island-specific
234 climatic variables and the number of exotics and their ratio to the total species richness on the islands.
235 Significantly highly correlating environmental variables (Spearman's $p < 0.05$, Spearman's $Rho > |0.6|$)
236 were removed prior to the analysis. Since there is no settled methodology to compare networks to each
237 other, two different approaches were taken: 1) island networks were compared based on their
238 associated species pairs, where distance matrices were calculated using the Jaccard distance on
239 presence-absence matrices of species associations; and 2) based on the differences in their calculated
240 network properties. In this latter case, similarity matrices were calculated using the Euclidean distances
241 of z-score scaled network properties. Environmental variables were also z-score scaled and a stepwise
242 redundancy analysis (dbRDA) process was conducted to find the optimal model. Whether or not island
243 networks topologies were significantly different was tested using the corresponding distance matrices in
244 an Analysis Of Similarities (ANOSIM) test with 10000 permutations, with the help of the *anosim()*
245 function implemented in the *vegan* (Oksanen et al. 2010) R package. To controlling Type I Error arising
246 from multiple comparisons, p-values in pairwise comparisons were adjusted using the false discovery
247 rate (FDR) correction.

248 To test if link formation between either combination of endemic, native, and introduced species
249 occurred non-randomly, we generated 5000 networks in an iterative process with keeping the original
250 network structure but randomly assigning the origin status to species. The proportion of each
251 combination pair to the overall link number was calculated and one-sample t-tests were used to
252 compute p-values to determine if association frequencies between categories of native status can be
253 random. A similar permutational approach was used to test whether or not some combinations of

254 categories of native status are more or less likely to collect negative links than it would be expected
255 from random processes. In this latter case though the ratio of the negative links to the number of links
256 within each combination pair was calculated and compared to the randomised distribution, using one-
257 sample t-tests. To investigate if there are differences in the frequency of endemic, native, and
258 introduced species having association links with each other we compared the number of links between
259 each combination using Kruskal-Wallis tests, and pairwise Wilcox-tests with p-values adjusted according
260 to the FDR method.

261 The relationship between major network topology measures and the number and the proportion of
262 exotics in the communities was investigated using linear mixed models with the island identity set as the
263 random term using the `lmer()` function in the `lme4` package (Bates et al. 2015 p. 4). All proportion
264 variables were square-root transformed prior to regression to approximate normality. P-values were
265 estimated according to Satterthwaite's method, as implemented in the `lmerTest` package (Kuznetsova et
266 al. 2017) in R. Marginal and the conditional R² values were extracted using the `r.squaredGLMM()`
267 function in the `MuMIn` package (Barton 2020). Since indigenous and exotic species richness strongly
268 correlated, to better disentangle the effects of exotics, similar models as above were fitted on networks
269 consisting of native species only and residuals from these models were used to re-fit models between
270 node properties and the number and proportion of exotics.

271 Both network-related and node-related properties were compared between native and exotic species
272 using Kruskal-Wallis tests and pairwise Wilcox tests with p-values adjusted for multiple testing according
273 to the FDR method. Linear mixed-models as above were used to investigate the effect of exotics (both
274 number and proportion in the whole community) on indigenous networks only.

275 Results

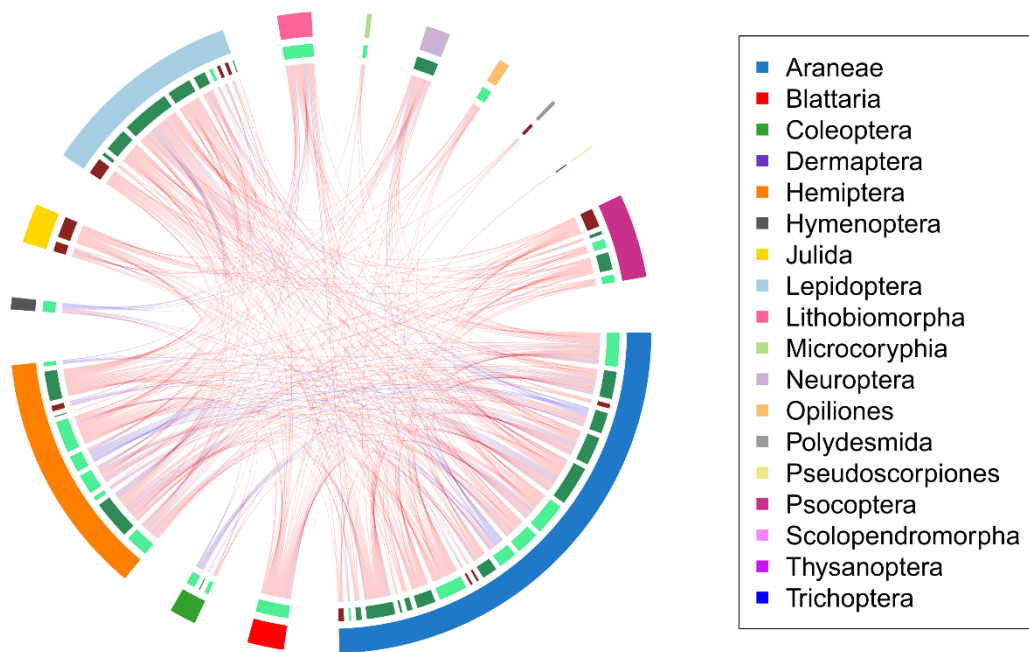
276 Our initial meta-network consisted of 161 nodes (species) and 398 edges, giving a 0.031 edge density
277 value. Of all species, 101 (52 endemics and 49 natives) were indigenous, 58 exotic, and 2 with an
278 unknown origin. Positive associations overwhelmingly dominated the meta-network (345 and 53
279 positive and negative links, respectively). The edge density and degree distribution of our meta-network
280 were significantly different from those that could have arisen from random networks. The degree of
281 nodes ranged from 1 to 44 with *Argyresthia atlanticella* Rebel, 1940, a moth species endemic to the
282 Azores, having the highest degree. *Lasius grandis* Forel, 1909, a native ant, and *Palliduphantes schmitzi*
283 (Kulczynski, 1899), an endemic spider, had the most negative link to other species (Figure 2,
284 Supplementary material 2).

285 Differences in island network topologies and driving factors

286 Islands networks significantly differed based on their topology measures (ANOSIM $p < 0.001$, $R = 0.175$).
287 After correcting for multiple comparisons, several pairwise differences between islands still remained
288 significant at the $p < 0.05$ significance threshold (Figure 3A-B). Although the number of nodes and the
289 number of edges were significantly different between islands (Kruskal-Wallis test, $p = 0.04$ and $p = 0.02$,
290 respectively), pairwise differences were not supported statistically. The connectance, the ratio of the
291 isolated nodes to all nodes, the relative vulnerability, normalised closeness and betweenness
292 centralities, and modularity, on the other hand, showed significant pairwise differences (Figure 1B,
293 Supplementary material 3). The number and proportion of the exotics on the islands, modelled mean
294 altitude, and the annual mean precipitation were the main factors driving these differences (dbRDA
295 model was significant at the $p=0.003$ level and explained 15.9% of constrained inertia) (Figure 3C). When
296 island networks were compared based on their association pairs, they differed significantly (ANOSIM p
297 < 0.001 , $R = 0.229$) but differences between individual islands were different than those when island

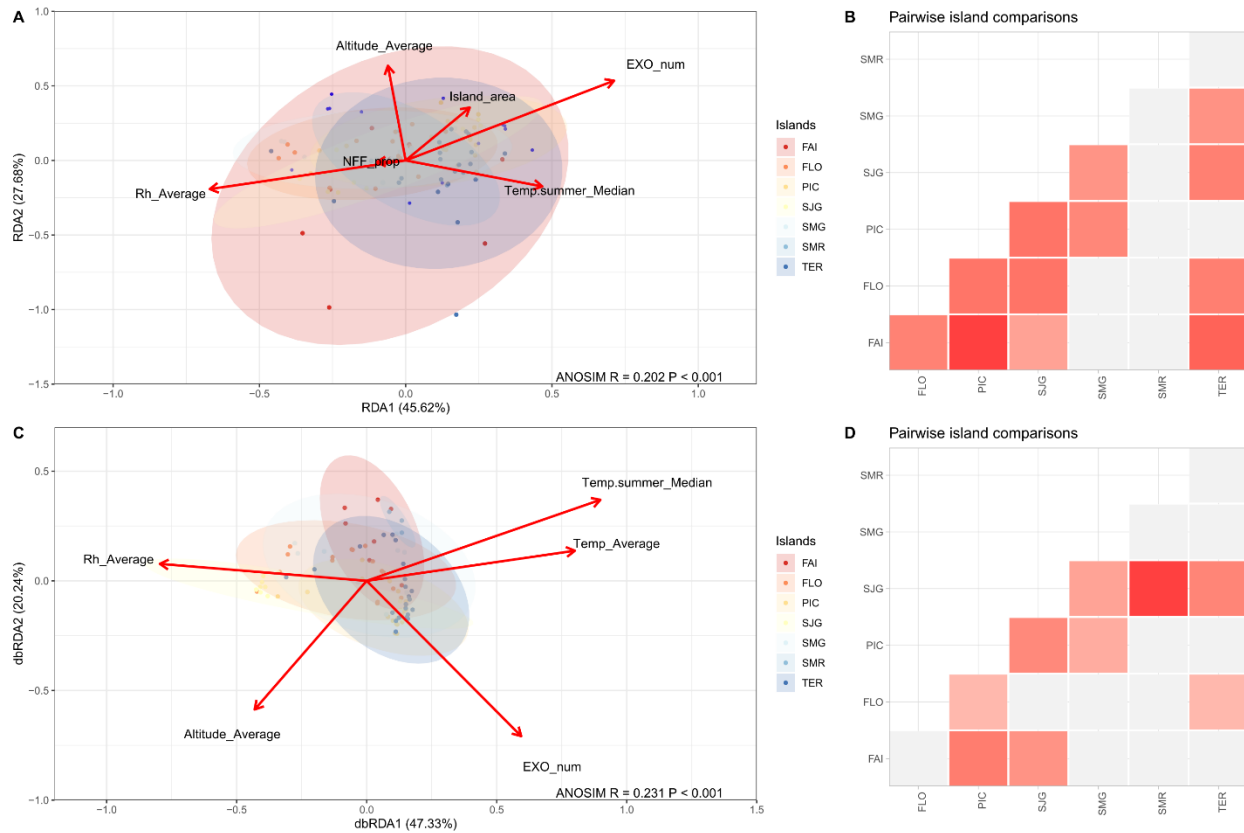
298 networks were compared based on their topology measures (Figure 3D). The major factors driving these
299 differences were the area of the native forest on an island, annual mean, and summer median
300 temperatures, and summer precipitation and average relative humidity (dbRDA model was significant at
301 the $p < 0.001$ level and explained 19.7% of constrained inertia).

Unconnected species



302
303 **Figure 2. Meta-network coloured according to higher taxa and nativity classes (A), and the number of**
304 **isolated species, grouped to endemics, natives, exotics, and unknown origins (B). Red links in the**
305 **network represent positive, blue links negative associations. Outer arc shows arthropod orders, inner**
306 **arc nativity classes. Arc segment length is proportional to the number of nodes the group has.**

307



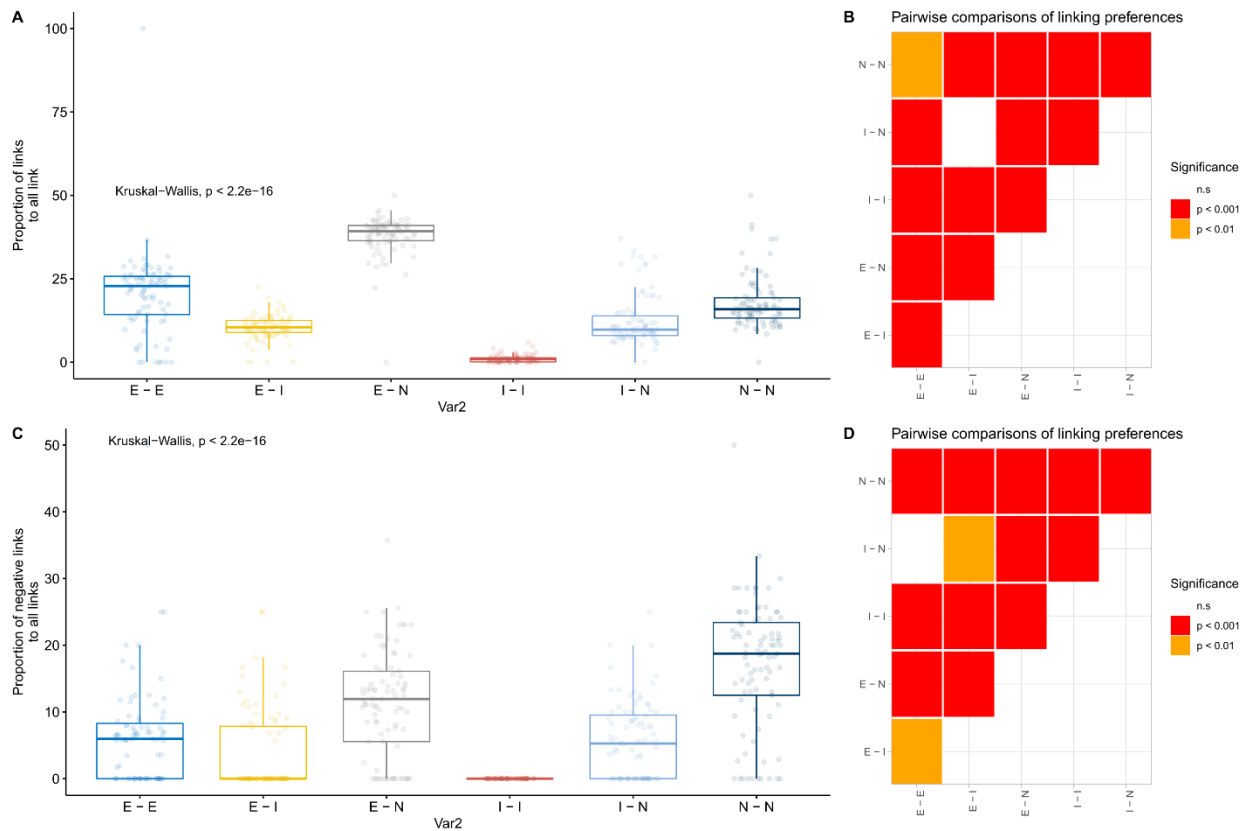
308
309 **Figure 3. The ordination and pairwise ANOSIM comparison of the island subnetworks based on their**
310 **network properties (A, B, respectively) and their species pair community (C< D, respectively).**

311

312 Effects of exotics on network topology

313 Simulations suggested that endemic to endemic, endemic to native, and native to native edges were less
314 common in the meta-network than could have arisen in networks with randomly reshuffled nativity
315 categories. At the same time, introduced species were more linked to the other groups than expected
316 by chance, including themselves. Moreover, natives had a lower chance than expected to have negative
317 links to both endemics and other natives. All other combination pairs showed a significantly greater
318 chance than random to have a higher proportion of negative links with each other (Supplementary
319 material 4). When linking frequencies were compared, endemic to endemic, native to native and
320 endemic to native links occurred in greater proportions than exotic to exotic, and exotic to
321 native/endemic (Figure 4A). In terms of the proportion of negative links, natives had negative

322 associations with themselves or with the other two categories in significantly higher proportions than
 323 any other combinations. Exotic to exotic negative links occurred in a significantly lower proportion than
 324 endemic to endemic ones (Figure 4B).
 325



326 **Figure 4. Preferential linking between endemic, native, and exotic species. The distribution of the**
 327 **proportion of both positive and negative links (A), and negative links only (C) to all links between**
 328 **nativity category pairs. Pairwise comparisons using pairwise Wilcox tests are shown on the right side**
 329 **(B, D, respectively). All p-values of pairwise Wilcox tests are adjusted according to the FDR method.**
 330

331
 332 Both the number of nodes and edges, as well as the ratio of negative edges showed significantly positive
 333 relationships with the number of exotics in the networks. On the contrary, the connectance, and the
 334 normalised closeness and betweenness centralities showed negative relationships (Table 1,
 335 Supplementary material 5).

336 **Table 1. R², f, and p-values for each network parameter as a function of the number and proportion of exotics in the community. Models ran**
 337 **for all site subnetworks, site subnetworks consisting of indigenous species only, and for the residuals of the model fit on indigenous species**
 338 **against the number of exotics.**

339

		Number of nodes	Number of edges	Proportion of isolated nodes	Proportion of negative edges	Mean degree	Connectance	Normalised closeness centrality	Normalised betweenness centrality	Modularity
Full network	R ²	0.676	0.371	0.173	0.289	0.217	0.445	0.303	0.254	0.261
– exotic number	F	159.371	29.589	3.814	12.493	2.417	63.17	38.641	4.093	1.392
	P	0	0	0.054	0.001	0.124	0	0	0.046	0.241
Full network	R ²	0.232	0.374	0.696	0.251	0.649	0.336	0.206	0.429	0.376
– exotic proportion	F	14.333	42.992	149.246	0.029	136.697	24.694	8.537	25.487	19.625
	P	0	0	0	0.866	0	0	0.004	0	0
Native network – exotic number	R ²	0.36	0.291	0.35	0.256	0.227	0.392	0.307	0.37	0.206
	F	41.103	15.74	5.89	0.058	2.807	45.073	30.493	4.241	4.446
	P	0	0	0.018	0.81	0.098	0	0	0.043	0.038
Native network – exotic proportion	R ²	0.282	0.38	0.455	0.378	0.521	0.254	0.179	0.308	0.275
	F	26.842	42.484	26.001	20.954	70.384	8.471	8.905	1.123	19.351
	P	0	0	0	0	0	0.005	0.004	0.293	0
Full network residuals – exotic number	R ²	0.597	0.063	0.199	0.034	0.233	0.197	0.106	0.065	0.128
	F	117.742	5.992	22.078	3.112	27.022	21.813	10.502	6.162	13.088
	P	0	0.016	0	0.081	0	0	0.002	0.015	0

340

341 However, when relationships between these measures and the proportion of exotic species in the
342 community were tested, only the proportion of isolated nodes and modularity revealed significantly
343 positive relationships but the number of nodes and edges, the mean degree, the ratio of negative edges,
344 the normalised betweenness centrality, and the connectance showed significantly negative
345 relationships. Relationships showed similar patterns when the proportions of exotics were fitted against
346 the residuals of the model fitted on the proportions of exotics against the properties of indigenous-only
347 networks (Table 1, Supplementary material 6).

348 [Differences between the node properties of indigenous and exotics](#)

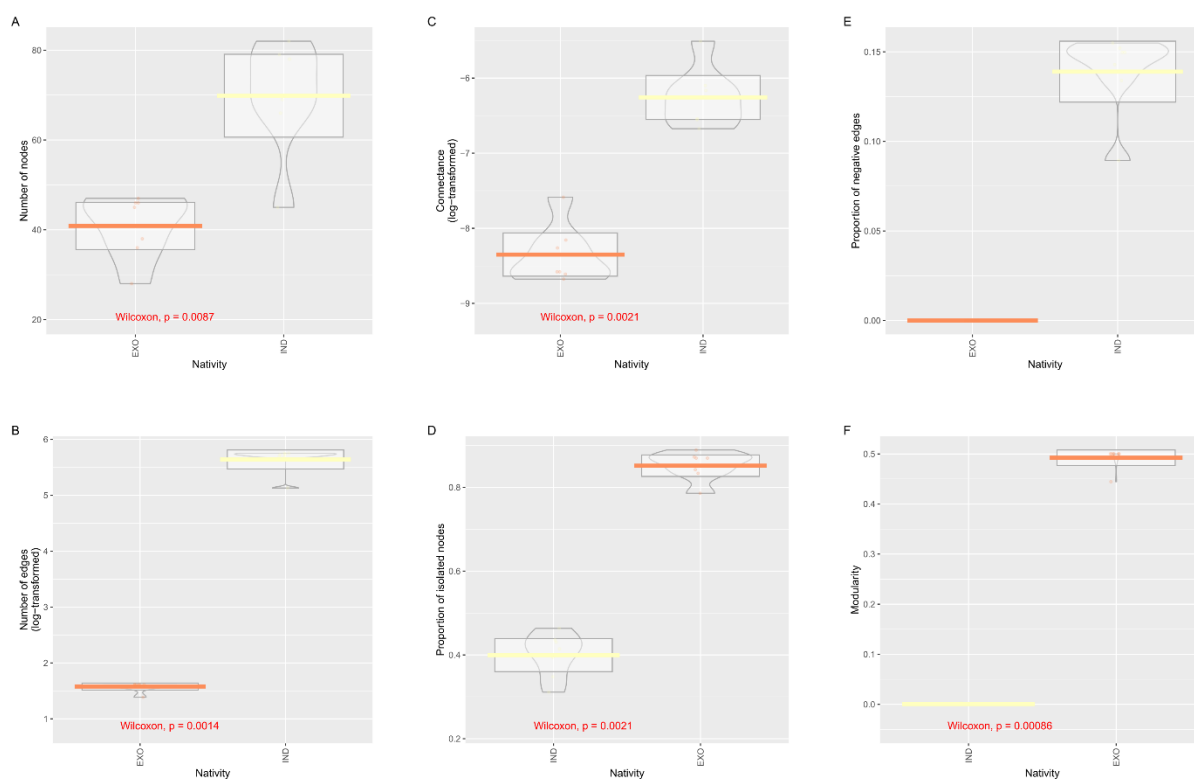
349 The mean and the relative degree, the normalised closeness and betweenness centralities, as well as the
350 number and ratio of positive links to other species, were greater for indigenous species in the meta-
351 network. However, indigenous and endemics only showed significant differences in their normalised
352 closeness centrality once isolated nodes (degree=0) were removed (Supplementary material 7)

353 [Differences in native and exotic networks](#)

354 When island subnetworks were split into networks consisting of only indigenous or exotic species,
355 differences emerged. Since there were more indigenous species than exotic, network topology
356 measures highly correlated to node number (such as number of edges, number of positive links, mean
357 degree etc.) were also significantly greater for native networks. Albeit they had no or little correlation to
358 the number of nodes, the proportion of isolated nodes, the connectance, and the normalised closeness
359 and betweenness centralities also showed differences (Figure 5).

360 When we investigated the effects of exotics on indigenous networks only, we found that number of
361 nodes (species number) and edges decreased with increasing exotic proportion. Exotics had a similarly
362 negative relationship with the mean degree and the normalised betweenness centrality. A positive

363 relationship was visible between the proportion of exotics and the proportion of isolated nodes, the
364 connectance, the normalised closeness centrality, and the modularity (Supplementary material 8).
365



366 **Figure 5. Comparison of network properties between indigenous-only and exotic-only networks:**
367 **number of nodes in the network (A), number of edges in the networks (B), the log-transformed value**
368 **of connectance (C), the proportion of the isolated nodes (D), the proportion of negative edges (E), and**
369 **the modularity based on the ‘fast and greedy’ community detection algorithm (F). Note that the**
370 **subnetworks in the figures are ordered according to the mean value of the focal network measure.**
371

372

373 Discussion

374 In this study, we analysed arthropod co-occurrence networks on seven Azorean islands and tested the
375 hypotheses that these networks reflect biogeographical patterns, are sensitive to abiotic environmental
376 differences, and that their topological features echo the imprint of exotic species in the community.

377 We found that co-occurrence networks of island arthropods showed non-random structuring patterns,
378 and that biogeography (i.e. island identity) was reflected on the network structure both when species
379 pairs, as network building blocks, and when network topological properties were compared (H1). Both
380 of our first and second predictions (P1, P2) that natural habitat size and abiotic factors drive network
381 structure in concert, were supported by the multivariate model. Thus, co-occurrence network analysis
382 seems to be suitable to detect inter-island differences and the dependence of network topology on
383 environmental factors is clear. Yet, although because island species richness strongly depends on the
384 size of the island (Whittaker et al. 2017) and natural habitat remnants behave as islands themselves
385 (Matthews 2021), we predicted natural habitat patch size will influence the structure of the association
386 networks, our results showed that the size of natural habitat has lower importance in shaping co-
387 occurrence networks than they have in driving community differences in indigenous Macaronesian
388 spiders (Cardoso et al. 2010). However, Cardoso et al. (2010) excluded exotic species from their analysis,
389 and in our cases, the number of exotics dominated the model, thus the disagreement with their findings
390 can be explained. Moreover, in our study, there was a moderately strong correlation between native
391 forest patch size and the number of exotics, which may have further obscured the clear effect of forest
392 patch size. Nevertheless, native habitat area and proportion showed a few, moderately strong,
393 correlations with network properties (Supplementary material 9), suggesting a limited power of this
394 variable to predict networks topologies.

395 Both the number and the proportion of exotics in the community influenced the structure of co-
396 occurrence networks (H3). As suggested by the species-area relationship (Whittaker et al. 2017), the
397 number of nodes showed a positive correlation with the island area, and so did the number of exotic
398 nodes. This is in line with the findings of Whittaker et al. (2014), who reported an increasing number of
399 exotics with increasing island area for both spiders and beetles in the Azores. The proportional increase
400 of edges did not match the increase of exotic nodes though, mostly because the newly recruited exotics

401 in the communities have no or few links to other species (i.e. the proportion of isolated increased). This
402 resulted in a general decline in the connectance, and, when the proportion of exotics to the entire
403 community was investigated, an increase of modularity; the opposite way we predicted (P5). These
404 trends are more pronounced when the effect of indigenous species is removed, suggesting that
405 indigenous mitigate changes in association network structure. Moreover, the declining number of nodes
406 as a function of the proportion of exotics in the community suggests uneven recruitment of new species
407 into the communities: when species richness increases, newcomers are mostly exotics. The fact that the
408 proportion of negative links did not show a significant relationship either as a function of the residuals
409 after the effect of natives had been removed, or when the proportion of the exotics was investigated
410 (i.e. P6 did not hold up), suggests that these species are rarely involved in direct competition with
411 indigenous ones. This pattern, and the high proportion of unconnected exotic species, on one hand,
412 suggest that the majority of the exotics do not occur in samples regularly enough to form detectable
413 associations with other species; only a few, dominant, exotics contribute to shaping network topologies
414 (Kay et al. 2018). This is in line with Florencio et al. (2015) who found that faunal homogenisation in the
415 Azores was not apparent from incidence-based community nestedness investigations, and reasoned
416 that although the prevalence of dominant exotic species was high, rare exotic species were replaced
417 both in space and time. On the other hand, our results support the earlier findings (Whittaker et al.
418 2014) that exotics, instead of competing with indigenous, occupied empty niches and increased the
419 realised trait space of the community (Rigal et al. 2018). However, the increasing proportion of negative
420 associations between indigenous species with the increasing proportion of exotics suggests an
421 increasing indigenous to indigenous competition as the effect of exotics.

422 We also showed a strong preferential linking in the community, and consequently, the assembly
423 structure was not random (H2). Endemic and native species linked to each other more frequently than
424 to exotics. This is somewhat controversial to what we expected, that since exotics are habitat generalists

425 and occur in many habitats, they will regularly co-occur with all species, and thus have a high number of
426 links (including negative ones). Similarly to the previous section, the reason for this may be the relatively
427 low number of exotic species being prevalent enough for association detection. Indeed, although native
428 habitat fragments are relatively small, most many exotic species may not reach the locations toward the
429 centre of patches where indigenous are frequent. Whether this happens through the resistance of local
430 communities to exotics or other reasons is yet to be investigated. Moreover, the number of endemic to
431 endemic links may have been inflated through species turnover within archipelago due to speciation.
432 Preferential linking through negative links was not obvious either and the trend in the proportion of
433 negative links in communities was also unclear (P6), suggesting little niche overlap and competition to
434 indigenous species in the Azores (e.g. Heleno et al. 2013).

435 Networks consisting of solely indigenous or exotic species also differed, as we predicted (P3). Exotic
436 species had different node properties than indigenous, but they showed a generally lower number of
437 links to other species and the proportion of negative links showed a significant relationship with the
438 number, but not with the proportion of exotics in the community (Thus, P7 was only partially upheld.).
439 This low degree resulted in lower connectance and centralities, and a greater proportion of isolated
440 nodes in exotic-only networks, compared to native-only networks (P4). As a consequence, connectance,
441 indeed, decreased and modularity increased with the increase of the number and proportion of exotic
442 species in communities (P5). Although, as seen above, these can be the results of exotic species blending
443 into indigenous communities without competing with indigenous species, from the high modularity of
444 exotic networks we also may speculate to their lower stability. Indeed, as a number of systems show
445 early signs of disintegration when stressed, particularly the weak links tend to break easily (Csermely
446 2004), increasing modularity is anticipated. Alarmingly, in our native-only networks, the modularity also
447 decreased with the increasing proportion of exotics in the community, as did the proportion of isolated
448 nodes and negative links. These suggest an obscure process of disintegration of native association

449 networks, driven by the increasing proportion of exotics, which, eventually may grow into a regime shift
450 (Rocha et al. 2015, Hui and Richardson 2018). This is in line with, Larson et al. (2016) and Hui (2021) who
451 showed that plant-pollinator interactions and fruit-bird mutualistic networks (respectively) change in a
452 similar manner when invaded by introduced species. Although co-occurrence networks cannot be
453 translated to interactions (Blanchet et al. 2020), species pairs that do not co-occur cannot interact
454 either, and hence these findings are highly concerning and in accordance with the recent observation
455 that exotic species diversity is increasing in Azorean native forests (Borges et al. 2020). Moreover, the
456 number of nodes was declining with the increasing proportion of exotics but the connectedness
457 increased, indicating that less connected species disappeared first, reinforcing the estimations by
458 Triantis et al. (2010) for a high level of extinction debt on the Azores.

459 Nonetheless, since species occurrences may also correlate with latent environmental factors, for
460 instance, the adjacent landscape of the natural forest patch, other drivers may also be in action. Thus,
461 before drawing casual links between exotic species' number and node properties and native species
462 richness, the underlying causes should be thoroughly investigated.

463 Our study provided ample evidence that island arthropod co-occurrence networks are sensitive to the
464 presence of exotic species and that the networks of exotic species differ from those of natives. These
465 structural sensitivities can make species co-occurrence networks ideal tools for providing early warning
466 signals of community changes induced by exotics. These signalling systems in the Anthropocene are
467 timely and essential to detect and mitigate deleterious effects of human-induced environmental change
468 on native habitats (Derocles et al. 2018, Fath et al. 2019). On the other hand, in the last decades, the
469 amount of biodiversity data multiplied, partly due to the advanced recording technology (e.g.
470 metabarcoding, environmental DNA), but also due to citizen science efforts. These untapped data could
471 be utilised for co-occurrence network analysis to understand large-scale ecological assembly rules and
472 geographic patterns of communities (Lima-Mendez et al. 2015, Ma et al. 2016) as well as for early

473 warning systems in conservation. A cautious approach has to be taken though. In our case, for instance,
474 negative links between species did not provide a useful measure for the effect of invasive species, most
475 likely because, as we speculated, the exotic arthropods on the Azores naturalised relatively well and
476 managed to exploit previously unoccupied niches causing little competition with natives, as it was
477 reported in the case of disturbed landscape such as managed pastures (Rigal et al., 2018). Whether or
478 not this process drives the patterns we found in native forests, can only be teased apart through
479 targeted field experiments.

480 Limitations

481 One of the main limitations of this study is inevitably derived from limitations of the method used;
482 although association networks are relatively easy to construct, they are not real-life interaction
483 networks, merely the predictions of them (Blanchet et al. 2020, Strydom et al. 2021). This is particularly
484 true because co-occurrence networks are scale dependent; although our sampling transects were
485 relatively small (150m), less mobile or microhabitat restricted species are unlikely to interact even at
486 that spatial scale. Therefore, a deeper insight is needed into the pairwise links and targeted tests or
487 literature searches should prove or disprove the existence of predicted interactions. Although the
488 dynamism of these networks is accounted for in our study (two separate networks were generated for
489 the two sampling rounds), deep dynamical processes are not analysed. This limitation is the direct
490 consequence of the lack of underpinning long-term datasets. This deficiency restricts our understanding
491 of processes overarching several decades, such as climate change, the temporal patterns of exotic
492 invasions, or continuous anthropogenic pressure, and likely prevents timely action to mitigate them
493 (Poisot et al. 2015, Tulloch et al. 2016). Moreover, species co-occurrence networks may also depend on
494 the seasonal dynamics of species of which we have little information. In this study, we did not focus on
495 differences resulting from taxonomical or functional grouping but these, most likely, exist. Whereas this

496 approach would plausibly be a fruitful area of research, a complete dataset of traits is crucial and,
497 besides taxonomy, a phylogenetic tree would also be desirable.

498 Conclusions

499 Here we show that changes in the topologies of arthropod co-occurrence networks in the Azores mirror
500 variances both in biotic and abiotic environments and thus they can help to gain a deeper insight into
501 natural and anthropogenic processes shaping island biogeography. Our findings demonstrate that
502 although Azorean exotic species have little competition to indigenous, their presence affects species
503 association networks and induce alarming reorganisations. Thus, developing standardised network
504 assessment methods and utilizing network information may help in developing early warning systems
505 for detecting the perilous impact of exotic species (Fath et al. 2019). Combining modern metabarcoding
506 techniques and standardised statistical methods for association network-building with cutting-edge
507 machine learning processes and literature-based trait data to routinely identify real-life interaction
508 networks would substantially advance our understanding of ecological assembly rules and improve our
509 predicting power to anticipate the future status of communities of high conservation interest (Evans et
510 al. 2016). Fully exploiting this toolkit is vital for island biodiversity conservation.

511

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643

644 Author contributions

645 G.P. and P.A.V.B. conceived the idea. Data were collected by the contributors of the BALA dataset
646 (Borges et al. 2016) and the environmental data were provided by E.B.A. Data analysis was conducted by

647 G.P., who also wrote the first version of the manuscript. The first draft was edited by P.C., F.R., M.B., and
648 P.A.V.B. The necessary funds were acquired by P.A.V.B. All authors contributed to editing the
649 manuscript. All authors have read the manuscript and agreed with its content.

650 [Data archiving statement](#)

651 Species list and distribution data are openly available in Borges et al. (2016). Computer codes, along with
652 summary environmental data will be made available on GitHub upon publication.

653 [Conflict of interest statement](#)

654 The authors claim no conflict of interest.

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663 .

- 664 **Supplementary material 1. Network measures calculated in the study and their ecological importance.**
- 665 **Supplementary material 2. List of all species in the meta-network with their taxonomic grouping**
666 **(Order, Family), nativity categorisation, and calculated node measures.**
- 667 **Supplementary material 3. Comparison of network properties of island subnetworks. Pirate plots**
668 **show the distribution of the data, the median, and the lower and higher quartiles. Kruskal-Wallis**
669 **tests are displayed, and pairwise differences are also shown if Wilcoxon tests are significant after**
670 **adjusting p-values with the FDR method.**
- 671 **Supplementary material 4. Preferential pairing between endemic, native, and exotic species. P-values**
672 **of the one-sided t-tests comparing the measured and expected values from the simulation process are**
673 **shown for all links and negative links only (A). The results of proportion tests between the frequencies**
674 **of links between exotics – natives and natives – natives (B), exotics – endemics and endemics –**
675 **endemics (C), and exotics – indigenous and indigenous – indigenous (D) species.**
- 676 **Supplementary material 5. Relationship between the number of exotic species and major network**
677 **properties in networks consisting of all species.**
- 678 **Supplementary material 6. Relationship between the number of exotic species and the residuals of**
679 **the model fitted against the major network properties in networks consisting of indigenous species**
680 **only.**
- 681 **Supplementary material 7. Differences between the node properties of indigenous and exotic species.**
- 682 **Supplementary material 8. Relationship between the number of exotic species and major network**
683 **properties in networks consisting of only native species.**
- 684 **Supplementary material 9. Correlation between all network properties, environmental variables, and**
685 **between network properties and environmental variables.**

