1   Uneven abundances determine nestedness in climbing plant-host

2   interaction networks

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28   Abstract

29   Nestedness is a common pattern in interaction networks. However, its ecological and

30   evolutionary meaning is under debate. Evidence shows that nestedness in mutualistic

31   networks may be just a consequence of the species–abundance distribution. This has

32   been questioned as abundance itself could be influenced by differences in generalism

33   between species. Host-parasite networks in plant communities also show nestedness

34   patterns, but their relationship with abundance has been seldom addressed. Importantly,

35   the potentially different effects of the number of interacting species (i.e. generalism

36   levels) on parasite and host abundance might help to understand the role of abundance

37   in determining both generalism and nestedness. Here we show that nestedness follows

38   abundance expectations in a climbing plant (structural parasite)- host interaction

39   network. Our results also point to a direct effect of abundance on both nestedness and

40   generalism levels because generalism does not deviate from abundance expectations for

41   both climbing plants and their hosts. Further, using an abundance index, which is

42   independent of species generalism, we found a similar level of disagreement between

43   generalism and abundance for both parties. Our findings evidence that the factors

44   underlying uneven abundance distributions can induce nestedness in interaction

45   networks. We stress the importance of neutral processes related to species dominance as

46   major determinants of nestedness in host-parasite networks.

47

48   **Keywords:** nestedness, host-parasite networks, species abundance, dominance, neutral

49   interaction processes, climbing-plant communities.

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Introduction

A central tenet in Ecology is to identify the mechanisms through which species interactions determine community properties in space and time. A popular way to address this issue is conceiving species interactions between two guilds (e.g. hosts and parasites or plants and pollinators) as bipartite networks, whose architectures reveal invariant interaction patterns across different ecosystems (Jordano et al., 2003), latitudinal gradients (Morris et al., 2014) or interaction types (Joppa et al., 2010). This has led to numerous studies trying to unravel the causes (e.g. Vázquez et al., 2009a), as well as the consequences (e.g. Bastolla et al., 2009) of these interaction structures. Among the potential set of patterns emerged from interaction networks, nestedness (i.e., the tendency of specialist species to interact with proper subsets of those interacting with generalist species; Bascompte et al., 2003) has received considerable attention. Nestedness has been largely reported in interaction networks from different ecosystems, including both mutualistic and host-parasite interactions (e.g. Joppa et al., 2010). Yet, despite its pervasiveness, the ecological and evolutionary significance of this pattern is still under debate.

Three main hypotheses have been proposed to account for the eco-evolutionary causes of nestedness (Fontaine, 2013; Ulrich et al., 2009). The first hypothesis suggest that nested interaction patterns would enhance community resilience (i.e. the speed to recover the equilibrum state after a disturbance, Okuyama and Holland, 2008; Thébault and Fontaine, 2010) and persistence (i.e. the number of existing species at equilibrium, Bastolla et al., 2009; Rohr et al., 2014; Saavedra and Stouffer, 2013; Thébault and Fontaine, 2010). However, little agreement has been reached about this possibility since no positive effects of nestedness on community resilience (Allesina and Tang, 2012; Staniczenko et al., 2013) and persistence (James et al., 2012; but see also Rohr et al.,

77 2014) were recorded afteraccounting for other significant factors (as interaction

78 strenght, Allesina and Tang, 2012; the number of mutualistic patners, James et al.,

79 2012; or interaction frequencies, Staniczenko et al., 2013). The second hypothesis

80 points to (co)evolutionary processes as responsible for nested patterns. Evidence for

81 this argument comes (i) from communities where the number of mutualistic patners

82 appear to be evolutionary conserved (Rezende et al., 2007), and (ii) from simulations

83 based on adaptive dynamics (McQuaid and Britton, 2013). Alternatively, some authors

84 have claimed for "nonadaptive community selection" to explain the preponderance of

85 nestedness patterns (Borrelli et al. 2015). However, no precise evolutionary mechanisms

86 have been directly related to the appearance and preponderance of nestedness (Fontaine,

87 2013). The third hypothesis attributes the origin of this pattern to neutral processes,

88 where interactions would be mainly governed by the relative abundance of the species

89 present in the community (neutral abundance hypothesis, e.g. Krishna et al., 2008;

90 Vázquez et al., 2009a). Here, the log-normal abundance distributions commonly found

91 in many communities would generate patterns of nested interactions (i.e. rare species

92 would be more likely to interact with the most abundant ones, which in turn would form

93 a core of highly-connected generalists). Despite the substantial evidence in this respect

94 (Canard et al., 2012; Dáttilo et al., 2013; Krishna et al., 2008; Sáyago et al., 2013;

95 Vázquez et al., 2009a), some authors cast doubts on this hypothesis due to the difficulty

96 in distinguishing whether a species is generalist due to its abundance or *vice versa* (e.g.

97 Fontaine, 2013; Krishna et al., 2008). Notice that, following a network vocabulary,

98 hereafter generalism will refer to a high number of observed interacting species,

99 independently of whether interacting species act as resources or consumers (e.g. a host

100 being attacked by many parasites will be named a generalist).

101   The work on nestedness in ecological interactions has been mainly developed

102   on mutualistic networks. This calls for questioning whether the proposed causes of

103   nested patterns hold for host-parasite networks (Graham et al., 2009; Lima et al., 2012;

104   Sfair et al., 2010). Among the three general hypotheses described above, only the

105   neutral–abundance hypothesis would hold for any interaction type (e.g. Canard et al.,

106   2012). In fact, nestedness –or any of its associated features– can be explained by the

107   distribution of species abundance in both host-parasite (Lima et al., 2012; Vázquez et

108   al., 2005; Vázquez et al., 2007) and mutualistic networks (e.g. Canard et al., 2012;

109   Dáttilo et al., 2013; Sáyago et al., 2013; Vázquez et al., 2009a). Importantly, the

110   problem of causality between abundance and generalism does not necessarily apply to

111   host-parasite networks. That is, while parasite species may increase their abundance by

112   increasing the number of host species used (i.e. their generalism), host species

113   abundance does not necessarily have to be positively influenced by the number of

114   parasite species using them. Such decoupled relationship between generalism and

115   abundance makes host-parasite networks suitable study models to assess whether there

116   is any direct effect of abundance on interaction nestedness.

117   In this work we investigate whether abundance may determine interaction

118   nestedness in host-parasite networks using a climbing plant–host network. Despite

119   climbing plants constitute important elements for the functioning and structure of forest

120   ecosystems (Schnitzer et al., 2015), their interaction networks have been scarcely

121   studied (Blick and Burns, 2009; Sfair et al., 2010; Blick and Burns, 2011). Climbing

122   plants are "structural parasites" of trees and shrubs (Stevens, 1987; Hegarty, 1991), so

123   they use (consume) the structural support resource provided by them, but may differ in

124   the range of hosts that they are able to use (Gianoli, 2015; Hegarty, 1991; Putz and

125   Holbrook, 1991). Importantly, while the abundance of a climbing plant species might be

126 enhanced by its generalism, host species should suffer the opposite effect (Carrasco-

127 Urra and Gianoli, 2009; Hegarty, 1991; Ingwell et al., 2010). This allowed us to delve

128 into the abundance–generalism causality problem. We firstly analyzed the consistency

129 between observed and expected nestedness based on abundance in the studied climbing

130 plant-host community. Secondly, given that the consequences of generalism are

131 different for parasite and host species, we also attempted to infer causality in the

132 relation between abundance and generalism. If abundance determines the realized

133 generalism in the local interactions, a strong and positive abundance–generalism

134 correlation for both hosts and climbing plants should be expected. On the contrary, if

135 generalism determines local abundance, the correlation between abundance and

136 generalism should be positive and strong for climbers but null (or even negative) for

137 their hosts.

138

Material and methods

140 *Study site and sampling design*

141   The study area is located in the Northern Central Iberian Plateau, Spain, within a

142 remnant temperate forest located at the margins of the Cega River (ETRS89 UTM 30N

143 coordinate: x 394682.55; y 4579316.17). This forest is included as a protected area in

144 the Natura Network 2000 (LIC-ES4180070). Although the area has a typical cool-

145 Mediterranean climate with 12 °C annual average temperature and 480 mm annual

146 precipitation, microclimate conditions associated with valley topography has allowed

147 the relict temperate vegetation to persist since the end of the last glacial period (Soriano

148 et al., 2002). The studied forest harbors over 50 species of trees, shrubs, and climbing

149 plants, including temperate shrubs such as *Lonicera xylosteum, Viburnum opulus,*

150 *Crataegus monogyna, Rhamnus cathartica, Cornus sanguinea, Prunus spinosa, Rubus*

151 *ulmifolius,* trees like *Corylus avellana, Populus nigra, Frangula alnus, Fraxinus*

152 *angustifolia* or *Alnus glutinosa,* and climbing plants such as *Hedera helix, Lonicera*

153 *peryclimenum, Humulus lupulus, Dioscorea communis,* or *Bryonia dioica* (Cuesta-Cano

154 et al., 2007).

155 To characterize the network of interactions between climbing plants and their

156 host trees we haphazardly established forty plots (10 m length, 5 m width) 200 m apart

157 from each other along the riparian forest of the Cega River. In each plot climber-host

158 interactions were recorded. An interaction between a climbing plant and a host species

159 was considered to occur when the attachment was evident, beyond the mere physical

160 contact between them. Interaction frequency was determined as the number of plots

161 where a species pair interacted. We used this measure of interaction frequency instead

162 of the number of interacting individuals because the difficulty in counting individuals

163 for some species could lead to skewed estimations (see Appendix 1 for photographs of

164 the community that illustrates this difficulty). Accordingly, the number of plots where a

165 given species occurred was used as a surrogate of species abundance in the community.

166 We preferred this proxy for abundance because: 1) estimates based on species cover

167 would lead to misleading estimations of the total surface available for climbing among

168 hosts (mainly due to differences in branch heights between trees and shrubs); 2)

169 estimations based on the observed number of interactions could lead to overestimation

170 of the effects of abundance (Vizentin-Bugoni et al., 2014); and 3) interaction frequency

171 was calculated as the number of plots where an interaction occurred, hence a suitable

172 and realistic abundance measure to contrast neutral expectations would be the number

173 of plots where species occur.

174

175 *Abundance and nestedness*

176   To explore the effect of species abundance on nestedness, we followed the

177   approach proposed by Vázquez et al. (2009a). This method projects the observed

178   number of interactions into a probability matrix based on species abundance. The

179   probability matrix was derived as the product of the vectors of host and climbing plant

180   abundance, with the host i and the climbing plant j receiving an interaction with a

181   probability based on the product of their relative abundance. The randomization

182   algorithm was run 1000 times, measuring nestedness using four different indices, based

183   on different definitions of nestedness. This approach allowed us to consider the different

184   aspects of nestedness due to the lack of a consensual definition for this concept

185   (Almeida-Neto et al., 2008; Ulrich et al., 2009). We employed two commonly used

186   nestedness indices for binary matrices: Temperature index (Temp) as implemented in

187   "BINMATNEST" (Rodríguez-Gironés and Santamaría, 2006) and "NODF"

188   (Almeida-Neto et al., 2008). For an easy comparison between indices, Temp values

189   were transformed as $N_{tm} = (100 - Temp)/100$ (Bascompte et al., 2003). Weighted

190   networks (i.e. those using interaction frequencies) have been found to be less affected

191   by unevenness in the sampling effort (Blüthgen, 2010). Therefore, two measures of

192   nestedness for quantitative matrices were also employed: "WINE" (Galeano et al.,

193   2009) and "Weighted NODF" (Almeida-Neto and Ulrich, 2011). Finally, since the

194   indices used can be related to matrix fill (or connectance; Almeida-Neto et al., 2008) the

195   procedure was repeated modifying the randomization algorithm to maintain the

196   observed matrix fill. This algorithm starts reassembling interactions until the observed

197   matrix fill is reached. Then, it allocates the remaining interactions within pairs of

198   species that have already received an interaction, also based on abundance probabilities

199   (Appendix 2).

200   We assumed that nestedness deviated from abundance expectations if observed

201   nestedness values were below 5 % and above 95 % of values obtained using null models

202   based on abundance iterations. Observed values being above the 95% of null model

203   values would point to other causes contributing to generate the nested pattern, while,

204   observed values below the 5% of null values would indicate other mechanisms (e.g.

205   reciprocal specialization) counteracting the effects of species abundance.

206

207   *Abundance vs. generalism*

208   Levels of generalism can be measured in several ways (Dormann, 2011), yet the number

209   of interaction partners (i.e. species degree; Jordano et al., 2003) is the measure more

210   directly related to nestedness patterns (at least in their binary form). Thus, we firstly

211   investigated whether the abundance–species degree relationship differs for climbing

212   plants and hosts. However, only attending to this measure the abundance-generalism

213   causality problem might still apply in the case of climbing plants. Further, even under a

214   non-neutral scenario host degree can be related to abundance simply because more

215   abundant host would have an increased probability to encounter climbing plants capable

216   to infect them (however this would also point, in any case, to important effects of

217   abundance). Hence, we also explored the relationship between abundance and the d'

218   specialization index (Blüthgen et al., 2006): e.g. a measure of specialism independent of

219   abundance. This index is a normalization between 0 and 1 of the Kullback-Leibler

220   relative entropy index (Kullback and Leibler, 1951), which is denoted as:

221
$$d_i = \sum_{j=1} \left(p'_{ij} \cdot ln \frac{p'_{ij}}{q_j} \right)$$

222   where p'_{ij} represents the frequency of interaction between the species $_i$ and species $_j$

223   divided by the total number of interactions of species $_i$, and q_j denotes the availability

224   of species $_j$, in our case calculated as its relative abundance (see Blüthgen et al., 2006

225   for details of the normalization procedure). Therefore, the index measures the deviation

226   between species use and species availability, regardless of the number of interactions

227   and, in turn, the effects of abundance. Species showing high deviations (i.e. specialists)

228   have values tending to 1, whilst those showing low deviations (i.e. generalists) have

229   values tending to 0. For the sake of simplicity we subtracted this index to 1 (i.e. 1 - d';

230   hereafter generalisation), to obtain higher values as generalisation level increases.

231   The Spearman's correlation coefficient was used to measure the correlation

232   among variables (i.e. between abundance and both species degree and generalization).

233   Further, as correlation does not imply causality the observed correlation coefficients

234   were also compared with those obtained in the null models based on abundance. A

235   significantly lower correlation was assumed if observed values fall below the lowest 5%

236   correlations of the null models. If generalism determines species abundance we should

237   find that the relationship between species generalisation and abundance is positive and

238   stronger than abundance expectations for climbing plants. In the case of hosts this

239   relationship should be similar or even lower than null model expectations based on

240   abundance – assuming that host fitness is either unaffected or strongly affected by

241   climbing plant infections, respectively. On the contrary, a low correlation between

242   generalization and abundance, together with a high correlation between species degree

243   and abundance (although matching abundance expectations) in both parties, would be

244   indicative of abundance as determinant of generalism.

245

246   All analyses were carried out in R environment (R core team, 2015). The indices of

247   nestedness, together with the d' index, were computed using the "bipartite" package

248   (Dormann et al. 2009), and the abundance-based null models were created using the

249 script provided in Vázquez et al. (2009) and a modified version of it to keep constant

250 matrix fill.

251

252 Results

253   We recorded a total of 26 host tree/shrub species, of which 24 (11 trees, 11

254 shrubs and two treelets) had associated climbing plants (Fig. 1). The only two species

255 that were not infested by climbers (*Pinus pinaster* and *Pyrus pyraster*) were actually

256 rare species –only occurring in one plot– and were thus excluded from the subsequent

257 analyses. On the other hand, ten climbing plant species were recorded, six herbaceous

258 vines and four woody climbers (Fig. 1).

259   Observed nestedness did not significantly deviate from the null models based on

260 abundance for all nestedness indices except NODF (N_{tm} = 0.75, P = 0.40; WINE = 0.52,

261 P = 0.39; and Weighted NODF = 18.1, P = 0.48; Fig. 2). NODF values fell below the

262 5% of null model values (NODF = 55.20, P = 0.004), which suggests that other factors

263 counteract the effects of abundance. However, this index was the most sensitive to

264 matrix fill. When matrix fill was accounted for, the observed NODF did not

265 significantly deviate from abundance-based null expectations (P = 0.15, Appendix 2).

266   Abundance and species degree were highly correlated for both parties

267 (Spearman's ρ = 0.84 and 0.88, for climbing plants and host respectively, Fig. 3a and

268 3b). In both cases the abundance–species degree correlations did not significantly

269 deviate from those obtained with the abundance-based null models (climbing plants:

270 mean null Spearman's ρ = 0.91, SD= 0.05, P = 0.892; host species: mean null

271 Spearman's ρ = 0.85, SD= 0.05, P = 0.226). Generalization levels were considerably

272 high in both cases (mean = 0.91, SD = 0.05 and mean = 0.85, SD = 0.12; for climbing

273 plants and hosts, respectively). However, it was weakly related with abundance for both

274   parties, being even negative in the case of climbing plants (Spearman's ρ = -0.1 and

275   0.10, for climbing plants and hosts respectively, Fig. 3c and 3d). These correlations

276   were never higher than null correlations based on abundance (climbing plants: mean

277   null Spearman's ρ = 0.71, SD= 0.18, P = 1; host species: mean null Spearman's ρ =

278   0.46, SD= 0.18, P = 0.961). Finally, generalization and species degree were not

279   significantly correlated for both climbing plants (Spearman's ρ = 0.30, P = 0.40) and

280   their hosts (Spearman's ρ =0.22, P = 0.31).

281

282   Discussion

283   Our results show that species abundance has a strong effect on the nestedness structure

284   of the studied parasite-host network. This relationship has been previously found for

285   mutualistic networks (Krishna et al., 2008; Vázquez et al. 2009a; Verdú and

286   Valiente-Banuet, 2011; Olito and Fox, 2014), but the causality problem between species

287   abundance and generalism has complicated the identification of the factor actually

288   driving the patterns of interaction nestedness in these networks (Krishna et al., 2008;

289   Fontaine, 2013). Parasite-host networks do not have this problem, at least in the case of

290   hosts, which allows delving into the causality of the abundance-generalism relationship.

291   Parasites can certainly benefit from being generalist by increasing the chance of

292   finding a suitable host, while hosts attacked by more species should not necessarily

293   show higher abundance or fitness. In this context, similar strong correlations between

294   abundance and species degree were recorded for climbing plants and their hosts, being

295   in both cases not significantly different from null expectations based on abundance

296   randomizations. These similarities between parasites and hosts point to abundance as

297   the main determinant of generalism in the studied interaction network. It could,

298   however, be argued that the abundance-generalism causality problem still holds for the

299   (structural) parasites. Yet, we found complementary evidence supporting species

300   abundance as the driver of generalism. Neither climbing plants nor their hosts showed a

301   significant relationship between generalization and both abundance and species degree.

302   Firstly, our results suggest that generalization levels does not have any apparent positive

303   impact on the abundance of climbing plants, as it is expected if abundance determines

304   generalism. Secondly, recorded results also show that species degree (which is the

305   measure of generalism most directly related to nestedness) is more strongly determined

306   by abundance than by generalization levels. The case of *V. vinifera* and *H. helix* clearly

307   exemplified these findings. The former is one of the species with highest generalisation

308   levels in the study site, showing also one of the lowest values for both species degree

309   and abundance (see Fig. 3). Conversely, *H. helix* shows the lowest generalisation level,

310   although it is one of the species with highest values of species degree and abundance

311   (see Fig. 3). Thus, it seems that the probability of infestation by a climbing plant

312   depends on the host abundance, while climbing plants are in general opportunistic

313   (Blick and Burns, 2011), being able to colonize new hosts as long as they have access

314   to them – regardless of different generalization levels. These results confirm the role of

315   abundance as a key factor for network properties at both the species (generalism) and

316   structural levels (nestedness) in the study system. Note that during the preparation of

317   this manuscript Fort et al. (2016) published further evidence of abundance as a cause of

318   generalism for mutualistic networks, which further support our findings.

319   Opposing to the hypothesis of abundance as determinant of nestedness patterns,

320   Suweis et al. (2013) found that increases in species abundance –accompanied by

321   increases in dominance– lead to increases in nestedness as a consequence of positive

322   interactions. Therefore they proposed that nestedness in mutualistic networks could be a

323   consequence of optimizing species abundance across all species present in the

324 community. However, our results do not support such interpretation –at least for host-

325 parasite networks– as we found that when assuming neutral interactions similar levels

326 of nestedness to empirical values can be recovered and that abundance determines

327 species degree. In fact, Blüthgen et al. (2008) found that higher degrees of dominance

328 lead to higher degrees of nestedness, simply through neutral processes in the allocation

329 of interactions, which would apply to networks of any sign (i.e. either mutualistic or

330 antagonistic). It could be argued that the mechanisms underpinning the interaction

331 patterns in mutualistic and antagonistic networks are fundamentally different, so the

332 agreement between abundance and nestedness would result from contrasting

333 mechanisms in different types of networks. However, following the principle of

334 parsimony (Sober, 1981; see also Blüthgen et al., 2008), it seems more likely that the

335 effect of abundance on nestedness is a direct result of the neutral distribution of

336 interactions throughout all the individuals present in the community. Indeed, a number

337 of studies in several types of networks have found similar effects of species abundance

338 (Vázquez et al., 2009a; Verdú and Valiente-Banuet, 2011; Lima et al., 2012; Dáttilo et

339 al., 2013; Sáyago et al., 2013; Olito and Fox, 2014; but see Canard et al., 2014;

340 Vizentin-Bugoni et al., 2014), supporting the general validity of this hypothesis for

341 explaining the nestedness structure of interaction networks.

342   Contrary to our findings, Canard et al. (2014) found that abundance did not

343 explain nestedness variation in ectoparasite-rodent networks. Nevertheless, it is

344 important to note that these results were based on the NODF index. In fact, the results

345 of the present study using such index were similar to those of Canard et al. (2014), but

346 we have also shown that they were strongly affected by matrix fill. When controlling for

347 matrix filling, nestedness did not significantly deviate from abundance expectations.

348 Thus, it is likely that the lack of relationship found by Canard et al. (2014) resulted from

349   the particular index they used. Indeed, these authors found good agreement between

350   abundance and network properties related to nestedness, such as levels of specialization.

351   Alternatively, there are clear biological differences between their study system and ours,

352   which could also partly explain the contrasting results. Ectoparasite-rodent interactions

353   are more intimate than climbing plant-host interactions, and interaction intimacy may

354   influence network structure significantly (Guimaraes et al., 2007; Pires and Guimarães,

355   2013).

356   It is important to note, that other factors besides species dominance and neutral

357   allocation of interactions could influence network properties, as the mentioned

358   interaction intimacy. In this sense, we do not argue that abundance is the sole factor

359   determining network structure. Other factors are known to contribute to network

360   properties, such as the spatio-temporal overlapping of individuals from different levels

361   (e.g. Vázquez et al., 2009a; Olito and Fox, 2014), trait matching (e.g. Vizentin-Bugoni

362   et al., 2014) or trait mismatching (Verdú and Valiente-Banuet, 2011). Hence, it seems

363   clear that both neutral and niche processes act together as drivers of interaction patterns.

364   Indeed, current efforts are focused on disentangling the relative contribution of both

365   types of processes to network structure (Vázquez et al., 2009a; Verdú and

366   Valiente-Banuet, 2011; Sáyago et al., 2013; Olito and Fox, 2014; Vizentin-Bugoni et

367   al., 2014). Here, we argue that future research efforts should also pay attention to which

368   combinations of the intrinsic conditions of ecological communities boost either neutral

369   or niche-based processes. As we have shown, these intrinsic conditions include uneven

370   abundance distributions, but spatial heterogeneity, intimacy levels, functional trait

371   diversity, phylogenetic diversity and even the diversity on the species geographic

372   affinities (Calatayud et al. 2016) should additionally be considered when analyzing

373   interaction networks. Detailed information from a diverse array of study systems is yet

374 required to determine the hierarchical contribution of all these factors to neutral or

375 niche-based processes (Vázquez et al., 2009b). Before such data are available, we

376 propose that the species-abundance distribution plays a major role in promoting

377 different levels of nestedness through the neutral allocation of species interactions.

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533

534   Figures

535   **Figure 1.** Climbing plant-host tree/shrub interaction network. Black boxes represent

536   species and their width corresponds to the number of single interactions (i.e. species

537   strength). Grey lines represent species interactions and line thickness indicates the

538   interaction frequency for each pair of interacting species. On the left, tree and shrub host

539   species are depicted by numbers (tr = tree, sh = shrub, tl = treelet). 1: *Ligustrum vulgare*

540   (sh), 2: *Pteridium aquilinum* (sh), 3: *Lonicera xylosteum* (sh), 4: *Crataegus monogyna*

541   (tl), 5: *Viburnum opulus* (sh), 6: *Populus nigra* (tr), 7: *Corylus avellana* (tr), 8: *Cornus*

542   *sanguinea* (sh), 9: *Prunus spinosa* (sh), 10: *Rhamnus cathartica* (sh), 11: *Fraxinus*

543   *angustifolia* (tr), 12: *Salix atrocinerea* (tr), 13: *Alnus glutinosa* (tr), 14: *Rubus ulmifolius*

544   (sh), 15: *Betula pendula* (tr), 16: *Salix purpurea* (tl), 17: *Rosa canina* (sh), 18: *Quercus*

545   *faginea* (tr), 19: *Frangula alnus* (tr), 20: *Alnus incana* (tr), 21: *Euonymus europaeus*

546   (tr), 22: *Juniperus communis* (sh), 23: *Salix fragilis* (tr), 24: *Cytisus scoparius* (sh). On

547   the right, climbing plants are depicted by letters (hv = herbaceous vine, wv = woody

548   vine). a: *Lonicera periclymenum* (wv), b: *Hedera helix* (wv), c: *Humulus lupulus* (hv),

549   d: *Galium aparine* (hv), e: *Vicia villosa* (hv), f: *Dioscorea communis* (hv), g: *Solanum*

550   *dulcamara* (wv), h: *Vitis vinifera* (wv), i: *Bryonia dioica* (hv), j: *Lathyrus sativus* (hv).

551

552   **Figure 2.** Distribution of nestedness based on species abundance among 1000 simulated

553   networks for the four used indices of nestedness: a) N_{tm}, b) NODF, c) WINE and d)

554   weighted NODF. The observed values (dotted lines) are above the lowest 5% and below

555   the highest 95% of the nestedness values derived from the abundance-based null models

556   (depicted in black). The only exception is NODF where the observed values are below

557   the lowest 5 % null values (but see also Appendix 2).

558 **Figure 3.** Relationships between abundance and both species degree (a and b, for

559 climbing plants and hosts respectively) and generalisation (c and d, for climbing plants

560 and hosts respectively). The points corresponding to *H. helix* and *V. vinifera* are labeled

561 as examples showing low and high generalisation levels (respectively), but high and low

562 values of abundance and species degree (also respectively, see main text). The

563 histogram on the bottom of each scatterplot represents the distribution Spearman's ρ

564 correlation coefficients between abundance and generalism estimates based on species

565 abundance among 1000 simulated networks. The observed values (dotted lines) are

566 above the lowest 5 % of the coefficients derived from the null models (depicted in

567 black) in the case of species degree, whereas observed values are below the lowest 5 %

568 null values for generalisation level.
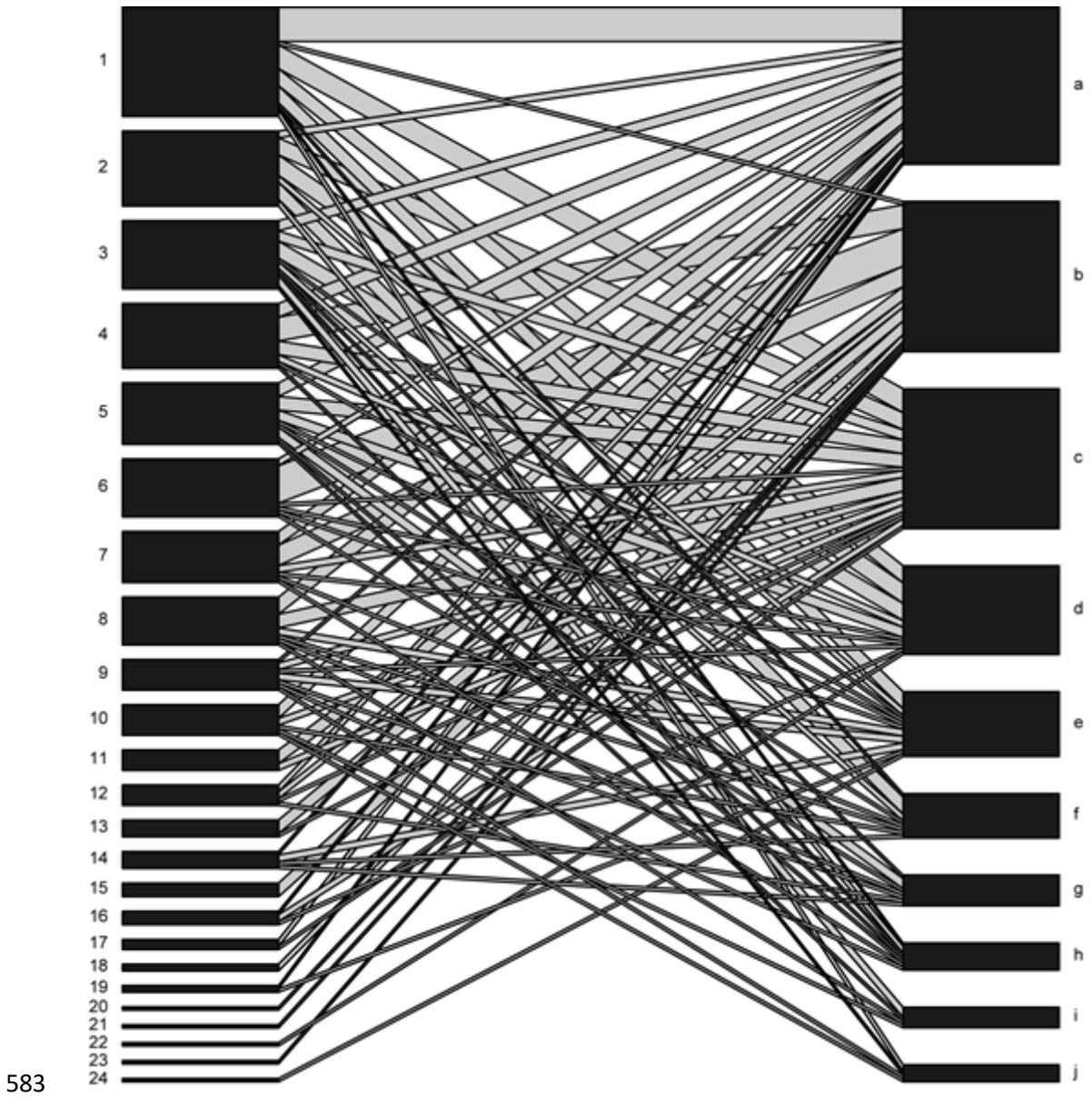
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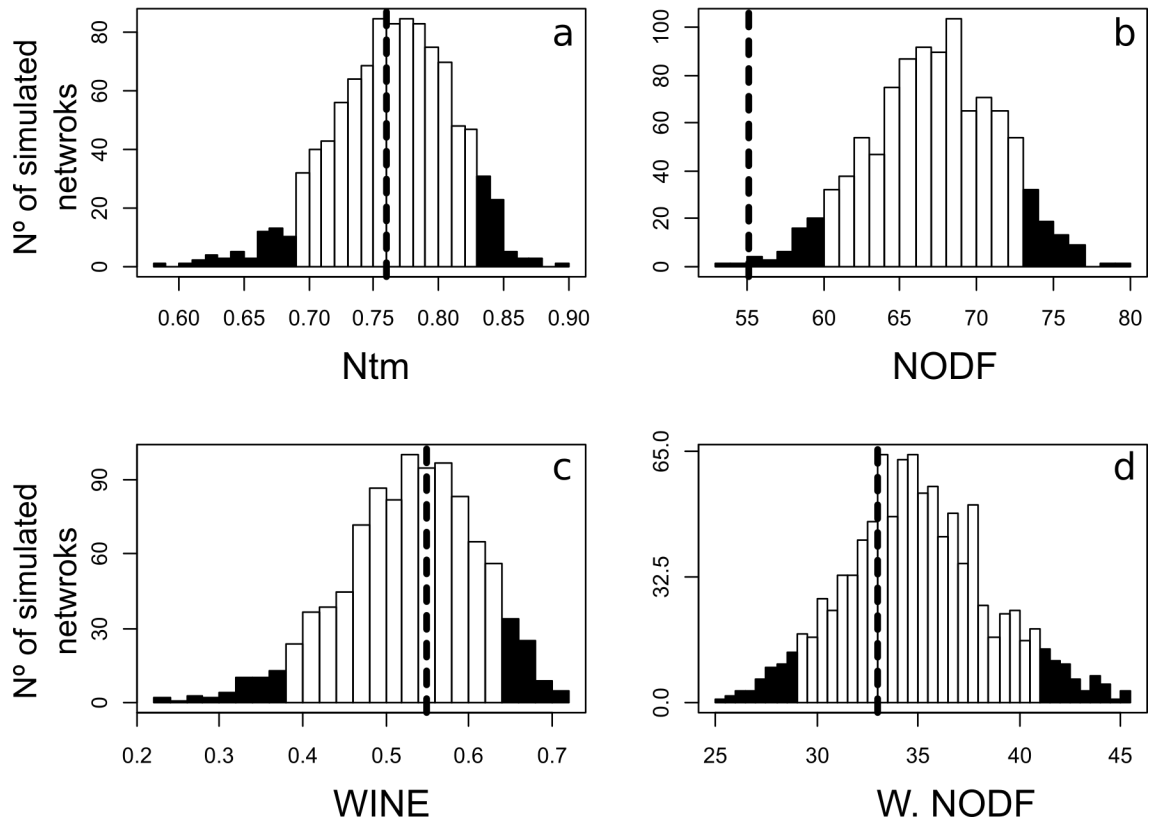
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585   **Figure 1.**

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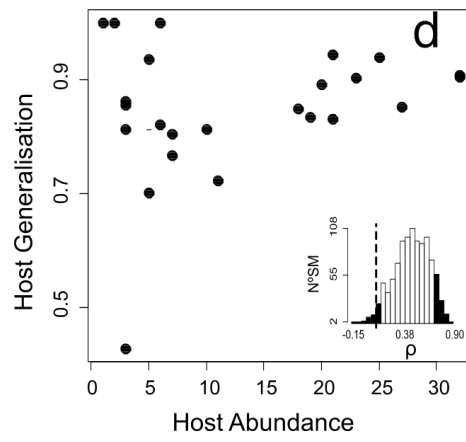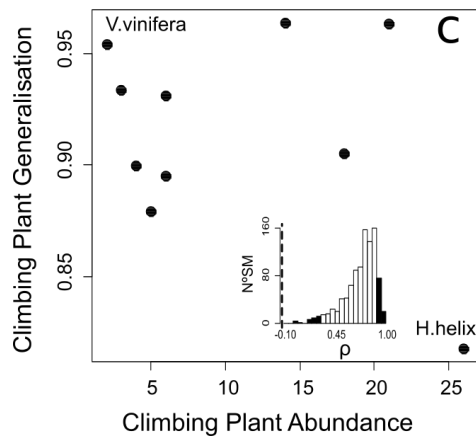
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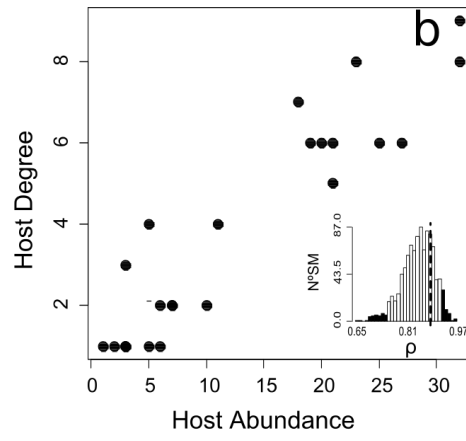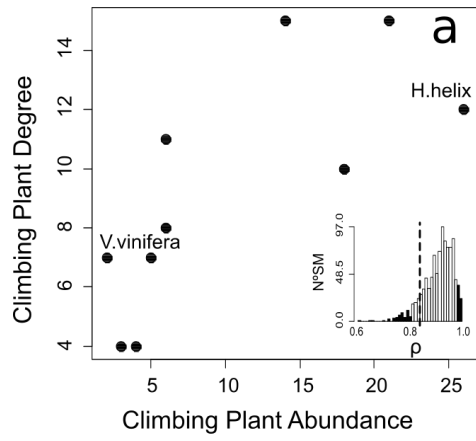
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Figure 3.

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