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1   Article

2   **Insights on the assembly rules of a continent-wide multilayer network**

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24

25 **Introductory paragraph**

26   How are ecological systems assembled? Here, we aim to contribute to answering this question by

27   harnessing the framework of a novel integrative hypothesis. We shed light on the assembly rules

28   of a multilayer network formed by frugivory and nectarivory interactions between bats and

29   plants in the Neotropics. Our results suggest that, at a large scale, phylogenetic trade-offs

30   separate species into different layers and modules. At an intermediate scale, the modules are also

31   shaped by geographic trade-offs. And at a small scale, the network shifts to a nested structure

32   within its modules, probably as a consequence of resource breadth processes. Finally, once the

33   topology of the network is shaped, morphological traits related to consuming fruits or nectar

34   determine which species are central or peripheral. Our results help understand how different

35   processes contribute to the assemblage of ecological systems at different scales, resulting in a

36   compound topology.

37

38 **Introduction**

39   Since Darwin's "tangled bank" metaphor[1], one of the most important quests in ecology has been

40   to unveil the assembly rules of ecological systems[2]. Different study models have been used in an

41   attempt to generate unifying principles, from sets of species (i.e., communities[3]) to systems

42   formed by species interactions (i.e., networks[4]). Knowing those rules is crucial for understanding

43   the architecture of biodiversity[5], restoring degraded environments[6], and controlling emerging

44   diseases[7], among other applications. However, identifying those rules remains one of the main

45   unsolved challenges in ecology[8].

2

46   Major advances in network science have shed light on some assembly rules that govern

47   interaction systems[9–11]. These breakthroughs permitted the ecological and evolutionary analysis

48   of monolayer networks formed by a single interaction type. Since then, there has been much

49   debate concerning the prevalent topology among interaction networks (nested or modular) and

50   which processes should generate those patterns (niche or neutral). Early evidence suggested that

51   antagonistic networks should be predominantly modular, while mutualistic networks should be

52   nested[12]. However, recent studies suggest that those topological archetypes are not exclusive to

53   particular interaction types[13], may occur in combination[14], and depend on geographic and

54   phylogenetic scales[15].

55   A novel conceptual framework, termed "the integrative hypothesis of specialization"

56   (IHS[16]), proposes that a balance between trade-offs[17] at larger scales and resource breadth

57   processes[18] at smaller scales shapes host-parasite networks. The IHS, in its updated form[19], is

58   based on premises that can be extrapolated from parasites to consumers in general: (i) types of

59   resources differ in their ability to be exploited by consumers; (ii) resources are more different

60   from one another at larger than smaller scales; and (iii) an adaptation to exploit a resource helps

61   exploit similar resources but becomes a maladaptation to exploit dissimilar resources.

62   Using the framework from the IHS and new models of multilayer networks[20], here we

63   aimed to understand the assembly rules of a system formed by bats and plants that interact with

64   one another through frugivory and nectarivory in the entire Neotropical region. From the IHS,

65   we deduced that different processes should shape the bat-plant network at different scales. If this

66   is true, firstly, there should be strong phylogenetic and geographic trade-offs in the network

67   studied, as it contains two interaction types and high phylogenetic diversity (one large bat family

68   and several plant families[21]), distributed over an entire biogeographic region. These trade-offs

3

69   should lead to strongly separated layers (large scale) and modules (intermediate scale). However,

70   within the modules (small scale) resource breadth processes should lead to a nested structure,

71   resulting in a compound topology: a modular network with modules internally nested. Secondly,

72   considering that some bat species are able to feed both on fruits and nectar[22], different

73   organismal traits related to those diets[22,23] should thus determine the relative importance of

74   different bat species for the structure of each layer and for bridging layers.

75   Our results support the IHS as a good model to explain the topology of interaction

76   networks. They also provide the first evidence of a compound topology in multilayer networks,

77   with different processes operating at different scales.

78

79   **Results**

80   The Neotropical bat-plant multilayer network analyzed here (Fig. 1a) is hyper-diverse and

81   massive. It is composed of 439 plant species, 73 bat species, 911 links of frugivory, 301 links of

82   nectarivory, and 18 dual links (i.e., links of both frugivory and nectarivory between the same bat

83   and plant species). The frugivory layer contains 307 plant species and 56 bat species, while the

84   nectarivory layer contains 139 plant species and 39 bat species. The 18 dual links were made

85   between 10 bat species and 8 plant species.

86   As predicted, the studied network showed a compound topology (Table 1, Fig.1b). The

87   modularity score for the whole multilayer structure (M = 0.53, Z_{free} = 49.18, P <0.001) was much

88   higher than expected by the free null model, which does not consider the network's modular

89   structure (see Methods for explanations of the null models). The same was observed for the

90   frugivory (M = 0.48, Z_{free} = 44.44, P <0.001) and nectarivory layers, respectively, using the free

4

91   null model (M = 0.63, Z_{free} = 24.94, P <0.001). In contrast, the entire multilayer structure was

92   slightly nested (NODF = 0.18, Z_{free} = 4.72, P_{free}< 0.001), as well as the frugivory (NODF = 0.29,

93   Z_{free} = 7.12, P_{free} < 0.001) and nectarivory layers (NODF = 0.16, Z_{free} = 2.39, P_{free} < 0.013). In

94   other words, the studied multilayer network is both modular and nested at the same time, but the

95   modular structure is stronger than the nested structure at larger scales.

96   Corroborating this result, nestedness between species of different modules (NODF$_{DM}$)

97   was lower than expected by the free null model in the nectarivory layer and the multilayer

98   network but, interestingly, equal to the expected value in the frugivory layer. This result suggests

99   that the modules impose greater constraints to nectarivory than to frugivory interactions.

100   Furthermore, nestedness in general (NODF), between species of the same module (NODF$_{SM}$),

101   and between species of different modules (NODF$_{DM}$) was higher than expected considering the

102   modular structure of the multilayer network and its layers. The exception was the nectarivory

103   layer, in which species of different modules (NODF$_{DM}$) show higher nestedness than expected

104   given the modules.

105   Geographic co-occurrence and phylogeny of bat species were also important predictors of

106   the network's compound structure. Most bat species analyzed have small geographic ranges,

107   while a few are broadly distributed. The species with the smallest range was *Lonchophylla*

108   *bokermanni* (23,309 km^2), whereas the species with the largest range was *Sturnira lilium*

109   (17,327,789 km^2). Mantel tests found no correlation between the geographic co-occurrence and

110   phylogenetic distances of bat species, which means that these bat clades are distributed in the

111   Neotropical Region independently of their evolutionary origin (Figure 2a). Though we found a

112   strong phylogenetic signal in the modules of the network (intermediate scale) we did not find

113   such signal in the interactions within the modules (small scale). Nevertheless, the contrary was

114   true for the geographic signal: it is strong at the scale of within-module interactions, but very

115   weak in the modules (Figure 2a). We found these same general trends (Figure 2b-c) when we

116   used partial Mantel tests to discount for mutual effects between the structuring factors and the

117   scales.

118   There was dependence between modules and interaction types ($\chi^2 = 554.33$, N = 12, P <

119   0.001), which means that some modules are formed mainly by nectarivorous bats and others by

120   frugivorous bats. Additionally, we detected a phylogenetic signal in layer composition (Figure

121   2d), where some bat clades are preferentially nectarivorous while others are preferentially

122   frugivorous, which corroborates the structuring power of phylogeny at a large scale. Then,

123   because of the dependence between layers and modules, we tested and confirmed that the

124   phylogenetic signal in the modules remains even when discounting the correlation with the

125   layers (Figure 2d). We conclude that phylogeny structures the layers of the network (large scale)

126   and the modules inside each layer (intermediate scale), and geographic co-occurrence structures

127   the interactions within each module (small scale). Finally, there was no phylogenetic signal in

128   bridge species, which make both interactions of frugivory and nectarivory (r = 0.04, Z = 0.75, P

129   = 0.21).

130   Few centrality metrics presented significant correlations with one another, whereas most

131   were only weakly correlated or not correlated (Supplementary Results 1). Centrality varied

132   largely among all species. It varied also between layers in the case of bridge species (Figure 3).

133   For these bridge species, there was no relationship between degree, betweenness centrality,

134   closeness, or eigenvector centrality across layers (all P > 0.05, Table 2, Supplementary Results

135   2). However, bat species with larger degree, betweenness centrality, and eigenvector centrality in

136   the frugivory layer had higher probabilities of being bridge species (all P < 0.05, Table 2,

6

137   Supplementary Results 2). In the nectarivory layer, none of the centrality metrics explained the

138   probability of a species being a bridge between layers.

139   Geographic range size did not affect the centrality of bat species. Among the

140   morphological attributes, body size and bite force were the most important predictors of species'

141   centrality. For the frugivory layer, the latent variable analysis (N = 16, df = 29) indicated that

142   eigenvector decreased with body size (coefficient = -0.524, P = 0.003), increased with bite force

143   (coefficient = 1.585, P < 0.001), and was not explained by the other latent and indicator variables

144   (Fig.4a). For the nectarivory layer (N = 15, df = 29), eigenvector increased with body size

145   (coefficient = 1.268, P < 0.001), decreased with bite force (coefficient = -1.841, P < 0.001), and

146   was not explained by the other variables (Fig.4b). For dual interactions, the model could not be

147   calculated due to the small number of observations. Finally, considering the entire multilayer

148   structure and a multilayer version of centrality (N = 18, df = 29), eigenvector increased with bite

149   force (coefficient = 0.517, P = 0.013), and was not explained by the other variables (Fig.4c).

150

Discussion

152   Our analysis of a continent-wide multilayer interaction network shows that, in order to build a

153   complex ecological system, a combination of processes operating at different scales is needed.

154   This finding supports the integrative hypothesis of specialization (IHS[16,19]), which we here

155   extend from parasite-host to plant-animal interactions.

156   Firstly, at large and intermediate scales, phylogenetic and geographic trade-offs generate

157   a multilayered and modular structure. After the influence of those trade-offs, at a small scale, the

158   modules of the network are internally nested and shaped first by geographic trade-offs. For

7

159   sympatric species, this nested structure is probably a result of resource breadth processes[18],

160   neutral processes related to differences in abundance[24], or universal processes observed in

161   different kinds of complex networks such as preferential attachment[25]. Scale-dependence has

162   been pointed out as a critical issue in biodiversity research[26] and here we show that the same is

163   true for species interactions. Secondly, after the network is shaped, biological traits determine

164   how important each species is for the structure of each layer of the network. Those traits

165   determine also which species bridge the layers by being frugivorous and nectarivorous at the

166   same time.

167   Organismal attributes, such as body size and bite force, predict eigenvector centrality in a

168   manner that is consistent with predictions from ecomorphological theory; species with greater

169   performance are expected to have access to a broader array of ecological resources[27]. Bite force

170   is a whole-organism performance trait that is tightly linked with the physical demands imposed

171   by diet[28]. Specialized neotropical frugivores have evolved foreshortened rostra and large jaw

172   adductors, which allows these species to have exceptionally forceful bites for their size and

173   consume fruit across a broader hardness spectrum than species that have weaker bite

174   forces[23,29,30]. Conversely, an elevated bite force is not a feeding performance requirement for

175   nectarivores, to whom an elongated skull and thus weaker bite forces, and a larger body size may

176   be an advantageous trait for accessing a broader array of flower sizes and types[31].

177   Our results suggest that the dilemma of identifying the predominant topology among

178   interaction networks (nested or modular) creates a false dichotomy. This interpretation is

179   supported not only by our results, but by evidence from other recent studies[14,15,32], which

180   highlight that modularity and nestedness are states along a continuum[3]. Ecologists foresaw this

181   continuum for interaction networks in the past[14], and it seems applicable to other types of

8

182   ecological systems, such as communities and metacommunities[3,33]. The IHS provides us with a

183   mechanistic model that predicts this compound topology[16,19]. In addition, the evidence provided

184   here also corroborates the importance of biological traits to the hierarchy of centrality in

185   interaction networks[34,35].

186   In conclusion, we found evidence that to build a continent-wide, hyper-diverse interaction

187   network, we need different processes operating at different scales. Our findings integrate

188   different debates in the ecological and parasitological literatures, and may also help understand

189   the emergence of hierarchical structures in other complex systems, such as social and economic

190   networks[36].

191

192   **Methods**

193   *Data set*

194   The data set used in the present study came from the Bat-Plant Interaction Database[37], which was

195   partially published in a book on seed dispersal by bats[38], and was later updated and used in other

196   studies on ecological networks[34]. In the present study, we added new data on bat-flower

197   interactions collected by the authors in Mexico, Costa Rica, and French Guiana, which were

198   published in different papers. The list of data sources is presented in Supplementary Table 1.

199

200   *Network building*

201   The original studies from which we sourced the bat-plant interaction data used a myriad of

202   methods, ranging from mist-netting to roost inspection and direct observation. In addition, these

203   studies varied in their focus, from single bat species or plant families, to whole bat-plant

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204   ensembles at a local scale[39]. Therefore, we decided to use binary data (i.e., presence or absence

205   of interactions) to build the multilayer network, as it would be very complicated to integrate and

206   standardize frequency data from different methods collected at different taxonomic scales.

207   Furthermore, binary data are more adequate to assess fundamental ecological niches[40,41], which

208   is the case of our study. The multilayer network was compiled at the scale of the whole

209   Neotropical Region. Henceforth, its nodes represent interactions across the entire geographic

210   range of species of bats and plants, and not just single local populations. Its binary links (edges)

211   thus represent dimensions of the fundamental niches of those species, and not their local realized

212   niches.

213   On each layer of the network a bat species and a plant species were connected to each

214   other by a link, whether an interaction of frugivory or nectarivory between them had been

215   recorded in the wild. Several species make links of both types, and thus belong to both layers of

216   the network. We call these "bridge species". Furthermore, a few bat and plant species were

217   connected to one another in both layers, making what we call here "dual links". In other words,

218   some bat species are both seed dispersers and pollinators of the same plant species.

219   Consequently, the multilayer network contained two types of links: frugivory and nectarivory.

220   Those link types were modeled as interconnected layers in the format of an edge list

221   (Supplementary Data 1). See also Supplementary Methods 1, where we explain how the

222   multilayer structure was modeled. Full Latin names of bats and plants are presented in

223   Supplementary Data 1. Network science terms used here are explained in detail in

224   Supplementary Table 2.

225

226   *Compound topology*

10

227   Compound topology analysis

228   To test whether each layer and the aggregated network were formed by internally nested modules

229   (compound topology, sensu[14]), we used a recently proposed protocol[19], which is based on the

230   following steps.

231   Step 1, find the best partition of a network and compare its modularity score to that

232   expected by a given null model of interest[42]. Step 2, compute the nestedness (NODF) of the entire

233   network and disentangle it into two components: nestedness between pairs of species of the same

234   module ($NODF_{SM}$) and nestedness between pairs of species of different modules ($NODF_{DM}$). Step

235   3, compare the observed values of $NODF_{SM}$ and $NODF_{DM}$ to their values expected both in the

236   absence (free null model) and in the presence (restricted null model) of the modular structure.

237   In a modular network, $NODF_{SM}$ should be higher than expected when interactions are

238   reshuffled regardless of the modular structure, *i.e.*, following the free null model. The reason is

239   that connectance of areas within the modules of the null matrices will be smaller than that of the

240   real matrix, and NODF increases monotonically with connectance[43]. Therefore, to test whether

241   interactions are more nested than expected given the modular structure, we compared the observed

242    $NODF_{SM}$ and $NODF_{DM}$ to the values expected by a null model that conserves the modular structure

243   (*i.e.*, keeps the observed connectance values within and between modules in the null matrices).

244

245   Null models

246   On the one hand, the free null model produces null matrices of the same size,

247   connectance, and species relative degrees. On the other hand, besides size, connectance, and

248   relative degrees, the restricted null model also conserves the modular structure of the original

11

249   matrix when generating the null matrices. This is made by weighting the *a priori* probability of

250   interaction among species C_i and resource R_j (P_{ij}) by the connectance of the matrix sub-area to

251   which the cell M_{ij} belongs[19].

252   For each layer, and the aggregated network, we generated 1,000 random matrices using

253   the free null model and another 1,000 matrices using the restricted null model. Next, for each

254   random matrix, we computed its overall NODF and decomposed it into $NODF_{SM}$ and $NODF_{DM}$

255   using the observed partitions of their corresponding real network. Finally, a Z-score was

256   calculated as $Z = [Value_{obs} - mean(Value_{sim})] / \sigma(Value_{sim})$, where $Value_{obs}$ is the observed value

257   of the metric and $Value_{sim}$ represents the values of the metric in the randomized matrices.

258   Observed and expected modularity values were also compared using Z-scores, but only for the

259   free null model, as it does not make sense to compare observed and expected modularities with a

260   null model that fixes the modules.

261

262   *Geographic and phylogenetic signals*

263   We used a combination of analyses to detect the signals of the geographic distribution and of the

264   phylogeny of bats at different scales of the multilayer network. In this analysis, we used only the

265   bat species that belong to the main component of the network, whose distribution data were

266   available in the IUCN red list global assessment (65 bat species). First, we computed five

267   pairwise distance matrices for bat species: phylogenetic, geographic, interactions, modules, and

268   layers.

269   To generate the phylogenetic distance matrix, we used the branch lengths in the most up-

270   to-date, species-level phylogeny of phyllostomids[44] (for 8 bat species not presented in the

12

271 phylogeny we used an alternative approach, see Supplementary Methods 2). For the pairwise

272 geographic distances, we used a measure of the overlap in the distribution of bat species

273 recovered from IUCN databases. Interaction, module, and layer pairwise distances were

274 calculated based on Jaccard Index (for details, see Supplementary Methods 2).

275 To test the signals, we performed a combination of Mantel and partial Mantel tests, and

276 used the Z-Score as a measure of effect size (observed correlation minus the average correlation

277 in randomized matrices, divided by the standard deviation). We tested the dependence between

278 modules and layers of the network using a chi-squared test of independence. Lastly, we used a

279 Mantel test to test for a phylogenetic signal in bridge species.

280

281 *Centrality and biological traits*

282 We assessed the relative importance of each bat species to the structure of each layer or the entire

283 multilayer network through the centrality metrics degree, closeness centrality, betweenness

284 centrality, complementary specialization, within-module degree, participation coefficient, and

285 eigenvector centrality. For details on their definition and calculation, see Supplementary Methods

286 1.

287 Using generalized linear models (GLMs) based on a quasi-Poisson distribution of errors,

288 we tested whether the centralities of bat species in the frugivory and the nectarivory layers were

289 correlated with one another. All models were checked for over- and sub-dispersion, and then tested

290 with an analysis of variance (ANOVA).

291 To test for a correlation between centrality indices of bat species in each layer (frugivory

292 and nectarivory) and the probability of a bat being a bridge species between the layers, we also

13

293   used generalized linear models (GLMs). Since the response variable was binary (bridge species:

294   yes or no), we used a binomial distribution of errors in those GLMs. We checked all models for

295   overdispersion, and then tested them with a chi-squared test. These two first sets of statistical tests

296   were conducted in R, using the package *lme4*[45] (see Supplementary Results 2).

297   To test the relationship between body size, skull morphology, feeding performance,

298   geographic range size, and centrality, we used a dataset on morphometric and performance traits

299   of phyllostomid bats for the whole Neotropics, compiled by R. Stevens and S. Santana from

300   published studies[23,29,46]. This dataset spans a large variety of morphometric and feeding

301   performance traits, which were collected from wild animals and museum specimens using

302   standardized methods[29]. As many of these are strongly correlated with one another, we relied on

303   previous studies to select traits considered most relevant to feeding function in the context of

304   frugivory and nectarivory (see Supplementary Results 1).

305   In relation to organismal traits, species with larger geographic range size are expected to

306   have broader diets within their trophic niches (e.g., frugivory or nectarivory), as they cannot rely

307   on specialized diets all over their distribuition[47,48]. Animals with larger body size are expected to

308   have broader diets, as they have higher energy requirements than small-bodied animals[34,49].

309   Frugivorous bats are expected to bite more forcefully than nectarivorous bats, considering

310   differences in hardness between solid and liquid diets[29]. Skull morphology is another important

311   trait related to diet in bats, as frugivorous species tend to have shorter and broader skulls than

312   nectarivorous species[22].

313   As there should be complex direct and indirect paths of influence among body size,

314   dietary morphology and performance, geographic range size, and centrality, we used a latent

315   variable analysis (LaVaAn) to disentangle these relationships. In all models, the response

14

316   variable, eigenvector centrality (eg.), was determined by three latent variables: body size (Siz),

317   bite force (Bit), and skull morphology (Skl), and one single indicator: geographic range size

318   (rng). The latent variable body size was composed of the exogenous variables body mass (Mss)

319   and forearm length (Frr). The latent variable Bit was composed of the exogenous variables

320   length of maxillary toothrow (LMT), breadth across upper molars (BUM), and maximum bite

321   force (MBF). The latent variable Skl was composed of the exogenous variables breadth of

322   braincase (BOB) and greatest length of skull (GLS). We built four similar models: one for the

323   frugivory layer, one for the nectarivory layer, one for dual interactions (i.e., the same bat and

324   plant species connected to one another in both layers), and one for the entire multilayer.

325   As not all bat species participate in both layers of the network, the sample size (N) of

326   each test was smaller than the number of bat species analyzed in the present study. All statistical

327   tests related to this prediction were carried out in R, using the package *lavaan*[50] (significance

328   level $\alpha = 0.05$ for all tests).

329

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348

349   **Author contributions**

350   MARM conceived the project. The first version of the working question, hypothesis, and

351   predictions was conceived by MARM together with RBPP and GMFF, and all authors

352   contributed to improving the central argument of the study. CG and MT acquired the literature

353   data and field data used to build the dataset of bat-plant interactions. SES reconstructed the bat

354   phylogeny. SES and RDS built the dataset on bat morphology and performance. FAR and NL

355   developed the new multilayer version of the centrality metrics. MARM, RLM, RBPP, GMFF,

356   FAR, and NL performed tasks related to data analysis and coding in R and Python. The first draft

357   of the manuscript was written by MARM, RBPP, GMFF, and RLM, and all authors contributed

358   to editing the text.

359

16

360 **Competing financial interests**

361 None to declare.

362

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475   **Figures**

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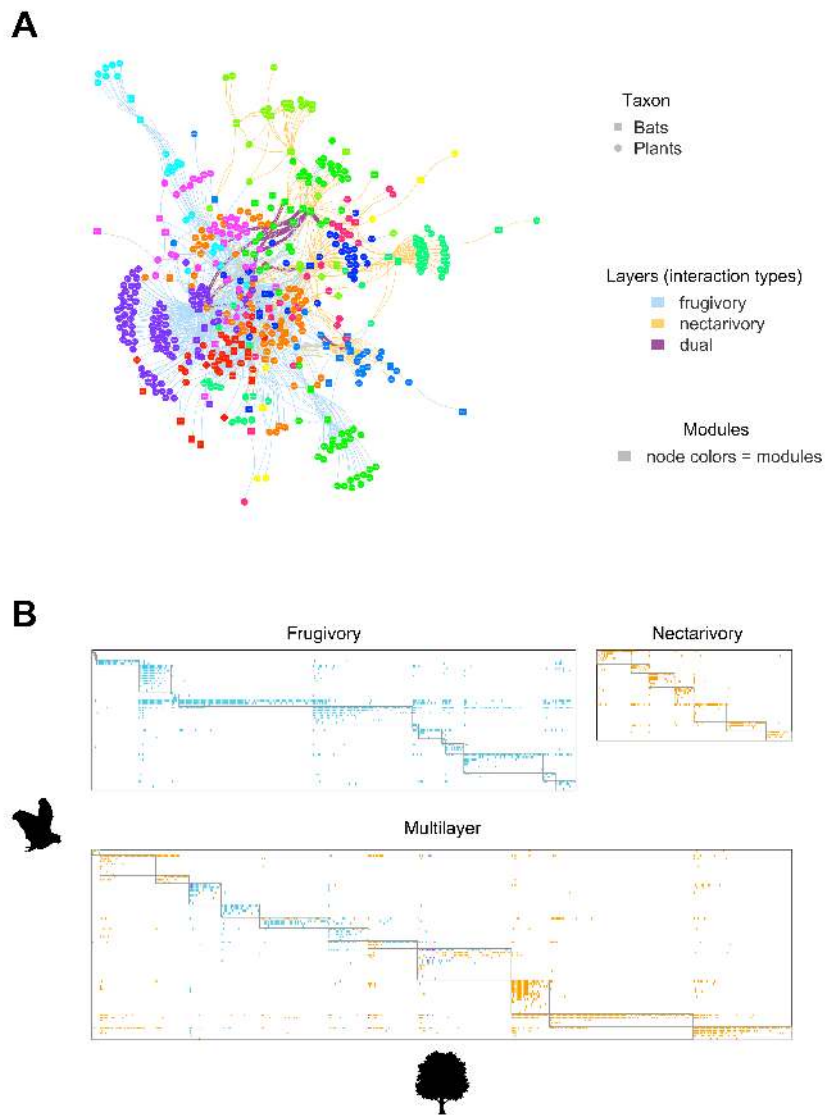
Figure 1. The multilayer bat-plant network, built for the entire Neotropical Region based on
interactions of frugivory and nectarivory recorded in the wild, showed a strong separation
between interaction types (layers) and guilds (modules). **A.** Multilayer graph; the layers represent
interactions of frugivory (blue), nectarivory (orange), and dual interactions (purple, i.e.,
interactions of both types between the same bat and plant species). Bat species are represented as
squares, plant species as circles, and interactions as lines. Node colors represent modules
detected in the network using the DIRT_LPAwb+ algorithm. **B.** Multilayer matrix; bat species
are represented in the rows, plant species in the columns, and filled cells represent interactions
(same colors as in the graph); boxes represent the modules found. See the full-sized graph with
species labels in Supplementary Data 1.
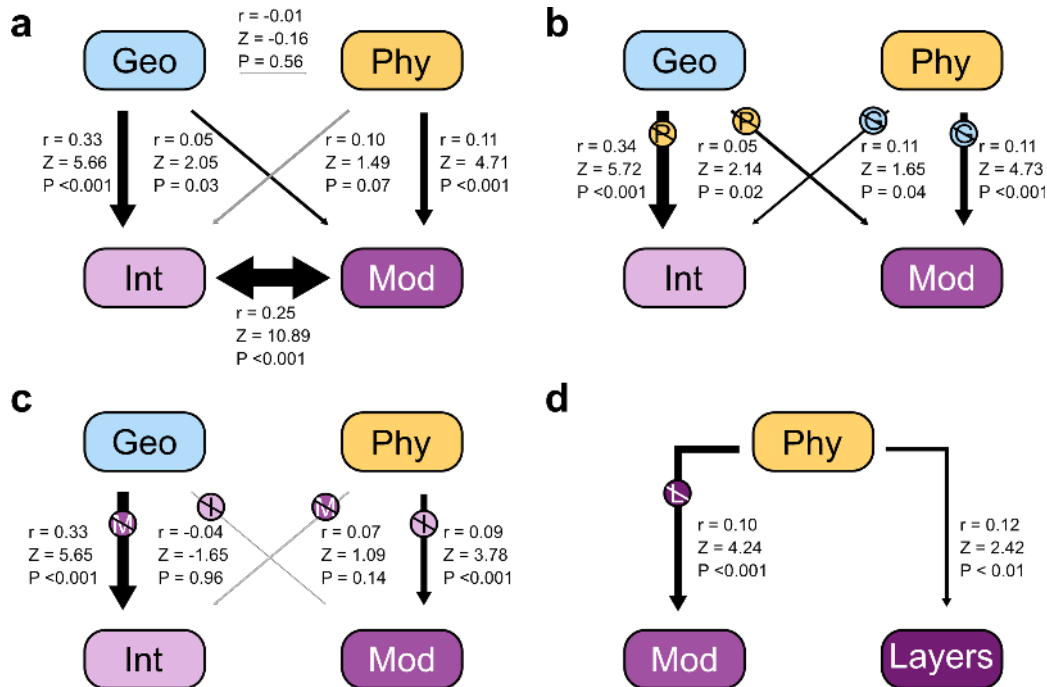
Figure 2. Phylogenetic (Phy) and geographic (Geo) signals at different scales of the multilayer network: interactions (Int) (small scale), modules (Mod) (intermediate scale), and layers (large scale). **A.** Results of Mantel tests for all the correlations between bat distances in phylogeny, geographic co-occurrence, interactions, and modules. **B.** We used partial Mantel tests to discount the mutual effects between phylogeny and geographic co-occurrence; therefore, when testing geographic signals at each scale, we conditioned the correlation on the phylogenetic distance, and vice-versa. **C.** We used partial Mantel tests but conditioning the correlations with distances in one scale on the distances in the other scale. **D.** We used a Mantel test to assess a phylogenetic signal in the layers of the network and then used a partial Mantel test to test the phylogenetic signal in the modules accounting for the distance between layers. Arrows in black represent significant correlations and in gray, non-significant correlations. Arrow width scaled by Z-scores. In partial Mantel tests, the crossed circle with a letter inside indicates on which distances the correlation tested (arrow) was conditioned (geographic – G, phylogenetic – P, modules – M, or interactions – I).

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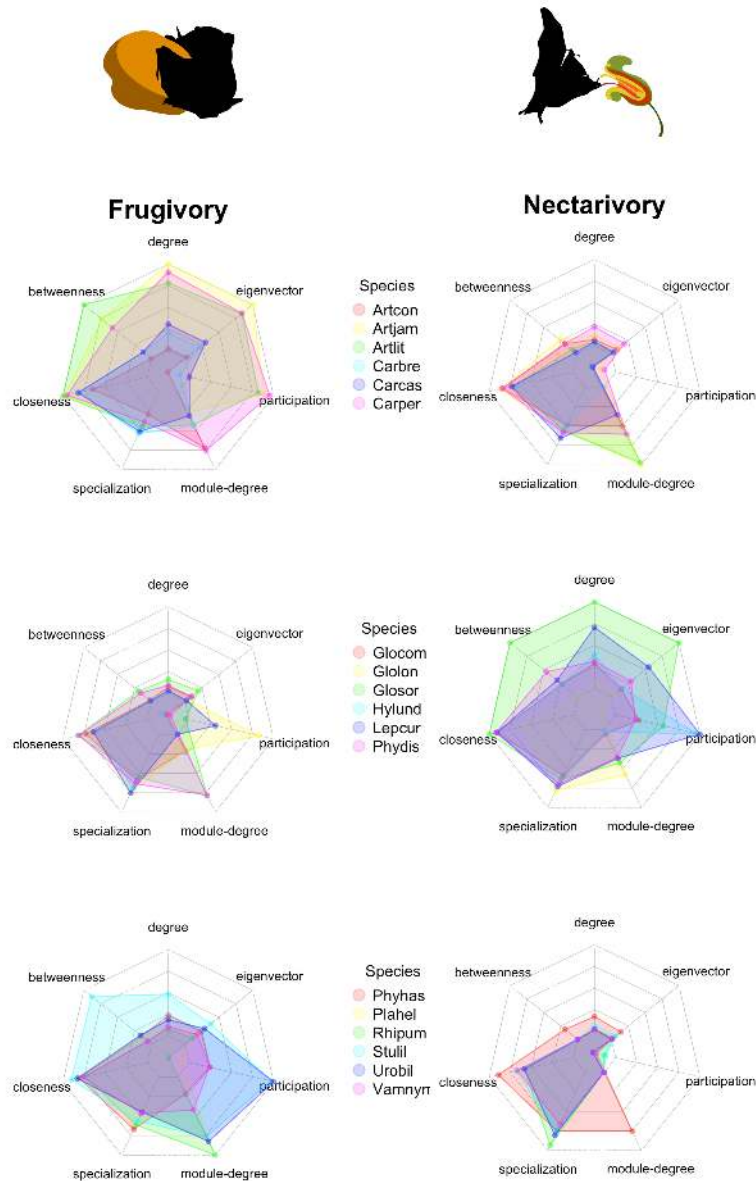
**Figure 3**. The centrality metrics varied largely in the same species between layers of the network (frugivory and nectarivory). Each axis of each spider chart represents a centrality metric calculated, and its original range of variation. Different bat species are represented by different colors. Only the most central species that occurred in both layers are presented here. Species codes were made using the first three letters of the genus and the first three letters of the epithet (e.g., Carper = *Carollia perspicillata*). See binomial nomenclature in Supplementary Data 1.
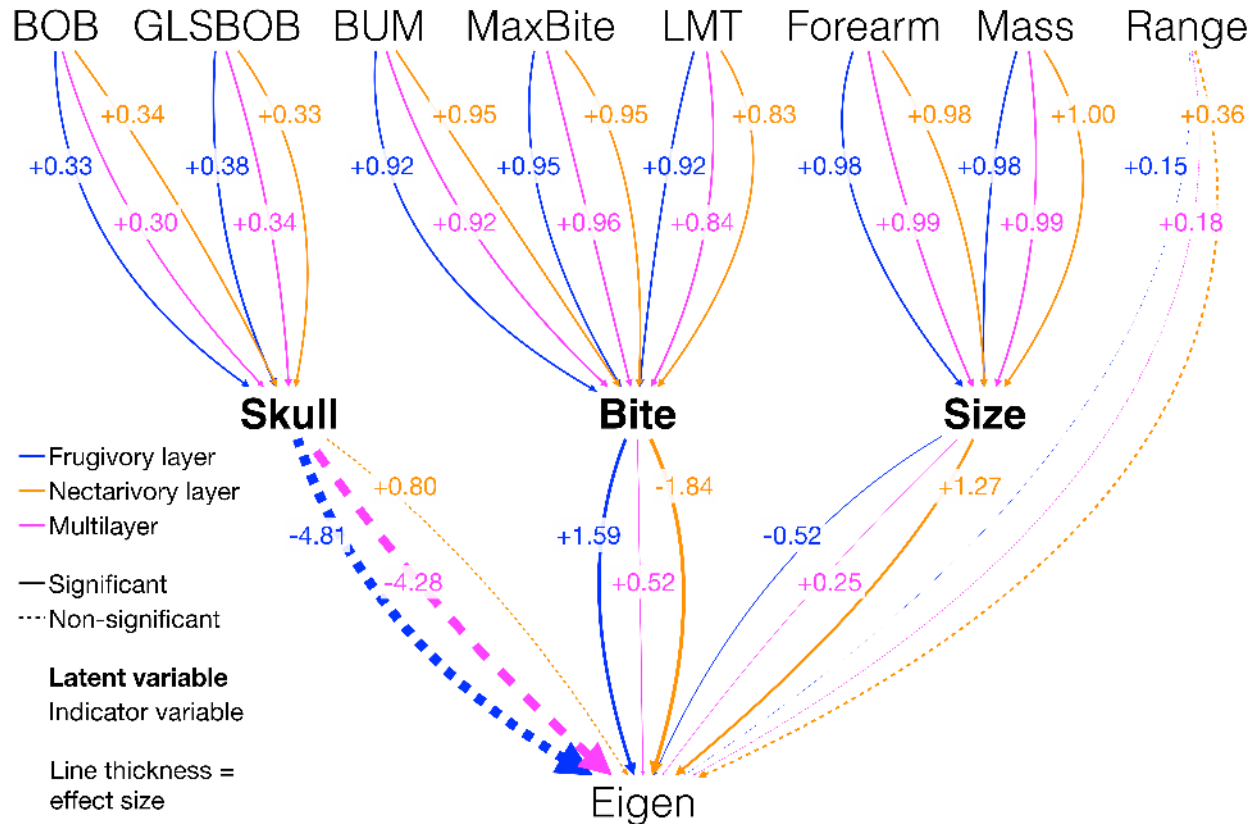
Figure 4. The eigenvector centrality (Eigen) of a bat species was determined by a combination of biological traits (indicators) related to morphology (the latent variables: Skull, Bite, Size) and geographic range size (Range). A bat species was more central in the frugivory layer, when it had a strong bite force (Bite) and small body (Size). In the nectarivory layer, larger bats (Size) with weak bite force (Bite) were the most central. In the complete multilayer structure, only bite force (Bite) was positively related to centrality. Numbers on the lines are the standardized coefficients of each path, and line thickness was drawn proportionally to this coefficient only for the latent variables (Skull, Bite, Size) and single indicator variable (Range). Significance was estimated only for those main variables. See full indicator names in Supplementary Results 1

519 **Tables**

520 Table 1. The multilayer network presented a compound topology, with a modular structure that

521 comprises internally nested modules. Scores of modularity (M) and nestedness (NODF) for the

522 entire multilayer matrix and its layers, including NODF scores calculated between species of the

523 same module (sm) and of different modules (dm). The scores were calculated for the studied

524 matrix (Obs), and also randomized according to the free and restricted null models. P-values (P)

525 were estimated based on a Monte Carlo procedures run for each null model (1,000 iterations),

526 which lead to expected scores (E) and Z-scores (Z). The free null model randomizes the entire

527 matrix, whereas the restricted null model conserves its modular structure. We did not run the

528 fixed null model for modularity. All scores were standardized varying from 0 to 1. Significance

529 level (α): 0.05.

	Obs	E_{free}	Z_{free}	P_{free}	E_{rest}	Z_{rest}	P_{rest}
Frugivory layer							
Mod	0.48	0.35	44.45	0.001	NA	NA	NA
NODF	0.29	0.22	7.00	0.001	0.23	6.44	0.001
$NODF_{sm}$	0.60	0.19	34.69	0.001	0.43	8.37	0.001
$NODF_{dm}$	0.23	0.22	0.92	0.179	0.19	4.04	0.002
Nectarivory layer							
Mod	0.63	0.47	24.95	0.001	NA	NA	NA
NODF	0.16	0.13	2.39	0.013	0.13	3.02	0.003
$NODF_{sm}$	0.55	0.13	37.41	0.001	0.35	8.41	0.001
$NODF_{dm}$	0.09	0.13	-4.82	0.999	0.09	-0.56	0.710
Multilayer							
Mod	0.53	0.38	49.18	0.001	NA	NA	NA
NODF	0.18	0.15	4.73	0.001	0.15	6.14	0.001
$NODF_{sm}$	0.55	0.14	53.32	0.001	0.40	8.85	0.001
$NODF_{dm}$	0.13	0.15	-2.23	0.994	0.11	3.58	0.001

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531   Table 2: The centrality of a bat species on one layer of the network did not predict its centrality
532   on the other layer. However, the higher the centrality of a bat species in the frugivory layer, the
533   higher its probability of being a bridge species (i.e., making interactions on both the frugivory
534   and the nectarivory layers). Relationships between centrality metrics calculated in different
535   layers of the network using GLMs. Significant P-values are highlighted in boldface. Significance
536   of the models of the set 1 was estimated using F tests, while for the sets 2 and 3 we used χ^2 tests.

Model	df	deviance	F	P
1. Centralities vs. layers				
ndeg.frug ~ ndeg.nect	20	0.027	0.269	0.610
bet.frug ~ bet.nect	20	0.003	0.033	0.857
clo.frug ~ clo.nect	20	0.002	2.208	0.153
eig.frug ~ eig.nect	20	0.018	4.870	0.832
2. Bridge species vs. frugivory				
ndeg ~ bridge	54	12.607		**0.000**
bet ~ bridge	54	16.125		**0.000**
clo ~ bridge	54	1.119		0.290
eig ~ bridge	54	14.940		**0.000**
3. Bridge species vs. nectarivory				
ndeg ~ bridge	41	0.073		0.787
bet ~ bridge	41	0.858		0.354
clo ~ bridge	41	1.759		0.185
eig ~ bridge	41	0.002		0.963

537   Legend: ndeg = normalized degree, bet = betweenness, clo = closeness, eig = eigenvector, frug =
538   frugivory layer, nect = nectarivory layer. Significance level (α): 0.05.

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540 **Supplementary information**

541 Supplementary Data 1. Dataset used to build the multilayer network, including an R code for

542 drawing it. Available on GitHub: https://github.com/marmello77/mello-etal-2018-SD1.

543 Supplementary Table 1. References used to build our dataset on bat-plant interactions in the

544 Neotropics.

545 Supplementary Table 2. A small dictionary of network science.

546 Supplementary Methods 1. Details on the calculation of centrality and the definition of the

547 multilayer structure and the calculation of multilayer versions of the main centrality metrics.

548 Supplementary Methods 2. Phylogenetic and geographic signals.

549 Supplementary Results 1. Correlograms of centrality for each layer of the network (A: frugivory,

550 B: nectarivory, and C: dual) and for the multilayer network (D).

551 Supplementary Results 2. Correlations between centrality metrics between layers. Trend lines are

552 presented only for statistically significant relationships. (a) Correlations between three centrality

553 metrics between layers for bat species that make interactions of frugivory and nectarivory. (b)

554 Relationship between the centrality of bat species in the frugivory layer and the probability of

555 being a bridge species (i.e., making dual links with the same plant species). (c) Relationship

556 between the centrality of bat species in the nectarivory layer and the probability of being a bridge

557 species (i.e., making dual links with the same plant species).

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