

Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests

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1 **Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests**

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- 80

81 Abstract

82
83 In the tropics, antagonistic seed predation networks may have different properties than mutualistic pollination and seed dispersal
84 networks, but the former have been considerably less studied. We tested whether the structure of antagonistic tripartite networks
85 composed of host plants, insects developing within seeds and fruits, and their insect parasitoids could be predicted from plant
86 phylogenetic distance and plant traits. We considered subsets of the networks (“subnetworks”) at three rainforest locations
87 (Panama, Thailand, Papua New Guinea), based on insect families, plant families or plant functional groups. We recorded 3,197
88 interactions and observed a low percentage of realized interactions, especially in Panama, where insect host specificity was higher
89 than in Thailand or New Guinea. Several factors may explain this, including insect faunal composition, incidence of dry fruits,
90 high fruit production and high occurrence of Fabaceae at the Panamanian site. Host specificity was greater among seed-eaters
91 than pulp-eaters and for insects feeding on dry fruits as opposed to insects feeding on fleshy fruits. Plant species richness within
92 plant families did not influence insect host specificity, but site characteristics may be important in this regard. Most subnetworks
93 were extremely specialized, such as those including Tortricidae and Bruchinae in Panama. Plant phylogenetic distance, plant basal
94 area and plant traits (fruit length, number of seeds per fruit) had important effects on several network statistics in regressions
95 weighted by sampling effort. A path analysis revealed a weak direct influence of plant phylogenetic distance on parasitoid
96 richness, indicating limited support for the “nasty host hypothesis”. Our study emphasizes the duality between seed dispersal and
97 seed predation networks in the tropics, as key plant species differ and host specificity tends to be low in the former and higher in
98 the latter. This underlines the need to study both types of networks for sound practices of forest regeneration and conservation.

99
100 **Key words:** Barro Colorado Island; functional group; nasty host hypothesis; plant phylogeny; quantitative food web; seed
101 predation.

102
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115 STS analyzed the data. All authors contributed to the writing of the manuscript, with notable input from YB, LRJ, STS, PTB,
116 SEM, VN, SJW, SG and OL.

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122 **Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests**

123

124 **Introduction**

125

126 Community assembly and the relationships among interacting species are frequently studied using ecological interaction networks
127 (Jordano et al. 2003, Blüthgen et al. 2006, Poisot et al. 2015, Dáttilo & Rico-Gray 2018), as the structure of these networks may
128 be critically linked to the dynamics and stability of interacting species within the community (Paniagua et al. 2009). Mutualistic
129 networks involving the processes of pollination and seed dispersal have been relatively well studied in tropical rainforests, often
130 emphasizing vertebrates (e.g., Olesen & Jordano 2002, Schleuning et al. 2012, Escribano-Avila et al. 2018). To date, antagonistic
131 networks, incorporating information on the frequency of each trophic interaction and emphasizing invertebrates in rainforests
132 have been assembled for leaf miners, gallers, leaf-chewers, their hosts and their parasitoids (review in Morris et al., 2014), and,
133 more rarely, for seed predators (Gripenberg et al. 2019).

134

135 In tropical rainforests, insects are the main seed predators, especially before seed dispersal (Janzen 1971). Insects that kill seeds
136 either before or after dispersal influence the population dynamics of individual plant species, and ultimately, plant diversity and
137 assemblage composition (Lewis & Gripenberg 2008). In addition to true seed predators, other functional groups of insects,
138 notably in Diptera and Lepidoptera, feed on the fleshy parts of fruits (Ctvrtecka et al. 2016). This guild of “pulp eaters” (as
139 opposed to “seed eaters”) can cause fruit abortion and fall, with consequences for plant population dynamics (Stephenson 1981).
140 In the tropics data regarding insect assemblages feeding on seeds/fruits are infrequent (Gripenberg 2018). So far, interaction
141 networks have been built for tephritid flies breeding in tropical flower heads (Prado & Lewinsohn 2004) or in tropical fruits
142 (Novotny et al. 2010), and for the whole assemblage of seed predators in one Panamanian rainforest (Gripenberg et al. 2019).

143

144 Concealed insect herbivores, such as seed/fruit predators, are more specialized than insect herbivores that feed externally
145 (Novotny & Basset 2005). Studies in tropical rainforests have often confirmed the high host specificity of seed/fruit predators
146 (Janzen 1980, Hopkins 1983, Nakagawa *et al.* 2003, Copeland et al. 2009, Ctvrtecka et al. 2014, Sam et al. 2017, Gripenberg et
147 al. 2019). Since foliar chemistry and plant phylogeny predict patterns of host use by caterpillars in tropical rainforests with high
148 concordance (Segar et al. 2017, Volf et al. 2017), we expect that plant phylogeny may also influence assemblages of seed/fruit
149 insects in tropical rainforests.

150

151 Resource availability, such as the production of young leaves, is key to understanding the local distribution of insect folivores in
152 tropical rainforests (e.g., Basset 2001). Likewise, it may be crucial to explain the structure and species interactions in assemblages
153 of insects feeding on seeds/fruits in tropical rainforests. In mutualistic networks, biotic specialization decreases with increasing
154 plant diversity, because high plant diversity may reduce relative plant abundance and related plant resources (Schleuning et al.
155 2012). However, antagonistic and mutualistic networks may be structured differently (Morris et al. 2014).

156

157 We expect that plant phylogeny (Segar et al. 2020), local plant diversity and abundance, seed availability and functional plant
158 traits (Basset et al. 2018) may influence interaction networks involving insects breeding in seeds and fruits in tropical rainforests.
159 In this contribution we test whether the structure of antagonistic tripartite networks composed of host plants, insects breeding in
160 seeds and fruits and their insect parasitoids at three representative rainforest locations within different biogeographical regions
161 can be predicted from different plant variables. Because of the high diversity of our study systems (see results), we consider
162 subsets of the overall networks (“subnetworks”) at each location, either based on insect families, plant families or plant traits. We
163 answer the following questions.

164

165 1. Accounting for host-plant phylogenetic relatedness, does herbivore host specificity vary among (a) insect families or feeding
166 guilds? (b) plant families or functional groups? and (c) three tropical forests?

167

168 One important variable accounting for network structure is specialization (Blüthgen et al. 2006), which is positively related to
169 host phylogenetic isolation (Jorge et al., 2017). Host specificity is likely to differ among insect guilds associated with fruit pulp
170 versus seeds, as seeds are better chemically protected than pulp (Janzen 1971). Plant traits may also influence seed predator load
171 and host specificity (Janzen 1971, 1980, Basset et al. 2018, Dahl et al. 2019). Low plant richness may favor high insect host
172 specificity, as suggested by comparisons of insect herbivores in temperate and tropical forests (Novotny et al. 2002).

173

174 2. Does plant phylogenetic relatedness or plant functional similarity explain the structure of interaction networks between seeds or
175 fruits and their insect predators across study sites or across different local subnetworks?

176

177 Related insect herbivores tend to feed on related host plants (Ehrlich & Raven 1964), because related plants may often
178 (Berenbaum 2001, Rønsted et al. 2012) but not always (Sedio et al. 2018) share similar chemical defences. In turn, specialized
179 herbivores, particularly seed predators, may be adapted to detoxify chemical defences (Kergoat et al. 2005). Hence, the structure
180 of plant-herbivore interaction networks may have a strong phylogenetic signal (Weiblen et al. 2006, Segar et al. 2020).

181 Alternatively, plant apparency theory (Feeny 1976) has been incorporated into a framework of three syndromes of plant defence,

182 including (1) tolerance/escape, (2) low nutritional quality and (3) high nutritional quality and defence (Agrawal & Fishbein
183 2006). Under this framework, plant functional traits may predict the structure of seed predator networks as well as, or better than,
184 plant phylogenetic relatedness.

185

186 **3.** Does the species richness of parasitoid assemblages feeding on seed/fruit predators reflect the traits of host plants, i.e. do the
187 effects of plants on herbivores cascade upwards to affect the next trophic level?

188

189 The nasty host hypothesis proposes that insect herbivores feeding on plant hosts with strong and/or distinctive chemical defenses
190 may support reduced loads of parasitoids because herbivore tissues may be more toxic to parasitoids (Gauld et al. 1992). Thus,
191 this hypothesis predicts that plant phylogenetic relatedness, as a surrogate for plant chemistry (Berenbaum, 2001), (a) should have
192 a significant effect on the species richness of parasitoids, (b) that this effect should be strong, and (c) that this effect should also
193 be positive (i.e., mean phylogenetic distance is predicted to be negatively correlated with parasitoid species richness).

194

195 **Material and methods**

196

197 **Study sites**

198

199 Our study sites are three ForestGEO lowland rainforest plots (Anderson-Teixeira et al. 2014) located in different biogeographical
200 regions. Salient characteristics of the plots and seed/fruit samples are detailed in Basset et al. (2018) and in Table 1. Neotropical:
201 Barro Colorado Island (BCI) is a 1,500-ha island created by the opening of the Panama Canal in 1914. The 50-ha plot is in the
202 heart of the island, which is near the center of more than 700 km² of protected forests. Oriental: the 24-ha plot at Khao Chong
203 (KHC) is in the protected forest of the Khao Ban Thad Wildlife Sanctuary in southern Thailand. Australasian: the 50-ha plot is
204 located in the 10,000 ha Wanang (WAN) Conservation Area in Papua New Guinea. Marked differences between BCI and the two
205 other sites include lower plant richness, higher percentage of species with dry seeds, higher percentage of Fabaceae species,
206 higher average seed rain per plant species and lower ratio of realized to potential interactions (Table 1).

207

208 **Plant surveys, phylogeny and functional traits**

209

210 Field methods were similar for all study sites (details in Basset et al. 2018, Gripenberg et al. 2019). Plant surveys spanned several
211 years at each site (Table 1; Appendix S1A). During the first study year at each site, we indiscriminately surveyed seeds and fruits

212 of locally abundant tree, shrub and liana (more rarely herb) species, to obtain an overview of the local community. During
213 subsequent study years at KHC and WAN, we restricted our sampling effort to the 10 plant families that were most common at
214 each plot. Eight of these focal families were common to all sites: Annonaceae, Arecaceae, Euphorbiaceae, Fabaceae, Lauraceae,
215 Meliaceae, Rubiaceae and Sapindaceae. Unless specified, results are detailed for all host plant species. Seeds and fruits collected
216 on plants or freshly fallen (without apparent decomposition) were opportunistically surveyed within and/or near permanent plots
217 (from an area < 1,500-ha corresponding to the smallest study area, BCI). Rearing sample units consisted of 1 to 200 seeds and/or
218 fruits collected from a single plant. We targeted as many individual plants as possible for each species, typically > 5. To evaluate
219 the phylogenetic relationships between sampled host plant species at each site, we estimated the relationships between our focal
220 species using the R package S.PhyloMaker (Qian & Yi 2016). We used the updated phylogeny and node ages derived from a
221 sequence-based study by Zanne et al. (2014) as a Megatree. Our focal species were placed within the Megatree where possible
222 and placed to family where not possible. This procedure generates three alternative topologies which differ with respect to the
223 resolution of unplaced taxa. We selected the phylogeny derived from “Scenario 3” as this has been shown to be robust to
224 uncertainty at the higher taxonomic level (Qian & Yi 2016). Note that polytomies in the phylogeny underestimated DSI* slightly
225 for herbivores feeding on a few species within a family. However, we expect this effect to be quite small, especially because it
226 does not apply to monophages that would still have maximum specialization.

227

228 To obtain similarity matrices of plant functional traits for each site, we first compiled a matrix of functional traits relevant to
229 seeds and fruits for each plant species, including numerical and categorical variables (Appendix S1B). We then used hierarchical
230 daisy clustering methods to identify functional groups. Finally, we used a mixed Principal Component Analysis (PCA) for
231 numerical and categorical variables to interpret the functional groups. Scores of each plant species on the PCA axes were used to
232 build similarity matrices of functional traits that were used in subsequent analyses. In sum, 1,186 plant species could be assigned
233 to one of five functional groups, coded A, B, C, D or E (A: often fleshy green fruits; B: often dry dehiscent fruits; C: often fleshy
234 orange fruits; D: often red fruits; E: often small fleshy black-green fruits). Appendix S1B provides details about the composition
235 of the matrix of functional traits, computational steps and relevant references, as well as the results obtained.

236

237 **Insect rearing and processing**

238

239 Methods for rearing seed/fruits insects are detailed in Basset et al. (2018) and Appendix S1C. Insects were identified with the
240 assistance of taxonomists (see Basset et al. 2018) and/or by molecular techniques (Appendix S1C). Insects reared from
241 seeds/fruits were assigned to the following guild categories (Basset et al. 2018): seed eaters (coded as SE: larva feeding mostly on
242 seed tissue), pulp eaters (PU: larva feeding mostly on mesocarp tissue), and parasitoids (PA: larva feeding on insect hosts). Seed

243 and pulp eaters consisted mainly of seven taxa that represented most of the material reared and are considered in analyses
244 restricted to insect taxa: Bruchinae, Scolytinae, Curculionidae others than Scolytinae (Coleoptera), Tortricidae, Pyralidae
245 (Lepidoptera), Stratiomyidae and Tephritidae (Diptera). Bruchinae were well represented only at BCI. Hereafter for sake of
246 simplicity, we refer to these seven taxa as “insect families”. For parasitoids, analyses were restricted to Braconidae and
247 Ichneumonidae because they represented most (69%) of the parasitoids reared from samples and their taxonomy was supported by
248 molecular data.

249

250 **Interactions, topologies and subnetworks**

251

252 Trophic relationships were inferred from the number of primary consumers reared from samples of seeds/fruits of host plant
253 species at the first trophic level (coded as level 1-2). For the third trophic level, we considered interactions between Braconidae
254 and Ichneumonidae and their insect hosts (coded as level 2-3). Contrary to interactions between the first and second trophic
255 levels, third level data only reflected expected interactions, not documented interactions, because parasitized hosts were not
256 isolated and reared individually, the parasitoids instead being reared from samples including relatively high numbers of seeds and
257 fruits. To assign putative hosts to each parasitoid species, we applied three simple rules, as detailed in Appendix S1D: (1) since
258 many parasitoid lineages are rather conservative in host use, we followed Quicke (2015) to select the most likely host order or
259 family. (2) In case of conflicts, we examined for each parasitoid species the consistency of co-occurrence with the putative host
260 species in all samples from which the parasitoid species was reared. (3) Eventually, we considered the highest abundance of
261 putative host reared in samples in which the parasitoid species was also reared. We considered expected interactions between
262 hosts plants and parasitoids (coded as level 1-3) to answer Question 3.

263

264 We constructed tripartite and quantitative interaction networks for the three full networks at BCI, KHC and WAN and for
265 meaningful subsets of the data. This approach was selected because of the complexity of the full networks, which involved an
266 order of magnitude more interacting species than most published networks (see Results; Schleuning et al. 2012, de Aguiar et al.
267 2019). Breaking a complex network into smaller sub-networks can reveal interesting patterns (Lewinsohn et al. 2006, de Aguiar et
268 al. 2019) and has been performed with networks including insects (Quinto et al. 2012), which are far more diverse than those
269 based on vertebrates (Schleuning et al. 2012). Each of our three full networks can be viewed as a collection of empirical
270 subnetworks built by sampling interactions of a particular taxonomic/functional group within a locality, a general approach which
271 is consistent with most published networks (de Aguiar et al. 2019). In addition, subnetworks were relatively independent from
272 each other, thus motivating analyses at the level of subnetworks (see “subnetwork structure” below). The meaningful subsets
273 (hereafter “topologies” for sake of brevity and in reference to how subnetworks are arranged) were based on (A) insect taxa: the

274 distribution of particular insect families on plant species (n=7 taxa, resulting in 19 subnetworks); (B) plant family: the
 275 distribution of insect species within particular plant families (n=8, 24 subnetworks); or (C) plant functional groups: the
 276 distribution of insect species on particular plant functional groups (n=5, 15 subnetworks). Topology (A) is more relevant to
 277 Questions 1 and 3 of the Introduction, whereas topologies (B) and (C) are more relevant to Question 2. Topologies (A) and (C)
 278 included insects reared from all host plants at each site, whereas for topology (B) we restricted the data to focal plant families.
 279 Further, for topologies (B) and (C) we also included in subnetwork illustrations plant species that were surveyed but yielded no
 280 reared insects (these “empty hosts” were not considered in the calculation of subnetwork statistics, see below). Variables as
 281 surrogates of either resource availability or sampling effort are discussed in Basset et al. (2018). Here, we consider that resource
 282 availability is most accurately tracked as the square root of the number of seeds collected for each plant species.

283

284 **Data analyses**

285

286 *Question 1: herbivore host specificity*

287

288 Quantitative metrics accounting for network-wide specialization (Blüthgen et al. 2006, Dormann et al. 2009) may be biased by
 289 sample size (Morris et al. 2014) and by non-random sampling of the plant phylogeny (Redmond et al. 2018). To overcome these
 290 challenges, we calculated herbivore specificity with the rescaled distance-based specialization index (DSI* - Jorge et al. 2014,
 291 2017), which measures trophic specialization by accounting for host phylogenetic relatedness and resource availability. This
 292 quantitative metric accounts for differences in abundance and sampling effort of consumers and is largely independent of sample
 293 size. Briefly, DSI* measures specialization as a deviation from a random expectation involving the mean pairwise phylogenetic
 294 distance between hosts and is rescaled to enable the comparison of consumers that differ in their recorded sample sizes. DSI*
 295 varies between -1 (maximum achievable generalization) and 1 (monophages or maximum achievable specialization; Jorge et al.
 296 2017). At each site we calculated DSI* for all seed- and pulp-eating insect species considering all host plant data available. DSI*
 297 was not calculated for parasitoid species, as, due to many missing data, we could not build reliably a phylogeny for insect
 298 herbivores.

299

300 To answer Questions 1a-1c, we first tested for differences in DSI* among herbivore taxa and guilds (pulp and seed eaters), plant
 301 families and functional groups, and study sites. We used non-parametric Kruskal-Wallis tests because DSI* values were skewed
 302 towards high specialization. Then, we used DSI* as the response variable in a model including taxa, guilds, sites and taxa:site and
 303 guild:site interactions as independent variables. To control for variation among insect families on DSI* (excluding Bruchinae,
 304 collected only at BCI), we performed a linear mixed model with site and insect guild as fixed effects and insect family as a

305 random effect. To control for variation among plant families, we performed a linear mixed model with mean DSI* of the
306 herbivores feeding on each plant species as the dependent variable, site and plant functional groups as fixed factors, and plant
307 family as a random factor. To evaluate the effect of local plant richness, we calculated the correlation between the average DSI*
308 of the insect assemblage feeding on each focal plant family at each study site (n=24 site-family combinations) and the species
309 richness of these plant families at each site.

310

311 *Question 2: subnetwork structure*

312

313 We addressed Question 2 by modeling indices for network properties at the level of the full network or subnetwork (hereafter
314 “network statistics”). Rather than focusing on any single metric, we calculated the following standard network statistics reflecting
315 network structure (Morris et al. 2014): degree of compartmentalization (number of compartments); weighted quantitative network
316 specialization index H_2' ; weighted quantitative generality (effective number of host species per consumer species); nestedness
317 (specialization asymmetry); weighted quantitative vulnerability (effective number of consumer species per host plant species);
318 and connectance (degree of redundancy in the study system). Appendix S1E describes these network statistics in greater detail.
319 All network statistics were calculated with the R package Bipartite (Dormann et al. 2018). We also reported the number of species
320 in both trophic levels and the sum of links for each subnetwork, as well as sampling intensity sensu Schleuning et al. (2012).
321 Models were estimated separately for topologies A-C (insect families, plant families and plant functional groups) and trophic
322 levels 1-2. We considered network statistics as independent data points in models, because of (a) no overlap between insect and
323 plant species across study sites; and (b) for a particular site and topology, the average pairwise species overlap between
324 subnetworks was 4.3%, 2.2% and 4.1% for herbivore families, plant families and functional groups, respectively. Network
325 statistics were also calculated for trophic levels 2-3 and 1-3 (see Question 3, below). We did not calculate network statistics when
326 subnetworks were too small (number of species in the lower level < 5).

327

328 We used null models to assess how network metrics deviated from those expected from a random distribution of interactions. Null
329 models were implemented for three full networks and 58 subnetworks using Patefield's algorithm ("r2dtable" in Bipartite's
330 nullmodel function, Dormann et al. 2018), in which the marginal species totals are constrained as per the respective observed
331 networks. We ran 1,000 randomisations for subnetworks and 200 for full networks (due to the time and CPU demands of running
332 analyses on large sparse networks). We evaluated whether network statistics differed significantly between study sites by
333 performing simple Kruskal-Wallis and Dwass-Steel tests. We refined this analysis by using three types of regression models. To
334 account for the effect of sampling effort, the number of observed interaction events (i.e., the number of links; Schleuning et al.,
335 2012) was used as a weighting factor in each regression. The first type of regression (hereafter “model type I”) included mixed

336 models with network statistics as dependent variables, sites and insect guilds as fixed factors and topologies (insect and plant
337 families, plant functional groups) as random factors.

338

339 Following Chamberlain et al. (2014), we modeled network statistics with beta regression (H2' and Connectance), generalized
340 linear models with Poisson (Number of compartments) or Gaussian (all other statistics) error distribution, separately for each
341 topology A-C. Models type II parsed the effects of plant phylogeny and of plant ecological variables (resource and functional
342 traits), and were calculated as:

343

344 Network statistic = MPD + FDis,

345

346 where MPD is the average plant relatedness (mean phylogenetic distance between plant species included in subnetwork,
347 calculated with the function `mpd` of the R package `Picante`, Kembel et al. 2010), and FDis is the functional dispersion within the
348 subnetwork, calculated with the function `fdisp` of the R package `FD` (Laliberté et al. 2014). FDis quantifies trait diversity as the
349 mean distance in multidimensional trait space of individual plant species to the centroid of all species (Laliberté & Legendre
350 2010). FDis was calculated with variables accounting for (a) plant resource (no. of stems and basal area in ForestGEO plots, seed
351 rain (g dry weight x m⁻²), equivalent to total fruit biomass and estimated from litterfall traps, Basset et al. 2018); and (b) plant
352 traits (fruit length and weight (partly related to seed size and biomass), number of seeds per fruit). We used the function `betareg`
353 of the R package `betareg` to perform beta regressions (Gruen et al. 2012). For other regressions, we performed model
354 simplification to extract the variables with significant predictive power with the built-in functions `glm` and `step` (backward
355 selection of variables) of the R package (R Core Team 2018). We eventually tested the significance of estimators by an ANOVA
356 (type 2 test) with the function `anova` in the R package 'car' (Fox and Weisburg 2019).

357

358 A last series of models considered more specifically the effects of plant variables (hereafter “models type III”):

359

360 Network statistic = Plant species richness + MPD + CWM₁ + CWM₂ + ... + CWM_n,

361

362 where Plant species richness was the number of confamilial species in ForestGEO plots (for topology B) or the number of plant
363 species in functional groups in ForestGEO plots (for topology C), and CWM_n was the community weighted mean of trait *n*,
364 weighted by the number of samples collected and calculated with function `dbFD` of R package `FD` (Laliberté et al. 2014; plant
365 species richness could not be included as an independent variable for the topology based on herbivore families). Independent
366 variables accounted for sampling effort, plant species richness, mean phylogenetic distance, plant resource and plant traits (as

367 defined in models type II; only continuous variables). Before analyses, highly correlated variables ($r > 0.7$) were removed from
368 models. Regressions were calculated and the significance of estimators tested as described previously.

369

370 *Question 3: parasitoid species richness*

371

372 To approach question 3, we computed a path analysis with a bottom-up flow of correlations implying direct and indirect
373 correlations between herbivore species richness, parasitoid species richness (dependent variables) and selected independent
374 variables. This analysis was performed at the level of the plant species, considering all plant species ($n = 618$) at the three sites
375 from which seed predators were reared. Independent variables included mean phylogenetic distance and variables related to plant
376 resource or plant traits (Appendix S1F). They were selected based on (a) a rationale for each path explained in Appendix S1F; and
377 (b) the best predictors in the regressions performed previously (see previous section and results). The mean phylogenetic distance
378 of a plant species to all other plant species was calculated with the function *cophenetic* of the R package *Picante* (Kembel et al.
379 2010). The model was calculated with the *Ωnyx* software (von Oertzen et al. 2015).

380

381 **Data deposition**

382

383 Interaction data were deposited in figshare, <https://doi.org/10.25573/data.11444571.v1>. Molecular insect data were deposited in
384 the following Barcode of Life projects (BOLD, www.boldsystems.org): BCI: 2,310 sequences in projects BCISP and PSPLP;
385 KHC: 398 sequences in KHCSP and KHCTE; WAN: 1,646 sequences in WANSP, FRUT and CURCU. Full data for specimens
386 sequenced (including those that failed), including images and host plants, are available on BOLD, accessible by DOI for the
387 datasets dx.doi.org/10.5883/DS-BCISP (BCI), dx.doi.org/10.5883/DS-KHCFRUIT (KHC) and [dx.doi.org/10.5883/DS-](https://dx.doi.org/10.5883/DS-PNGFRUIT)
388 PNGFRUIT (WAN).

389

390 **Results**

391

392 We collected 1,163 kg of seeds and fruits, which produced 80,600 insects across the three sites (Table 1). The composition and
393 species richness of the insect material is discussed elsewhere (Basset et al. 2018). This contribution analyzes the 3,197
394 interactions across a total of 1,176 plant, 1,015 herbivore and 318 parasitoid species at the three study sites (Table 1). Only 0.58%
395 of the potential 553,160 interactions were realized (Table 1). Since most properties of subnetworks do not represent properties of
396 whole networks (Jordano 2016), we detail network statistics for the full networks (level 1-2) of BCI, KHC and WAN in Table 1,

397 for comparison with other studies. These results emphasize differences between BCI and the other two sites, which we analyze
 398 in more depth by considering subnetwork data.

399

400 **Question 1: insect host specificity**

401

402 Differences in the median value of DSI* across insect families were significant ($W=114.0$, $p < 0.001$, $d.f.=6$; Fig. 1b). Bruchinae
 403 were by far the most specialized taxa, followed by Pyralidae, Curculionidae, Scolytinae, Tortricidae, Tephritidae and
 404 Stratiomyidae (Fig. 1b). Seed eaters were significantly more specialized than pulp eaters (Mann-Whitney test, $U=91.8$, $p < 0.001$,
 405 $d.f.=1$; Fig. 1c). There were also significant differences between the median DSI* of insect faunas feeding across plant families
 406 ($W= 50.9$, $p > 0.001$, $d.f.=7$). For example, on average, insects feeding on Fabaceae were rather specialized whereas those feeding
 407 on Meliaceae were less so (Fig. 1d). Differences in median of DSI* for insects feeding across plant functional groups were also
 408 significantly different ($W= 53.1$, $p < 0.001$, $d.f.=4$). In particular, insects feeding on plants belonging to functional group B (dry
 409 dehiscent fruits) were far more specialized than those feeding on group C plants (fleshy orange fruits; Fig. 1e). Overall, insects
 410 feeding on dry fruits were significantly more specialized than those feeding on fleshy fruits (Mann-Whitney test, $U=39.9$, $p <$
 411 0.001 , $d.f.=1$; Fig. 1f). The percentage of true monophagous species ($DSI*=1$) was higher at BCI (69.5%) than at KHC (25.3%)
 412 and WAN (18.9%) and the median of DSI* was significantly different across sites (Kruskal-Wallis test, $W=201.8$, $p < 0.0001$,
 413 $d.f.=2$; Fig. 1a).

414

415 The mixed linear model with DSI* as dependent variable and insect family as random factor indicated that the effect of site was
 416 significant, but not that of insect guild (seed eater versus pulp eater; Table S1). When considering the mean DSI* of insect species
 417 feeding on plant families, a similar model indicated that the effects of both site and plant functional group (coded A to E, see
 418 Appendix S1B) were significant, but not their interaction (Table S1). There was no correlation between the average DSI* of
 419 insects feeding on the eight focal plant families at the three study sites and the local species richness of these plant families ($r = -$
 420 0.16 , $p = 0.45$; Fig. S1).

421

422 **Question 2: variables affecting the structure of subnetworks**

423

424 We illustrate nine of the 58 subnetworks studied (Fig. 2) and detail characteristics of all subnetworks in Appendix S2. In null
 425 models, most (95.6%) observed network statistics deviated significantly from those expected from a random distribution of
 426 interactions (Table S2), with nestedness involved in nearly all cases where the deviation was not significant (Table S2). The
 427 distribution of the six main network statistics is summarized in Fig. 3 for the topology based on insect herbivore families and

428 trophic levels 1-2. BCI subnetworks had significantly more compartments, significantly higher degree of specialization ($H2'$),
429 and significantly lower effective number of host species per consumer species (generality) than KHC and WAN. In particular, for
430 all herbivore families, $H2'$ was also higher at BCI than at other sites (Appendix S2). Subnetworks based on Bruchinae,
431 Tortricidae, Curculionidae and Pyralidae were in general more specialized than those based on Tephritidae, Scolytinae and
432 Stratiomyidae (Appendix S2). Food webs based on stratiomyid flies were rather unspecialized, rarely parasitized by braconids and
433 their subnetwork at WAN represented the most unspecialized subnetwork of all subnetworks analyzed. Conversely, the most
434 specialized subnetwork was based on Tortricidae at BCI, followed closely by Bruchinae at BCI (Appendix S2). Other network
435 variables were not significantly different between sites (Fig. 3). Mixed models weighting the effect of sampling effort (models
436 type I), for the topology based on insect families, confirmed the strong effect of sites on the number of compartments, $H2'$ and
437 generality (Table S3).

438

439 For the topology based on plant families, BCI had significantly more compartments than KHC and WAN, and KHC had
440 significantly larger effective number of consumer species per host plant species (vulnerability) than BCI and WAN (Fig. S1).
441 Nestedness and Connectance were not significantly different between sites for any of the topologies considered (Fig. S1). For the
442 topology based on plant functional groups, the number of compartments and $H2'$ were significantly higher at BCI than at the
443 other sites, whereas generality and vulnerability were significantly lower at BCI (Fig. S2). Mixed models weighting the effect of
444 sampling effort (models type I) for both topologies based on plant families and functional groups confirmed the significant effect
445 of site on all network statistics (Table S3).

446

447 When parsing the effects of plant phylogeny and ecological variables (models type II, Table S4), the significance of effects could
448 be ranked overall as mean phylogenetic distance (MPD) > functional dispersion (FDis). MPD was a significant predictor of
449 network statistics calculated for plant functional groups (topology C), while FDis was more important to predict network statistics
450 calculated for plant families (topology B). Note that for models based on plant families, the effect of MPD may be low due to the
451 limited range of MPD within plant families. This also applies for FDis in models based on plant functional groups.

452

453 Not surprisingly, models best explained by CWM (models type III) were related to plant functional groups (65-98% of variance
454 explained, Table 2). Over the different topologies, the variation explained by the type III models was greatest for number of
455 compartments and least for generality. Several variables were reasonably good predictors of subnetwork structure, in order of
456 importance seed rain, mean phylogenetic distance and number of plant species, as well as number of seeds per fruit (Table 2).
457 Plant species richness was a good predictor of network statistics (connectance, nestedness, generality), only for topology B based
458 on plant families. In models describing network statistics for plant functional groups, variables related to plant traits were

459 important to predict H2', while variables related to plant resources were important for number of compartments, vulnerability,
460 connectance and nestedness (Table 2).

461

462 **Question 3: species richness of herbivores and parasitoids**

463

464 Our path analysis model explained 19% of the variance in the number of parasitoid species supported by each plant species (Fig.
465 4). As expected, significant paths existed between plant traits and herbivore species richness, and between plant resources and
466 herbivore species richness. Mean plant phylogenetic distance influenced plant traits but not directly herbivore species richness.
467 The strongest direct paths (as judged from standardized path coefficients) influencing parasitoid species richness originated from
468 herbivore species richness (positive), mean phylogenetic distance (negative) and basal area (positive). Thus, although the effect of
469 mean plant phylogenetic distance was significant and negative on parasitoid species richness (as predicted by the nasty host
470 hypothesis of Gauld et al. 1992), its direct path was about five times smaller than the corresponding direct path originating from
471 herbivore species richness, pointing to other explanations.

472

473 **Discussion**

474

475 In this contribution we examined the interaction networks involving seeds and fruits, the insects feeding on them and their
476 parasitoids, at three tropical sites. To analyze the 3,197 interactions reported, we considered three "topologies" (how subnetworks
477 are arranged) resulting in 58 different subnetworks, which were largely independent from each other. This strategy was possible
478 because of the very low overlap of interacting species between subnetworks but may not be applicable to other types of networks,
479 such as mutualistic networks. Topology A, based on families of seed predators, may be useful to entomologists, whereas
480 topologies B and C (based on plant families and functional groups) may be more interesting to botanists. Some interactions may
481 not have been documented in our study system, since attack rates were rather low (8.5% of seeds/fruits attacked, Basset et al.
482 2018) and substantial sampling effort may be required to rear insects attacking seeds and fruits, For example, Ctvrtecka et al.
483 (2014) consider a minimum sample size of 5kg of fruits/seeds per plant species adequate to rear weevils feeding on fruits/seeds.
484 This condition was achieved for only 3% of our plant species. Low sampling effort may result in inflated insect host specificity
485 and network specialization (Blüthgen et al. 2006). Sampling effort in the field (collecting seeds/fruits, rearing insects) was higher
486 at BCI than at the other sites (Table 1). Hence, we believe that the high host specificity documented at BCI is not an artefact.
487 Another obvious limitation in our study was the indirect documentation of linkages between insect herbivores and parasitoids (see

488 Methods). Some of the linkages reported here will need confirmation but given the limited data on tropical seed predators they
489 are nevertheless valuable.

490

491 **Insect host specificity**

492

493 Insect host specificity varied significantly between insect families. While some seed- or fruit-feeding taxa are known to be
494 extremely specialized in rainforests (Bruchinae: Janzen 1980, Curculionidae: Cvrtecka et al. 2014), others are less so
495 (Tephritidae: Novotny et al. 2010). These trends were confirmed in our study, which also indicated that Stratiomyidae, a taxon
496 rarely considered in studies of frugivorous insects, are less specialized pulp eaters than Tephritidae. Seed-eaters were more host-
497 specific than pulp-eaters, confirming that insect host specificity for tropical herbivore guilds in both temperate and tropical forests
498 decreases in the sequence: seed-eaters > leaf-miners > pulp-feeders > leaf-chewers > sap-suckers > xylophages > root-feeders
499 (Novotny & Basset 2005). This partially reflects the plant's allocation of nitrogen and chemical defences to the tissues consumed
500 by these guilds, as young leaves are sometimes better defended than seeds (Janzen 1971, 1980, Bazzaz et al. 1987, Zangerl &
501 Bazzaz 1992, Kergoat et al. 2005). Insects feeding on dry fruits were also more host specific than those feeding on fleshy fruits.
502 Insect host specificity varied significantly among plant families and functional groups, and the effect of site was important in
503 most of our analyses. Overall, we observed the lowest percentage of realized interactions and highest insect host specificity at
504 BCI. This trend was apparent when considering both entire networks (Table 1) and subnetworks (Figs 1,3). Similar levels of host
505 specificity for entire networks and across subnetworks may be explained by the preponderance of highly specialized fruit/seed
506 consumers, with very few generalist consumers present in more than one subnetwork.

507

508 This high insect host specificity at BCI is likely to result from the following factors. (1) Insect faunal composition: highly host
509 specific and diverse Bruchinae are prevalent at BCI and absent from KHC and WAN. (2) Fruit fleshiness: BCI has the highest
510 proportion of dry fruits (supporting highly host specific insects), possibly because of lower rainfall at BCI as compared to our
511 other sites (Kissling et al. 2009). (3) Fruit production: BCI has on average four times higher seed rain per plant species than KHC
512 or WAN (i.e., high fruit production and low plant species richness: Table 1). Our regressions confirmed the importance of
513 variables such as basal area or seed rain to predict insect specialization. (4) Fabaceae: there is a high percentage of Fabaceae
514 species at BCI (Table 1), which support many host-specific insect species.

515

516 In mutualistic networks, such as pollination and seed dispersal networks, specialization decreases with increasing plant diversity.
517 An explanation may be that high plant diversity reduces relative plant abundance and related plant resources, resulting in hard
518 evolutionary constraints on specialists (Schleuning et al. 2012, Escribano-Avila et al. 2018). Antagonistic networks may be

519 different (Morris et al. 2014). Lewinsohn and Roslin (2008) discuss the species richness and host specificity of folivorous
520 insects in tropical rainforests, and our BCI data appear to follow their contention that high species richness may be promoted by
521 more insect species per plant species (Table 1) or higher herbivore host specificity (Fig. 1a). In sum, low plant richness and high
522 insect host specificity at BCI suggests that antagonistic networks based on seed predation may follow the same rules as
523 mutualistic networks, with low plant richness strengthening interactions and favoring high insect host specificity (Novotny et al.
524 2002).

525

526 **Subnetwork structure**

527

528 Our analyses emphasized the strong effects of site on the different network statistics. Plant assemblages at different rainforests
529 may be phylogenetically different or may possess different traits, or both. Tree assemblages are phylogenetically distinct in many
530 rainforests (Webb 2000) and there are important differences in seed functional traits between our rainforest sites (Appendix S1B:
531 Table App2-S1; Dahl et al., 2019). Plant phylogenetic distance had an important effect on subnetwork structure (e.g.,
532 specialization H2' and generality in subnetworks based on insect families), but this effect was not overwhelming, as variables
533 related to plant traits or plant resource were also important in this regard. A more explicit inclusion of the hierarchical structure of
534 phylogenies in predicting interaction identities might provide increased explanatory power. Ideally, further analyses would
535 include phylogenies for hosts, herbivores and parasitoids (Ives and Godfray 2006), but herbivore and parasitoid phylogenies are
536 not currently available. Plant traits such as fruit length and number of seeds per fruit, were important predictors of network
537 statistics (Table 2). Other variables related to host phenology, such as the duration of fruiting season and its synchronization
538 within/among years, may well be important in this regard (Janzen 1976), but they could not be tested in this study, for lack of
539 reliable data at all sites. Variables accounting for plant resource (basal area, seed rain) were also important whereas the effect of
540 mean phylogenetic distance was not excessive. This would lend support to the modified plant defence theory (Agrawal &
541 Fishbein 2006). Both plant resource and plant traits were reasonably good predictors of subnetwork structure, particularly for
542 models based on plant functional groups, emphasizing the interest in this topology as a predictive framework for subnetwork
543 structure.

544

545 **Upward cascades in the subnetworks**

546

547 The nasty host hypothesis (Gauld et al. 1992) argues that tropical plants often possess highly active chemical defenses, which may
548 lead to greater host specialization and sequestration of secondary compounds in insect herbivores, and reduced loads of
549 parasitoids on particularly well-defended host plants. However, to date, evidence in favor of this hypothesis is mixed (Quicke

550 2012, Morris et al. 2014). Alternatively, Smilanich et al. (2009) observed that secondary metabolites sequestered by herbivores
551 may compromise their immune response, making them more vulnerable to successful parasitism (the “vulnerable host
552 hypothesis”). In our study system, we used plant phylogenetic distance as a surrogate for plant chemistry (Berembaum 2001), as
553 chemical data for tropical fruits and seeds are limited (Gripenberg et al. 2018). Our path model indicated that most of the
554 explained variance in parasitoid species richness on host plants could be attributed to a direct path originating from herbivore
555 species richness, whereas the corresponding path originating from mean plant phylogenetic distance was less important.

556

557 The nasty host hypothesis (Gauld et al. 1992) explains parasitoid loads on plants principally with regard to plant chemistry. Were
558 this hypothesis correct, we would have expected a large direct path from mean plant phylogenetic distance to parasitoid species
559 richness. The larger direct path observed from herbivore species richness to parasitoid species richness seems rather consistent
560 with both the resource concentration and resource base hypotheses (Root 1973, Price 1992), predicting that local assemblages of
561 parasitoids may be more diverse when their herbivore hosts are diverse (Hawkins & Lawton 1987) and vulnerable (Smilanich et
562 al. 2009).

563

564 **Conclusions**

565

566 The stability of mutualistic networks is promoted by a highly connected and nested architecture, whereas stability in antagonistic
567 networks is promoted by a compartmentalized and weakly connected structure (Morris et al. 2014). The subnetworks with the
568 highest number of compartments were those based on Curculionidae, Fabaceae and functional group B (large dry fruits, protected
569 and dehiscent) at BCI. Webs that are strongly compartmentalised (i.e. have high modularity) might be expected to be stable
570 (across modules) because changes in abundance (or extinction) of individual species (within modules) are less likely to cascade to
571 affect nodes in other parts of the network beyond the affected compartment or module (Thébaud and Fontaine 2010). In
572 antagonistic insect-plant networks where the host is immobile (a property that distinguishes them from many other food webs),
573 modularity will often result from trait matching and phylogenetic conservatism in plant traits. High levels of trait matching in
574 most cases will make insect herbivores particularly prone to co-extinction following loss of their host plants. Interactions such as
575 those for Stratiomyidae at Wanang which display lower trait matching may be more robust to random plant species loss but the
576 subnetwork overall will be less resilient to the loss of key nodes rich in fleshy fruit (e.g. well-connected plant genera).

577

578 Seed dispersal networks have on average a low specialization ($H2'$) compared to our seed predation subnetworks (Blüthgen et al.
579 2007: average 0.28; average 0.79 for all our subnetworks). Low $H2'$ promotes high redundancy and increased seed dispersal
580 (Blüthgen et al. 2007). Everything else being equal, plant species supporting generalist dispersers but specialized seed predators

581 with low attack rates may be able to produce large number of viable seeds and may be at an advantage over other plant
582 competitors. This is in line with the plant defence syndrome of high nutritional quality and defence (Agrawal & Fishbein 2006).
583 Further, reviewing seed dispersal networks in the tropics, Escribano-Avila et al. (2018) indicated that woody plants bearing small
584 juicy berries containing many tiny seeds often represent keystone species. From the viewpoint of conserving insects feeding on
585 fruits/seeds, the plants most important in seed predation networks are those which support many insect species (i.e., with high
586 number of consumer species per host plant species, vulnerability). Although we did not study many of the plant families
587 considered by Escribano-Avila et al. (2018), we note that our plant families with high vulnerability (Appendix S2) usually do not
588 bear berries with tiny seeds. This indicates that, from a conservation viewpoint, key plant species in the tropics may differ
589 between networks of seed dispersal and seed predation.

590

591 In summary, our study emphasizes the duality between seed dispersal and seed predation networks in the tropics as the former are
592 not very specific whereas the latter are far more specialized and may include different key plant species. From the viewpoint of
593 forest regeneration and conservation, this underlines the need to study both types of network including a variety of potential key
594 plant species.

595

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607

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734 Supplementary material at xxx.

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737 **Table 1.** Salient characteristics of the study sites and their plant, insect and network interactions. Plot data are from Anderson-
 738 Teixeira *et al.* (2014).

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Variable	BCI	KHC	WAN
Site physiognomy and structure:			
Coordinates	9.15°N, 79.85°W	7.54°N, 99.80°E	5.24°S, 145.08°E
Elevation (m)	120-160	120-330	90-180
Annual average Rainfall (mm)	2551	2665	3366
Annual average daily maximum air temperature (°C)	26.3	27.1	26.5
Number of tree species/ genera/ families recorded in plot	299/181/59	593/285/82	508/245/77
Percentage of plant spp. with dry seeds/fruits	56.8	26.0	28.0
Percentage of Fabaceae species to total spp. richness in plot	14.0	3.1	4.8
Total fruit production (seed rain; dry g x m ⁻² x yr ⁻¹)	108.0	7.0	10.8
Average fruit production per species (dry g x m ⁻² x yr ⁻¹)*	0.596	0.141	0.157
Plant samples:			
Years of collection	2010-2013	2013-2015	2013-2015
Number of plant species/plant families surveyed	497/82	357/66	332/67
No. plant species surveyed within the 10 focal families	218	171	170
Total number of seeds or fruits collected	208,508	39,252	122,976
Total weight of samples (kg)	380.2	343.2	439.9
Insect samples:			
Total number of insects reared	27,610	17,555	35,434
Number of individuals / species of seed eaters**	11,059/311	2,100/59	3,935/77
Number of individuals / species of pulp eaters**	5,670/214	7,265/161	9,403/193
Number of individuals / species of parasitoids***	775/161	359/61	961/96
Interactions:			
Number of interactions realized / % realized-potential****	892/0.26	917/1.01	1,388/1.20
Plant species with most seeds/fruit reared	<i>Mikania leiostachya</i>	<i>Caryota mitis</i>	<i>Mastixiodendron pachyclados</i>
Most abundant herbivore species	<i>Pagiocerus frontalis</i>	<i>Coccotrypes myristicaceae</i>	<i>Coccotrypes</i> sp.n.3
Most abundant parasitoid species	Dorylinae sp. 156	Alysiinae sp. 13	<i>Diospilus</i> sp. 2
Network statistics for full network (level 1-2):			
Average DSI* ± s.e.	0.906±0.013	0.577±0.029	0.503±0.028
Number of compartments	85	20	9
H2'	0.914	0.664	0.657
Generality	1.85	6.84	5.15
Nestedness	0.96	1.61	2.20
Vulnerability	2.23	4.69	6.05
Connectance	0.006	0.021	0.022

740 * Plant species recorded in litterfall traps

741 ** Seven focal taxa only, see methods

742 *** Braconidae and Ichneumonidae only

743 **** No. of interactions between levels 1-2 and 2-3; percentage of realized to potential interactions

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745 **Table 2.** Summary of the best regression models (type III) with network statistics as dependent variables, for each topology considered (A-C). Independent variables include
746 Mean Phylogenetic Distance (MPD) and the community weighted mean (CWM) of functional traits (see text for details). *** p< 0.001, ** p<0.01, * p<0.05, independent
747 variables listed according to decreasing standardized coefficients, best estimators indicated in bold.

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Topology/ Subnetwork variable	Significant variables	R ²	F	p	AIC
A. Insect families					
Specialization H2'	MPD*** , Fruit length***, Basal area***, No. seed per fruit***, Seed Rain***	0.400	2457.1	<0.001	-3670.1
Connectance	n.s.	-	-	-	-
No. compartments	Seed Rain*** , Fruit length***, MPD***, Basal area***, No. seed per fruit***	0.581	2637.9	<0.001	26903.0
Generality	MPD**	0.500	15.9	<0.001	104.1
Nestedness	n.s.	-	-	-	-
Vulnerability	Fruit length*	0.342	5.2	0.022	94.5
B. Plant families					
Specialization H2'	No. seed per fruit*** , Basal area***, MPD***, Fruit length***, Seed Rain***	0.107	446.1	<0.001	-1999.3
Connectance	No. plant species*** , MPD***, Basal area***, No. seed per fruit***, Fruit length***	0.618	1948.5	<0.001	-7143.4
No. compartments	Basal area*** , Seed Rain***, Fruit length***, No. plant species***, MPD**	0.925	18.5	<0.001	5481.6
Generality	No. plant species* , Fruit length*	0.351	3.4	0.037	44.6
Nestedness	No. plant species***	0.467	8.8	0.002	150.4
Vulnerability	n.s.	-	-	-	-
C. Plant functional groups					
Specialization H2'	No. seeds per fruit*** , Basal area***, Seed rain***, MPD***, Fruit length***	0.696	4169.4	<0.001	-10018.1
Connectance	Seed Rain*** , MPD***, Fruit length***, No. seed per fruit***, Basal area***	0.749	5125.6	<0.001	-20987.9
No. compartments	Seed Rain*** , Basal area***, Fruit length***, No. seed per fruit***, No. plant species***	0.987	56.9	<0.001	13211.0
Generality	n.s.	-	-	-	-
Nestedness	MPD*** , Basal area*	0.650	11.2	0.002	60.7
Vulnerability	Seed rain*** , Basal area**, MPD*	0.835	9.1	0.002	52.3

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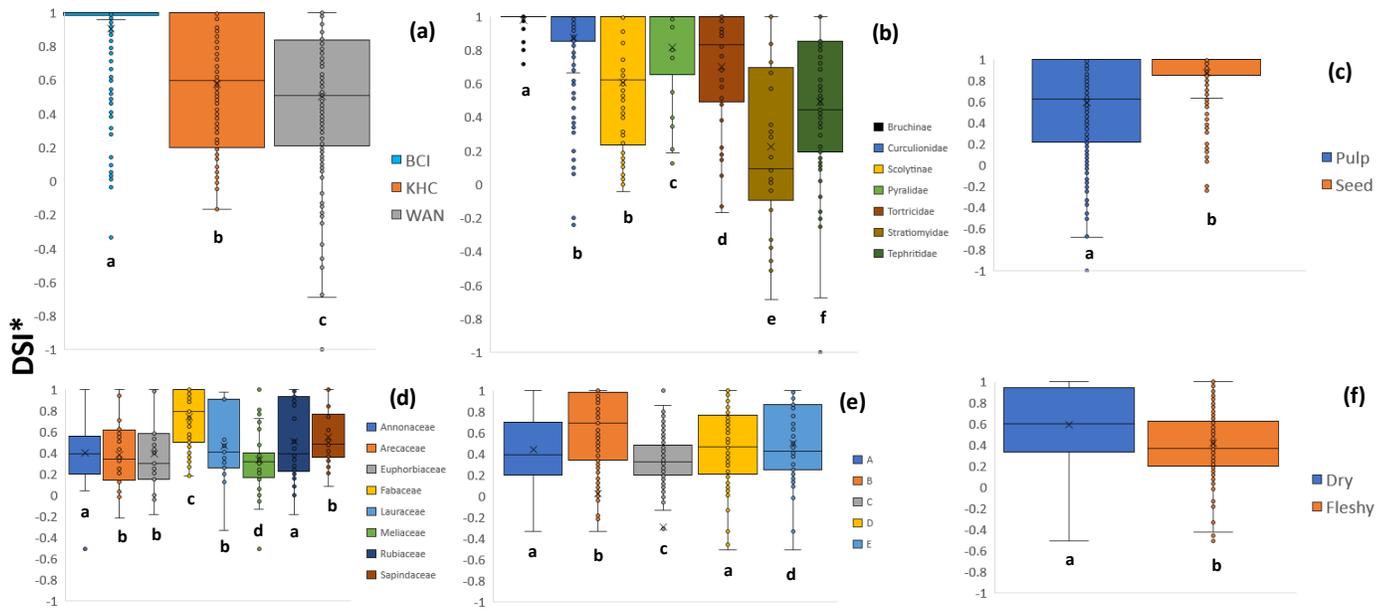
FIGURE CAPTIONS

Fig. 1. Summary distribution of the specialization index DSI*. Box and whisker plots across (a) sites, (b) insect families, (c) insect guilds, (d) plant families, (e) seed functional groups and (f) categories of fruit fleshiness. Groups with different letters are significantly different (Dwass-Steel tests, $p < 0.05$).

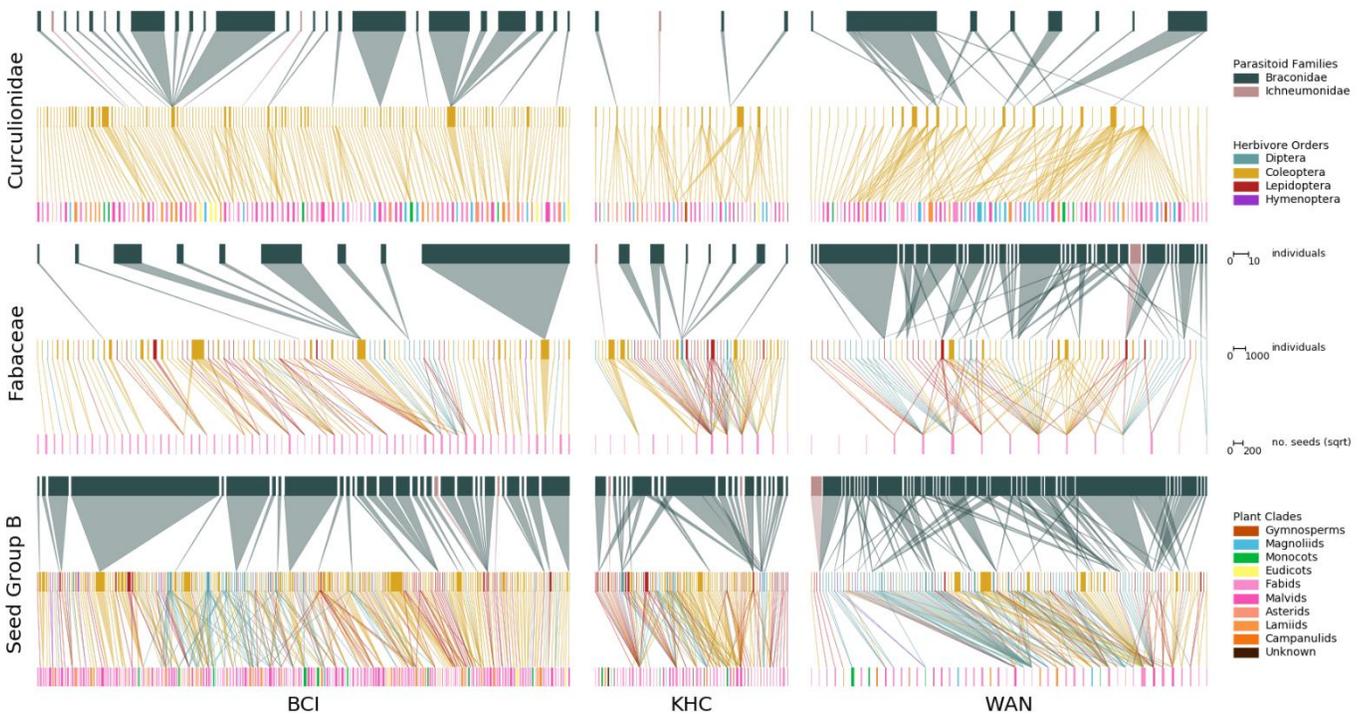
Fig. 2. Examples of interaction subnetworks at BCI (left), KHC (middle) and WAN (right). Top: topology based on insect family, here the Curculionidae (without Scolytinae). Middle: topology based on plant family, here the Fabaceae (including plant species lacking insects attacking seeds or fruits). Bottom: topology based on plant functional group, here Group B (dry fruits, protected, dehiscent and relatively large, see Appendix S1B). For each subnetwork, the abundance of parasitoid species (top series of rectangles) and herbivore species (middle series of rectangles) are represented by the number of individual reared, whereas the abundance of plant species (bottom series of rectangles, coloured by plant clades following APG IV: Chase *et al.*, 2016) are represented by the square root of the number of seeds collected. Parasitoid families, herbivore orders and plant clades are identified by distinct colours as coded on the right. The scale for each level is also indicated on the right. All subnetwork nodes are ordered as to minimize the number of crossed interactions. From left to right and top to bottom these subnetworks are coded as HB-CURC-BCI, HB-CURC-KHC, HB-CURC-WAN, PL-FABA-BCI, PL-FABA-KHC, PL-FABA-WAN, FG-B-BCI, FG-B-KHC and FG-B-WAN in Appendix S2.

Fig. 3. Summary distribution of the six main network level statistics across study sites (BCI, KHC, WAN) for subnetworks based on insect herbivore families and trophic levels 1-2 (plants-insect herbivores; $n=18$). The Bruchinae subnetwork for BCI was not included as it has no equivalent at other study sites. Groups with different letters are significantly different (Dwass-Steel tests, $p < 0.05$).

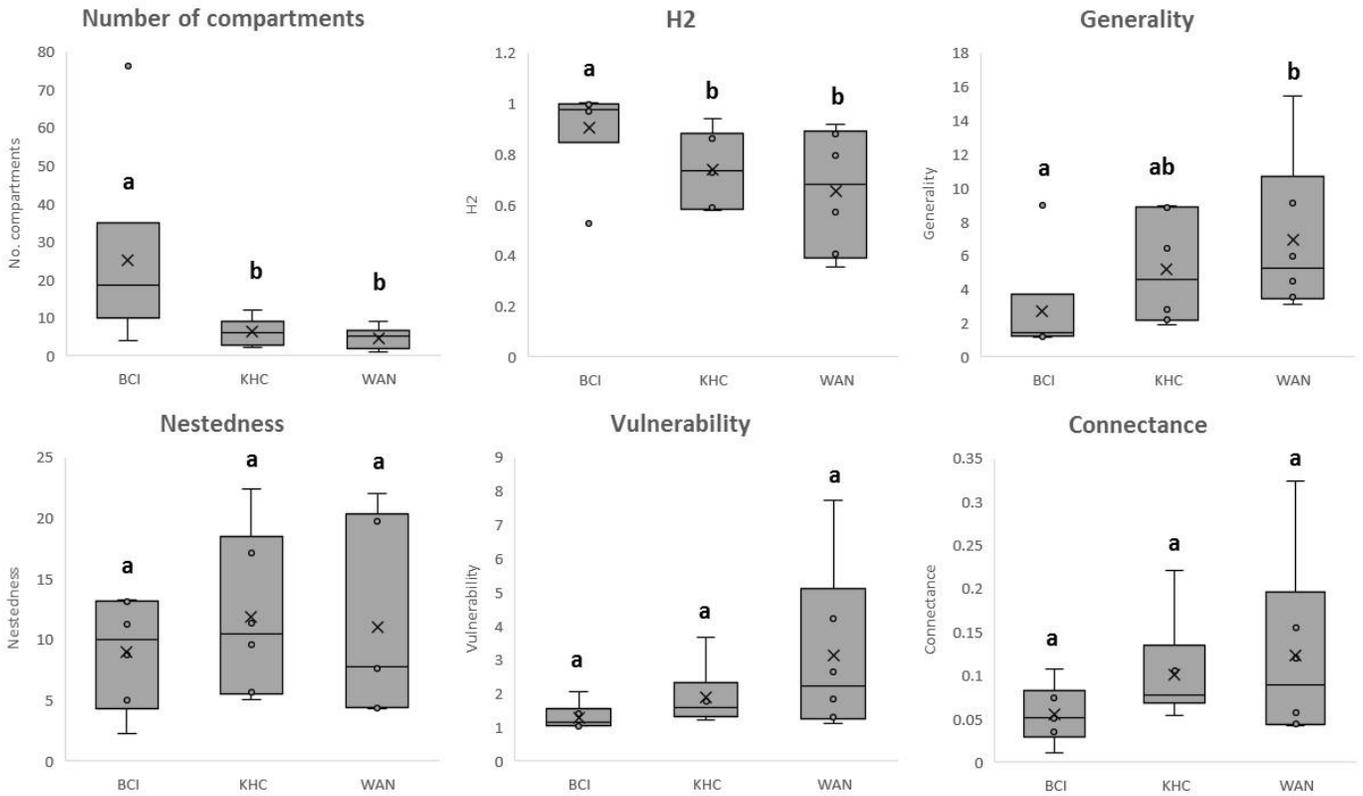
Fig. 4. Results of path analysis testing direct and indirect correlations between the species richness of seed- and fruit-eating insects (HerbSpp), parasitoid species richness (ParaSpp), mean phylogenetic distance (MPD), plant traits (fruit length, Length and ordination scores delineating plant functional groups, PCA1) and plant resource (basal area, BA and seed rain, SeedRain), for 618 host plant species. Standardized path coefficients are in parentheses. Significant ($p < 0.05$) and insignificant paths are indicated by solid and dashed lines, respectively. The rationale of the model is detailed in Appendix S1F.



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784 **Fig. 1.** Summary distribution of the specialization index DSI*. Box and whisker plots across (a) sites, (b) insect families, (c)
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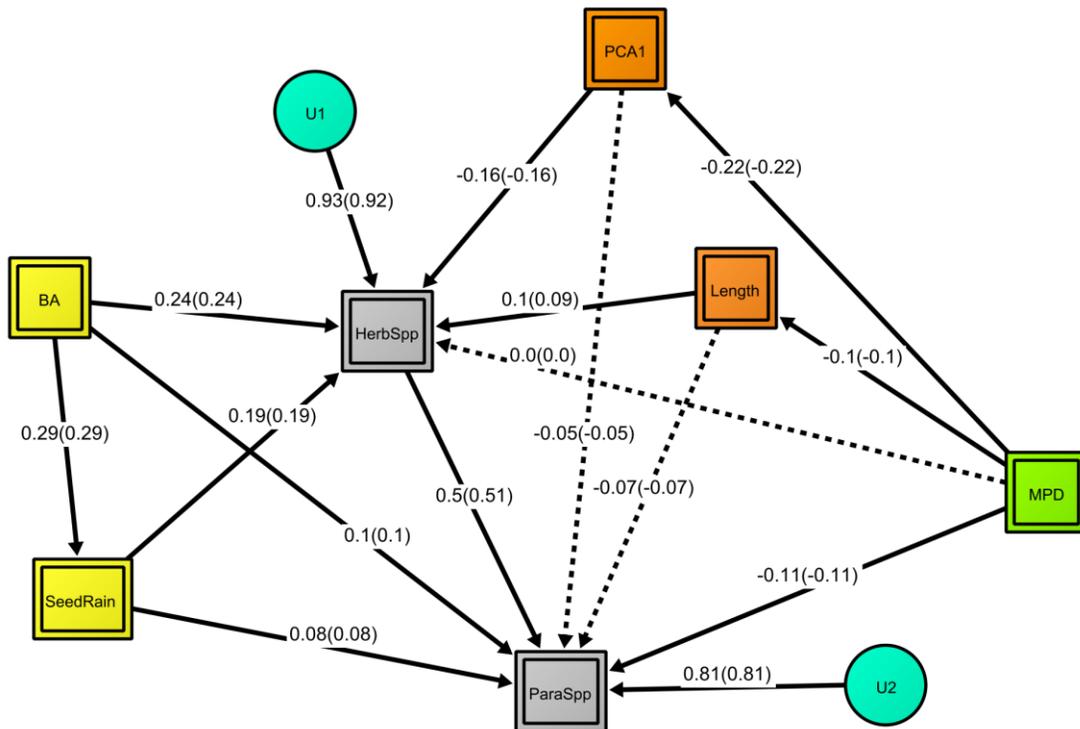


788
789 **Fig. 2.** Examples of interaction networks at BCI (left), KHC (middle) and WAN (right). Top: topology based on insect family,
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799 KHC and FG-B-WAN in Appendix S2.



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