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5 **Does biological intimacy shape ecological network structure? A test using a**
6 **brood pollination mutualism on continental and oceanic islands**

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33 collected data; DHH, RLGR, PRG, and EAN conducted analyses; DHH, RLGR, EAN, and PRG
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35

36 **ABSTRACT**

37

38 (1) Biological intimacy—the degree of physical proximity or integration of partner taxa
39 during their life cycles—is thought to promote the evolution of reciprocal specialization
40 and modularity in the networks formed by co-occurring mutualistic species, but this
41 hypothesis has rarely been tested.

42 (2) Here, we test this “biological intimacy hypothesis” by comparing the network
43 architecture of brood pollination mutualisms, in which specialized insects are
44 simultaneously parasites (as larvae) and pollinators (as adults) of their host plants to that
45 of other mutualisms which vary in their biological intimacy (including ant-
46 myrmecophyte, ant-extrafloral nectary, plant-pollinator, and plant-seed disperser
47 assemblages).

48 (3) We use a novel dataset sampled from leafflower trees (Phyllanthaceae: *Phyllanthus* s. l.
49 [*Glochidion*]) and their pollinating leafflower moths (Lepidoptera: *Epicephala*) on three
50 oceanic islands (French Polynesia) and compare it to equivalent published data from
51 congeners on continental islands (Japan). We infer taxonomic diversity of leafflower
52 moths using multilocus molecular phylogenetic analysis, and examine several network
53 structural properties: modularity (compartmentalization), reciprocity (symmetry) of
54 specialization, and algebraic connectivity.

55 (4) We find that most leafflower-moth networks are reciprocally specialized and modular, as
56 hypothesized. However, we also find that two oceanic island networks differ in their
57 modularity and reciprocal specialization from the others, as a result of a supergeneralist
58 moth taxon which interacts with 9 out of 10 available hosts.

59 (5) Our results generally support the biological intimacy hypothesis, finding that leafflower-
60 moth networks (usually) share a reciprocally specialized and modular structure with other
61 intimate mutualisms such as ant-myrmecophyte symbioses, but unlike non-intimate
62 mutualisms such as seed dispersal and non-intimate pollination. Additionally, we show
63 that generalists—common in non-intimate mutualisms—can also evolve in intimate
64 mutualisms, and that their effect is similar in both types of assemblages: once generalists
65 emerge they reshape the network organization by connecting otherwise isolated modules.

66

67 Keywords: biological intimacy hypothesis, coevolution, *Epicephala*, *Glochidion*, modularity,
68 network evolution, *Phyllanthus*, reciprocal specialization

69

70 **RÉSUMÉ**

71

72 (1) L'intimité biologique – le niveau de proximité physique ou d'intégration biologique de
73 différentes espèces au cours de leurs cycles de vie – est considérée comme un facteur
74 favorisant l'évolution de la spécialisation réciproque et la modularité dans les réseaux
75 écologiques formés par des espèces mutualistes, mais cette hypothèse n'a été que
76 rarement testée.

77 (2) Ici, nous testons cette « hypothèse d'intimité biologique » en comparant l'architecture de
78 deux types de réseaux mutualistes. Le premier type de réseaux comprend des interactions
79 de haute intimité biologique, telles que celles entre les insectes spécialisés qui sont en
80 même temps pollinisateurs (durant le stade adulte) et parasites (durant le stade larvaire)
81 de leurs plantes-hôtes, et celles entre les fourmis et les myrmécophytes. Le second type

82 de réseaux comprend quant à lui des mutualistes dont l'intimité biologique diffère de celle
83 trouvée dans le premier type de réseaux. Cela correspond aux interactions entre les
84 fourmis et les plantes aux nectaires extra-floraux, les plantes et leur pollinisateurs, ainsi
85 que les plantes et les animaux qui dispersent leurs graines.

86 (3) Nous utilisons des données échantillonnées à partir d'arbres du clade *Glochidion*
87 (Phyllanthaceae : *Phyllanthus s. l.*), aussi appelés *mahame* ou *mānono* en langue
88 tahitienne, et leurs papillons de nuit pollinisateurs du genre *Epicephala* (Lepidoptera) sur
89 trois îles océaniques (Tahiti, Moorea, et Huahine, archipel de la Société, Polynésie
90 française) et les comparons à des données équivalentes déjà publiées sur quatre îles
91 continentales (Japon). Nous en déduisons la diversité taxonomique des papillons en
92 utilisant l'analyse phylogénétique moléculaire multilocus, et examinons plusieurs
93 propriétés structurelles des réseaux obtenus : la modularité (compartimentation), la
94 réciprocité (symétrie) de spécialisation, et la connectivité algébrique.

95 (4) Nous trouvons que la plupart des réseaux *Glochidion-Epicephala* ont une structure
96 spécialisée de manière réciproque et modulaire, comme prédit par l'hypothèse.
97 Cependant, nous trouvons également que les réseaux de deux des îles océaniques (Tahiti
98 et Huahine) diffèrent des autres par leur modularité et spécialisation réciproque, résultant
99 de la présence d'un papillon super-généraliste interagissant avec 9 sur 10 plantes-hôtes
100 disponibles.

101 (5) De manière générale, nos résultats soutiennent l'hypothèse d'intimité biologique en
102 montrant que les réseaux *Glochidion-Epicephala* ont (généralement) une structure
103 spécialisée de manière réciproque et modulaire, similaire à celle des symbioses fourmis-
104 myrmécophytes mais différente de celle des mutualistes non-intimes tels que les

105 disperseurs des graines, et la pollinisation non-intime. De plus, nous montrons que les
106 généralistes (souvent observés chez les mutualistes non-intimes) peuvent aussi évoluer
107 chez les mutualistes intimes, et que leur effet est similaire dans les deux types
108 d'assemblages : l'arrivée de généralistes provoque une ré-organisation de l'architecture
109 des réseaux, connectant des modules jusqu'alors isolés.

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112

113 **Introduction**

114 Evolutionary biologists have been fascinated by ecological specialization for over a
115 century (Darwin 1862), but how specialization varies among biotic interactions has received
116 renewed attention in ecology and coevolutionary biology (Thompson, 1994; Bascompte,
117 Jordano, Melián, & Olesen, 2003; Olesen, Bascompte, Dupont, & Jordano, 2007). Species
118 interaction networks commonly vary depending on the biological intimacy of the interactions,
119 where intimacy is defined as the degree of physical proximity or integration of partner taxa
120 during their life cycles (Ollerton, 2006). Partners in highly intimate or symbiotic mutualisms
121 (such as ant-myrmecophyte, brood pollination, anemone-anemonefish, and eukaryotic host-
122 bacterial symbiont interactions) spend substantial portions of one or both species' life cycles in
123 close physical proximity to, or even inside the tissues of, the other. In contrast, partners in less
124 intimate mutualisms (such as non-symbiotic pollination, seed dispersal, and host-cleaner fish
125 mutualisms) spend smaller fractions of their lifespans in contact with each partner and interact
126 with more partners over the course of their lifespans (Thompson, 1994, 2005). In what can be
127 termed the “biological intimacy hypothesis”, the networks formed by species engaged in highly
128 intimate interactions appear to be reciprocally specialized and highly modular at fine taxonomic
129 scales, whereas less intimate interactions are less reciprocally specialized and less modular
130 (Thompson, 2005; Guimarães et al., 2007; Pires & Guimarães, 2013; Thompson, Adam,
131 Hultgren, & Thacker, 2013). Consistent with this hypothesis, there is evidence that intimate
132 ecological interactions can be expected to be species-poor (Raimundo, Gibert, Hembry, &
133 Guimarães, 2014), non-nested (Guimarães et al., 2007) and highly modular (Fontaine et al.,
134 2011). This reciprocal specialization and modularity has been attributed to a number of
135 processes, including the opportunities for selection afforded by the close physical contact

136 between partners (Thompson, 2005; Guimarães et al., 2007) and the historical effects of descent
137 from non-mutualistic ancestors (Thompson, 1994).

138 The role of biological intimacy in determining the structure of interactions among species
139 is of interest because ecological and evolutionary dynamics, and the feedbacks between both, are
140 expected to show marked differences between high- and low-intimacy mutualisms.

141 Coevolutionary theory (Thompson, 2005) suggests adaptive co-diversification and reciprocal
142 specialization can be major drivers of the strong modularity found in empirical high-intimacy
143 mutualistic networks (Guimarães et al., 2007; Fontaine et al., 2011). On the other hand, theory
144 predicts that low-intimacy mutualisms involving generalist and phylogenetically unrelated
145 species would favor trait convergence and increased network connectivity (Guimarães, Jordano,
146 & Thompson, 2011), which, combined to adaptive interaction rewiring (Ramos-Jiliberto,
147 Valdovinos, Moisset de Espanés, & Flores, 2012; Zhang, Hui, & Terblanche, 2011), would
148 explain the recurrence of nestedness in low-intimacy mutualistic networks (Guimarães et al.,
149 2011; Fontaine et al., 2011).

150 However, despite these theoretical predictions, the hypothesis that biological intimacy
151 promotes modularity and reciprocal specialization in mutualisms has been tested very few times
152 empirically, primarily using ant-myrmecophyte networks. In these symbiotic interactions, ant
153 colonies inhabit hollow domatia on the inside of plant organs and in turn defend their plant hosts
154 from herbivores (Rico-Grey & Oliveira, 2007). Ant-myrmecophyte assemblages are
155 characterized by high reciprocal specialization (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen,
156 2007; Guimarães et al., 2007) and high modularity (Guimarães et al., 2007; Dáttilo, Izzo,
157 Vasconcelos, & Rico-Grey, 2013; Cagnolo & Tavella, 2015) especially compared to less-
158 intimate assemblages formed by extrafloral nectary-bearing plants and their ant visitors

159 (Blüthgen et al., 2007; Guimarães, Rico-Gray, dos Reis, & Thompson, 2006; Guimarães et al.,
160 2007; Dáttilo, 2012). Other intimate mutualisms between tropical marine shrimp and gobies
161 (Thompson et al., 2013) and between ants and myrmecophilous lycaenid butterfly caterpillars
162 (Cagnolo & Tavella, 2015) show similarly high reciprocal specialization as do ant-
163 myrmecophyte networks, suggesting that the biological intimacy hypothesis may apply broadly
164 across taxonomically disparate mutualisms; data are, however, more mixed for other intimate
165 mutualisms, such as that between anemones and anemonefish (Ollerton, McCollin, Fautin, &
166 Allen, 2007; Ricciardi, Boyer & Ollerton, 2010).

167 In this paper, we test the biological intimacy hypothesis by comparing the network
168 architecture of plant-insect brood pollination mutualisms (characterized by high biological
169 intimacy) to that of other types of mutualistic assemblages which vary in their intimacy. Brood
170 pollination mutualisms include those between figs and fig wasps, leafflowers and leafflower
171 moths, and yuccas and yucca moths (Hembry & Althoff, 2016). In these interactions, specialized
172 insects pollinate flowers of their host plants, but also oviposit in the flowers, where their larvae
173 consume seeds or other floral tissue. Consequently, these associations are characterized by high
174 biological intimacy, with a portion of the insects' life cycle (egg and larval stages, and pupation
175 and even mating in some cases) taking place inside host reproductive tissue and the insect larvae
176 relying on the host for food (Cook & Rasplus, 2003; Kato, Takimura, & Kawakita, 2003;
177 Pellmyr, 2003; Luo, Yao, Wang, Zhang, & Hembry 2017). Classically, these interactions were
178 thought to obey a “one-to-one” paradigm in which locally, each pollinator species uses one
179 unique host plant, and each plant species is pollinated by a unique pollinator species exclusive to
180 it (Ramírez, 1970; Janzen, 1979); although recent data on host specificity do not uphold the
181 “one-to-one” paradigm strictly in many cases, it is clear that these interactions are still extremely

182 specialized at the species level, and host-associated adaptation may drive speciation, thereby
183 ensuring high host-specificity (Thompson, 2005; Hembry & Althoff, 2016).

184 The brood pollination mutualism we use in this paper as an independent test of the
185 biological intimacy hypothesis is that between leafflower plants (Phyllanthaceae; *Phyllanthus*
186 sensu lato) and leafflower moths (Lepidoptera: Gracillariidae: *Epicephala*). Leafflower moths
187 are the sole known pollinators of several clades of leafflowers (in the genus *Phyllanthus* sensu
188 stricto, as well as the genera *Glochidion* s. l. and *Breynia*); they actively pollinate the flowers of
189 their host, and then oviposit into the ovaries such that the larvae feed on a subset of the
190 developing seeds (Kato, et al., 2003; Kawakita & Kato, 2006; Hembry, Okamoto & Gillespie,
191 2012; Zhang, Wang, Li, Hu, Yang & Wang, 2012c; Luo et al., 2017). Those leafflower lineages
192 that are pollinated by leafflower moths have no other known pollinators. Like myrmecophyte-
193 dwelling ants and other brood pollinating insects, leafflower moths spend a large portion of their
194 life cycles on or in their hosts' tissues: *Epicephala* eggs are laid inside leafflower host tissue,
195 larvae consume developing seeds inside leafflower fruit, and adults appear to spend a substantial
196 fraction of their existence on hosts engaging in active pollination and oviposition (Kato, et al.,
197 2003, Zhang et al., 2012c, Luo et al., 2017) and possibly also mating (Zhang, Hu, Li & Wang,
198 2012a).

199 Here we assemble data from the literature on networks between *Glochidion* (the best-
200 studied clade of leafflowers) and *Epicephala* moths on continental islands in Asia (the Ryukyu
201 Islands), and gather a novel dataset based on field collections and rearing for *Glochidion*-
202 *Epicephala* networks on oceanic islands in the South Pacific (Tahiti, Moorea, and Huahine).
203 Each of the seven islands considered here has 3-5 species of *Glochidion*. First, we infer a
204 phylogeny of Society Island *Epicephala* moths to ask how many minimally monophyletic taxa

205 exist. Moth taxa may use multiple hosts, so we also ask if any of these minimally monophyletic
206 taxa show signs of phylogenetic differentiation by geography or by host plant species, thereby
207 indicating extreme specialization in natural communities. Second, we use ecological network
208 analyses to examine patterns of specialization in brood pollination mutualisms and test the
209 biological intimacy hypothesis based on a comparison with other types of mutualisms that vary
210 in their biological intimacy (including ant-myrmecophyte, ant-extrafloral nectary, plant-
211 pollinator, and plant-seed disperser assemblages).

212

213 **Materials and Methods**

214 ***Study system background:*** The 300 described species of *Glochidion* are widely distributed in the
215 tropical Asia-Pacific region (Govaerts, Frodin & Radcliffe-Smith, 2000), but information about
216 patterns of species-specificity between these trees and *Epicephala* moths is available only from
217 Japan, China, and southeastern Polynesia. In Japan, each of the five native species of *Glochidion*
218 is locally pollinated by 1-2 species of *Epicephala*, and each species of *Epicephala* locally
219 pollinates only one species of *Glochidion* (Kawakita & Kato, 2006, 2016). Many Chinese
220 *Epicephala* are known from only single host species, although most of these are based on
221 relatively few collection localities (Zhang, Hu, Wang, & Li, 2012b; Li & Zhang, 2016);
222 however, two *Epicephala* are associated with one host at two sites in southwest China (Li &
223 Zhang, 2016), and three co-occurring *Epicephala* species appear to all use the same two
224 sympatric *Glochidion* species on Hainan Island (Li, Wang & Hu, 2015). Finally, at least three
225 multiple, distantly related *Epicephala* species co-occur in the Society Islands (French Polynesia);
226 one of these is a widespread generalist morphospecies (Clade Z) associated with 12 host species
227 across 13 islands in the Society, Cook, and Austral archipelagos (Hembry et al., 2013). Single

228 *Epicephala* species using different *Glochidion* host species in different parts of their range have
229 been reported in all three of these regions (Kawakita & Kato, 2006; Hembry et al., 2013; Li &
230 Zhang, 2016).

231 Here, we examine *Glochidion-Epicephala* networks on continental (Ryukyu Islands,
232 Japan) and oceanic (Society Islands, French Polynesia) islands (Appendix S1: Fig. S1). The
233 Ryukyu Islands are subtropical—near the northern climatic limit of this predominantly tropical
234 mutualism—and continental in origin, having been connected during glacial maxima to Taiwan
235 and the Asian continent. Four of the five *Glochidion* and at least one of the *Epicephala* in this
236 regional assemblage are also found elsewhere in continental or insular East Asia (Deng & Wang,
237 1993; Li & Gilbert, 2008; Zhang et al., 2012b). In contrast, the Society Islands are tropical and
238 oceanic, formed by volcanoes passing over a stationary hotspot in the earth’s mantle over the
239 past 4.6 Ma (Guillou et al., 2005). They have never been connected to each other (with one
240 exception) nor to other island groups or continents. All but one of the 14 described *Glochidion*
241 species from this archipelago are endemic, as are two of the three known *Epicephala* taxa
242 (Florence, 1997; Wagner & Lorence, 2011; Hembry et al., 2013; Hembry, 2017).

243 **Sampling:** *Epicephala* moths were sampled on the islands of Huahine, Moorea, and Tahiti by
244 collecting fruits from 10 *Glochidion* species in the field, aiming to maximize the number of
245 individual trees per species sampled for moths. Excluding unique maximum and minimum
246 values (for the endangered *P. papenooense* and the extremely widespread *P. taitensis*), we
247 collected 1-2 moths each from 3-12 individual trees per species, from 1-4 localities per tree
248 species per island ($n = 89$ individual moths, including 11 individuals used in Hembry et al.,
249 2013). Larvae from fruits were reared in plastic bags or rearing containers. Larvae and adults
250 were preserved in 96% ethanol. Because *Glochidion* is nested within a paraphyletic *Phyllanthus*

251 s. l. (Kathriarachchi et al., 2006), all these *Glochidion* have names in *Phyllanthus* which are used
252 in the main text (Appendix S1: Table S1; Wagner & Lorence, 2011). See Appendix S1 and
253 Appendix S1: Tables S1 and S2 for additional detail on Society Islands *Glochidion* and specimen
254 collection data.

255 **Molecular methods:** We amplified using polymerase chain reaction and Sanger-sequenced 2000
256 bp of DNA from three loci (mitochondrial COI, and nuclear ArgK, and EF1- α) from adult and
257 larval *Epicephala* specimens (GenBank accession numbers MH110346-MH110560), and
258 combined them with previously published equivalent data for the same taxa (Gen Bank accession
259 numbers KC912865- KC912869, KC912871, KC912873, KC912884- KC912885, KC912892-
260 KC912893, KC912918- KC912919, KC912921- KC912923, KC912925, KC912927,
261 KC912941-KC912942, KC912949- KC912950, KC912976- KC912977, KC912979- KC912981,
262 KC912983, KC912985, KC912998- KC912999, KC913006- KC913007, and MH110346-
263 MH110560, Hembry et al., 2013). Sequences were aligned using MUSCLE (Edgar, 2004) and
264 analyzed using Bayesian phylogenetic inference in MrBayes 3.1 (Ronquist & Huelsenbeck,
265 2003). We used support values (posterior probabilities) recovered in the phylogenetic analysis to
266 indicate potential groupings and differentiation of moth individuals by host plant species or by
267 island. This is the same approach used in the fields of phylogeography, host-associated
268 differentiation in the insect phylogenetics literature, and molecular species delimitation to look
269 for differentiation among closely related populations or young species. For additional details, see
270 Appendix S1.

271 **Network analysis:** To summarize patterns of host-moth interactions, weighted graphs (network
272 diagrams) were drawn for each of the three Society Islands. We used species designations for
273 *Glochidion* following existing taxonomy (Florence, 1997; Wagner & Lorence, 2011), and treated

274 each of the three minimally monophyletic clades of *Epicephala* recovered in the phylogenetic
275 analysis as a taxon. Although recognition of insect taxa based on monophyletic groups
276 recovered through molecular phylogenetic analysis alone has been criticised (Carstens, Pelletier,
277 Reid, & Satler, 2013), we consider it to be warranted here because the same approach was used
278 in the previous study of host-specificity in *Glochidion* and *Epicephala* (Kawakita & Kato, 2006),
279 making our results directly comparable. In the network description, lines represent interactions
280 between *Epicephala* taxa and *Glochidion* species, with line thickness representing number of
281 *Epicephala* individuals reared from each host plant taxon (i.e., outcomes of interaction events).
282 We assembled analogous networks for four continental islands in the Ryukyu Archipelago using
283 a molecular phylogeny inferred using the same loci in a different study (Kawakita & Kato,
284 2006), and checked them against additional host data from a recent taxonomic monograph
285 (Kawakita & Kato, 2016). This earlier study had sampled 1 moth each from 1-7
286 individual trees per species, from 1 locality per tree species per island (with two exceptions
287 where much greater numbers of individual moths were sampled from multiple individuals of two
288 tree species). Regional networks (Society Islands and Ryukyu Archipelago) were assembled by
289 summing interaction events across the three and four local networks, respectively.

290 Small networks (roughly, those with under 10 nodes) have long been of interest to
291 network science but many available methods for network analysis do not perform well for small
292 networks (Amaral et al., 2004). We analyzed three structural properties of the local and regional
293 networks: modularity (compartmentalization), reciprocity (symmetry) of specialization, and
294 algebraic connectivity. Modularity is a measure of the extent to which the network is broken into
295 modules (also called “compartments” or “subwebs”), which are weakly or not at all connected to
296 one another. Modularity was measured using the metric defined by Newman & Girvan (2004)

297 and the simulated annealing algorithm (Guimerà & Amaral, 2005), both as implemented in
298 MODULAR (Marquitti, Guimarães, Pires, & Bittencourt, 2014). We note here that the fact that a
299 network consists of several isolated modules is not, in and of itself, a guarantee that the network
300 is significantly modular. Indeed, it is a well-known result from random graph theory that random
301 processes can generate a network formed by multiple isolated components. Consequently,
302 assessments of the significance of modularity, such as the ones we use here, assess significance
303 relative to theoretical networks generated by null model 2 of Bascompte et al. (2003) in which
304 the probability of two species i and j interacting is proportional to the average of their relative
305 degrees, in which the relative degree is the number of partners of a species divided by the species
306 richness of the set of potential partners.

307 Reciprocity (or symmetry) of specialization describes the extent to which species in
308 each side of a bipartite network (e.g., animals and plants) have similarly narrow or broad ranges
309 of partner species with which they interact. For instance, a network in which each plant species
310 interacts with only one animal species and vice versa would have extremely high reciprocal
311 specialization, whereas a network in which all plants were specialists but all animals were
312 extreme generalists would not be reciprocally specialized (rather, it would be asymmetrically
313 specialized). Reciprocity was calculated using Blüthgen's H_2' (Manley, 1997; Blüthgen,
314 Menzel & Blüthgen, 2006), a measure of reciprocity of specialization across an entire network,
315 implemented in their online calculator (<http://rxc.sys-bio.net/>) and in the R package bipartite
316 (Dormann, Fründ, Blüthgen, & Gruber, 2009).

317 Algebraic connectivity (Fiedler, 1973; Abreu, 2007) is a well-known descriptor of the
318 robustness of complex networks, since it measures the extent to which it is difficult to cut the
319 network into different disconnected components, with higher c values implying more robust

320 networks (Jamakovic & Mieghem, 2008). The second smallest eigenvalue of the Laplacian of a
321 graph G defines its algebraic connectivity (here defined as c), and G is connected if and only c is
322 different from zero (Fiedler, 1973; Abreu, 2007). For networks depicting species interactions,
323 algebraic connectivity is a proxy for the extent to which ecological and evolutionary effects
324 propagate throughout a species assemblage. If the graph is disconnected, i.e. $c = 0$, isolated
325 subwebs exist and any given effect will never reach all coexisting species. On the other hand,
326 the higher the c -value, effects such as abundance fluctuations or trait convergence are more
327 likely to affect multiple species within the network, because there are interactions connecting
328 different groups in the network (Guimarães et al., 2011). We used standardized connectivity
329 measures defined by c/c_{\max} , so that resulting algebraic connectivity measures range between 0
330 and 1.

331 Finally, we compared the range of H_2' and c values obtained here with those from a
332 dataset of other bipartite mutualistic networks (Appendix S1: Table S5) obtained from the
333 Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/>), using the biological
334 intimacy index introduced by Ollerton (2006) to compare mutualisms with higher and lower
335 intimacy (Appendix S2, Table S6). For additional detail about network analyses see Appendix
336 S1.

337 Although Society Islands *Glochidion* have received recent comprehensive taxonomic
338 attention (Florence, 1997; Wagner & Lorence, 2011), some co-occurring species are extremely
339 similar morphologically (*P. florencei* and *P. huahineense* on Huahine; *P. manono* and *P. st-*
340 *johnii* on Moorea; *P. orohenense* and *P. taitensis* on Tahiti; Appendix S1). We ran additional
341 analyses on “alternate” local networks in which these co-occurring species pairs were fused into
342 single taxa.

343

344 **Results**345 **Lack of host-plant-associated phylogenetic structure in Society Islands *Epicephala***

346 *Epicephala* from Huahine, Moorea, and Tahiti belong to three minimally monophyletic
347 clades (Fig. 1), corresponding to the three previously reported clades from these islands (Hembry
348 et al., 2013); no previously unknown lineage of *Epicephala* was recovered. One clade is
349 restricted to Tahiti and Moorea (Y1), another is restricted to Huahine (Y2), and the third is found
350 across all three islands (Z). Clade Y2 is presumably found also on the neighboring Leeward
351 islands of Raiatea and Tahaa, based on the overlap in sampling with Hembry et al. (2013). Clade
352 Y1 primarily uses different host species allopatrically (*Phyllanthus nadeaudii* on Moorea and *P.*
353 *manono* on Tahiti) and Clade Y2 uses morphologically very similar hosts (*P. huahineense* and *P.*
354 *florencei*) sympatrically on Huahine. However, Clade Z uses nine different hosts across the three
355 islands, and is the predominant pollinator for multiple pairs and trios of morphologically
356 distinctive *Glochidion* species within the same island (particularly *P. florencei*/*huahineense* and
357 *P. temehaniensis* on Huahine, and *P. grayanus* and *P. taitensis/orohenense* on Tahiti). However,
358 despite being distributed across multiple islands and multiple host plant species, none of these
359 three *Epicephala* clades show any subclades with posterior probabilities greater than 0.50
360 containing all or most individuals from particular subsets of islands or host-plant species, and
361 thus show no evidence for within-clade differentiation corresponding to either geography or
362 host-plant species.

363 **Modularity of *Glochidion*-*Epicephala* networks**

364 We find that the four Asian networks and one of the Polynesian networks (Moorea) are
365 significantly modular, while the remaining two Polynesian networks (Huahine and Tahiti) are

366 not significantly modular (Table 1; Fig. 2; $p < 0.0001$ for the Asian and Moorea networks, $p =$
367 0.18 for Huahine, $p = 0.17$ for Tahiti). The modular networks each contain 2-4 modules which
368 are not connected to each other. Each module contains 1-2 species each of *Glochidion* and
369 *Epicephala* (with 2-3 species total per module). These patterns are reflected in the structure of
370 the regional networks formed by these local ones; the regional Ryukyu Islands network is
371 significantly modular ($Q = 0.72$, $p < 0.0001$), while the Society Islands network is not ($Q = 0.30$,
372 $p = 0.33$; Table 1; Fig. 2; see Table S3 for number of *Glochidion* species, *Epicephala* clades, and
373 interactions per network).

374 The lack of modularity on Tahiti and presence of modularity on Moorea are upheld even
375 if each of two morphologically similar species pairs of *Glochidion* are treated as a single taxon in
376 the network analysis (Table 1; Tahiti: $Q = 0.17$, $p = 0.18$; Moorea: $Q = 0.50$, $p < 0.0001$).
377 However, collapsing the morphologically similar and sympatric species pair on Huahine changes
378 modularity there ($Q = 0.17$) so that it becomes barely statistically significant ($p = 0.045$).

379 **High reciprocal specialization in all but two networks**

380 We find substantial variation in reciprocal specialization among these networks (Table 1).
381 The networks from Huahine and Tahiti have low values of standardized H_2' (Huahine: 0.488;
382 Tahiti: 0.0) compared to those from Moorea and the four Asian networks have extremely high
383 H_2' (1.00 in all cases). Collapsing morphologically similar species pairs of *Glochidion* raises H_2'
384 for both Huahine (1.00) and Tahiti (0.747); the Tahiti species are still less reciprocally
385 specialized than the taxa of other networks considered here. These results are consistent with
386 those from the modularity analyses. All significantly modular networks have high values of
387 reciprocal specialization, whereas the two non-modular networks have lower values of reciprocal
388 specialization. The correlation between modularity and reciprocal specialization is significant

389 (Pearson's product-moment correlation, $p = 0.025$, d. f. = 5, $t = 3.0287$). The values of reciprocal
390 specialization found across the seven local networks considered here are relatively high
391 compared with other networks, but there is some overlap with lower-intimacy plant-pollinator
392 networks (Fig. 3).

393 **Algebraic connectivity**

394 The variation in the degree of modularity and specialization among networks suggest that
395 these networks vary in their algebraic connectivity. We detected high algebraic connectivity for
396 Huahine ($c = 0.83$) and Tahiti networks ($c = 0.586$), whereas Moorea and the four Asian
397 networks hold disconnected components ($c = 0$) that imply biological processes arising from
398 ecological interactions are likely to operate independently within each of these disconnected
399 subwebs (Appendix S1: Table S4). The number of network components was higher for the Asian
400 networks (3-4 components) compared to Moorea (2 components). The use of alternate plant
401 taxonomies does not affect the algebraic connectivity results (Appendix S1: Table S4). With
402 regards to the regional networks, we find a qualitative difference between the Ryukyu Islands,
403 which contains disconnected components ($c = 0$), and the Society Islands, which forms a single,
404 connected regional web but with low global connectivity ($c = 0.213$). The range of variation in
405 algebraic connectivity among these seven local networks is roughly equivalent to that seen
406 across all mutualisms (Fig. 4; Appendix S1: Fig. S2 shows number of components).

407 **Presence of more than one *Epicephala* clade on a single host tree individual on oceanic** 408 **islands**

409 Finally, out of 15 individual *Glochidion* trees from which two moths were sampled, these
410 results find two cases in which more than one *Epicephala* taxon visits the same individual tree.

411 Both these examples involve moth clades Y2 and Z on Huahine; one is from *P. florencei* and
412 another from *P. huahineense*.

413

414 **Discussion**

415 **a) Limited differentiation by geography but none by host-plant in Society Islands**

416 *Epicephala*

417 Using molecular phylogenetic methods, we find no genetic differentiation of *Epicephala*
418 on different host plants, and limited differentiation by geography (namely, clades Y1 and Y2 on
419 the Windward and Leeward Society Islands, respectively; Fig. 1). As a result of this lack of host-
420 associated divergence in *Epicephala*, several examples of a minimally monophyletic *Epicephala*
421 taxon associating with more than one species of *Glochidion* host sympatrically are seen (*P.*
422 *temehaniensis*, *P. florencei*, and *P. huahineense* on Huahine, *P. st-johnii* and *P. manono* on
423 Moorea, and *P. grayanus*, *P. taitensis*, and *P. orohenense* on Tahiti). Such a pattern of sympatric
424 pollinator sharing is not known in Japanese *Glochidion* (Kawakita & Kato, 2006), but limited
425 examples have been reported for two Chinese *Glochidion* (Li et al., 2015) and the leafflower
426 genus *Breynia* (Zhang et al. 2012c).

427 Our lack of evidence for host-associated differentiation in Society Islands *Epicephala* is
428 in contrast to an earlier study using the same loci and phylogenetic approach, which found
429 clearly distinct monophyletic *Epicephala* species, each of which pollinated only a single
430 *Glochidion* at any site in Japan (Kawakita & Kato, 2006). However, similarly to the present
431 study, that earlier study did not find any evidence for host-associated phylogenetic differentiation
432 in either of two *Epicephala* (*E. obovatella* and *E. corruptrix*), which are both associated with two
433 closely related, allopatrically distributed *Glochidion* hosts (*G. obovatum* and *G. rubrum*) across

434 Japan and Taiwan. Phylogenetic differentiation on different host plants is widely known in
435 phytophagous insects (Singer & Stireman, 2005; Ohshima & Yoshizawa, 2006; Althoff, 2008),
436 although intriguingly, it has rarely been reported in oligophagous brood-pollinators (but see
437 Leebens-Mack & Pellmyr, 2004) despite expectations that mutualistic coevolution might
438 promote species-specific diversification (Kiestler, Lande, & Schemske, 1984; Godsoe, Yoder,
439 Smith, & Pellmyr, 2008; but see Hembry & Althoff, 2016).

440 This study does find evidence of geographic differentiation in one clade (clade Y) of
441 *Epicephala* between the Windward (Tahiti and Moorea) and Leeward (Huahine and islands to its
442 northwest) island groups within the Society archipelago, as suggested by a previous study
443 (Hembry et al., 2013). Clade Y is older than Clade Z and has previously been found to show
444 geographic differentiation among archipelagos within Polynesia. The strait between Huahine and
445 Moorea (150 km) is the most important phylogeographic barrier in Society Islands animals,
446 including several insect taxa (Hembry & Balukjian, 2016). Both *Epicephala* clades Y1 and Z in
447 this study fail to show phylogeographic divergence associated with the straits between Tahiti and
448 Moorea (17 km). In this respect, *Epicephala* differ from most Society Islands arthropod,
449 mollusk, and bird taxa which have been examined (Hembry & Balukjian, 2016).

450 Why the diversification of *Epicephala* in the Society Islands has not been more sensitive
451 to isolation on different islands and to host plant diversity is unclear. Potential explanations
452 include the decoupling of plant and moth diversification (Hembry & Althoff, 2016), insufficient
453 time (< 2.7 Ma since the formation of Huahine, Guillou et al., 2005; < 1 Ma since the
454 colonization of Clade Z, Hembry et al., 2013), and insufficient geographic isolation and area
455 (Hembry & Balukjian, 2016). Finally, *Epicephala* may be undergoing recent diversification that
456 is invisible to molecular phylogenetic analysis. Even if such diversification is occurring,

457 however, the patterns seen here can be considered to represent the state of *Epicephala* in the
458 recent evolutionary past.

459 **Support for the biological intimacy hypothesis**

460 This study applies network analysis methods to the study of brood pollination
461 mutualisms, and our results are generally consistent with the hypothesis that interaction intimacy
462 promotes reciprocal specialization and modularity in ecological networks (Thompson, 1994,
463 2005; Guimarães et al., 2007). Across both continental and oceanic island assemblages,
464 reciprocal specialization (H_2') is high compared to less intimate interactions such as ant-
465 extrafloral nectary, non-brood pollination, and seed dispersal mutualisms. Modularity varies
466 across *Glochidion-Epicephala* networks as is the case in both intimate and non-intimate
467 mutualisms (Olesen et al., 2007), although all continental and one oceanic (Moorea) island
468 networks show significant modularity. In the combination of these two structural properties,
469 leaf-flower-moth networks are thus structurally similar to ant-myrmecophyte networks (Blüthgen
470 et al., 2007; Guimarães et al., 2007; Dáttilo et al., 2013; Cagnolo & Tavella, 2015); with regards
471 to their high reciprocal specialization, they are similar also to the intimate mutualism between
472 *Alpheus* shrimps and gobies (Thompson et al., 2013). These findings thus constitute an important
473 independent test of the biological intimacy hypothesis.

474 Although these findings lend support to the biological intimacy hypothesis, we note that
475 we do not have comprehensive data available on the structure of networks formed by *Glochidion*
476 and *Epicephala* in the tropical continental regions where the majority of species in both genera
477 are found, and local assemblages can be more species-rich (Hembry et al., 2013). Both the
478 Ryukyu and Society Islands are near the range limits of this predominantly tropical continental
479 mutualism, and we might expect different patterns to appear at these range margins compared to

480 the range center (Mueller, Mikheyev, Solomon, & Cooper, 2011; see below). Finally, the
481 Ryukyu networks (which we compiled from a phylogenetic study not explicitly examining
482 network architecture) were not as intensively sampled as our Polynesian networks, so it is
483 possible that further sampling there may uncover additional moth species or links. We also note
484 that although a number of studies have examined attributes of network structure in other intimate
485 mutualisms (Ollerton et al., 2007; Ricciardi et al., 2010; Cagnolo & Tavella, 2015), they have
486 not explicitly tested both reciprocal specialization and modularity in the same assemblages.
487 Additional studies testing the biological intimacy hypothesis in these and other intimate
488 mutualisms (such as other ant-myrmecophile and brood pollination assemblages) would be
489 extremely valuable.

490 **Possible deviation from the biological intimacy hypothesis on two oceanic islands**

491 Although our results are broadly consistent with the biological intimacy hypothesis, two
492 leafflower-moth networks—both from oceanic islands (Huahine and Tahiti)—do show
493 differences in their structural properties compared to the others examined here. Both these
494 networks show lower reciprocal specialization and higher algebraic connectivity than their
495 counterparts on continental islands and the third oceanic island (Moorea), and unlike them, lack
496 significant modularity. The range of variation in their algebraic connectivity (interpreted as the
497 propensity to propagate indirect effects) is equivalent to that seen across all mutualisms (Figs 3-
498 4). These patterns suggest that some properties of oceanic islands, such as their young age and
499 geographic isolation, may in some cases permit networks formed by intimate mutualistic
500 assemblages to evolve differences in structure from those that would evolve on older or less
501 isolated landmasses.

502 It is not known whether the Tahiti and Huahine networks represent stable endpoints
503 engendered by the unique attributes of oceanic islands (toward which the Moorea network may
504 also evolve in the future), or whether they will evolve to become more reciprocally specialized
505 and modular like *Glochidion-Epicephala* interactions on the neighboring island of Moorea or on
506 continental islands. These patterns show no discernable relationship with island age or size,
507 suggesting that very different network structures can evolve within 2.7 Myr (the age of Huahine;
508 Guillou et al., 2005) given a similar starting set of lineages and islands. Variation in ecological
509 network structure among islands within an oceanic archipelago has been reported previously
510 (Trøjelsgaard et al., 2013).

511 We note that it is also not clear whether the reciprocally specialized and modular network
512 structure of *Glochidion-Epicephala* interactions in the Ryukyus is representative of that found
513 between these taxa in continental tropical regions in Asia and Australasia. *Glochidion-*
514 *Epicephala* networks in the Ryukyus are near the northern distributional limit of this mutualism,
515 and may represent a subset from a more diverse regional assemblage found on Taiwan and
516 continental Asia, as contemporary ranges of *Glochidion* and *Epicephala* species would suggest
517 (Deng & Wang, 1993; Li & Gilbert, 2008; Zhang et al., 2012b; Kawakita & Kato, 2016). This
518 assemblage may also have been heavily influenced by glacial cycles; patterns of presence and
519 absence of *Glochidion* pollen in the Quaternary palynological record from Taiwan and Okinawa
520 (Liew, Huang & Kuo, 2006; Fujiki & Ozawa, 2008; Lee & Liew, 2010) are consistent with this
521 interpretation. More data on the diversity, distributions, and host use of *Epicephala* in other parts
522 of Asia would be valuable in this context.

523 **Generalist taxa in intimate mutualisms**

524 Proximately, the deviations from a reciprocally specialized and modular structure seen in
525 the Tahiti and Huahine networks are due to the presence of a generalist *Epicephala* taxon (clade
526 Z of Hembry et al., 2013) which interacts with 9 of the 10 available host *Glochidion* species, and
527 is the predominant or exclusive pollinator of many of these species (Fig. 2). Generalists are
528 characteristic of non-intimate mutualistic assemblages, as part of the core of their nested
529 architecture (Guimarães et al., 2007). Generalists are thought to function to promote trait
530 convergence and to stabilize mutualistic networks (Thompson, 2005; Guimarães et al., 2006,
531 2011). To the best of our knowledge, generalists are rarely reported from intimate mutualistic
532 networks (but see the anemonefish *Amphiprion clarkii*; Ollerton et al., 2007). The term “super-
533 generalist” has been used to refer to generalists that interact with very high proportions of
534 available partner species in a local assemblage, such as generalist pollinators which visit a very
535 large proportion of available plant species on islands (Olesen, Eskildsen & Venkatasamy 2002)
536 or honeybees or large-bodied seed dispersing vertebrates in other communities (Guimarães et al.,
537 2011). We note here that Clade Z is similar to such super-generalists in that it interacts with
538 nearly all available *Glochidion* hosts in the Society Islands. Whether Clade Z’s broad host
539 breadth is therefore a result of it being found on oceanic islands (“interaction release,” Traveset
540 et al., 2015) or similarly generalized *Epicephala* species are found on continents remains unclear.
541 Regardless, these results contrast with the traditional “one-to-one” paradigm that has been
542 widespread in the study of brood pollination mutualisms (Ramírez, 1970; Janzen, 1979).

543 How clade Z and the other taxa within the Society Islands regional network coevolve is
544 therefore of great interest. Since interspecific floral odor differences mediate *Epicephala*
545 specificity in Japanese *Glochidion* (Okamoto, Kawakita, Goto, Svensson, & Kato, 2013), it may
546 be that Clade Z is undergoing incipient divergence and speciation through association with

547 ecologically distinct *Glochidion* species (Hembry, 2017). Such divergence would implying that
548 being a generalist is unstable within an intimate mutualistic network. Alternately, Clade Z may
549 be promoting the evolution of trait convergence or structural stability within its network
550 (Guimarães et al., 2011), suggesting that generalists can arise in intimate mutualisms and that
551 they have stabilizing effects. The implications of this widespread pollinator sharing for
552 interspecific gene flow among Polynesian leafflower trees has yet to be explored. Finally, our
553 results also suggest the possibility of using biogeographic variation in network structure as a
554 window onto how networks evolve through time and space.

555

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577

578 **Authors' contributions**

579 DHH, RLGR, and PRG conceived the ideas; DHH, EAN, LA, and CG collected the data; DHH,
580 RLGR, EAN, and PRG analysed the data; DHH, RLGR, EAN, and RGG led the writing of the
581 manuscript. All authors contributed critically to the drafts and gave final approval for
582 publication.

583

584 **Data accessibility**

585 Data (specimen locality data, DNA sequences novel to this study, tree file, and interaction
586 networks) available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1224pr2>
587 All *Epicephala* moth DNA sequences used are available from GenBank (see accession numbers
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589

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771 **Figure 1.** Phylogeny of *Epicephala* moths collected from 10 *Glochidion* species on Tahiti,
 772 Moorea, and Huahine. Tip labels indicate host *Glochidion* species (names following Wagner &
 773 Lorence, 2011) and collection number. Colored nodes indicate posterior probabilities; black: $x \geq$
 774 0.99, grey: $0.90 \leq x < 0.99$, white: $x < 0.90$. For additional collection data, see Appendix S1:
 775 Table S2.

776 **Figure 2:** Local and regional networks examined in this study. Line thicknesses proportional to
 777 number of interaction events, but are not proportional among networks. Data for Asia, and
 778 numbers corresponding to previously undescribed *Epicephala* taxa, from Kawakita & Kato
 779 (2006). The Asian *Epicephala* species indicated by numbers in the figure correspond to the
 780 following described species: *E. sp. 2 = E. anthophilia*; *E. sp. 3 = E. perplexa*; *E. sp. 4 = E.*
 781 *corruptrix*; *E. sp. 5 = E. lanceolatella*; *E. sp. 6 = E. bipollenella* (Kawakita & Kato, 2016).
 782 Regional networks simply represent the sums of all local networks.

783 **Figure 3:** Comparison of standardized reciprocal specialization (H_2') among continental and
 784 oceanic island *Glochidion-Epicephala* networks (this study) and other types of mutualistic
 785 networks. Labels as follows: AP, ants and extrafloral nectary-bearing plants; PP, plants and
 786 pollinators; PS, plants and seed dispersers; AM, ants and myrmecophytic plants; GE(A), Asian
 787 leafflowers (*Glochidion*) and leafflower moths (*Epicephala*); GE(P), Polynesian leafflowers
 788 (*Glochidion*) and leafflower moths (*Epicephala*). For biological intimacy (i) details, see
 789 Appendix S2 and Table S6.

790 **Figure 4:** Comparison of algebraic connectivity among continental and oceanic island
 791 *Glochidion-Epicephala* networks (this study) and other types of mutualistic networks. Labels as
 792 follows: AP, ants and extrafloral nectary-bearing plants; CC, clients (e.g., fishes) and cleaner

793 fishes; PP, plants and pollinators; PS, plants and seed dispersers; AF, sea anemones and
794 anemonefishes; AM, ants and myrmecophytic plants; GE(A), Asian leafflowers (*Glochidion*) and
795 leafflower moths (*Epicephala*); GE(P), Polynesian leafflowers (*Glochidion*) and leafflower
796 moths (*Epicephala*). For biological intimacy (*i*) details, see Appendix S2 and Table S6.

Clade Y1 (Moorea, Tahiti)

Clade Y2
(Huahine)

Clade Z (Huahine, Moorea, Tahiti)

nadeaudii 09124a
nadeaudii 07329a
manono 11090a
nadeaudii 09112b
nadeaudii 09107a
manono 07413a
nadeaudii 09123a
nadeaudii 09121a
manono 11072a
taitensis 07376a
manono 09100a
nadeaudii 09114d
nadeaudii 09109a

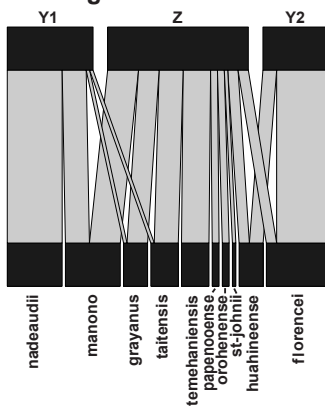
nadeaudii 09147a
manono 11071b
nadeaudii 09110b
manono 09101a
grayanus 11057a
nadeaudii 09129a
nadeaudii 09114k
nadeaudii 09121e
nadeaudii 09112a
manono 07429a
nadeaudii 09128a
nadeaudii 09123b

florencei 11110b
florencei 11110a
florencei 11106b
huahineense 08478a
florencei 08473a
florencei 11105a
florencei 11106a
florencei 11111a
florencei 08473b
huahineense 08474a
florencei 08472a
florencei 11108a
florencei 11111b
florencei 11124a
florencei 11107a
florencei 11126b
florencei 11122a
huahineense 11109b
huahineense 11109a
grayanus 11059a
temehaniensis 11129a
temehaniensis 11137a
manono 09142a
manono 08432a
huahineense 11113a
papencocense 08pape07a
grayanus 07434a
manono 07335b
taitensis 07411b
temehaniensis 08030a
grayanus 11056a
taitensis 11082a
grayanus 08anaoriia
taitensis 07219a
?grayanus 07420a
?orohenense 07372a
taitensis 11093b
taitensis 07419a
st-johnii 07442a
?taitensis 11068a
temehaniensis 11138a
manono 07391a
taitensis 07404a
manono 07440a
st-johnii 07442b
huahineense 08478b
florencei 11123a
florencei 11126a
manono 09143a
orohenense 08485a
?taitensis 11073a
grayanus 11083b
grayanus 11053a
temehaniensis 11120a
orohenense 07356a
temehaniensis 08030b
huahineense 11125a
manono 11140a
manono 07438b
sp 11139a
temehaniensis 11133a
florencei 11123b
temehaniensis 11132a
manono 07438a

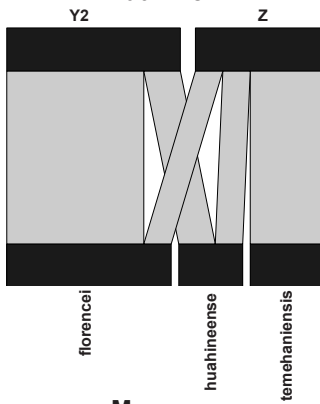
ex obovatum

POLYNESIA

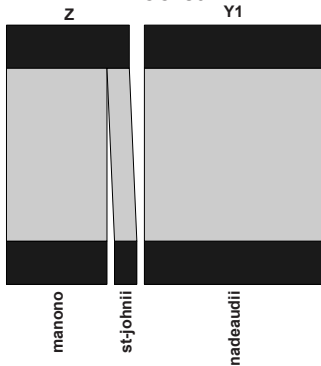
Regional network



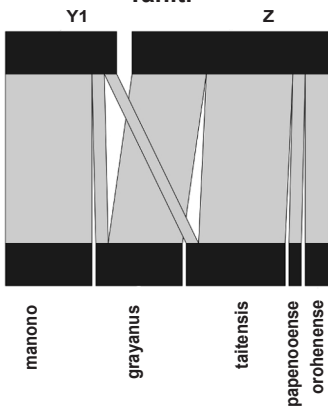
Huahine



Moorea

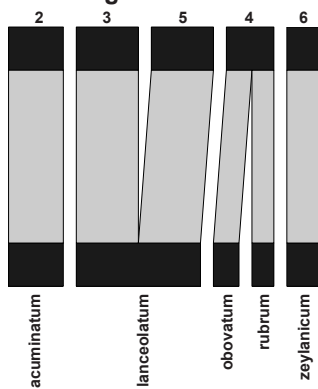


Tahiti

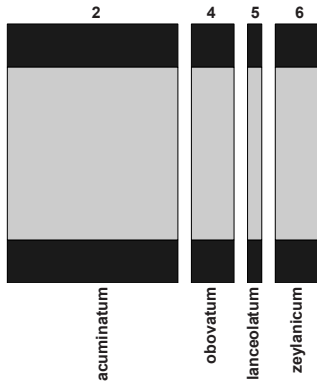


ASIA

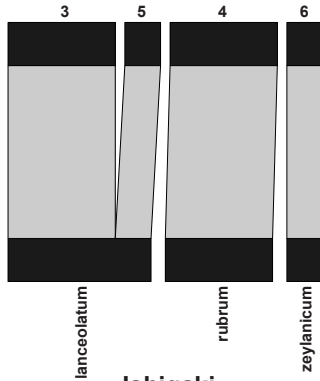
Regional network



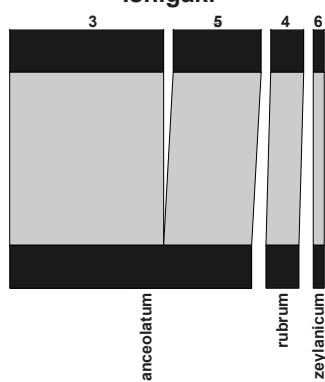
Amami



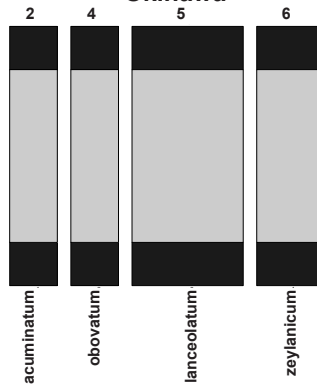
Iriomote

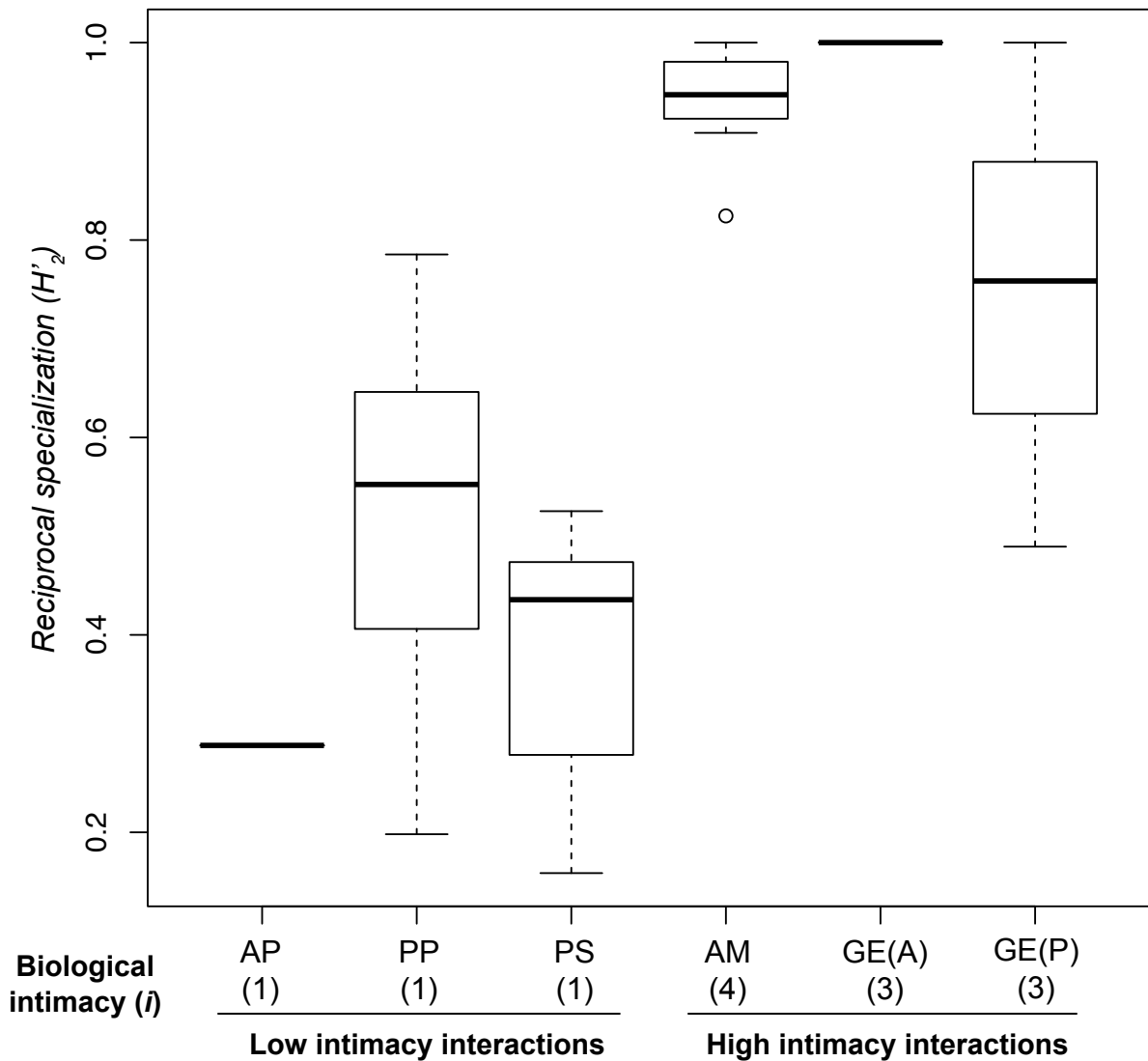


Ishigaki



Okinawa





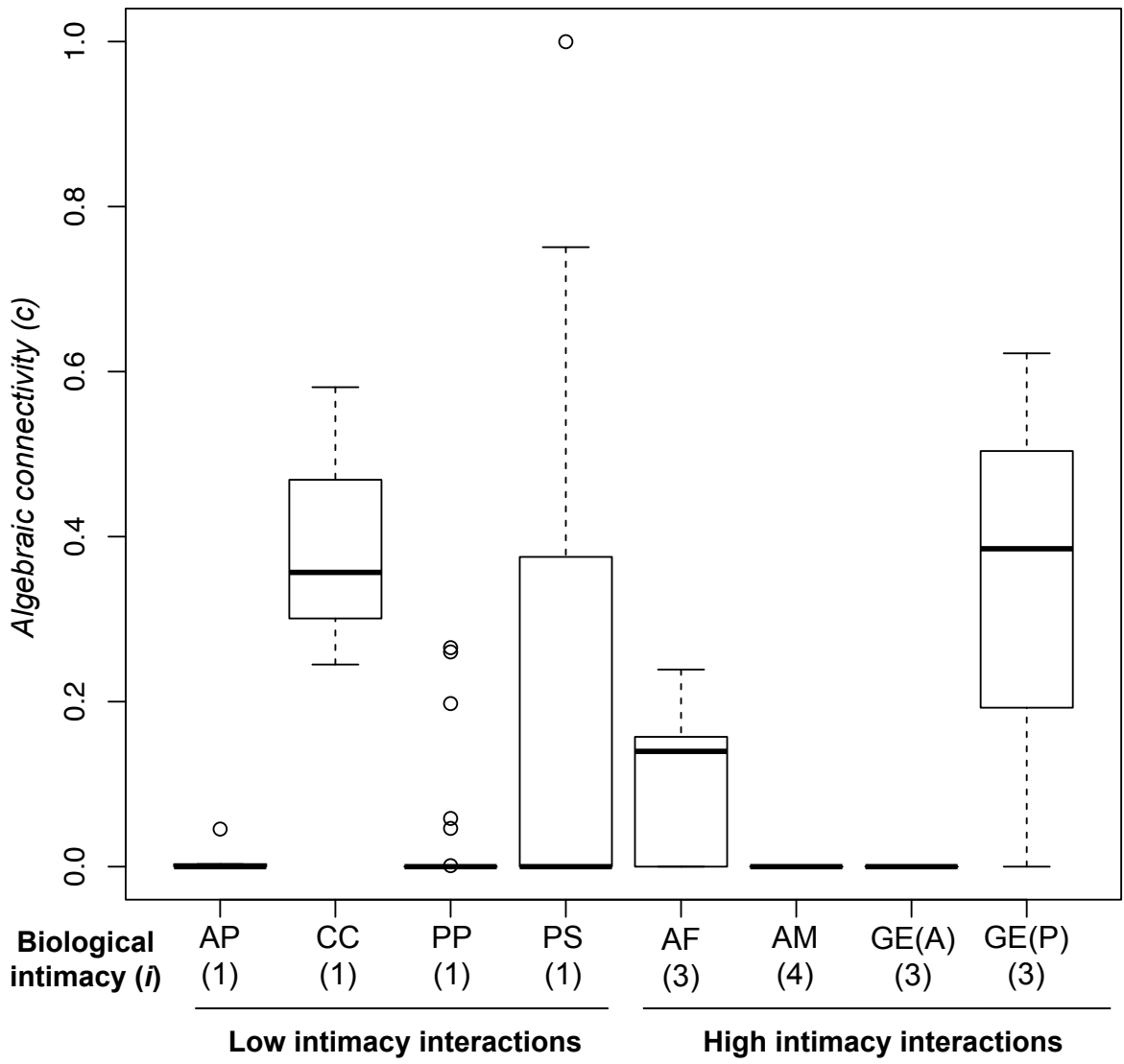


Table 1. Modularity and reciprocal specialization (H_2') values for local and regional *Glochidion-Epicephala* networks in the Society Islands (oceanic islands; Polynesia) and Ryukyu Islands (continental islands, Asia). “Alternate plant taxonomies” refer to cases where morphologically similar but described as different *Glochidion* species were treated together as a single taxon in the network analyses (*Phyllanthus florencei* and *P. huahineense* on Huahine; *P. manono* and *P. st-johnii* on Moorea; *P. orohenense* and *P. taitensis* on Tahiti). *P*-values for reciprocal specialization are for 1000 randomizations. * Actual value obtained was $H_2' = 1.05$. This value is slightly greater than 1 because it is an artefact of the heuristic implementation of Blüthgen et al. (2006)’s formula available in the online calculator at <http://rxc.sys-bio.net/>.

Island/region	Modularity			Reciprocal specialization		
	Number of modules	Modularity	<i>P</i>	<i>H</i> ₂ ' standardized	<i>H</i> ₂ '	<i>P</i>
<i>Society Is. (Polynesia)</i>						
Huahine	2	0.080	0.182	0.488	1.39	0.0001
Moorea	2	0.444	< 10 ⁻⁶	1	0.869	0.0001
Tahiti	2	0.204	0.171	0	1.95	0.6546
<i>Society Is. (alternate plant taxonomies)</i>						
Huahine (alt.)	2	0.167	0.045	1	0.971	0.0001
Moorea (alt.)	2	0.500	< 10 ⁻⁶	1	0.676	0.0001
Tahiti (alt.)	2	0.167	0.181	0.747	1.45	0.0001
<i>Ryukyu Is. (Asia)</i>						
Amami	4	0.750	< 10 ⁻⁶	1	1.03	0.0001
Okinawa	4	0.750	< 10 ⁻⁶	1	1.32	0.0001
Ishigaki	3	0.625	< 10 ⁻⁶	1	1.07	0.0001
Iriomote	3	0.625	< 10 ⁻⁶	1	1.26	0.0001
<i>Regional networks</i>						
Ryukyu Islands	4	0.722	0.004	1*	1.71	0.0001
Society Islands	3	0.304	0.334	0.655	2.39	0.0001

First Appendix (Appendix S1) for Hembry DH, Raimundo RLG, Newman EA, Atkinson L, Guo C, Guimarães PR, Jr., and Gillespie RG, “Does biological intimacy shape ecological network structure? A test using a brood pollination mutualism on continental and oceanic islands.” *Journal of Animal Ecology*

Materials and Methods

The islands: Tahiti, Moorea, and Huahine are the three youngest of the Society Islands with *Glochidion*, located in the central south Pacific (Figure S1). These islands are aligned from the northwest (Huahine) to the southeast (Tahiti) in an age progression reflecting the motion of the Pacific Plate over a stationary hotspot in the earth’s mantle. K-Ar dated basalt samples from each of these islands suggest that Huahine was volcanically active from 2.1-2.7 Ma, Moorea from 1.3-1.8 Ma, and Tahiti (which consists of three volcanoes) from 0.3-1.3 Ma (1). Tahiti is the tallest at 2241 m (Mt. Orohena), with Moorea at 1207 m (Mt. Tohica) and Huahine at 670 m (Mt. Turi). *Glochidion* is absent from two small, low islands (Maiao and Mehetia) that are located within 100 km of Moorea and Tahiti (2,3). Although Huahine, Moorea, and Tahiti have never been connected to one another, Moorea and Tahiti are relatively close (17 km at their closest point) and are cartographically grouped together as the Windward Islands. Moorea and Huahine are farther apart (150 km), and Huahine is cartographically grouped together with other nearby islands to its northwest as the Leeward Islands. Each of these islands is similar in size (Tahiti 1045 km²; Moorea, 134 km²; Huahine 75 km²) to those continental islands (e.g., Okinawa, 1200 km²; Amami Oshima 712 km²; Ishigaki, 139 km²) examined in the previous study of *Epicephala* host specificity (4).

The plants: In this study we examined ten species of *Glochidion* trees native to the islands of Tahiti, Moorea, and Huahine (Table S1), all of which have synonyms in *Phyllanthus* (5) due to the fact that the traditional circumscription of *Glochidion* s. l. is nested phylogenetically within a paraphyletic *Phyllanthus* (6). Only one species is found on more than one of the islands examined (*P. manono* on both Moorea and Tahiti), while another three (*P. florencei*, *P. temehaniensis*, and *P. st-johnii*) are also found on other Society Islands (7). The species were last revised by Florence (5), prior to transfer to *Phyllanthus* by Wagner and Lorence (7). With the exception of two coexisting species pairs that are distinguished solely by the presence/absence of pubescence (*P. orohenense* and *P. taitensis* on Tahiti; *P. florencei* and *P. huahineense* on Huahine (5)) and another species pair which morphologically intergrades among populations (*P. manono* and *P. st-johnii* on Moorea; D. Hembry, unpublished data), these species are all morphologically distinct and can primarily be distinguished based on pistillate floral morphology. They are found from sea level to ~1500 m elevation on the three islands, on basaltic substrate, in a variety of mesic and wet forest and degraded vegetation types (5,7,8). *Phyllanthus huahineense* and *P. florencei* are additionally found on (although not restricted to) calcareous substrate on offshore islets or cays (*motu* in Tahitian) on Huahine (5,7,8). Multiple species are found growing sympatrically or along elevational contact zones at many locations on these islands (8).

The insects: All *Epicephala* species in the Society Islands are undescribed, but they have been reported from all 10 *Glochidion* species considered here (9). Previous phylogenetic analysis (10) suggests that at least three clades of *Epicephala* are present on Tahiti, Moorea, and Huahine: one

clade on *Phyllanthus manono* on Tahiti and *P. nadeaudii* on Moorea; one clade on *P. huahineense* and *P. florencei* on Huahine; and one clade on the remaining taxa (*P. temehaniensis* on Huahine, *P. st-johnii* and *P. manono* on Moorea, and *P. taitensis*, *P. papenooense*, *P. orohenense*, and *P. grayanus* on Tahiti). *Epicephala* moths were sampled by collecting fruits from *Glochidion* species in the field and rearing larvae from them in either plastic bags or plastic rearing containers. Adult larvae (and in a few cases, larvae) were preserved in 96% ethanol for later DNA extraction. Strictly, this procedure generates data on trophic interactions rather than pollination interactions, but based on the natural history of this interaction (11) the former is expected to serve as an informative proxy for the latter. Numbers of *Epicephala* specimens sampled from each species of tree on each island are shown in Table 1. Collection information on the specimens collected is shown in Table S2. In 15 cases, multiple moths were collected from the same tree individuals. Voucher specimens of the individual *Glochidion* hosts were collected for all of the trees sampled for *Epicephala* larvae in this study. *Glochidion* were identified by the lead author (DHH) and vouchers have been deposited in the University Herbarium (UC) at the University of California, Berkeley, California, USA.

Molecular methods: Total genomic DNA was extracted from the thoraxes of ethanol-preserved adult *Epicephala*, and in a few cases, from the posterior ends of ethanol-preserved larvae as well using DNEasy kits (Qiagen Corp., Hilden, Germany). We amplified 2000 bp of DNA from three loci (mitochondrial cytochrome oxidase I, nuclear arginine kinase, and nuclear elongation factor 1- α) using polymerase chain reaction using previously published primers (12,13). Previously published PCR protocols (14) were used for the two nuclear loci but with the annealing temperatures modified to 48° C for ArgK and 55° C for EF-1 α . Products were purified using ExoSAP (Affymetrix, Foster City, CA) and Sanger sequenced, with raw sequences edited in Sequencher (Gene Codes Corporation, Ann Arbor, MI). Sequences are GenBank accession numbers MH110346-MH110560 for these new data. To the new sequence data we added previously published sequence data (Gen Bank accession numbers KC912865- KC912869, KC912871, KC912873, KC912884- KC912885, KC912892- KC912893, KC912918- KC912919, KC912921- KC912923, KC912925, KC912927, KC912941-KC912942, KC912949- KC912950, KC912976- KC912977, KC912979- KC912981, KC912983, KC912985, KC912998- KC912999, KC913006- KC913007, and MH110346-MH110560) for the same loci for 11 *Epicephala* from Huahine, Tahiti, and Moorea (10). Sequences were aligned using MUSCLE (14) and analyzed using Bayesian phylogenetic analysis in MrBayes 3.1 (15), with a model partitioned by codon position in each gene, for a total of nine partitions. The model GTR+G was used for each partition. An *Epicephala* from *Glochidion obovatum* on Honshu, Japan was used as the outgroup based on a previous analysis (10). The analysis was run for 20 million generations, with convergence assessed using Tracer 1.5 (16). The first 25% of sampled trees were discarded as burn-in.

Ecological network analysis: We analyzed three structural properties of the local and regional networks: modularity (compartmentalization), reciprocity (symmetry) of specialization, and algebraic connectivity. Modularity is a measure of the extent to which the network is broken up into modules (also called “compartments” or “subwebs”), which are weakly or not at all connected to one another. Modularity was measured using the simulated annealing algorithm implemented in MODULAR (17). We used Barber’s index and set the initial temperature factor = 2, cooling factor = 1.01, number of interaction factors = 1 (following MODULAR’s default

values) and evaluated significance using “null model 2” from Bascompte *et al.* (18). *P*-values for each network are based on 1,000 null models.

Reciprocity (or symmetry) of specialization describes the extent to which species in each side of a bipartite network (e.g., animals and plants) have similarly narrow or broad ranges of partner species with which they interact. For instance, a network in which each plant species interacts with only one animal species and vice versa would have extremely high reciprocal specialization, whereas a network in which all plants were specialists but all animals were extreme generalists would not be reciprocally specialized (rather, it would be asymmetrically specialized).

Reciprocity was calculated using Blüthgen’s H_2' (19-21), a measure of reciprocity of specialization across an entire network, implemented in their online calculator (<http://rxc.sys-bio.net/>) and the H_2 fun function implemented within the R package bipartite (22). A Pearson’s product-moment correlation was used to test for correlation between modularity and reciprocal specialization across all the local networks. Finally, we visually compared the range of H_2' values obtained here with those from a dataset of other bipartite mutualistic networks (see Table S4) obtained from the Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/>).

Algebraic connectivity (23) is a network metric that describes how well a graph is connected (24). The second smallest eigenvalue of the Laplacian of a graph G defines its algebraic connectivity (here defined as c), and G is connected if and only if c is different from zero (23,24). The algebraic connectivity is a well-known descriptor of the robustness of complex networks, since it measures the extent to which it is difficult to cut the network into different disconnected components, with higher c values implying more robust networks (25). For networks depicting species interactions, algebraic connectivity is a proxy to the extent to which ecological and evolutionary effects propagate throughout a species assemblage. If the graph is disconnected, i.e. $c = 0$, isolated subwebs exist and any given effect will never reach all coexisting species. On the other hand, the higher the c -value, effects such as abundance fluctuations or trait convergence are more likely to affect multiple species within the network, because there are interactions connecting different groups in the network (26). Specifically, we used standardized algebraic connectivity measures defined by c/c_{\max} , so that resulting connectivity measures range between 0 and 1. To calculate the number of disconnected components (the independent subwebs within a disconnected graph), we computed the number of eigenvalues of the Laplacian of G equal to zero (25). We visually compared the range of c values obtained here with those from a dataset of other bipartite mutualistic networks (see Table S4) obtained from the Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/>).

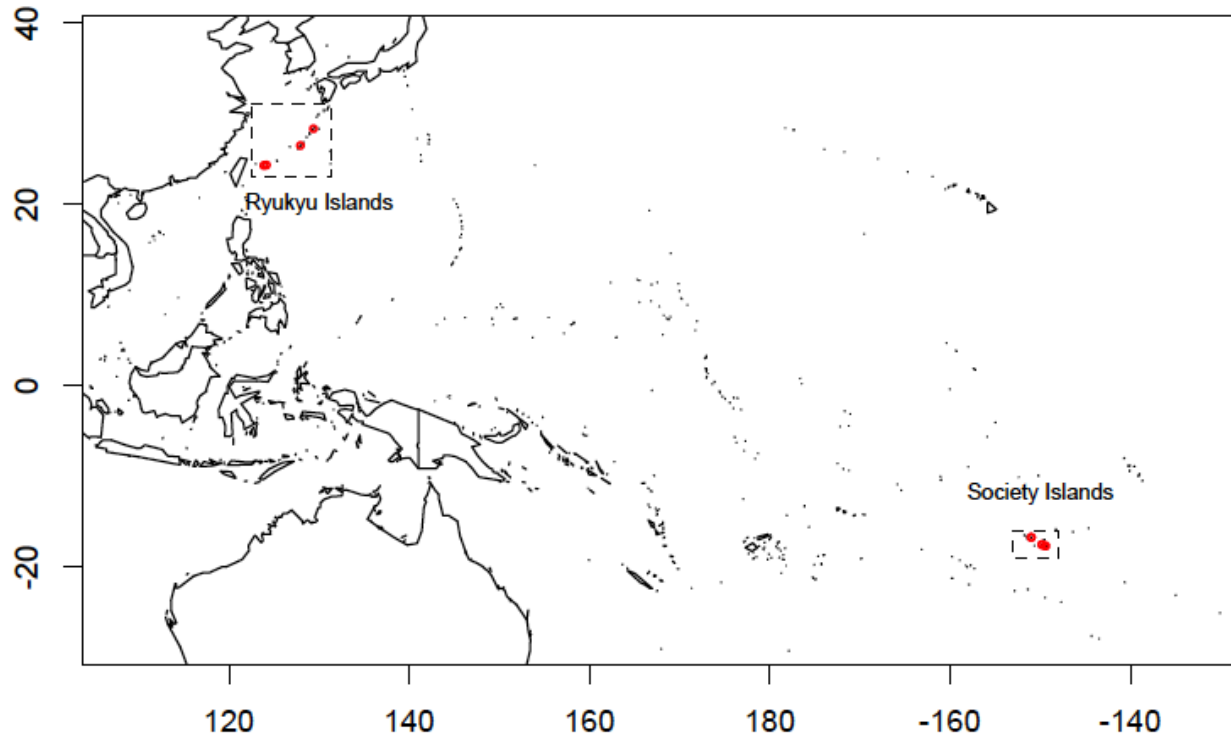
References for Appendix S1

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Figure S1. A. Map of sites from which networks were sampled in the Asia-Pacific region. Society Islands networks were sampled in this study, and Ryukyu Islands networks are from Kawakita and Kato (2006).



B. Map of the Society Islands, French Polynesia. The three islands where sampling was conducted, and their maximum ages, are indicated.

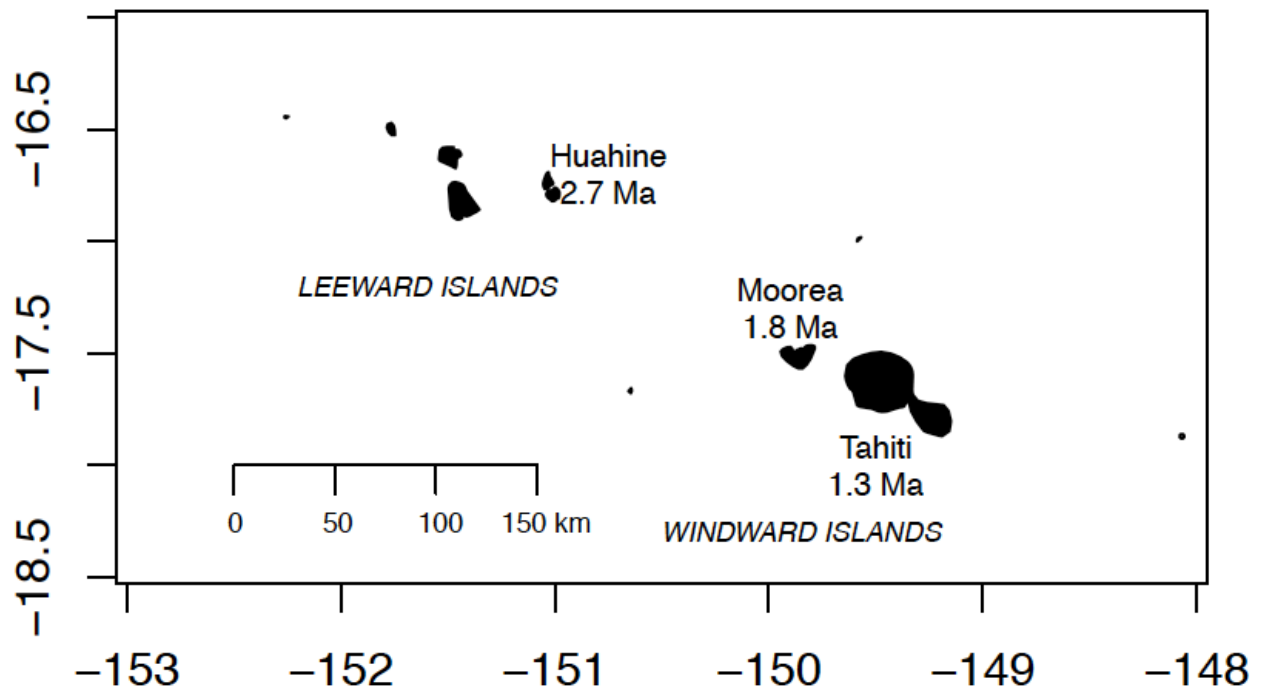


Table S1. *Glochidion* species present on the islands of Tahiti, Moorea, and Huahine (elevational data from Florence (1)).

Name	Synonym	Distribution	Elevational range (m a.s.l.)
<i>P. florencei</i>	<i>G. societatis</i>	Huahine*	0-225
<i>P. huahineense</i>	<i>G. huahineense</i>	Huahine	1-4
<i>P. temehaniensis</i>	<i>G. temehaniense</i>	Huahine†	0-600
<i>P. nadeaudii</i>	<i>G. nadeaudii</i>	Moorea	420-800
<i>P. st-johnii</i>	<i>G. myrtifolium</i>	Moorea‡	30-680
<i>P. manono</i>	<i>G. manono</i>	Moorea, Tahiti	30-1000
<i>P. grayanus</i>	<i>G. grayanum</i>	Tahiti	60-1040
<i>P. orohenense</i>	<i>G. orohenense</i>	Tahiti	900-1750
<i>P. papenooense</i>	<i>G. papenooense</i>	Tahiti	ca. 500
<i>P. taitensis</i>	<i>G. taitense</i>	Tahiti§	50-1500

* Also present on Raiatea, Tahaa, Maupiti, and Rimatara (1), although the Rimatara taxon is likely to belong to a distinct species (2)

† Also present on Raiatea and Tahaa

‡ Also present on Raiatea, Tahaa, and Bora Bora

§ Collected once on Moorea (1); never found on that island in this study.

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Table S2: Collection data for *Epicephala* moth specimens examined in this study. Each specimen ID number corresponds to an individual moth specimen, where their format indicates whether or not the moth individual was collected from the same individual tree as other moth individuals. For instance, DHH-08-030A and DHH-08-030B represent two moths, both collected from the same *Phyllanthus temehaniensis* tree on Huahine. (DHH-08-030 corresponds to the herbarium voucher of this tree.)

Specimen ID	Island	Host species	Locality
DHH-08-030A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-08-030B	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-08-472A	Huahine	<i>florencei</i>	Fare
DHH-08-473A	Huahine	<i>florencei</i>	Fare
DHH-08-473B	Huahine	<i>florencei</i>	Fare
DHH-08-474A	Huahine	<i>huahineense</i>	Fare
DHH-08-478A	Huahine	<i>huahineense</i>	Fare
DHH-08-478B	Huahine	<i>huahineense</i>	Fare
DHH-11-105A	Huahine	<i>florencei</i>	Motu de Maeva, yard of Pension Fare Maeva
DHH-11-106A	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-106B	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-107A	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-108A	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-109A	Huahine	<i>huahineense</i>	Motu de Maeva, road to airport
DHH-11-109B	Huahine	<i>huahineense</i>	Motu de Maeva, road to airport
DHH-11-110A	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-110B	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-111A	Huahine	<i>florencei</i>	Motu de Maeva
DHH-11-111B	Huahine	<i>florencei</i>	Motu de Maeva, road to airport
DHH-11-113A	Huahine	<i>huahineense</i>	Motu de Maeva, east end
DHH-11-120A	Huahine	<i>temehaniensis</i>	Mt. Turi
DHH-11-122A	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-123A	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-123B	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-124A	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-125A	Huahine	<i>huahineense</i>	Mt. Mou'a Tapu
DHH-11-126A	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-126B	Huahine	<i>florencei</i>	Mt. Mou'a Tapu
DHH-11-129A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-11-132A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-11-133A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-11-137A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi

DHH-11-138A	Huahine	<i>temehaniensis</i>	Mt. Pohue Rahi
DHH-11-139A	Huahine	putative <i>temehaniensis</i> x <i>florencei</i>	Mt. Pohue Rahi
DHH-07-329	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-07-335B	Moorea	<i>manono</i>	'Opunohu Valley: Sommet des Trois Pinus
DHH-07-391A	Moorea	<i>manono</i>	Mt. Fairurani
DHH-07-438A	Moorea	<i>manono</i>	near Marae Teti'iroa
DHH-07-438B	Moorea	<i>manono</i>	near Marae Teti'iroa
DHH-07-440A	Moorea	<i>manono</i>	Mou'aroa
DHH-07-442A	Moorea	<i>st-johnii</i>	Vaianaë
DHH-07-442B	Moorea	<i>st-johnii</i>	Vaianaë
DHH-08-432A	Moorea	<i>manono</i>	Col des Trois Cocotiers
DHH-09-107A	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-109A	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-110B	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-112A	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-112B	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-114D	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-114K	Moorea	<i>nadeaudii</i>	Mt. Rotui
DHH-09-121A	Moorea	<i>nadeaudii</i>	Mt. Mou'aputa
DHH-09-121E	Moorea	<i>nadeaudii</i>	Mt. Mou'aputa
DHH-09-123A	Moorea	<i>nadeaudii</i>	Mt. Fairurani
DHH-09-123B	Moorea	<i>nadeaudii</i>	Mt. Fairurani
DHH-09-124A	Moorea	<i>nadeaudii</i>	Mt. Fairurani
DHH-09-128A	Moorea	<i>nadeaudii</i>	Mt. Fairurani
DHH-09-129A	Moorea	<i>nadeaudii</i>	Mt. Fairurani
DHH-09-142A	Moorea	<i>manono</i>	'Opunohu Valley: Sommet des Trois Pinus
DHH-09-143A	Moorea	<i>manono</i>	'Opunohu Valley: Sommet des Trois Pinus
DHH-09-147A	Moorea	<i>nadeaudii</i>	Pitons de Vaianaë
DHH-11-140A	Moorea	<i>manono</i>	Opunohu Valley, near Belvédère
DHH-07-219A	Tahiti	<i>taitensis</i>	Mt. Marau
DHH-07-356A	Tahiti	<i>orohenense</i>	Mt. Aora'i: Fare Mato
DHH-07-372A	Tahiti	? <i>orohenense</i>	Mt. Aora'i
DHH-07-376A	Tahiti	<i>taitensis</i>	Mt. Aora'i
DHH-07-404A	Tahiti	<i>taitensis</i>	Mt. Marau road, stand à tirs
DHH-07-411B	Tahiti	<i>taitensis</i>	Mt. Marau
DHH-07-413A	Tahiti	<i>manono</i>	Papeno'o Valley
DHH-07-419A	Tahiti	<i>taitensis</i>	Papeno'o Valley

DHH-07-420A	Tahiti	? <i>grayanus</i>	Papeno'o Valley
DHH-07-429A	Tahiti	<i>manono</i>	Papeno'o Valley
DHH-07-434A	Tahiti	<i>grayanus</i>	Belvédère de Taravao
DHH-08-485A	Tahiti	<i>orohenense</i>	Mt. Marau
DHH-08-ANAORIIA	Tahiti	<i>grayanus</i>	Papeno'o Valley: Anaori'i Plateau
DHH-08-PAPE07A	Tahiti	<i>papenooense</i>	Papeno'o Valley: Anaori'i Plateau
DHH-09-100A	Tahiti	<i>manono</i>	Taravao Plateau: Toahotu
DHH-09-101A	Tahiti	<i>manono</i>	Taravao Plateau: Toahotu
DHH-11-053A	Tahiti	<i>grayanus</i>	Hitia'a lavatubes
DHH-11-056A	Tahiti	<i>grayanus</i>	Hitia'a lavatubes
DHH-11-057A	Tahiti	<i>grayanus</i>	Hitia'a lavatubes
DHH-11-059A	Tahiti	<i>grayanus</i>	Hitia'a lavatubes
DHH-11-068A	Tahiti	? <i>taitensis</i>	Mt. Aora'i
DHH-11-071B	Tahiti	<i>manono</i>	Mt. Aora'i
DHH-11-072A	Tahiti	<i>manono</i> (pubescent)	Mt. Aora'i
DHH-11-073A	Tahiti	<i>taitensis</i>	Pic Vert
DHH-11-082A	Tahiti	<i>taitensis</i>	Belvédère de Taravao
DHH-11-083B	Tahiti	<i>grayanus</i>	Belvédère de Taravao
DHH-11-090A	Tahiti	<i>manono</i> (pubescent)	col du Tahara'a
DHH-11-093B	Tahiti	<i>taitensis</i>	col du Tahara'a

Table S3. Total numbers of plant and moth species and interactions per network. Columns labeled as follows: *P* = number of *Glochidion* species (plants) in the network; *A* = number of *Epicephala* species (animals) in the network; *I* = total number of interactions or links in the network.

	<i>P</i>	<i>A</i>	<i>I</i>
Island/region			
<i>Society Is. (Polynesia)</i>			
Huahine	3	2	5
Moorea	3	2	3
Tahiti	5	2	7
<i>Society Is. (alternate plant taxonomies)</i>			
Huahine	2	2	3
Moorea	2	2	2
Tahiti	4	2	6
<i>Ryukyu Is. (Asia)</i>			
Amami	4	4	4
Okinawa	4	4	4
Ishigaki	3	4	4
Iriomote	3	4	4
<i>Regional networks</i>			
Society Islands	10	3	15
Ryukyu Islands	5	5	6

Table S4. Algebraic connectivity of *Glochidion-Epicephala* networks. Columns labeled as follows: *c* = the algebraic connectivity, i.e., the value of the second smallest eigenvalue of the Laplacian matrix of each empirical network; NC = number of components within the networks; S = mean number of species per component; SP = mean number of plant species per component; SA = mean number of animal species per component.

	<i>c</i>	<i>c</i> standardized	NC	S	SP	SA
Island/region						
<i>Society Is. (Polynesia)</i>						
Huahine	0.830	1.00	1	5.00	3.00	2.00
Moorea	0.000	0.000	2	2.50	1.50	1.00
Tahiti	0.586	0.706	1	6.00	4.00	2.00
<i>Society Is. (alternate plant taxonomies)</i>						
Huahine (alt.)	0.586	0.706	1	4.00	2.00	2.00
Moorea (alt.)	0.000	0.000	2	2.00	1.00	1.00
Tahiti (alt.)	0.586	0.706	1	6.00	4.00	2.00
<i>Ryukyu Is. (Asia)</i>						
Amami	0.000	0.000	4	2.00	1.00	1.00
Okinawa	0.000	0.000	4	2.00	1.00	1.00
Ishigaki	0.000	0.000	3	2.33	1.00	1.33
Iriomote	0.000	0.000	3	2.33	1.00	1.33
<i>Regional networks</i>						
Society Islands	0.213	0.257	1	13.0	10.0	3.00
Ryukyu Islands	0.000	0.000	4	2.50	1.25	1.25

Table S5. Empirical networks used to contrast structural patterns of *Glochidion-Epicephala* networks with other mutualisms. L, Mutualisms of low interaction intimacy. H, Mutualisms of high interaction intimacy. AP, Interactions between ants and plants with extrafloral nectaries. PP, Interactions between free living animal pollinators and flowering plants. PS, Interactions between animals that disperse seeds and plants. CC, Interactions between marine cleaner species and their client fishes. AF, Interactions between anemone fish and sea anemones. AM, Interactions between myrmecophyte plants and ants. The 47 quantitative networks used for the reciprocal specialization analysis are marked with an X in the column (H'_2). The algebraic connectivity analysis used binary versions of all the listed networks ($n = 72$). A single locality may have more than one network due to sampling in different habitats or sites.

Intimacy	System	Locality	Country	Reference	H'_2
L	AP	Cape Tripulation	Australia	Blüthgen <i>et al.</i> 2004	X
L	AP	San Benito	Mexico	Guimarães <i>et al.</i> 2007a	
L	AP	La Mancha	Mexico	Guimarães <i>et al.</i> 2007a	
L	AP	Parque Clavijero	Mexico	Guimarães <i>et al.</i> 2007a	
L	AP	Valle de Zapotitlan	Mexico	Guimarães <i>et al.</i> 2007a	
L	PP	Cordón del Cepo	Chile	Arroyo <i>et al.</i> 1982	
L	PP	Cordón del Cepo	Chile	Arroyo <i>et al.</i> 1982	
L	PP	Cordón del Cepo	Chile	Arroyo <i>et al.</i> 1982	
L	PP	New Brunswick	Canada	Barrett & Helenuum 1987	X
L	PP	Catimbau Park	Brazil	Bezerra <i>et al.</i> 2009	X
L	PP	Tenerife	Spain	Dupont & Hansen 2003	
L	PP	Latnjajaure	Sweden	Elberling & Olesen 1999	X
L	PP	Lake Hazen	Canada	Hocking 1968	
L	PP	BRG National Park	Mauritius	Kaiser-Bunbury <i>et al.</i> 2010	X
L	PP	Kosciusko Park	Australia	Inouye & Pyke 1988	X
L	PP	Laguna Diamante	Argentina	Medan <i>et al.</i> 2002	
L	PP	Rio Blanco	Argentina	Medan <i>et al.</i> 2002	
L	PP	Melville Island	Canada	Mosquin <i>et al.</i> 1967	X
L	PP	Aigrettes Island	Mauritius	Olesen <i>et al.</i> 2002	X
L	PP	Flores Island	Portugal	Olesen <i>et al.</i> 2002	X
L	PP	Wahroonga	South Africa	Ollerton <i>et al.</i> 2003	X
L	PP	Calabozo	Venezuela	Ramírez 2004	
L	PP	Itatim	Brazil	Santos <i>et al.</i> 2010	
L	PP	Brownfield Woods	United States	Schemske <i>et al.</i> 1977	X
L	PP	Dolman Ridge Road	Canada	Small 1976	X
L	PP	Arroyo Goye	Argentina	Vázquez & Simberloff 2003	X
L	PP	Cerro Lopez	Argentina	Vázquez & Simberloff 2003	X
L	PP	Llao Llao	Argentina	Vázquez & Simberloff 2003	X
L	PP	Mascardi	Argentina	Vázquez & Simberloff 2003	X

L	PP	Quetritihue	Argentina	Vázquez & Simberloff 2003	X
L	PP	Norfolk	UK	Dicks <i>et al.</i> 2002	X
L	PP	Norfolk	UK	Dicks <i>et al.</i> 2002	X

Table S1. (continued)

L	PP	AP National Park	N. Zealand	Primack 1983	
L	PS	Princeton	USA	Baird 1980	X
L	PS	Mount Missi	P. N. Guinea	Beehler 1983	X
L	PS	Caguana	Puerto Rico	Carlo <i>et al.</i> 2003	X
L	PS	Cialitos	Puerto Rico	Carlo <i>et al.</i> 2003	X
L	PS	Cordillera	Puerto Rico	Carlo <i>et al.</i> 2003	X
L	PS	Fronton	Puerto Rico	Carlo <i>et al.</i> 2003	X
L	PS	Campinas	Brazil	Galetti and Pizo 1996	X
L	PS	Barro Colorado Island	Panamá	Poulin <i>et al.</i> 1999	X
L	PS	Soberania Park	Panamá	Poulin <i>et al.</i> 1999	X
L	PS	Kakamega Forest	Kenya	Schleuning <i>et al.</i> 2011	X
L	PS	LC Mission Beach	Australia	Crome 1975	X
L	PS	Oxford	UK	Sorensen 1981	X
L	PS	Hato Raton	Spain	Jordano 1985	X
L	PS	Xpujil	Mexico	Kantak 1979	
L	PS	Kuala Lompat	Malaysia	Lambert 1987	
L	PS	CMBR Station	P. New Guinea	Mack 1994	
L	PS	Rio Negro	Brazil	Donatti <i>et al.</i> 2011	
L	CC	Saint Crox	Virgin Islands	Johnson & Ruben 1988	
L	CC	Abrolhos	Brazil	Guimarães <i>et al.</i> 2007b	
L	CC	Bonaire	Neth. Antilles	Wicksten 1998	
H	AF	Bahowo	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Bualo	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Fukui	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Jalan Masuk	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Kasegaran Point	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Likuan	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Mandolin	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Mike's Point	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Sachiko	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Tanjung Kopi	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AF	Tanjung Pisok	Indonesia	Ricciardi <i>et al.</i> 2010	
H	AM	Manu Park	Peru	Davidson <i>et al.</i> 1989	X
H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X
H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X
H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X
H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X

H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X
H	AM	Amazonas State	Brazil	Guimarães <i>et al.</i> 2007a	X
H	AM	Manaus	Brazil	Fonseca & Ganade 1996	X

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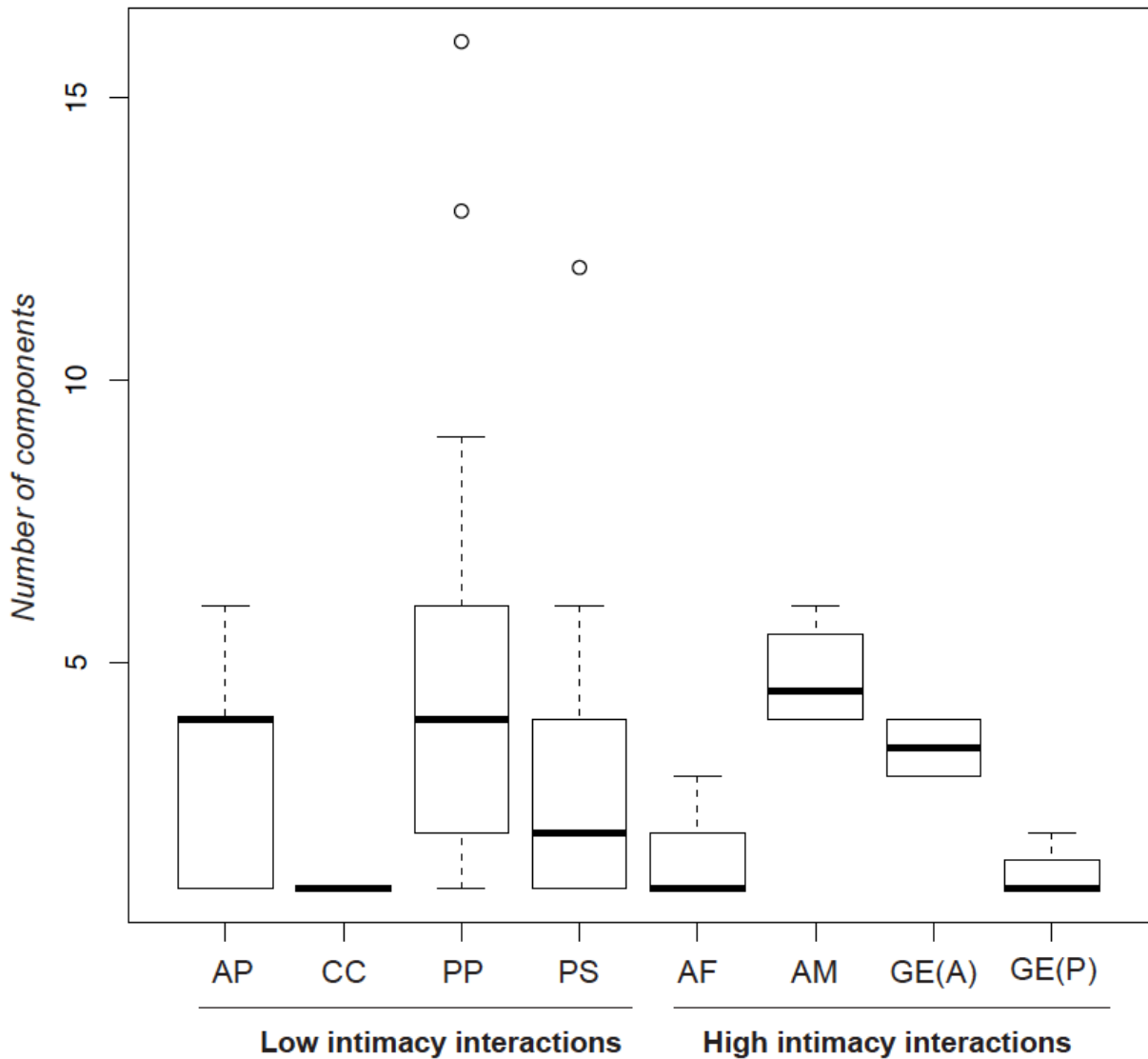
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Figure S2. Numbers of components per network across the mutualistic networks used for calculation of algebraic connectivity (see Table S3, Figure 6 in main text). Labels as follows: AP, ants and extrafloral nectary-bearing plants; CC, clients (e.g., fishes) and cleaner fishes; PP, plants and pollinators; PS, plants and seed dispersers; AF, sea anemones and anemonefishes; AM, ants and myrmecophytic plants; GE(A), Asian leafflowers (*Glochidion*) and leafflower moths (*Epicephala*); GE(P), Polynesian leafflowers (*Glochidion*) and leafflower moths (*Epicephala*).



Second Appendix (Appendix S2).

Biological intimacy index. We used the biological intimacy index (i) originally defined by Ollerton (2006) to quantify the degrees of biological integration between interacting species in the mutualisms shown in Figures 3 and 4 (Table S1). The index is the sum of four elements whose values can range according to the criteria described below:

- physical dependence: the value of this element is 0 if species show no dependence, 1 when they dependent on each other only during part of the life cycle, or 2 when species are attached during their entire life cycles.
- trophic dependence: the value of this element is 0 if species are independent regarding their trophic requirements, 1 if species the trophic dependence is partial, or 2 if the trophic dependence between species is total.
- physiological integration: the value of this element is 0 if no physiological integration occurs, i. e., the interactions is extracorporeal; 1 if species are physiologically integrated during part of the life cycle; or 2 if physiological integration occurs during species' entire life cycles.
- vertical transmission: the last element of Ollerton's index is 0 if vertical transmissions do not occur or 1 if vertical transmissions occur.

Table S6. Computation of Ollerton's biological intimacy index for the different mutualisms considered in this study. AP, ants and extrafloral nectary-bearing plants; PP, plants and pollinators; PS, plants and seed dispersers; CC, clients (e.g., fishes) and cleaner fishes. AM, ants and myrmecophytic plants. AF, sea anemones and anemonefishes. GE, leafflowers (*Glochidion*) and leafflower moths (*Epicephala*).

Mutualism type	Physical Dependence	Trophic Dependence	Physiological Integration	Vertical Transmission	Biological Intimacy (i)
AP	0	1	0	0	1
PP	0	1	0	0	1
PS	0	1	0	0	1
CC	0	1	0	0	1
AF	1	1	1	0	3
AM	2	1	1	0	4
GE	1	1	1	0	3

Reference for Appendix S2

Ollerton, J. (2006) Biological barter: patterns of specialization compared across different mutualisms. *Plant-pollinator interactions: from specialization to generalization* (eds N.M. Waser & J. Ollerton), pp. 411-435. University of Chicago Press, Chicago, IL, USA.