



RESEARCH ARTICLE

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

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Abstract

1. Biological intimacy—the degree of physical proximity or integration of partner taxa during their life cycles—is thought to promote the evolution of reciprocal specialization and modularity in the networks formed by co-occurring mutualistic species, but this hypothesis has rarely been tested.
2. Here, we test this “biological intimacy hypothesis” by comparing the network architecture of brood pollination mutualisms, in which specialized insects are simultaneously parasites (as larvae) and pollinators (as adults) of their host plants to that of other mutualisms which vary in their biological intimacy (including ant-mycophyte, ant-extrafloral nectary, plant-pollinator and plant-seed disperser assemblages).
3. We use a novel dataset sampled from leafflower trees (Phyllanthaceae: *Phyllanthus* s. l. [*Glochidion*]) and their pollinating leafflower moths (Lepidoptera: *Epicephala*) on three oceanic islands (French Polynesia) and compare it to equivalent published data from congeners on continental islands (Japan). We infer taxonomic diversity of leafflower moths using multilocus molecular phylogenetic analysis and examine several network structural properties: modularity (compartmentalization), reciprocity (symmetry) of specialization and algebraic connectivity.
4. We find that most leafflower-moth networks are reciprocally specialized and modular, as hypothesized. However, we also find that two oceanic island networks differ in their modularity and reciprocal specialization from the others, as a result of a supergeneralist moth taxon which interacts with nine of 10 available hosts.
5. Our results generally support the biological intimacy hypothesis, finding that leafflower-moth networks (usually) share a reciprocally specialized and modular structure with other intimate mutualisms such as ant-mycophyte symbioses, but unlike nonintimate mutualisms such as seed dispersal and nonintimate pollination.

Additionally, we show that generalists—common in nonintimate mutualisms—can also evolve in intimate mutualisms, and that their effect is similar in both types of assemblages: once generalists emerge they reshape the network organization by connecting otherwise isolated modules.

KEYWORDS

biological intimacy hypothesis, co-evolution, *Epicephala*, *Glochidion*, modularity, network evolution, *Phyllanthus*, reciprocal specialization

1 | INTRODUCTION

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

The role of biological intimacy in determining the structure of interactions among species is of interest because ecological and evolutionary dynamics, and the feedbacks between both, are expected to show marked differences between high- and low-intimacy mutualisms. Co-evolutionary theory (Thompson, 2005) suggests adaptive codiversification and reciprocal specialization can be major drivers of the strong modularity found in empirical high-intimacy mutualistic

networks (Fontaine et al., 2011; Guimarães et al., 2007). On the other hand, theory predicts that low-intimacy mutualisms involving generalist and phylogenetically unrelated species would favour trait convergence and increased network connectivity (Guimarães, Jordano, & Thompson, 2011), which, combined to adaptive interaction rewiring (Ramos-Jiliberto, Valdivinos, Moisset de Espanés, & Flores, 2012; Zhang, Hui, & Terblanche, 2011), would explain the recurrence of nestedness in low-intimacy mutualistic networks (Fontaine et al., 2011; Guimarães et al., 2011).

However, despite these theoretical predictions, the hypothesis that biological intimacy promotes modularity and reciprocal specialization in mutualisms has been tested very few times empirically, primarily using ant–myrmecophyte networks. In these symbiotic interactions, ant colonies inhabit hollow domatia on the inside of plant organs and in turn defend their plant hosts from herbivores (Rico-Gray & Oliveira, 2007). Ant–myrmecophyte assemblages are characterized by high reciprocal specialization (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007; Guimarães et al., 2007) and high modularity (Cagnolo & Tavella, 2015; Dáttilo, Izzo, Vasconcelos, & Rico-Gray, 2013; Guimarães et al., 2007) especially compared with less intimate assemblages formed by extrafloral nectary-bearing plants and their ant visitors (Blüthgen et al., 2007; Dáttilo, 2012; Guimarães, Rico-Gray, dos Reis, & Thompson, 2006; Guimarães et al., 2007). Other intimate mutualisms between tropical marine shrimp and gobies (Thompson et al., 2013) and between ants and myrmecophilous lycaenid butterfly caterpillars (Cagnolo & Tavella, 2015) show similarly high reciprocal specialization as do ant–myrmecophyte networks, suggesting that the biological intimacy hypothesis may apply broadly across taxonomically disparate mutualisms; data are, however, more mixed for other intimate mutualisms, such as that between anemones and anemonefish (Ollerton, McCollin, Fautin, & Allen, 2007; Ricciardi, Boyer, & Ollerton, 2010).

In this study, we test the biological intimacy hypothesis by comparing the network architecture of plant–insect brood pollination mutualisms (characterized by high biological intimacy) to that of other types of mutualistic assemblages which vary in their intimacy. Brood pollination mutualisms include those between figs and fig wasps, leafflowers and leafflower moths, and yuccas and yucca moths (Hembry & Althoff, 2016). In these interactions, specialized insects pollinate flowers of their host plants, but also oviposit in the flowers, where their larvae consume seeds or other floral tissue.

Consequently, these associations are characterized by high biological intimacy, with a portion of the insects' life cycle (egg and larval stages, and pupation and even mating in some cases) taking place inside host reproductive tissue and the insect larvae relying on the host for food (Cook & Rasplus, 2003; Kato, Takimura, & Kawakita, 2003; Pellmyr, 2003; Luo, Yao, Wang, Zhang, & Hembry, 2017). Classically, these interactions were thought to obey a "one-to-one" paradigm in which locally, each pollinator species uses one unique host plant, and each plant species is pollinated by a unique pollinator species exclusive to it (Janzen, 1979; Ramírez, 1970); although recent data on host specificity do not uphold the "one-to-one" paradigm strictly in many cases, it is clear that these interactions are still extremely specialized at the species level, and host-associated adaptation may drive speciation, thereby ensuring high host specificity (Hembry & Althoff, 2016; Thompson, 2005).

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

Here, we assemble data from the literature on networks between *Glochidion* (the best-studied clade of leafflowers) and *Epicephala* moths on continental islands in Asia (the Ryukyu Islands), and gather a novel dataset based on field collections and rearing for *Glochidion*–*Epicephala* networks on oceanic islands in the South Pacific (Tahiti, Moorea, and Huahine). Each of the seven islands considered here has 3–5 species of *Glochidion*. First, we infer a phylogeny of Society Island *Epicephala* moths to ask how many minimally monophyletic taxa exist. Moth taxa may use multiple hosts, so we also ask if any of these minimally monophyletic taxa show signs of phylogenetic differentiation by geography or by host-plant species, thereby indicating extreme specialization in natural communities. Second, we use ecological network analyses to examine patterns of specialization in brood pollination mutualisms and test the biological intimacy hypothesis based on a comparison with other types of mutualisms that vary in their biological intimacy (including ant-myrmecophyte, ant-extrafloral nectary, plant-pollinator and plant-seed disperser assemblages).

2 | MATERIALS AND METHODS

2.1 | Study system background

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

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

2.2 | Sampling

Epicephala moths were sampled on the islands of Huahine, Moorea and Tahiti by collecting fruits from 10 *Glochidion* species in the field, aiming to maximize the number of individual trees per species sampled for moths. Excluding unique maximum and minimum values (for the endangered *P. papenooense* and the extremely widespread *P. taitensis*), we collected 1–2 moths each from 3 to 12 individual trees per species, from 1 to 4 localities per tree species per island ($n = 89$ individual moths, including 11 individuals used in Hembry

et al., 2013). Larvae from fruits were reared in plastic bags or rearing containers. Larvae and adults were preserved in 96% ethanol. Because *Glochidion* is nested within a paraphyletic *Phyllanthus* s. l. (Kathiriarachchi et al., 2006), all these *Glochidion* have names in *Phyllanthus* which are used in the main text (Appendix S1, Table S1; Wagner & Lorence, 2011). See Appendix S1 and Tables S1 and S2 for additional detail on Society Islands *Glochidion* and specimen collection data.

2.3 | Molecular methods

We amplified using polymerase chain reaction and Sanger-sequenced 2,000 bp of DNA from three loci (mitochondrial COI, and nuclear ArgK and EF1- α) from adult and larval *Epicephala* specimens (GenBank accession numbers MH110346–MH110560) and combined them with previously published equivalent data for the same taxa (GenBank 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, Hembry et al., 2013). Sequences were aligned using MUSCLE (Edgar, 2004) and analysed using Bayesian phylogenetic inference in MRBAYES 3.1 (Ronquist & Huelsenbeck, 2003). We used support values (posterior probabilities) recovered in the phylogenetic analysis to indicate potential groupings and differentiation of moth individuals by host-plant species or by island. This is the same approach used in the fields of phylogeography, host-associated differentiation in the insect phylogenetics literature and molecular species delimitation to look for differentiation among closely related populations or young species. For additional details, see Appendix S1.

2.4 | Network analysis

To summarize patterns of host-moth interactions, weighted graphs (network diagrams) were drawn for each of the three Society Islands. We used species designations for *Glochidion* following existing taxonomy (Florence, 1997; Wagner & Lorence, 2011) and treated each of the three minimally monophyletic clades of *Epicephala* recovered in the phylogenetic analysis as a taxon. Although recognition of insect taxa based on monophyletic groups recovered through molecular phylogenetic analysis alone has been criticised (Carstens, Pelletier, Reid, & Satler, 2013), we consider it to be warranted here because the same approach was used in the previous study of host specificity in *Glochidion* and *Epicephala* (Kawakita & Kato, 2006), making our results directly comparable. In the network description, lines represent interactions between *Epicephala* taxa and *Glochidion* species, with line thickness representing number of *Epicephala* individuals reared from each host plant taxon (i.e., outcomes of interaction events). We assembled analogous networks for four continental islands in the Ryukyu Archipelago using a molecular phylogeny inferred using the same loci in a different study (Kawakita & Kato, 2006) and checked them

against additional host data from a recent taxonomic monograph (Kawakita & Kato, 2016). This earlier study had sampled 1 moth each from 1 to 7 individual trees per species, from 1 locality per tree species per island (with two exceptions where much greater numbers of individual moths were sampled from multiple individuals of two tree species). Regional networks (Society Islands and Ryukyu Archipelago) were assembled by summing interaction events across the three and four local networks, respectively.

Small networks (roughly, those with under 10 nodes) have long been of interest to network science, but many available methods for network analysis do not perform well for small networks (Amaral et al., 2004). We analysed 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 into modules (also called “compartments” or “subwebs”), which are weakly or not at all connected to one another. Modularity was measured using the metric defined by Newman and Girvan (2004) and the simulated annealing algorithm (Guimerà & Amaral, 2005), both as implemented in MODULAR (Marquitti, Guimarães, Pires, & Bittencourt, 2014). We note here that the fact that a network consists of several isolated modules is not, in and of itself, a guarantee that the network is significantly modular. Indeed, it is a well-known result from random graph theory that random processes can generate a network formed by multiple isolated components. Consequently, assessments of the significance of modularity, such as the ones we use here, assess significance relative to theoretical networks generated by null model 2 of Bascompte et al. (2003) in which the probability of two species i and j interacting is proportional to the average of their relative degrees, in which the relative degree is the number of partners of a species divided by the species richness of the set of potential partners.

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' (Blüthgen, Menzel, & Blüthgen, 2006; Manley, 1997), a measure of reciprocity of specialization across an entire network, implemented in their online calculator (<http://rxc.sys-bio.net/>) and in the R package bipartite (Dormann, Fründ, Blüthgen, & Gruber, 2009).

Algebraic connectivity (Abreu, 2007; Fiedler, 1973) is a well-known descriptor of the robustness of complex networks, as 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 (Jamakovic & Miegheem, 2008). 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

c is different from zero (Abreu, 2007; Fiedler, 1973). For networks depicting species interactions, algebraic connectivity is a proxy for the extent to which ecological and evolutionary effects propagate throughout a species assemblage. If the graph is disconnected, that is $c = 0$, 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 (Guimarães et al., 2011). We used standardized connectivity measures defined by c/c_{\max} , so that resulting algebraic connectivity measures range between 0 and 1.

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

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

3 | RESULTS

3.1 | Lack of host-plant-associated phylogenetic structure in Society Islands *Epicephala*

Epicephala from Huahine, Moorea and Tahiti belong to three minimally monophyletic clades (Figure 1), corresponding to the three previously reported clades from these islands (Hembry et al., 2013); no previously unknown lineage of *Epicephala* was recovered. One clade is restricted to Tahiti and Moorea (Y1), another is restricted to Huahine (Y2), and the third is found across all three islands (Z). Clade Y2 is presumably found also on the neighbouring Leeward Islands of Raiatea and Tahaa, based on the overlap in sampling with Hembry et al. (2013). Clade Y1 primarily uses different host species allopatrically (*Phyllanthus nadeaudii* on Moorea and *P. manono* on Tahiti), and Clade Y2 uses morphologically very similar hosts (*P. huahineense* and *P. florencei*) sympatrically on Huahine. However, Clade Z uses nine different hosts across the three islands and is the predominant pollinator for multiple pairs and trios of morphologically distinctive *Glochidion* species within the same island (particularly *P. florencei*/*huahineense* and *P. temehaniensis* on Huahine, and *P. grayanus* and *P. taitensis/orohenense* on Tahiti). However, despite being distributed across multiple islands and multiple host-plant species, none of these three *Epicephala* clades show any subclades with posterior probabilities $>.50$ containing all or most individuals from particular subsets

of islands or host-plant species and thus show no evidence for within-clade differentiation corresponding to either geography or host-plant species.

3.2 | Modularity of *Glochidion*–*Epicephala* networks

We find that the four Asian networks and one of the Polynesian networks (Moorea) are significantly modular, while the remaining two Polynesian networks (Huahine and Tahiti) are not significantly modular (Table 1; Figure 2; $p < .0001$ for the Asian and Moorea networks, $p = .18$ for Huahine, $p = .17$ for Tahiti). The modular networks each contain 2–4 modules which are not connected to each other. Each module contains 1–2 species each of *Glochidion* and *Epicephala* (with 2–3 species total per module). These patterns are reflected in the structure of the regional networks formed by these local ones; the regional Ryukyu Islands network is significantly modular ($Q = 0.72$, $p < .0001$), while the Society Islands network is not ($Q = 0.30$, $p = .33$; Table 1; Figure 2; see Table S3 for number of *Glochidion* species, *Epicephala* clades and interactions per network).

The lack of modularity on Tahiti and presence of modularity on Moorea are upheld even if each of two morphologically similar species pairs of *Glochidion* is treated as a single taxon in the network analysis (Table 1; Tahiti: $Q = 0.17$, $p = .18$; Moorea: $Q = 0.50$, $p < .0001$). However, collapsing the morphologically similar and sympatric species pair on Huahine changes modularity there ($Q = 0.17$) so that it becomes barely statistically significant ($p = .045$).

3.3 | High reciprocal specialization in all but two networks

We find substantial variation in reciprocal specialization among these networks (Table 1). The networks from Huahine and Tahiti have low values of standardized H_2' (Huahine: 0.488; Tahiti: 0.0) compared with those from Moorea, and the four Asian networks have extremely high H_2' (1.00 in all cases). Collapsing morphologically similar species pairs of *Glochidion* raises H_2' for both Huahine (1.00) and Tahiti (0.747); the Tahiti species are still less reciprocally specialized than the taxa of other networks considered here. These results are consistent with those from the modularity analyses. All significantly modular networks have high values of reciprocal specialization, whereas the two nonmodular networks have lower values of reciprocal specialization. The correlation between modularity and reciprocal specialization is significant (Pearson's product-moment correlation, $p = .025$, $df = 5$, $t = 3.0287$). The values of reciprocal specialization found across the seven local networks considered here are relatively high compared with other networks, but there is some overlap with lower intimacy plant-pollinator networks (Figure 3).

3.4 | Algebraic connectivity

The variation in the degree of modularity and specialization among networks suggests that these networks vary in their algebraic

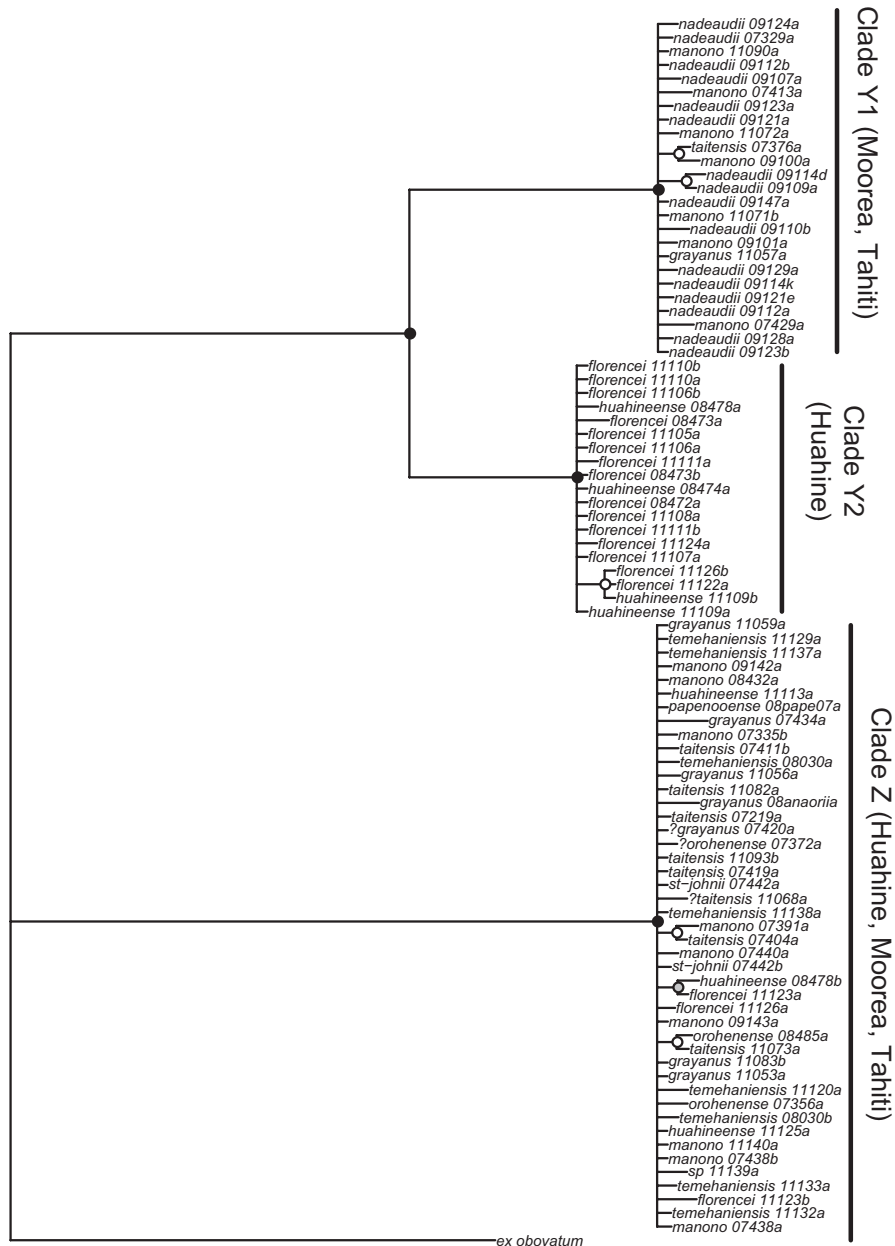


FIGURE 1 Phylogeny of *Epicephala* moths collected from 10 *Glochidion* species on Tahiti, Moorea and Huahine. Tip labels indicate host *Glochidion* species (names following Wagner & Lorence, 2011) and collection number. Coloured nodes indicate posterior probabilities; black: $x \geq 0.99$, grey: $0.90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

connectivity. We detected high algebraic connectivity for Huahine ($c = 0.83$) and Tahiti networks ($c = 0.586$), whereas Moorea and the four Asian networks hold disconnected components ($c = 0$) that imply biological processes arising from ecological interactions are likely to operate independently within each of these disconnected subwebs (Table S4). The number of network components was higher for the Asian networks (3–4 components) compared with Moorea (2 components). The use of alternate plant taxonomies does not affect the algebraic connectivity results (Table S4). With regard to the regional networks, we find a qualitative difference between the Ryukyu Islands, which contains disconnected components ($c = 0$), and the Society Islands, which forms a single, connected regional web but with low global connectivity ($c = 0.213$). The range of variation in algebraic connectivity among these seven local networks is roughly equivalent to that seen across all mutualisms (Figure 4; Figure S2 shows number of components).

3.5 | The presence of more than one *Epicephala* clade on a single host tree individual on oceanic islands

Finally, of 15 individual *Glochidion* trees from which two moths were sampled, these results find two cases in which more than one *Epicephala* taxon visits the same individual tree. Both these examples involve moth clades Y2 and Z on Huahine; one is from *P. florencei* and another from *P. huahineense*.

4 | DISCUSSION

4.1 | Limited differentiation by geography but none by host plant in Society Islands *Epicephala*

Using molecular phylogenetic methods, we find no genetic differentiation of *Epicephala* on different host plants and limited

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 1,000 randomizations

Island/region	Modularity			Reciprocal specialization		
	Number of modules	Modularity	<i>p</i>	H_2' standardized	H_2'	<i>p</i>
Society Is. (Polynesia)						
Huahine	2	0.080	.182	0.488	1.39	.0001
Moorea	2	0.444	<10 ^{−6}	1	0.869	.0001
Tahiti	2	0.204	.171	0	1.95	.6546
Society Is. (alternate plant taxonomies)						
Huahine (alt.)	2	0.167	.045	1	0.971	.0001
Moorea (alt.)	2	0.500	<10 ^{−6}	1	0.676	.0001
Tahiti (alt.)	2	0.167	.181	0.747	1.45	.0001
Ryukyu Is. (Asia)						
Amami	4	0.750	<10 ^{−6}	1	1.03	.0001
Okinawa	4	0.750	<10 ^{−6}	1	1.32	.0001
Ishigaki	3	0.625	<10 ^{−6}	1	1.07	.0001
Iriomote	3	0.625	<10 ^{−6}	1	1.26	.0001
Regional networks						
Ryukyu Islands	4	0.722	.004	1 ^a	1.71	.0001
Society Islands	3	0.304	.334	0.655	2.39	.0001

^aActual 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/>.

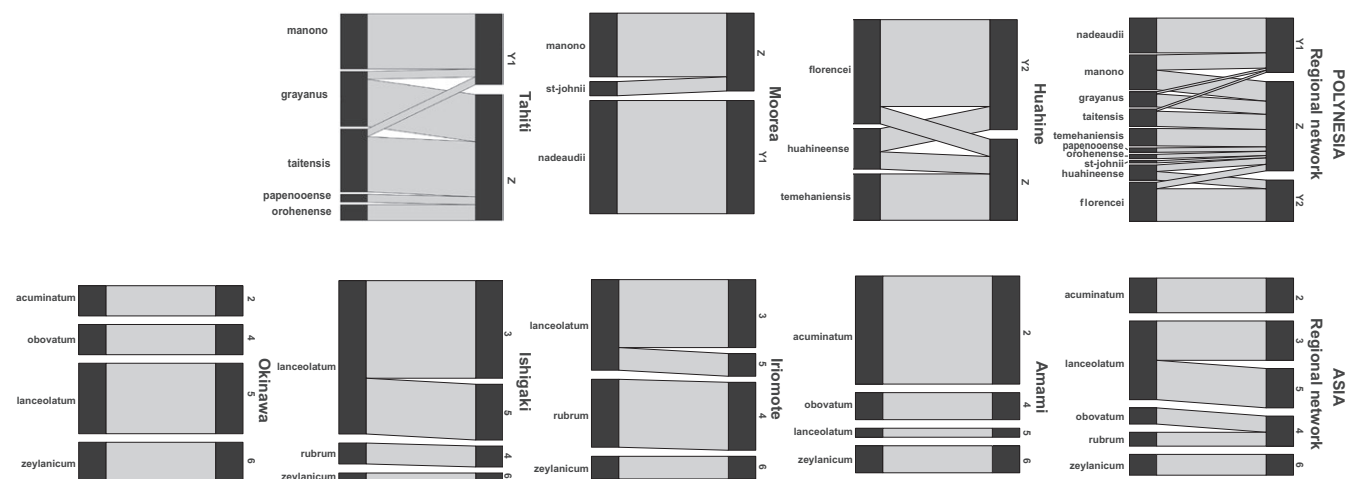


FIGURE 2 Local and regional networks examined in this study. Line thicknesses proportional to number of interaction events, but are not proportional among networks. Data for Asia and numbers corresponding to previously undescribed *Epicephala* taxa, from Kawakita and Kato (2006). The Asian *Epicephala*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

differentiation by geography (namely, clades Y1 and Y2 on the Windward and Leeward Society Islands, respectively; Figure 1). As a result of this lack of host-associated divergence in *Epicephala*, several examples of a minimally monophyletic *Epicephala* taxon associating with more than one species of *Glochidion* host sympatrically

are seen (*P. temehaniensis*, *P. florencei* and *P. huahineense* on Huahine, *P. st-johnii* and *P. manono* on Moorea, and *P. grayanus*, *P. taitensis*, and *P. orohenense* on Tahiti). Such a pattern of sympatric pollinator sharing is not known in Japanese *Glochidion* (Kawakita & Kato, 2006), but limited examples have been reported for two Chinese *Glochidion* (Li

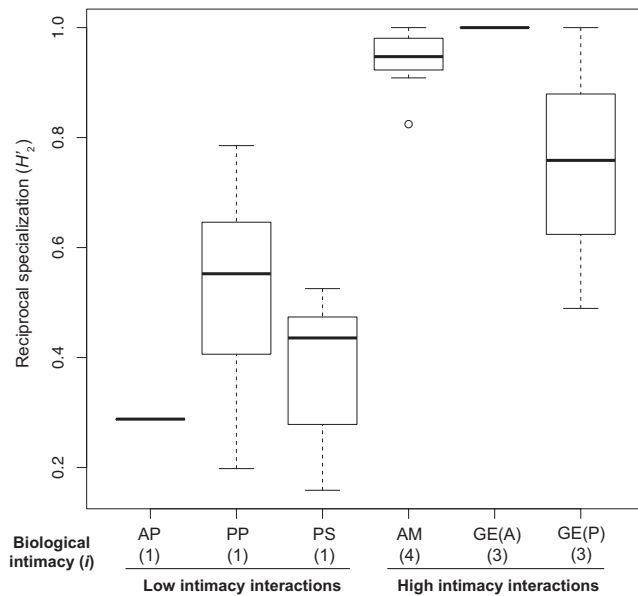


FIGURE 3 Comparison of standardized reciprocal specialization (H_2') among continental and oceanic island *Glochidion*–*Epicephala* networks (this study) and other types of mutualistic networks. Labels as follows: AP, ants and extrafloral nectary-bearing plants; PP, plants and pollinators; PS, plants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

et al., 2015) and the leafhopper genus *Breynia* (Zhang, Wang, et al., 2012).

Our lack of evidence for host-associated differentiation in Society Islands *Epicephala* is in contrast to an earlier study using the same loci and phylogenetic approach, which found clearly distinct monophyletic *Epicephala* species, each of which pollinated only a single *Glochidion* at any site in Japan (Kawakita & Kato, 2006). However, similar to the present study, that earlier study did not find any evidence for host-associated phylogenetic differentiation in either of two *Epicephala* (*E. obovatella* and *E. corruptrix*), which are both associated with two closely related, allopatrically distributed *Glochidion* hosts (*G. obovatum* and *G. rubrum*) across Japan and Taiwan. Phylogenetic differentiation on different host plants is widely known in phytophagous insects (Althoff, 2008; Ohshima & Yoshizawa, 2006; Singer & Stireman, 2005), although intriguingly, it has rarely been reported in oligophagous brood-pollinators (but see Leebens-Mack & Pellmyr, 2004) despite expectations that mutualistic co-evolution might promote species-specific diversification (Kiester, Lande, & Schemske, 1984; Godsoe, Yoder, Smith, & Pellmyr, 2008; but see Hembry & Althoff, 2016).

This study does find evidence of geographic differentiation in one clade (clade Y) of *Epicephala* between the Windward (Tahiti and Moorea) and Leeward (Huahine and islands to its northwest) island groups within the Society archipelago, as suggested by a previous study (Hembry et al., 2013). Clade Y is older than Clade Z and has previously been found to show geographic differentiation among

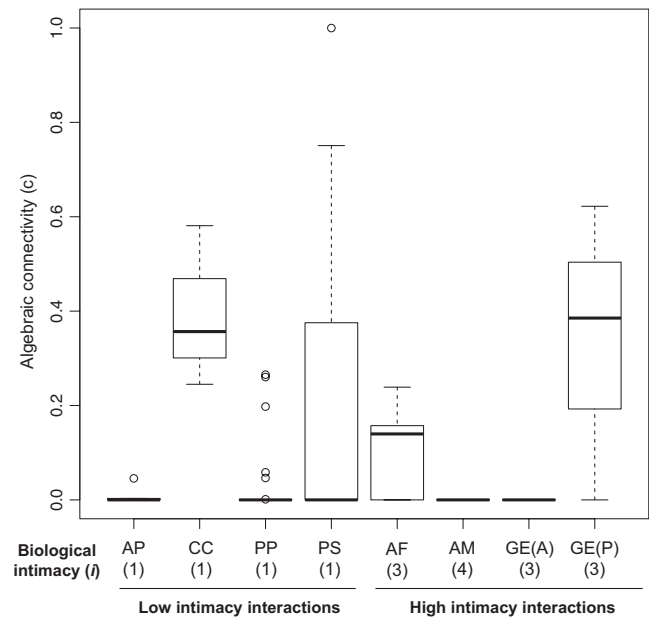


FIGURE 4 Comparison of algebraic connectivity among continental and oceanic island *Glochidion*–*Epicephala* networks (this study) and other types of mutualistic networks. Labels as follows: AP, ants and extrafloral nectary-bearing plants; CC, clients (e.g., fishes) and cleaner fishes; PP, plants and pollinators; PS, plants and seed dispersers; AF, sea anemones and anemonefishes; AM, ants and myrmecophytic plants; GE(A), Asian leafhoppers (*Glochidion*) and leafhopper moths (*Epicephala*); GE(P), Polynesian leafhoppers (*Glochidion*) and leafhopper moths (*Epicephala*). For biological intimacy (i) details, see Appendix S2 and Table S6

archipelagos within Polynesia. The strait between Huahine and Moorea (150 km) is the most important phylogeographic barrier in Society Islands animals, including several insect taxa (Hembry & Balukjian, 2016). Both *Epicephala* clades Y1 and Z in this study fail to show phylogeographic divergence associated with the straits between Tahiti and Moorea (17 km). In this respect, *Epicephala* differ from most Society Islands arthropod, mollusc and bird taxa which have been examined (Hembry & Balukjian, 2016).

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

4.2 | Support for the biological intimacy hypothesis

This study applies network analysis methods to the study of brood pollination mutualisms, and our results are generally consistent with

the hypothesis that interaction intimacy promotes reciprocal specialization and modularity in ecological networks (Guimarães et al., 2007; Thompson, 1994, 2005). Across both continental and oceanic island assemblages, reciprocal specialization (H_2') is high compared with less intimate interactions such as ant-extrafloral nectary, non-brood pollination and seed dispersal mutualisms. Modularity varies across *Glochidion*–*Epicephala* networks as is the case in both intimate and nonintimate mutualisms (Olesen et al., 2007), although all continental and one oceanic (Moorea) island networks show significant modularity. In the combination of these two structural properties, leaf-fig-moth networks are thus structurally similar to ant-myrmecophyte networks (Blüthgen et al., 2007; Cagnolo & Tavella, 2015; Dáttilo et al., 2013; Guimarães et al., 2007); with regard to their high reciprocal specialization, they are similar also to the intimate mutualism between *Alpheus* shrimps and gobies (Thompson et al., 2013). These findings thus constitute an important independent test of the biological intimacy hypothesis.

Although these findings lend support to the biological intimacy hypothesis, we note that we do not have comprehensive data available on the structure of networks formed by *Glochidion* and *Epicephala* in the tropical continental regions where the majority of species in both genera are found, and local assemblages can be more species-rich (Hembry et al., 2013). Both the Ryukyu and Society Islands are near the range limits of this predominantly tropical continental mutualism, and we might expect different patterns to appear at these range margins compared with the range centre (Mueller, Mikheyev, Solomon, & Cooper, 2011; see below). Finally, the Ryukyu networks (which we compiled from a phylogenetic study not explicitly examining network architecture) were not as intensively sampled as our Polynesian networks, so it is possible that further sampling there may uncover additional moth species or links. We also note that although a number of studies have examined attributes of network structure in other intimate mutualisms (Cagnolo & Tavella, 2015; Ollerton et al., 2007; Ricciardi et al., 2010), they have not explicitly tested both reciprocal specialization and modularity in the same assemblages. Additional studies testing the biological intimacy hypothesis in these and other intimate mutualisms (such as other ant-myrmecophile and brood pollination assemblages) would be extremely valuable.

4.3 | Possible deviation from the biological intimacy hypothesis on two oceanic islands

Although our results are broadly consistent with the biological intimacy hypothesis, two leaf-fig-moth networks—both from oceanic islands (Huahine and Tahiti)—do show differences in their structural properties compared with the others examined here. Both these networks show lower reciprocal specialization and higher algebraic connectivity than their counterparts on continental islands and the third oceanic island (Moorea), and unlike them, lack significant modularity. The range of variation in their algebraic connectivity (interpreted as the propensity to propagate indirect effects) is equivalent to that seen across all mutualisms (Figures 3 and 4). These patterns suggest

that some properties of oceanic islands, such as their young age and geographic isolation, may in some cases permit networks formed by intimate mutualistic assemblages to evolve differences in structure from those that would evolve on older or less isolated landmasses.

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

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

4.4 | Generalist taxa in intimate mutualisms

Proximately, the deviations from a reciprocally specialized and modular structure seen in the Tahiti and Huahine networks are due to the presence of a generalist *Epicephala* taxon (clade Z of Hembry et al., 2013) which interacts with nine of the 10 available host *Glochidion* species and is the predominant or exclusive pollinator of many of these species (Figure 2). Generalists are characteristic of nonintimate mutualistic assemblages, as part of the core of their nested architecture (Guimarães et al., 2007). Generalists are thought to function to promote trait convergence and to stabilize mutualistic networks (Guimarães et al., 2006, 2011; Thompson, 2005). To the best of our knowledge, generalists are rarely reported from intimate mutualistic networks (but see the anemonefish *Amphiprion clarkii*; Ollerton et al., 2007). The term “supergeneralist” has been used to refer to generalists that interact with very high proportions of available partner species in a local assemblage, such as generalist pollinators which visit a very large proportion of available plant species on islands (Olesen, Eskildsen, & Venkatasamy, 2002) or honeybees or large-bodied seed dispersing vertebrates in other

communities (Guimarães et al., 2011). We note here that Clade Z is similar to such supergeneralists in that it interacts with nearly all available *Glochidion* hosts in the Society Islands. Whether Clade Z's broad host breadth is therefore a result of it being found on oceanic islands ("interaction release," Traveset et al., 2015) or similarly generalized *Epicephala* species are found on continents remains unclear. Regardless, these results contrast with the traditional "one-to-one" paradigm that has been widespread in the study of brood pollination mutualisms (Janzen, 1979; Ramírez, 1970).

How clade Z and the other taxa within the Society Islands regional network coevolve is therefore of great interest. As inter-specific floral odour differences mediate *Epicephala* specificity in Japanese *Glochidion* (Okamoto, Kawakita, Goto, Svensson, & Kato, 2013), it may be that Clade Z is undergoing incipient divergence and speciation through association with ecologically distinct *Glochidion* species (Hembry, 2017). Such divergence would imply that being a generalist is unstable within an intimate mutualistic network. Alternately, Clade Z may be promoting the evolution of trait convergence or structural stability within its network (Guimarães et al., 2011), suggesting that generalists can arise in intimate mutualisms and that they have stabilizing effects. The implications of this widespread pollinator sharing for interspecific gene flow among Polynesian leafflower trees have yet to be explored. Finally, our results also suggest the possibility of using biogeographic variation in network structure as a window onto how networks evolve through time and space.

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AUTHORS' CONTRIBUTIONS

D.H.H., R.L.G.R. and P.R.G. conceived the ideas; D.H.H., E.A.N., L.A. and C.G. collected the data; D.H.H., R.L.G.R., E.A.N. and P.R.G. analysed the data; D.H.H., R.L.G.R., E.A.N. and R.G.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data (specimen locality data, DNA sequences novel to this study, tree file and interaction networks) available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1224pr2> (Hembry et al., 2018). All *Epicephala* moth DNA sequences used are available from GenBank (see accession numbers above under "Section 2").

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SUPPORTING INFORMATION

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