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Biol. Lett. published online 7 September 2011
doi: 10.1098/rsbl.2011.0771

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<http://rsbl.royalsocietypublishing.org/content/suppl/2011/09/02/rsbl.2011.0771.DC1.html>

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Repeated colonization of remote islands by specialized mutualists

David H. Hembry^{1,*}, Tomoko Okamoto² and Rosemary G. Gillespie¹

¹Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA 94720, USA

²Graduate School of Human and Environmental Studies, Kyoto University, Kyoto, Japan

*Author for correspondence (hembry@berkeley.edu).

Mutualisms are ubiquitous in nature, but constraints imposed by specialization may limit their ability to colonize novel environments synchronously. The ability of mutualisms to reassemble following disturbance is central to understanding their response to global change. Here, we demonstrate that a highly specialized pollination mutualism considered to be obligate (Phyllanthaceae: *Glochidion*; Lepidoptera: Gracillariidae: *Epicephala*) has colonized some of the world's most isolated archipelagoes, and we record, to our knowledge, for the first time the presence of *Epicephala* moths from 19 host *Glochidion* species on 17 islands in the Pacific Ocean. Our findings appear to offer a remarkable example of mutualism persistence in an insect–plant interaction characterized by reciprocal specialization and mutual dependence. These findings also appear to contradict the island biogeography paradigm that taxa with specialized biotic interactions are unlikely to colonize oceanic islands.

Keywords: mutualism persistence; dispersal; specialization; Phyllanthaceae; *Epicephala*; southeastern Polynesia

1. INTRODUCTION

Mutualisms are pervasive in nature, but both theory and data suggest that they are intrinsically unstable because of conflicts between partners [1]. Additionally, reciprocal specialization between mutualists that are not vertically transmitted might pose constraints on their ability to successfully colonize new environments. As early as 1878, Wallace [2] hypothesized that the lack of suitable pollinators is a major constraint on the colonization of remote islands by flowering plants [3]. Island angiosperms are predominantly pollinated by wind or generalist insects and depend on generalist vertebrates for fruit dispersal [4]. Difficulties of synchronous co-establishment are thought to also restrict island colonization by plants or animals that require specialized fungal symbionts [5,6]. Alternatively, specialized mutualisms may be lost when plants colonize islands in the absence of mutualists [7,8].

Obligate, pollinating seed-predation mutualisms, such as between figs and fig wasps [9] and yuccas

and yucca moths [10] would appear to be especially ill-suited to island colonization. In these mutualisms, specialized insects pollinate the host plants' flowers, but feed as larvae on a subset of the host's seeds; these interactions have high reciprocal species-specificity, but are not vertically transmitted [9,10]. These mutualisms are either absent, or not species-rich, on oceanic islands. Native yuccas are absent from islands off North America, including the West Indies [10]. Native figs and fig wasps are widely distributed on Pacific islands, but are species-poor on most oceanic islands and absent from Hawaii [11,12]. The islands of southeastern Polynesia (Cook Islands, French Polynesia and Pitcairn Islands), the region in the Pacific farthest from continents (≥ 6000 km from Australia, ≥ 4800 km from Mexico and ≥ 3000 km from Fiji), are considered to have only one native, non-endemic fig species (*Ficus prolixa*) [5,11,13], which is apparently pollinated by a single wasp species throughout its range [12,13].

A similar mutualism between *Glochidion* trees (Phyllanthaceae) and *Epicephala* moths (Lepidoptera: Gracillariidae) is widely distributed throughout tropical Asia and Australasia [14]. *Glochidion* are monoecious, with minute, unisexual flowers that do not produce nectar [5]. Female flowers have a reduced perianth, fused styles and concealed stigmas [14]; this suite of traits has evolved convergently in four other *Epicephala*-pollinated Phyllanthaceae lineages [15]. Two Japanese *Glochidion* species have been shown to be self-compatible (A. Kawakita 2011, personal communication). *Epicephala* are the sole-known pollinators of *Glochidion* [14,16]; each *Glochidion* species appears to be associated with only one or two *Epicephala* species and vice versa [16]. Adult *Epicephala* pollinate their host in a highly stereotyped behaviour in which they transfer pollen to the host's concealed stigmas with the proboscis and then oviposit into the ovaries; larvae consume a subset (typically 30%) of the host's seeds [14]. Female *Epicephala* bear pollen on proboscis hairs; these hairs are absent in males (and females of one non-pollinating *Epicephala* lineage known from another genus of Phyllanthaceae) [15].

Glochidion are also found throughout the oceanic islands of Micronesia and Polynesia, except Hawaii [17]. The 25 described species in southeastern Polynesia constitute one of the largest endemic plant radiations in this biodiversity hotspot [5,18–20]. Twenty of these 25 species are considered single-archipelago endemics; most islands have one to three species, but the larger Society Islands have four to seven species [5,19]. These *Glochidion* retain the reduced flowers with fused styles and concealed stigmas seen in continental taxa [5]; style fusion is a strong predictor of *Epicephala* pollination in Phyllanthaceae [15]. Within Polynesia and Micronesia, however, *Epicephala* have only been reported from Samoa [21] and the Marquesas Islands [22], suggesting that this mutualism may have been lost as *Glochidion* colonized the remote Pacific [23]. It is unlikely that *Glochidion* and *Epicephala* could establish on a new island through a single dispersal event, since if a fruit containing an *Epicephala* larva were to land on a new island, the moth would eclose several years before a germinated *Glochidion* would be mature enough to produce flowers. Here, we report on the

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2011.0771> or via <http://rsbl.royalsocietypublishing.org>.

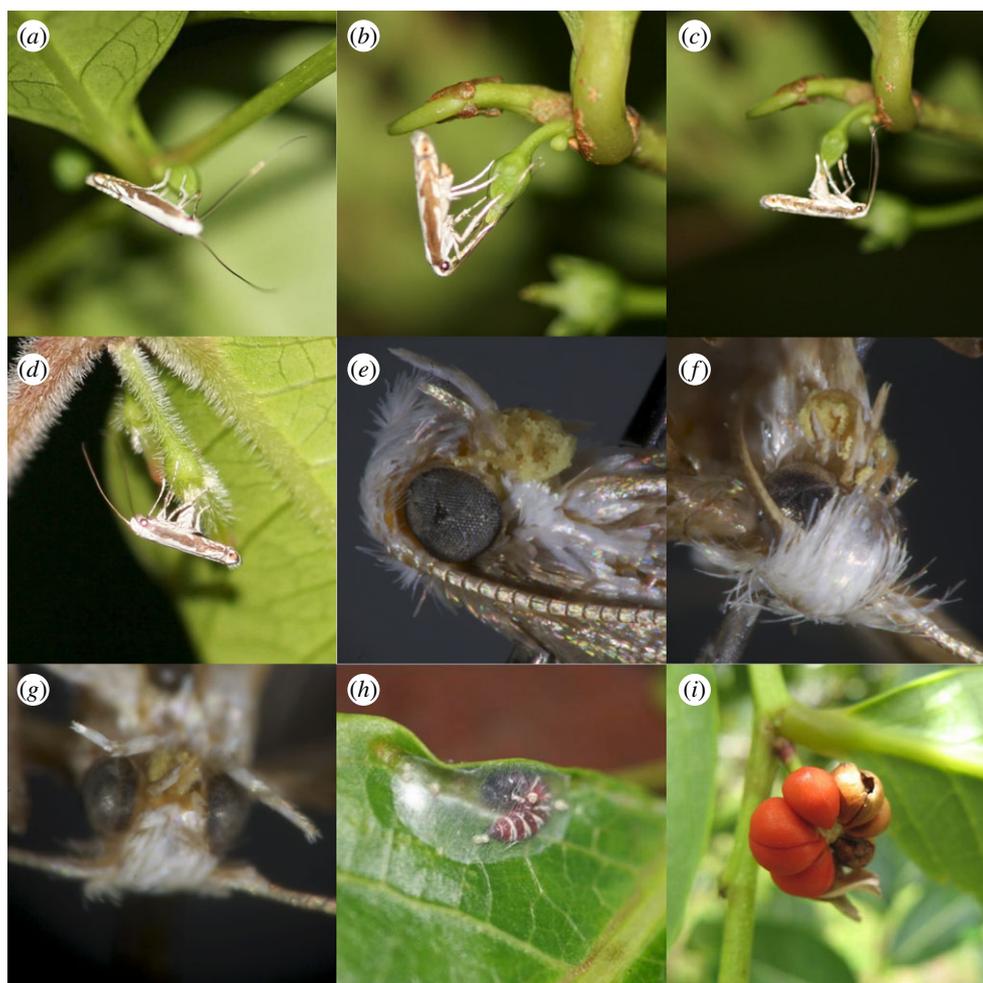


Figure 1. *Glochidion*–*Epicephala* interaction on Pacific islands. (a) *Epicephala* moth visiting male *G. grayanum* flower, Tahiti. (b) *Epicephala* inserting proboscis into female *G. grayanum* flower, Tahiti. (c) *Epicephala* inserting ovipositor into female *G. grayanum* flower, Tahiti. (d) *Epicephala* inserting ovipositor into female *G. temehaniense* flower, Raiatea. (e) Pollen on the proboscis of an *Epicephala* captured after being observed pollinating and ovipositing into flowers of *G. temehaniense*, Raiatea. (f) Pollen on the proboscis of a female *E. spinula* collected in 1968 on Nuku Hiva, Marquesas Islands. (g) Pollen on the proboscis of a female *Epicephala* collected in 1953 on Pohnpei, Micronesia. (h) *Epicephala* larva emerged from *G. grayanum* fruit and spinning a cocoon, Tahiti. (i) Dehiscent fruit of *G. manono*, showing intact seeds (red, left) and seeds consumed by *Epicephala* larva (right, brown), Moorea.

first survey of the presence of *Epicephala* moths on *Glochidion* trees in southeastern Polynesia, and assess whether on these islands *Epicephala* show evidence of pollinating *Glochidion* flowers.

2. MATERIAL AND METHODS

(a) Rearing

Glochidion fruit were collected from 22 species on 18 islands in the Cook Islands and the Society, Austral, Marquesas and Tuamotu archipelagoes in French Polynesia (see the electronic supplementary material) and kept in plastic bags to rear larvae. Fruit were also dissected to search for *Epicephala* larvae. Adult *Epicephala* were recognized by the two-lobed valvae of the male genitalia, sclerotized ovipositor and forewing pattern. Female *Epicephala* were examined for pollen-bearing hairs on the proboscis [16].

(b) Flower observations

We observed flowers of [1] *Glochidion grayanum* at the Belvédère, Taravao Plateau, Tahiti (Society Islands, French Polynesia; 560 m elevation, 17°46.7' S, 149°15.5' W) on the nights of 21 November 2007, 27–28 July 2008 and 7 March 2009; and [2] *Glochidion temehaniense* on Te Mehani Rahi Plateau on Raiatea (Society Islands; 400 m elevation, 16°46.0' S, 151°27.9' W) on the nights of 30–31 July 2006 and 15–16 July 2008, for a total of 15 h between 18.00 and 1.00 h. All flower visitors were observed and photographed

while on flowers, captured, preserved dry in glassine envelopes and examined for pollen. *Epicephala* specimens were photographed using a Microptics XLT digital imaging system (Ashland, USA), and automontaged using COMBINEZM [24].

(c) Examination of museum specimens

We additionally examined four female *Epicephala* specimens from the Smithsonian Institution for pollen. These specimens were collected by J. F. Gates Clarke on Fatu Hiva and Nuku Hiva (Marquesas; two specimens of *Epicephala spinula*) in 1968 [22] and on Pohnpei (Micronesia; two specimens of an undescribed species) in 1953.

3. RESULTS

We reared *Epicephala* adults from larvae in fruits of 17 species of *Glochidion* from 14 islands in four archipelagoes in French Polynesia and obtained *Epicephala* larvae from the fruits of four additional species of *Glochidion* from five islands in three archipelagoes in the Cook Islands and French Polynesia (figure 1*h,i* and electronic supplementary material). Three species of *Glochidion* examined yielded no *Epicephala* (electronic supplementary material); in these cases, 0–1 fruiting trees and less than five fruits were found. This is, to

our knowledge, the first published report of *Epicephala* from the Society, Austral, Tuamotu or southern Cook archipelagoes. Based on the valvae of male genitalia, male adult specimens represent five distinct morphospecies endemic to southeastern Polynesia (*E. spinula* and four undescribed species), each of which appears geographically restricted to one to three archipelagoes. All female *Epicephala* had proboscis hairs similar to those of pollinating *Epicephala* in Asia, and unlike non-pollinating *Epicephala* [15]. We also reared *Tritopterna* (Lepidoptera: Tortricidae); these are non-pollinating seed parasites of *Glochidion* in Asia [25].

We photographed and captured *Epicephala* visiting flowers of *G. grayanum* on Tahiti and *G. temehaniense* on Raiatea (Society Islands). *Epicephala* were observed visiting male flowers (figure 1a), pollinating female flowers with their proboscides (figure 1b) and subsequently ovipositing into the flowers' ovaries (figure 1c,d). Photographs show the insertion of the proboscis into both male and female flowers (figure 1a,b). Captured *Epicephala* bore pollen on their proboscides (figure 1e). Only three other insects were observed perched on the cylindrical flowers: one bug (Hemiptera: Miridae) and two midges (Diptera: Nematocera). None of these were observed contacting the vicinity of the recessed stigma and none bore pollen when examined. We also found that museum specimens of *Epicephala* from the Marquesas and Micronesia bore pollen (figure 1f,g).

4. DISCUSSION

We find that both *Glochidion* trees and *Epicephala* moths have colonized the remote Pacific, and that on at least several islands, *Epicephala* pollinate *Glochidion* as in continental Asia and Australasia [14]. Conservation of traits involved with mutualism (proboscis hairs; minute flowers with fused styles and concealed stigmas) between Asia and Polynesia suggests this interaction may be mutualistic throughout southeastern Polynesia. Although many insects are found on *Glochidion* foliage and some occasionally perch on flowers, our results do not suggest that they transport pollen or actively pollinate in the manner of *Epicephala*.

Successful colonization of remote islands by specialized mutualists that probably do not disperse together may appear paradoxical, and in contrast to the island biogeography paradigm that taxa with specialized biotic interactions should not be able to establish on islands [3]. It is unclear what mechanism has permitted this interaction to reassemble on these islands, but several hypotheses are possible. Reassembly may be permitted by long plant generation time, high insect dispersal rates or facultative species-specificity between *Glochidion* and *Epicephala* lineages that have no recent coevolutionary history. Although all evidence to date suggests that this mutualism is obligate [14,16], and we have no evidence of alternative pollinators, vegetative propagation or selfing, we cannot rule out the possibility that any of these processes may operate at a low rate that permits the persistence of a small *Glochidion* population on an island until later colonization by *Epicephala*.

Glochidion and *Epicephala* in southeastern Polynesia appear to constitute a remarkable example of the colonization of some of the youngest and remotest

landmasses on the planet by specialized mutualists that probably do not disperse together. This finding is of interest given concerns over the disruption of pollination systems, the increasing disturbance of island ecosystems, the rarity of many island plants and the response of mutualisms to global change.

We thank Priscille Frogier, the Délégation à la Recherche and Direction de l'Environnement (French Polynesia), and the National Research Council (Cook Islands) for permits; Jean-Yves Meyer, Gerald McCormack, Neil Davies, Emile Brotherson, Landry Chiou, Elin Claridge, Pascal Erhel, Curtis Ewing, Frida Fareea, François-Xavier and Sandrine Geneslay, Kau Henry, Craig Hetherington, Eric and Catherine Pellé, Erica Spotswood, Ravahere Taputuarai, the late Bernard Tevehini, Alan Tuara, Tou Unuia, April Yang, the Faraire family, and UCB ESPM C107 students (2007, 2009) for field assistance; Jean-Yves Meyer for *Glochidion hivaoaense* specimens; Bruce Baldwin, John Brown, Don Davis, Jacques Florence, Makoto Kato, Atsushi Kawakita, Tosio Kumata, Peter Oboyski, Issei Ohshima, George Roderick, William Sykes, Kip Will and students for other assistance; and Atsushi Kawakita, Jean-Yves Meyer, and three reviewers for comments. This research was supported by funds from NSF DEB-0451971 and the Moore Foundation to R.G.G., the NSF-GRFP, Sigma Xi, and Margaret Walker to D.H.H., and the Sumitomo Foundation to T.O.

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