Repeated colonization of remote islands by specialized mutualists

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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 prolifera) [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 monoeocious, 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 larva would be mature enough to produce flowers. Here, we report on the
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 CommerZM [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 1h,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 or 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 Triopterna (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.

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