



Phytophagous insect community assembly through niche conservatism on oceanic islands

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ABSTRACT

Aim To determine whether a community of phytophagous insects on oceanic islands (the fauna of insects feeding internally on *Glochidion* trees in south-eastern Polynesia) was assembled predominantly through niche conservatism or adaptive radiation.

Location The islands of south-eastern Polynesia (southern Cook, Austral, Society, Tuamotu-Gambier and Marquesas archipelagos) in the Cook Islands and French Polynesia.

Methods Internally feeding insects were collected as larvae from 23 endemic species of *Glochidion* (Euphorbiaceae s.l., Phyllanthaceae: *Phyllanthus* s.l.) trees on 20 islands in south-eastern Polynesia, reared and identified. Rearing records were compared with host records previously known from the literature and museum collections of closely related taxa in Asia and Australasia.

Results Ninety per cent of insect specimens collected fall into five taxa previously known to attack *Glochidion* in Asia and Australasia (≥ 6000 km distant), indicating a strong role for niche conservatism in the assembly of this community. Three of these taxa, two seed-feeding moths (Gracillariidae: *Epicephala*; Tortricidae: *Tritopterna*) and a leaf-mining moth (Gracillariidae: *Diphtheroptila*) are only known from Phyllanthaceae or Euphorbiaceae s.l. on continents. Two more taxa, another leaf-mining moth (Gracillariidae: *Caloptilia*) and a leaf-rolling moth (Tortricidae: *Dudua*), contain many species known only from Phyllanthaceae on continents, and are also very likely to represent examples of niche conservatism. Conversely, many numerically dominant insect taxa known from *Glochidion* on continents (such as parasitoid Hymenoptera) are not reported from south-eastern Polynesia. This indicates that the insular community represents a subset of those taxa from the continental community, consistent with the well-established Pacific diversity gradient.

Main conclusions These findings indicate that niche conservatism can play an important role in the assembly of phytophagous insect communities on oceanic islands, despite the constraints that specialization might be expected to pose on successful establishment. As a result of this niche conservatism, these communities may represent less species-rich versions of continental tropical communities rather than non-analogue insular ecosystems.

Keywords

Adaptive radiation, *Caloptilia*, community assembly, *Diphtheroptila*, niche conservatism, oceanic islands, Phyllanthaceae, phytophagous insects, south-eastern Polynesia, *Tritopterna*.

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INTRODUCTION

The roles of adaptive radiation and niche conservatism in community assembly are a major area of inquiry in commu-

nity ecology and biogeography (Ackerly, 2004; Melville *et al.*, 2006; Donoghue, 2008; Crisp *et al.*, 2009; Moen *et al.*, 2009). Nowhere are these questions more clearly relevant than on islands. The islands of the world are known for a number of

spectacular adaptive radiations, but a quick consideration of the limited number of such examples (Darwin, 1859; Perkins, 1913; Lack, 1947; Carlquist, 1974; Schluter, 2000; Carlquist *et al.*, 2003; Gillespie, 2004; Pratt, 2005; Grant & Grant, 2008; Losos, 2009) will make it clear that adaptive radiations are not inevitable on islands (Stuessy *et al.*, 2006; Losos, 2010), and that niche conservatism is also likely to be widespread in island taxa. Here, adaptive radiation is defined as the evolution of ecological differences among members of a rapidly multiplying lineage (*sensu* Schluter, 2000); it encompasses the evolution of ecological differences between sister lineages, including what is referred to as *in situ* evolution (e.g. Moen *et al.*, 2009). Niche conservatism is defined as conservation of important ecological traits among members of a diversifying lineage; it includes non-adaptive radiations (Rundell & Price, 2009). Whether island biotas are assembled through adaptive radiation or by niche conservatism over evolutionary time-scales ultimately has great implications for the study of community assembly, as well as island community structure and function.

Research on community assembly on oceanic islands has primarily focused on single lineages that undergo adaptive radiations to form an entire guild or community of species, such as passerine birds, lizards, spiders and snails (Lack, 1947; Chiba, 2004; Gillespie, 2004; Harmon *et al.*, 2007, 2008; Grant & Grant, 2008). In contrast, few studies have explicitly compared adaptive radiation and niche conservatism in phytophagous (plant-feeding) insect lineages on oceanic islands (but see Roderick & Percy, 2008; Percy, 2011). This neglect is surprising given that insects are a major proportion of both island and continental faunas, and that 'niches', 'ecomorphs' and 'communities' can be defined with much greater precision in specialized phytophagous insects than in many other radiations. Plants on remote islands can provide colonizing insects with numerous opportunities to radiate adaptively by shifting to novel hosts and speciating, but this outcome is not inevitable. The phytophagous insect community on a given host-plant taxon on an island or archipelago can consist of any combination of the following: (1) generalist species that feed on other plant taxa on the same island; (2) specialized species whose closest relatives elsewhere feed on the same plant taxon (niche conservatism); (3) specialized species whose closest relatives feed on some other plant taxon (adaptive radiation); (4) empty niches (plant resources not used by any insects).

The colonization of remote islands by specialized plant-feeding insects – or any other ecologically specialized organism – poses a paradox. Specialists that disperse independently to remote islands might not be able to establish if their host or prey is absent (Holt, 2010). It is unlikely that a woody host plant and insects specialized to feed on it could colonize a new island in a single dispersal event because any insects would reach reproductive maturity several years before a germinated host plant was mature enough to serve as a host. Synchronous colonization could, however, be permitted by insect dormancy or asexual plant propagules that

reproduce vegetatively but also carry insects. Consistent with the hypothesis that it is difficult for specialized insects to colonize islands, it has long been noted that island plant taxa often lack their co-evolved mutualistic and parasitic insects from the mainland (Janzen, 1973, 1975; Armbruster & Baldwin, 1998; Terborgh, 2010), and some ecologically dominant insular phytophagous insects are host-plant generalists (e.g. *Rhyncogonus* weevils in south-eastern Polynesia; Claridge, 2006).

A number of putative examples of adaptive radiation by insects onto different host-plant taxa on oceanic islands are known (Gagné, 1968, 1997; Gressitt, 1978; Zimmerman, 1978; Paulay, 1985; Asquith, 1995; Percy, 2003; Jordal & Hewitt, 2004; Jordal *et al.*, 2004; Magnacca *et al.*, 2008; Goodman, 2010; Bennett & O'Grady, 2011; Polhemus, 2011). In contrast, few examples exist of specialized host associations being conserved among oceanic archipelagos or between oceanic archipelagos and continents (Wiebes, 1994; Garin *et al.*, 1999; Staddon *et al.*, 2010). There is some degree of overlap between these two processes, as it has been hypothesized that the progenitors of some adaptive radiations were only able to establish on islands because of the presence of hosts closely related to the ancestral hosts (Asquith, 1995; Gagné, 1997; Percy, 2003), and some of these adaptive radiations could also be considered as exhibiting niche conservatism because they did not leave their ancestral host family (Percy, 2003; Jordal & Hewitt, 2004). Furthermore, adaptive radiations may contain subclades which show niche conservatism. For the purposes of this paper, we will be considering each end of this continuum: cases of niche conservatism in which insect lineages remain associated with the same host-plant family, and cases of adaptive radiation in which insect lineages radiate onto multiple host-plant families. This analysis includes both endemic as well as non-endemic native insect species.

One system ideally suited for examining niche conservatism in phytophagous insects on oceanic islands is the radiation of endemic species of trees in the genus *Glochidion* J.R. Forst. & G. Forst. (Phyllanthaceae; Euphorbiaceae *sensu lato*) in south-eastern Polynesia (Fig. 1a). The approximately 300 described species of *Glochidion* are distributed from tropical Asia and Australasia across the south Pacific as far east as the Pitcairn Islands (Govaerts *et al.*, 2000). In both Asia and the Pacific islands, *Glochidion* species are found in a wide range of wet to mesic habitats, and many show an affinity for open areas with a history of disturbance (Butaud *et al.*, 2008; Kawakita, 2010). The community of phytophagous insects on *Glochidion* in Asia and Australia is well known (De Prins & De Prins, 2005; Horak, 2006; Kawakita *et al.*, 2010; D.H.H., unpublished data, A. Kawakita, Kyoto University, pers. comm., 2010), and includes many internally feeding taxa (those whose larvae live and feed inside the tissues of their host plant) which are likely to have constrained host preferences. It is already known that the sole pollinator of *Glochidion* in Asia, namely *Epicephala* Meyrick (Lepidoptera: Gracillariidae), whose larvae also feed internally on

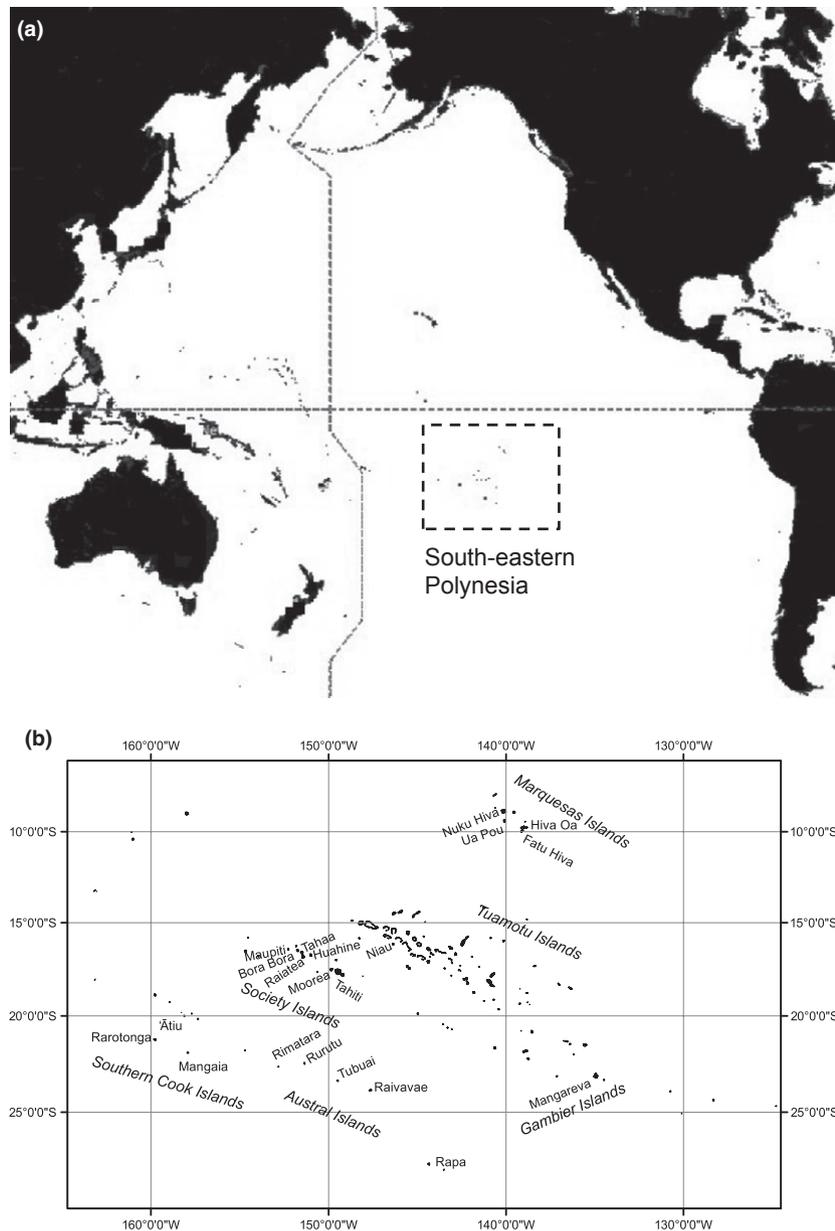


Figure 1 (a) Map of the Pacific Basin with south-eastern Polynesia indicated. (b) Map of south-eastern Polynesia, with archipelagos and islands mentioned in text indicated.

Glochidion, has successfully co-colonized south-eastern Polynesia with its host (Hembry *et al.*, 2012). The islands of south-eastern Polynesia are some of the world's islands that are most isolated from continents (≥ 6000 km from Australia and ≥ 3000 km from Fiji; Fig. 1a) and are all formed by midplate volcanoes, meaning that they are likely to pose numerous ecological opportunities for phytophagous insect colonizers.

The goal of this study is to determine the roles of adaptive radiation (host shifts), niche conservatism (conserved host associations) or generalist host associations in the assembly of the insect community on *Glochidion* trees on remote Pacific islands. To accomplish this, we ask what internally feeding insect taxa (at the family and genus level) are associated

with *Glochidion* in south-eastern Polynesia and whether the close relatives of these taxa feed on *Glochidion*, Phyllanthaceae or other hosts in Asia and Australasia. Finally, we address putative mechanisms that may be responsible for these biogeographic patterns.

MATERIALS AND METHODS

Field collection and rearing

Internally feeding insect larvae were collected from 202 trees representing 23 species of *Glochidion* on 20 islands in the southern Cook, Austral, Society, Tuamotu-Gambier and Marquesas archipelagos in the Cook Islands and French

Polynesia (Fig. 1b) over a period of 3 years from 2007 to 2009. Insect larvae were searched for visually and reared from fruits, leaf mines, leaf rolls, tied leaves, the surface of leaves and pupae found on *Glochidion* species. Rearing was carried out in plastic bags or in plastic rearing containers in the field. To assess whether leaf-mining gracillariids had host ranges broader than *Glochidion*, we reared all other leaf-mining insect larvae found on other host plants during this field-work in south-eastern Polynesia. We also examined the three native, extant species of *Phyllanthus* L. *sensu stricto* (s.s.) in this region (*Phyllanthus societatis* on 'Ātiu in the Cooks, *Phyllanthus pinaiensis* on Moorea in the Societies, and *Phyllanthus pacificus* in the Marquesas) for leaf-feeding and seed-feeding insects. The only other potentially native species of Phyllanthaceae in south-eastern Polynesia is *Bischofia javanica*, of doubtful indigenous status and extreme rarity (McCormack, 2007; Butaud *et al.*, 2008); we did not examine it.

Most adult insects that eclosed, and some larvae, were preserved in ethanol for future molecular work. Rearing from larvae provides stronger records of host-plant use than some other methods (e.g. sweeping). Most larvae from the Cook Islands were killed immediately in ethanol because it was prohibitive to obtain an import permit into French Polynesia, where the lead author (D.H.H.) was based. Rearing records from the Cook Islands thus do not accurately reflect abundances in the field.

Voucher specimens of *Glochidion* (the same as in Hembry *et al.*, 2012) have been deposited in the Herbarium Pacificum (BISH), Bishop Museum, Honolulu, HI, USA (Cook Islands specimens), and the University Herbarium (UC), University of California, Berkeley, CA, USA (French Polynesian specimens). Voucher specimens of moths will be deposited in the Bishop Museum.

Literature and museum search for host records

To determine whether host associations from south-eastern Polynesia represented examples of niche conservatism, we concurrently conducted a literature search for other host records world-wide for each of the most abundant insect genera collected in the field (which were all moths). For additional information on host associations of Gracillariidae, we examined host records of specimens at the Hokkaido University Museum (Sapporo, Japan), based on the extensive field rearing surveys by Tosio Kumata in tropical Asia. Specifically, we aimed to determine whether each of the genera under consideration is known only from Phyllanthaceae or Euphorbiaceae *sensu lato* (s.l.) on continents and on Pacific islands; such cases would represent examples of niche conservatism.

Although niche conservatism is usually assessed through the analysis of traits on a phylogeny, the taxonomy-based approach we used here is valid for assessing niche conservatism in this system because extensive information on the relevant ecological trait (host plant) was available from the literature and museum collections for each of these genera.

Taxonomic status of Pacific island *Glochidion*

Numerous analyses support the monophyly of *Glochidion* s.l. within a paraphyletic *Phyllanthus* s.s. (Kathriarachchi *et al.*, 2006; Kawakita & Kato, 2009; Luo *et al.*, 2011). Accordingly, Hoffman *et al.* (2006) proposed that the genus *Glochidion* be placed in synonymy within a monophyletic *Phyllanthus* s.l., but refrained from formally transferring all *Glochidion* species to *Phyllanthus* because of the large number of species and the numerous synonymous epithets requiring resolution. For the Flora of the Marquesas project, Wagner & Lorence (2011) transferred all described Polynesian *Glochidion* species to *Phyllanthus* and erected new species epithets where necessary to prevent homonymy. Because we expect all species of *Glochidion* s.l. eventually to be given valid names in *Phyllanthus* (Chakrabarty & Balakrishnan, 2009), here we use the Wagner & Lorence combinations (if available) in *Phyllanthus* to refer to individual species of *Glochidion* s.l. from south-eastern Polynesia. However, we use the name *Glochidion* to refer to *Glochidion* s.l. (the clade *Glochidion*, including the Polynesian species), *Glochidion* s.s. to refer to continental *Glochidion*, and *Phyllanthus* s.s. to refer to species not in *Glochidion* s.l. (e.g. the traditional circumscription of *Phyllanthus* ignoring Wagner & Lorence). There are four native species of *Phyllanthus* s.s. in south-eastern Polynesia (Florence, 1997; McCormack, 2007). For synonyms, see Wagner & Lorence (2011).

RESULTS

Field surveys

A total of 509 individual insects were reared from internally feeding larvae and pupae on *Glochidion* species on 20 islands (Table 1; see Appendices S1 & S2 in Supporting Information). This number is much lower than the total number of insects collected, due to mortality during the rearing process. Based on our experience of learning to recognize different larval taxa and their feeding damage during this process, we believe that the sample of insects reared is an accurate reflection of the insect fauna collected as larvae. Ninety per cent of these insect specimens fall into five taxa that are also known to attack *Glochidion* in Asia and Australasia (Table 1, Appendix S3). These taxa are *Epicephala* (Lepidoptera: Gracillariidae; 50% of the total), leaf-mining *Diphtheroptila* Vári moths (Gracillariidae; 16%), leaf-mining *Caloptilia* Hübner moths (Gracillariidae; 1%), seed-feeding *Tritopterna* Meyrick moths (Tortricidae; 18%) and leaf-rolling *Dudua* Walker moths (Tortricidae; 4%). These moths were identified to genus, pending future molecular and taxonomic studies.

To the best of our knowledge, these are the first published records of *Diphtheroptila* from the Society, Austral and Tuamotu archipelagos; of *Caloptilia* from the Societies; of *Tritopterna* from the northern Australs; and of *Dudua* from the northern Australs and Tuamotus.

Table 1 Results of the rearing survey of insects feeding on *Glochidion* s.l. as larvae in south-eastern Polynesia, compared with information from continental faunas. The number of specimens of each insect taxon reared from *Glochidion* s.l. in each archipelago is indicated; specimens are identified to genus for Lepidoptera and to family for other orders. Numbers do not include larvae or pupae that died before adult eclosion. Archipelagos are subdivided to reflect geology and geography: the Australs are divided into the Northern Australs and Rapa, and the Societies into the Leeward and Windward Islands. Niau is in the Tuamotus. Percentage total refers only to south-eastern Polynesian samples from this survey, out of the total of 509 insect specimens reared (Appendix S1).

Taxa	Regions										Total	Percentage
	Japan	Southeast Asia	Australia	Southern Cooks	Northern Australs	Rapa	Societies (Leeward)	Societies (Windward)	Niau	Marquesas		
<i>Epicephala</i> (Lepidoptera)	P	P	P	P*	3	22	97	104	3	26	255	50%
<i>Diphtheroptila</i> (Lepidoptera)	P	P	P	1	12	0	24	43	2	0	82	16%
<i>Caloptilia</i> (Lepidoptera)	P	0	P	1	0	1	1	2	0	1	6	1%
<i>Tritopterna</i> (Lepidoptera)	P	P	P	1	10	13	20	26	0	22	92	18%
<i>Dudua</i> (Lepidoptera)	P	0	P	1	8	0	9	2	2	P*	22	4%
Frass-tube gelechioids (Lepidoptera)	0	0	0	0	0	0	0	8	0	0	8	2%
Bucculatricidae (Lepidoptera)	P	0	0	0	0	0	0	0	0	0	0	0%
<i>Peragrarchis</i> (Lepidoptera)	P	0	0	P*	0	0	0	0	0	0	0	0%
<i>Cryptoblabe</i> (Lepidoptera)	P	0	0	0	0	0	0	0	0	0	0	0%
Stem-boring moths (Lepidoptera)	P	P	0	0	0	0	0	0	0	0	0	0%
<i>Aristotelia</i> (Lepidoptera)	0	P	0	0	0	0	0	0	0	0	0	0%
Agromyzidae (Diptera)	P	0	0	0	0	2	P†	0	0	0	2	0%
Attelabidae (Coleoptera)	0	P	0	0	0	0	0	0	0	0	0	0%
Braconidae (Hymenoptera)	P	P	0	0	0	0	0	0	0	0	0	0%

*Previously reported on *Glochidion* s.l. (Clarke, 1986; McCormack, 2007; Hembry *et al.*, 2012) but not reared in this study.

†Agromyzid mines present but adults never successfully reared.

The remaining 10% of insect specimens reared represent several rare taxa. The two most distinctive were an unidentified moth (Lepidoptera: Gelechioidea) whose leaf-scraping larvae made frass and silk tubes along the upper surface of *Glochidion* leaves, and leaf-mining flies (Diptera: Agromyzidae). Frass-tube gelechioids and their distinctive feeding damage were restricted to the Windward Society Islands (Tahiti and Moorea); similar frass and silk tubes were never observed on other native or introduced plants (D.H.H., unpublished notes). *Glochidion*-mining agromyzids and their mines, which are distinctive, were restricted to the Leeward Societies and Rapa, although they were only successfully reared on Rapa. However, agromyzids were observed and reared from a number of other native and introduced plant genera on many islands (D.H.H., unpublished data) and will not be considered further.

A striking feature of the rearing survey was the small number of hymenopterans, including parasitoids, which eclosed (10 individuals), despite the hundreds of lepidopteran larvae reared. Those we did find were from leaf-rolls (one each from Maupiti and Moorea, Societies), frass-tube gelechioids (two from Tahiti), or leaf-mines (three from Ua Pou, Marquesas). Three braconids were reared from unrecorded host larvae on Fatu Hiva (Marquesas). In contrast, seed-feeding or *Epicephala*-parasitic braconids are common in *Glochidion* fruit in Asia, Fiji and American Samoa (D.H.H., unpublished data; A. Kawakita, pers. comm., 2010).

No leaf-mining larvae or empty mines were found on *Phyllanthus wilderi* on Mangareva (Gambier Islands), in contrast to all other archipelagos. Although we examined three species of native *Phyllanthus* s.s. for insect larvae in seeds and leaves, the only insects found were *Diphtheroptila* mining

the leaves of *Phyllanthus pinaiensis* on Moorea (Societies). Very few other leaf-mining Lepidoptera were found on other native plants, consistent with earlier surveys which suggested a depauperate fauna (Clarke, 1971, 1986). Taxa found were *Macarostola* (Gracillariidae) on *Metrosideros* (Myrtaceae) in the Societies, northern Australs and Rapa (previously reported by Clarke, 1971); unidentified larvae not successfully reared from *Pipturus*, *Boehmeria*, and *Cypholophus* (Urticaceae) in the Societies and northern Australs; and unidentified microlepidoptera on *Myrsine* (Myrsinaceae) in the Societies.

Literature and museum surveys for host records

Literature and museum surveys revealed that of the five abundant moth genera on *Glochidion* s.l. in south-eastern Polynesia, three (*Epicephala*, *Diphtheroptila*, *Tritopterna*) were previously only known from Phyllanthaceae or Euphorbiaceae s.l. on both continents and islands (Meyrick, 1880, 1907, 1969; Vári, 1961; Robinson *et al.*, 1994; Kato *et al.*, 2003; De Prins & De Prins, 2005; Horak, 2006; Kawakita & Kato, 2009; Kawakita *et al.*, 2010; Hu *et al.*, 2011; T. Kumata, Hokkaido University, pers. comm., 2010). The remaining two genera (*Caloptilia* and *Dudua*) are known from multiple host-plant families world-wide (Clarke, 1976; De Prins & De Prins, 2005; Horak, 2006), but contain multiple described species (five species of *Caloptilia* and six species of *Dudua*, including both island and continental species) that have only been reported from *Glochidion* s.l. (Bradley, 1953; Kumata, 1966, 1982; Esaki *et al.*, 1971; Clarke, 1976, 1986; De Prins & De Prins, 2005; Horak, 2006; Kawakita *et al.*, 2010; Robinson *et al.*, 2010). Complete host record information is provided in Appendix S3.

DISCUSSION

Conserved host associations and niche conservatism between Asia and Polynesia

This study finds that the numerically dominant insect taxa that feed internally on *Glochidion* trees in south-eastern Polynesia are taxa which also feed on the same host plants in the west Pacific and Asia. The three most abundant of these taxa (*Epicephala*, *Diphtheroptila*, *Tritopterna*; 84% of the insects reared) are only known from Phyllanthaceae or Euphorbiaceae s.l. in Asia and Australasia (Meyrick, 1880, 1907, 1969; Vári, 1961; Robinson *et al.*, 1994; Kato *et al.*, 2003; De Prins & De Prins, 2005; Horak, 2006; Kawakita & Kato, 2009; Kawakita *et al.*, 2010; Hu *et al.*, 2011; T. Kumata, pers. comm., 2010) and so their presence on *Glochidion* in south-eastern Polynesia represents examples of niche conservatism. This result is robust to phylogenetic analysis, because each of these insect genera is specialized on this host-plant family. If *Glochidion*-feeding *Caloptilia* (Kumata, 1966, 1982; Clarke, 1986; Kawakita *et al.*, 2010; Robinson *et al.*, 2010) and *Glochidion*-feeding *Dudua* (Bradley, 1953; Esaki *et al.*, 1971;

Clarke, 1976, 1986; Horak, 2006) are each monophyletic across the Asia-Pacific region (Appendix S3), they may also represent examples of niche conservatism. The association of this set of taxa with the same host plants in both the Asian and Australasian (sub)tropics and the central Pacific indicates a substantial role for niche conservatism in the assembly of this phytophagous insect community. More importantly, they indicate that specialization on particular host plants does not prevent insects from successfully colonizing islands, provided their hosts are present.

Whereas these results demonstrate the role of niche conservatism in the assembly of this insect community, they do not preclude the possibility that some of these lineages have adaptively radiated onto other host-plant families since colonizing this region. (This possibility is, however, unlikely in the case of *Diphtheroptila* and *Caloptilia*, given that leaf-miner larvae were searched for and reared on all other woody plant taxa.) These results also do not bear on the possibility that these insects have evolved narrower or broader host breadth within *Glochidion* or Phyllanthaceae than their continental relatives (Kawakita *et al.*, 2010), or on the process of lineage diversification within each taxon across south-eastern Polynesia. Finally, although the species-level taxonomy and genetics of each of the four parasitic moth genera has not yet been examined, it is likely that each of these taxa has diverged into endemic lineages in south-eastern Polynesia due to their geographic isolation from continental relatives. Such endemic diversification is known for south-eastern Polynesian *Epicephala* species (Hembry *et al.*, 2012).

Such niche conservatism between continents and oceanic islands across ≥ 6000 km of ocean has rarely been demonstrated (Wiebes, 1994; Hembry *et al.*, 2012). However, despite the great distance between Asia/Australasia and south-eastern Polynesia, because of the high density of islands in this region, inter-island distances are always ≤ 1000 km. Specialized phytophagous insects might be able to colonize this area in a stepwise fashion by using islands of the western and central Pacific archipelagos as stepping stones to colonize south-eastern Polynesia. Consequently, the effective isolation of south-eastern Polynesia to colonists may be much less than its distances from the nearest continents suggests. Most of the western and central Pacific islands have *Glochidion* on them, with the exception of atolls (Smith, 1981; Govaerts *et al.*, 2000). Furthermore, many atolls would have emerged to 100-m elevation during Pleistocene sea-level minima (Dickinson, 2004); *Glochidion* today grows on the modern analogues of these emerged atolls (e.g. Anaa, Niau, Makatea in the Tuamotus; Florence, 1997; Butaud *et al.*, 2008). As a result, herbivorous insects specialized on *Glochidion* may have been able to colonize the islands of the south Pacific in a stepping-stone fashion, and establish successfully on each new island as long as their host was already present there.

It is extremely unlikely that human-mediated dispersal has played a role in the assembly of this community. *Glochidion*

trees are not considered to have been among the plants transported by Polynesians between archipelagos (Whistler, 2009), and there is no evidence in the ethnobotanical literature or language dictionaries from the Cooks or French Polynesia that *Glochidion* were planted or facilitated by Polynesians (Chabouis & Chabouis, 1954; Pétard, 1986; Buse, 1995; Académie Tahitienne, 1999; Whistler, 2009). If *Glochidion* were transported by Polynesians, it would be expected that some species would be shared between the Polynesian homeland (Samoa and Tonga; Kirch, 2000) and south-eastern Polynesia, or between archipelagos within south-eastern Polynesia. However, all south-eastern Polynesian taxa in *Glochidion* are endemic to south-eastern Polynesia, with one exception, *Phyllanthus concolor* in Fiji and Rarotonga (Wagner & Lorence, 2011), which is likely to comprise two distinct taxa based on molecular data (D.H.H., unpublished data). Additionally, with one exception which is probably over-lumped (*Phyllanthus florencei*; D.H.H., unpublished data) all species are single-archipelago endemics (Florence *et al.*, 1995; Florence, 1997; Wagner & Lorence, 2011). There is no widespread, low-elevation species of *Glochidion* throughout south-eastern Polynesia, and today they rarely grow near sea level where the majority of people live.

Pacific diversity gradient

We also find that the insect fauna feeding on *Glochidion* trees in south-eastern Polynesia is a subset of the taxa known to feed on *Glochidion* in Asia and the west Pacific (Table 1). Taxa absent from south-eastern Polynesia include: leaf-mining bucculatricid moths (Japan; A. Kawakita, pers. comm., 2010); unidentified stem-boring moths (in Japan and Malaysia; A. Kawakita & D.H.H., unpublished data); another seed-feeding moth taxon (Pyralidae: *Cryptoblabe*; Kawakita *et al.*, 2010); leaf-rolling weevils (Attelabidae in Malaysia; D.H.H., unpublished data); braconid wasps (Hymenoptera), some species of which parasitize *Epicephala* larvae and some of which gall *Glochidion* fruit (A. Kawakita & D.H.H., unpublished data; Japan, Malaysia, Fiji, American Samoa); and *Aristotelia galeotis* (Gelechiidae) (Robinson *et al.*, 1994). The apparent absence of many of these taxa in south-eastern Polynesia is consistent with the Pacific diversity gradient, in which species or lineage diversity of numerous terrestrial and nearshore marine taxa decreases, and taxonomic disharmony increases, from west to east across the Pacific Basin (reviewed in Steadman, 2006; however, this pattern is in some cases confounded by island area).

The absence of certain taxa (predicted by theory; Holt, 2010) may have strong effects on the densities of other community members. For instance, almost no parasitoids were obtained despite the huge number of lepidopteran larvae reared. The absence of parasitoids may be responsible for the high densities of *Diphtheroptila* seen on many islands in south-eastern Polynesia. Likewise, the absence of braconids (with the possible exception of Fatu Hiva in the Marquesas), which either compete with or parasitize *Epicephala* larvae in

Asia (R. Goto, Kyoto University, pers. comm., 2011), may have a strong effect on the stability and fitness outcome of the mutualism between *Glochidion* and *Epicephala* in Polynesia. These effects may have important consequences that lead to differences in community structure and function between islands and continents.

Adaptive radiation and niche conservatism in phytophagous insects on islands

This study finds that niche conservatism plays an important role in assembling this phytophagous insect community on remote oceanic islands thousands of kilometres from continents. Is this a common pattern for phytophagous insects on islands? Besides this study, a few examples are known of apparent niche conservatism between oceanic archipelagos, or between archipelagos and continents. These include multiple lineages of leaf beetles in the Canary Islands (Garin *et al.*, 1999) which conserved their ancestral host associations but failed to diversify *in situ*; the pollinating seed-predatory fig wasp *Platyscapha innumerabilis* (Hymenoptera: Agaonidae), which apparently uses the same fig host (*Ficus prolixa*) in the Cooks, Marquesas and Guam (Fullaway, 1913; Grandi, 1939; Wiebes, 1994; Staddon *et al.*, 2010); and leaf-mining *Macarostola* moths (Gracillariidae) on *Metrosideros* in the southern Cooks, Australs and Societies (Clarke, 1971; McCormack, 2007; this study). In contrast, numerous putative adaptive radiations onto different host-plant families have been reported, primarily from the Hawaiian insect fauna. These include Hawaiian *Drosophila* (Magnacca *et al.*, 2008), Hawaiian *Plagithmysus* beetles (Cerambycidae; Gressitt, 1978), Hawaiian *Nesophrosyne* leafhoppers (Cicadellidae; Bennett & O'Grady, 2011), Hawaiian leaf-mining *Philodoria* moths (Gracillariidae; Zimmerman, 1978), multiple clades of Hawaiian plant bugs (Miridae: *Nesiomiris*, *Cyrtopeltis*, *Sarona*, *Orthotylus*; Gagné, 1968, 1997; Asquith, 1995; Polhemus, 2011), *Nesosydne* planthoppers in Hawaii and the eastern Pacific (Delphacidae; Goodman, 2010), *Miocalles* weevils on Rapa, Austral Islands (Curculionidae; Paulay, 1985) and *Liparthrum* bark beetles in the Canary Islands and Madeira (Curculionidae; Jordal *et al.*, 2004).

Taken at face value, these examples suggest that niche conservatism may be uncommon in phytophagous insects on islands; in other words, it might be more likely that niches on host plants will be filled by adaptive radiation *in situ* than by specialist insects colonizing from elsewhere. What, then, determines whether phytophagous insects on oceanic islands continue to attack their ancestral hosts or evolve to attack new hosts? Broadly, there are two categories of explanations: factors intrinsic to the organisms themselves (evolutionary constraints or evolvability) and factors extrinsic to the organisms (ecological opportunity) (Schluter, 2000; Losos, 2010). Intrinsic factors would include aspects of the biology of host-plant specialization that make host shifts difficult to evolve. It is well-recognized that host-plant specialization is a complex trait, and many barriers exist to host-shifts

(Schoonhoven *et al.*, 1998; Matsubayashi *et al.*, 2010), although the extent to which host shifts are evolutionarily constrained may vary across insect groups. Extrinsic factors in this case would include island area and age, the presence of suitable host plants, and the absence of competitors (presumably correlated with isolation).

It is worth noting that most of the putative examples of adaptive radiation in host use are seen in Hawaii (Gagné, 1968, 1997; Gressitt, 1978; Zimmerman, 1978; Asquith, 1995; Magnacca *et al.*, 2008; Bennett & O'Grady, 2011). In principle, the colonizing insect fauna should be similar across all these midplate Pacific archipelagos, and thus the intrinsic evolutionary constraints for the fauna as a whole on each archipelago should be similar. In contrast, south-eastern Polynesia differs from Hawaii in two extrinsic factors that might predispose its biota towards less adaptive radiation: first, it is less isolated (because of the presence of many intermediate islands), and second, its islands are much smaller (Tahiti, by far the largest at 1000 km², would be the fifth largest of the Hawaiian Islands). Consequently, assuming the observed patterns are not an artefact of investigator bias (see below), it is possible that in this plant–insect community in south-eastern Polynesia dispersal occurs sufficiently frequently and ecological opportunities are sufficiently restricted that dispersal plays a more important role than adaptive radiation in assembling its biota relative to Hawaii. It is worth noting that radiations of many other taxa (including passerine birds, woody Asteraceae, lobeliads and *Tetragnatha* spiders) have far less ecological diversity in south-eastern Polynesia than in Hawaii (Carlquist, 1974; Gillespie, 2003a,b, 2004; Steadman, 2006; Fleischer *et al.*, 2008; Givnish *et al.*, 2009; Lerner *et al.*, 2011; Price & Wagner, 2011). This hypothesis would imply that adaptive radiation onto new host plants is difficult, and overcome only when islands are sufficiently large and/or isolated to reduce the importance of dispersal and increase that of *in situ* evolution, as in Hawaii.

These apparent patterns of many adaptive radiations in certain archipelagos and a few examples of niche conservatism in others may, however, also result in part from investigator bias. Hawaii and the Canaries have been well studied because of their proximity to North America and Europe, and extremely isolated islands such as Rapa have long attracted a great deal of interest from entomologists (Clarke, 1971; Paulay, 1985). It is likely that there are unreported and unrecognized adaptive radiations of phytophagous insects in south-eastern Polynesia. Ultimately, our understanding of adaptive radiation and niche conservatism in these systems is hampered by our poor understanding of phytophagous insect diversity and their host associations among archipelagos and between archipelagos and continents. Comparisons of the same taxa across multiple archipelagos, as well as standardized surveys of insects in numerous functional groups associated with the same host-plant taxon between archipelagos and continents, would be particularly revealing. These kinds of studies would be illuminating not only in our understanding of the evolution of host breadth and host shifts in

phytophagous insects, but in our understanding of the roles of niche conservatism and adaptive radiation in assembling biological communities in general.

CONCLUSIONS

This study finds that specialization to particular hosts does not necessarily prevent phytophagous insects from colonizing remote oceanic islands, and that consequently, niche conservatism can play a strong role in the assembly of these phytophagous insect communities. These findings indicate that even remote oceanic island communities can represent less species-rich examples of their tropical continental equivalents, and have implications for efforts to understand why certain organisms remain phylogenetically conservative in their ecology, whereas others undergo adaptive radiation.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Rearing records by plant species and island.

Appendix S2 Illustrations of insects and feeding damage.

Appendix S3 Literature and museum host records.

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BIOSKETCH

David Hembry is a recent PhD from the University of California, Berkeley, interested in co-evolutionary diversification, the evolution of specialization and Pacific biogeography. This paper is part of his PhD thesis on the co-phylogenetics, biogeography and network structure of the *Glochidion–Epicephala* mutualism in south-eastern Polynesia. He is headed to a post-doctoral research position at Kyoto University.

Author contributions: D.H.H. conceived the ideas; D.H.H. and T.O. conducted the fieldwork; D.H.H., T.O. and G.M. conducted rearing; D.H.H. identified specimens and analysed the data; D.H.H. and R.G.G. wrote the paper.

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