Molecular phylogeography of the Society Islands (Tahiti; South Pacific) reveals departures from hotspot archipelago models

David H. Hembry1,2,3* and Brad Balukjian4

1Center for Ecological Research, Kyoto University, Otsu, Shiga, Japan, 2Department of Molecular and Cell Biology, University of California, Berkeley, CA, USA, 3Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA, 4Department of Biology, Laney College, Oakland, CA, USA

*Correspondence: Dr. David H. Hembry, University of Arizona, Department of Ecology and Evolutionary Biology, P.O. Box 210088, Tucson, AZ 85721, USA
E-mail: hembry@email.arizona.edu

ABSTRACT

Aim Phylogeographical and modelling studies have suggested that the biotas of oceanic hotspot archipelagos (such as the Hawaiian, Canary and Galápagos islands) diversify in parallel with the formation of the islands on which they live. Here, we review the phylogeography of the native terrestrial biota of the Society Islands, an archipelago formed < 4.6 Ma, to test this model.

Location Society Islands, French Polynesia (Pacific Ocean).

Methods We reviewed 49 phylogenetic and phylogeographical studies incorporating Society Island terrestrial animal and plant taxa. We ask: (1) Where are the sister groups of Societies lineages distributed? (2) Are Societies-endemic ‘radiations’ monophyletic or polyphyletic? (3) What between-island barriers are seen in the phylogeography of Societies taxa? (4) What within-island barriers are seen in the phylogeography of Societies taxa? (5) How old is the Societies biota?

Results Most Societies lineages are closely related to those in other tropical Pacific archipelagos, particularly the Cook, Austral and Marquesas Islands (< 2000 km distant). More genera show strong evidence for polyphyly (13 genera) than for monophyly (4 genera) in the Society Islands. The most common within-archipelago phylogeographical barrier corresponds to the straits (150 km) between the Windward Society and Leeward Society Islands. Only a few groups, primarily species-rich invertebrate radiations, show divergence among or within islands. Published divergence time estimates suggest that much of the Societies biota may be much younger than the age of the archipelago.

Main conclusions Much of the Societies biota does not appear to have diversified in parallel with the formation of the archipelago, differing from ‘progression rule’ and general dynamic models for the diversification of oceanic archipelago biotas. Rather, many Societies ‘radiations’ may have been assembled via repeated, independent colonizations, which may have entailed extensive macroevolutionary turnover of colonizing lineages. These patterns have implications for the biogeography of other Pacific hotspot archipelagos.

Keywords oceanic hotspot archipelago, Pacific, phylogeography, repeated colonization, Society Islands, Tahiti

INTRODUCTION

The Society Islands have loomed large in the Western imagination since first contact between Tahitians and Europeans in 1767. These islands, of which the most famous are Tahiti, Bora Bora and Moorea, are an oceanic archipelago formed by volcanoes in the central South Pacific. However, despite an early visit by Darwin (1839), and extensive endemism in their biota (Meyer, 2004), they have received less attention from evolutionary biologists than other oceanic
archipelagos such as the Hawaiian, Galápagos and Macaronesian islands.

The Society Islands are one of several linear hotspot archipelagos on the Pacific Plate, along with the Hawaiian, Marquesas, Cook-Austral and Samoan islands (Fig. 1a). All these archipelagos were likely formed by stationary hotspots under the Pacific Plate (Clouard & Bonneville, 2005). All have roughly the same orientation, with an age progression of youngest islands at the south-east end of the archipelago and the oldest at the north-west end; the existing high islands of many of these archipelagos are less than or equal to 5 Myr in age (Duncan & McDougall, 1976; Clouard & Bonneville, 2005). Because these and other oceanic archipelagos are formed de novo by volcanism, their biotas are assembled entirely via long-distance dispersal and in situ diversification. They thus have long been considered laboratories for studying processes such as speciation, adaptive radiation, community assembly and macroevolutionary diversification dynamics (Darwin, 1859; MacArthur & Wilson, 1967; Carliquist, 1974; Coyne & Orr, 2004; Grant & Grant, 2008; Gillespie & Baldwin, 2009).

Extensive phylogenetic study of the biota of Hawaii has suggested that the linear age progression of its islands drives common phylogeographical patterns in the diversification of its biota (Wagner & Funk, 1995; Roderick & Gillespie, 1998; Cowie & Holland, 2008; Gillespie & Baldwin, 2009). The most widely emphasized aspect of this model is termed the ‘progression rule’, in which an endemic clade radiates in parallel with the sequential formation of the islands (Wagner & Funk, 1995). This implies that earlier diverging (more ‘basal’) lineages are found on older islands and later diverging (more ‘derived’) lineages are found on younger islands, and that many of these radiations are similar in age to the archipelago itself (5.1 Ma for the main Hawaiian Islands). In
addition, many Hawaiian radiations show other common patterns. Most, even the most species-rich ones, are monophyletic. Furthermore, evidence for both between- and within-island speciation is seen, due to the large size of islands, the fact that many islands are made of multiple volcanoes and the distances between islands. Similar patterns have been reported in other well-studied oceanic archipelagos (Canaries and Galápagos; Juan et al., 2000; Parent et al., 2008), and have inspired highly influential conceptual models for the way in which island ontogeny governs the diversification of insular biotas, such as the general dynamic model (Whittaker et al., 2008) and the overshoot hypothesis (Gillespie & Baldwin, 2009).

Whether these conceptual models or elements thereof apply to the diversification of the biotas of other Pacific Plate hotspot archipelagos remains unclear and in some cases, contentious because these island groups are much smaller in total area than the Hawaiian Islands and are much less isolated from each other. They also lack the elevational, climatic and topographic complexity of the Hawaiian archipelago. Taxonomists have long noted that these islands have fewer and smaller endemic radiations (radiations composed entirely of locally endemic species), and less ecological diversity within these radiations, than is the case in Hawaii (see summary in Keast, 1996). Consequently, some authors (in the absence of phylogenetic data) have argued that within the Pacific, Hawaii is a ‘special case’ in which the large size, topography, spatial arrangement and isolation of its islands permit such spectacular radiation (Keast, 1996; Hembry et al., 2013b). Conversely, other authors have argued based on phylogenetic data that particular radiations on other Pacific archipelagos (Societies: Bradley, 2003; Marquesas: Cibois et al., 2004; Australs: Garb & Gillespie, 2006) show progression rule patterns, potentially due to the same underlying geological mechanisms as in Hawaii. No comprehensive phylogeographical synthesis of any of these other archipelagos has been conducted (but see Gillespie et al., 2008).

Here we perform the first phylogeographical synthesis of the Society Islands terrestrial biota (vascular flora and fauna). Among Pacific Plate hotspot archipelagos, the biodiversity and phylogeography of this archipelago is the next-best-studied after Hawaii. We ask the following questions: (1) Where are the sister groups of Societies lineages distributed? (2) Are Societies-endemic radiations monophyletic or polyphyletic? (3) What major between-island phylogeographical patterns are seen in Societies taxa? (4) What within-island phylogeographical patterns are seen in the Societies? (5) How old is the Societies biota? Finally, we compare these findings to those from other Pacific hotspot archipelagos, particularly Hawaii.

### GEOLOGY AND BIODIVERSITY OF THE SOCIETY ISLANDS

The Society Islands, politically part of French Polynesia, are located in the central south Pacific at roughly 16–18° S, 149–152° W (Fig. 1a,b). They are likely formed by the activity of a stationary hotspot under the Pacific Plate, leading to a SW–NE gradient in island age from the youngest high island, Mehetia (0.0–0.3 Ma, 2.3 km²; Diraison et al., 1991) to the oldest high island, Maupiti (4.2–4.5 Ma, 8 km²; Blais et al., 2002; Guillou et al., 2005; Uto et al., 2007; Table 1; Fig. 2). Collectively, the western set of islands (Maupiti, Bora Bora, Tahaa, Raiatea, Huahine, Tupai, Maupihia, Motu One and Manuae) are classified as the Leeward Islands (Raromata‘i in Tahitian or Îles-sous-le-Vent in French), and the eastern set (Moorea, Tahiti, Maiao, Tetiaroa, Mehetia) as the Windward Islands (Ni‘amata‘i in Tahitian or Îles-du-Vent in French). This age progression and the division of the archipelago into two ‘subarchipelagos’ suggest two hypotheses for between-island patterns in the diversification of the Societies biota (Fig. 3). In the first (Fig. 3a), branching order may follow the age progression of the islands in a progression rule, and in the second (Fig. 3b), Leeward and Windward taxa may form separate clades.

The largest island, Tahiti, is made up of three volcanoes (Tahiti Nui, Taravao and Taira’apu/Tahiti Iti). The subaerial portions of Tahaa, Raiatea, Huahine, Moorea and Tahiti Nui are thought to have been formed in a three-stage process, with an initial period of volcanism, followed by caldera collapse, followed by additional lava flows (Diraison et al., 1991). In the case of Tahiti Nui, the volcanic activity is thought to have been continuous from 1.3 Ma to at least 0.5 Ma, punctuated by two caldera collapses (one each on the north and south sides of the volcano) between 0.87 and 0.85 Ma, resulting in subaerial and submarine landslides (Hildenbrand et al., 2004, 2006); erosion and the formation of deep valleys has taken place over 0.5 Ma to the present (Hildenbrand et al., 2008). These processes could potentially drive within-island diversification, particularly within Tahiti.

The high islands of the Society Islands therefore overlap in age (0–4.6 Ma) with many other midplate, linear volcanic archipelagos and islands on the Pacific Plate (Fig. 1a; Clouard & Bonneville, 2005). However, they are younger

<table>
<thead>
<tr>
<th>Island</th>
<th>Sub-archipelago</th>
<th>Age (Ma)</th>
<th>Area (km²)</th>
<th>Maximum elevation (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maupiti</td>
<td>Leeward</td>
<td>4.2–4.6</td>
<td>8</td>
<td>380</td>
</tr>
<tr>
<td>Bora Bora</td>
<td>Leeward</td>
<td>3.1–3.5</td>
<td>29</td>
<td>727</td>
</tr>
<tr>
<td>Tahaa</td>
<td>Leeward</td>
<td>2.6–3.3</td>
<td>90</td>
<td>590</td>
</tr>
<tr>
<td>Raiatea</td>
<td>Leeward</td>
<td>2.4–2.8</td>
<td>168</td>
<td>1017</td>
</tr>
<tr>
<td>Huahine</td>
<td>Leeward</td>
<td>2.1–2.7</td>
<td>75</td>
<td>669</td>
</tr>
<tr>
<td>Maiao</td>
<td>Windward</td>
<td>1.7–1.9</td>
<td>8.8</td>
<td>154</td>
</tr>
<tr>
<td>Moorea</td>
<td>Windward</td>
<td>1.3–1.8</td>
<td>134</td>
<td>1207</td>
</tr>
<tr>
<td>Tahiti</td>
<td>Windward</td>
<td>0.3–1.3</td>
<td>1045</td>
<td>2241</td>
</tr>
<tr>
<td>Mehetia</td>
<td>Windward</td>
<td>0.0–0.3</td>
<td>2.3</td>
<td>435</td>
</tr>
</tbody>
</table>
than the Austral and Northwest Hawaiian islands (Clouard & Bonneville, 2005). Unsampled seamounts to the west of the Societies, if part of the same alignment, would date to 7–8 Ma, but whether or not they were ever subaerial is unclear (Duncan & McDougall, 1976; Clouard & Bonneville, 2005); this is in contrast to the long history of subaerial islands in the Hawaiian archipelago (Price & Clague, 2002). As a result, it is unclear whether the Societies could have been colonized by any terrestrial organisms prior to the emergence of Maupiti 4.6 Ma. The closest archipelagos at the present time to the Societies are the Tuamotus (≥220 km), the Australs (≥550 km) and the southern Cooks (≥680 km).

The Societies vary greatly in maximum elevation and consequently in habitat diversity (Fig. 4). The largest and second-youngest island, Tahiti, is nearly twice as high (2241 m) as the next highest islands (Moorea, 1207 m; Raiatea, 1017 m); it has a far greater area of montane cloud forest than any other island (Meyer, 2010). Greater areas of high-elevation habitat presumably existed on Tahiti and older islands in the geological past but have since eroded away (Hildenbrand et al., 2004). Similarly to other Pacific archipelagos, the south-eastern side of all islands is the wetter, windward side and the north-west side is the drier, leeward side. Before human colonization, all these islands were covered by wet or mesic tropical forest, or cloud forest at higher elevations (Meyer, 2004). Low elevations on all these islands have been greatly transformed by human impacts beginning with Polynesian colonization ≥1000 BP and accelerating with Western colonialism and the introduction of invasive plants and livestock (Meyer, 2004; Kahn et al., 2015a,b). Consequently, the lowest high islands (Maupiti: 380 m; Maiao: 154 m; Mehetia: 435 m) retain almost no original vegetation (Meyer, 1999, 2007; Meyer et al., 2009).

Like that of many other Pacific archipelagos, the native terrestrial biota consists entirely of taxa whose ancestors were able to colonize by over-water dispersal (Fig. 5). Bryophytes and ferns are diverse and major components of the flora; angiosperms show high levels of endemism with some notable endemic radiations; native conifers are absent (Florence, 1997). Terrestrial arthropods are mostly small-bodied, with notable exceptions (cicada, dragonflies; Nishida, 2008). Smaller bodied insects usually show high levels of endemism, with some spectacular endemic radiations (Craig & Curie, 1999; Claridge, 2006; Liebherr, 2013) but also evidence for human-induced extinction (Kahn et al., 2015b). Where introduced predators are rare, several species of land crabs are common at low elevations. Freshwater fishes and decapod crustaceans are restricted to species which are either catadromous or are descended from catadromous ancestors (Keith et al., 2002). Terrestrial gastropods are highly diverse with some major endemic radiations, but have suffered extensive human-induced extinction (Lee et al., 2014). Native terrestrial vertebrates are restricted to birds, and among these, human-induced extinction has been extensive (Steadman & Pahalvan, 1992; Steadman, 2006). Of the terrestrial birds which remain extant, many appear to have been historically endemic to the Societies, but evidence for endemic radiations is limited (Steadman, 2006). Although most authors consider all species of terrestrial reptiles to be introduced (Steadman, 2006), one species of gecko may be native (but not endemic; Fisher, 1997). Many native species of ferns, angiosperms (particularly strand plants), terrestrial crabs and seabirds are widely distributed in the tropical Pacific.

**BIOGEOGRAPHICAL AFFINITIES OF SOCIETIES TAXA**

We compiled phylogenetic studies that include Society Islands taxa (see Appendix S1 in Supporting Information, Fig. 5; including Wright et al., 2001; Gemmill et al., 2002; Howarth et al., 2003; Tronchet et al., 2005; Swenson et al.,

---

*Fig. 2 Cartoon representing the chronological sequence of the Society Islands. Y-axis indicates maximum elevation at the present-day, and x-axis indicates intervals of active volcanism for each island. Sizes and spacing of islands not to scale; atolls (Tupai, Tetiaroa, Maunae, Motu One, Maupihaa) omitted.*
Sister relationships of Society Island taxa are varied, but current data indicate that they are entirely restricted to other archipelagos within the Pacific, Australia and New Zealand (Fig. 6a). Out of 44 Societies clades examined, a majority of both plant (14/23) and animal (17/21) lineages show sister-group relationships with taxa on oceanic archipelagos in the Pacific (south-eastern Polynesia, Samoa or Hawaii; Fig. 6c,d). Just under half of plant lineages (11/23) but a large majority of animal lineages (15/21) show sister-group relationships with taxa in other archipelagos within south-eastern Polynesia (the southern Cook, Austral, Tuamotu, Marquesas, Gambier or Pitcairn Islands). The unevenness of sampling across Pacific archipelagos in these studies suggests that relationships within south-eastern Polynesia are likely underestimated for plants (e.g. in *Psychotria*). The largest number of taxa show sister-group affinities to the Cook Islands (13 taxa), the Austral Islands (12 taxa) or the Marquesas Islands (9 taxa). When only studies are considered in which taxon sampling both inside and outside the Societies is considered ‘extensive’ or ‘comprehensive’ (13 studies total), the greatest number of lineages show affinities with the Cooks (7 taxa), Marquesas (4 taxa) and Australs (3 taxa), although these examples are dominated by angiosperms and birds (Fig. 6b).

Nine plant lineages show sister relationships with western Polynesian archipelagos (Samoa, Futuna, Tonga or Fiji), whereas no Societies animal clades have western Polynesian taxa as their closest relatives outside the archipelago. Three plant taxa are found to be nested within (*Astelia, Fuchsia*) or sister to (*Melicep*) New Zealand clades (Berry et al., 2004; Harbaugh et al., 2009; Birch & Keeley, 2013), although no animals show relationships with New Zealand taxa. In contrast, two animal lineages (*Bembidion* beetles and *Coridromius* bugs) show sister relationships with Australian taxa (Liebherr & Maddison, 2013; Tatarinc & Cassis, 2013), whereas no plant lineages do. One bird species (the critically endangered Tahiti Monarch *Pomarea nigra*) is apparently most closely related to species from Micronesia (Andersen et al., 2015a).

These studies also reveal a number of cases in which Societies taxa are not sister to congeners on other high islands in south-eastern Polynesia, indicating that different archipelagos in this region were likely colonized independently. In plants, particularly good examples of this are *Astelia* (Birch & Keeley, 2013), *Psychotria* (Barbá & et al., 2014), *Coprosma* (Cantley et al., 2014) and *Melicep* (Harbaugh et al., 2009). In animals, *Psilinopus* fruit doves are perhaps the best-supported example (Cibois et al., 2014); *Tetragnatha* spiders (Casquet et al., 2015) and *Pomarea* monarchs (Andersen et al., 2015a) are other likely examples. As has been previously argued (Gillespie, 2002; Garb & Gillespie, 2006), these examples suggest that independent colonizations of adjacent archipelagos are common in Pacific biogeography.

Finally, Tahiti has a number of ‘unique’ lineages whose closest relatives are distant from the Societies. These include
the small trees *Fuchsia* (of New Zealand origin; Berry et al., 2004) and *Polyscias* (sister to a clade of apparently Melanesian taxa; Eibel et al., 2001); the tree snail *Succinea pudorina* (apparently of Hawaiian origin; Holland & Cowie, 2009), and the beetle *Bembidion* (sister to Australian taxa; Maddison & Liebherr, 2013). The small herb *Peperomia fosbergii* (possibly related to Hawaiian congeners) may be an additional example (Bradley, 2003). Whether these lineages directly colonized Tahiti from elsewhere and were never present on other adjacent islands, or have since been extirpated on these other islands, is unclear.

All these results suggest that the Societies biota shows the most phylogenetic affinities with the geographically nearest island groups within south-eastern Polynesia (Cooks, Australs and Tuamotus) as well as the largest (by land area) oceanic island groups on the Pacific Plate (Marquesas, Hawaii and Samoa), as would be predicted by island biogeography theory (MacArthur & Wilson, 1967). Generally, nearly all of these Societies taxa are ultimately of Asian/Australasian origin, in contrast with the pattern in Hawaii, where many lineages are of New World origin (Cowie & Holland, 2008; Baldwin & Wagner, 2010; but see Garb & Gillespie, 2006).

**POLYPHYLY OF SOCIETIES TAXA (MULTIPLE COLONIZATIONS OR SOCIETIES AS A SOURCE AREA)**

More genera (at least thirteen) show evidence of polyphyly or paraphyly in the Society Islands than strongly supported monophyly (four; Table 2). Some of polyphyletic/paraphyletic groups are best interpreted as repeated independent colonizations of the Societies from elsewhere: these include the forest herbs *Peperomia* (Piperaceae; Bradley, 2003), the understorey shrubs *Cyrtandra* (Gesneriaceae; Clark et al., 2009), *Psychotria* (Rubiaceae; Barrabé et al., 2012, 2014) and *Melicope* (Rutaceae; Meyer et al., 2012), succineid snails (Holland & Cowie, 2009), *Tetragnatha* spiders (Gillespie, 2002; Gillespie et al., 2008; Casquet et al., 2015), *Epicephala* moths (leafflower moths; Hembry et al., 2013a) and kingfishers (the Chattering Kingfisher *Todiramphus tutus* and the Society Kingfisher *T. veneratus*; Andersen et al., 2015b). *Peperomia, Cyrtandra, Melicope, Epicephala, Tetragnatha* and Succineidae all show evidence of the repeated colonization of the same island (Table 2). Other groups are more likely to represent radiations within the Societies that then colonized other archipelagos; the strongest example of this are *Partula* snails, in which the single endemic species from Rarotonga (Cook Islands) is nested within the species-rich Societies radiation (Lee et al., 2014). Given that the Societies are larger in total land area than any of their adjacent archipelagos, and that they are older than some surrounding islands (e.g. Rarotonga and re-uplifted islands such as Rurutu, Rimatara and some of the north-western Tuamotus and southern Cooks), their role as a source of propagules for adjacent archipelagos is to be expected. Other examples of polyphyletic groups are more ambiguous with respect to the history of colonization of the Societies.

**Figure 4** Vegetation and landscapes of the Society Islands. (a) Maupiti (4.2–4.6 Ma, 380 m elev., 8 km²) is the oldest high island in the archipelago. (b) Mt. Ohiri (590 m elev.), the highest mountain on Tahaa (2.6–3.3 Ma) (c) Montane scrub dominated by *Gahnia* (Poaceae) and *Pandanus* (Pandanaceae) on Te Mehani Rahi Plateau, Raiatea (2.4–2.8 Ma) (d) View of the highly dissected interior of Tahiti Nui (0.3–1.25 Ma), Tahiti from the summit of Mt. Aorai (2066 m elev.) (e) Cloud forest dominated by Weinmannia (Canoniaceae) and *Cyathoe* (Cyatheaceae) on Mt. Marau, Tahiti Nui, Tahiti. (f) Mehetia (0.03 Ma-present, 435 m elev., 2.3 km²) is the youngest subaerial and only geologically active, island in the Societies.
In contrast, only a few plant and animal taxa examined show strongly supported monophyly within the Societies. These are the sandalwood *Santalum insulare* (Santalaceae; Butaud et al., 2005; Harbaugh & Baldwin, 2007), the forest herbs *Opiohiriza* (Rubiaceae; Nakamura et al., unpublished data), *Misumenops* crab spiders (Garb & Gillespie, 2009) and *Coridromius* plant bugs (Tatarnic & Cassis, 2013). Additional taxon sampling outside the Societies might render either *Opiohiriza* or *Coridromius* polyphyletic. Except for *Opiohiriza*, none of these taxa are particularly diverse in the Societies, suggesting that most of the larger endemic ‘radiations’ in the Society Islands may be polyphyletic.

**BETWEEN-ISLAND PHYLOGEOGRAPHICAL BARRIERS IN THE SOCIETIES**

By far, the most common phylogeographical division seen in Societies taxa is between the Windward and Leeward Society Islands (Fig. 3b). This represents the largest interisland distance in the Societies (150 km between Huahine and...
Moorea), and consequently an important role for allopatry in the diversification of the Societies biota. This pattern is seen in a number of animal taxa, including Misumenops crab spiders (Garb & Gillespie, 2006, 2009), the two older Epicephala lineages (Hembry et al., 2013a), Pseudoloxops plant bugs (Balukjian, 2013), Rhyncogonus weevils (Claridge, 2006),

Figure 6 Maps representing the distributions of closely related taxa to Societies-endemic lineages. Lines between the Societies and other archipelagos/regions are not meant to imply directionality. Line segment thicknesses and colours correspond to numbers of taxa showing particular sister-group relationships. A Societies taxon may be closely related to taxa in multiple other regions in cases where phylogenetic reconstructions are ambiguous (e.g. polytomies). Regions to which lines point are as follows: Cook Islands, Marquesas Islands, Tuamotu Islands, Austral Islands, Gambier Islands, Pitcairn Islands, Hawaii, Samoa, Tonga, Fiji, Wallis and Futuna, Caroline Islands (Micronesia), New Caledonia, Australia and New Zealand. (a) All taxa. (b) Studies in which sampling of extant taxa inside and outside the Societies is either ‘extensive’ or ‘comprehensive’. (c) Angiosperms only. (d) Animals only.

Table 2 Taxa showing evidence for monophyly or polyphyly/paraphyly of particular genera in the Society Islands.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Pattern</th>
<th>Co-occurrence on same island</th>
<th>Sampling within Societies</th>
<th>Sampling outside Societies</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peperomia (Piperaceae)</td>
<td>Polyphyly</td>
<td>Yes (Tahiti)</td>
<td>Comprehensive</td>
<td>Partial</td>
</tr>
<tr>
<td>Cyrtandra (Gesneriaceae)</td>
<td>Polyphyly</td>
<td>Yes (Huahine)</td>
<td>Limited</td>
<td>Partial</td>
</tr>
<tr>
<td>Psychotria (Rubiaceae)</td>
<td>Polyphyly</td>
<td>Unknown</td>
<td>Limited</td>
<td>Partial</td>
</tr>
<tr>
<td>Ixora (Rubiaceae)</td>
<td>Paraphyly</td>
<td>N/A</td>
<td>Partial</td>
<td>Partial</td>
</tr>
<tr>
<td>Melicope (Rutaceae)</td>
<td>Polyphyly</td>
<td>Yes (Tahiti)</td>
<td>Extensive</td>
<td>Partial</td>
</tr>
<tr>
<td>Succineidae</td>
<td>Polyphyly</td>
<td>Yes (Tahiti)</td>
<td>Unclear</td>
<td>Extensive</td>
</tr>
<tr>
<td>Partula (Partulidae)</td>
<td>Paraphyly</td>
<td>N/A</td>
<td>Extensive</td>
<td>Extensive</td>
</tr>
<tr>
<td>Tetragnathidae (Tetragnathidae)</td>
<td>Polyphyly</td>
<td>Yes (Tahiti, Moorea)</td>
<td>Extensive</td>
<td>Partial</td>
</tr>
<tr>
<td>Epicephala (Gracillariidae)</td>
<td>Polyphyly</td>
<td>Yes (Tahiti, Moorea, Huahine, Raiatea)</td>
<td>Comprehensive</td>
<td>Partial</td>
</tr>
<tr>
<td>Rhyncogonus (Curculionidae)</td>
<td>Paraphyly</td>
<td>N/A</td>
<td>Comprehensive</td>
<td>Comprehensive</td>
</tr>
<tr>
<td>Acrocephalus (Acrocephalidae)</td>
<td>Paraphyly</td>
<td>N/A</td>
<td>Comprehensive</td>
<td>Comprehensive</td>
</tr>
<tr>
<td>Todiramphus (Alcedinidae)</td>
<td>Polyphyly</td>
<td>No</td>
<td>Extensive</td>
<td>Comprehensive</td>
</tr>
<tr>
<td>Ptilinopus purpureus (Columbidae)</td>
<td>Paraphyly</td>
<td>N/A</td>
<td>Extensive</td>
<td>Comprehensive</td>
</tr>
<tr>
<td>Santalum insulare (Santalaceae)</td>
<td>Monophyly</td>
<td>N/A</td>
<td>Comprehensive</td>
<td>Partial</td>
</tr>
<tr>
<td>Ophiurhiza (Rubiaceae)</td>
<td>Monophyly</td>
<td>N/A</td>
<td>Comprehensive</td>
<td>Unclear</td>
</tr>
<tr>
<td>Misumenops (Thomisidae)</td>
<td>Monophyly</td>
<td>N/A</td>
<td>Comprehensive</td>
<td>Unclear</td>
</tr>
<tr>
<td>Coridromius (Miridae)</td>
<td>Monophyly</td>
<td>N/A</td>
<td>Unclear</td>
<td>Unclear</td>
</tr>
</tbody>
</table>
Todiramphus kingfishers (Andersen et al., 2015b), the sandalwood Santalum insulare (Butaud et al., 2005) and probably also the Grey-green Fruit Dove Ptilinopus purpuratus (Cibois et al., 2014). Acrocephalus reed warblers may also be consistent with this pattern as well (Cibois et al., 2008, 2011). There are, however, exceptions: Huahine Partula are sister to the rest of the radiation (Lee et al., 2014).

A few animal taxa (Tetragnathidae, Pseudoloxops, Acrocephalus, perhaps Ptilinopus purpuratus) show evidence for distinct clades or sister-species on Tahiti and Moorea (Cibois et al., 2008, 2011, 2014; Gillespie et al., 2008; Balukjian, 2013), although other animals do not show this divergence (Misumenops: Garb & Gillespie, 2009; Epicephala: Hembry et al., manuscript; Todiramphus veneratus: Andersen et al., 2015b). Partula have multiple clades endemic to Tahiti and Moorea respectively, as well as clades containing taxa from both islands (Lee et al., 2014), and one sister-species relationship between a Tahiti-endemic and a Moorea-endemic species is known in Simulium (Joy & Conn, 2001). Although molecular phylogenetic data are not available, multiple pairs of presumed sister-species (based on morphology) in Mecyclothorax ground beetles distributed on the western part of Tahiti Nui and Mt. Tohiea on Moorea suggest a role for repeated independent dispersal and between-island speciation in this large insect radiation (Liebherr, 2012).

The only groups which show evidence for inter-island divergences or single-island endemic clades within the Leeward Islands are Partula, Pseudoloxops and Rhyncogonus, all of which are highly species-rich in the archipelago (Claridge, 2006; Balukjian, 2013; Lee et al., 2014). Finally, many plant taxa examined (Glomisidion, Ixora, Melicope tahitensis lucida) show no phylogeographical structure within the archipelago (Mouly et al., 2009; Meyer et al., 2012; Hembry et al., 2013a), although this is in part likely due to the markers used (but see Wikstroemia; Meyer et al., 2012). The only group that shows a pattern consistent with any form of a ‘progression rule’ (Fig. 3a) is one clade of Rhyncogonus, which may have initially diversified on Raiatea before colonizing the older islands Tahaa and Bora Bora, as well as the younger islands Huahine, Moorea and Tahiti.

The fact that by far the most widely seen phylogeographical barrier is the one between the Windwards and Leewards suggests two possible historical biogeographical explanations, which are not mutually exclusive. First, the interisland distances within the Windwards and within the Leewards (at present, 5–52 km) might not be great enough to restrict gene flow in many of these taxa. With the exception of Raiatea and Tahaa, these islands were not connected during recent glacial maxima. The other possibility is that colonization of the Societies by some of these lineages has been so recent that only the greatest inter-island separation has been effective as a barrier driving phylogeographical differentiation. Although these hypotheses are difficult to distinguish given available data, the former suggests that the diversification of the Societies biota operates differently than in other well-studied oceanic archipelagos, in which single-island-endemic lineages are more widely reported. The second would imply that a substantial part of the Societies biota is much younger than the archipelago itself (see data below). Finally, many groups that are likely to show phylogeographical structure have yet to be examined at all using molecular methods (see Future Directions).

**WITHIN-ISLAND PHYLOGEOGRAPHICAL BARRIERS**

Several invertebrate radiations in the Society Islands show evidence for diversification within islands. Limited gene and taxon sampling suggests possible divergences between the two major volcanoes of Tahiti (Tahiti Nui and Taïarapu) in succineid snails (Holland & Cowie, 2009), the snail Samoana burchi (Lee et al., 2009) and the spider Tetragnathidae rava (Gillespie et al., 2008). The radiations of Partula snails, Pseudoloxops plant bugs, Rhyncogonus weevils and Simulium blackflies show evidence for both within-island speciation (as well as between-island speciation: above). Partula contains a number of mitochondrial clades containing multiple species all endemic to the same island (seen on Raiatea, Huahine, Moorea and Tahiti), suggesting within-island diversification in both the Leewards and Windwards (Lee et al., 2008, 2014). Sister-species relationships in Pseudoloxops plant bugs show evidence of diversification within islands in six cases compared to between islands in two cases. The former include potential cases of diversification within Tahiti, even potentially within single massifs (e.g. Aorai; Balukjian, 2013). Rhyncogonus weevils show diversification within Tahiti, with speciation driven by isolation on different mountains/massifs evidenced by two allopatrically distributed species pairs (Claridge, 2006). Both these pairs consist of allopatrically distributed sister-species, one endemic to the western Tahitian massif comprised of the mountains Marau, Aorai, Pito Hiti and Pihiateta, and one endemic to the eastern Tahitian massif of Mt. Mauru (at eastern and western ends of the remnants of the main shield of Tahiti Nui; Hildenbrand et al., 2004). Phylogenetic patterns are consistent with speciation within Raiatea and within Bora Bora in Rhyncogonus as well. Diversification within Tahiti is also likely in Simulium blackflies – most of the 25 species in this endemic radiation are endemic to Tahiti, and several sister-species pairs within Tahiti are seen the phylogeny (Joy & Conn, 2001; Joy et al., 2007). Finally, many pairs of presumed sister-species based on morphology in the spectacular radiation of Mecyclothorax ground beetles (101 spp. on Tahiti, 7 spp. on Moorea) are reported from different massifs or peaks within Tahiti Nui (Liebherr, 2013). Localized distributions of some Nabis damselflies (Heteroptera: Nabidae) species endemic to Tahiti suggest the possibility of within-island speciation in this well-studied endemic radiation (Polhemus, 2010).

These studies above suggest that isolation on the two main volcanoes of Tahiti (Tahiti Nui and Taïarapu) may promote population divergence (and perhaps incipient speciation) in some snails and spiders. There is also good
evidence that the erosion of the main shield of Tahiti Nui drove speciation in some of the archipelago’s most diverse insect radiations (*Rhyncogonus*, *Simulium* and *Mecyclothorax*) – primarily through the isolation of populations on different peaks and massifs. Most importantly, these results show that the largest islands in the archipelago (particularly Tahiti and Raiatea, but also Huahine, Moorea and possibly Bora Bora) are or have been large enough in the recent geological past to permit within-island speciation and radiation in small-bodied invertebrates.

**HOW OLD IS THE SOCIETIES BIOTA?**

Limited evidence for phylogeographical divergence among adjacent islands within the Windward and Leeward Society Islands, and abundant evidence for repeated colonizations by closely related lineages, suggest that much of the extant Societies biota may in fact be much younger than the archipelago itself. A corollary of this hypothesis is that over evolutionary time-scales, turnover among lineages on the Society Islands may be high (although in some cases, these lineages may be extremely closely related). Do estimated divergence times of Societies clades support this hypothesis?

Many phylogeographic studies of Societies taxa have incorporated divergence time estimates (see Appendix S2). Excluding groups whose estimates are calibrated using geological ages of the Societies themselves (internal calibrations) or for which taxon sampling within the Societies is extremely limited, the crown ages of nearly all (8 out of 10) Societies endemic clades have been dated to $\leq$ 2 Ma (corresponding to younger than the Leeward Islands but older than the Windwards; Fig. 7). These include all of the bird radiations that have been dated, two plant taxa (*Sclerotheca* and *Santalum*; Givnish *et al.*, 2009) and one snail clade (*Samoana*). Divergence time estimates for the split of Societies taxa from their nearest known relatives elsewhere (stem ages) show more spread, although most of those are less than 6 Ma in age (Fig. 7). None of these studies incorporate species-tree-based divergence time estimation. The primary sources of error in these studies are likely due to missing extant taxa (which is particularly likely to affect stem-age estimates, and estimates in arthropods), and the use of published rates rather than calibrations and reliance on mitochondrial data. See main text for details.
phylogenetic analysis reveals that and Tuamotu P. parvirostris (extant member of this genus, the Tuamotu Sandpiper sandpiper genus colonization of now awash Societies volcanoes from a place where they may represent multiple colonizations of the Societies. Divergence between the extinct Tahitian endemic P. leucoptera and Tuamotu P. parvirostris dates to only 1.7 Ma. However, phylogenetic analysis reveals that Prosobonia shares a most recent common ancestor with its closest living relatives (other sandpipers and turnstones) 20–35 Ma. The ancestors of this lineage probably colonized the remote Pacific during the Oligocene, long before the formation of any of the extant high islands.

FUTURE DIRECTIONS

Although in recent years, an increasing number of investigators have focused on the Society Islands and a number of emergent patterns are seen across Societies taxa, much remains unclear both about the biodiversity of this archipelago and its patterns of molecular biogeography. Here we suggest major gaps in our knowledge and promising phenomena for future research:

1. Many of the most diverse groups in the Society Islands have not been studied using molecular phylogenetic or even taxonomic approaches, which constrains our ability to draw conclusions about patterns like within- and between-island speciation, biogeographical barriers and progression rules. Candidate groups for future taxonomic and phylogenetic work include (in plants) Myrsine (Myrsinaceae), Bideus (Asteraceae), Ixora (Rubiaceae), Psychotria (Rubiaceae), Cyrtandra (Gesneriaceae), (in animals) Campsicnemis (Diptera: Dolichopodidae), Mecyclothorax (Coleoptera: Carabidae), Campylopoeus (Coleoptera: Curculionidae), Atylana (Hemiptera: Nogodinidae), Nabis (Hemiptera: Nabidae), Campyllomma (Hemiptera: Miridae), Oliarius (Hemiptera: Cixiidae) and Lallemandana (Hemiptera: Cercopidae). Some major insect radiations are likely unrecognized; based on their diversity elsewhere (e.g. Rapa), Miocalles (Coleoptera: Curculionidae) and Dichelopa (Lepidoptera: Tortricidae) are likely to yield interesting patterns (Clarke, 1971; Paulay, 1985).

2. Similarly, the biodiversity of some important places in the Societies has not been sampled, constraining our ability to test certain hypotheses. Many of these locations are logistically difficult to access and in some cases have never been visited by scientists, requiring the use of helicopters or dedicated teams with extensive experience under mountain conditions. Candidate locations include the highest summits of the Leeward Islands (particularly Otemanu on Bora Bora, which has never been visited by scientists, and Ohiri on Tahaa and Toomaru on Raiatea, which have only recently been visited a few times; J.-Y. Meyer, pers. comm., 2014), and unclimbed summits on Tahiti (e.g. Tevaitoi on Tahiti Nui and Ronui on Taitaarau; J.-Y. Meyer and R. Taputuarai, pers. comm., 2014).

3. Molecular dating and phylogeographical patterns suggest that a large component of the Societies biota might be young relative to the age of the existing high islands (4.6 Ma). The Societies may thus be frequently colonized, but have very high turnover. This hypothesis can be tested with additional molecular dating studies and modelling approaches.

4. Many studies suggest that the Societies may function as a ‘stepping stone’ or ‘source area’ for the biota of different archipelagos within south-eastern Polynesia (and beyond). Further studies with widespread sampling from diverse groups may reveal an important role for this archipelago in eastern Pacific biogeography, particularly islands younger than 4.6 Ma in neighbouring archipelagos, such as Rarotonga and the uplifted northern Austral, southern Cooks and western Tuamotus.

5. The Societies offer opportunities to study interactions between different colonizations of the archipelago by closely related lineages (e.g. multiple colonizations by Cyrtandra, Epicephala; possibly also Peperomia, Tetragnatha).

6. Within-island patterns have received relatively little attention in the Societies, but have been found to be very interesting in other archipelagos.

CONCLUSIONS

The molecular evolution and diversification of the biota of the Society Islands shows a number of general patterns across taxa within the archipelago. Many Society Islands taxa show sister relationships with other archipelagos in south-eastern Polynesia (particularly the Cook, Austral and Marquesas Islands) or other tropical Pacific islands. Many plants show affinities with western Polynesia, Fiji and New Zealand, while few animals do. Most genera are polyphyletic within the Societies, representing either multiple independent colonizations of the archipelago or dispersal from the Societies to other archipelagos. The straits between the Leeward and Windward Islands are an important biogeographical barrier in many animal groups examined. Very few taxa examined show strong evidence for phylogeographical differentiation among islands within the Leeward or Windward groups; the few exceptions are the most species-rich invertebrate radiations, which have diversified both among and within islands. Finally, there is no strong evidence for a progression rule in the diversification of Societies radiations; only one taxon may be consistent with it.

Two major caveats apply to these conclusions. Many studies which include Societies taxa sample a small fraction of the diversity within the archipelago, and only a few studies (focused on low-diversity bird and plant groups) sample...
extant diversity comprehensively throughout the Pacific. Additionally, these studies do not account for human-mediated extinction, either following Polynesian colonization or European colonialism. In some cases, the extent of diversity loss remains unclear: a few sediment cores near sea level have revealed previously unknown native insect diversity on Moorea (Kahn et al., 2015b), and only one site (on Huahine) is known for sub-fossil birds in the whole archipelago (Steadm an & Pahlavan, 1992). Better sampling of extant taxa should, at least, further refine these preliminary conclusions, particularly for plants.

Interestingly, the common patterns seen in Societies phylogeography are largely different from those that would be predicted from past phylogeographical work in Hawaii (Wagner & Funk, 1995; Roderick & Gillespie, 1998; Cowie & Holland, 2008; Baldwin & Wagner, 2010). Many endemic radiations in Hawaii are monophyletic, resulting from single colonizations. Hawaii is also generally not argued to be an important source area for other islands or biogeographical regions (although exceptions to this pattern have been recently argued: Harbaugh & Baldwin, 2007; O’Grady & DeSalle, 2008; Harbaugh et al., 2009). Hawaii does not show a single, widespread phylogeographical barrier between two subsets of islands in the same manner as the Leeward/Windward barrier seen in the Societies; instead, it more often shows a weak form of the progression rule in which early-diverging (‘basal’) lineages are found on older islands. Adaptive radiation, and diversification within- and between islands, is more pronounced in the biota of Hawaii (and of other archipelagos such as the Galápagos). Many of these differences may be ascribed to the smaller size, lower elevation, ephemerality and reduced isolation of the islands in the Societies both to each other and to other oceanic archipelagos (Keast, 1996; Hembry et al., 2013b).

There are two major implications of these patterns. First, the evolution of the biota of the Society Islands differs from that not just of Hawaii and several phylogeographical studies from other archipelagos, but from the basic observations underlying the general dynamic (Whittaker et al., 2008) and overshoot (Gillespie & Baldwin, 2009) models for the evolution of oceanic island biotas. These patterns suggest that the Societies may instead be an archipelago which is frequently colonized from the outside, and has high turnover of clades arising from these colonizing lineages. In some ways, the Societies more resemble elements of the taxon cycle and supertramp hypotheses articulated by Wilson (1961) and Diamond (1974) for islands further west in the Pacific. Even if some of the un-investigated, species-rich radiations in the Societies prove to have diversified in parallel with the formation of the archipelago, such a finding would not change the overall pattern reported here. Our conclusions do not mean that the general dynamic or overshoot models are wrong or not useful for the archipelagos on which they are based, but simply that they may be of limited applicability for the Society Islands.

Second, these findings also have important implications for other hotspot archipelagos in the Pacific whose biogeography is less well-known. In terms of size, spatial arrangement and topographic complexity the Societies are more similar to many other archipelagos – particularly the Marquesas, Cook-Austral and Samoan islands – than to Hawaii. Conversely, in terms of their location in close proximity to the southern Cook, northern Austral and Tuamotu archipelagos, the Societies are much less isolated than are the Marquesas and Hawaiian islands, or Rapa. Future research will reveal whether the diversification and assembly of the biotas of other Pacific hotspot archipelagos are more similar to the Societies or Hawaiian models.

ACKNOWLEDGEMENTS

We thank Bruce Baldwin, Michael Balke, David Clague, Jean-Yves Meyer, Dan Polhemus, Erica Newman and Nik Tatarnic for discussion, Erica Spotswood and Laura Stevenson for the bird photos, Erica Newman, Jimmy O’Donnell and Morgan Tingley for assistance with figures, Bruce Baldwin, Elin Claridge, Darko Cotoras, Rosemary Gillespie, Kari Goodman, Jun Ying Lim, Jean-Yves Meyer and three anonymous referees for comments on an earlier version of this manuscript, and many other people for their assistance and friendship in the field while these ideas were originally being formulated. DHH was supported by NSF grant OISE-1159509 and also thanks Chicken and Mo’o for their companionship at Gump Station. This is contribution number 215 of the University of California, Berkeley’s Gump South Pacific Research Station.

REFERENCES


**SUPPORTING INFORMATION**

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

**Appendix S1** Distributions of sister groups to Society Island lineages.

**Appendix S2** Estimated divergence times for the crown ages of Societies-endemic clades and their divergences from sister groups outside of the Societies.

**BIOSKETCHES**

David Hembry is a postdoctoral researcher at the University of Arizona interested in the evolution of interactions, particularly those between leafflower moths (*Epicephala*) and leafflower plants (*Phyllanthus* s. l.) in the Society Islands and elsewhere in the world.

Brad Balukjian is adjunct faculty at Laney College in Oakland, California and is interested in island biogeography and the taxonomy of understudied Hemiptera (which means all Hemiptera).

Editor: Lawrence Heaney