# Dispersal and diversification: macroevolutionary implications of the MacArthur–Wilson model, illustrated by *Simulium* (*Inseliellum*) Rubstov (Diptera: Simuliidae)

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## Abstract

**Aim** Provide an empirical test of the 'radiation zone' hypothesis of the MacArthur–Wilson theory of island biogeography using the taxon-pulse hypothesis of Erwin and Brooks Parsimony Analysis (BPA) on *Simulium* (*Inseliellum*) Rubstov.

**Location** Micronesia, Cook Islands, Austral Islands, Society Islands, Marquesas Islands, Fiji and New Caledonia.

**Methods** Primary and secondary BPA of the phylogeny of *Inseliellum*.

**Results** Primary BPA showed that 15% of the taxon area cladogram contained area reticulations. Secondary BPA (invoking the area duplication convention) generated a clear sequence of dispersal for *Inseliellum*. The sequence follows a Micronesia – Cook Islands – Marquesas Islands – Society Islands dispersal, with a separate dispersal from the Cook Islands to the Austral Islands less than 1 Ma. A radiation in the island of Tahiti (Society Islands) produced numerous dispersals from Tahiti to other islands within the Society Islands system. Islands close to Tahiti (source island) have been colonized from Tahiti more often than islands far from Tahiti, but a higher proportion of those species colonizing distant islands have become distinct species.

**Main conclusions** The dispersal sequence of *Inseliellum* exhibits both old to young island dispersal and young to old island dispersal. This is due to habitat availability on each island. *Inseliellum* is a model system in exemplifying the 'radiation zone' hypothesis of MacArthur and Wilson. As well, islands close to the source are colonized more often that those far from the source, but colonization of islands far away from the source results in a higher proportion of speciation events than for islands close to the source. The diversification of *Inseliellum* corresponds to a taxon-pulse radiation, with a centre of diversification on Tahiti resulting from its large area and abundant freshwater habitats. This study illustrates the utility of BPA in identifying complex scenarios that can be used to test theories about the complementary roles of ecology and phylogeny in historical biogeography.

## Keywords
*Inseliellum*, Pacific Islands, phylogenetic biogeography, Brooks parsimony analysis, MacArthur–Wilson model, taxon pulse radiations.

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## INTRODUCTION

The theory of island biogeography developed by MacArthur & Wilson (1963, 1967) has been the major hypothesis of dispersal, colonization, and evolution of insular species. For over 40 years, it has lead researchers and students to regard islands as natural experiments of evolutionary processes. The MacArthur–Wilson model predicts that the number of species (species richness) is increased by new colonization, but decreased by extinctions. When the rates of colonization and extinction are equal, equilibrium is achieved (MacArthur & Wilson, 1963, 1967). The model also predicts that species richness is affected by distance and area. Large islands are more species-rich than small islands due to lesser extinctions, and near islands are more species-rich than far islands due to greater colonizations (MacArthur & Wilson, 1963, 1967).

MacArthur & Wilson (1963) recognized that species richness on islands is not strictly due to colonization. They hypothesized that 'radiation zones' exist in island faunas – adaptive radiation increases with distance from the major source region (the source being an island within the archipelago). Within-island speciation could thus be a major contributor to species richness. Until recently, however, the bulk of research using the MacArthur–Wilson model has neglected the element of within-island speciation.

Heaney (2000) produced a series of macroevolutionary (i.e. phylogenetic) predictions derived from MacArthur & Wilson's (1963) hypothesis of 'radiation zones'. Islands close to sources of colonizers will not exhibit as much speciation as islands far from a source. This is because colonization on a far island will be a rare event, giving colonizers less chance of experiencing gene flow with parental populations, which would hinder speciation. Small islands will not exhibit as much speciation as large islands, simply because there is not as much opportunity in terms of absolute space and probably in terms of spatial heterogeneity. Thus, there is reason to believe that macroevolutionary aspects of island biogeography complement ecological aspects. That is: (1) within-island radiations should occur most often on far, large islands; (2) colonization should occur more often on near than far islands; (3) speciation should occur more often on far islands than on near islands. Heaney (2000) applied these ideas to Philippine murid rodents, and proposed that rare successful colonization of islands from the mainland had been followed by within-island diversification. Using the same assumptions as Heaney (2000), Losos & Schluter (2000) showed that intra-island speciation, rather than colonization, was the primary source of new species of *Anolis* lizards on Caribbean islands larger than 3000 km$^2$; they did not, however, investigate the historical sequence of colonization of those islands.

A leading model of evolutionary radiations resulting from colonization and within-area diversification is the 'taxon pulse' proposed by Terry Erwin (Erwin, 1979, 1981, 1985) (see also Bouchard et al., in press; Erwin & Adis, 1982; Liebherr & Hajek, 1990) is similar to that proposed by (Darlington, 1943) and named 'taxon cycle' by Wilson (1959, 1961). Both models assume that: (1) taxa and adaptations arise in a 'center of origin' (where the highest diversity for a taxon can be found) and (2) distributional ranges of taxa periodically fluctuate around a more stable, continuously occupied centre. During expansion phases of the habitat, peripheral patches are colonized. Conversely, during contractions of the habitat, these patches become isolated. Taxon cycles occur over long periods of time and are driven mostly by dispersal along a broad advancing front during expansion of suitable habitat leading to peripheral isolate speciation. This model of evolutionary radiation has not been applied rigorously to oceanic island systems. Many patterns exhibited by Hawaiian taxa appear to be consistent with interpretation of this model. However, the taxon-pulse hypothesis of Erwin was not discussed in Wagner & Funk (1995). Craig (1983) and Craig et al. (2001) suggested a taxon-pulse for *Inseliellum*, but without specifying details on the sequence of events that would characterize a taxon-pulse.

Testing the 'radiation zone' hypothesis, and the predictions made by MacArthur & Wilson (1963) and Heaney (2000), and the taxon pulse hypothesis, require the use of a method of historical biogeography capable of representing dispersal events explicitly, including those producing reticulated historical relationships among islands. Brooks parsimony analysis (BPA) (Brooks, 1981, 1990; Wiley, 1988; Brooks et al., 2001; Brooks & McLennan, 2002) is such a method. BPA has been used with success in other systems (Harlin, 1996; Ruedi, 1996; Van Soest & Hajdu, 1997; de Jong, 1998; Marshall & Liebherr, 2000; Brooks et al., 2001; Duffels & Turner, 2002; Green et al., 2002; McLennan & Brooks, 2002). In addition, if the ages of the islands and their colonization abilities are known, then correlations between the ages of clades and the diversity of clades can be made.

## METHODS

### *Inseliellum* and phylogeny

We have chosen the black fly (Diptera: Simuliidae) subgenus *Inseliellum* for our study clade. There are currently 48 described species in the subgenus *Inseliellum*. They occur on the islands of Guam (northern Mariana Islands), Chuuk (Caroline Islands), Rarotonga (Cook Islands), and the Marquesas, Society and Austral Island chains (French Polynesia) (Fig. 1) (Craig & Joy, 2000; Craig et al., 2001). Craig & Currie (1999) reconstructed a morphological phylogeny of 34 species of *Inseliellum*, which was later revised by Craig et al. (2001) with the incorporation of six new species (Fig. 2). Craig & Joy (2000) and Craig et al. (2001) presented reasons for excluding the remaining eight nominal species assigned to the subgenus. Joy & Conn (2001) reconstructed a molecular phylogeny of 27 Society Island species of *Inseliellum*, and the relationships of that subset of species were in agreement with the morphological tree.
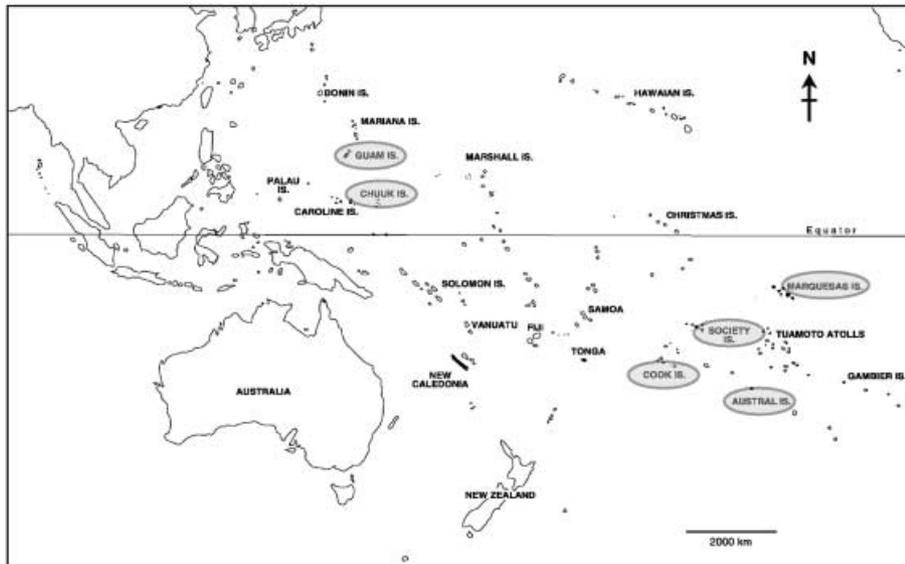
**Figure 1** Distribution of *Inseliellum* (shaded areas) in the South Pacific (adapted from Craig *et al.*, 2001).

### Island descriptions with regard to *Inseliellum*

Historical biogeographical analysis is aided by an understanding of the age, number of species of *Inseliellum* present, number of endemic species of *Inseliellum* present, and presence of suitable habitat for the islands where *Inseliellum* spp. reside. The most important habitat feature is the presence of fresh running water. An island must have permanent fresh running water to maintain a black fly fauna. A discussion on the evolution of running water habitat is given in Craig *et al.* (2001). The island data here were taken from three sources: Craig (1997), Dickinson (1998) and Craig *et al.* (2001).

#### Guam and Chuuk
Guam is the southernmost island of the Bonin and Mariana Arcs. It is *c.* 1060 km north of Chuuk. Guam is *c.* 43.8–13.5 Myr and contains one black fly species, *Simulium guamense* (Craig *et al.*, 2001). Chuuk is a member of the Caroline Islands, and is one of the larger, higher islands. The age of Chuuk ranges from 14.8 to 4.0 Myr and is now a series of small islands. One of these islands (Tol) also contains one black fly species, *S. trukense* (Craig *et al.*, 2001). These species are both endemic to their respective islands.

#### Austral Islands
The only member of the Austral Islands known to support black flies is Rurutu. The age of the island ranges from 12.8 to 0.3 Myr and contains an endemic species, *S. rurutuense* (Craig, 1997; Dickinson, 1998; Craig *et al.*, 2001).

#### Cook Islands
Rarotonga is also unique to the Cook Islands in supporting black flies. It is the youngest island in the southwest segment of its chain (2.3–1.1 Myr), and is the only island in the Cook Island chain with permanent running water. Rarotonga contains two black fly species (both endemic), *S. teruamanga*, and *S. mataverense* (Craig, 1997; Dickinson, 1998; Craig *et al.*, 2001).

#### Marquesas Islands
This chain consists of eleven islands, seven supporting a black fly fauna. The islands will be given from the northwest to the southeast. Eiao is 5.78–4.98 Myr, and contains one species, *S. sechani*. Nuku Hiva is 4.34–2.99 Myr and contains three species, *S. sechani*, *S. buissoni*, and *S. hukaense*. *Simulium buissoni* and *S. hukaense* are also present on Ua Huka, together with *S. gallinum* and *S. uaense* (which is endemic to Ua Huka). The age of Ua Huka is from 3.24 to 1.36 Myr. Ua Pou is 5.61–1.78 Myr and contains three species, *S. gallinum*, *S. hukaense* and *S. adamsoni*. Hiva Oa also has *S. gallinum*, *S. adamsoni*, and additionally, *S. rivierei*. Hiva Oa is the second-youngest island in the chain (2.55–1.66 Myr). Tahuata is 2.09–1.82 Myr and is the youngest island in the chain, and contains one species, *S. gallinum*. Fatu Hiva is the most southeastern island that supports black flies, and is 2.55–1.33 Myr. Four species are present on Fatu Hiva: *S. gallinum*, *S. adamsoni*, *S. rivierei*, and *S. pichoni* (which is endemic to Fatu Hiva) (Craig, 1997; Dickinson, 1998; Craig *et al.*, 2001).

#### Society Islands
Six islands in this chain support a black fly fauna. The islands will be given from the northwest to the southeast. Bora Bora is northwest of Tahaa, close enough to be within sight. The age of the island is 4.15–3.12 Myr, and contains one black fly species, *S. malardei*. Tahaa is only 4 km north of Raiatea, and is 3.30–2.60 Myr. Two black fly species are found on Tahaa:
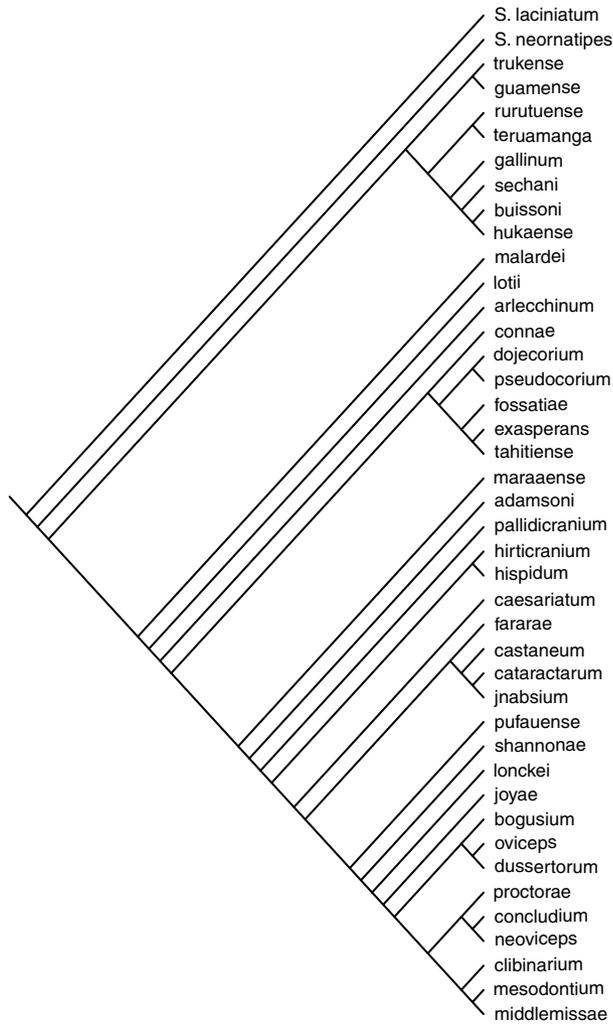
**Figure 2** Reconstructed phylogeny of *Inseliellum* redrawn from Craig *et al.* (2001).

*S. malardei*, and *S. lotii*. Raiatea is the second-largest island in the chain, and is 3.4–2.4 Myr. *Simulium malardei*, *S. lotii*, *S. oviceps* s.l., *S. castaneum*, *S. pufaense*, *S. bogusium*, and *S. proctorae* (the latter four endemic to Raiatea) are found on the island. Huahine is slightly northwest of Tahiti, and is 3.15–1.95 Myr. Like Tahaa, Huahine has the two species, *S. malardei* and *S. lotii*. Moorea is 16 km northwest of Tahiti, and is 2.25–1.20 Myr. Eleven species are found on Moorea, namely *S. malardei*, *S. lotii*, *S. pseudocorium* (endemic to Moorea), *S. exasperans*, *S. cataracatarum*, *S. shannonae*, *S. oviceps* s.l., *S. dussertorum*, *S. concludium*, *S. neovicpes*, and *S. middlemissae*. Tahiti is the largest of the Society Islands, and contains the greatest number of *Inseliellum*. The age of Tahiti is 1.75–0.25 Myr. Twenty-eight species are found on Tahiti, the following are endemic to Tahiti: *S. arlecchinum*, *S. connae*, *S. dojeycorium*, *S. fossatiae*, *S. tahitiense*, *S. maraaense*, *S. pallidicranium*, *S. hirticranium*, *S. hispidum*, *S. caesariatum*, *S. fararae*, *S. jnabsium*, *S. lonckei*, *S. joyae*, *S. clibanarium*, *S. admixtum*, and

*S. middlemissae*. The following are not endemic to Tahiti: *S. malardei*, *S. lotii*, *S. exasperans*, *S. castaneum*, *S. cataractarum*, *S. shannonae*, *S. oviceps* s.l., *S. dussertorum*, *S. concludium*, *S. neoviceps*, and *S. middlemissae*.

## Historical biogeographical analysis

Brooks parsimony analysis (Brooks, 1981; Wiley, 1988; Brooks *et al.*, 2001; Brooks & McLennan, 2002) was used to analyse the phylogenetic (Fig. 2) and distributional data. Phylogenetic biogeographers attempt to document as full and parsimoniously as possible the geographical context of speciation in co-occurring clades. This includes the possibility that the same area may have been the site of more than one episode of speciation.

We converted the phylogenetic tree for *Inseliellum* into a taxon-area cladogram by replacing the names of species with their geographical areas (Fig. 3). We then prepared two BPA matrices, one (for primary BPA) in which each island occurs
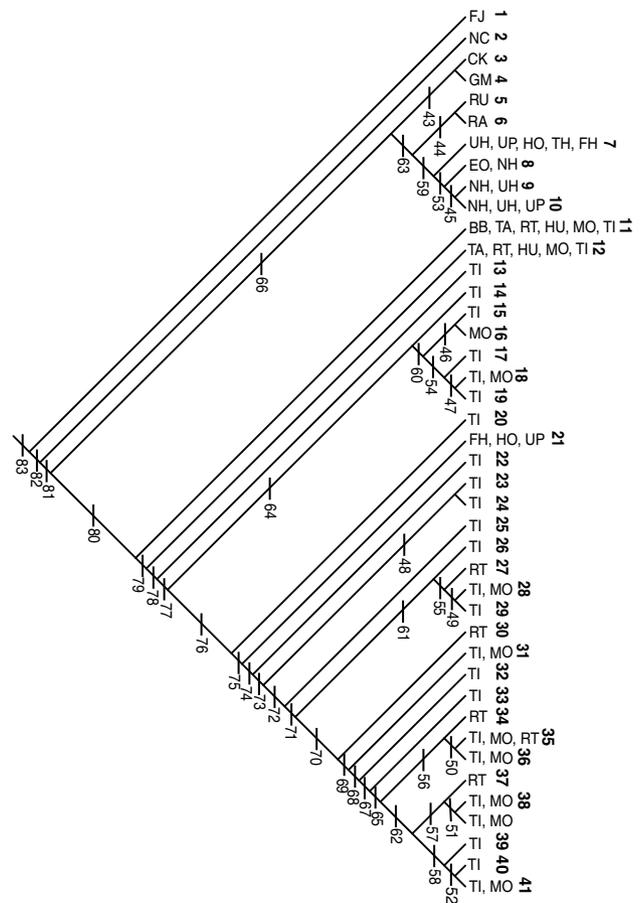


**Figure 3** Phylogenetic tree for *Inseliellum* numbered for biogeographical analysis. FJ, Fiji; NC, New Caledonia; CK, Chuuk; GM, Guam; RU, Rurutu; RA, Rarotonga; UH, Ua Huka; UP, Ua Pou; HO, Hiva Oa; TH, Tahuata; FH, Fatu Hiva; EO, Eiao; BB, Bora Bora; TA, Tahaa; RT, Raiatea; HU, Huahine; MO, Moorea; and TI, Tahiti.

**Table 1** Primary BPA matrix listing the geographical distributions for *Inseliellum* and binary codes representing the phylogenetic relationships of *Inseliellum*

| Area | Species | Binary code |
| --- | --- | --- |
| FJ | 1 | (A) 1000000000 0000000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000000 0000000000 0000000000 001 |
| NC | 2 | (A) 0100000000 0000000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000000 0000000000 0000000000 011 |
| GM | 4 | (A) 0001000000 0000000000 0000000000 0000000000 |
|  |  | (B) 0010000000 0000000000 0000010000 0000000000 111 |
| CK | 3 | (A) 0010000000 0000000000 0000000000 0000000000 |
|  |  | (B) 0010000000 0000000000 0000010000 0000000000 111 |
| RA | 6 | (A) 0000010000 0000000000 0000000000 0000000000 |
|  |  | (B) 0001000000 0000000000 0010010000 0000000000 111 |
| RU | 5 | (A) 0000100000 0000000000 0000000000 0000000000 |
|  |  | (B) 0001000000 0000000000 0010010000 0000000000 111 |
| EO | 8 | (A) 0000000100 0000000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0010000010 0010010000 0000000000 111 |
| NH | 8, 9, 10 | (A) 0000000111 0000000000 0000000000 0000000000 |
|  |  | (B) 0000100000 0010000010 0010010000 0000000000 111 |
| UH | 7, 9, 10 | (A) 0000001011 0000000000 0000000000 0000000000 |
|  |  | (B) 0000100000 0010000010 0010010000 0000000000 111 |
| UP | 7, 10, 21 | (A) 0000001001 0000000000 1000000000 0000000000 |
|  |  | (B) 0000100000 0010000010 0010010000 0000111111 111 |
| HO | 7, 21 | (A) 0000001000 0000000000 1000000000 0000000000 |
|  |  | (B) 0000000000 0000000010 0010010000 0000111111 111 |
| TH | 7 | (A) 0000001000 0000000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000010 0010010000 0000000000 111 |
| FH | 7, 21 | (A) 0000001000 0000000000 1000000000 0000000000 |
|  |  | (B) 0000000000 0000000010 0010010000 0000111111 111 |
| BB | 11 | (A) 0000000000 1000000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000000 0000000000 0000000001 111 |
| TA | 11, 12 | (A) 0000000000 1100000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000000 0000000000 0000000011 111 |
| RT | 11, 12, 27, 30, 34, 35, 37 | (A) 0000000000 1100000000 0000001001 0001101000 |
|  |  | (B) 0000000001 0000111000 0100101111 1111111111 111 |
| HU | 11, 12 | (A) 0000000000 1100000000 0000000000 0000000000 |
|  |  | (B) 0000000000 0000000000 0000000000 0000000011 111 |
| MO | 11, 12, 16, 18, 28, 31, 35, 36, 38, 39, 42 | (A) 0000000000 1100010100 0000000100 1000110110 |
|  |  | (B) 0100011011 1101111101 1101000011 1111111111 111 |
| TI | 11, 12, 13, 14, 15, 17 18, 19, 20, 22, 23, 24, 25, 26, 28, 29, 31, 32, 33, 35, 36, 38, 39, 40, 41, 42 | (A) 0000000000 1111101111 0111110110 1110110111 |
|  |  | (B) 1100011111 1101111101 1101101111 1111111111 111 |

FJ, Fiji; NC, New Caledonia; CK, Chuuk; GM, Guam; RU, Rurutu; RA, Rarotonga; UH, Ua Huka; UP, Ua Pou; HO, Hiva Oa; TH, Tahuata; FH, Fatu Hiva; EO, Eiao; BB, Bora Bora; TA, Tahaa; RT, Raiatea; HU, Huahine; MO, Moorea; and TI, Tahiti.

only once (Table 1) and the other (for secondary BPA) in which each island is represented for each instance in which a species evolved on that island (Table 2). The data for each matrix were entered into MacClade 4.0 (Maddison & Maddison, 2001) and analysed using PAUP* 4.0b8 (Swofford, 1998). A heuristic search was executed using the default PAUP settings. All characters were equally weighed and were run unordered.

## RESULTS

Analysis of the primary BPA data matrix (Table 1) produced three equally parsimonious trees (TL 96, CI 0.85, RI

0.89). The 50% majority rule consensus tree is shown in Fig. 4. Multiple trees with CI of 0.85 indicate that *c*. 15% of the areas have a reticulate history with respect to the species living there. Explicit and most parsimonious representation of area reticulations is achieved through the use of what is called the 'area duplication convention', or secondary BPA (Brooks *et al.*, 2001; Brooks & McLennan, 2002). Analysis of the secondary BPA data matrix (Table 2) produced a single most parsimonious tree (TL 82, CI 1.00, RI 1.00) (Fig. 5). Fiji is the most basal area, with New Caledonia being the second most basal area. This is in agreement with the hypothesis by Edwards (1932) and Craig (1983) and later Craig & Currie (1999) that

**Table 2** Secondary BPA matrix listing the geographical distributions for *Inseliellum* and binary codes representing the phylogenetic relationships of *Inseliellum*. Area abbreviations are the same as in Table 1

| Area | Species | Binary code |
|---|---|---|
| FI | 1 | 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 001 |
| NC | 2 | 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000000 011 |
| CK | 3 | 0010000000 0000000000 0000000000 0000000000 0010000000 0000000000 0000010000 0000000000 111 |
| GM | 4 | 0001000000 0000000000 0000000000 0000000000 0010000000 0000000000 0000000000 0000000000 111 |
| RU | 5 | 0000100000 0000000000 0000000000 0000000000 0001000000 0000000000 0010010000 0000000000 111 |
| RA | 6 | 0000010000 0000000000 0000000000 0000000000 0001000000 0000000000 0010010000 0000000000 111 |
| UH (G) | 7 | 0000001000 0000000000 0000000000 0000000000 0000000000 0000000010 0010010000 0000000000 111 |
| UP (G) | 7 | 0000001000 0000000000 0000000000 0000000000 0000000000 0000000010 0010010000 0000000000 111 |
| HO (G) | 7 | 0000001000 0000000000 0000000000 0000000000 0000000000 0000000010 0010010000 0000000000 111 |
| TH (G) | 7 | 0000001000 0000000000 0000000000 0000000000 0000000000 0000000010 0010010000 0000000000 111 |
| FH (G) | 7 | 0000001000 0000000000 0000000000 0000000000 0000000000 0000000010 0010010000 0000000000 111 |
| EO (S) | 8 | 0000000100 0000000000 0000000000 0000000000 0000000000 0010000010 0010010000 0000000000 111 |
| NH (S) | 8 | 0000000100 0000000000 0000000000 0000000000 0000000000 0010000010 0010010000 0000000000 111 |
| NH (B) | 9 | 0000000010 0000000000 0000000000 0000000000 0000100000 0010000010 0010010000 0000000000 111 |
| UH (B) | 9 | 0000000010 0000000000 0000000000 0000000000 0000100000 0010000010 0010010000 0000000000 111 |
| NH (H) | 10 | 0000000010 0000000000 0000000000 0000000000 0000100000 0010010010 0010010000 0000000000 111 |
| UH (H) | 10 | 0000000010 0000000000 0000000000 0000000000 0000100000 0010010010 0010010000 0000000000 111 |
| UP (H) | 10 | 0000000010 0000000000 0000000000 0000000000 0000100000 0010010010 0010010000 0000000000 111 |
| BB (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| TA (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| RT (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| HU (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| MO (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| TI (M) | 11 | 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000001 111 |
| TA (L) | 12 | 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 111 |
| RT (L) | 12 | 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 111 |
| HU (L) | 12 | 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 111 |
| MO (L) | 12 | 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 111 |
| TI (L) | 12 | 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000011 111 |
| TI (A) | 13 | 0000000000 0010000000 0000000000 0000000000 0000000000 0000000000 0000000000 0000000111 111 |
| TI (C) | 14 | 0000000000 0001000000 0000000000 0000000000 0000000000 0000000000 0001000000 0000001111 111 |
| TI (D) | 15 | 0000000000 0000100000 0000000000 0000000000 0000010000 0000000001 0001000000 0000001111 111 |
| MO (P) | 16 | 0000000000 0000010000 0000000000 0000000000 0000010000 0000000001 0001000000 0000001111 111 |
| TI (F) | 17 | 0000000000 0000001000 0000000000 0000000000 0000000000 0001000001 0001000000 0000001111 111 |
| TI (E) | 18 | 0000000000 0000000100 0000000000 0000000000 0000001000 0001000001 0001000000 0000001111 111 |
| MO (E) | 18 | 0000000000 0000000100 0000000000 0000000000 0000001000 0001000001 0001000000 0000001111 111 |
| TI (T) | 19 | 0000000000 0000000010 0000000000 0000000000 0000001000 0001000001 0001000000 0000001111 111 |
| TI (MA) | 20 | 0000000000 0000000001 0000000000 0000000000 0000000000 0000000000 0000000000 0000011111 111 |
| FH (AD) | 21 | 0000000000 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000111111 111 |
| HO (AD) | 21 | 0000000000 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000111111 111 |
| UP (AD) | 21 | 0000000000 0000000000 1000000000 0000000000 0000000000 0000000000 0000000000 0000111111 111 |
| TI (PA) | 22 | 0000000000 0000000000 0100000000 0000000000 0000000000 0000000000 0000000000 0001111111 111 |
| TI (HI) | 23 | 0000000000 0000000000 0010000000 0000000000 0000000100 0000000000 0000000000 0011111111 111 |
| TI (HS) | 24 | 0000000000 0000000000 0001000000 0000000000 0000000100 0000000000 0000000000 0011111111 111 |
| TI (CA) | 25 | 0000000000 0000000000 0000100000 0000000000 0000000000 0000000000 0000000000 0111111111 111 |
| TI (FA) | 26 | 0000000000 0000000000 0000010000 0000000000 0000000000 0000000000 1000000000 1111111111 111 |
| RT (CS) | 27 | 0000000000 0000000000 0000001000 0000000000 0000000000 0000100000 1000000000 1111111111 111 |
| TI (CT) | 28 | 0000000000 0000000000 0000000100 0000000000 0000000010 0000100000 1000000000 1111111111 111 |
| MO (CT) | 28 | 0000000000 0000000000 0000000100 0000000000 0000000010 0000100000 1000000000 1111111111 111 |
| TI (J) | 29 | 0000000000 0000000000 0000000010 0000000000 0000000010 0000100000 1000000000 1111111111 111 |
| RT (PU) | 30 | 0000000000 0000000000 0000000001 0000000000 0000000000 0000000000 0000000001 1111111111 111 |
| TI (SH) | 31 | 0000000000 0000000000 0000000000 1000000000 0000000000 0000000000 0000000011 1111111111 111 |
| MO (SH) | 31 | 0000000000 0000000000 0000000000 1000000000 0000000000 0000000000 0000000011 1111111111 111 |
| TI (LO) | 32 | 0000000000 0000000000 0000000000 0100000000 0000000000 0000000000 0000000111 1111111111 111 |
| TI (JO) | 33 | 0000000000 0000000000 0000000000 0010000000 0000000000 0000000000 0000001111 1111111111 111 |
| TI (BO) | 34 | 0000000000 0000000000 0000000000 0001000000 0000000000 0000010000 0000101111 1111111111 111 |
| TI (O) | 35 | 0000000000 0000000000 0000000000 0000100000 0000000001 0000010000 0000101111 1111111111 111 |
| MO (O) | 35 | 0000000000 0000000000 0000000000 0000100000 0000000001 0000010000 0000101111 1111111111 111 |

**Table 2** *continued*

| Area | Species | Binary code |
|---|---|---|
| RT (O) | 35 | 0000000000 0000000000 0000000000 0000100000 0000000001 0000010000 0000101111 1111111111 111 |
| TI (DU) | 36 | 0000000000 0000000000 0000000000 0000010000 0000000001 0000010000 0000101111 1111111111 111 |
| MO (DU) | 36 | 0000000000 0000000000 0000000000 0000010000 0000000001 0000010000 0000101111 1111111111 111 |
| RT (PR) | 37 | 0000000000 0000000000 0000000000 0000001000 0000000000 0000001000 0100101111 1111111111 111 |
| TI (CL) | 38 | 0000000000 0000000000 0000000000 0000000100 0000000000 1000001000 0100101111 1111111111 111 |
| MO (CL) | 38 | 0000000000 0000000000 0000000000 0000000100 0000000000 1000001000 0100101111 1111111111 111 |
| TI (N) | 39 | 0000000000 0000000000 0000000000 0000000010 0000000000 1000001000 0100101111 1111111111 111 |
| MO (N) | 39 | 0000000000 0000000000 0000000000 0000000010 0000000000 1000001000 0100101111 1111111111 111 |
| TI (CB) | 40 | 0000000000 0000000000 0000000000 0000000001 0000000000 0000000100 0100101111 1111111111 111 |
| TI (ME) | 41 | 0000000000 0000000000 0000000000 0000000000 1000000000 0100000100 0100101111 1111111111 111 |
| TI (MD) | 42 | 0000000000 0000000000 0000000000 0000000000 0100000000 0100000100 0100101111 1111111111 111 |
| MO (MD) | 42 | 0000000000 0000000000 0000000000 0000000000 0100000000 0100000100 0100101111 1111111111 111 |

G, *guamense*; S, *sechani*; B, *buissoni*; H, *hukaense*; M, *malardei*; L, *lotii*; A, *arlecchinum*; C, *connae*; D, *dojeycorium*; P, *pseudocorium*; F, *fossatiae*; T, *tahitiense*; E, *exasperans*; MA, *maraaense*; AD, *adamsoni*; PA, *pallidicranium*; HS, *hipsidum*; HI, *hirticranium*; CA, *caesariatum*; FA, *fararae*; CS, *castaneum*; J, *jnabsium*; CT, *cataractarum*; PU, *pufauense*; SH, *shannonae*; LO, *lonckei*; JO, *joyae*; BO, *bogusium*; DU, *dussertorum*; O, *oviceps*; CB, *clibanarium*; MD, *middlemissae*; ME, *mesodontium*; PR, *proctorae*; CL, *clibanarium*; N, *neoviceps*.

*Inseliellum* was derived from a westerly origin (New Caledonia), although Fiji does lie between New Caledonia and the Cook Islands (Fig. 1). Nested within those areas is a group containing areas from Micronesia, Cook Islands, Austral Islands, Society Islands, and Marquesas Islands. The basal most clade within that group is made up of
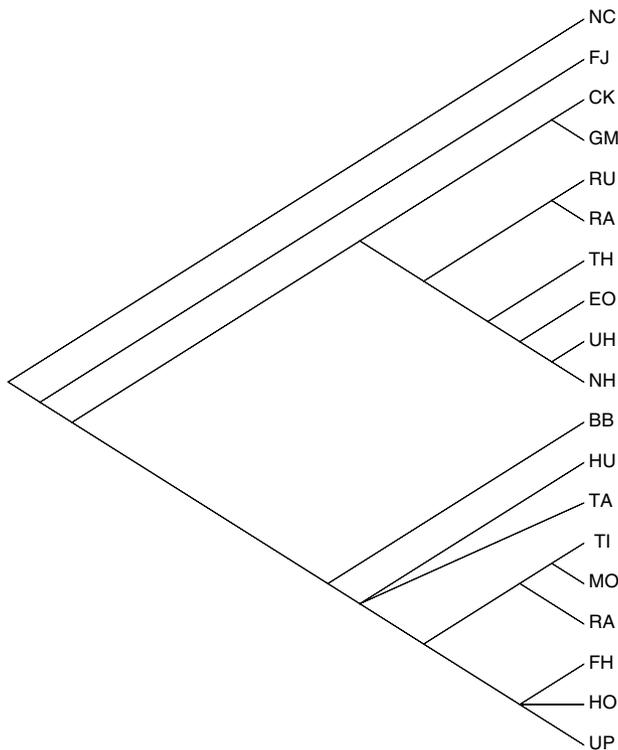


**Figure 4** Area cladogram (50% majority-rule) produced by primary BPA of *Inseliellum*. Area abbreviations are the same as in Fig. 3.

Guam, Chuuk, Rarotonga, Rurutu, and the Marquesas Islands. The remainder of the tree comprises areas from the Society Islands; mainly Tahiti, Moorea, and Raiatea. It is of note, however, that there is one instance of the Marquesas Islands in this clade.

Figure 5 is optimized under the 'area affect' of the Mac-Arthur–Wilson model, i.e. islands with a larger area will be more species-rich than smaller islands. Thus, over time, it can be assumed that larger islands have produced enough species to begin colonizing near-by islands. In the Marquesas Islands, Nuku Hiva and Hiva Oa are the two largest islands with areas of 345 and 318 km$^2$, respectively (Craig *et al.*, 2001). In the Society Islands, Tahiti and Raiatea are the two largest islands with areas of 1040 and 173 km$^2$, respectively.

The larval and pupal stages of simuliids are aquatic, so the evolution of running water habitats on the islands should be considered. Craig *et al.* (2001) estimated the upper time limits of running water formation within these islands, thus the earliest possible times of colonization of islands will be considered in the historical biogeographical analysis.

### Chuuk and Guam

Dispersal from the west led to the colonization of Chuuk and Guam, each island containing one black fly species. According to Craig *et al.* (2001), Guam was suitable for colonization by simuliids at 20 Myr. Further molecular evidence indicates that *S. trukense* (Chuuk, 14 Myr) is the most distantly related lineage of *Inseliellum* (Craig & Joy, 2000).

### Cook and Austral Islands

Only Rarotonga (in the Cook Islands) has black flies (two species), and has an approximate age of 1.5 Myr, while Rurutu (Austral Islands) has an approximate age of 1.0 Myr (one species) (Craig & Craig, 1986; Craig *et al.*, 2001). It is interpreted from Fig. 5 that dispersal is in a Cook Island to Austral Island sequence.

**Figure 5** Secondary BPA area cladogram for *Inseliellum* with duplicated areas. G, *guamense*; S, *sechani*; B, *buissoni*; H, *hukaense*; M, *malardei*; L, *lotii*; A, *arlecchinum*; C, *connae*; D, *dojeycorium*; P, *pseudocorium*; F, *fossatiae*; T, *tahitiense*; E, *exasperans*; MA, *maraaense*; AD, *adamsoni*; PA, *pallidicranium*; HS, *hipsidum*; HI, *hirticranium*; CA, *caesariatum*; FA, *fararae*; CS, *castaneum*; J, *jnabsium*; CT, *cataractarum*; PU, *pufauense*; SH, *shannonae*; LO, *lonckei*; JO, *joyae*; BO, *bogusium*; DU, *dussertorum*; O, *oviceps*; CB, *clibanarium*; MD, *middlemissae*; ME, *mesodontium*; PR, *proctorae*; CL, *clibanarium*; N, *neoviceps*. Area abbreviations are the same as in Fig. 3, and numbers accompanying slash marks refer to species (from Fig. 3).

*Marquesas Islands*
The rest of the Chuuk/Guam/Cook/Austral/Marquesas clade is the result of dispersal from the Cook Islands into the Marquesas (Fig. 5). The first branch shows a reticulating pattern, but considering island areas, Hiva Oa (in the southern portion of the Marquesas) may have been colonized first, and the species that is found there, *S. gallinum* may have dispersed to other areas. However, as these islands are under constant erosion by the ocean, an island with a larger area is usually younger than islands with smaller areas. In

this case, Eiao is the oldest island, with an age ranging up to 5.75 Myr (Craig *et al.*, 2001). The next dispersal shown is to Nuku Hiva (in the northern portion of the Marquesas), which contains three black fly species. Repeated dispersal from Nuku Hiva to Ua Huka and Ua Pou may be the sequence in this northern group of islands. The earliest possible colonization time for the Marquesas is 6 Myr (Craig *et al.*, 2001).

*Society Islands*
The next dispersal shown in Fig. 5 is to Tahiti. The rest of the secondary area cladogram represents a marked within-Tahiti radiation, with numerous dispersals out of Tahiti to neighbouring islands (Table 3). The earliest possible colonization time of Tahiti is 1.75 Myr (Craig *et al.*, 2001). This large radiation supports the first prediction made by this paper, within-island radiations should occur most often on far, large islands. *Simulium malardei* and *S. lotii* are the two most widespread species, both with reticulating histories. The dispersals are to Tahaa, Raiatea, Huahine, Moorea and Bora Bora (only in *malardei*) (Fig. 5). The remainder of the tree (minus *S. malardei*) shows dispersal from either Tahiti to Moorea, or Tahiti to Raiatea. These dispersal sequences indicate interesting events. For example, dispersal from Tahiti to Moorea [TI (E) to MO (E) in Fig. 5] represents a dispersal event to another area with no change of species in the new area (*S. exasperans*). Another example, dispersal from Tahiti to Raiatea [TI (FA) to RT (CS) in Fig. 5] represents a dispersal event to another area with a change of species in the new area. The distance from Tahiti to Moorea is 16 km, while the distance from Tahiti to Raiatea is 200 km. Patterns like these are summarized in Table 3 and shown diagrammatically in Fig. 6. This exemplifies the second and third prediction made by Heaney (2000), that colonization should occur more often on near than far islands and speciation should occur more often on far islands than on near islands. The only outlier to this section of the tree is *S. adamsoni*, which shows dispersal out of Tahiti back to the Marquesas Islands. This species has been problematic in the phylogeny of *Inseliellum*, and dispersal back to older source islands is not impossible (Craig & Currie, 1999; Craig *et al.*, 2001).

**DISCUSSION**

*Inseliellum* spp. conform to the basic expectations of the MacArthur–Wilson model. Larger islands contain more species than smaller islands (e.g. Tahiti 28 species, Rurutu one species), and islands near the source of colonizers are more species-rich than islands far from the source (e.g. Moorea 11 species, Raiatea seven species).

The 'radiation zone' hypothesis of MacArthur & Wilson (1963) and the extension of that hypothesis by Heaney (2000), tested by the secondary area cladogram of *Inseliellum* (Fig. 5), also seems to be corroborated. If adaptive radiation increases with distance from a major source island, then there should be patterns of endemic and non-endemic species on islands, moving away from the source

**Table 3** Dispersal sequences, number of dispersals and speciation events due to dispersal of *Inseliellum* interpreted from the secondary area cladogram (Fig. 5). The proximity of the islands to each other is also given

| Dispersal sequence | Dispersals | Speciation events | Proximity (km) |
|---|---|---|---|
| Chuuk–Guam | 1 | 1 | 1200 |
| Rarotonga–Rurutu | 1 | 1 | 1800 |
| Hiva Oa–(Ua Huka, Ua Pou, Tahuata, Fatu Hiva) | 1 | 0 | 6.25–106.25 |
| Nuku Hiva–Eiao | 1 | 0 | 262.5 |
| Nuku Hiva–Ua Huka | 1 | 0 | 43.75 |
| Nuku Hiva–(Ua Huka, Ua Pou) | 1 | 0 | 43.75–50 |
| Tahiti–(Bora Bora, Tahaa, Raiatea, Huahine, Moorea) | 1 | 0 | 16–256.25 |
| Tahiti–(Tahaa, Raiatea, Huahine, Moorea) | 1 | 0 | 16–200 |
| Tahiti–Moorea | 8 | 1 | 16 |
| Tahiti–Raiatea | 4 | 4 | 200 |
| Tahiti–(Fatu Hiva, Hiva Oa, Ua Pou) | 1 | 1 | 1800–1900 |
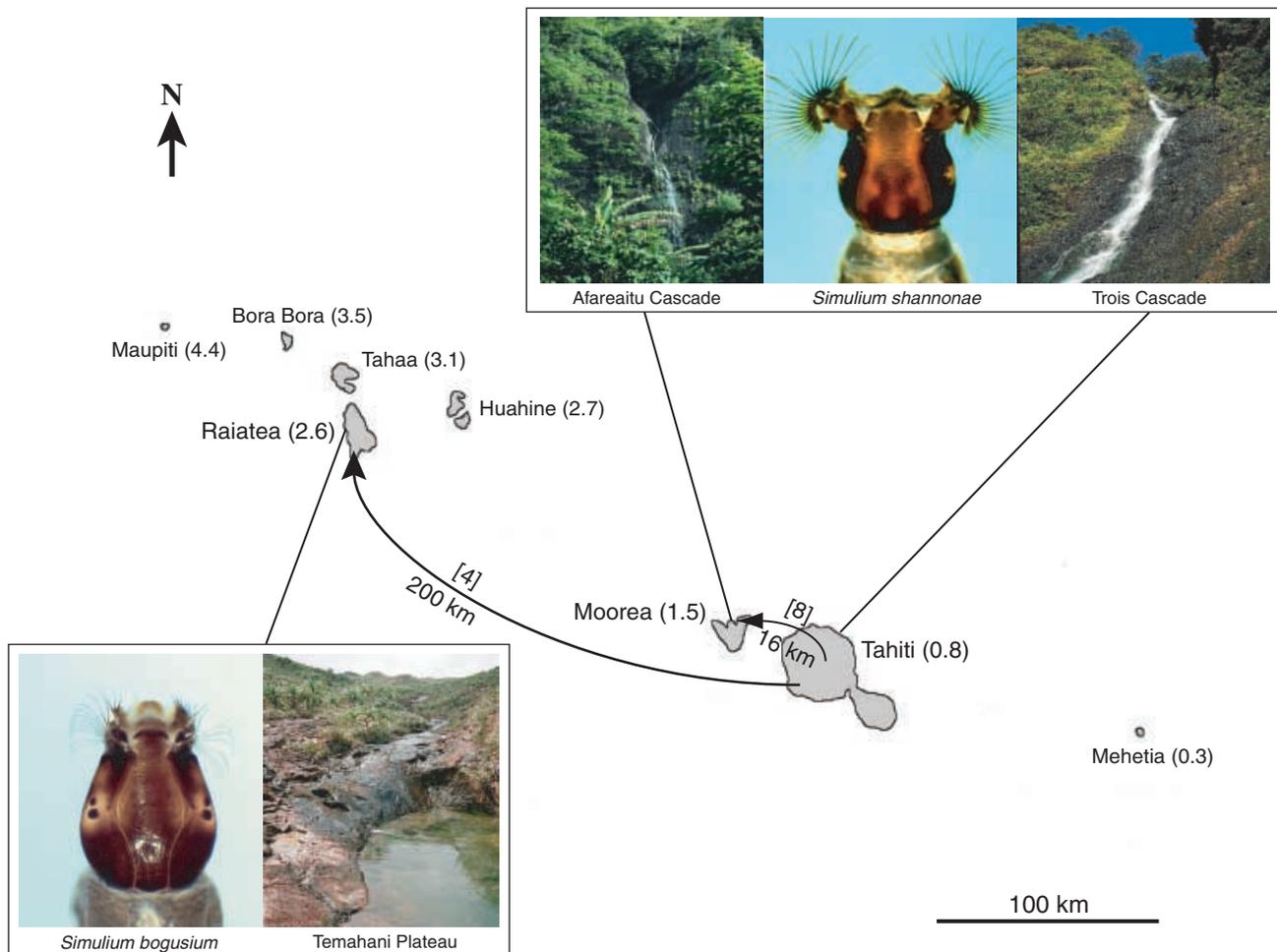


**Figure 6** Map of the Society Islands showing dispersal paths of *Inseliellum* out of Tahiti. The upper-right box shows an example of a species (dorsal side of larval head) present in both Tahiti and Moorea, *S. shannonae* (with its respective habitat in each island), while the box in the lower-left shows an example of a species present only in Raiatea, *S. bogusium* (with its respective habitat). Numbers in square brackets indicate the number of dispersal events to the island that the arrow leads to, and numbers in round brackets indicate the average ages of islands according to Craig *et al.* (2001). All photographs courtesy of Douglas A. Craig.

island (Heaney, 2000). More specifically, an island that is close to species-rich source would have many of the same species present through direct colonization and high rates of gene flow between the two islands. Conversely, if an island is far enough away from the source, gene flow will decrease enough to allow anagenesis to take place, and endemic species will evolve (Heaney, 2000). The secondary BPA area cladogram demonstrates this effect, beginning with Tahiti as the source island for subsequent colonization events. The Society Islands are arranged distance-wise (nearest to farthest) as follows: Tahiti, Moorea, Huahine, Tahaa, Raiatea, Bora Bora. Any dispersal from Tahiti to Moorea has not led to an endemic species except for that of *S. pseudocorium* [Moorea (P) in Fig. 3]. Moorea is thus close enough to Tahiti (16 km) to maintain gene flow between the two islands. Three of seven dispersals from Tahiti to Raiatea (Fig. 3) have led to three endemic species on Raiatea; 200 km away from Tahiti, Raiatea may be near the mid-point of the dispersal range of *Inseliellum*.

Finally, the phylogenetic pattern of sequential colonization of islands, the large within-Tahiti radiation of species, and subsequent dispersal with at least some speciation, demonstrated by the secondary BPA area cladogram, are also consistent with a taxon pulse radiation. Craig (1983), Craig *et al.* (2001) and Joy & Conn (2001) previously suggested that *Inseliellum* had undergone a taxon pulse, based on the extensive range of larval habitat type, and reported secondary reinvasions of habitats within Tahiti, and these results support their conclusions.

## CONCLUSIONS

This study supports the contention that the macroevolutionary and ecological elements of island biogeography are complementary, as proposed by MacArthur & Wilson (1963) and Heaney (2000). For *Inseliellum* spp., most within-island radiation occurred on a far, large island (Tahiti); (2) colonization occurred more often on near than on far islands (Tahiti-Moorea); and (3) speciation resulting from colonization occurred more often on far than on near islands (Tahiti–Moorea–Raiatea). This study also indicates that taxon pulse radiations may occur in the context of colonization of oceanic islands as well as on larger contiguous terrestrial stages, and evidence of their occurrence can be discovered using BPA. It will be interesting to see the results of similar analyses of additional clades in the same, and different islands; of particular interest would be analysis of the large phylogenetic data base for taxa inhabiting the Hawaiian Islands (Wagner & Funk, 1995).

## ACKNOWLEDGMENTS

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