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DR. ROSEMARY GILLESPIE (Orcid ID : 0000-0003-0086-7424)

DR. GEORGE RODERICK (Orcid ID : 0000-0001-7557-2415)

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ANCIENT BIOGEOGRAPHY OF GENERALIST PREDATORS ON REMOTE OCEANIC ISLANDS

R. G. Gillespie^{1,3}, M. S. Brewer^{1,2}, G. K. Roderick¹

1. Environmental Science, Policy, and Management, University of California, Berkeley,
California 94720-3114

2. Department of Biology, East Carolina University, Greenville, NC 27828-4353

3. corresponding author: R. G. Gillespie, gillespie@berkeley.edu

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28 **Abstract**

29 **Aim**

30 Remote islands are known for providing spectacular examples of adaptive radiation, with
31 ecological divergence across a lineage giving rise to multiple species, each specialized for a
32 particular niche. These isolated environments also provide some of the best examples of recent
33 colonization, often human-mediated, with a single generalist taxon distributed over vast regions.
34 Highlighted by this dichotomy is a tendency of taxa to become more specialized over time. The
35 current study focuses on two spider taxa (family Uloboridae) each occupying a broad range of
36 habitats: *Tangaroa tahitiensis* in the Austral and Society islands of French Polynesia and
37 *Daramulunia gibbosa* in Fiji. We ask whether the generalist tendency of each is associated with
38 recent colonization of widespread species or, rather, maintained over extended evolutionary time.

39 **Location**

40 South Pacific: Fiji (18°S, 175°E), Society (18°S, 150°W), and Austral (23°S, 150°W)
41 archipelagoes.

42 **Methods**

43 Mitochondrial COI and nuclear 18S rDNA were sequenced and analysed using maximum
44 likelihood (RAxML) and Bayesian approaches with concurrent divergence dating calibrated with
45 a general arthropod molecular clock. Ancestral ranges were reconstructed independently for
46 French Polynesia and Fiji (RASP).

47 **Results**

48 While both *T. tahitiensis* and *D. gibbosa* occur broadly from sea-level to cloud forest, each has a
49 separate and ancient origin within their respective archipelagoes, the pattern of colonization
50 matching the geographical arrangement of the islands.

51 **Main conclusions**

52 Populations of two spider species, *T. tahitiensis* in the Australs and Societies and *D. gibbosa* in
53 Fiji, are extreme generalists with broad physiological tolerances throughout their respective
54 ranges. Yet, every population displays single island endemism and deep genetic divergences
55 between islands indicating a long history on individual landmasses, a finding that contradicts the
56 tendency for organisms to show increasing specialization associated with endemism.

57

58 **Keywords**

59 Austral, Fiji, Pacific, Society Islands, spiders, island biogeography, taxon cycle, Uloboridae,
60 endemic, specialist

61

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62 Introduction

63 The biogeography of remote islands has attracted considerable attention as it provides insights
64 into general patterns of adaptation and speciation, and how these are dictated by the combined
65 effect of isolation and time. Early concepts of the dynamic nature of isolation and adaptation
66 were provided by Wilson (1961) who described cycles of island colonization by generalist
67 species, followed by adaptation and increasing specialization (see also Losos & Ricklefs, 2009).
68 More recent studies lend support to the idea that the ecology of taxa on isolated islands changes
69 over time, with successful colonizers (or invaders) initially tending to be abundant with large
70 ranges (Williamson & Fitter, 1996; Economo & Sarnat, 2012). Thus, taxa with attributes of high
71 numbers and generalized ecological affinities might be expected to be recent colonists; those that
72 are specialized with small ranges are likely to be the products of a longer history of adaptation
73 and specialization. The islands of the Pacific (Fig. 1) are an ideal system with which to examine
74 the ecological signatures associated with biogeographic patterns of age and adaptation across
75 various degrees of isolation (Gillespie *et al.*, 2008a). Indeed, the islands of the South Pacific
76 have provided the classic setting for both the original hypotheses (Wilson, 1961) and subsequent
77 tests (Economo & Sarnat, 2012; Jönsson *et al.*, 2014) of taxon cycles and related phenomena
78 regarding evolutionary change in distribution.

79 The current study highlights an intriguing system presented by hackled orb-weaving spiders,
80 family Uloboridae, in the South Pacific (see Appendix S1). On the islands ranging from the
81 Societies and Australs in French Polynesia, westward across to Fiji and north to Micronesia, the
82 family is a dominant component of the spider fauna, represented by different, and largely non-
83 overlapping, genera, in particular *Daramulunia*, *Tangaroa* and *Purumitra*: Morphological
84 characters suggest that the genera in the South Pacific are not phylogenetically close to each
85 other and affinities show little association with geography (Opell, 1979) (Appendix S1, Fig. S1).
86 The generic-level endemism suggests deep divergences, which is striking because of the lack of
87 species-level diversity. The genus *Tangaroa* is represented by five species distributed across the
88 mid-Pacific, including *T. tahitiensis* (one of the subjects of the current study) in the Societies and
89 Australs (Berland, 1934); *Waitkera* by a single species, *W. waitakerensis* in New Zealand (Opell,
90 1979, 2006); *Purumitra* by two species, *P. grammica* in southern Micronesia and *P. australiensis*
91 in Queensland Australia (Lehtinen, 1967); and *Daramulunia* (the second subject of the current

92 study) by two species, *D. gibbosa* and *D. tenella*, in Fiji and Samoa (Lehtinen, 1967; Opell,
93 1979).

94 At variance with the precinctive nature of the genera, *Tangaroa tahitiensis* from French
95 Polynesia and *Daramulunia gibbosa* from Fiji are habitat generalists (Claridge *et al.*, 2014),
96 building orb webs low in the vegetation, and occurring from sea level, often to the mountain
97 summits (Table 1). The abundance of individuals and broad ecological tolerance of the
98 populations might suggest recent colonization, even subsequent to human arrival. If so, the levels
99 of generic endemism in the area (Fig. S1) are surprising, and warrant exploration. Alternatively,
100 if the group has a long history in the region, its widespread and generalist nature is inconsistent
101 with the taxon cycle proposed for many ant (Wilson, 1961; Economo & Sarnat, 2012) and bird
102 (Ricklefs, 2015) taxa.

103 French Polynesia is spread over 2.5 million km² of ocean in the South Pacific (similar to Europe
104 in extent). The Society Islands form the largest archipelago, with individual islands sequentially
105 ordered from south-east to north-west by increasing age up to 4.3 million years (Ma) for the
106 current high islands, due to the north-westward movement of the Pacific tectonic plate over
107 stationary volcanic plumes (Clouard & Bonneville, 2005) (Fig. 1). The Austral Archipelago lies
108 approximately 500 km to the south-west of the Society Islands at their closest points (between
109 the islands of Tahiti and Rurutu), and extends over 1500 km, the main islands ranging from 12.2
110 to 4.5 Ma, with secondary volcanic activity beneath Rurutu c. 2-1 Ma. The two main islands in
111 the Fiji archipelago are Viti Levu and Vanua Levu (Fig. 1), where the earliest emergence is
112 estimated at ca. 25 Ma (Sarnat & Economo, 2012), though much of the land probably only
113 became available about 4 Ma (Rodda, 1994), and through a burst of volcanic activity about 3
114 Ma, in particular in Taveuni, but also in Vanua Levu and Koro (Colley, 2009).

115 The generalist habitat tendencies of *T. tahitiensis* and *D. gibbosa* are notable in the context of the
116 striking habitat differences that characterize terrestrial environments of the central Pacific
117 (Mueller-Dombois & Fosberg, 2013). The interactions between trade winds and steep
118 topography forcing rapid cooling of upward moving winds, gives rise to a tremendous variation
119 of microclimates within a given island (Meyer, 2011), including hot and variably dry coastal
120 areas, cooler low elevation and then montane forests, with rainfall dictated by position on the

121 island relative to the trade winds, whether leeward or windward side, and cloud forest at the
122 highest elevations on some of the larger and high islands, characterized by waterlogged soils
123 with copious mosses, ferns, and epiphytic plants, and very high levels of endemism.

124 The affinities of the multiple uloborid genera in the Pacific region, together with the restricted
125 distributions of each, suggest a complicated biogeographic scenario (Fig. S1). At the same time,
126 the abundance and widespread nature of *T. tahitiensis* and *D. gibbosa*, coupled with the overall
127 similarities in their ecology, would suggest that their distribution represents recent colonization
128 associated with human transportation. Yet, given that the taxa within the different islands tend to
129 be endemic at the generic level, it is difficult to reconcile the history underlying the
130 biogeographic pattern. Given this paradox, the current study set out to examine the
131 biogeographic affinities of uloborid taxa, in particular *T. tahitiensis* and *D. gibbosa*, in the South
132 Pacific, focusing on the archipelagoes of Fiji, and the Societies and Australs in French Polynesia.
133 Using mitochondrial and nuclear DNA sequence data, we test the following hypotheses: (1) The
134 taxa are recent arrivals associated with humans, in which case we expect minimal genetic
135 population structure across the islands within each species (Gillespie *et al.*, 2008b).
136 Alternatively, (2) the taxa have a longer history within each archipelago and on each island, for
137 which we predict deeper phylogenetic divergence, but also more time for evolutionary shifts to
138 take place. Further, the taxon cycle concept will be supported if lineages show an evolutionary
139 shift from being widespread habitat generalists to ecological specialists (Economo & Sarnat,
140 2012).

141

142

143 **Methods**

144 ***Taxon sampling and habitat characterization*** The current study sampled populations from
145 both representatives of *Daramulunia* (*D. gibbosa* and *D. tennela*) from three islands in Fiji, and
146 *Tangaroa tahitiensis* from the Society Islands, and the Austral Islands (see Appendix S1).
147 Additional specimens from Genbank were included to assess the age and monophyly of genera
148 and possibly to infer direction of colonization (Table 1). Genera included were: (1) from the
149 Pacific, *Waitkera* from New Zealand and the Asian *Octonoba* (no specimens of *Purumitra* were

150 available); (2) the related widespread genera *Philoponella* and *Uloborus*, and (3) *Hyptiotes* and
151 *Miagrammopes* that appear to be more distantly related (Fig. S1) (Opell, 1979). *Deinopis spinosa*
152 was included as an outgroup to all uloborids.

153 For *Daramulunia* and *Tangaroa* locations (forest/habitat type, elevation) and habit of the spiders
154 (web, microhabitat) were noted upon collection (Table 1). We distinguished four forest/habitat
155 types. Coastal strand habitat (0-50m) is found on almost all Pacific islands; it is hot and dry with
156 xeric, scrubby vegetation but has been extensively modified through development. Low
157 elevation wet and dry forest (90-300/1000m) has rainfall of 2000-3700 mm on the wet side and
158 1000 – 3000 mm on the leeward side. Low elevation forest which comprises all of the non-
159 coastal area in the small and moderately elevated (< 500m) Austral islands of Raivavae, Tubuai
160 and Rurutu, has been heavily impacted through grazing by introduced ungulates or conversion to
161 agriculture and secondary vegetation, particularly in the French Polynesia (Meyer, 2004).
162 Cooler montane rainforests (400/600 m up to 600/1000m) have rainfall 2000-3750 mm. Cloud
163 forests are found at higher elevations on some of the larger and higher islands, e.g., above 550 m
164 on Rapa (Meyer, 2011) and 900m in Fiji.

165 **Molecular methods** DNA was extracted from two legs of each representative specimen (Table 1)
166 with a Qiagen DNeasy Tissue Kit using the included protocol, with a final elution volume of 100
167 μ L of genomic extraction for each individual. Voucher specimens were stored in the Essig
168 Museum of Entomology, University of California, Berkeley. Remaining genomic DNA has been
169 stored at -80C in the Gillespie and Roderick Laboratory, UC Berkeley. Mitochondrial
170 cytochrome c oxidase subunit I (COI) was amplified via a single primer pair, while the
171 nuclear 18S rDNA was amplified in two pieces, primer pairs [COI] C1-J-1751 and C1-N-2191
172 (Simon *et al.*, 1994) and [18S] 1F and 5R or 5F and 9R (Giribet *et al.*, 1999). These markers
173 were chosen for their utility in resolving phylogenetic relationships in arachnids at various levels.
174 The protein-coding COI was amplified using 35 cycles of 30s at 95°C melting temperature,
175 followed by 30s at an annealing temperature of 55°C, and an extension step of 45s at 72°C with
176 initial melting and final-extension steps as above. No additional buffering agents were required
177 for these reactions, although some specimens required lowering the annealing temperature to
178 48°C to amplify the COI fragment. For the 18S, the PCR protocol, modified from (Hedin &
179 Maddison, 2001), used 35 cycles of 30s at 95°C melting temperature, followed by 30s at an

180 annealing temperature of 52°C and an extension step of 45s at 72°C, with 3s added to this
181 extension for every cycle after the first. These cycles were preceded by an initial melting at 95°C
182 for 2 minutes, with a 7-minute final extension at 72°C. A 1% final volume of dimethyl sulfoxide
183 (DMSO) was included in the 18S amplifications to stabilize the PCR pre-mixes. A 3µL portion
184 of all PCR products was run out on 1.5% TBE/agarose gels to assess amplification product size,
185 purity and concentration. PCR products were cleaned using Qiagen QiaQuick PCR Purification
186 Kit, and cycle sequenced in both directions using dye terminators. Cycle sequencing products
187 were analysed using an ABI 377 gel sequencer or an ABI 3730 capillary autosequencing
188 machine. All loci were sequenced in two directions, and complementary sequence pairs were
189 aligned and used to check for errors in alignment and base-calls using SEQUENCHER 3.1.1 (Gene
190 Codes Corporation).

191 *Multiple sequence alignment, phylogenetic analyses, and divergence dating* Sequences for each
192 locus (COI and 18S) were aligned using MAFFT 7 (Kato et al., 2002; Kato and Toh, 2008)
193 under the default settings and edited by hand in MESQUITE 3 (W. Maddison and D. Maddison,
194 2010). The COI alignment was examined for breaks in coding frame by translating to amino
195 acids in MESQUITE. Both alignments were trimmed on each end to reduce poorly aligned regions
196 and poor coverage across the dataset. Appropriate models of molecular evolution and
197 partitioning schemes were determined using KAKUSAN4 4.0.2011.05.28 (Tanabe, 2007) under
198 the Bayesian information criterion variant 4 (sample size is equal to the number of sites in the
199 alignment) and adjusted for the target programs. The datasets were concatenated for downstream
200 analyses using FASCONCAT 1.0 (Kuck and Meusemann, 2010). Maximum likelihood trees
201 were reconstructed in RAXML 7.4.2 (Stamatakis, 2006) for the concatenated dataset under the
202 GTRCAT model. The outgroup (*Deinopis spinosa*) was specified. Tree searches comprised
203 1,000 random addition sequence replicates (RAS) and 1,000 bootstrap replicates. Bayesian tree
204 searches with concurrent divergence dating on the concatenated dataset were conducted in
205 BEAST 1.8.1 (Drummond and Rambaut, 2007) with two partitions (18S and COI) under the
206 TN93+I+G model and a Yule speciation prior. Runs comprised 50,000,000 generations, and
207 trees were sampled every 1,000 generations.

208 *Estimating divergence times* Because of the uncertainty in establishing island age (Forest, 2009)
209 and inevitable circularity of using island age for calibration, we applied a general arthropod

210 molecular clock estimate of 3.54% per million years (i.e., 0.0177 per clade rates) (Papadopoulou
211 *et al.*, 2010) to the COI partition with a strict clock; the 18S rate was estimated under a
212 lognormal relaxed clock model. Bayesian inference was used following the methods of
213 Drummond *et al.* (2006) implemented in BEAST (Drummond & Rambaut, 2007) and visualized
214 with FIGTREE (Rambaut, 2014). Two independent BEAST analyses were conducted and
215 combined using LOGCOMBINER. The first 10% of each run was discarded as burn-in.
216 Convergence of parameters was accessed using TRACER (<http://beast.bio.ed.ac.uk/tracer>), and the
217 trees were summed using TREEANNOTATOR.

218 *Ancestral range reconstructions* The geographic range evolution was reconstructed for each of
219 the *Tangaroa* and *Daramulunia* subclades extracted from the BEAST tree using the
220 “extract.clade” function in the R package ‘APE’ (Paradis *et al.*, 2004). Contemporary island
221 ranges were coded for the following *Daramulunia* terminal taxa Fiji (Viti Levu), Fiji (Koro), and
222 Fiji (Taveuni). The *Tangaroa* terminal range encodings were Australs (Tubuai), Australs
223 (Rurutu), Australs (Raivavae), Australs (Rapa), Societies (Moorea), Societies (Tahiti), Societies
224 (Raiatea). The ancestral ranges were reconstructed independently for each group under the
225 Dispersal-Extinction-Cladogenesis (DEC) (Ree and Smith, 2008) and Bayesian-Binary (Yu *et*
226 *al.*, 2010) in RASP 3.2 (Yu *et al.*, 2015). Default priors were used and the analysis comprised
227 chains run for 10,000 generations, sampled every 100 generations, with the first 20% discarded
228 as burn-in.

229

230 **Results**

231 *Taxon sampling and habitat characterization.* Spiders were collected throughout the islands of
232 Fiji, the Society Islands, and the Austral Islands (Table 1). *Daramulunia gibbosa* in Fiji and *T.*
233 *tahitiensis* in French Polynesia were both common throughout the archipelagoes of Fiji and the
234 Societies and Australs respectively, and in every known habitat type. Populations of both species
235 were collected from the hot and dry beach and coastal forest, through low elevation forest,
236 montane forest, and up into the wet and cool cloud forest; and in habitats that were entirely

237 modified (gardens, roadsides) to largely intact cloud forests (Table 1). All spiders were found to
238 build webs, and were invariably collected low in the vegetation.

239 *Multiple sequence alignment, phylogenetic analyses, and divergence dating.* The final
240 concatenated alignment comprised 2,156 nucleotides (1,580 – 18S; 576 – COI). The GAMMA-
241 based $-\log$ likelihood value for the best scoring RAxML tree was -7252 , and the mean $-\log$
242 likelihood value from the combined BEAST runs were -7981 (3.54%/my rate) and -8034 (island
243 calibration). All BEAST ESS values were >200 (posterior ESS = 5,081; likelihood ESS =
244 6,114). The topologies (Appendix S2, Fig. S2 for the RAxML tree; Fig. 2 for the BEAST tree)
245 were largely congruent, but showed varying levels of support under each optimality criterion.
246 Many areas of conflict between the trees were between terminals on the same island. In general,
247 the BEAST tree had better support, even when accounting for the inflated nature of posterior
248 probabilities and was the preferred topology for downstream analyses (Fig. 2).

249 The BEAST analyses recovered all genera as reciprocally monophyletic. Dating results were
250 very similar in terms of topology, and produced ages with higher confidence (i.e., tighter 95%
251 confidence intervals) at younger nodes (Fig. 2). The lack of confidence in deep node age
252 estimates is likely exacerbated by the breakdown of phylogenetic signal in COI at such deep
253 evolutionary time. The estimates of divergence using the standard rate are consistent with spiders
254 colonizing some time after the islands initially formed. The family Uloboridae last shared a
255 common ancestor with the Deinopidae ~ 24 (17-32) Ma. *Daramulunia* diverged from a clade
256 containing *Philoponella* ~ 11 (7.7-15) Ma (stem group age). Within *Daramulunia*, *D. tenella*
257 split from *D. gibbosa* ~ 6.4 (4.4-8.9) Ma, and within *D. gibbosa*, the monophyletic clade found
258 exclusively on Viti Levu split from the remaining island members of the genus ~ 5.2 (3.5-7.1)
259 Ma. The clade found on Koro diverged from relatives on Taveuni ~ 2.9 (1.7-4.3) Ma. The split
260 between *Tangaroa* inhabiting the Australs and Societies and *Waitkera* was inferred to have
261 occurred ~ 14 (9.7-20) Ma, with the date of first colonization of the two archipelagoes between
262 14 - 5 Ma. Approximate divergence ages for *Tangaroa* were as follows: between Tubuai and the
263 rest of the group ~ 4.7 (3.2-6.8) Ma; between Rurutu and the rest of the group ~ 3.4 (2.4-4.7) Ma;
264 the Societies from (Raivavae+Rapa) ~ 3.1 (2.2-4.3) Ma; and Raivavaie from Rapa ~ 1.5 (0.8-2.3)
265 Ma.

266 *Ancestral range reconstructions* Both genera, *Tangaroa* (Fig. 3A) and *Daramulunia* (Fig. 3B),
267 have had a long history within the islands of French Polynesia and Fiji respectively. *Tangaroa*
268 shows a pattern of colonization, roughly from older to younger islands, with each island
269 supporting its own monophyletic population. The pattern of colonization is consistent with
270 geology rather than geography, given the initial arrival point appears to be Tubuai (the oldest
271 continuous land mass in the area), with the most derived population on the youngest island of
272 Rapa. However, the timing of colonization is more recent than the age of the islands, suggesting
273 that geographic distance may have been the major contributor to the pattern of colonization.
274 Populations on the islands of the Societies appear to come from the northern Australs, with a
275 pattern of colonization that shows no relationship to island age, though this may be due in part to
276 the lack of samples from the oldest islands of Bora Bora and Tahaa. *Daramulunia* in Fiji shows a
277 similar pattern of island monophyly, with colonization roughly reflecting geological history (Fig.
278 3B), with the estimated age of the colonization events being consistent with the ages of Koro or
279 Taveuni, although we do not yet have samples from a number of the other islands in the area.
280 The major difference within Fiji (as compared to the Austral and Society islands) is that there has
281 been a speciation event within *Daramulunia* likely on the island of Viti Levu.

282

283 **Discussion**

284 The results, in combination with previous morphological data indicating deep divergences
285 between lineages (Opell, 1983; Coddington, 1990), suggest that the family Uloboridae has an
286 ancient history in the Pacific. Given that we were not able to sample all taxa across the Pacific,
287 and because support values were weak at deeper nodes, it is not possible to determine specific
288 relationships between genera. However, the data are consistent with earlier results (Opell, 1979,
289 1983) that the two genera which served as the focus of the current study, *Daramulunia* and
290 *Tangaroa*, do not share a recent ancestry (Fig. S1) and both have been in the area for a longer
291 time than most of the islands on which they are currently found. More comprehensive sampling
292 throughout the region is needed to test explicitly the patterns of colonization, but the key point is
293 that, although the spiders appear to be ecological generalists, the biogeographic pattern suggests
294 an ancient origin rather than recent colonization.

295 We now consider the biogeography of *T. tahitiensis* and *D. gibbosa* within their respective
296 archipelagoes of French Polynesia and Fiji, but emphasize the caveat that we are using gene trees
297 to reconstruct ancestral range states. At the species level, given the limited data for 18S, this
298 largely reflects mtCOI data, which can provide a misleading picture of species relationships.
299 Among the spiders, for example, it is possible that effects such as sex biased long distance
300 dispersal (Goodacre *et al.*, 2009) could be entirely missed. However, two aspects of the results
301 give at least some confidence that the data are reflecting a biologically meaningful pattern: first,
302 we find monophyly (without exception) of populations on a given island; and second, the
303 variation between islands is consistently much greater than within (Meyer & Paulay, 2005).
304 Together, these results suggest a scenario of few colonizations involved in island establishment
305 (Shaw & Gillespie, 2016).

306 ***Tangaroa in French Polynesia.*** Colonization by *T. tahitiensis* in the Austral Islands is roughly
307 consistent with both the spatial geography and geology of the Austral islands, though populations
308 on a given island appear to be somewhat younger than the geological ages of the islands
309 themselves (Fig. 2). Although sampling is insufficient to estimate the precise time of arrival on
310 the island, the oldest sampled population is from Tubuai, with subsequent colonization of the
311 progressively younger and more distant islands of Rurutu, Raivavae and Rapa. Interestingly, a
312 similar pattern of ancient colonization of the Austral Islands has been found in populations of the
313 crab spider species *Misumenops rapaensis*. Like *T. tahitiensis*, *M. rapaensis* occurs throughout
314 the Austral Islands with large genetic distances between populations on each island; uncorrected
315 genetic distance between Rurutu and Tubuai is 8.4%, a value nearly as much as the maximal
316 distance computed across an entire radiation of 16 Hawaiian taxa (Garb & Gillespie, 2006).
317 Applying the same standard rate of divergence of COI as used in the current study (3.54%), the
318 divergence of *M. rapaensis* in the Australs seems to have occurred over an approximately similar
319 timeframe as that found here for *Tangaroa*, and with a similar pattern of initial divergence on the
320 older islands to the northwest and subsequent island hopping to the progressively younger islands
321 in the south east.

322 Among insects from the Australs, recent works shows that the weevil genus *Rhyncogonus* has a
323 long history in the region, following the same sequence though even older than the spiders and
324 with species diversification within and between islands (Claridge *et al.*, 2016). Similar sequential

325 colonization has also been documented for blackflies (*Inseliellum*, Simuliidae) (Craig & Porch,
326 2013), with large genetic distances between island populations.

327 The colonization of the Society Islands by *T. tahitiensis* from within the Australs is worth
328 comment. The specimen from the youngest island of Tahiti shows a divergence from the
329 Australs at ca. 3.1 (2.2-4.3) Ma (Fig. 2), which is considerably older than the age of either
330 Moorea (1.9 Ma), the most likely inferred ancestral range (Fig. 3A), or Tahiti (1.0 Ma). In the
331 same way, divergence of at least two of three *Rhyncogonus* weevil lineages on Tahiti predates
332 the formation of Tahiti (Claridge *et al.*, 2016). The apparent paradox may be explained by the
333 complexity of the island systems in the region, including older islands in the Society archipelago
334 as well as the likely existence of intermittent paleo-islands in the area between the Society and
335 Austral archipelagoes. This region is characterized by a complex pattern of aerial and submarine
336 volcanoes arising from a heterogeneous plume emanating from the South Pacific superswell
337 (Bonneville *et al.*, 2006) and many of the identified guyots are ancient (Clouard, 2000).

338 ***Daramulunia in Fiji.*** Our sampling is insufficient to provide a specific date for the colonization
339 of Fiji by *Daramulunia*, though it could be as old as ca. 11 Ma (7.7-15 Ma). The earliest
340 colonization for Fijian terrestrial arthropod lineages has been estimated at 17–10 Ma in a lineage
341 of ants (Sarnat & Moreau, 2011). In other taxa, colonization time estimates are slightly younger:
342 *Copelatus* (Monaghan *et al.*, 2006) and *Rhantus* (Balke *et al.*, 2007) diving beetles and
343 *Lordomyrma* ants (Lucky & Sarnat, 2009) have all been reported to have colonized between 13
344 and 5 Ma. Yet, some taxa appear to have reached the islands much more recently, e.g., halictine
345 bees, which appear to have a Pleistocene origin (Groom *et al.*, 2013).

346 For *Daramulunia*, *D. tenella*, a bright green species characteristic of high elevation wet forest,
347 diverged early, and most likely on Viti Levu. Within *D. gibbosa*, the split between Viti Levu and
348 the other islands occurred around 5.2 (3.5-7.1) Ma, with the credibility interval placing it well
349 within the timing of volcanic eruption (and first subaerial appearance) of Koro at ca. 4 Ma
350 (Rodda, 1994). Divergence between Koro and Taveuni is estimated at ca. 2.9 (1.7-4.3) Ma,
351 which is older than the age of Taveuni, an effect likely due to incomplete sampling of islands.

352 ***Multiple island endemics?*** The only major recognized speciation event in the group likely
353 occurred on Viti Levu (Fiji) between *D. tenella*, which is restricted to cloud forest on Viti Levu

354 and Taveuni (Koro has no cloud forest), and *D. gibbosa* (Fig. 3B). In contrast, the widespread *T.*
355 *tahitiensis* and *D. gibbosa* are both single species. Barcoding studies have suggested a 2%
356 divergence threshold as a cutoff value for species delimitation based on the distribution of intra
357 and inter-specific genetic distance among taxa (Pereira *et al.*, 2013), although this value is
358 fraught with issues as to what defines species boundaries (Meyer & Paulay, 2005). In particular,
359 when divergent lineages are allopatric, it is not clear whether they fulfill the species designation
360 (Mutanen *et al.*, 2012). However, the divergence between the different island populations of both
361 *T. tahitiensis* and *D. gibbosa* shown here indicates that the taxa warrant further scrutiny for
362 taxonomic status. Indeed, recent examination of *Tangaroa* within the Cook islands, has revealed
363 subtle differences in leg spination and genital morphology that support species designation
364 (Salvatierra *et al.*, 2015). Yet, whether or not species status is warranted, the question remains as
365 to why generalist and ecologically similar taxa show such deep genetic divergences.

366 ***The paradox - generalists with ancient origins.*** The most striking aspect of the current study is
367 the ecological enigma: the two species of spiders, *T. tahitiensis* and *D. gibbosa*, are both
368 ecological generalists, invariably found from sea level to the summit of the mountains; some
369 mtDNA haplotypes on Rapa are identical between populations inhabiting the vastly contrasting
370 sites of the hot and often dry beach/ ocean cliffs and the cool and very wet cloud forest on the
371 mountain summit (550m) of the same island. Moreover, populations show little morphological
372 variation, despite occurring over vast geographic distances. Such patterns of ecological tolerance
373 coupled with abundance and lack of variation are classic signatures of recently arriving (invasive
374 or other) species (Williamson & Fitter, 1996; Sakai *et al.*, 2001). However, the current study
375 shows that both *T. tahitiensis* and *D. gibbosa* have been extant in the region since before the
376 Pliocene. Given the close matching of the colonization pattern to the geographical arrangement
377 of islands across the landscape, in turn associated with their geological formation, it is likely that
378 the lineages simply “hopped” between paleo-islands, reaching the current islands some time after
379 their appearance, but with no evidence of recent (< 1 Ma) movement between islands (with the
380 exception of Moorea and Raiatea).

381 A small number of other lineages are also known to show ancient allopatric divergence despite
382 little ecological change (Schneider & Moritz, 1999). Most of these diversification events appear
383 to have been the result of changes in topography that, instead of opening up new habitats, have

384 served simply to isolate a previously more widespread species. For example, isolated
385 mountaintops and other continental refugia can lead to long periods of evolution in isolation,
386 without any ecological change giving rise to patterns of considerable genetic distance between
387 morphologically similar species from different isolates. Similarly, diversification of snails on
388 islands has frequently been attributed to topographical isolation (e.g. Crete, (Gittenberger, 1991);
389 Madeira, (Cameron *et al.*, 1996)). In general it appears that ancient divergence in these groups
390 has not been accompanied by any adaptive shifts.

391 The question posed by the current study on the two species of uloborid spiders is: Why do taxa
392 that show ancient divergence, also show the signature of early colonizers by displaying broad
393 physiological tolerances and being locally abundant? The generalist strategy appears also to be
394 found in the related New Zealand species *Waitkera waitakerensis* which is frequently the most
395 numerous orb-weaver in forests and found in kauri-podocarp-hardwood, lowland podocarp-
396 hardwood, and lowland hardwood forests (Opell, 2006). Thus, lack of ecological specialization
397 may be common to the different genera of uloborids throughout the Pacific, with Pacific island
398 genera being represented by an average of 2.5 species (1-5 species) (Fig. S1), and *D. tennella*
399 being the only example of ecological specialization. The overall lack of specialization is
400 particularly striking in comparison with other spider lineages in Hawaii as well as the islands of
401 French Polynesia, which frequently show extreme habitat specialization, often associated
402 adaptive diversification (Gillespie, 2016).

403 The generalist nature of these ancient and highly diverged lineages also runs counter to the well-
404 known pattern of the taxon cycle (Wilson, 1961) developed for ants in exactly the same region:
405 taxa tend to go through a cycle of colonization into lowland marginal habitats, but then evolve
406 towards lower population densities and greater ecological specialization, and ultimately
407 extinction, allowing relative age of a taxon in the archipelago to be assessed based on taxonomic
408 differentiation among island populations (Ricklefs, 2012). Such cycles have also been identified
409 through detailed molecular studies of West Indian birds (Ricklefs & Bermingham, 2002).
410 Mechanisms to explain this pattern are based mostly on the development of interactions with
411 other members of the community: colonizing species tend to be highly productive populations
412 without many parasites or predators; over time, 'counteradaptation' leads to a reduction in
413 population productivity with concomitant habitat contraction and reduced abundance (Ricklefs,

414 2011).

415 Ecological generalism might be maintained in any situation which favours environmental
416 averaging, such as higher rates of spatial diffusion, mutation, and local extinction (empty patches
417 filled from the surroundings) (Loeuille & Leibold, 2014), conditions that might be expected in
418 organisms subsequent to initial colonization of an area. If high rates of colonization and gene
419 flow are maintained, or if extinction remains high, then generalism might also be maintained.
420 But if spatial diffusion is low, as shown in the current study, then the expectation is for
421 development of specialization. Yet, the Pacific uloborids appear to be ancient generalists,
422 inhabiting vast areas of Oceania over very long time periods. We can speculate on several non-
423 exclusive possible reasons as to why this group of spiders shows such an anomalous pattern:
424 First, lack of specialization may be due to the small size of many of the islands, as diversification
425 often requires a minimum area (Losos & Schluter, 2000). However, other spider lineages in
426 many of these same islands show extreme ecological specialization (Gillespie *et al.*, 2008a).
427 Second, the biology of uloborid spiders may prohibit specialization: The spiders are unusual in
428 lacking cheliceral venom glands; instead, they employ a strategy of wetting and densely
429 wrapping their prey (Weng *et al.*, 2006). If venoms play a role in species diversification, as has
430 been suggested in Hawaiian spiders (Binford, 2001), lack of venoms may make specialization on
431 specific prey types less likely. Third, although divergence between islands may be ancient, their
432 ecological generalism and abundance may be a recent effect of predator extinctions: It is well
433 known that the native birds on these islands have suffered massive extinction, and also that
434 spiders can respond strikingly to the absence of arthropodivorous birds (Rogers *et al.*, 2012). A
435 final possibility is that, after the initial establishment, additional lineages were somehow unable
436 to establish. The taxon cycle is predicated on the establishment of new competitors in the
437 generalist niche (Wilson, 1961). Priority effects may be sufficiently strong such that new
438 colonists cannot displace the resident species (Shaw & Gillespie, 2016). Priority effects may
439 also help explain the lack of overlap between these different lineages that have complementary
440 distributions in the Pacific (Fig. S1).

441 Additional studies are clearly needed to determine the processes involved in promoting or
442 preventing ecological specialization. Given that the endemic island lineages in the current study
443 are frequently found in low elevation sites that are monopolized by non-native species, the

444 results have further implications for understanding attributes of taxa and communities that might
445 allow them to persist or resist invasion by non natives.

446

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457

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612

613 **Supporting Information**

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

615 **Appendix S1.** Morphological Affinities of Pacific Uloboridae

616 **Appendix S2.** Maximum likelihood phylogeny – RaxML tree

617 **Appendix S3.** Collecting sites across the archipelagos.

618

619 **Biosketch**

620 **Rosemary Gillespie** has been working on the evolutionary biogeography of Pacific spiders for
621 almost 30 years. Her research uses islands of known age and isolation to assess the combined
622 temporal and spatial dimension of biogeography (see EvoLab, <http://evolab.berkeley.edu>). Author
623 contributions: RGG conceived the ideas, conducted the fieldwork, much with GKR, and led the
624 writing of the paper. RGG and MSB collected the molecular data; RGG, MSB, and GKR analysed
625 the data.

626

627 Editor: Luis Valente

628

629

630 Table 1. Habitat characteristics for spiders collected from the different sites in Fiji (*Daramulunia*
631 *gibbosa*, *Dg*, and *D. tenella*, *Dt*) and the archipelagos of the Societies and Australs (*Tangaroa*
632 *tahitiensis*, *Tt*) used for the current study (for complete list with localities, see Appendix S3).

633 Column “H” represents the habitat type, from white (coastal or beach) to vertical lines (low
634 elevation forest), horizontal lines (montane forest) and black (cloud forest). Column “D”

635 represents the level of disturbance/ modification of the habitat in which the spider was collected
636 from light hatch (entirely modified), to vertical lines (modified/ secondary vegetation),
637 horizontal lines (largely native) and black (almost entirely native). Sp. = species. * Habitat is
638 forest unless otherwise noted. Elv = elevation (m). NS – no sequences data for this marker.

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639 **Table 1.**

Island	Sp	H	D	Elv (m)	Forest * habitat	GenBank accession#	
						18S	COI
FIJI							
Viti Levu	<i>Dg</i>			150	low	KX668549	KU956064
Viti Levu	<i>Dg</i>			150	low	KX668550	KU956084
Viti Levu	<i>Dg</i>			150	low	KX668551	KU956073
Viti Levu	<i>Dg</i>			520	montane rain	NS	KU956083
Viti Levu	<i>Dg</i>			575	montane rain	KX668554	KU956087
Viti Levu	<i>Dg</i>			780	montane rain	KX668552	KU956085
Viti Levu	<i>Dg</i>			933	cloud	NS	KU956072
Viti Levu	<i>Dt</i>			933	cloud	NS	KU956086
Taveuni	<i>Dg</i>			90	low	NS	KU956079
Taveuni	<i>Dg</i>			700	montane rain	KX668553	KU956078
Taveuni	<i>Dt</i>			700	montane rain	NS	KU956081
Taveuni	<i>Dt</i>			700	montane rain	NS	KU956080
Koro	<i>Dg</i>			115	low	NS	KU956077
Koro	<i>Dg</i>			342	low	NS	KU956076
Koro	<i>Dg</i>			465	low	NS	KU956075
Koro	<i>Dg</i>			505	low	NS	KU956088
Koro	<i>Dg</i>			505	low	NS	KU956074
AUSTRALS & SOCIETIES							
Raivavae	<i>Tt</i>			400	montane	NS	KU956063
Raivavae	<i>Tt</i>			400	montane	NS	KU956057
Rapa	<i>Tt</i>			5	coastal	KU956091	KU956062
Rapa	<i>Tt</i>			5	coastal	NS	KU956070
Rapa	<i>Tt</i>			450	montane	NS	KU956061
Rapa	<i>Tt</i>			450	montane	NS	KU956056
Rapa	<i>Tt</i>			600	cloud	NS	KU956055
Rapa	<i>Tt</i>			650	cloud	NS	KU956058
Rurutu	<i>Tt</i>			120	low	NS	KU956059
Rurutu	<i>Tt</i>			120	low	NS	KU956060
Tubuai	<i>Tt</i>			50	low	NS	KU956082
Moorea	<i>Tt</i>			270	low	NS	KU956065
Moorea	<i>Tt</i>			280	low	NS	KU956071
Moorea	<i>Tt</i>			400	montane	KU956089	KU956066
Moorea	<i>Tt</i>			115	cloud	NS	KU956068
Raiatea	<i>Tt</i>			949	cloud	KU956090	KU956069
Tahiti	<i>Tt</i>			210	cloud	NS	KU956067

641

642

643 Figure captions

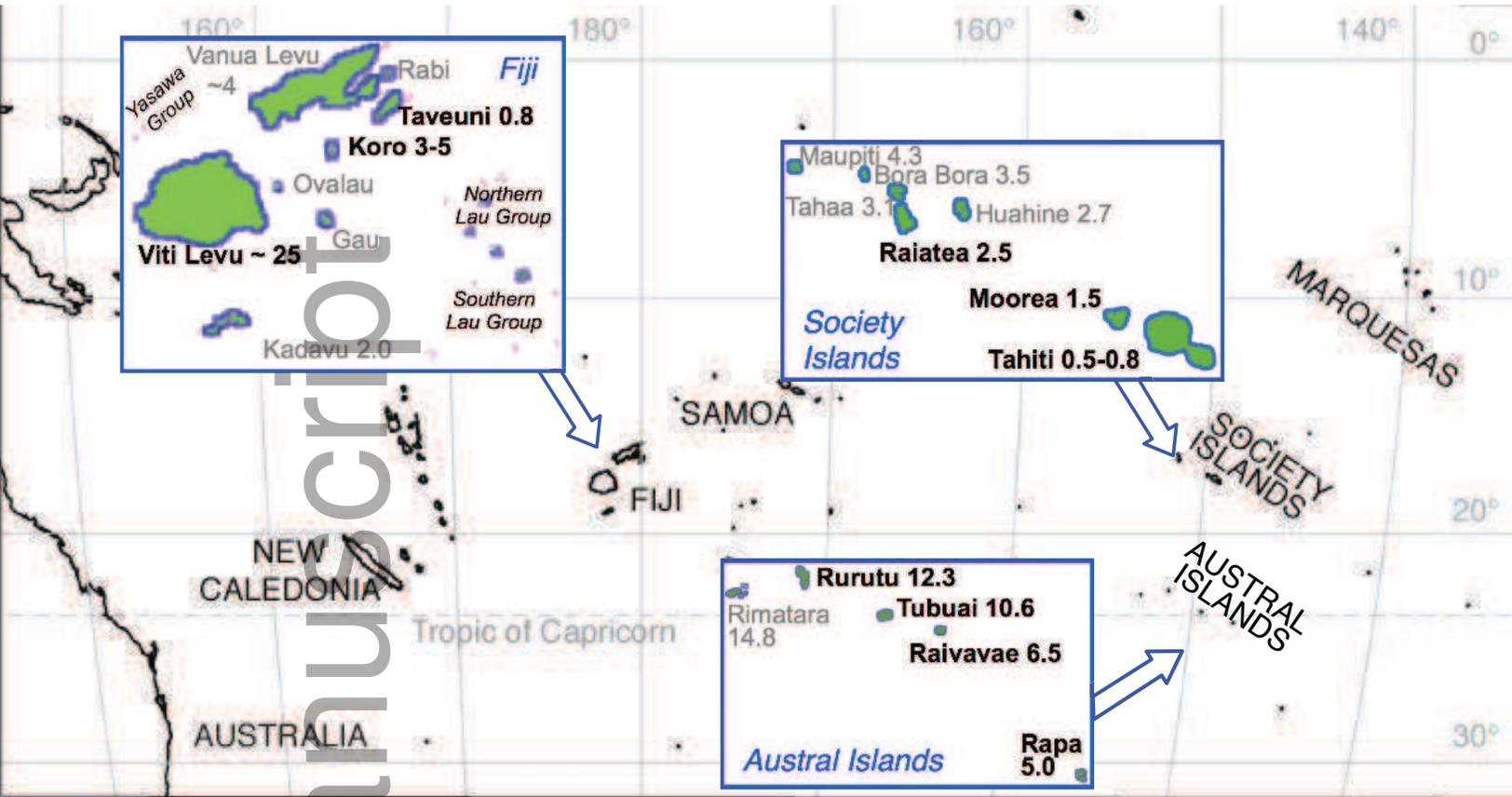
644 **Figure 1.** Island groups in the south Pacific, noting Fiji, and the archipelagoes of the Societies
645 and Australs in French Polynesia shown as a Mollweide projection. Geologic ages (Ma) are
646 provided for each of the main islands. Fiji originated as an ancient continental island, made up of
647 Viti Levu and Vanua Levu, though the subaerial (above water) extent is much younger; the
648 smaller islands in between are largely volcanic in origin and also much younger than the oldest
649 rocks. Dates represent the earliest emergence of Viti Levu, Vanua Levu and Koro (Sarnat &
650 Economo, 2012) and the estimated Pliocene age of Koro (Colley, 2009). In French Polynesia,
651 both the Society and Austral chains are separate volcanic hotspots, with the Australs being
652 considerably older than the Societies; dates are for mean island ages (Craig *et al.*, 2001; Clouard
653 & Bonneville, 2005).

654
655 **Figure 2.** Phylogenetic relationships among Pacific Uloboridae. The BEAST tree with dating of
656 major nodes (see text) shows that the Fiji *Daramulunia* and the French Polynesia *Tangaroa* are
657 roughly similar in age, and supports the suggested affinity of *Tangaroa* with *Waitkera* (Opell,
658 1979; Coddington, 1990) and of *Daramulunia* as a separate group from *Tangaroa*. Calibrations
659 are given using the standard arthropod molecular clock estimate of 3.54% per million years
660 (Papadopoulou *et al.*, 2010). Posterior probabilities are given at each node. Bars indicate the age
661 range (95% highest posterior density interval, HPD) at each node.

662
663 **Figure 3.** A. Biogeography of *Tangaroa* in the archipelagoes of the Societies and Australs of
664 French Polynesia islands. Based on the Dispersal-Extinction-Cladogenesis model (DEC or
665 Lagrange) as implemented in RASP, the figure shows that the different islands are monophyletic,
666 the biogeography dictated mostly by hops from one island to the next closest island, though
667 mostly in order of geological appearance and associated geographical distance. The inset shows
668 the island arrangement, with arrows indicating the inferred pattern of colonization from one
669 island to the next. B. Biogeography of *Daramulunia* in the archipelago of Fiji. Based on RASP
670 analysis, the figure shows that the different islands are monophyletic. The green box indicates *D.*
671 *tenella*; all other populations are *D. gibbosa*. Although sampling of islands was limited to Viti

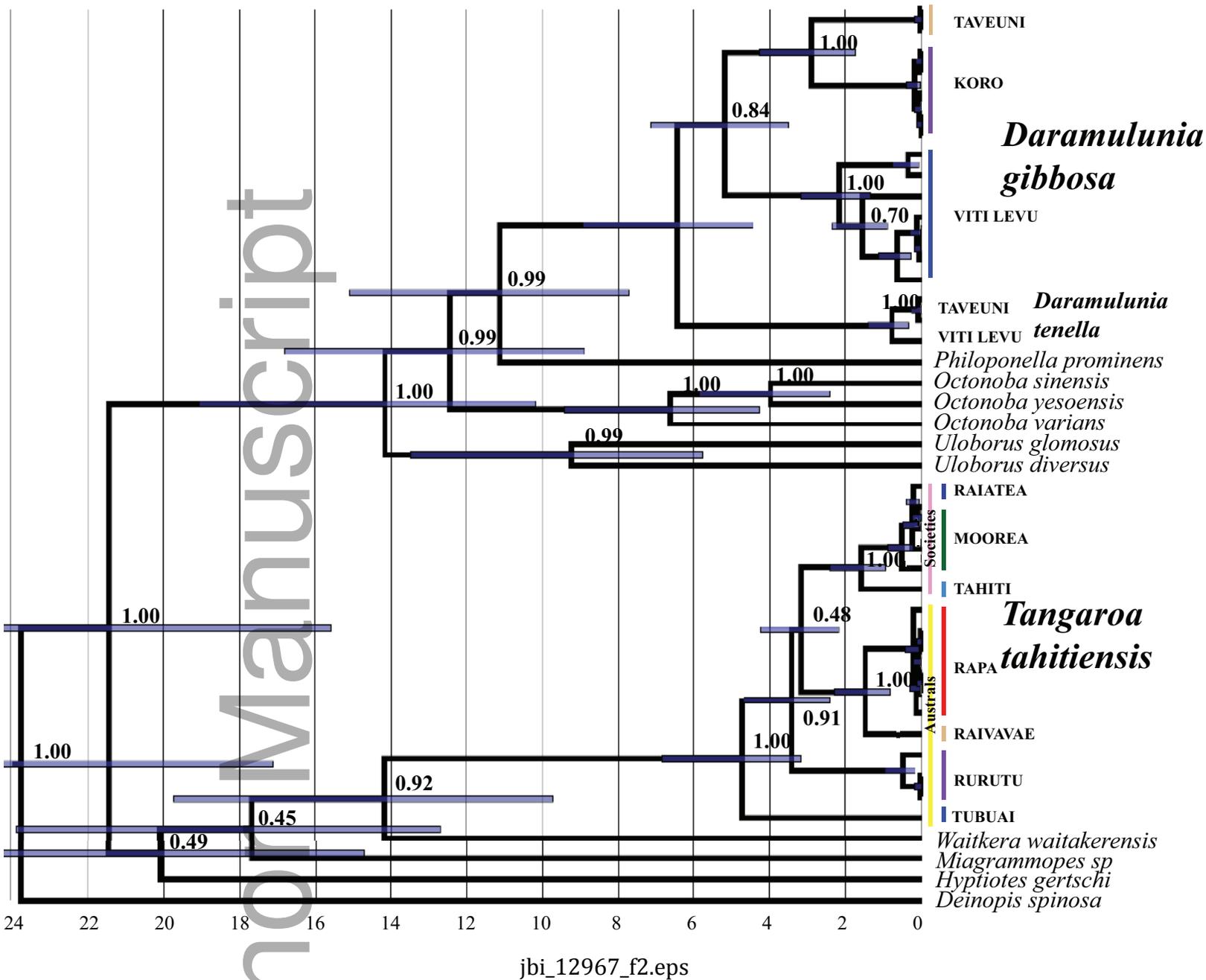
672 Levu, Koro, and Taveuni, the biogeography is consistent with hops between islands in order of
673 geological appearance. The inset shows the island arrangement, with arrows indicating the
674 inferred pattern of colonization from one island to the next.

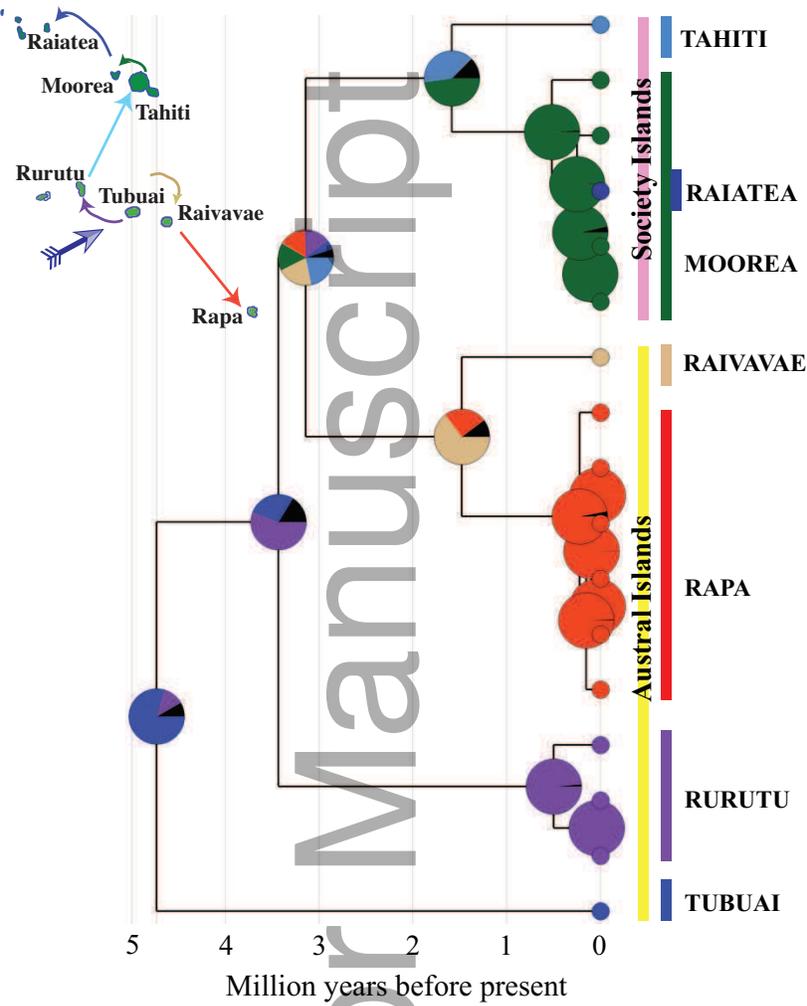
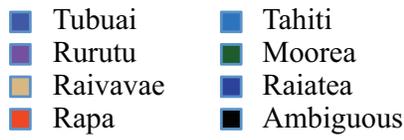
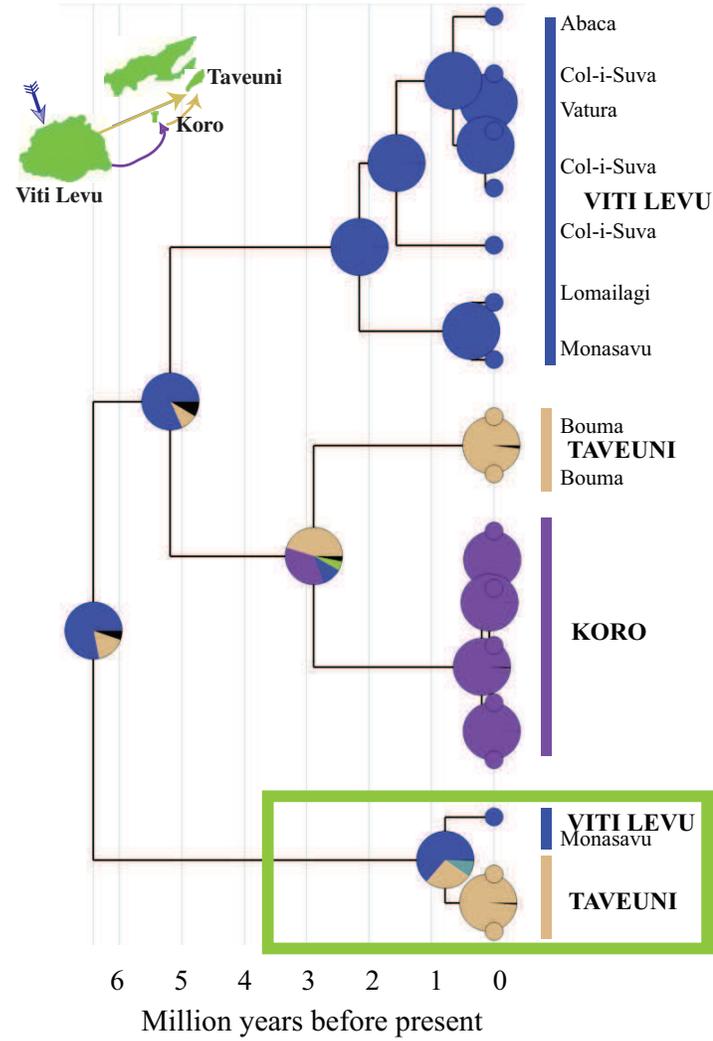
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