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Aedes polynesiensis in the Society Islands: environmental correlates of isoenzyme differentiation

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Abstract. Isoenzyme genetic differentiation of *Aedes polynesiensis* mosquitoes in Raiatea island, French Polynesia, was evaluated by two models of population structure based on seven gene-enzyme systems: Ak, Est, Got, Gpi, Hk, Mdh and Pgm. The ecological model tested whether genetic differentiation is congruent with habitat differences. The isolation model evaluated whether genetic differentiation is proportional to geographical distribution. The ecological model found no significant differentiation between populations of *Ae.polynesiensis* from beach and forest ecotopes, whereas the isolation model was consistent with the data. However, incipient speciation is opposed by the source–sink system of population dynamics in such small neighbouring islands, where *Ae.polynensiensis* extinction is readily followed by reinvasion causing considerable gene flow between island populations.

Key words. *Aedes polynesiensis*, isoenzymes, ecological habitats, genetic differentiation, population genetics, French Polynesia.

Introduction

Aedes (*Stegomyia*) *polynesiensis* Marks, a day-biting mosquito vector of dengue (Rosen *et al.*, 1954) and Bancroftian filariasis (Zahar *et al.*, 1980), has spread through the South Pacific islands from east to west with Polynesian migrations (Buxton & Hopkins, 1927; Davis, 1949). Its ecological plasticity was apparently responsible for the success in this wide dispersal (Marks, 1954; Belkin, 1962). The original natural breeding-sites were probably flooded tree-holes. *Ae.polynesiensis* is now adapted to a wide variety of water-filled man-made containers such as buckets, discarded tyres and drums, wells and water cisterns (Jackowsky, 1954; Lardeux, 1992; Samarawickrema *et al.*, 1993); this mosquito also colonizes coconut shells, rock holes and crab holes. The capacity to tolerate salt concentrations up to 1.5% NaCl (Ingram, 1954) contributes to its successful establishment in new areas where tree-holes are non-existent and crab holes numerous. In French Polynesia, most crab holes harbouring *Ae.polynesiensis* are generated by the gecardinid crab, *Cardisoma carnifex* (Herbst) (Klein & Rivière, 1982).

Polynesian islands can be classified into various ecological and topological types, depending on their geological age. Older mountainous volcanic islands have rainforests covering deep valleys, with abundant breeding places for *Ae.polynesiensis* in flooded rock and tree-holes. Surrounding the high islands, the coastal beaches have abundant terrestral crab populations with holes that constitute the most productive breeding sites of *Ae.polynesiensis*. Coconut shells are ubiquitous. The low islands are mostly atolls, i.e. coral rings 2–3 m above sea level, with *Ae.polynesiensis* breeding prolifically in the innumerable crab holes. Motu are flat islands on the coral reef surrounding volcanic islands, with ecological characteristics similar to the those of the atolls.

Genetic differentiation of *Ae.polynesiensis* according to habitat types was not detected by Silberstein (1978) based on a single esterase enzymatic locus. However, a recent study of *Ae.polynesiensis* by Failloux *et al.* (1996) using multilocus analysis demonstrated strong genetic differentiation between mosquitoes of this species on a motu and those on the main island of Raiatea (lat. 16°50′S, 151°30′W), one of the high volcanic islands of the Society archipelago. Ecological specialisation has also been described: *Ae.polynesiensis* from atolls are autogenous (Rivière, 1983), i.e. they can lay a first batch of eggs without having blood-fed, an adaptation to very nutritive larval habitats (e.g. crab holes), where mammalian hosts are scarce. Coincidence of these two phenomena, i.e. reduced gene flow and ecological specialization, could lead to speciation.

The present investigation of *Ae.polynesiensis* genetic divergences in the Raiatea island group evaluates whether differentiation is

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more correlated with isolation than with ecological difference. Mosquitoes were sampled from several isolated motu surrounding Raiatea, and from various habitat types on the main island.

Material and Methods

Mosquitoes. Adult females of *Ae.polynesiensis* were collected landing on human bait (Bonnet *et al.*, 1956) at fourteen localities during April 1995 (Table 1, Fig. 1). Mosquito specimens were taken to the laboratory alive, identified morphologically, placed in vials and killed by liquid nitrogen storage until used for enzyme characterization.

Sampling localities (Table 1). Six motu were sampled: five of these were small sandy islands on the coral reef, windy and exposed with little vegetation: crab holes and coconut shells were the principal larval breeding sites of *Ae.polynesiensis*. The sixth motu (Haaio) had more substantial geological formation, with soil unstead of coral supporting the growth of dense vegetation with tree holes as well as crab holes for breeding sites of *Ae.polynesiensis*. Beaches around the main island of Raiatea were sandy, with plentiful crabs holes as prolific mosquito larval habitats. Forest habitats in Raiatea dense inland vegetation, hot and humid, with numerous flooded tree-holes, mainly in *Inocarpus fagifer* Parkinson (Fabaceae).

Isoenzyme characterization. Electrophoretic procedures used were described by Pasteur *et al.* (1988). Single adult homogenates were submitted to starch gel electrophoresis in TME 7.4 buffer systems. Seven enzymes were studied: Pgm (phosphoglucomutase, E.C. 2.7.5.1.), Est (esterase, EC 3.1.1.1.), Mdh (malate dehydrogenase, E.C. 1.1.1.37.), Ak (adenylate kinase, E.C. 2.7.4.3.), Hk (hexokinase, E.C. 2.7.1.1.), Got (glutamate oxaloacetate transaminase, EC 2.6.1.1.) and Gpi (Glucophosphoisomerase, E.C.5.3.1.9.). The Mangaréva strain of *Ae.polynesiensis* from Gambiers archipelago (lat. 23°10′S, 135°00′W) was used for control mobility (Failloux *et al.*, 1997).

Table 1. Ecotope samples of *Aedes polynesiensis* from Raiatea island group, April 1995. 'Motu' are dry, flat, sandy small islands situated on the coral reef barrier. 'Beach' surrounds the main island. 'Forest' is tree-clad humid inland places on the main island.

Sample No.	Name	Ecotope	Locality
1	Ofetaro	Motu	Uturoa
2	Taoru	Motu	Uturoa
3	Tipaemaua	Motu	Avera
4	Oatara	Motu	Opoa
5	Haaio	Motu/forest	Fetuna
6	NaoNao	Motu	Fetuna
7	Opeha	Beach	Avera
8	Opoa	Beach	Opoa
9	Plage	Beach	Opoa
10	Tahoata	Beach	Fetuna
11	Tupua	Forest	Uturoa
12	Hotopuu	Forest	Opoa
13	Aihau	Forest	Fetuna
14	Nuutere	Forest	Fetuna

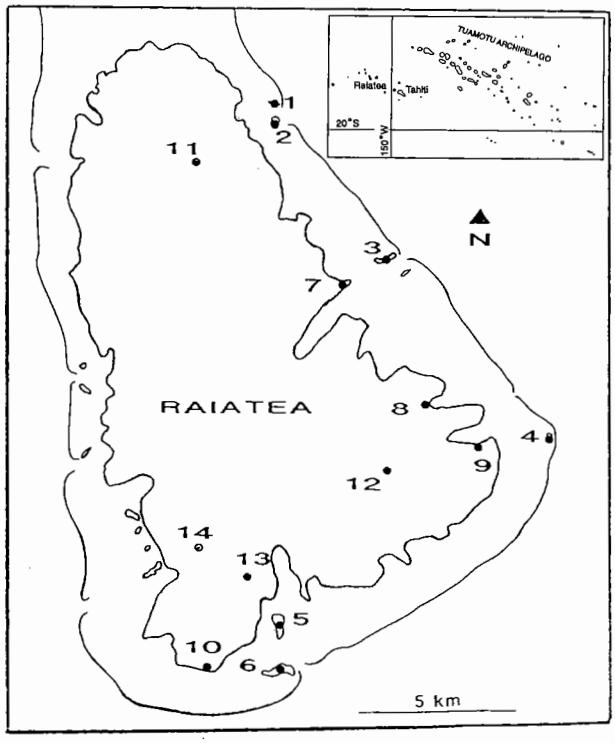

Fig. 1. Sampling stations in Raiatea island group among the Society Islands. Inset: location of Raiatea in relation to Tahiti and the other Polynesian islands.

Statistics. Data were analysed using 'Genepop' software version 2.0 (Raymond & Rousset, 1995). Statistical independence of each pair of loci was first tested by option 2 of 'Genepop'. Genotypic differentiation was measured by the Weir & Cockerham (1984) F_{st} estimator (measuring the fraction of all genetic variation due to the difference between subpopulations), and was tested by using an *F*st-based exact test as available in 'Genepop' ver. 2.0. An overall measure of differentiation for all loci was obtained using the weighting proposed by Weir & Cockerham (1984), and Fisher's (1970) method was used for a global test across loci. The significance level for each test was adjusted by the sequential Bonferroni method (Holm, 1979) to take the other tests into account. Isolation by distance was tested according to Slatkin (1993), following Pasteur *et al.* (1995).

Results

Enzyme polymorphism

The seven enzymes examined revealed eleven putative enzymatic gene loci. Mpi electrophoretic profiles were uninterpretable: Gpi was monomorphic: Hk1 and Hk3 displayed one predominant allele (frequency from 0.95 to 1) and one or two rare alleles in some samples. These four loci were not considered further. Est-1 was also excluded from the analysis due to possible selection acting at this locus (Failloux *et al.*, 1996). Genetic analysis was therefore based on the five remaining loci: Pgm, Mdh, Got1, Got2 and Est2 (Table 2).

Table 2. Allelic frequencies observed at five loci for fourteen *Ae.polynesiensis* samples from three ecotopes (see text for explanations). (*N*) refers to the sample size. Alleles are coded by a letter.

	Main island																			
	Motu								Beach						Forest					
Locus	1	2	3	4	5	6	Mean	SD	7	8	9	10	Mean	SD	11	12	13	14	Mean	SD
Pgm																				
(N)	30	30	30	30	30	30			29	29	30	29			30	30	30	30		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.005	0.01
B	0.82	0.55	0.58	0.77	0.68	0.62	0.67	0.11	0.72	0.74	0.68	0.67	0.70	0.03	0.70	0.62	0.77	0.67	0.69	0.06
C	0.18	0.45	0.47	0.23	0.32	0.38	0.34	0.12	0.28	0.26	0.32	0.33	0.30	0.03	0.30	0.37	0.23	0.33	0.31	0.06
Mdh																				
(N)	30	30	32	30	30	30			28	29	30	30			34	30	30	28		
A	0.13	0.17	0.03	0.45	0.00	0.13	0.15	0.16	0.04	0.00	0.00	0.00	0.01	0.02	0.00	0.02	0.07	0.00	0.02	0.03
B	0.87	0.83	0.97	0.55	0.98	0.87	0.84	0.16	0.96	1.00	0.97	0.97	0.97	0.02	1.00	0.93	0.93	1.00	0.96	0.04
C	0.00	0.00	0.00	0.00	0.02	0.00	0.003	0.01	0.00	0.00	0.03	0.03	0.01	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Got1																				
(N)	30	32	32	30	30	30			28	29	30	30			34	30	30	28		
A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.01	0.02	0.04	0.02	0.05	0.02	0.030	0.01
C	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	0.93	0.95	0.97	1.00	0.96	0.03	0.94	0.98	0.95	0.98	0.96	0.02
D	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.02	0.03	0.00	0.02	0.02	0.02	0.00	0.00	0.00	0.005	0.01
Got2																				
(N)	29	31	32	30	30	30			27	30	30	30			34	30	30	28		
A	0.29	0.16	0.06	0.02	0.28	0.10	0.15	0.11	0.15	0.27	0.30	0.28	0.25	0.07	0.31	0.28	0.27	0.21	0.27	0.04
B	0.60	0.81	0.94	0.98	0.72	0.90	0.82	0.14	0.85	0.73	0.70	0.72	0.75	0.07	0.69	0.72	0.73	0.79	0.73	0.04
C	0.11	0.03	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Est2																				
(N)	30	30	32	30	30	30			28	30	30	30			34	30	30	30		
A	0.01	0.00	0.00	0.00	0.00	0.00	0.002	0.004	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
B	0.02	0.00	0.00	0.02	0.03	0.05	0.02	0.02	0.00	0.02	0.05	0.05	0.03	0.02	0.04	0.01	0.07	0.02	0.03	0.03
C	0.97	1.00	1.00	0.98	0.97	0.95	0.98	0.02	1.00	0.98	0.95	0.95	0.97	0.02	0.96	0.97	0.93	0.98	0.96	0.02
D	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.005	0.01

Linkage disequilibrium

The five loci studied were found to assort independently. Genotypic equilibrium between pairs of loci within each population was statistically significant in all but three cases out of ninety tests performed, not different from the expected proportion under the null hypothesis for the significance level of 0.05. None of these three cases remained significant when the number of tests performed was taken into account (Holm, 1979). As the latter procedure is conservative, another approach was undertaken to detect the possibility of a low but systematic disequilibrium: for each pair of loci the *P*-values of the above tests were combined across populations (Fisher's method). Statistical independence was not rejected: $P > 0.05$ for all pairs of loci.

Population differentiation

Comparing all samples (Table 3), their isoenzyme differentiation was highly significant ($P < 10^{-5}$) and relatively elevated ($F_{st} = 0.042$), conforming with the degree of local differentiation reported within Raiatea island (Failloux *et al.*, 1997).

A model (Fig. 2A) of local differentiation according to ecological characteristics was then evaluated. This model assumes that samples from the same hatibat type are not differentiated. This prediction was fulfilled for forest ($F_{st} = -0.009$, $P > 0.5$) and beach ($F_{st} = -0.009$, $P > 0.5$) habitats on the main island of Raiatea, but not for motu habitats (Table 3) where the local differentiation ($F_{st} = 0.084$) was highly significant ($P < 10^{-5}$). The ecological model was used to assess differentiation between samples from different habitats using pooled data for samples from forest habitats versus samples from beach habitats (lacking intra-habitat diversity). When tested for inter-habitat differentiation between these pooled samples, the degree of differentiation was found to be low ($F_{st} = -0.005$) and not significant ($P > 0.05$). Hence the ecological model of local differentiation was not supported by the present data.

The model (Fig. 2B) of differentiation due to local isolation was employed to test for the possibility of reduced gene flow between the main island and surrounding motu. This model assumes that samples from the two ecotopes (beach and forest) on Raiatea main island are not differentiated, samples from motu

Table 3. Measure and test of genotypic differentiation among populations of *Ae.polynesiensis* in Raiatea at different levels of subdivisions. F_{st} refers to the Weir & Cockerham (1984) estimator of the *F*st parameter. Unbiased estimate of *P*-values of the F_{st}-based exact test are given in parentheses. Bold characters indicate significant ($P < 0.05$) values.

	*F*st (*P*-value)					
Subdivision:	Pgm	Mdh	Got1	Got2	Est2	All
All samples	0.010	0.179	0.003	0.034	0.001	0.042
	(0.07)	(**<10⁻⁵**)	(0.24)	(**0.002**)	(0.42)	(**<10⁻⁵**)
Model A						
Intra habitat						
Forest	–0.002	0.020	–0.012	–0.022	–0.002	–0.009
	(0.44)	(0.16)	(0.74)	(0.86)	(0.46)	(0.65)
Beach	–0.012	–0.003	–0.007	–0.009	0.005	–0.009
	(0.85)	(0.62)	(0.64)	(0.53)	(0.36)	(0.86)
Motu	0.036	0.166	–	0.094	0.003	0.084
	(**0.005**)	(**<10⁻⁵**)	–	(**0.0004**)	(0.30)	(**<10⁻⁵**)
Inter habitat						
Forest *v* Beach	–0.004	–0.001	–0.003	–0.007	–0.003	–0.005
	(0.74)	(0.41)	(0.53)	(0.76)	(0.63)	(0.88)
Model B						
Main island	–0.008	0.005	–0.010	–0.018	–0.001	–0.011
	(0.78)	(0.23)	(0.83)	(0.88)	(0.47)	(0.85)
Motu *v* Main island						
Motu 1	0.024	0.157	0.002	0.020	–0.005	0.029
	(0.08)	(**0.001**)	(0.36)	(0.15)	(0.77)	(**0.005**)
Motu 2	0.039	0.228	0.003	0.004	0.010	0.039
	(**0.035**)	(**<10⁻⁴**)	(0.35)	(0.25)	(0.22)	(**0.0001**)
Motu 3	0.020	–0.010	–0.003	0.087	0.011	0.043
	(0.09)	(0.93)	(0.34)	(**0.01**)	(0.22)	(0.03)
Motu 4	0.002	0.658	0.002	0.134	–0.004	0.194
	(0.30)	(**<10⁻⁵**)	(0.35)	(**0.002**)	(0.71)	(**<10⁻⁵**)
Motu 5	–0.009	–0.010	0.002	–0.016	–0.009	–0.011
	(0.89)	(0.93)	(0.35)	(0.82)	(1.0)	(0.98)
Motu 6	0.005	0.156	0.002	0.051	–0.005	0.033
	(0.24)	(**0.003**)	(0.37)	(**0.04**)	(0.71)	(**0.008**)

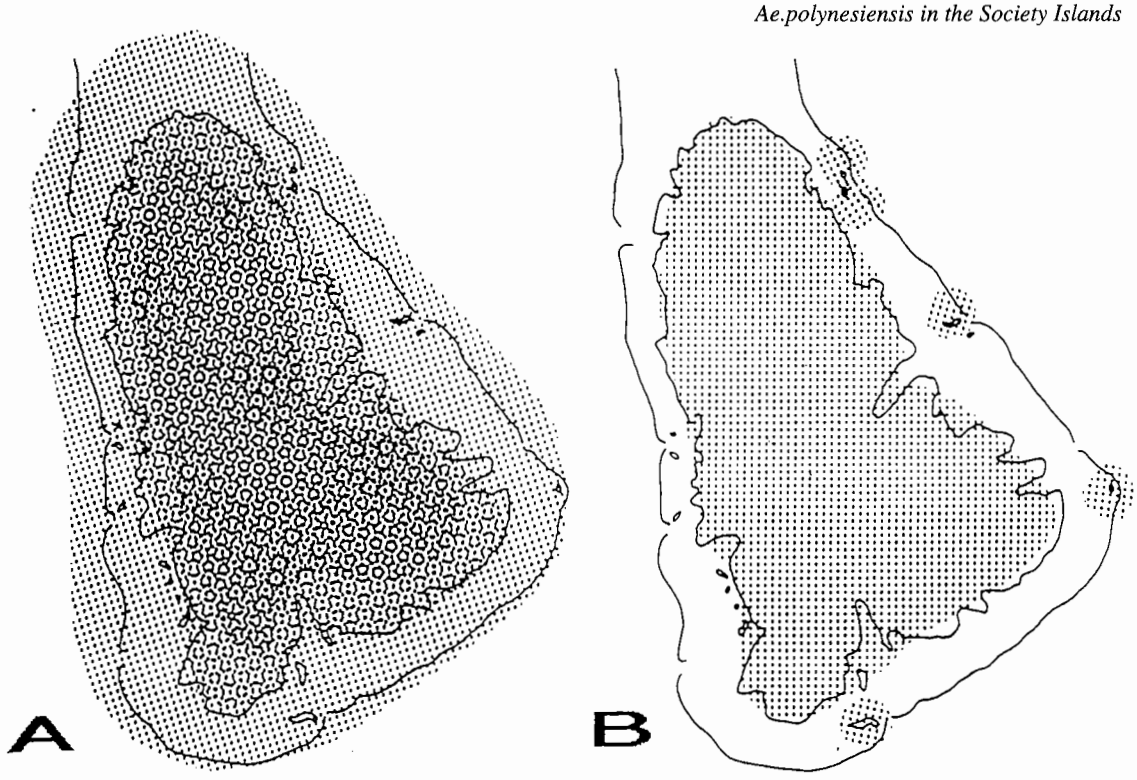

Fig. 2. Main models of population subdivision tested: subpopulation areas shown by differential shading. (A) Ecological differentiation; each ecological habitat is genetically homogenous and differentiated from the others. (B) One large undifferentiated population on the main island and differentiated populations on each isolated motu.

are expected to be significantly differentiated from each other and from the mainland. Among all samples from Raiatea main island (Table 3), differentiation is low (F_{st}=–0.011) and non-significant (P=0.85). In addition, F_{st} estimates between pairs of samples do not increase (P>0.8) with the geographical distance separating the samples, suggesting an absence of isolation by distance in Raiatea main island. When these samples are pooled and compared with each of the six motu samples (Table 3), differentiation was significant in five cases (F_{st}: 0.029 to 0.19, P=0.00001 to 0.03) but not for motu 5 (F_{st}=–0.011; P=0.98). These results are consistent with the model of differentiation by isolation between the main island and the motu. Comparisons between motu showed a high differentiation ($P<10^{-5}$).

Discussion

Isoenzyme frequency differences were confirmed among *Ae.polynesiensis* mosquito populations from islands of the Raiatea group in French Polynesia. This supports the classic geographical isolation concept of genetic divergence, potentially leading to speciation (MacArthur & Wilson, 1967). Conversely, no differentiation was found between *Ae.polynesiensis* samples from beach and forest ecotopes, so the ecological model of population divergence was rejected. The relative homogeneity of *Ae.polynesiensis* populations from contrasted habitats may be due simply to their lack of isolation until comparatively recently. These two models are not exclusive and both could operate at the same time. The absence of divergence and of isolation by distance within the Raiatea main island suggest that seawater separating the main island from the motu plays a larger role in genetic differentiation than geographical distances *per se*.

Flat oceanic islands, motu and atolls, are mainly coralline. The part of the island with the recent extension of copra production (*Cocos nucifera* L.), have replaced indigenous trees such as *Pisonia grandis* (L.) that provided tree-hole breeding places of *Ae.polynesiensis*. Nowadays, *Ae.polynesiensis* breeds mainly in crab holes (Rosen, 1954) and wet coconut shells which are particularly abundant in poorly maintained coconut groves (Bonnet *et al.*, 1956). Crab burrows generally have their main chamber flooded at ground water level, providing water for larvae and shelter for adult *Ae.polynesiensis* (Klein & Rivière, 1982). Whereas water-filled coconut shells are very exposed to evaporation, crab holes are less sensitive to climate variations, but they are vulnerable to inundation by seawater during storms and hurricanes. Local extinctions of *Ae.polynesiensis* in such habitats have been documented, e.g. three in 1982 (Rivière, 1988), although larvae may survive in breeding places such as the tree-holes of *Pisonia grandis*, axils of 'taro' plants (*Colocasia esculenta* L.), and in elevated coral structures, 'feo', sometimes found in the centre of an atoll. After local extinction of *Ae.polynesiensis* occurs on a motu, recolonization probably comes from the main island, either via adult mosquito flight dispersal or via accidental transportation of dormant mosquito eggs in containers via human traffic motivated by coconut harvesting and tourist activities. After local extinction occurs on an atoll, recolonization is more likely to be by mosquito flight from a nearby atoll. In French Polynesia, most atolls are found in the Tuamotu archipelago, where *Ae.polynesiensis* probably constitutes a metapopulation (Olivieri

et al., 1990) with frequent extinctions and recolonizations of local subpopulations.

If associated with local adaptation, such as selection for autogeny as well as differentiation and other genetic factors, isolated motu populations are theoretically prone to speciation (Coyne, 1992). However, the polynesian motu are generally too small and unstable for speciation to occur. Recolonization may involve few individuals, enhancing random diversity due to founder effects.

Gene flow between the main island and motu is reminiscent of a source–sink system (Dias, 1996), where adaptation in the sink population (motu) is diluted by gene influx from the source population on Raiatea island. *Ae.polynesiensis* populations in motu are usually self-sustaining, and are therefore not a true sink, although recolonization following occasional extinctions demonstrates the occurrence of gene flow despite the genetic differentiation detected in this study. Speciation could not operate in this scenario. It remains to be seen whether incipient speciation can be detected in places where motu are either larger, more numerous (thus enhancing the survival probability of *Ae.polynesiensis* populations during adverse climatic conditions) or more isolated from different ecological habitats preventing gene pool swamping in source–sink systems. Some isolated and inhabited atolls of the Tuamotu archipelago (Fig. 1) are good candidates to investigate such possibilities.

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