Influence of quaternary sea-level variations on a land bird endemic to Pacific atolls

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Little is known about the effect of quaternary climate variations on organisms that inhabited carbonate islands of the Pacific Ocean, although it has been suggested that one or several uplifted islands provided shelter for terrestrial birds when sea-level reached its highest. To test this hypothesis, we investigated the history of colonization of the Tuamotu reed-warbler (*Acrocephalus atyphus*) in southeastern Polynesia, and found high genetic structure between the populations of three elevated carbonate islands. Estimates of time since divergence support the hypothesis that these islands acted as refugia during the last interglacial maximum. These findings are particularly important for defining conservation priorities on atolls that endure the current trend of sea-level rise owing to global warming.

Keywords: atolls; sea-level variations; refugia; reed-warblers; phylogeography

1. INTRODUCTION

Changes in global climate during the Pleistocene and Holocene have had major impact on land biota (Lomolino *et al.* 2005). For many organisms, genetic population structure has been found to reflect these climatic oscillations (Hewitt 2000). Biota were also modified indirectly by the eustatic sea-level variations that led to the creation of new islands, which often achieved higher levels of endemism by isolation through time (e.g. Vasconcelos *et al.* (2006) for reptiles in the Mediterranean islands; Mayr & Diamond (2001) for birds in the Solomon Is.). In the tropical oceans, sea-level variations have had more influence on low-lying atolls than on the large, elevated, volcanic or carbonate islands for which area and age mainly determine the richness and diversity of biota (Mayr 1941). Most atolls within the Pacific Ocean cap old volcanoes rooted in oceanic lithosphere. Deep drilling has shown that atolls were emergent limestone plateaus with rugged karstic relief during glacial Quaternary periods, when sea-levels were below the present sea-level. For example in the Tuamotu archipelago, southeastern Polynesia (figure 1a), data from Moruroa reveal that sea-level was 135–143 m lower during the peak of the last glaciation (17–23 kyr ago; Camoin *et al.* 2001). The Tuamotu archipelago (the largest chain of atolls in the world with 76 atolls spread over ca 1750 km) formed at that time a series of high islands. When sea-level rose during interglacial periods, reef growth formed the layer-cake sequences of carbonate deposits that enclosed the eroded limestone plateaus. However, when sea-level was at its highest

(highstand maxima), the eustatic rise in global sea-level resulted in the flooding of the atoll piles (Pirazzoli & Montaggioni 1986; Woodroffe 2008). The flooding of these islands implies that insular biota regressed and eventually disappeared before the conditions were again favourable after the decline in sea-level.

This sequence of extinction and recolonization has been investigated for several marine organisms in the Tuamotu (Arnaud-Haond *et al.* 2003; Fauvelot *et al.* 2003; Thompson *et al.* 2005). These studies focused on lagoon specialists that suffered from the decline or suppression of shallow waters during glacial episodes. Currently, little is known about the effect of Quaternary climate variations on terrestrial organisms that live in the atolls of the Pacific Ocean. The Tuamotu reed-warbler (*Acrocephalus atyphus*) is an endemic small passerine bird that inhabits at least 74 per cent of the atolls of the archipelago and was probably more widespread before its habitat was recently altered by humans. Previous phylogenetic studies on reed-warblers in the Pacific suggested that the Tuamotu reed-warbler diverged from the northern Marquesas reed-warbler (*A. percernis*) approximately 600 kyr ago (Cibois *et al.* 2007a, 2008). Hence, the Tuamotu reed-warbler withstood the Quaternary sea-level variations, implying that one or several islands provided refugia for the birds during the peak of sea-level highstands. Thibault (1974) hypothesized that one or several carbonate islands that were uplifted in the early Pleistocene as the result of lithospheric loading by the Tahiti-Moorea-Mehetia complex (Montaggioni 1989) might constitute these refugia. To test this hypothesis, we analysed the variation of mitochondrial sequences and nuclear markers of reed-warblers from several atolls of the Tuamotu, including the main elevated carbonate islands as well as low-lying atolls that currently reached no more than 3 m above sea level.

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Figure 1. (a) Location of the Tuamotu archipelago in the Pacific Ocean. (b) mtDNA haplotype tree. The three haplotypes found in the Tuamotu are indicated by black, grey and white dots. The northern Marquesas reed-warbler was used as an outgroup. Hatch marks along branches represent nucleotide changes.

2. MATERIAL AND METHODS

(a) Sampling

A total of 168 reed-warbler samples were collected from 10 atolls (see the electronic supplementary material, table S1) in 2004–2008. Sample size per atoll varied from 8 to 21 individuals (see the electronic supplementary material, table S2). Birds were caught with mist-nets, using playback of recorded songs, and blood and/or tail feather was sampled for genetic analyses. Because of the strong territorial habits of reed-warblers, most of the individuals attracted and caught were males.

(b) Mitochondrial DNA

The mitochondrial control region II was amplified and sequenced with the primers BCML4 and FTH3 (Hansson *et al.* 2008). Genomic DNA was extracted, amplified and sequenced using standard protocols. Contiguous sequences derived from the set of sequence fragments were created using SEQUENCHER (Genecodes, Ann Arbor, Michigan). Three individuals of the northern Marquesas reed-warbler were used as outgroups. All sequences are deposited in GenBank (accession no. GU045 564–GU045 568).

(c) Microsatellite loci

Ten microsatellite loci originally developed for the Seychelles brush warbler (*Acrocephalus sechellensis*) were genotyped: Ase9, Ase12, Ase13, Ase18, Ase19, Ase34, Ase40, Ase42, Ase51 and Ase55 (Richardson *et al.* 2000). Microsatellite

fragments were amplified using a touch-down polymerase chain reaction (PCR) as described in the original publication. Genotyping was conducted on a 310 Genetic Analyzer (Applied Biosystem) using multiplex PCR (Qiagen). Results were visualized using GENE SCAN ANALYSIS 3.1.2. (Applied Biosystem). Four loci (Ase9, Ase40, Ase19 and Ase55) were not polymorphic for the Tuamotu reed-warblers and were not included in the analysis. The genetic diversity of the remaining six loci (Ase13, Ase18, Ase34, Ase12, Ase51 and Ase42) was quantified for allelic richness, observed and expected heterozygosity. These statistics were estimated using ARLEQUIN (Excoffier *et al.* 2005) and Microsatellite Analyser (Dieringer & Schöterer 2003). Deviations from Hardy–Weinberg genotype frequency equilibrium were tested with ARLEQUIN (10 000 permutations). Subpopulation structure (Wahlund effect), presence of null alleles, inbreeding or selection at or near a microsatellite locus can cause HWE departures (Dakin & Avise 2004). The atolls Hardy–Weinberg equilibrium morphology (contiguous ring of land or islets connected by small arms of the sea) and their small size suggest that reed-warbler populations are panmictic within an island and subpopulation structure is unlikely. Presence of null alleles was tested with FREENA (Chapuis & Estoup 2007). Our dataset, which did not include genetic information from related individuals, was not designed to test for inbreeding or selection at or near a microsatellite locus.

(d) Genetic analysis

We used PAUP (Swofford 2003) to reconstruct the phylogenetic tree using the mitochondrial data with neighbour-joining (NJ, uncorrected distances) and maximum parsimony (MP, heuristic search, 100 replicates) algorithms. Population genetic structure was estimated using the microsatellite data and RST-CALC (Goodman 1997). This method is useful for microsatellite data because it assumes a stepwise mutation model, and differences in sample size between populations and variation between the variance of loci are also incorporated in the estimation of R_{st} . However, Gaggiotti *et al.* (1999) suggested that F_{st} should be used when samples sizes are moderate or small (less than 10) and number of loci low (less than 20); consequently, F_{st} values estimated using ARLEQUIN were shown as well. Sequential Bonferroni corrections were applied when appropriate. Bayesian assignment of individuals to clusters without using prior information of the sampling locations was conducted using STRUCTURE 2 (Pritchard *et al.* 2000) and the microsatellite data. The inferred number of clusters, K , was tested from $K = 1$ to 10. Each run was pursued for 1 000 000 iterations, with a burn-in period of 100 000. A correlated allele frequency and admixture model were used. Convergence was assessed with five independent runs. The inferred number of clusters K was estimated using the value of K with the highest probability: posterior probabilities were computed as indicated in Pritchard *et al.* (2000), and an additional ad hoc statistic (ΔK) was also estimated, following the simulation study of Evanno *et al.* (2005). Isolation by distance was estimated for the population structure inferred by the microsatellite data with Mantel tests, 1000 replicates, conducted in ARLEQUIN. We compared the pairwise R_{st} with the pairwise distances between atolls (distance values in logarithm). Estimation of recent immigration rates (i.e. proportion of migrants) between islands was conducted using BAYESASS 1.3 (Wilson & Rannala 2003) and the microsatellite data. This Bayesian method was favoured over estimations based on F_{st} analogues that require equilibrium conditions (Widlock & McCauley 1999). Twenty million Markov chain Monte Carlo iterations were run, with a burn-in of 1 000 000 iterations and a sample frequency of 2000. Preliminary runs used delta values (i.e. maximum parameter change per iteration) ranging from 0.05 to 0.30, to ensure optimal mixing and maximize log likelihood values as suggested in the software documentation. Confidence intervals were also compared with simulations when there was no information in the data. The final delta values were set to 0.15, 0.05 and 0.15 for the parameters estimated for allele frequency, migration and inbreeding, respectively. Input files for BAYESASS were created using the file converter FORMATOMATIC 0.8.1 (Manoukis 2007).

The average divergence between the mitochondrial haplotypes (D) was used to provide a first estimate for time since divergence between the three uplifted atolls with the expression $t = (D/2\mu)g$, where μ is the mutation rate and g the generation time (2 years, based on other reed-warblers species; Bensch & Hasselquist 1999). To compare with continental populations of great reed-warbler (*Acrocephalus arundinaceus*), we followed Hansson *et al.* (2008) for the range estimation of the mutation rate (10–20% sequence divergence per Myr; see Hansson *et al.* for the original references). We also used IMA (Hey & Nielsen 2007) to estimate time since divergence between the three uplifted atolls using

a coalescence model. Analyses were conducted first with the mitochondrial dataset only, and second with mitochondrial and microsatellite datasets combined in the same input file. Several runs were sampled with a burn-in period of 10^5 steps and sampling period of 10^6 steps, using 10 to 100 chains and a geometric heating scheme. We examined different parameter values (from 10 to 100) for estimating θ and t , as suggested in the software documentation. Similar results were obtained when varying these parameter values. A range of mutation rates can be given as prior to the analysis for scaling parameter estimates in demographic units. We used the range of divergence rates described above for our 527 base pairs control region sequences and let IMA calculate mutation rates scalars for the other loci (i.e. no mutation rate was specified for the microsatellite loci). Runs were monitored by observing effective sample size (ESS) values and inspecting parameter plots for trends. Preliminary runs suggested that convergence was difficult to reach when all parameters were estimated: consequently, we simplified the model and assumed that the migration rates between the three refugia were null ($m1 = m2 = 0$). This assumption was suggested by the haplotype network and supported by the results of the BAYESASS analysis (see below).

3. RESULTS

Only three haplotypes were obtained for the mitochondrial control region sequences in the Tuamotu, with six transitions between each pair of haplotypes (corresponding to a divergence of 0.011). The mitochondrial haplotype tree (identical using NJ or MP algorithms) indicates reciprocal monophyly and differentiation between the three uplifted islands, Ana'a, Niau and Makatea, with no variation within population and no variation for the seven other atolls that all share the same haplotype, identical to that found in Makatea (figure 1b). Two haplotypes were obtained for the three individuals of the northern Marquesas reed-warbler, which diverged by one transition among them. Variability of the six microsatellite loci is summarized in the electronic supplementary material. R_{st} averaged over the six loci was high (0.22; 95% CI 0.15–0.34), and pairwise R_{st} indicated significant genetic structure between 53 per cent pairs of atolls (table 1). Non-significant values were found mainly for comparison involving Takapoto (78% of its pairwise values), Manihi (67%) and Napuka (67%). We obtained similar results with F_{st} (overall $F_{st} = 0.29$, table 1).

Bayesian clustering analysis revealed five as the best estimation for the number of clusters among Tuamotu reed-warblers (figure 2 and the electronic supplementary material, figure S1). The posterior probability of K was maximum for $K = 5$ and close to zero for all remaining values of K . ΔK also indicated a strong signal for $K = 5$. Assignment results were very similar for the second best model ($K = 4$; figure 2). Three of the inferred five clusters corresponded to the three main uplifted islands, Makatea, Ana'a and Niau (see the electronic supplementary material, table S3). The two remaining clusters did not have a simple geographical interpretation, although almost half (48%) of the individuals from Tikehau and Takapoto were assigned to the same cluster. Most of the individuals from the other low-lying atolls were not

Table 1. Pairwise R_{st} estimates (below diagonal) and F_{st} (above diagonal) averaging the variance components over loci. (Values in bold are those significantly different from zero after Bonferroni correction.)

	Fa'aite	Takapoto	Ana'a	Makatea	Napuka	Hao	Manihi	Mataiva	Niau	Tikehau
Fa'aite		0.0159	0.1488	0.3256	0.1185	0.1100	0.0196	0.2549	0.2855	0.2295
Takapoto	0.0327		0.2448	0.3944	0.1873	0.2252	0.0805	0.3400	0.3578	0.2602
Ana'a	0.0100	0.0631		0.4786	0.2237	0.1078	0.2107	0.2757	0.3726	0.4152
Makatea	0.2044	0.2429	0.1468		0.2944	0.4879	0.2177	0.3707	0.3213	0.4117
Napuka	0.1467	0.0499	0.1839	0.2718		0.1910	0.0571	0.0901	0.0363	0.4654
Hao	0.1586	0.0509	0.2031	0.2940	0.0729		0.1975	0.3270	0.3371	0.4897
Manihi	0.0052	0.0019	0.0633	0.2327	0.0571	0.1423		0.1932	0.2138	0.2470
Mataiva	0.1362	0.0688	0.1378	0.2315	0.0097	0.2087	0.0578		0.174	0.4779
Niau	0.1556	0.1017	0.2261	0.2902	0.0084	0.1627	0.0480	0.1033		0.5487
Tikehau	0.0033	0.2132	0.0047	0.1920	0.4735	0.5399	0.1476	0.4798	0.4790

Figure 2. Bayesian assignment probabilities of individuals to clusters. Colour indicates the probability of an individual's genotype to be assigned to a particular lineage. Three of the clusters correspond to the main uplifted islands, Makatea, Ana'a and Niau. Average likelihood values for $K=1$ to 10 over five independent runs were -1246.9 , -1155.8 , -1102.3 , -1066.6 , -1064.8 , -1105 , -1111.9 , -1087.8 , -1102.6 and -1141.04 , respectively (see also the electronic supplementary material, figure S1). Assignment results are shown for $K=5$ (the model selected by ΔK) and $K=4$ (second best model).

assigned significantly to a particular cluster, except for three individuals from Fa'aite, two from Mataiva and six from Hao that were assigned with $p > 80\%$ to the Ana'a cluster. Estimation of migration rates with nuclear markers suggested that dispersal between islands is currently a very rare event: none of the recent migration rates among populations differ significantly from zero ($m \approx 0.02$; see the electronic supplementary material, table S4). Additionally, no pattern of isolation by distance was detected between populations ($r = 0.015$, $p = 0.46$, Mantel test between the R_{st} pairwise matrix and the distance between atolls matrix). Assuming a constant molecular clock for the control region sequences, we obtain a first estimation of divergence time for the three uplifted islands, Ana'a, Niau and Makatea between 57 and 114 kyr. Divergence times estimated under a coalescence model were similar for mitochondrial data (approx. 100 kyr) but younger estimates (4–25 kyr) were found when microsatellite data were added (table 2 and the electronic supplementary material, figure S2).

Table 2. Divergence times between uplifted islands from the coalescence model. (Results from the longest run are shown, with ESS more than 200 and no trend observed in the parameters plot. Effective population size estimates were consistent among uplifted island pairs and suggested values of less than 10 000 individuals per island (see the electronic supplementary material, figure S3). These estimates are compatible with the small size of these islands.)

	T (years), peak values with 90% highest probability density
mitochondrial DNA (mtDNA) only	
Makatea–Ana'a	102 000 (13 500–190 000)
Makatea–Niau	90 000 (13 500–190 000)
Ana'a–Niau	102 000 (13 000–195 000)
mtDNA and microsatellites	
Makatea–Ana'a	25 000 (5000–120 000)
Makatea–Niau	11 000 (3500–46 000)
Ana'a–Niau	4000 (4000–46 000)

4. DISCUSSION

Mitochondrial data indicate the reciprocal monophyly of three groups: (i) Ana'a, (ii) Niau and (iii) Makatea and the seven other atolls. The nuclear markers also identify three clusters that correspond to the main uplifted islands, but the situation for the remaining localities (the low-lying atolls) is less defined: most of the individuals from the low-lying atolls were not assigned significantly (i.e. with $p > 80\%$) to a cluster and in particular none were assigned to the cluster corresponding to Makatea. No climatic or geologic data suggest a drastic and recent reduction of reed-warbler numbers in Makatea that could have induced a shift in its microsatellite profile. On the other hand, reed-warblers colonized at least 58 low-lying atolls spread over several hundreds of kilometres. The seven low-lying atolls studied represent a wide selection within the archipelago (figure 1a) and no pattern of isolation by distance was detected between populations (see results of the Mantel test). However, several intermediate populations were obviously not sampled and this could confuse the assignment analysis. Additionally, each new atoll was probably colonized by a very small number of individuals because unlike other insular passerines like white-eyes (*Zosterops*), reed-warblers do not form flocks. We did not observe a significant reduction

of genetic variation for the low-lying atolls (see the electronic supplementary material), but further analyses may be necessary to investigate the effect of founder events in the low-lying atoll populations.

Overall we observed that F_{st} (mitochondrial) was greater than F_{st} (nuclear), which is consistent with differences in coalescence time for mitochondrial and nuclear loci owing to differences in effective population size (Zink & Barrowclough 2008). Because males of Tuamotu reed-warblers are highly territorial, it is probable that dispersal is female-biased like other *Acrocephalus* species (Eikenaar *et al.* 2008). The reciprocal monophyly of the marker with maternal mode of inheritance (i.e. the mitochondrial marker) suggests that dispersal between islands does not occur frequently: for example, Fa'aite is the closest atoll to Ana'a (70 km apart) but their populations do not share the same mitochondrial haplotype. This observation is consistent with the estimation of migration rates with nuclear markers, suggesting that dispersal between islands is rare. Thus, the assignment of a few individuals from low-atolls to Ana'a in the STRUCTURE analysis is more likely to result from incomplete lineage sorting owing to the larger effective population size of nuclear markers than to recent dispersal between islands.

Estimates of divergence times between the three uplifted islands post-date the last interglacial maximum (Marine Isotope Stage 5e at approx. 125 kyr ago) when sea level reached approximately 6 m above the present sea surface in the Pacific Ocean (Camoïn *et al.* 2001; Dickinson 2001). Results from the mitochondrial data analysis suggest that the three uplifted islands acted as refugia during this highstand, whereas the younger estimates found with nuclear markers could be linked to their longer coalescence time. Similar results were obtained for bird populations inhabiting sky islands in North America, with earlier estimates found using the microsatellite data combined with the mitochondrial sequences (McCormack *et al.* 2008). Mitochondrial data suggest moreover that when sea-levels fell, Makatea was the main source for the recolonization of the low-lying atolls, which all possessed the same haplotype. Makatea is the most elevated carbonate island in the Tuamotu, reaching 113 m above sea level, with an area of 28.4 km². It consists of a large plateau encircled by cliffs, with no lagoon. Even though its habitat has been extensively altered, there are more reed-warblers in Makatea than on other Tuamotu islands (Cibois *et al.* 2007b). Because of its large size and elevation, it is probable that this island acted as the main reservoir for Pleistocene recolonization events in the Tuamotu.

Nuclear data suggest that recent migration rate is very low between islands; consequently, the low genetic structure found for Takapoto, Napuka and Manihi (table 1) is more likely to be owing to incomplete lineage sorting after a recent recolonization than to current exchange of genetic materials with other populations. This low differentiation could be linked to a recent episode of highstand in the mid-Holocene (5–2 kyr ago), when the sea-level rose to 0.8–1 m above the present sea-level (Pirazzoli & Montaggioni 1988; Dickinson 2004). This increase in sea-level had a limited overall impact on reed-warbler populations, but could have led to a drastic reduction or disappearance of reed-warblers on some atolls owing to their remoteness or geomorphology. Likewise,

modifications of the shoreline owing to the Holocene highstand were demonstrated when studying the human coastal settlements in Tonga (Dickinson *et al.* 1994) and the same influence was suspected for human settlement in the Tuamotu (Pirazzoli & Montaggioni 1986).

The inundation of low atolls during sea-level highstands is often proposed as one of the causes for the low endemism of flora in the Tuamotu, in addition to the islands' remoteness and small size (Mueller-Dombois & Fosberg 1998). Prebble & Dowe (2008) suggested that the extirpation and extinction of several palm species on oceanic islands may have resulted from rising sea-level. However, fossil evidence is lacking on atolls because of inadequate depositional settings. Plant endemism is highest in Makatea and Niau, which have for instance their one endemic palm tree (genus *Pritchardia*, Arecaceae). It is thus probable that these islands, and perhaps other uplifted islands, also acted as refugia for plants during sea-level highstands. Additional genetic studies on endemic terrestrial organisms will be necessary to investigate the global role played by uplifted islands during Quaternary sea-level maxima.

5. CONCLUSION

The results of this study provide insight into the effects of past sea-level variations on the terrestrial fauna of atolls in the Pacific Ocean. The current trend for sea-level increase owing to global warming is likely to affect insular habitats in the near future, especially on the low-lying atolls. Estimates of the global average sea-level rise by the end of the twenty first century vary according to studies and models, but an increase close to 1 m is not improbable (Church & White 2006; Pfeffer *et al.* 2008). This would place the Tuamotu in a situation comparable to the mid-Holocene highstand that affected the population of reed-warblers in several low-lying atolls. It is probable that an increase of 1 m is sufficient to damage the land biota of the narrowest and lowest islands, especially during storms or tsunamis (Woodroffe 2008). Climate change over the last 30 years has already produced shifts in both the distributions and abundances of organisms, and estimates of extinction risks linked to climate change are considerable (Thomas *et al.* 2004). In this context, we stress the importance of the conservation of the three elevated carbonate islands' populations, Niau, Ana'a and Makatea, which are most likely to survive the next sea-level maximum. The preservation of the population of Makatea is particularly crucial because this island was the main source for recolonization events. Substantial conservation effort is required for this island which has already suffered severe habitat destruction owing to phosphate extraction during the twentieth century (Gargominy *et al.* 2006).

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