

## On the origin of sympatric fruit doves in a small and remote Pacific archipelago

By Alice Cibois\*, Jean-Claude Thibault, Jean-Yves Meyer and  
Eric Pasquet

### Abstract

Fruit doves of the genus *Ptilinopus* (Columbidae) form a large group of more than 50 species that have been successful in colonizing most of the Pacific Ocean, with sympatric species on several small oceanic islands. A new phylogeny of this genus and allies (Cibois et al. 2014) showed that all these cases of sympatry derived from multiple independent colonizations, with the exception of the Marquesas Islands (Eastern Polynesia) where the two fruit doves that occurred sympatrically are sister species: the Red-moustached Fruit Dove *Ptilinopus mercierii* and the White-capped Fruit Dove *Ptilinopus dupetithouarsii*. Both Marquesas fruit doves coexisted on several Marquesas islands until the recent extinction of the Red-moustached Fruit Dove. Here, we analyse their morphology, review their life history, and discuss the two most likely scenarios for the divergence of the two species, in light of the geological history of the Marquesas hotspot volcanoes (5.5 -1.1 Ma). The microallopatry scenario takes into account the large initial size of the islands and involves partitioning of the fruit doves distributions within the same island, whereas in the intra-archipelago scenario, the birds' speciation occurred on different islands, in conjunction with their sequential emergence. We discuss both hypotheses and conclude that the estimated time of divergence of the two species and the known ecology of the birds favor the intra-archipelago scenario.

\*Corresponding author. E-mail: [alice.cibois@ville-ge.ch](mailto:alice.cibois@ville-ge.ch)

This **early view** paper has been peer-reviewed and accepted for publication in *Pacific Science*. However, it has not been copy-edited nor has it undergone typesetting for *Pacific Science*. The final published paper will look different due to formatting changes, but scientific content will remain the same.

## Introduction

The occurrence of sympatric speciation, i.e. the divergence within the same place of distinct groups of organisms that could be recognized as taxonomic species, is a much debated subject in evolutionary biology (Fitzpatrick et al. 2008). Evidence supporting this is scarce (Coyne and Corr 2004), and in many cases an allopatric phase of differentiation, occurring at a very small scale (e.g. “microallopatry”), cannot be ruled out. Most examples of putative sympatric speciation are from islands, where the isolation of populations can be easily evaluated. For birds, the few possible cases are reviewed in Coyne and Price (2000) and in Grant and Grant (2010). The three best examples of sympatric speciation are all from relatively small oceanic islands (less than 10,000 km<sup>2</sup>): buntings (*Nesospiza* spp., Thraupidae) in the Tristan da Cunha group (Ryan et al. 2007), finches (*Geospiza* spp., Thraupidae) in the Galapagos Islands (Grant and Grant 2010), and storm-petrels (*Oceanodroma* spp., Hydrobatidae) in Eastern Atlantic islands (Friesen et al. 2007). The latter case refers to a special scenario of allochrony, i.e. the occurrence on the same island of two distinct breeding periods, specific to each divergent population.

Birds are usually considered highly mobile and this could explain the rarity of sympatric speciation in this group. However, bird populations can be isolated by a barrier at a very small scale on the same island or archipelago: for instance, the Mascarene Grey White-eye (*Zosterops borbonicus*, Zosteropidae) show population differentiation caused by altitude or natural barriers like lava fields on Réunion Island in the Indian Ocean (Mila et al. 2010), and in the Fiji archipelago in the Pacific Ocean, the Orange Fruit Dove group (*Chrysoena* spp.) is composed of species endemic to islands separated by sea distances less than 100 km (Gibbs et al. 2001). These examples suggest that microallopatric speciation does occur for insular birds, despite their initial dispersal capacity that permitted the colonization of remote oceanic islands.

Among insular birds, the fruit doves (*Ptilinopus* spp. and their close allies *Drepanoptila*, *Alectroenas* and *Chrysoena*; Columbidae) represent one of the groups having species that occur

sympatrically on the same island. With more than 50 species, fruit doves are distributed on both sides of the Wallace Line (Gibbs et al. 2001). They are particularly diverse on the large continental island of New Guinea, which was found to be the ancestral area for several nodes within the phylogeny, as shown in the biogeographic analysis of the group (Cibois et al. 2014). All fruit doves are arboreal and frugivorous, and many species playing an important role in seed dispersal of insular ecosystems (Shanahan et al. 2001a,b, Steadman 1997b, Steadman and Freifeld 1999). On oceanic islands, all cases of sympatric fruit doves correspond to the coexistence of two species, except in Fiji where three species (Crimson-crowned Fruit Dove *Ptilinopus porphyraceus*, Many-colored Fruit Dove *P. perousii*, and Orange Fruit Dove *Chrysoena victor*) coexist on the same small island (Laucala, 12 km<sup>2</sup>) (Watling 1989 and pers. com.). In each case, the sympatric species have colonized the island independently and at different times (Cibois et al. 2014). This result supports the hypothesis that for fruit doves, like for most birds, speciation occurs in allopatry.

We found, however, an exception to this pattern in the Marquesas Islands (Eastern Polynesia), where the two fruit doves that occurred sympatrically on several islands in historical times are also sister species on the phylogenetic tree: the Red-moustached Fruit Dove *Ptilinopus mercierii* and the White-capped Fruit Dove *Ptilinopus dupetithouarsii*. Their divergence was estimated at ca. 2 Ma (Cibois et al. 2014). This result supports the hypothesis of Diamond (1977) of one rare case of “*intra-archipelago speciation*”, as opposed to the double colonization scenario proposed by most authors (Cain 1954, Goodwin 1967, Holyoak and Thibault 1978, Mayr 1940, 1942, Ripley and Birckhead 1942). But how did this speciation occur on one of the most remote archipelagos in Oceania? Our aim in this paper is first to review the life history and to analyze the morphology of the two species. Then, we present geological information on the volcanic formation of the Marquesas archipelago, and discuss the most likely scenarios for the emergence of the two sympatric fruit doves.

## MATERIALS AND METHODS

We compiled data on the Marquesas fruit doves biology from the available literature and from the examination of specimens stored in the following museums: MNHN Muséum National d'Histoire Naturelle (Paris), AMNH American Museum of Natural History (New York), NHM Natural History Museum (Tring), NML National Museum Liverpool, and USNM National Museum of Natural History, Smithsonian Institution (Washington). The first detailed account of the Marquesas avifauna comes from the Whitney South Sea Expedition, led by the AMNH in 1921-22, and the unpublished journals of this expedition were a major source of information on the fruit doves biology (Beck ms, Quayle ms). We conducted a morphometric analysis on measurements of 15 White-capped Fruit Doves and 8 Red-moustached Fruit Doves collected on Hiva Oa (all adult males, specimens held at the AMNH and NML). Measurements consisted of wing length, bill length from skull, bill length from nostril, bill width (at nostril), bill height (at nostril), tarsus length, and tail length. Measurements were first examined through an ANOVA (one-way analyse of variance,  $K=2$ ,  $N=23$ ) using R (R Core team 2013). Then we used principal components analysis (PCA) on standardized variables to summarize patterns of variation in the morphometric data in producing independent composite variables (PC axes). The PCA analysis was conducted using the package ggbiplot in R (Vu 2011). The fruit doves molecular phylogeny and analysis of plumage evolution were conducted by Cibois et al. (2014). The genes used for the molecular phylogeny were three mitochondrial genes (ND2, ND3, COI) and two nuclear genes (FGB exons 5 to 6 and intron 5, and RAG1); however mitochondrial genes only were sequenced for the extinct Red-moustached Fruit Dove. Finally, we summarized the information available from the literature on the volcanic formation of the Marquesas archipelago.

## RESULTS

### *Distribution of Marquesas fruit doves*

The Red-moustached Fruit Dove (hereafter RMFD) is now extinct. It was a polytypic species with nominate *mercierii* (DES MURS & PRÉVOST, 1849) on Nuku Hiva, known by a single specimen collected in 1848 and held at the MNHN (Voisin et al. 2004), and *tristrami* (SALVADORI, 1892) on Hiva Oa, with 12 specimens found in collections: 1 at the NML (the type), 7 at the AMNH, 1 at the USNM, and 3 at the NHM. Sub-fossil records from Ua Huka, identified as cf. *P. mercierii*, suggest the possibility of a more widespread distribution within the archipelago in the past (Fig.1) (Steadman 1989). The RMFD was never seen again on Nuku Hiva after its discovery. On Hiva Oa, it was rare at the beginning of the 20th century (Ripley and Birckhead 1942) and disappeared before the 1970s (Holyoak and Thibault 1984). The White-capped Fruit Dove (hereafter WCFD) is a polytypic species with nominate *dupetithouarsii* (NEBOUX, 1840) in the Northern Marquesas (Nuku Hiva, Ua Huka, Ua Pou), and *viridior* (MURPHY, 1924) in the Southern islands of the archipelago (Hiva Oa, Tahuata, Mohotani, Fatu Iva). Today the WCFD is common on the main islands of the archipelago (Fig.1) and absent on islands where resources of fleshy fruits are absent, due to a degraded vegetation cover (Eiao) or a naturally depauperate flora (Hatutaa, Fatu Huku, Hatu Iti).

### *Life history*

Although data are scarce for the RMFD, evidence suggests that both species were frugivorous like all fruit doves (Gibbs et al. 2001). Several expeditions observed the two species foraging in the same tree, suggesting they occupied the same habitats (Beck ms, Quayle ms, Schmeltz and Krause 1881). On Nuku Hiva, the only known specimen of RMFD was collected in a tree near the shore (Voisin et al. 2004) where the WCFD was common, as it is still today. On Hiva Oa in 1922, the Whitney South Sea Expedition recorded the RMFD mostly inland, whereas the WCFD

was abundant all over the island. Berck (ms) and Quayle (ms) also mentioned that both species perched in the same trees, feeding together on fruits.

#### *Plumage variation*

Both species present a similar pattern of green on the upperparts and yellow or orange on the belly. They differ mostly by the crown and malar patches, red in the RMFD, white in the WCFD (Fig.1). The plumage of the nominate *mercierii* differs slightly from that of *tristrami* (see Gibbs et al. 2001), but the unique known specimen of the nominate taxon is old and its coloration could have been altered. Differences of coloration are well-marked in the WCFD subspecies: the nominate *dupetithouarsii* presents a pronounced orange patch of the belly contrasting with the grey breast, whereas in *viridior* the orange belly-patch is less extensive and the breast is green (Gibbs et al. 2001, Murphy 1924).

#### *Morphological analysis*

All measurements of the RMFD are significantly smaller than values of the WCFD (ANOVA  $P < 0.05$ ; degrees of freedom  $K-1=1$ ,  $N-K=21$ ;  $F$  between 31.9 and 4.9); for instance on average RMFD's wing length is  $138.9 \pm 3.9$  mm, whereas WCFD's is  $148.3 \pm 3.8$  mm. The first axis of the PCA explained most of the variation (51.5%), with the main contribution of wing length, bill length from nostrils, and bill width. Bill height and bill length from skull are the main characters that accounted for the variation of the second axis (19.4% of total variation). The results of the PCA (Fig. 2) show that the RMFD specimens are distinct from the WCFD in Hiva Oa, suggesting that the two sympatric taxa did not present the same morphology.

#### *Molecular phylogeny*

Both RMFD and WCFD belong to a monophyletic group that colonized most Pacific archipelagos, often referred as the “*purpuratus*” group (Cain 1954, Cibois et al. 2014). They are the first lineage to branch off this clade, and are sister-taxa in all analyses with good support (i.e. posterior probabilities  $>0.95$  and bootstrap values  $>70\%$ ; only the *mercierii* clade is not well

supported in the Bayesian analysis, a result probably due to the shorter sequences of some individuals) (Fig. 3). The sampling was based on several RMFD from Hiva Oa (toe pads from specimens held at the AMNH and from the type specimen held at the NML). Unfortunately it was not possible to study the nominate subspecies from Nuku Hiva because we could not retrieve DNA from the only known specimen. The two subspecies of WCFD were sequenced based on fresh material from several islands (Fatu Iva, Nuku Hiva, Tahuata, Ua Huka, and Ua Pou). No reciprocal monophyly was found between the two WCFD subspecies. Although the sampling was limited to a few individuals per islands, the absence of a geographical structure in the genetic data suggested either ongoing gene flow between islands or incomplete lineage sorting between the two subspecies. The fruit dove phylogenetic tree was calibrated using a relaxed clock and fossil data. The Marquesas fruit dove clade represents the first of the two colonizations of Eastern Polynesia, estimated at ca. 5 Ma. The second colonization of Eastern Polynesia involved the Cook, Society, Tuamotu, Austral archipelagos and Henderson Island, and took place more recently at ca. 2 Ma. The genetic distance between the two Marquesas taxa was 1.4% (mitochondrial sequence data, uncorrected distance), and the estimate of time of divergence of the two species was 1.8 Ma (95% CI 0.8 – 2.8 Ma).

#### *Plumage evolution*

The analysis of plumage coloration showed that the red crown (including all variations from orange to purple) is the plesiomorphic state for this character for all fruit doves of the “*purpuratus*” group (Cibois et al. 2014). Three taxa evolved from this red coloration, which is based on carotenoid pigments (Mahler et al. 2003), to other colors probably based on structural coloration (Gill and McGraw 2006): blue in Blue-capped Fruit Dove *P. monacha* (Moluccas), grey in Silver-capped Fruit Dove *P. richardsii* (Melanesia), and white in WCFD in the Marquesas. Experiments have shown that in a feather of the American Goldfinch *Carduelis tristis*, the yellow color was actually produced by a combination of carotenoids pigments with an

underlying white structural coloration (Shawkey and Hill 2005). Thus the white color of the WCFD's crown and malar patches probably results from the disappearance of the carotenoid pigments that are still present in the RMFD. This major change in plumage coloration could constitute a signal for species selection, by character reinforcement in sympatric species after speciation in allopatry (Liou and Price 1994, Sætre et al. 1997).

Fruit doves exhibit in general little intra-specific plumage variation but geographical phenotypic variation occurs in some species: one of the most extreme cases is found within the Rose-crowned Fruit Dove *P. regina*, where a clinal variation of the crown color is observed between populations from Australia (pinkish-red) to Indonesia (pale grey with light lilac tint) (Baptista et al. 1997). Morphs are usually defined as the presence within a species of individuals of the same sex and age with distinct plumages that are genetically determined (Buckley 1987). Because the main difference between RMFD and WCFD lies in a change of their crown and malar patch color, one can ask whether two distinct morphs formed within the same species. This seems however unlikely because of the size difference between the taxa, as well as the deep divergence found in the molecular phylogenetic tree.

#### *Marquesas Islands geology*

The Marquesas archipelago (141°-138° W long. and 7°-11°S lat.) is composed of 11 islands and seamounts, spread over 470 km along a northwest–southeast axis (Fig. 1). Like most islands of Polynesia they are of volcanic origin, formed by a “hotspot” where magma extruded from the earth's mantle through the crust, building huge shield volcanoes. Over time, the weight of a new island, associated with motion from the hotspot, caused a relatively rapid decrease in island elevation and area (Moore et al. 1989, Moore et al. 1994). This phenomenon was particularly spectacular in the Marquesas (Brousse et al. 1990, Desonie and Duncan 1993, Guille et al. 2002, Moore et al. 1989, Moore et al. 1994). Estimates of whole-rock <sup>40</sup>K-<sup>40</sup>Ar isotope ages are given for every island in Table 1 (Guille et al. 2002, Legendre et al. 2005, 2006). Older islands are

located in the northwest (from Eiao to Ua Pou), and younger ones in the southeast (from Hiva Oa to Fatu Iva). The volume of the main islands was considerably larger before the collapse of their caldera: the bulk of underwater debris was estimated from half of the original shield volcano (Nuku Hiva, Ua Huka, and Fatu Iva) to even three-quarters for Eiao (Filmer et al. 1994, Wolfe et al. 1994). Although no modeling was conducted on the Marquesas to estimate the original elevation of the islands, the collapse of a large part of the original volcanoes likely led to a significant decrease of the islands elevation.

Nuku Hiva, where the two fruit doves occurred in the same habitats, is the largest of the northern old islands and very likely played an important role in the beginning of the fruit doves colonization of the Marquesas. Its morphology is typical for the archipelago, with a succession of caldera walls encased toward the south (Brousse et al. 1978, Le Dez et al. 1996). The two main volcanoes (the external volcano Tekao and the internal Taiohae) were active during the 4.8-3.1 Ma period, with a major collapse of Tekao that formed the Toovii plateau around 4 Ma (Le Dez et al. 1996). On Ua Huka and Ua Pou, the areal volcanic activity was particularly long (ca. 2 Ma), interspersed by a period of volcanic quiescence (Guille et al. 2002, Legendre et al. 2005, 2006). This long period of activity could have delayed the establishment of habitats favorable to fruit doves.

The volcanic activities for the southern islands are mostly contemporaneous during the 3-1.6 Ma period, although Fatu Iva is likely the youngest formation of this group (Guille et al. 2002). The largest southern island, Hiva Oa, was formed by a series of volcanoes along a west-east line, characterized by the collapse of the calderas that formed the cliffs surrounding the summits of the island today (Le Dez et al. 1996). The time of this collapse is unknown. The total radiometric data obtained for this group suggest that the aerial volcanic activity lasted for 1.3 Ma.

## DISCUSSION

The two species of fruit doves lived together on at least three islands of the archipelago: Nuku Hiva, Ua Huka and Hiva Oa. Life history data, albeit scarce for the extinct RMFD, indicate that both species shared the same resources and did not live in separate habitats. Although sympatric speciation, linked with different ecological adaptations, cannot be completely ruled out, we consider this hypothesis highly unlikely based on the absence of obvious ecological differences between the two species. Then, two main scenarios can be proposed to explain the speciation in the Marquesas: 1) microallopatry (within island speciation), and 2) intra-archipelago speciation.

The microallopatry hypothesis takes into account the large volume of the main islands, especially in the old northern group, which existed between their emergence and the collapse of the volcanoes' calderas. According to the molecular phylogeny, the fruit doves colonized the archipelago not long after its formation at ca. 5 Ma. At this time, the largest island was Nuku Hiva, where the two fruit doves were still found in historic times (Fig. 4, Period 1). Eiao and Hatuta'a are older, but they were most probably smaller and the presence of fruit doves has never been documented there in historic times. The maximum altitude of Nuku Hiva at the time of its emergence is unknown (1227 m today), but its volume was likely twice that of today (estimated at up to 13,000 km<sup>3</sup>; Wolfe et al. 1994). Its surface was probably covered by large patches of different native habitat types: coastal (littoral) forests, dry (xeric) and semi-dry (mesic) forests in the lowlands, wet (rain) forests in the valleys and uplands, and cloud forests in the mountains. Such diversity could shelter different populations of fruit doves that became isolated by a partitioning of their distributions, in microallopatry (Fig. 4, Period 2). This situation could have lasted until the major collapse of the caldera, ca. 4 Ma: this period of one million years is probably sufficient for speciation in insular birds (see for instance Fleischer et al. 1998 for Hawaiian creepers). Then the collapse of the caldera led to the reduction of half of the island size and put in contact the two populations (Fig. 4, Period 3). The conjunction of isolation and

character displacement at secondary contact could have then led to the different phenotypes of the two taxa, which subsequently colonized the rest of the archipelago (Fig. 4, Period 4). This scenario implies that, at least in Nuku Hiva, the island resources were sufficient, since a short time after its emergence, to sustain several species of frugivorous birds. Although the paleoflora of the Marquesas remains to be studied (Melinda Allen, pers. com.), its sub-fossil record supports this hypothesis with six frugivorous (or partially frugivorous) species that coexisted on several islands in prehistoric times: the two *Ptilinopus* spp. and the Marquesan Imperial Pigeon *Ducula galeata* (Columbidae), plus two extinct *Vini* spp. and the Ultramarine Lorikeet *Vini ultramarina* (Psittacidae) (Steadman 2006). Today the large *Ducula galeata* and the WCFD often share the same fruit resources, but the largest fruits can only be eaten by the Imperial Pigeon, suggesting a possible niche distinction linked to fruit size (McConkey et al. 2004 and pers. obs.). The body size difference between the Marquesan Imperial Pigeon and the WCFD is however much greater than the difference between the WCFD and the RMFD, which probably ate fruits of similar diameter.

The second possible scenario involves an intra-archipelago speciation and takes into account the sequential emergence of the islands. As in the microallopatry hypothesis, the colonization of fruit dove took place in the Northern part of the Marquesas, probably in the largest island Nuku Hiva (Fig. 5, Period 1). From there, this ancestral fruit dove colonized all islands of the archipelago, reaching the southern group after its emergence (Fig. 5, Period 2). Then the two fruit dove populations became isolated, separated by more than 100 km: during this time of isolation their genomes accumulated mutations by drift and local adaptation, and subsequently formed two distinct taxa (Fig. 5, Period 3). Finally, a change in climate or wind regime, or a general increase in the populations' number could have allowed the two taxa to resume inter-island dispersal, leading to sympatric distributions on at least three islands of the archipelago (Fig. 5, Period 4).

The microallopatry scenario implies that the speciation process has been limited to a single island, similar to what happened to the white-eyes on Réunion Island (Mila et al. 2010). Although this scenario provides a simpler explanation for the presence of both fruit doves in the archipelago (a global dispersal after the establishment of the two taxa), the general mobility of fruit doves argues against the isolation of two populations on the same island. Today, the availability of pigeons' and doves' food resources is irregular on Polynesian islands, with the seasonal fruit production of native or endemic species (e.g. the banyan fig-tree *Ficus prolixa* var. *prolixa*). The birds' movements within islands are well known, flying over mountain passes regularly in the search of fruiting trees (Holyoak and Thibault 1984, pers. obs.). The only known exception takes place on the small Henderson Island (37 km<sup>2</sup>), where the Scarlet-capped Fruit Dove (*P. insularis*) may be territorial (Graves 1992). It is difficult however to evaluate what we know of the fruit doves ecology in the context of the initial island conditions, when islands were larger and higher, with pristine native habitats. Those were extensively altered during the last millennium, first by the Polynesians, then by the Westerners (Allen et al. 2011, Bailleul 2001). Regardless of the ecology of the birds, the divergence time of the two taxa, estimated at ca. 2 Ma based on molecular characters, favors the intra-archipelago scenario because it corresponds well to the emergence time of the southern islands group. Part of this scenario (Period 2) evokes the monarchs' (*Pomarea* spp, Monarchidae) colonization of the Marquesas: the phylogeny of the species was consistent with the sequential appearance of the islands, from the northern and oldest group to the southern and youngest islands (Cibois et al. 2004). But the last part of the intra-archipelago scenario (Period 4) also implies a back colonization from younger islands to older ones, a pattern found in the Hawaiian flora and fauna (Cowie and Holland 2008, Havran et al. 2009) but undocumented in the Marquesas Islands. In the microallopatry scenario, the isolation of the two taxa supposedly ended with the reduction of size of the island caused by the collapse

of the main caldera, estimated at ca. 4 Ma: this event predates the divergence time of the two taxa, thus making this scenario less likely.

## CONCLUSION

Our review of the Marquesas fruit doves' life history, morphology and phylogeny, coupled with geological data on the islands, is in favor of the intra-archipelago scenario for the divergence of the two taxa. It is worth noting, however, that this conclusion depends partly on the time of divergence obtained in a previous phylogenetic analysis (Cibois et al. 2014). The past occurrence of other *Ptilinopus* species in the Marquesas can also mislead our analysis: the two Marquesas fruit doves may not be sister species, or one of them could have hybridized with an extinct species and kept the other species's mtDNA haplotype by introgression (see Rheindt and Edwards 2011 for a review of genetic introgression in birds). However we found the existence of other extinct fruit doves unlikely because the sub-fossil record of the archipelago has been well-studied, with new extinct taxa found in all the major landbird groups. Based on this record and on the results of the molecular phylogeny, we consider a sister species relationship between the RMFD and the WCFD to be the most parsimonious hypothesis.

Regardless of the pattern of colonization, on the same island or on separate islands distant by more than 100 km, the occurrence of sympatric sister species is still unique among fruit doves in Oceania: in Fiji, the three *Chrysoena* species that belong to the same radiation do not occur on the same islands. In the Marquesas, the other cases of congeneric sympatric species involve crakes (*Zapornia* spp., Rallidae) and lorikeets (*Vini* spp., Psittacidae), most of them being extinct today. The morphological examination of the sub-fossil data suggests that these taxa originated from multiple independent colonizations (Steadman 2006). Unfortunately, the only genetic study including sub-fossils failed to obtain DNA data from material extracted from Marquesas archeological excavations (Kirchman 2012, on Rallidae). Further phylogenetic studies should be conducted on other sub-fossil material in order to test the colonization patterns of these birds.

Both Marquesas fruit doves conjointly inhabited several islands for a long time, until the extinction of the RMFD less than a century ago. The reasons for its extinction are unclear, but human activities probably played a major role. Habitat degradation (deforestation, fires, introduction of predatory animals, grazing ungulates, and invasive plants), and the hunt for red feathers, a color praised by Polynesians (Stokes 1925), may have conjointly driven the RMFD's extinction (Steadman 1997a). Conversely, the WCFD is still common today throughout its range and even beneficated from introduced fruiting trees as new food resources (Holyoak and Thibault 1984). This suggests that the RMFD was a more vulnerable species, either associated during parts of its life cycle to a type of native habitat becoming rare, or sensitive to introductions and disturbances. Because its extinction precludes the ecological study of the coexistence of the two related species, the sympatric Marquesas fruit doves will remain an enigma for this remote Oceanic archipelago, where islands are relatively small compared to Hawaiian Islands or the Galapagos.

## ACKNOWLEDGMENTS

We are grateful to the following people and institutions: Joel Cracraft, Mary Lecroy and Paul Sweet (American Museum of Natural History), Donna Dittmann and Frederick Sheldon (Louisiana State University), Sharon Birks (University of Washington, Burke Museum), Jon Fjeldså (Zoological Museum of Copenhagen), Clemency Fisher and Tony Parker (National Museums Liverpool), Robert Prys-Jones and Mark Adams (Natural History Museum, Tring), and Erica Spotswood (University of Berkeley). For their help and support during fieldworks in French Polynesia, J-C.T. and A.C. thank Philippe Raust and Thomas Ghestemme (Société d'Ornithologie de Polynésie), Claude Serra (Direction de l'Environnement, French Polynesia), and the Institut de Recherche pour le Développement (IRD Tahiti). We are also grateful to Dick Watling (Environment Consultants Fiji) and Melinda Allen (University of Auckland) for providing additional information, and to Richard Camp, an anonymous reviewer and Curtis Daehler for their helpful comments on the manuscript.

Table 1. Present physical characteristics of the main Marquesas Islands, as synthesized in Guille et al. (2002) and Legendre et al. (2005, 2006).

<b>Island</b>	<b>Age of volcanic activities (Ma)</b>	<b>Area (km<sup>2</sup>)</b>	<b>Elevation (m)</b>
<u>Northern group:</u>			
Eiao	5.5-4.9	40	578
Hatuta'a	4.9-4.7	4	428
Nuku Hiva	4.8-3.1, 4.7-3.0	380	1227
Ua Huka	3.1-2.4, 1.1-0.7	77	884
Ua Pou	4.0, 2.9-2.3	105	1252
<u>Southern group:</u>			
Hiva Oa	3.9-1.8, 2.9-1.6, 1.9-1.8	320	1276
Tahuata	2.9-1.8, 2.0	70	1050
Mohotani	2.3-2.1	15	520
Fatu Iva	2.5-1.9, 1.2	84	960

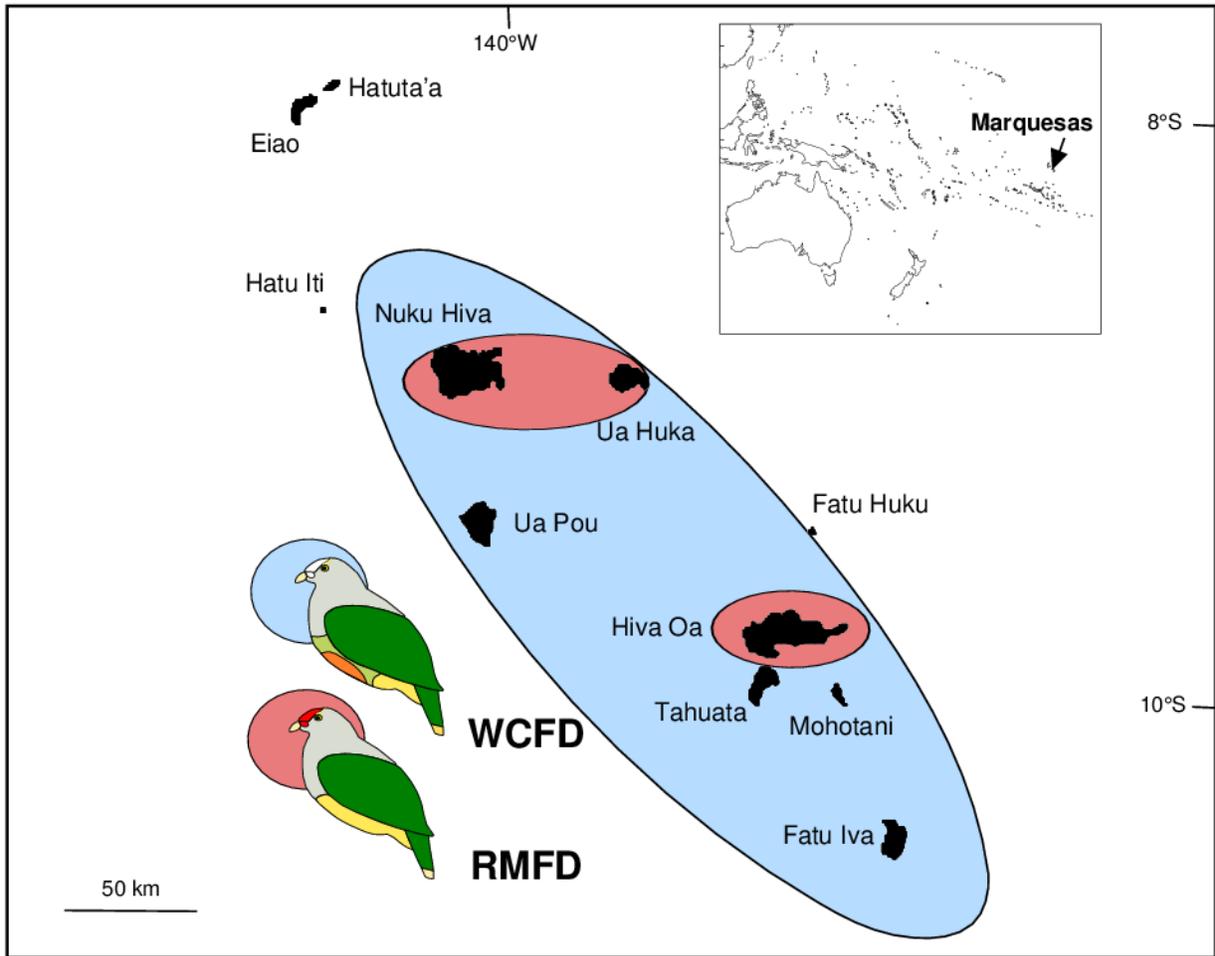


Figure 1. Map of the Marquesas Islands and known distribution of the Red-moustached Fruit Dove (RMFD) and White-capped Fruit Dove (WCFD).

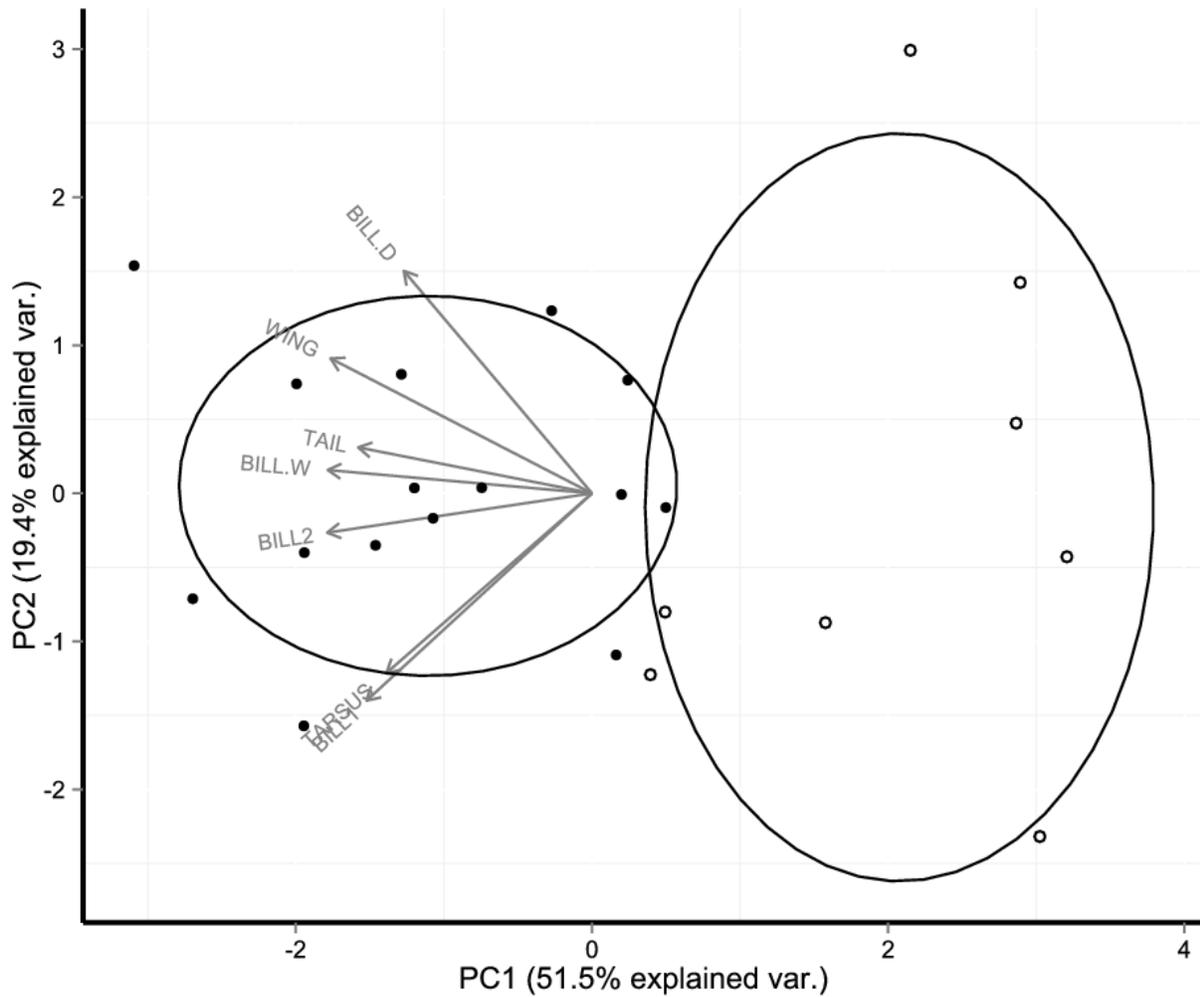


Figure 2. PCA of the Marquesas fruit doves. Black circles represent the RMFD, white circles the WCFD. Arrows indicate the direction of the variables: WING wing length, BILL1 bill length from skull, BILL2 bill length from nostril, BILL.W bill width (at nostril), BILL.D bill height (at nostril), TARSUS tarsus length, and TAIL tail length.

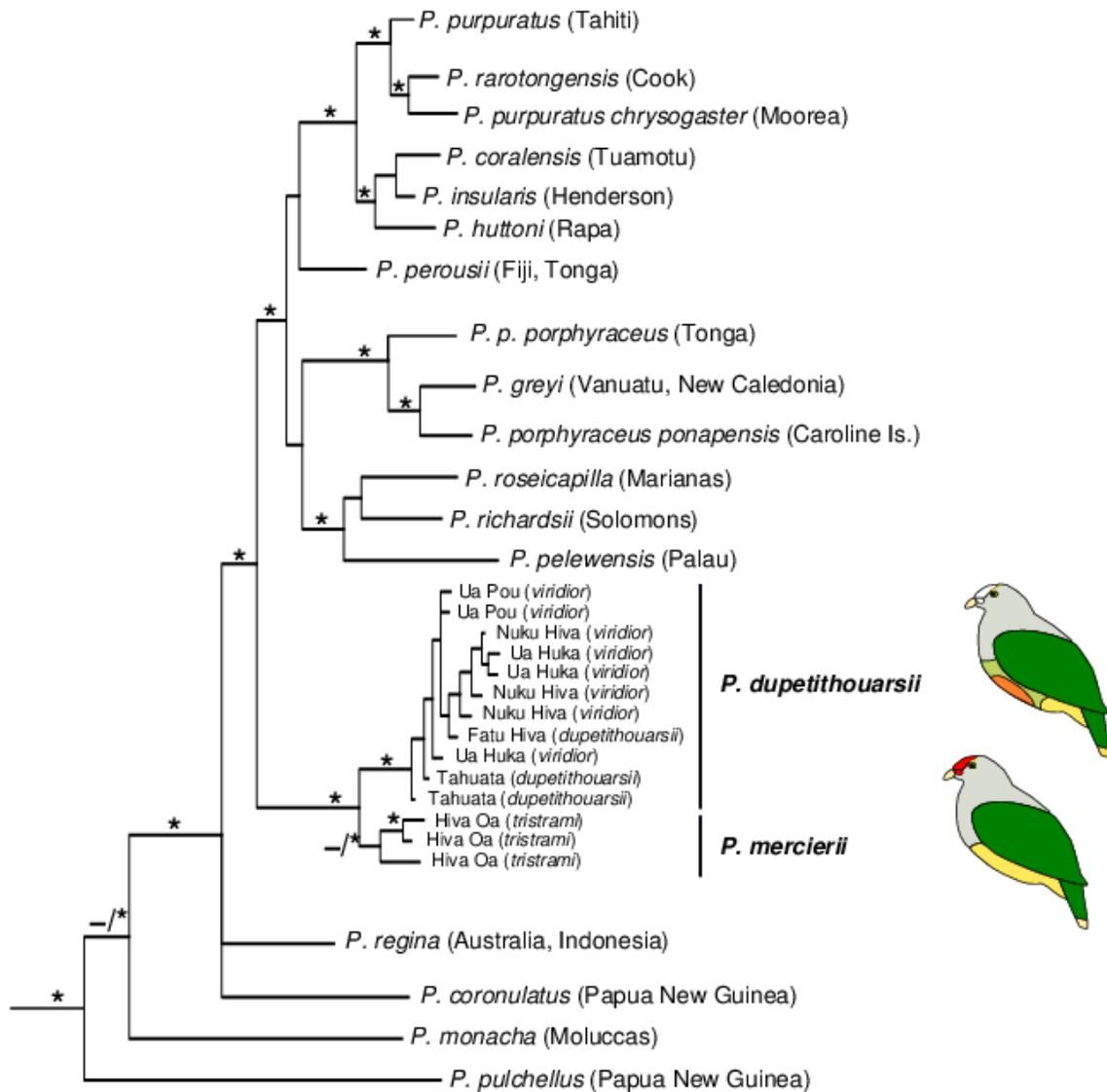


Figure 3. Phylogeny of the “*purpuratus*” group, modified from Cibois et al. (2014). Asterisks indicate nodes supported by posterior probabilities (PPs)  $\geq 0.95$  and bootstrap (BT) values  $\geq 70\%$ . When support differs between methods, PPs are indicated first and BT second with support below significance labeled by a dash (see original paper for details).

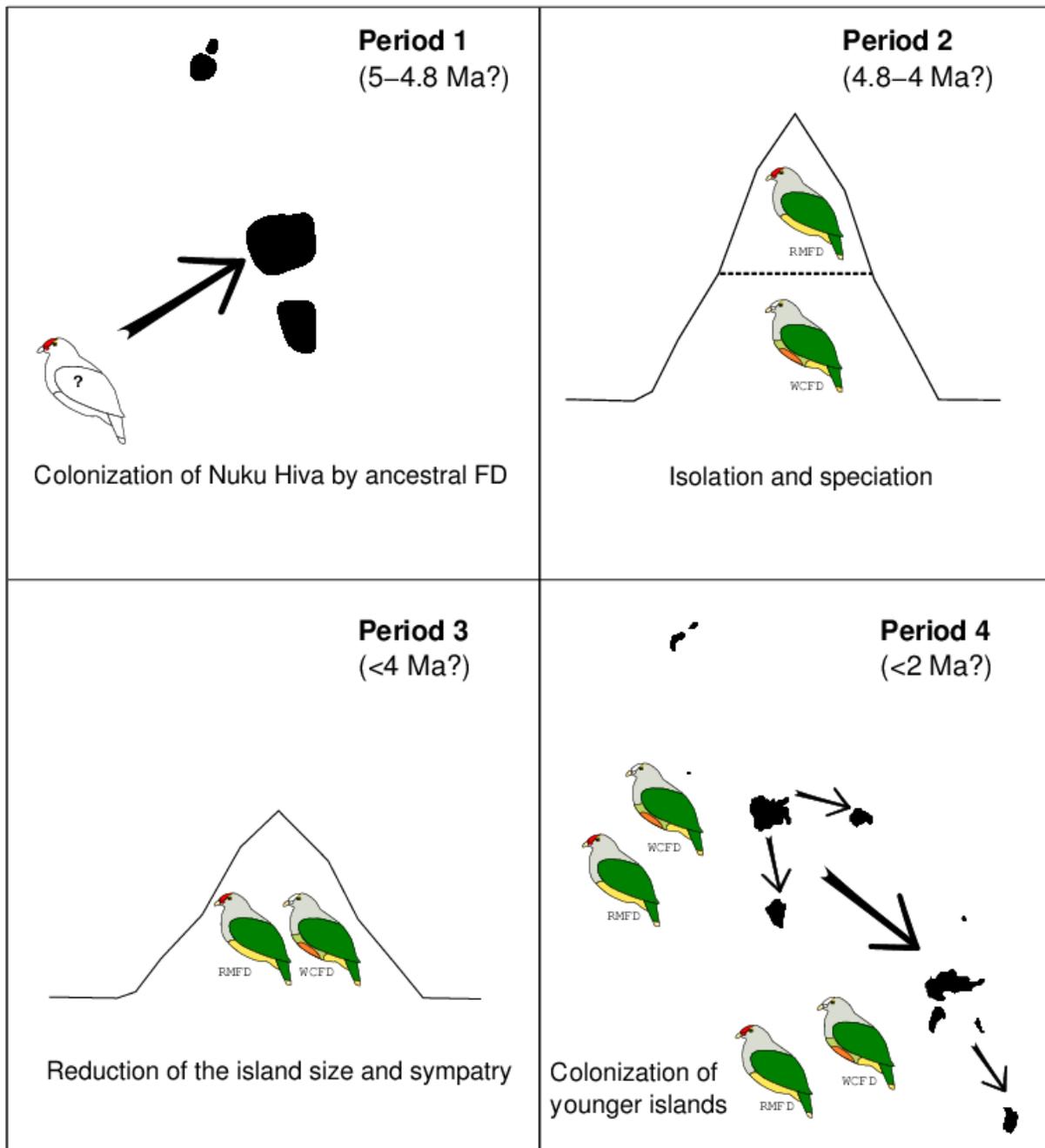


Figure 4. The microallopatry scenario. For each period, only the emergent islands are mapped, first with an enlarged size that corresponds to the island before the collapse of its main volcano.

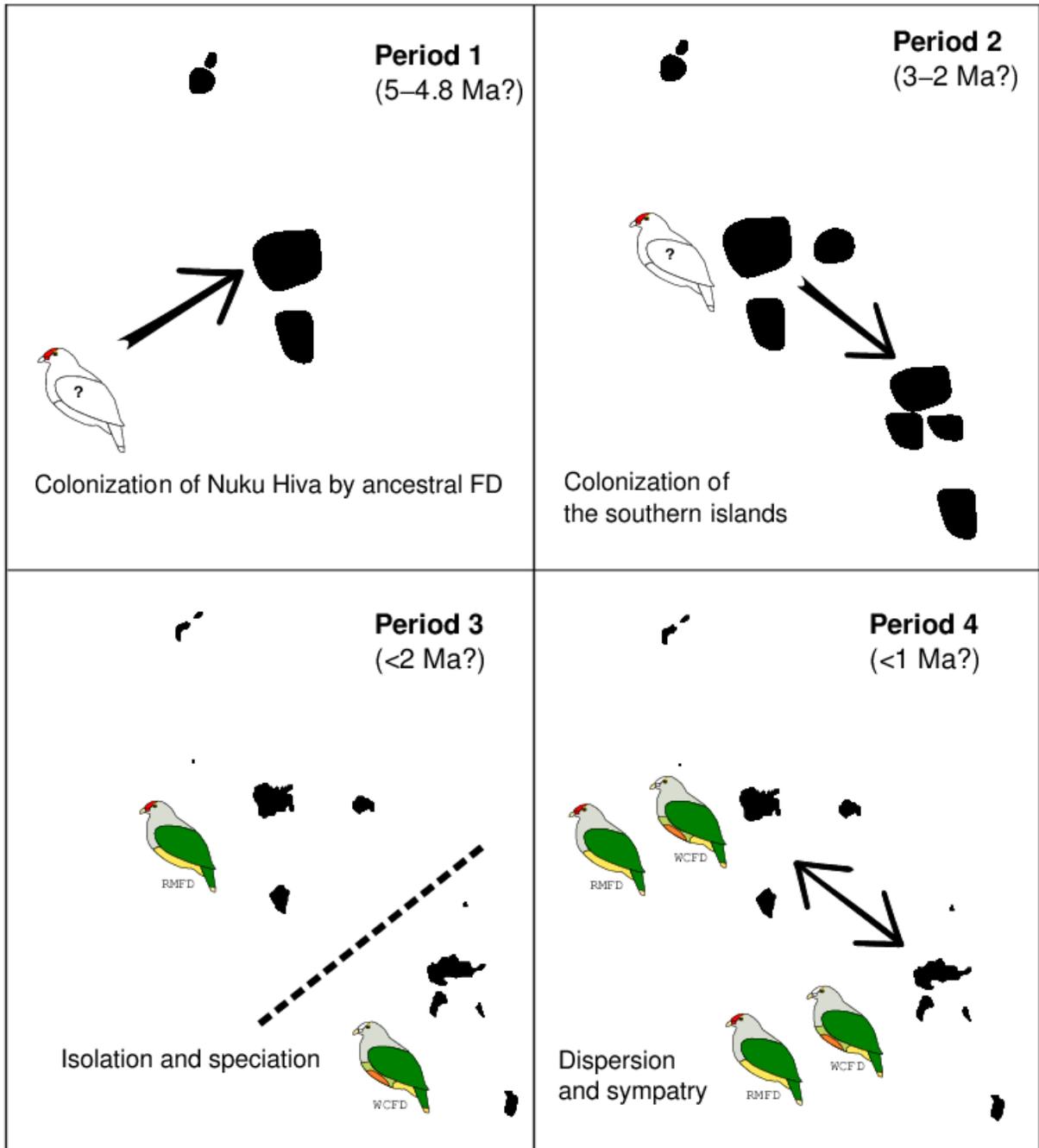


Figure 5. The intra-archipelago scenario. For each period, only the emergent islands are mapped, first with an enlarged size that corresponds to the island before the collapse of its main volcano.

## LITERATURE CITED

- Allen, M. S., K. Butler, J. Flenley, and M. Horrocks. 2011. New pollen, sedimentary, and radiocarbon records from the Marquesas Islands, East Polynesia: Implications for archaeological and palaeoclimate studies. *Holocene* 21: 473-84.
- Bailleul, M. 2001. Les îles Marquises. Histoire de la Terre des Hommes du XVIII<sup>e</sup> siècle à nos jours. Ministère de la Culture de Polynésie française, Tahiti.
- Baptista, L. F., P. W. Trail, and H. M. Horblit. 1997. Family Columbidae (Pigeons and doves). Pages 60-243 in J. del Hoyo, A. Elliot and J. Sargatal eds. Handbook of the Birds of the World. Vol. 4. Sandgrouse to Cuckoos. Lynx Edicions, Barcelona.
- Beck, R. H. ms. Journal during the Whitney South Sea Expedition (books E, F). Typescript copy at the Department of Ornithology, American Museum of Natural History, New York.
- Brousse, R., H. G. Barszczus, H. Bellon, J.-M. Cantagrel, C. Diraison, H. Guillou, and C. Leotot. 1990. Les Marquises (Polynésie française): vulcanologie, géochronologie, discussion d'un modèle de point chaud. *B. Soc. Geol. Fr.* 8: 933-49.
- Brousse, R., G. Guille, and R. C. Maury. 1978. Volcanisme et pétrologie de l'île de Nuku Hiva dans les îles Marquises (Pacifique Central). Pages 145-54 in F. S. Polignac ed. "Marquises", Cahiers du Pacifique. Paris.
- Buckley, P. A. 1987. Mendelian genes. Pages 1-44 in F. Cooke and P. A. Buckley eds. Avian Genetics. Academic Press, London.
- Cain, A. J. 1954. Subdivisions of the genus *Ptilinopus* (Aves, Columbidae). *Bull. Br. Mus. Nat. Hist. Zool.* 2: 267-84.
- Cibois, A., J.-C. Thibault, C. Bonillo, C. E. Filardi, D. Watling, and E. Pasquet. 2014. Phylogeny and biogeography of the fruit doves (Aves: Columbidae). *Mol. Phyl. Evol.* 70: 442-53.

- Cibois, A., J.-C. Thibault, and E. Pasquet. 2004. Biogeography of eastern Polynesian monarchs (*Pomarea*): an endemic genus close to extinction. *Condor* 106: 837-51.
- Cowie, R. H., and B. S. Holland. 2008. Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands. *Philos. T. R. Soc. B* 363: 3363-76.
- Coyne, J. A., and H. A. Corr. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Coyne, J. A., and T. D. Price. 2000. Little evidence for sympatric speciation in island birds. *Evolution* 54: 2166-71.
- Desonie, D. L., and R. A. Duncan. 1993. Temporal and geochemical variability of volcanic products of the Marquesas hotspot. *J. Geophys. Res.* 98: 17,649-17,65.
- Diamond, J. M. 1977. Continental and insular speciation in Pacific land birds. *Syst. Zool.* 26: 263-8.
- Filmer, P. E., M. K. McNutt, H. F. Webb, and D. J. Dixon. 1994. Volcanism and archipelagic aprons in the Marquesas and Hawaiian Islands. *Mar. Geophys. Res.* 16: 385-406.
- Fitzpatrick, B. M., J. A. Fordyce, and S. Gavrilets. 2008. What, if anything, is sympatric speciation? *J. Evol. Biol.* 21: 1452-9.
- Fleischer, R. C., C. E. McIntosh, and C. L. Tarr. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstruction and K-Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Mol. Ecol.* 7: 533-45.
- Friesen, V. L., A. L. Smith, E. Gómez-Díaz, M. Bolton, R. W. Furness, J. González-Solís, and L. R. Monteiro. 2007. Sympatric speciation by allochrony in a seabird. *P. Natl. Acad. Sci. USA* 104: 18589-94.
- Gibbs, D., E. Barnes, and J. Cox. 2001. *Pigeons and doves. A guide to the pigeons and doves of the world*. Pica Press, Sussex.
- Gill, G. E., and K. J. McGraw. 2006. *Bird Coloration, Volume 1: Mechanisms and Measurement*. Harvard University Press, Harvard.

- Goodwin, D. 1967. Pigeons and doves of the world. Trustees of the British Museum (Natural History), London.
- Grant, P. R., and B. R. Grant. 2010. Sympatric speciation, immigration, and hybridization in island birds. Pages 142-162 in J. B. Losos and R. E. Ricklefs eds. The theory of island biogeography revisited. Princeton University Press, Princeton, NJ.
- Graves, G. R. 1992. The endemic land birds of Henderson Island, southeastern Polynesia: notes on natural history and conservation. *Wilson Bull.* 104: 32-43.
- Guille, G., C. Legendre, R. C. Maury, M. Caroff, M. Munsch, S. Blais, C. Chauvel, J. Cotten, and H. Guillou. 2002. Les Marquises (Polynésie française): un archipel intraocéanique atypique. *Geol. Fr.* 2: 5-37.
- Havran, J. C., K. J. Sytsma, and H. E. Ballard. 2009. Evolutionary relationships, interisland biogeography, and molecular evolution in the Hawaiian violets (*Viola*: Violaceae). *Am. J. Bot.* 96: 2087-99.
- Holyoak, D., and J.-C. Thibault. 1978. Notes on the phylogeny, distribution and ecology of frugivorous pigeons in Polynesia. *Emu* 78: 201-6.
- Holyoak, D. T., and J.-C. Thibault. 1984. Contribution à l'étude des oiseaux de Polynésie orientale. *Memoir. Mus. Natl. Hist.* 127: 1-209.
- Kirchman, J. J. 2012. Speciation of Flightless Rails on Islands: A DNA-Based Phylogeny of the Typical Rails of the Pacific. *Auk* 129: 56-69.
- Le Dez, A., R. C. Maury, P. Vidal, H. Bellon, J. Cotten, and R. Brousse. 1996. Geology and geochemistry of Nuku Hiva, Marquesas: temporal trends in a large Polynesian shield volcano. *Oceanogr. Lit. Rev.* 43.
- Legendre, C., R. C. Maury, S. Blais, H. Guillou, and J. Cotten. 2006. Atypical hotspot chains: evidence for a secondary melting zone below the Marquesas (French Polynesia). *Terra Nova* 18: 210-6.

Legendre, C., R. C. Maury, M. Caroff, H. Guillou, J. Cotten, C. Chauvel, C. Bollinger, C. Hémond, G. Guille, S. Blais, P. Rossi, and D. Savanier. 2005. Origin of exceptionally abundant phonolites on Ua Pou Island (Marquesas, French Polynesia): partial melting of basanites followed by crustal contamination. *J. Petrol.* 46: 1925-62.

Liou, L. W., and T. D. Price. 1994. Speciation by Reinforcement of Premating Isolation. *Evolution* 48: 1451-9.

Mahler, B., L. S. Araujo, and P. L. Tubaro. 2003. Dietary and sexual correlates of carotenoid pigment expression in dove plumage. *Condor* 105: 258-67.

Mayr, E. 1940. Speciation phenomena in birds. *Am. Nat.* 74: 249-78.

Mayr, E. 1942. *Systematics and the Origin of Species*. Harvard University Press, Cambridge, MA.

McConkey, K. R., H. J. Meehan, and D. R. Drake. 2004. Seed dispersal by Pacific Pigeons (*Ducula pacifica*) in Tonga, Western Polynesia. *Emu* 104: 369-76.

Mila, B., B. Warren, P. Heeb, and C. Thebaud. 2010. The geographic scale of diversification on islands: genetic and morphological divergence at a very small spatial scale in the Mascarene grey white-eye (Aves: *Zosterops borbonicus*). *BMC Evol. Biol.* 10: 158.

Moore, J. G., D. A. Clague, R. T. Holcomb, P. W. Lipman, W. R. Normark, and M. E. Torresan. 1989. Prodigious submarine landslides on the Hawaiian Ridge. *J. Geophys. Res.* 94: 17465-84.

Moore, J. G., W. R. Normark, and R. T. Holcomb. 1994. Giant Hawaiian landslides. *Annu. Rev. Earth Pl. Sc.* 22: 119-44.

Murphy, R. C. 1924. Birds collected during the Whitney South Sea Expedition. I. *Am. Mus. Novit.* 115: 1-111.

Quayle, E. H. ms. Journal during the Whitney South Sea Expedition (books G, H, I, K, L). . Typescript copy at Department of Ornithology, American Museum of Natural History, New York.

- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Rheindt, F. E., and S. V. Edwards. 2011. Genetic introgression: an integral but neglected component of speciation in birds. *Auk* 128: 620-32.
- Ripley, S. D., and H. Birkhead. 1942. Birds collected during the Whitney South Sea Expedition. 51. On the fruit-pigeons of the *Ptilinopus purpuratus* group. *Am. Mus. Novit.* 1192: 1-14.
- Ryan, P. G., P. Bloomer, C. L. Moloney, T. J. Grant, and W. Delpont. 2007. Ecological speciation in South Atlantic island finches. *Science* 315: 1420-3.
- Sætre, G.-P., T. Moum, S. Bures, M. Kra, M. Adamjan, and J. Moreno. 1997. A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* 387: 589-92.
- Schmeltz, J. D. E., and R. Krause. 1881. Die Ethnographisch-Anthropologische Abtheilung des Museum Godeffroy in Hamburg. L. Friederichsen & Co., Hamburg.
- Shanahan, M., R. D. Harrison, R. Yamuna, W. Boen, and I. W. B. Thornton. 2001a. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *J. biogeogr.* 28: 1365-77.
- Shanahan, M., S. So, S. G. Gompton, and R. Gorlett. 2001b. Fig-eating by vertebrate frugivores: a global review. *Biol. Rev.* 76: 529-72.
- Shawkey, M. D., and G. E. Hill. 2005. Carotenoids need structural colours to shine. *Biol. Lett.* 1: 121-4.
- Steadman, D. W. 1989. Extinction of birds in Eastern Polynesia. A review of the record, and comparison with other island groups. *J. Archaeol. Sci.* 16: 177-205.

- Steadman, D. W. 1997a. Extinctions of Polynesian birds: reciprocal impacts of birds and people. Pages 51-79 in P. V. Kirch and T. L. Hunt ed. *Historical Ecology in the Pacific Islands*. Yale University Press, New Haven and London.
- Steadman, D. W. 1997b. The historic biogeography and community ecology of Polynesian pigeons and doves. *J. biogeogr.* 24: 737-53.
- Steadman, D. W. 2006. *Extinction & Biogeography of tropical Pacific birds*. University of Chicago Press, Chicago.
- Steadman, D. W., and H. B. Freifeld. 1999. The food habit of Polynesian pigeons and doves: a systematic and biogeographic review. *Ecotropica* 2: 13-33.
- Stokes, J. F. G. 1925. Notes on Polynesian featherwork. *J. Polynesian Soc.* 34: 24-35.
- Voisin, C., J.-F. Voisin, C. Jouanin, and R. Bour. 2004. Liste des types d'oiseaux des collections du Muséum d'Histoire naturelle de Paris. 13: Gangas et Pigeons (Pteroclididae et Columbidae), première partie. *Zoosystema* 26: 107-28.
- Vu, V. Q. 2011. ggbiplot: A ggplot2 based biplot. R package, version 0.55.  
<http://github.com/vqv/ggbiplot>.
- Watling, D. 1989. Notes on the fauna of Laucala and Matagi Islands, Fiji. *Domodomo* 1989: 59-64.
- Wolfe, C. J., M. K. McNutt, and R. S. Detrick. 1994. The Marquesas archipelagic apron: Seismic stratigraphy and implications for volcano growth, mass wasting, and crustal underplating. *J. Geophys. Res.* 99: 13591-608.