Biodiversity of the Austral Islands, French Polynesia

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Photos 1er de couverture

a : Pacifigeron rapensis (photo J.-Y. Meyer)
b : Lamellidea oblonga (photo O. Gargominy)
c : Vini kuhlii (photo B. Fontaine)
d : Ischnura rurutana (photo R. Englund)
e : Mt Taraia cliffs, Raivavae (photo J.-Y. Meyer)

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m : Capparis cordifolia (photo J.-Y. Meyer)
n : Microcystis fосbergi fosbergi (photo O. Gargominy)

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Cet ouvrage doit être référencé comme suit :
Timothy J. Motley (1965-2013)

In Memoriam

I first met Tim when we were both "young" PhD students working in Hawaii in the mid-1990s. We started professionally collaborating in 1999, when he came to French Polynesia to study Kadua (syn. Hedyotis, Rubiaceae) and other Pacific island plants. We first conducted fieldwork together on the high volcanic islands of Bora Bora, Raiatea, and Tahiti (Society archipelago), searching for rare endemic species like Fitchia cordata on Mt Pahia in Bora Bora, Geniostoma clavatum on Temehani plateau in Raiatea, and Scaevola tahitensis on Mt Marau in Tahiti.

In early 2001, Tim, then working for the New York Botanical Garden, was awarded a grant from the National Geographic Society to study the flora of the remote island Rapa Iti, in the Austral archipelago. This fit in well with my nascent research plans to survey the terrestrial biodiversity of the entire archipelago which was poorly known. The resulting two-month expedition from February to March 2002 organized by Tim, was assisted by field botanists Steven Perlman and Kenneth Wood of the National Tropical Botanical Garden (Kauai, Hawaiian Islands ?), ethnobotanist Ron Fenstemacher, and by my logistical support on the island for the first two weeks. The expedition's outcome was to expand the flora of Rapa by about ten percent, with a dozen new island records for indigenous plants that weren't previously found there and eight unique endemic species that were new to science!

This expedition was a milestone in my career for both its scientific impact and the human adventure involved. In subsequent years I took other biologists (botanists, entomologists, malacologists, and ornithologists) throughout the Austral islands to continue further biotic surveys. This exhaustive field research led to a conference in Tahiti, held in 2005 at Institut Louis Malardé, on the biodiversity and richness of the natural history of the Austral archipelago. Tim was an invited speaker to this conference, where he presented a paper and co-authored two others. He also contributed two papers to this current volume and provided data for use in a third chapter of this book, a book he unfortunately will never read. Tim was an associate professor of Botany at Old Dominion University in Virginia, happily married, and had even recently become a father, when he passed away suddenly and quite unexpectedly, in March 2013.

While Tim was internationally recognized as an excellent Pacific Island systematist and botanist, it was his great enthusiasm for fieldwork and his conscientiousness in the lab that inspired and convinced me, a plant ecologist and field botanist, of the fundamental importance of conducting phylogenetic and phylogeographical studies for conservation purposes. Because of our common interest in Pacific island floras, both Tim and I were selected as members on a panel studying "Extinction in the Islands of Oceania" for a symposium held at the Australian National University in Canberra, Australia, in 2006, invited by a colleague, palaeoecologist Matiu Prebble, who was also a member of the survey expeditions to the Austral islands. Tim's path and mine continued to cross over the years, as we both remained focused on research in the Pacific. Tim honored me in 2008, by naming one of the newly discovered endemic species of fern on Rapa, Elaphoglossum meyeri. We last met at the "Evolution of Life in Pacific Islands" conference in Honolulu in 2011, where we had kava (Piper methysticum) with Ron Fenstemacher, as we three had often done on Rapa after our long days of fieldwork there. Tim's last message to me came in January 2013, with a final version of his paper on taro cultivars... and a picture of his two-year old son, Anton. He wrote that he was "happy the Austral Islands book will be moving forward soon, I hope".

Through the time we worked together and the adventures we shared, Tim became more than a close research colleague, he was a true friend, and so we had always expected to maintain our rewarding professional collaboration for many years to come, and, we had even hoped to revisit Rapa together again, one fine day...
Mt Taraia cliffs and view on Vaianaua, Raivavae, March 2008 (Photo J.-Y. Meyer).
Mts Hiro and Araua, Raivavae (Photo J.-Y. Meyer).
Knowledge of terrestrial biodiversity and ecosystem composition, structure and function, is crucial for the sustainable management of natural resources and the conservation of threatened endemic species and native habitats. This is especially true for small islands with limited resources and human capacities, which also often harbor high levels of endemism and unique biota (Wagner & Funk 1995). The Austral Islands (also called "the Australs") are an isolated archipelago in French Polynesia, a French territory in the South Pacific, located between 500 and 1250 km from the main island of Tahiti (Society Islands, Fig. 1). The most remote island in the chain, Rapa (also called "Rapa Iti" as opposed to "Rapa Nui", Easter Island, which is a Chilean territory located to the southeast) can be considered a biodiversity hotspot in and of itself. However, biological data for this archipelago was outdated and/or highly incomplete, and thus of limited use to land managers, research scientists, and other potential users (e.g., conservationists from NGO's and local nature protection groups). Therefore, a biodiversity inventory of the Australs would be research priority.

The most recent and most extensive scientific expeditions to the Austral Islands were those of the Bayard Dominick Expedition between 1921-22, and the Mangarevan Expedition in 1934, both funded by the Bernice P. Bishop Museum, Honolulu (Hawaii). More than 50 years afterwards, in the 70s and 80s the Service Mixte de Contrôle Biologique (SMCB) of the Direction des Centres d’Expérimentations Nucléaires (DIREC), Centre d’Expérimentation du Pacifique (CEP), organized a series of expeditions with French marine and terrestrial biologists from IRD (formerly called ORSTOM) and the Muséum national d'Histoire naturelle in Paris. However, little
data was published relating to terrestrial ecosystems, and that which was focused primarily on vascular plants (see DIRCEN 1986 and references in chapter by Meyer et al., this volume).

During the past 20 years, other contemporary research surveys were conducted by lone researchers, including botanical field trips by J. Florence in 1988 and 1992 funded by IRD, by J.-Y. Meyer in 1998 (Tubuai, Rurutu) and 1999 (Rurutu), funded by the Délegation à la Recherche de la Polynésie française (French Polynesia Department of Research), and an expedition to Rapa by T. Motley, R. Fenstemacher, S. Perlman and K. Wood in 2002 funded by the National Geographic Society. However, no comprehensive assessment was ever published on the flora of the Austral Islands. By comparison, a special issue on the vascular flora of the Marquesas was compiled by Lorence in 1997 following a series of botanical expeditions between 1988 (a collaborative program with IRD, the National Tropical Botanical Garden in Hawaii and the Smithsonian Institution of Washington) and 2005 (with the Délegation à la Recherche and the Délegation à l’Environnement de la Polynésie française, Tahiti), which has resulted in a website dedicated to the Marquesan flora, housed by the Smithsonian Institution (Wagner & Lorence 2002).

In order to address these gaps in our knowledge and growing environmental concerns a series of multidisciplinary scientific expeditions were conducted in 2002 (November-December), 2003 (November-December) and 2004 (November) to the five inhabited islands of Raivavae, Rapa, Rimatara, Rurutu and Tubuai. The uninhabited small rocky islets of Marotiri, located 75 km southeast of Rapa, and the atoll of Maria, about 210 km north of Rimatara, were not surveyed because of the extreme difficulty of accessing them by boat. The expeditions were funded by the Contrat de Développement Etat-Polynésie française 2000-2004 (France-French Polynesia Development Contract) through a larger research program aimed to inventory and evaluate the biodiversity of French Polynesia (Inventaire et Valorisation de la Biodiversité en Polynésie française) proposed by the Délegation à la Recherche de la Polynésie française. The total budget allocated to the Expéditions scientifiques aux Australes was 10 million XPF, i.e. about 84 000 €, managed by the Institut Louis Malardé (ILM).

The main goals of these expeditions, as stipulated in the contracts signed between ILM with each participant (or "missionaries"), were to:

- Map the different terrestrial and freshwater native habitats, to assess their conservation status, and to localize the natural areas of high ecological value;
- Conduct inventories (as exhaustive as possible) of native and alien vascular plants and animals (mammals, birds, molluscs, insects and arthropods);
- Estimate the distribution and abundance of the threatened species, and to assess their conservation status;
- Identify the past and current threats on species and their habitats;
- Study the dynamics and evolution of the terrestrial biota compared with historic data;
- Propose recommendations for biodiversity conservation and natural resources management to both the local community and authorities (mayors offices) and the Government of French Polynesia (mainly the Ministries of Environment and Agriculture).

<table>
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<tr>
<td>Délégation à la Recherche de la Polynésie française &amp; Institut Louis Malardé, Tahiti</td>
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<td>1</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Muséum national d’Histoire naturelle, Paris</td>
<td>France</td>
<td>2</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>Bernice Pauahi Bishop Museum, Honolulu</td>
<td>USA</td>
<td>1</td>
<td>x</td>
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<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Université de Polynésie française &amp; Service du Développement Rural, Tahiti</td>
<td>French Polynesia</td>
<td>1</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
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<td>x</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
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<tr>
<td>IRD, Paris</td>
<td>France</td>
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<tr>
<td>University of British Columbia, Vancouver</td>
<td>Canada</td>
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<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Australian National University, Canberra</td>
<td>Australia</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
J.-Y. Meyer, hired as research scientist at the Délegation à la Recherche in 2002, was appointed as the expedition leader, and in charge of setting up a team of local, French and foreign scientists (Table 1) with field experience in French Polynesia and/or the Pacific Islands (e.g. Hawaii), and with recognized expertise on specific taxa (e.g. vascular plants, forestry, birds, mollusks, insects, spiders, fossil pollen). Some of the expedition members were senior scientists, other were PhD students at that point in time.

**OUTCOMES**

The expeditions were unique for several reasons: they were the first to be conducted in French Polynesia during the 21st century; the small field-teams (seven-eight people) were able to travel to remote islands (Rimatara and Rapa by cargo boat), survey all the different habitat types (from low elevation coastal areas to high elevation cloud forests) including rough terrains (limestone cliffs, wetlands and precipitous peaks and ridges) in a minimum amount of time; they were well-integrated into the Polynesian lifestyle and adapted to the local logistic constraints in these islands (small planes, boat travels, guesthouses). Expedition members were able to synthesize collection data, sharing their results with the local authorities and communities during meetings at the local mayor’s offices (“mairies”). The expeditions were covered by the local media (local newspapers La Dépêche de Tahiti, local television TNTV) on the most inhabited islands of Rurutu and Tubuai.

The results obtained during these scientific expeditions, have greatly improved the knowledge of the ecology, biogeography, evolutionary and...
conservation biology of the Austral Islands terrestrial biota: several plant and invertebrate (insects and molluscs) species previously unknown to science were discovered, species that were only collected during the 20's and 30's expeditions were found again, new records for some Austral Islands endemic or native species were reported for other islands, there were only a few contemporary extinctions recorded, but many historical extinctions, based on palynological studies (see chapter by Prebble, this volume) and subfossil land snail deposits (see chapter by Gargominy & Fontaine, this volume). The conservation status of many of the endemic taxa was revised.

A symposium entitled the "Austral Islands Biodiversity Conference" was organized in Tahiti in 2005 (8-10 Nov.) at the Institut Louis Malardé (Papeete), hosted by both the Ministry of Education and Research and the Ministry of Environment, to synthesize and share the main results. A total of 15 talks were given, including additional talks from invited speakers who didn’t participate in the 2002-2004 field expeditions, dealing with vegetation mapping of Tubuai using satellite images
It took almost five years for all the participants to write the 11 scientific papers (including this one) and five more years for the two editors and the publisher (Service des Publications scientifiques of the Muséum national d’Histoire naturelle) to prepare this book entitled Terrestrial Biodiversity of the Austral Islands, dedicated to science for conservation and management. Very few other fieldtrips and conservation projects were carried out during this past decade (a palaeoecological study conducted in the wetlands of Rurutu and Raivavae by the Australian National University of Canberra in 2008, the construction by the "Association Raumatariki" of a fence to protect a semi-dry forest remnant on Rapa in 2011, a plant and bird inventory on Maria atoll in 2013, all projects conducted in collaboration with J.-Y. Meyer of the Délegation à la Recherche), demonstrating the importance of publishing this book, as a baseline for existing knowledge, and highlighting the urgent need to promote conservation action in the archipelago. There are still no protected terrestrial areas in the Austral Islands, compared with the Society Islands, which has a single natural park (Te Faaiti on Tahiti since 1989), a management area (Temehani Ute Ute plateau, Raiatea, created in 2010) and natural uninhabited reserves since 1971 (Scilly and Bellinghausen atolls); or the Marquesas (Eiao, Hatutu, Mohotani have been natural reserves since 1971, Vaikivi natural park and reserve created in 1997), and the Tuamotus (the Fakarava Biosphere Reserve since 2006).

An online database of the terrestrial biodiversity of the Austral Islands, based on a model developed for the Cook Islands, located some 700 km to the west in Rarotonga (McCormack 2007) would be very useful, and the Cook Islands database could even be used as a starting point, as most of the terrestrial native biota is shared with the Austral Islands.

The results of this scientific, but also human adventure, have greatly improved the knowledge of the ecology, biogeography, evolutionary and conservation biology of the Austral Islands terrestrial biota, and we hope this book will inspire further research, conservation and management programs.

CONCLUSIONS

(B. Stoll from the Université de Polynésie française), phylogeny and evolution of reed-warblers in the Eastern Pacific (A. Cibois, Natural History Museum of Geneva, Switzerland), marine biodiversity (R. Galzin, Université de Perpignan, France, and CRIOBE-EPHE biological marine station, Moorea) and the marine algal flora of Rapa (A. N’Yeurt, Université de Polynésie française).
Corallieous islets ("motus") in the lagoon of Tubuai (Photo J.-Y. Meyer).
The Austral Islands (or Australis, formerly known as the Tubuai Islands) are located between 21-28°S latitude and 144-155°W longitude. The archipelago along with the Society, the Tuamotu, the Marquesas and the Gambier Islands makes up the French Overseas Territory known as French Polynesia (Fig. 2). The Australs and the Gambier form the southernmost part of this territory.

The Austral archipelago is a chain of seven oceanic islands stretching over 1300 km (from west to east: Maria, Rimatara, Rurutu, Tubuai, Raivavae, Rapa and Marotiri), more than 5400 km distant from the coast of Australia and over 7300 km from the coast of South America. The archipelago is located between 575 km and 1275 km from the main island of Tahiti (Society).

Table 2: Characteristics of the Austral Islands and comparison with the three largest islands of French Polynesia
* Data from Maury et al. this volume; ** data from Clouard & Bonneville 2005.

<table>
<thead>
<tr>
<th>Island</th>
<th>Island type*</th>
<th>Age (Myr)</th>
<th>Area (km²)</th>
<th>Max. elev. (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maria</td>
<td>atoll</td>
<td>4.8-28.6**</td>
<td>0.53</td>
<td>3</td>
</tr>
<tr>
<td>Rimatara</td>
<td>composite</td>
<td>&gt;15**</td>
<td>8.06</td>
<td>106</td>
</tr>
<tr>
<td>Rurutu</td>
<td>composite</td>
<td>12.7-12</td>
<td>32.35</td>
<td>389</td>
</tr>
<tr>
<td>Tubuai</td>
<td>High volcanic</td>
<td>8.9-10</td>
<td>45.00</td>
<td>422</td>
</tr>
<tr>
<td>Raivavae</td>
<td>High volcanic</td>
<td>6.4-5.4</td>
<td>20.35</td>
<td>483</td>
</tr>
<tr>
<td>Rapa</td>
<td>High volcanic</td>
<td>4.8-4.1</td>
<td>40.50</td>
<td>650</td>
</tr>
<tr>
<td>Marotiri</td>
<td>rocky islets</td>
<td>3.8-3.1</td>
<td>0.11</td>
<td>113</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td><strong>147.44</strong></td>
<td></td>
</tr>
<tr>
<td>Tahiti (Society)</td>
<td>High volcanic</td>
<td>0.43-1.17**</td>
<td>1 045.10</td>
<td>2 241</td>
</tr>
<tr>
<td>Moorea (Society)</td>
<td>High volcanic</td>
<td>1.50-1.86**</td>
<td>141.80</td>
<td>1 207</td>
</tr>
<tr>
<td>Nuku Hiva (Marquesas)</td>
<td>High volcanic</td>
<td>3.59-4.38**</td>
<td>339.50</td>
<td>1 227</td>
</tr>
</tbody>
</table>

These volcanic islands are between 3 and 30 Myr in age, and are the result of the activity of colinear hotspots (Table 2). Although politically the Austral and Cook Islands are two separate entities, geologically they are part of the same volcanic chain: the Cook-Austral chain which extends from Mangaia in the Cook Islands to the Macdonald Seamount (Maury et al. this volume).
Figure 2: The Austral archipelago in French Polynesia (Map ORSTOM - LCA).

Coastal limestone vegetation, Rimarata (Photo J.-Y. Meyer).
The total surface area of the seven islands of the Australs combined is only c. 148 km², i.e. almost equivalent to the surface area of Moorea (Society), and represents only 4% of the total land area of French Polynesia (Table 2).

Within the Australs there are three volcanic high islands (Tubuai with its summit Mt Taitaa, 422 m, Raivavae with Mt Hiro, 438 m, and Rapa with Mt Perau, 650 m, the highest peak in the archipelago), with associated sandy islets ("motus" in Tubuai and Raivavae which are formed on the barrier reef) or offshore rocky islets (e.g. Karapoo Rahi near Rapa, Hotuatua near Raivavae). There are two composite islands ("makatea" islands sensu Nunn 1994) (Rurutu with its summit Mt Taatioe, 389 m and Rimatara with Mt Uahu, 84 m) made up of a volcanic center surrounded by raised limestone or coralline substrate (called "mato"). At the south-eastern end of the archipelago there are a group of ten extremely isolated rocky islets, Marotiri, the highest reaching 110 m elevation and at the north-western end the remote atoll, Maria, 230 km from Rimatara, and made up of four small "motus". The diversity of geomorphological features and associated natural habitats include impressive raised coral limestone karst cliffs on Rurutu, large marsh areas containing some of the largest intact wetlands in French Polynesia on Tubuai, steep and dissected reliefs on Rapa reminiscent of those found on the high volcanic islands of the Marquesas and the Society Islands.
The climate is subtropical to tropical, with mean annual temperatures of c. 23°C (20-26°C) on Tubuai and Rurutu, and 20.6°C on Rapa (18-23°C). The minima recorded on Tubuai and Rurutu are at 9.2-9.4°C and 8.5°C on Rapa (Laurent et al. 2004). Rapa is the coldest and the wettest island of French Polynesia with 2560 mm average annual rainfall (and a maximum of 3798 mm in 1965), and Rimatara is the driest of the Australs (1663 mm average annual rainfall) (Laurent et al. 2004). The rainy season is typically between December and April, except for Rapa where precipitation is continuous throughout the year.

Five of the Austral Islands (Tubuai, Rurutu, Raivavae, Rimatara and Rapa) are inhabited, whence the Polynesian name "Tuhaa pae" (literally the five pieces); Marotiri and Maria atoll are currently uninhabited. The archipelago’s population is 6820, 3% of the population of French Polynesia. Rurutu and Tubuai are the most densely populated (with over 2000 inhabitants each), though Rimatara has the highest population density, with more than 100 inhabitants per square kilometer. Rapa is the least populated island, with only 515 inhabitants living in two villages (Haurei or Ahurei, and Area) a population density of only 13 inhabitants per square kilometer (Table 3).

For a long time the Australs were among the most isolated islands of French Polynesia, though now airports are found on four of the inhabited islands, two being recently opened (2002 in Raivavae, 2006 in Rimatara). Rapa is only accessible by cargo boat.
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...they had on the natural habitat were profound, especially in the lowland for agriculture (e.g. taro fields). Likewise, recent development projects, such as airport construction on Raivavae and Rimatara, raise important environmental concerns as well as socio-economic issues. The long-term impacts of land management practices (e.g. gravel extraction at the foot of Mt Tonarutu, rubbish dumps in the wetlands of Tubuai and Rimatara, agricultural development on Rurutu) and associated human disturbances (e.g. invasion of Strawberry guava *Psidium cattleianum* on the summits of Tubuai and Rapa, widespread burning of the summits of Rurutu in 2004 and the wetlands of Tubuai in 2010) may be equally profound.

Table 3: Characteristics of the Austral Islands human population. *Institut de la Statistique de Polynésie française (www.ispf.pf).*

<table>
<thead>
<tr>
<th>Island name (ancient name)</th>
<th>Polynesian Colonization</th>
<th>European discovery</th>
<th>Approx. population size upon discovery</th>
<th>Population (2002)*</th>
<th>Population (2012)*</th>
<th>Density (inhab./km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maria</td>
<td>?</td>
<td>1824 (Gardner)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td>Rimatara</td>
<td>10-14th century</td>
<td>1811 (Henry)</td>
<td>1 200</td>
<td>791</td>
<td>873</td>
<td>108.3</td>
</tr>
<tr>
<td>Rurutu</td>
<td>10th century</td>
<td>1769 (Cook)</td>
<td>6 000</td>
<td>2 098</td>
<td>2 322</td>
<td>71.8</td>
</tr>
<tr>
<td>Tubuai (Tupuai)</td>
<td>10th century</td>
<td>1777 (Cook)</td>
<td>3 000</td>
<td>1 979</td>
<td>2 170</td>
<td>48.2</td>
</tr>
<tr>
<td>Raivavae (Vavitu)</td>
<td>10th century</td>
<td>1775 (Gayangos)</td>
<td>3 000</td>
<td>991</td>
<td>940</td>
<td>46.2</td>
</tr>
<tr>
<td>Rapa (Oparo)</td>
<td>1515-1635</td>
<td>1791 (Vancouver)</td>
<td>2 000</td>
<td>470</td>
<td>515</td>
<td>12.9</td>
</tr>
<tr>
<td>Marotiri (Bass)</td>
<td>?</td>
<td>1800 (Bass)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>-</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td><strong>14 700</strong></td>
<td><strong>6 329</strong></td>
<td><strong>6 820</strong></td>
<td></td>
<td><strong>46.3</strong></td>
</tr>
<tr>
<td>Tahiti (Society archipelago)</td>
<td>500 B.C.</td>
<td>1769 (Wallis)</td>
<td>100 000</td>
<td>168 773</td>
<td>183 480</td>
<td>175.6</td>
</tr>
<tr>
<td>Nuku Hiva (Marquesas archipelago)</td>
<td>150 B.C.</td>
<td>1791 (Ingraham)</td>
<td>8 000</td>
<td>2 649</td>
<td>2 967</td>
<td>8.8</td>
</tr>
</tbody>
</table>
Geology
Southern rock, Marotiri islets, the youngest emerged land of the Australs archipelago (Photo C. Debitus).
**Hotspot Chain**

René C. Maury, Christelle Legendre, Catherine Chauvel, Gérard Guille, Sylvain Blais, Hervé Guillou & Philippe Rossi

The Southeastern Polynesian oceanic domain is characterised by an unusual density of volcanic islands, seamounts and atolls. The Marquesas, Tuamotu, Pitcairn-Gambier, Society and Austral-Cook archipelagoes highlight the importance of past and present volcanic activity in the area. All these linear chains are built on top of a Pacific oceanic crust, which is 250 to 750 m shallower than expected given its age. Thus, the Southeastern Polynesian islands lie on top of a huge oceanic bulge, the largest of the planet, called the "South Pacific Superswell" (McNutt & Fischer 1987). It corresponds to a region of anomalously hot mantle (Cazenave & Thoraval 1994) that is also characterised by unusual geochemical features (Duncan & Compston 1976; Hart 1984), sometimes referred to as the South Pacific Isotope and Thermal Anomaly or "SOPITA" (Staudigel et al. 1991). Recent seismic tomography results show that the thermal anomaly is due to the presence in the lower mantle of unusually hot materials rising from the core-mantle boundary (Zhao 2001) and called "superplumes" by Courtillot et al. (2003).

In Southeastern Polynesia, the surface expression of the "superplume" is not a giant and very active volcanic edifice such as Hawaii, but a number of rather quiet young volcanoes, sometimes emerged such as Mehetia ("Me’eti’a") but more commonly immerged as shallow seamounts (Adams SE of Pitcairn, Moua Pihaa near Mehetia, Macdonald and Arago in the Austral Islands). Most of them are located at the South-East end of a volcanic chain and are thought to indicate the present positions of the corresponding hotspots; however, the recently discovered Arago seamount is located in the central part of the Austral-Cook linear chain. This is not the only originality of the Austral Islands chain, which is also the longest in Southeastern Polynesia (2300 km from Macdonald to Aitutaki in the Cook Islands). It includes very old volcanic islands with ages of c. 10 Ma for Tubuai and Raivavae, 12 Ma for Rurutu and even 19 Ma for Mangaia (Cook Is.), while in the other Southeastern Polynesian archipelagoes volcanic edifices older than 6 Ma have been converted to atolls.

Finally, the Austral Islands are famous among the international community of geochemists for the very unusual composition of most of their lavas, which display abnormally radiogenic lead isotopic compositions, due to their mantle source with a high U/Pb ratio. As the U/Pb ratio is called $\mu$, this uncommon geochemical signature is often referred to as High $\mu$ (HIMU, Zindler & Hart 1986). Since the discovery of this imprint in Tubuai lavas (Vidal et al. 1984), c. 35 studies of the Austral-Cook lavas have dealt with their geochemical characteristics to understand their origin. Unfortunately, the geological knowledge of the Austral Islands has not taken this path, and the early reconnaissance investigations (Chubb 1927; Obellianne 1955; Aubert de la Rüe 1959) have been followed by a surprisingly small number of field studies (Mottay 1976) compared to the Society and Marquesas Islands. The only available recent geological maps are those of Rurutu, Tubuai and Raivavae Islands (Maury et al. 2000, 2011; Guille et al. 2011).

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**THE AUSTRAL-COOK VOLCANIC CHAIN**

... General features and submarine geology

The Austral-Cook volcanic chain (Fig. 3A) extends over 2300 km from Macdonald Seamount to Aitutaki, and as the Society and Pitcairn-Gambier-Mururoa linear chains, it follows an ESE-WNW direction (N115°E) with an active seamount at the SE end. The alignment is related to the 11 cm/yr motion of the Pacific plate over the hotspot (Duncan & McDougall 1976). However, the Austral Islands chain displays many unusual features besides its uncommon length and the presence of several very old volcanic islands. In particular, the relationship between age and distance to Macdonald plot (Fig. 3B) is very abnormal and does not show a single and good linear trend, as is normally the case elsewhere and, in particular, for the Society chain (Guillou et al. 2005) and the Pitcairn-Gambier chain. Indeed, young volcanic activity (<2 Ma) is observed not only at the SE end of the chain but also in the central part (Rurutu-Arago) and even at the NW end (Rarotonga and Aitutaki, Cook Is.). The archipelago is cut in the middle by a major discontinuity, the Austral Fracture Zone (AFZ) which represents a fossil transform fault linked to the Pacific-Farallon oceanic ridge (the ancestor...
Rarotonga trend
Atiu trend
B
Aitutaki
30°
25°
20°
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et al
those measured on bulk rocks (Laughlin on groundmass or on separated phases have been preferred to Maury. (1984), Diraison (1991), Turner & Jarrard (1982), Matsuda et al data from Dalrymple Fig. 3A and 3B are modified from Chauvel: Plot of age versus distance to the Macdonald seamount.
2 000 fathoms (3 650 m) isobaths.
However, a recent study taking uted to its thermal rejuvenation acquired during c. 42 Ma at Macdonald, 56 Ma at Rapa, 63 Ma at Raivavae to 70 Ma at Tubuai and 82 Ma at Rurutu (Mayes et al. 1990; Munschy et al. 1998; Bonneville et al. 2002). The bulge of the oceanic crust below the archipelago is small compared to the Tuamotu bulge (Sichoix et al. 1998), and its highest point lies about 4 500 m below sea level (Sichoix & Bonneville 1996; Sichoix 1997; Bonneville & Sichoix 1998). The elastic thickness of the Austral-Cook lithosphere has been considered abnormally low (Calmant & Cazenave 1986), a feature attributed to its thermal rejuvenation acquired during its passage over underlying hot spots (Cazenave & Thoraval 1994). However, a recent study taking into account all the volcanic events which affected this lithosphere (Adam & Bonneville 2008) concludes that its elastic thickness is normal.
Figure 3A may give an impression of relative simplicity, because almost all of the hundreds of seamounts, which disturb the seafloor topography, are not shown. The understanding of their distribution and ages is still very weak, as evidenced by the recent discovery of the potentially active seamount Arago (cruise in 1999, publication in 2002), halfway between Tubuai and Rurutu. However, the combination of satellite-derived altimetric data and oceanographic cruises quickly increases our knowledge relative to the early studies of Lambeck & Coleman (1982) and Baudry et al. (1988). In particular, McNutt et al. (1997) discovered two chains of “old” seamounts southeast of the Australs, and named them the Ngatemato and Taukina chains after the ruling families of Rapa. The ages of these seamounts range from c. 34 to 22 Ma, and most likely they formed close to the Pacific ridge axis (near the present location of the Foundation Seamounts) on an oceanic lithosphere which was only about 10 Ma old at the time. More recent investigations (Clouard et al. 2003; Adam et al. 2005; Bonneville et al. 2006) led to the recognition of a number of other seamounts, belonging to three volcanic stages with ages ranging respectively, between 58 and 40 Ma, 33 and 20 Ma and less than 20 Ma. The youngest set (e.g., seamounts ZEP2-12 West of Rimatara and ZEP2-19 South of Raivavae, Fig 3) coincides with the activity of the Macdonald and Arago hotspots, and the 33-20 Ma with that of the near-ridge Ngatemato and Taukina plumes, but the origin of the oldest seamounts remains unclear. They were necessarily emplaced very close to the active ridge, possibly through ridge-plume interactions, because their ages are only slightly younger than that of the oceanic crust on which they lie. “Old” samples were also dredged from the flanks of Marotiri and Raivavae, suggesting that some, if not many, of the Austral-Cook islands are built over older seamounts resulting from the activity of previous plumes.

Lava types
Austral island lavas are mostly basaltic, and they show the typical characteristics of Ocean Island Basalts (OIB). Relative to Mid Ocean Ridge Basalts (MORB) they display selective enrichments in incompatible elements, e.g. alkali and alkaline earth elements (K, Rb, Ba, Sr) as well as in high field strength elements (Nb, Zr, Ti, Hf) and light rare earth elements (La, Ce, Nd) (Dupuy et al. 1988, 1989). Within a given island, the major element compositions are also usually variable, the critical point being the ratio between total alkalis (Na2O + K2O) and silica (SiO2). With increasing values of this ratio, five types of basalts can be distinguished:
- Quartz tholeiites, which contain silica in excess with respect to the sum of alkalis,
- Olivine tholeiites, which are silica-saturated,
i.e. the proportions of silica and alkalis are equilibrated;
• Alkali basalts, which have a slight excess of alkalis, and can contain small amounts of feldspathoids (e.g. less than 5% nepheline);
• Basanites, which are strongly silica-undersaturated, and often bear rather high percentages of feldspathoids in their groundmass (nepheline, sodalite, analcite);
• Nephelinites, which are so silica-poor that they are feldspar-free and contain only ferromagnesian minerals (olivine, pyroxenes, iron oxides) plus feldspathoids and glass.

These basaltic types can be distinguished on a total alkalies-silica (TAS) plot (Fig. 4) by their variable contents in (Na₂O + K₂O) and SiO₂. Such associations may be explained by variable partial melting degrees of a peridotitic mantle source: for very low melting degrees (e.g. 1-3%), the liquids are very rich in alkalis (nephelinites), and with increasing fusion the SiO₂/(Na₂O + K₂O) ratios of the melts increases up to quartz tholeiites (for c. 15% melting). In addition, many Polynesian basalts have accumulated large crystals of olivine and/or clinopyroxene (up to 50% or even 60%), and are thus alkali- and silica-poor but very rich in MgO (up to 25%). These are called picrobasalts, among which two varieties are often distinguished: olivine-rich picrobasalts (“oceanites”) and pyroxene-rich picrobasalts (“ankaramites”).

The evolution of basaltic magmas usually involves separation of olivine, pyroxenes, plagioclase feldspars, etc. and leads to more alkali- and silica-rich derived melts, which are also classified using the TAS diagram (Fig. 4). Alkali basaltic magmas commonly evolve towards hawaiites, mugearites,
benmoreites and trachytes, while the differentiation of basanitic magmas usually leads to tephritic, tephriphonolitic and phonolitic magmas. These correlations were demonstrated in 1927 for French Polynesian magmas par Alfred Lacroix, and they are still accepted.

### Isotopic compositions: HIMU and the other pieces of the Austral puzzle

The considerable isotopic heterogeneity of Polynesian magmas (Vidal et al. 1984) mimics that of their mantle sources, because isotopic ratios are not affected by partial melting processes. At least four kinds of isotopic end-members are required to describe their composition (Zindler & Hart 1986), providing that these end-members can mix in variable proportions: DMM (Depleted MORB Mantle), EM 1 (Enriched Mantle type 1), the composition of which is usually considered as resulting from the ancient incorporation of pelagic sediments, EM 2 (Enriched Mantle type 2) which is thought to contain an old detrital sedimentary component, and finally the famous High µ (HIMU) end-member, identified for the first time in Tubuai lavas by Ph. Vidal et al. (1984). This discovery has triggered a number of geochemical studies on Austral-Cook lavas, with the aim of understanding the meaning of such unusual compositions for the heterogeneity of the Earth’s mantle and the origin of mantle plumes (Matsuda et al. 1984; Palacz & Saunders 1986; Dupuy et al. 1988, 1989; Nakamura & Tatsumoto 1988; Vidal et al. 1989; McDonough & Chauvel 1991; Staudegül et al. 1991; Chauvel et al. 1992; Vidal 1992; Hauri & Hart 1993; Hauri et al. 1993; Hémond et al., 1994; Hanan & Graham 1996; Woodhead 1996; Chauvel et al. 1997; Kogiso et al. 1997; Dostal et al. 1998; Salters & White 1998; Hanyu et al. 1999; Hanyu & Nakamura 2000; Schiano et al. 2001; Bonneville et al. 2002; Lassiter et al. 2003; Nishio et al. 2005; Bonneville et al. 2006; Pfänder et al. 2007; Jackson & Dasgupta 2008; Chan et al. 2009; Parai et al. 2009; Vlastelíc et al. 2009).

Although there is still a debate concerning the origin of HIMU end-member, the most widely accepted opinion is that it comes from the ancient (1 or 2 Ga) incorporation into the mantle of residues of subducted oceanic crust that experienced selective extraction of lead with respect to uranium during the dehydration process accompanying their subduction (Chauvel et al. 1992; Kogiso et al. 1997; Kawabata et al. 2011). Most authors envision that these residues were carried down to the mantle-core boundary and stored there until their incorporation into ascending mantle plumes (Hofmann 1988).

### GEOLOGICAL FEATURES AND HISTORY OF THE AUSTRAL ISLANDS

#### Macdonald Seamount

This active seamount was discovered in 1967 from hydrophone records of acoustic signals during eruption (Norris & Johnson 1969), and named in honor of the American volcanologist Gordon Macdonald. Since its discovery, the seamount was monitored by the French Polynesia seismic network (Talandier & Okal 1984). It has been very active from 1977 to 1989, with more than 20 eruptive events (among which 8 from June 1987 to April 1988), including spectacular shallow submarine explosions in September 1988 and January 1989 (Cheminée et al. 1991).

Macdonald volcano is a large submarine cone, with a basal diameter of 45 km at a depth of 3950 m, which lies over Eocene (c. 42 Ma old) Pacific crust. Several volcanic ridges, which from submersible observations correspond to lava channels and/or lava flows, extend in a radial fashion from the top down the slopes (Stoffers et al. 1989). These ridges define a star-shaped pattern with a preferential N-S orientation which coincides with a regional fault pattern of the underlying oceanic crust (Binard et al. 1991), and they are similar to the rift zones of Hawaiian volcanoes. The summit is a rather flat plateau (150 m x 100 m) lying at a depth of 39-40 m, and made of basaltic flows covered by recent lapilli. It is capped by small (and short-lived) spatter cones which form steep-sided pinnacles reaching depths of 23 to 30 m only. It seems likely that Macdonald will emerge at the surface in the near future. Soon after its discovery, it has been proposed that it marks the present position of the hotspot responsible for the formation of the Austral-Cook archipelago (Johnson & Malahoff 1971).

Numerous volcanic samples have been collected from Macdonald by dredging, during submersible explorations and even directly from pyroclastic falls (Brousse & Richer de Forges 1980; Barsczus & Liotard 1985; Hekinian et al. 1991; Hémond et al. 1994). They show a considerable diversity (Fig. 4), largely because the 20th century pyroclastic explosions deposited on the summit and on the flanks of the volcano blocks of older materials (Hekinian et al. 1991), on which ages up to 0.35 Ma have been measured. Basalts range from olivine tholeiites to nephelinites through alkali basalts, basanites and picrobasalts. Hawaiitites, tephrites and a single mugearite have also been identified. Debris of granular rocks (dolerites and olivine gabbros) are thought to have been removed from deep intrusions by the explosive eruptions. Much older (c. 34 to 22 Ma) samples have also been dredged on the slopes of several seamounts close to Macdonald, e.g. on Ra seamount (29.21 ± 0.62 Ma, McNutt et
al. 1997), and it is possible that the active volcano itself was built on an older edifice belonging to the Ngatemano volcanic chain.

Marotiri

The ten very small islets collectively referred to as Marotiri (or Bass) are the southermost emerged lands of French Polynesia. They represent the still emerged parts of a c. 50 m deep circular plateau 5 km in diameter, which corresponds to the top of a conical volcanic edifice. These islets reach altitudes of 8 to 113 m, and their surfaces range from a few m$^2$ to 0.035 km$^2$. They are composed of a pile of subaerial basaltic flows, the individual thickness of which range from 50 cm to 10 m, with occasional interbedded pyroclastic deposits (reddish ash layers and tuffs). The massive parts of the lava flows are usually separated by autoclastic breccias, and their dips are lower than 15°.

Twelve samples have been collected by N.O. Marara in 1979 and 1982 from islets NW (alt. 10 m), SE (alt. 113 m) and W (alt. 99 m) and described by Liotard & Barsczus (1985) and Dupuy et al. (1988, 1989). They include picrobasalts (oceanites), basanites, tephrites and hawaiites (Fig. 4), and a granular rock (plagioclase-rich olivine gabbro) has also been recovered. The ages of these samples range from 3.29 ± 0.16 to 3.21 ± 0.32 Ma (Diraison 1991). In addition, two samples dredged from the submarine slopes of the volcano have been dated at 3.78 ± 0.18 Ma and 31.95 ± 0.82 Ma, respectively (McNutt et al. 1997). The latter age indicates that the Pliocene (3.8-3.2 Ma) Marotiri volcano grew on the top of a much older seamount belonging to the Late Eocene-Oligocene Ngatemato volcanic chain.

Rapa

This rather large island (c. 40 km$^2$) has been less studied from a geological point of view than Tubuai and Rurutu, because of its remote location 1240 km South of Papeete and the lack of airport facilities. Early investigators (Marshall 1918; Chubb 1927; Obellianne 1955) spent only a few days in the island. The first detailed study of Rapa was that of Mottay (1976), who collected samples analysed by Maury et al. (1978) and Brousse et al. (1981). During the DIRCEN-SMCC Expedition in 1984, R. Brousse and P. Gelugne collected many samples that were later dated by Diraison (1991), and they published in 1986 a detailed account of the geology and petrology of Rapa. A simplified version of their map (Brousse & Gelugne 1986) is shown in figure 5.

Rapa has an unusual shape because of the very deep Ahurei bay that penetrates into the core of the island. There, a rather flat zone interpreted as the bottom of a caldera is rimmed by two almost vertical ridge lines: the inner one is rather continuous and encircles almost completely Ahurei bay; the outer one, which culminates at Mt Maurua, Mt Perau (650 m) and Mt Pukumia, is interrupted by the Iri and Anarua bays and lacks in the northern part of the island. These ridge lines have been interpreted by Mottay (1976) as the caldera walls of two successive volcanoes, the inner one being the youngest and having grown inside the caldera of the older (and outer) volcano. However, the study of their geomorphologic features led Brousse & Gelugne (1986) to consider them as two nested caldeiras, with respective diameters of 6 and 3 km, belonging to a single volcanic edifice. This interpretation has
been supported by ten 40K-40Ar ages (Diraison 1991) which indicate a relatively short period of subaerial activity (4.8 to 4.1 Ma), consistent with the lifetime of a single shield volcano.

Rapa island lies on a rather flat submarine plateau of ovoid shape, c. 16 km in diameter at a depth of 50 m; the size of the island should thus have been several times its present one during the sea level minima related to Quaternary glaciations (Brousse & Gelugne 1986). The rather dissymetric shape of Rapa, with its higher summits in the western half of the island, its north-south trending and almost linear east coast, the opened eastwards caldeiras and the unusual configuration of Ahurei bay, all suggest that one, or more likely, several sector collapse events have affected its eastern and central zone. They probably led to the destruction of the eastern part of the initial shield volcano by submarine debris avalanches, as envisioned for other Polynesian islands, e.g. Moorea (Le Dez et al. 1998) or Nuku Hiva (Maury et al. 2006). Smaller collapse events may have been responsible for the formation of the Ahurei bay by connecting the central (inner) caldeira with the eastern coast. The dissymetric shape of the island is still partly responsible for the numerous recent landslides that affected the inner caldera wall (Brousse & Gelugne 1986). Another noticeable tectonic feature of Rapa lies in the orientations of the numerous dykes, which show two frequency maxima corresponding to the NW-SE trend of the archipelago and to the conjugate NE-SW direction (Brousse & Gelugne 1986).

Rapa is mostly made of a pile of subaerial basaltic flows, the individual thickness of which range from 1 to 10 m, which dip gently (8°-15°) towards the periphery of the island. Following Brousse & Gelugne (1986), the distinction shown in figure 5 between an outer and an inner volcano is purely morphologic, as these areas represent two parts of a single shield edifice separated by the collapse of the inner caldeira. Indeed, the lithology of the two parts is identical, and there is no reliable age difference.
that the lignite was deposited into a small lake or swamp, possibly within a previous lava lake (Brousse & Gelugne 1986). Most intrusions lie along a NW-SE trend parallel to the island elongation (Brousse & Gelugne 1986); one intrusion is exposed in the center of the caldeira (Motu Tapui inside Ahurei or Haurei bay). Pyroclastic breccias are not very abundant in Rapa: the most common type corresponds to strombolian-type scoria, lapilli and ash deposits occurring in several locations shown in figure 5, the largest ones being in Iri bay and in the southernmost part of Rapa (Karapoo Nui and Karapoo Iti islands). The Puputa parasitic cone in the NE of Rapa is relatively well preserved: it consists of strombolian breccias with intercalated basanitic flows containing numerous xenoliths of depleted mantle rocks, i.e. harzburgites (Berger et al. 1986). Submarine (hydromagmatic) pyroclastic breccias have been identified in Agaira (Angairao) bay.

Rapa lavas are chemically very heterogeneous (Fig. 4). Although the most common lavas are basanites, tholeiitic basalts, alkali basalts and nephelinites occur as well as olivine- or clinopyroxene-rich varieties (picrobasalts). The basaltic magmas evolve towards intermediate melts (tephrites, hawaiites, mugearites, andesites), and ultimately into trachytic and phonolitic melts. The genesis of the Rapa series is ascribed to fractional crystallisation of basaltic magmas under almost anhydrous and oxygen-poor conditions, leading to delayed fractionation of titanomagnetite and strong enrichment in iron of olivines and pyroxenes (Maury et al. 1978; Brousse et al. 1981; Brousse & Gelugne 1986). Intermediate lavas commonly occur as flows intercalated within the basaltic pile. Trachytes and phonolites form intrusions, e.g. Mt Ruatara and Mt Vairu; the largest massif is located in Agaira (Angairao) bay (Fig. 5).

An unusual deposit of lignite (brown coal), up to 2 m thick, associated with volcaniclastic sand and clay-rich layers, occurs at an altitude of 180 m south of Mt Vairu, below the inner ridge line (Fig. 5). It is interbedded within the basaltic pile and cut by a picrobasaltic (ankaramitic dyke), whose glass is converted into palagonite (Lacroix 1927), a typical product of interaction between basaltic magma and water. These features suggest that the lignite was deposited into a small lake or swamp, possibly within a previous lava lake (Brousse & Gelugne 1986).

Rapa is devoid of coral reef barrier or of fringing reef, and its shores are composed of volcaniclastic sands mixed with biodetritic debris (mostly Lithothamnium and shells). A Quaternary shore terrace has been identified at + 5 to + 15 m in Tupuaki bay (Chubb 1927; Brousse & Gelugne 1986).

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**Raivavae**

Raivavae is a 16 km² volcanic island that culminates at 438 m at Mt Hiro and is rimmed by a typical barrier reef delineating a 2 to 3 km wide lagoon. Unlike most of the other Austral islands, it has an elongated shape trending WSW-ENE, parallel to the nearby Austral Fracture Zone (AFZ) which lies only c. 35 km to the NW. It represents the emerged remnants of a much larger volcano, which has collapsed generating two large submarine debris avalanches (Clouard & Bonneville 2004). A 50 km long submarine ridge prolongates the island towards the South-West (Adam & Bonneville 2008). Gravimetric data (Clouard et al. 2000) document positive residual isostatic anomalies centered on this ridge, which might correspond to a set of mafic intrusions or to the summit of a magma reservoir.

The salient geomorphological feature of Raivavae is a typical barrier reef delineating a 2 to 3 km wide lagoon. Unlike most of the other Austral islands, it has an elongated shape trending WSW-ENE, parallel to the nearby Austral Fracture Zone (AFZ) which lies only c. 35 km to the NW. It represents the emerged remnants of a much larger volcano, which has collapsed generating two large submarine debris avalanches (Clouard & Bonneville 2004). A 50 km long submarine ridge prolongates the island towards the South-West (Adam & Bonneville 2008). Gravimetric data (Clouard et al. 2000) document positive residual isostatic anomalies centered on this ridge, which might correspond to a set of mafic intrusions or to the summit of a magma reservoir.
An Atypical Hotspot Chain

(...) evolved towards trachytic and phonolitic melts (Fig. 4) through intermediate (hawaiitic, mugearitic and benmoreitic) lava compositions. From a petrologic point of view, the Anatonu series resembles in many respects the Rapa series (Maury et al. 1978, 2009).

The oldest exposed unit of Rairua volcano is a more than 200 m thick pile of basaltic breccias crosscutting the northern cliff as well as the Vaiuru area; and a western (and younger) one centered around the Rairua-Mahanatoa depression, interpreted as a caldera (Mottay op. cit.). However, such a view has not been corroborated by K-Ar dating. Five ages measured by Duncan and McDougall (1976) range from 6.96 ± 0.35 Ma to 6.07 ± 0.30 Ma, and do not support the hypothesis of a westward migration of emplacement ages. Four out of five additional ages measured by Diraison (1991) are also very close to 6.5 Ma (6.43 ± 0.32 Ma to 6.32 ± 0.32 Ma). In addition, a tholeiitic basalt dredged on the SW flank of the Raivavae edifice, at a depth of 2 950 m, was dated at 33.3 ± 0.5 Ma and 31.9 ± 0.5 Ma on separated plagioclase (Bonneville et al. 2006). The latter ages suggest that the Late Miocene Raivavae volcanoes were emplaced over a much older seamount belonging to the Ngatemato chain. Lassiter et al. (2003) published detailed informations on the geochemistry of Raivavae lavas, including major, trace elements and Sr, Nd, Hf, Pb, and Os isotopes. Although these authors did not try to decipher the geological structure of the island, they identified two geochemical groups:

- Lavas derived from a HIMU-type mantle source, which include mainly basanites and picrobasalts (ankaramites);
- Lavas derived from a mantle containing an important DMM (Depleted MORB Mantle) component.

The simplified geological map of Raivavae shown in figure 6 has been drawn from the results of a mapping program conducted from 2005 to 2010 (Guille et al. 2011; Maury et al. 2011). We recognise two distinct volcanoes:

- The old Rairua volcano, made of nephelinites, basanites, alkali basalts and picrobasalts (clinopyroxene-rich ankaramites) derived from HIMU-type mantle sources;
- The younger, although dissected, Anatonu shield volcano built of plagioclase-phyric tholeiitic and less commonly alkalic basalts, which originated from partial melting of a more depleted mantle with a subdued (DMM-HIMU-EM) signature (Maury et al. 2013).

The Anatonu basaltic magmas evolved towards tholeiitic and phonolitic melts (Fig. 4) through intermediate (hawaiitic, mugearitic and benmoreitic) lava compositions. From a petrologic point of view, the Anatonu series resembles in many respects the Rapa series (Maury et al. 1978, 2009). The oldest exposed unit of Rairua volcano is a more than 200 m thick pile of basaltic breccias crosscut...
by a dense network of basanitic and alkali basaltic dykes, most of which trend WSW-ENE, parallel to the AFZ and the trend of the island. They outcrop along the axis of the island, and are overlain either:

- By the Rairua basanitic flows which form the Mt Tavaetu plateau in the western part of Raivavae;
- Or by the younger plateaus of Anatonu volcano, e.g. below Mt Maunau, Mt Taraia and Mt Matotea.

These breccias also crop out at the pass (altitude 200 m) separating the Mt Hiro ridge from its eastern equivalent, i.e. the Mouatapu-Turivao ridge. In this latter location, they occur as a c. 20 m thick pile of volcaniclastic (laharic) breccias and conglomerates interbedded with clay-rich layers, both of them deposited in a lacustrine or shallow submarine environment. This pile is probably overlain by Miocene northwards-dipping sediments (bioclastic limestones; ms in Fig. 6) emplaced on the lower slopes near Anatonu village (Obellianne 1955; Maury et al. 2011). However, most of the breccias outcropping at lower altitudes do not appear reworked. Their characteristics resemble those of shallow submarine autoclastic or hydromagmatic basaltic deposits, and they contain small (often fragmented) pillows set into a palagonite-rich matrix. Because of their common yellowish color, they were apparently mistaken for trachytic breccias by former authors (Obellianne 1955; Mottay 1976). The occurrence of chlorine-rich melt inclusions in the olivine crystals from old Raivavae lavas (Lassiter et al. 2002) suggests that these melts have interacted with seawater. Two fresh basanitic and alkali basaltic dykes crosscutting these breccias have given unspiked K-Ar ages of 10.58 ± 0.23 Ma and 9.12 ± 0.19 Ma, respectively. They display a typical HIMU signature (Maury et al. 2011, 2013), as well as other dykes in the same position and the Tavaetu plateau lava flows (Lassiter et al. 2003). The basal (picrobasaltic) and summital (basanitic) flows of the Tavaetu lava pile have given significantly younger unspiked K-Ar ages of 7.41 ± 0.16 Ma and 7.37 ± 0.16 Ma, respectively.

The Anatonu shield volcano is mostly composed of an up to 400 m thick pile of plagioclase-phyric tholeiitic basalts, with intercalated alkali basaltic, hawaiitic, mugearitic and benmoreitic flows, up to 10 m thick. These flows form six gently dipping plateaus, which are, by order of decreasing size, those culminating at Mts Hiro, Taraia, Matotea, Mouatapu, Taamora, and Tapioi, respectively (Fig. 6). Their unspiked K-Ar ages range from 6.41 ± 0.14 Ma to 5.36 ± 0.11 Ma. The youngest of them is the Tapioi plateau, the basal and summital flows of which have been dated to 5.74 ± 0.12 Ma and 5.36 ± 0.11 Ma, respectively (Maury et al. 2011, 2013). All these lavas display a subdued isotopic signature intermediate between DMM, HIMU and EM end-members (Maury et al. 2013), as well as other Anatonu volcano flows and dykes and the phonolitic and trachytic plugs (Lassiter et al. 2003). The variations of the dips and
the thickness of the Mt Hiro plateau pile along the northern cliff of the island suggest that these flows were emplaced into a paleodepression dug into the Rairua breccias. Other witnesses of Anatonu volcanic activity are six phonolitic and trachytic domes and plugs, which crosscut either the Rairua breccias (Mt Rareterepa trachytic plug, dated at $6.42 \pm 0.14$ Ma) or more commonly the Anatonu shield plateaus (e.g. Mt Turivao). They define a WSW-ENE trend, from Mt Rareterepea to the two phonolitic plugs of Motu Hatuatu at the eastern edge of the island. This trend is parallel to the AFZ and to the main direction of the dykes crosscutting the Rairua breccias. All these features suggest that a deep fracture parallel to the nearby AFZ controlled closely the emplacement of Raivavae magmas.
The geological evolution of Raivavae is therefore characterized by two temporally distinct volcanic events with contrasted geochemical signatures, separated by a c. 1 Myr long time gap. The development of Rairua submarine breccias in Raivavae suggests a c. 200 m uplift of the island after the first event.

**Tubuai**

Tubuai, the largest of the Austral islands (45 km²), has an ovoid shape (9.5 x 5 km) and is encircled by a large barrier reef (16 x 10.5 km) that isolates a wide lagoon. The morphology of Tubuai is typical of an old volcanic edifice: two residual reliefs corresponding to the western Hanareho volcano and to the central/eastern strongly dissected Herani volcano emerge from a thick cover of Quaternary bioclastic sands and alluvial deposits. The island represents the summit of a large conical volcanic edifice, the base of which has an average diameter of 100 km (Monti & Pautot 1975) and lies over a 4500 m deep oceanic crust of Upper Cretaceous age (c. 70 Ma; Mayes et al. 1990; Munschy et al. 1998). This edifice is characterised by gentle submarine slopes (8° to 10°) and a very flat summit (above the -500 m isobath), the shape of which indicates an important coral reef limestone cover. Tubuai has been quoted very early for the occurrence of nephelinites, basanites and phonolites (Lacroix 1927, 1928) but the first geological descriptions of the island (Marshall 1918; Chubb 1927; Obellianne 1955; Aubert de la Rue 1959) were very brief. In 1976, R.A. Duncan and I. McDougall published the first accurate K-Ar datings of Tubuai lavas, and G. Mottay collected a sample set extended by R. Brousse in 1979. This set was used for detailed geological and petrologic investigations (Brousse 1980; Brousse & Maury 1980) together with additional datings (Bellon 1980). It allowed P. Vidal et al. (1984) to document the first occurrence in the South Pacific of lavas displaying a highly radiogenic lead isotopic signature (later called HIMU). The name of Tubuai became famous to geochemists for its unusual composition, and this discovery was followed by numerous other studies. The geological mapping of the island was completed between 1989 and 1995 (Maury et al. 1994, 2000a, 2000b).

Tubuai mafic lavas range in composition from alkali basalts and picrobasalts (mostly clinopyroxene-rich ankaramites) to basanites and nephelinites (Fig. 4). These types of lavas were emitted more or less successively: alkali basalts and picrobasalts were emplaced at 10 Ma (Fig. 7), and were followed by basanites between 10 and c. 9.4 Ma. Both types were only emplaced within the eastern Herani volcano, where basanitic flows systematically overlie alkali basaltic flows. The alkali basalt sequence, up to 350 m thick, makes up the basal part of the Herani volcano, and this pile of individual 1 to 10 m thick flows crosscut by numerous dykes crops out in the radial valleys diverging from Mt Taitaa. Their main vents were located north of Mt Panee, where strombolian alkali basaltic breccias reach a thickness of 170 m. Individual basanitic flows are generally thicker (c. 10 m) than alkali basaltic ones, but they made a thinner pile (< 130 m). They were mostly emitted from the summit of Mt Panee and from the ridge located north of Mt Taitaa, where basanitic strombolian scoriae, lapilli and bombs are common. These flows form three plateaus dipping gently towards the periphery of the island: the main one, dated at 9.37 ± 0.07 Ma, corresponds to the ridge connecting Mt Panee to Mt Taitaa and extends towards the north coast (Fig. 7), while the two others cap the Mt Herani (West) plateau (10.04 ± 0.07 Ma and 9.56 ± 0.06 Ma) and the Mt Herani (East) plateau (9.62 ± 0.06 Ma), respectively.

Nephelinite eruptions occurred only within the western Hanareho volcano. They were either contemporaneous (9.68 ± 0.07 Ma) with basanites or younger (8.89 ± 0.06 Ma). These rocks occur as individual decametric flows forming a more than 300 m thick pile. Crosscut by several nephelinitic necks and radial dykes, they make the frame of the crescent-shaped ridge of the western Hanareho volcano, which connects Mts Haurii, Tonarutu, and Pahatu. Their main vents were located north of Mt Panee, where strombolian alkali basaltic breccias reach a thickness of 170 m. Individual basanitic flows are generally thicker (c. 10 m) than alkali basaltic ones, but they made a thinner pile (< 130 m). They were mostly emitted from the summit of Mt Panee and from the ridge located north of Mt Taitaa, where basanitic strombolian scoriae, lapilli and bombs are common. These flows form three plateaus dipping gently towards the periphery of the island: the main one, dated at 9.37 ± 0.07 Ma, corresponds to the ridge connecting Mt Panee to Mt Taitaa and extends towards the north coast (Fig. 7), while the two others cap the Mt Herani (West) plateau (10.04 ± 0.07 Ma and 9.56 ± 0.06 Ma) and the Mt Herani (East) plateau (9.62 ± 0.06 Ma), respectively.
An Atypical Hotspot Chain

Basanitic and nephelinitic magmas evolved towards tephritic melts (e.g. TB9 from Mt Pirita dated at 9.46 ± 0.07 Ma) and the phonolitic islet Motu Taitaa (8.78 ± 0.06 Ma) within the Hanareho volcano, the large Mt Taitaa intrusive needle (8.78 ± 0.06 Ma) and the phonolitic islet Motu Volu, the large Mt Taitaa intrusive needle (Fig. 7), and ultimately towards tephritic melts (e.g. TB9 from Mt Pirita dated at 9.46 ± 0.07 Ma) and the phonolitic islet Motu Olai located west of Tubuai (not shown in Fig. 7).

All the lavas exposed on the island likely derive from a single type of enriched mantle source displaying a strong HIMU imprint (Vidal et al. 1984; Dupuy et al. 1989; Chauvel et al. 1992). Enriched mantle xenoliths are rather abundant in Tubuai lavas (Berger & Brousse 1980; Berger 1985). Those found in Mt Pirita tephrites show evidence for enrichments linked to interaction with carbonatite melts (Liotard & Barsczus 1989; Hauri 1993). Strongly enriched mantle clinopyroxenites, found within nephelinites, could represent an analog of their source (Caroff et al. 1997). As a whole, the mafic lava succession observed on the island could result from variable degrees of melting of an isotopically homogeneous mantle source, which decreased through time from 8-5% (alkali basalts) to 3-1.5% (nephelinites) while depth of melting was simultaneously decreasing (Caroff et al. op. cit.). Thus, alkali basaltic and basanitic lavas from the Hanareho volcano likely derived from the partial melting, at a depth of c. 60 km, of asthenospheric plume-related garnet+spinel lherzolites, while the Hanareho nephelinites resulted from the low-degree fusion at c. 50 km of lithospheric spinel pyroxenites previously contaminated by plume melts (Caroff et al. op. cit.).

Arango Seamount

The occurrence of a young seamount between Tubuai and Rurutu, marking the present position of the Rurutu hotspot, was predicted before its discovery (Turner & Jarrard 1982; Chauvel et al. 1997; Guille et al. 1998). During the ZEPOLFY2 cruise in 1999, samples were dredged from a very shallow seamount, with its top only 26.5 m below sea level, located at 23°26.4’ S and 150°43.8’ W, (Bonneville et al. 2002, 2006). Already called Arango Seamount after a French Navy ship that discovered its summit in 1993, it was also known from the local fishers as Tino Mana. This submarine edifice shows three rift zones equivalent to those recognised for MacDonald. Their principal orientations, N170° and N70°, correspond to that of structural discontinuities inherited from the Farallon ridge, and to that of the nearby AFZ, respectively. The edifice is composed of three coalescent volcanoes, among which the highest (Arango) is a regular cone overlapping the two lower and older ones. Samples of nephelinite and hawaiite, both occurring as pillow-lavas, were collected between depths of 900 and 600 m on its southern flank. Nepheline crystals and groundmass separated from a nephelinite gave K-Ar ages of 0.230 ± 0.004 Ma and 0.013 ± 0.002 Ma, respectively (Bonneville et al. op. cit.), allowing to designate Arago as the potentially active seamount overlying the Rurutu hotspot (Fig. 3).

Rurutu

Rurutu, a 38.5 km² island culminating at 389 m (Mt Manureva) is from a geological point of view the most unusual among the Austral islands, because it is made of two volcanic series of very different ages, Upper Miocene (12.7 to 12.1 Ma) and Pleistocene (1.1 to 1.0 Ma), separated by a 100 m thick uplifted Late Miocene carbonate platform. Already quoted by Charles Darwin (1842), the latter was the subject of a very long controversy regarding its origin (Marshall 1913, 1929; Chubb 1927; Hoffmeister 1930), which ended only rather recently (Stoddard & Spencer 1987; Dickinson 1998). The first geological sketches of Rurutu were drawn by Chubb (1927) and Obellianne (1955), but Duncan & McDougall (1976) and Duncan & Compston (1976) were the first to date two very distinct volcanic events in Rurutu, later confirmed by Turner & Jarrard (1982) and Diraison (1991). The discovery of HIMU-type lavas in the nearby island of Tubuai led to a number of geochemical studies including Rurutu samples
The geological map shown in figure 8 results from fieldwork conducted between 1992 and 1996 (Guille et al. 1998; Maury et al. 2000a, 2000b).

Rurutu island represents the summit of a large submarine edifice (with a diameter of 100 km at -4500 m) which displays a five-starshaped morphology corresponding probably to the rift zones of the initial volcano. Dredgings on a 1350 m deep seamount (ZEP2-7) located slightly west of Rurutu recovered basalts similar in age and geochemistry to the Late Miocene lavas cropping out in the island (12.2 ± 0.2 Ma, Bonneville et al. 2006).

Rurutu lavas are exclusively mafic (Fig. 4): the Late Miocene ones, which display a strong HIMU signature, consist of alkali basalts, hawaiites and picrobasalts, although a single tholeiitic basalt has also been identified (Chauvel et al. 1997; Guille et al. 1998). Pleistocene mafic lavas are more silica-undersaturated, and include basaltes and tephrites. They display an attenuated HIMU imprint (Chauvel et al. op. cit.). The two types show rather contrasted major and trace element features, and thus can be easily distinguished (and mapped) using simple geochemical diagrams, e.g. TAS (Fig. 4 Guille et al. 1998). The origin of the attenuated HIMU signature of Pleistocene lavas is attributed to the interactions between plume-related asthenospheric magmas derived from the Arago hotspot and the Rurutu lithospheric mantle, which had previously been enriched by carbonatite melts during the Late Miocene volcanic episode (Chauvel et al. op. cit.).

Three main geological units are exposed in Rurutu (Fig. 8):

- The Late Miocene volcanics, which constitute the central NS trending ridge of the island, from Moerai to Naairoa;
- The Late Miocene limestones, which overlie unconformably the old volcanics, forming a series of plateaus up to 100 m high along the coasts of Rurutu, and which dip gently (15°-20°) towards the periphery of the island;
- And finally the Pleistocene lava pile, which overlies unconformably either the limestones or directly the old volcanics. Their maximal thickness (150 m) and largest development are observed at Mt Manureva, but they also cap several other plateaus in the southern part of the island.

Figure 8: Geological map of Rurutu, simplified from Guille et al. (1998).
glass shards altered to yellowish palagonite. These units are crosscut by a dense network of dykes. Then, volcanic activity became subaerial, emplacing at the top of the pile columnar-jointed alkali basaltic flows, up to 10 m thick, which often fill up paleodepressions dug into the submarine units. Some laharc breccia deposits are also intercalated within this sequence.

The contact between the Late Miocene volcanics and the overlying (transgressive) bioclastic limestones is marked by layers of volcanioclastic breccias with abundant basaltic pebbles set into a clay-rich matrix. In the southern part of the island, near Nairobi, manganese-rich deposits occur in this contact zone (Chubb 1927; Obellianne 1955).

These limestones are rich in coral debris and show discrete layering. They contain abundant Lepidocyclina sp., the occurrence of which demonstrates their Miocene age, and their faunistic associations indicate deposition between c. 10.5 and 6.5 Ma (Bourrouilh-Le Jan 1984). They form steep cliffs facing either the periphery or the central part of the island. The origin of the latter (internal) cliffs has been a matter of considerable debate, and is now explained by the erosion/dissolution processes caused by surface waters draining the old volcanic edifice (Stoddard & Spencer 1987). These circulations led to the development of a typical karstic morphology with dolines, lapiés, caves, exits of underground streams, etc.

The Pleistocene (1.1 to 1.0 Ma) volcanic activity emplaced mainly basanites and tephrites. Basanitic flows are usually c. 10 m thick and often display columnar jointing. They crop out below the tephritic pile of Manureva plateau in the north of Rurutu, and as isolated flows near the southern edge of the island. They also occur as hydromagmatic breccias forming the beautifully preserved maar structure of Nairobi (Fig. 8). These breccias, up to 30 m thick, were emplaced either above the bioclastic limestones or the old volcanics. They are layered, with occasional base surge features and gentle peripheral dips (<10°), and contain basanitic cauliflower bombs together with abundant angular limestone blocks. The tephritic lava flows range in thickness from 10 up to 30 m, especially when they fill up paleodepressions, and often display columnar jointing. They were emitted from strombolian cones, the biggest of which (Mt Manureva) shows a preserved crater opened northwards, with an up to 150 m thick breccia pile made of lapilli, red scoriae and occasional fusiform bombs.

The common occurrence of Late Miocene shallow submarine volcanics and bioclastic limestones clearly indicates that Rurutu has been uplifted after the end of deposition of the limestones, i.e. at less than 6.5 Ma (Guille et al. 1998). On the other hand, a coastal Pleistocene lava flow near the airport shows evidence for autofragmentation by interaction with seawater, indicating that the sea level at 1.1 Ma was similar to the present-day level, and thus that the uplift of Rurutu had already ended (Maury et al. 2000b). In addition, the coastal limestone cliffs show very distinct notches at altitudes of +8 to +10 m, dated at 122 ka by the Th/U method (Pirazzoli & Veeh 1987; Pirazzoli & Salvat 1992). Such age and position are consistent with the Riss-Wurm interglacial period of high sea level (Dickinson 1997, 1998), and suggest a lack of recent uplift of the island. Thus, the origin of the surrection of Rurutu is probably linked to its passage over the Arago hotspot, leading to a thermal rejuvenation of the underlying lithosphere and corresponding local uplift of the seafloor.

**Rimatara and Seamount ZEP2-12**

The westernmost among the Austral islands, and the smallest among the inhabited ones, displays an almost circular shape, with an average diameter of 3 km, and a typical residual morphology. It is rimmed by coral sands and by an uplifted coral reef limestone unit, up to 500 m wide and reaching an altitude of 11 m (Obellianne 1955). The central part of the island, which is usually separated from the uplifted reefal limestone by swamps, reaches an
An alternative possibility is to envision an atypical hotspot chain

The presence beneath Macdonald Seamount of a hotspot responsible for the edification of at least some of the Austral-Cook Islands (Johnson & Malahoff 1971) is not questioned. However, since Duncan & McDougall (1976) and Turner & Jarrard (1982), all authors agree that the Austral-Cook linear hotspot chain is not as simple as the Hawaiian or Society archipelagoes, as it obviously shows their progressive age variation (e.g. Guillou et al. 2005) and geomorphologic evolution (Dickinson 1998). The complex age-distance relationships depicted in figure 3B are rather intriguing, especially regarding the succession, in some islands (Rurutu, Aitutaki) or seamounts (Arago), of two volcanic events separated by more than 5 Ma. Rejuvenation of volcanism may occur in Hawaiian-type islands well after the end of the main building stage, when the island passes over a plume "tail" deflected away from the hotspot by overlying lithosphere motion (Ribe & Christensen 1999; Thoraval et al. 2006). However, the spatial and temporal scales of such a process (c. 150 km and 1.5 Ma in the Marquesas, Legendre et al. 2006) are not consistent with those observed in the Austral-Cook chain.

An alternative possibility is to envision a more or less continuous volcanic activity along a c. 2300 km long hot line, as proposed by Bonatti & Harrison (1976) and Bonatti et al. (1977) for the Easter island chain. However, this hypothesis is not consistent with the three relatively regular age trends shown in figure 3B, which have been termed the Tubuai, Atiu and Rarotonga trends (Chauvel et al. 1997). The occurrence of such trends, recently supported by age data on seamounts discovered during the ZEPOLYF2 cruise (Bonneville et al. 2006), is consistent with the hypothesis of at least three coeval hotspots (Fig. 3) respectively located beneath Macdonald, Arago, and in a still unknown position SE of Rarotonga (Turner & Jarrard 1982; Diraison 1991; Chauvel et al. 1997). Of course, the incoming difficulty is then to explain how and why three hotspots could be aligned precisely in the ESE-WNW direction corresponding to the Pacific plate motion. The geometric technique of relocating hotspots from seamount tracks (Wessel & Kroenke 1997, 1998) does not help to solve these problems, because it relocates adequately Rurutu-Arago and Rarotonga, but surprisingly not the most obvious hotspot in the region, i.e. Macdonald.

Other authors (e.g. Diament & Baudry 1987; Bonneville et al. 2002, 2006; Adam & Bonneville 2008) consider two separate trends corresponding to the northern and southern rows of islands, respectively (Fig. 3A). In this hypothesis, the southern row, from Macdonald to Marotiri, Rapa, Mangaia and Rarotonga, should be credited of two coeval hotspots and presents an apparent 1500 km gap between Rapa and Mangaia. For the northern one, Raivavae to Tubuai, Arago, Rurutu, Rarotara, Mauke, Atiu and Aitutaki, the situation becomes even more complicated because the young volcanism in Aitutaki (and of course at Arago) needs to be explained, and it is also necessary to postulate that an unknown hotspot located SE of Raivavae became extinct after the edification of this island. In addition, the HIMU signatures and petrologic types of Mangaia, Rarotara, Rurutu (old), Tubuai and Raivavae (old) lavas are quite unusual but very similar, and point out to their derivation from the same mantle plume. Finally, the present-day diameters of the Macdonald (100 km) and Society (160 km) hotspots are smaller than the bulk width of the Cook-Austral chain (200 km), but the latter size is considered acceptable for a mantle plume (Morgan 1972; Wylle 1988).

Unusual mantle sources of Austral magmas

Recent geochemical data on Austral islands (Schiano et al. 2001; Lassiter et al. 2003) and seamounts (Bonneville et al. 2006) have lead to the recognition of mantle heterogeneities much larger than previously expected (Vidal 1992) beneath the archipelago. From seamount data, this
heterogeneity increased through time to reach its maximum at less than 20 Ma. Such a feature is consistent with a progressive heterogeneity of the Pacific lithospheric mantle, induced by its passage over several different hotspots (Dupuy et al. 1993). The "contamination" of young Rurutu (and probably Arago) plume-derived magmas by the overlying lithosphere, which acquired its HIMU signature during the Late Miocene volcanic activity (Chauvel et al. 1997) is a good example of such interactions leading to increased heterogeneities.

If the origin of the HIMU signature of many Austral-Cook lavas appears no more as a controversial topic, its distribution within the archipelago is still not well understood. The most extreme HIMU imprint is documented at Mangaia (Woodhead 1996); it is still very strong in Tubuai, "old" Rurutu (Chauvel et al. 1992) and "old" Raivavae lavas (Lassiter et al. 2003; Maury et al. 2013), but attenuated in "young" Rurutu lavas (Chauvel et al. 1997) and in Arago lavas (Bonneville et al. 2002). The HIMU flavor is much weaker in the other Cook islands, as well as in "young" Raivavae, Rapa, Marotiri and Macdonald (Hémont et al. 1994). The hypothesis that the Austral Fracture Zone might represent a major mantle limit (Lassiter et al. 2003) is clearly not consistent with the location of Raivavae south of it (Fig. 3A). Complex geochemical models involving:

• melting of highly heterogeneous mantle plume materials,

• followed by variable contamination of these melts by the Pacific lithosphere,

have been proposed (Lassiter et al. 2003; Bonneville et al. 2006). A temporal evolution of the composition of the Macdonald mantle plume, involving the recent contribution of mantle containing a younger sediment component has also been considered (Hémont et al. 1994). Additional hypotheses postulate the contribution of other materials, e.g. old subcontinental lithosphere (Schiano et al. 2001) or subduction-modified mantle (Lassiter et al. 2003). However, the dating of HIMU-type "old" Raivavae (Rairua) lavas to 10.6-7.4 Ma allows us to propose a much simpler explanation for the HIMU-type lavas. Indeed, the "strong" HIMU signature, documented since 19 Ma in Mangaia (Woodhead 1996) seems to disappear after the edification of Tubuai and Rairua volcanoes. In Raivavae Island, a 1 Myr long gap is documented between their emplacement and that of the "young" Anatomu volcano which displays a more subdued DMM-HIMU-EM isotopic signature. This gap, much shorter than that observed in Rurutu, seems inconsistent with the hypothesis of a passage of Raivavae over two different hotspots (Maury et al. 2013). Moreover, the oldest (4.8 Ma) Rapa lavas, isotopically rather similar to those of Marotiri and Macdonald, were emplaced only 0.6 Myr after the youngest ones from Raivavae (5.4 Ma), although they lie 500 km closer to the present Macdonald hotspot (Fig. 3).

Therefore, the whole volcanic history of Raivavae seems related to the late stages of activity of a predominantly HIMU plume which generated successively Mangaia, Rurutu (old) and Tubuai lavas. Numerical simulations of the evolution of thermal and thermo-chemical plumes (Farnetani et al. 2002; Farnetani & Hoffmann 2009) suggest that small heterogeneous mantle domains are present in the thermal boundary layer feeding the plume. During the ascent of the latter, they are converted into long-lived elongated and narrow filaments within the plume conduit. Such filaments would melt sporadically, and then eventually communicate their specific geochemical fingerprint to small volumes of basaltic lavas (Farnetani & Hoffmann 2009).

The changes which occurred in Raivavae between 7.4 and 6.4 Ma involved an increase of partial melting degrees (from basanitic and alkali basaltic to tholeiitic magmas) and an attenuation of their HIMU signature. They could be ascribed to the contribution of a new filament of specific composition within a predominantly HIMU plume.

... Superplume and plumelets
The very deep origin, close to the core-mantle boundary, of HIMU type plume component is generally admitted. Despite the considerable length of the Austral-Cook archipelago, it does not fit the characteristics of hotspot chains derived from mantle plumes arising directly from the core-mantle boundary, e.g. those of Hawaii, La Réunion and Iceland (Clouard & Bonneville 2001; Courtillot et al. 2003). Analogical (Davaille 1999; Davaille et al. 2002, 2005) and numerical (Ogawa 2007) models show that large thermochemical plumes ("superplumes") can ascend within the lower mantle as very large domes of hot materials, and remain anchored there for more than 100 Myrs (type 2 plumes of Courtillot et al. 2003). A number of much smaller and short-lived plumes ("plumelets") can form from the top of the "superplume" and uprise through the asthenospheric upper mantle. They can be chemically heterogeneous, and display variable geochemical signatures, as they tap very different regions of the lower mantle and may include several filaments with specific geochemical signatures (Farnetani & Hoffmann 2009).

The short tracks of Arago (Atiu trend) and Rarotonga suggest that the corresponding plumes are young and potentially short-lived "plumelets" (e.g. Dickinson 1998). Given the existence of a "superplume" in the lower mantle beneath French Polynesia, as evidenced by its very hot character (Zhao 2001), one may consider the Macdonald, Arago and Rarotonga (?) "plumelets" emanated from it, as short-lived columns of hot mantle materials ascending through the upper mantle (Courtillot et al. 2003). The ascent of such plumelets is likely favored by existing discontinuities and
zones of weakness in the upper mantle, and the track left by a previous plume can certainly create such weaknesses. Indeed, recent numerical models (Sleep 2008) demonstrate that hot plume materials can be channeled at the top of the asthenosphere. There, they can be guided by the track of an older hotspot along which the oceanic lithosphere has been thermally eroded. It is thus possible to explain the three coeval present-day hotspots by considering that the oldest plumelet, i.e. the Macdonald HIMU-type one, started to create an ESE-WNW island/seamount chain (the Tubuai trend) c. 20 Ma ago (Mangaia), and at the same time left its track in the upper mantle as a weakness zone extending from Mangaia to Raivavae. There, its strong HIMU imprint vanished at 7.4 Ma; between 6.4 and 5.4 Ma, a different filament of more subdued DMM-HIMU-EM isotopic signature melted to form Anatonu lavas. More or less simultaneously:

- another plumelet (the present Macdonald plumelet) generated Rapa and then Marotiri lavas,
- and the Arago plumelet ascended along the same track beneath Aitutaki and Atiu (Fig. 3), creating the Atiu trend. They were later followed, at less than 4 Ma, by the still poorly known Rarotonga plumelet.

**CONCLUSION**

The spatial, temporal and geomorphologic evolutions from the active Macdonald Seamount to Marotiri, Rapa, Raivavae and Tubuai are relatively simple, as expected from a Hawaiian-type hotspot-related linear volcanic chain. However, the presence in the row of the Austral-Cook Islands of a second hotspot, presently located beneath Arago Seamount, led to the uplift of Rurutu more than 10 Ma after the end of its Late Miocene activity, and to the emplacement of young volcanics over the old ones and the uplifted limestones. The complexity of the mantle sources of Austral magmas is attributed:

- To the ascent through the upper mantle of several heterogeneous plumelets sometimes made of distinct filaments, tapping different source regions located within the South Pacific superplume;
- And to heterogeneities in the Pacific lithospheric mantle, created during its successive passage over several mantle plumes. We propose that the location of several hotspots along the same track is due to the channelling of hot plumelet materials at the top of the asthenosphere, where they were guided by the thermally eroded base of the oceanic lithosphere.
Fauna
Adult Red tailed tropicbird (Phaethon rubricauda) sitting in ferns, Tubuai (Photo J-Y. Meyer).
Hunting, introduction of predators (e.g. dog, pig, the Polynesian rat *Rattus exulans*), and habitat destruction (e.g. burning for cultivation) by the early Polynesian inhabitants has resulted in the decline and extinction of numerous bird species on the small and remote islands of Polynesia (Steadman 2006). In the past, birds were a significant source of protein for Polynesians as well as an important component of their everyday life, being celebrated culturally in songs, legends, and sculptures (Lavondès 1975; Steadman 1997); see cradle song on the right. Many species which survived the changes induced by the first human settlers (e.g. parrots *Cyanoramphus* spp., shorebirds *Prosobonia* spp., etc.) disappeared after the arrival of Europeans, this second wave of extinction coincided with the introduction of the Black rat (*Rattus rattus*) and raptors, the destruction of habitat by grazing animals (cattle, goat, sheep), and possibly the arrival of introduced avian disease (see van Riper & Scott 2001 for Hawaii Islands). The process continues today, as demonstrated by the recent decline and extinction of several species of monarchs (*Pomarea* spp.) (Thibault et al. 2002; Cibois et al. 2004) on islands in the Marquesas (e.g. Ua Pou, Fatu Hiva), following the documented arrival of the Black rat. Similarly the recent introduction of behaviorally dominant birds, such as the Red vented bulbul (*Pycnonotus cafer*) threatens native landbird species in Tahiti (Thibault et al. 2002).

In the Austral Islands the incomplete knowledge of the avifauna, up to now, has prevented the evaluation of the levels of endemicity and population status, necessary for developing appropriate conservation strategies. Two expeditions to the Austral Islands in 2002 and 2004 funded by the Délégation à la Recherche (French Polynesia Government) in collaboration with the Institut Louis Malardé (Tahiti), in order to address the gaps in our knowledge. In this chapter we present a synthesis of historical and field data on the avifauna of each island, (landbirds, seabirds and introduced birds), evaluating population densities and the status of species, when possible, and finally proposing conservation priorities for the archipelago.

The historical data for the birds of the Austral Islands was collected from a variety of scattered sources, dating from the beginning of the 20th century. Some of the data comes from published literature; other data comes from unpublished manuscripts and letters written by several ornithologists (Table 4 gives details of these sources). The islands of Rapa and Raivavae have been the most frequently and intensely studied by ornithologists, Maria has been visited just twice and Marotiri’s rocky islets just once. The historical data gives a reasonable overview of the species found in the archipelago, but the data is too scattered and inconsistent to provide an insight into population trends for most species, especially seabirds, where abundance fluctuates dramatically during breeding cycles and between years, depending on the abundance of food sources.

### AVIFAUNA OF THE AUSTRAL ISLANDS

#### Landbird assemblages

Only six native landbird species inhabit the Austral Islands (Table 5). Three have a wide range in the Pacific and are found in most archipelagos (Pacific reef heron *Egretta sacra*, Pacific black duck *Anas superciliosa*, Spotless crake *Porzana tabuensis*). Two species are endemic to a single island: the Fruit dove *Ptilinopus huttoni* (locally called “koko”) inhabits Rapa and the Reed warbler *Acrocephalus rimitarae*, Rimatara. Another species, Kühl’s...
Group of Pacific black ducks (*Anas superciliosa*), Raivavae (Photo J.-C. Thibault).

Table 4: Chronology of main historical sources relating ornithological work since the early 20th century for which a report, book or paper were accessible.

<table>
<thead>
<tr>
<th>References</th>
<th>Maria</th>
<th>Rimatara</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Raivavae</th>
<th>Rapa</th>
<th>Marotiri</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seale (undated)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fosberg (1972)</td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>J.-C. Thibault (this work)</td>
<td>27 Sept.-12 Oct. 1974</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>J.-C. Thibault (Thibault &amp; Varney 1991a, b)</td>
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<td></td>
<td></td>
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<tr>
<td>Ehrhardt (1986)</td>
<td></td>
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<tr>
<td>McCormack &amp; Kürzle (1996), McCormack (pers. comm.)</td>
<td>5-11 Aug. 1992</td>
<td></td>
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<tr>
<td>Second hand data reported in <em>Te Manu</em> (39): 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>July 1992</td>
<td></td>
<td></td>
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<tr>
<td>McCormack et al. (2000)</td>
<td></td>
<td></td>
<td>June 2000</td>
<td></td>
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</tr>
<tr>
<td>J.-C. Thibault (this work)</td>
<td>18 Nov.-18 Dec. 2002</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Fontaine (2002)</td>
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<tr>
<td>Pierce et al. (2003)</td>
<td>11-12 Apr. 2003</td>
<td></td>
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<tr>
<td>J.-C. Thibault (this work)</td>
<td>25 Oct.-6 Nov. 2004</td>
<td></td>
<td></td>
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<tr>
<td>Gaskin (2007)</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Te Manu (39): 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>21 Sept. 2006</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Iorikeet *Vini kuhlii* (locally called "vini 'ura"), has a disjunct distribution, being present on Rimatara and two islands in the Kiribati archipelago, where population numbers are estimated to be in excess of one thousand (King 1973); bones of fossil remains attributed to this species have also been found in the Cook Islands (Steadman 2006). The Rimatara reed warbler was originally described as a sub-species of *Acrocephalus vaughani* from the Pitcairn Islands group, on the basis of morphometrics (Murphy & Mathews 1929). However, recent molecular phylogenetic work shows that the species is more closely related to the Reed warblers of Mangaia (*A. kerearako*) and Mitiaro (*A. kaoko*) in the Cook Islands (Cibois et al. 2007).
Landbird population sizes, trends and habitat

Where available, data on estimated population size are presented in Table 5. The Pacific reef heron is widespread in Polynesia, but does not breed in the most southern islands (Rapa and Pitcairn group, except Oeno atoll [Brooke 1995a]). Although it is a common visitor. The Pacific black duck is present on all Austral Islands excepted Marotiri, taking advantage of wetlands associated with taro cultivation. The Spotless crake occupies the same islands in small numbers, except on Rapa, where the population was relatively large in 1989.

It seems that the Rapa fruit dove was only observed at low densities in the early 20th century during the Whitney South Sea Expedition (WSSE)’s visit. In 1989, the population was small (Table 5), its range corresponding to patches of the native forest. The extent of which has continued to decrease in size, due to fires and grazing by feral animals (cattle, horses, and goats). The dove occupies less than 10 forest patches with and area over 10 ha each (Thibault & Varney 1991b). In 2002, the Fruit dove was observed in several patches, especially the forest which covers the slope of the main summit (Mt Perau, 650 m) (B. Fontaine pers. comm.).

Table 5: Presence and abundance of breeding landbird species on islands in the Austral Islands. Vérin (1969) mentions the occurrence of a Fruit-dove attributed to *Ptilinopus purpuratus* on Rurutu, but he fails to give details of the source data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Rimatara</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Raivavae</th>
<th>Rapa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pacific reef heron (<em>Egretta sacra</em>)</td>
<td>2004: 5-15 pairs (1)</td>
<td>2003: present (6), (7)</td>
<td>2003: present (6)</td>
<td>2002: &lt;50 individuals (9)</td>
<td>Rare visitor recorded once in 1974 (10)</td>
</tr>
<tr>
<td>Spotless crake (<em>Porzana tabuensis</em>)</td>
<td>Despite active searching Quayle (undated) failed to find it in 1921. One record only, in 2002 (2)</td>
<td>Present, but seems very rare (7)</td>
<td>1974: common in fern-land, taro cultivation and wetlands (8). No recent data</td>
<td>2002: present inland (9)</td>
<td>1989: common on mainland (taro cultivation, fern-land) and islets (Tarakoi, Taaturu)</td>
</tr>
<tr>
<td>Rapa fruit dove (<em>Ptilinopus huttoni</em>)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Discovered during the 19th century. 1974-1990: 175-368 individuals (12). 2002: present in woody areas up to 600 m (11)</td>
</tr>
<tr>
<td>Kühl’s lorikeet (<em>Vini kuhlii</em>)</td>
<td>Discovered in the 19th century. See Table 6</td>
<td></td>
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</tr>
<tr>
<td>Rimatara reed warbler (<em>Acrocephalus rimitarae</em>)(1)</td>
<td>Discovered by the WSSE. 2004: 1 777-2 567 individuals well-distributed in all habitats (5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Total number of species | 5 | 3 | 3 | 3 | 3

(1) Correct name is *rimitarae* and not *rimatarae* (cf. IUCN 2004); use of *rimitarae* by Murphy & Mathews (1929) is not a mistake, as people used also the name Rimatara at the beginning of the 20th century (Jourdain 1970).
The Rapa fruit dove is threatened with extinction due to the loss of the remaining patches of suitable habitat, which will only persist if grazing by feral goats and cows is controlled. Population numbers of the Kuhl’s lorikeet and the Reed warbler on Rimatara are relatively high (Table 5). Several counts of the Lorikeet were attempted during the last few years (Table 6), but no trend was detected and differences most likely reflect the different methods used by the different observers. Both species occupy disturbed habitats: cultivated areas and secondary forest. Recent observations suggest that their populations remain stable. The Lorikeet is able to utilize both wild and cultivated plants opportunely (flower, nectar, fruit) (Table 7). The Warbler is present almost everywhere on the island, it was even observed in the swamp and the central fern-covered hill, though breeding occurs mainly in wooded areas (coconut groves with undergrowth, in cultivated areas, coastal forest, and natural forest on limestone [Thibault & Cibois 2006]). Most of the island’s surface is covered with agricultural plantations or coconut groves with undergrowth, these habitats are relatively stable in range and suitable for the Reed warblers, though the common use of fire to clear vegetation is clearly a threat to these birds. Native forest is restricted to a limestone area that constituted, until recently, c. 21 % of the total surface of the island (170 ha). The building of an airport in 2002 has cleared c. 65 ha of the most representative part of this forest (i.e. 40 % according to Meyer et al. 2005). Thus we estimate that the habitat of several dozen Reed warblers and Kuhl’s lorikeet has been permanently destroyed by this development.

### Seabird Endemism

The Austral Islands are characterized by a high diversity of seabirds, especially in the Procellariiformes: most of the species breeding in Eastern Polynesia can be found in the Austral Islands (i.e. at least 12 species; Table 8). Breeding seabirds include two endemic species (*Puffinus myrtae*, *Fregetta grallaria titan*) from Rapa and possibly Marotiri (both discovered in the early 20th century, by H.J. Kelsall in 1925 and the WSSE in 1921, respectively). There is also a petrel that was found on Raivavae that may constitute a new taxa, related to *Pterodroma leucoptera* (Bretagnolle 2001). Molecular studies have recently showed that *Puffinus myrtae*, described initially as part of the *P. assimilis* species-group, is in fact related to *P. newelli* from Hawaii (Austin et al. 2004). *F. grallaria titan*, a sub-species described on the basis of its large size (Murphy 1928), might constitute a full species on the basis of its specific vocalization, which is very distinct from those of others populations (V. Bretagnolle pers. comm.), but molecular analyses will be necessary to confirm this hypothesis. The Small petrel that probably breeds on the ridges of Raivavae has been tape-recorded in 1989 (Seitre & Seitre undated), then photographed in 1993 (A. Guillemont unpublished data), but no biometric data are available (except the dismembered wings of an individual killed by a cat, held at the National Museum, Wellington, New Zealand) and as yet, no molecular analyses have been performed. As most species of petrels are nocturnal and often breed in inaccessible areas, knowledge is far from complete and several populations will probably be discovered in the future. An unidentified petrel was photographed on Mt Hanaheno (Tubuai) in 1980 (Ehrhardt 1980) and an unfamiliar vocalization was heard at dusk on Mt Perau (Rapa) in December 2002 (B. Fontaine pers. comm.).

**Table 6: Comparisons of population estimates of Kuhl’s lorikeet, made between 1992 and 2004. No definite trend can be extrapolated.**

<table>
<thead>
<tr>
<th>Estimated numbers (individuals)</th>
<th>Date</th>
<th>Method</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>905</td>
<td>5-11 August 1992</td>
<td>transect</td>
<td>McCormack &amp; Künzlé (1996)</td>
</tr>
<tr>
<td>c. 750</td>
<td>2000</td>
<td>transect</td>
<td>McCormack et al. (2000)</td>
</tr>
<tr>
<td>1042</td>
<td>3-23 August 2002</td>
<td>point-counts</td>
<td>Blanvillain (2002)</td>
</tr>
</tbody>
</table>
Table 7: List of plant species observed as a food source of Kühl's lorikeet. The majority of species are cultivated plants, observers have rarely visited the native forest, though there are several species present there which could provide food resources (namely: Hernandia nymphaefolia, H. moerenhoutiana [Hernandiaceae], Barringtonia asiatica [Lecythidaceae], Calophyllum inophyllum [Guttiferae], Homalium sp. [Salicaceae], Procris pedunculata [Urticaceae], Capparis cordifolia [Capparaceae]).

<table>
<thead>
<tr>
<th></th>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>Falcataura molucanna (= Albizia molucanna, Paraseianthes falcata) (Mimosaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adenanthera pavonina (Mimosaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Albizia lebbeck (Mimosaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inga feuilles (= I. ynga, I. edulis) (Mimosaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Casuarina equisetifolia (Casuarinaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Mangifera indica (Anacardiaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Ceiba pentandra (Malvaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Erythrina variegata (Fabaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Syzygium jambos (Myrtaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Musa spp. (Musaceae)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Cocos nucifera (Areaceae)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Hibiscus rosa-sinensis/nobilis (Malvaceae)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Persea americana (Lauraceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cordyline fruticosa (Lilaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barringtonia asiatica (Lecythidaceae)</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Guettarda speciosa (Rubiaceae)</td>
<td>X</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Morinda citrifolia (Rubiaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ficus tinctoria (Moraceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Passiflora maliformis (Passifloraceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bauhinia monandra (Fabaceae)</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Psidium guajava (Myrtaceae)</td>
<td>X</td>
<td></td>
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</tr>
</tbody>
</table>

The taxonomic status of the Blue gray noddy, Procellsterna cerulea, needs revision. Holyoak & Thibault (1984) considered that plumage color variation in P. cerulea populations in the South Pacific was clinal, with a gradient from darker birds in Hawaii in the north of the range to lighter birds in the southeast in Lord Howe and Easter Island. However, Gochfeld & Burger (1996) separated the taxon into two species; populations from the north of the range (Hawaii to the Austral Islands) were included in P. cerulea and populations from the south (Lord Howe to San Ambrosio, through Easter Island) were included in P. albivitta.

**Comparison of seabird diversity between islands**

Among the Austral Islands, Raivavae has the highest species diversity, including many Sternidae and Procellariiformes, although absolute numbers are very low, approaching local extinction in three species (Murphy's, Kermadec and the Herald petrel).
Table 8: Presence and abundance of breeding seabird species on islands in the Austral Islands. For details on islets of Raivavae see Table 9, and for data on Rapa’s islets obtained in 1974 and 1990 see Thibault & Varney (1991a).


<table>
<thead>
<tr>
<th>Species</th>
<th>Island</th>
<th>Presence</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Murphy’s petrel <em>Pterodroma ultima</em></td>
<td>Maria (1)</td>
<td>Possible breeder</td>
<td>&lt;10 pairs. Definitely known only from Motu Papararuu (J.-J. Philippeneau); possible breeder inland (F. Lacan)</td>
</tr>
<tr>
<td>Kermadec petrel <em>Pterodroma neglecta</em></td>
<td>Rimatara (2)</td>
<td>Several sightings; but no breeding record</td>
<td>Breed on mainland and 4 islets. (&gt;500&lt;1 000 pairs)</td>
</tr>
<tr>
<td>Herald petrel <em>Pterodroma (arminjoniana) heraldica</em></td>
<td>Rurutu (3), (4)</td>
<td>One collected by WSSE. Probable breeder in low number inland (G. McCormack pers. comm., (14))</td>
<td>Breed on 2 islets. (&gt;250&lt;1 645 pairs)</td>
</tr>
<tr>
<td>Black winged petrel <em>Pterodroma nigripennis</em></td>
<td>Tubuai (7), (14)</td>
<td>Founded on ridges inland, but breeding sites unknown (Seitre &amp; Seitre undated; A. Guillemont unpublished)</td>
<td>Collected at sea (9) and recorded offshore (11)</td>
</tr>
<tr>
<td>Collared petrel <em>Pterodroma d. leucoptera</em></td>
<td>Raivavae (7), (8)</td>
<td>Breeding on 5 islets. (&lt;100 pairs)</td>
<td></td>
</tr>
<tr>
<td>Tahiti petrel <em>Pseudobulweria rostrata</em></td>
<td>Rapa (6), (8)</td>
<td>Several breeders collected (9). Several thousands displaying (11), “abundant” (13)</td>
<td></td>
</tr>
<tr>
<td>Christmas shearwater <em>Puffinus nativitatis</em></td>
<td>Several pairs on Motu Hotuatua</td>
<td>Breeding in small number on Motu Ofai (6)</td>
<td>Breed on 4 islets. (&gt;150&lt;1 000 pairs)</td>
</tr>
<tr>
<td>Wedge tailed shearwater <em>Puffinus pacificus</em></td>
<td>Tropical shearwater <em>Puffinus bailloni</em></td>
<td>Breeding on a coral islet according to Quayle (undated); breed in low numbers on Motu Ofai (6)</td>
<td>Breeder (13)</td>
</tr>
<tr>
<td>Newell’s shearwater <em>Puffinus (newelli) myrtae</em></td>
<td></td>
<td>Breeding on mainland and 5 islets. (&gt;500&lt;1 000 pairs)</td>
<td></td>
</tr>
<tr>
<td>White bellied storm petrel <em>Fregata (grallaria) titan</em></td>
<td></td>
<td>Breeding on 4-5 islets. (&gt;300&lt;550 pairs). “Breeding most likely” (13)</td>
<td></td>
</tr>
<tr>
<td>Polynesian storm petrel <em>Nesofretta fuliginosa</em></td>
<td></td>
<td>Breeding on 2-4 islets. (&gt;200&lt;1 000 pairs). “Breeding most likely” (13)</td>
<td></td>
</tr>
<tr>
<td>Red tailed tropicbird <em>Phaethon rubricauda</em></td>
<td></td>
<td>Breed in the natural forest (&lt;5 pairs)</td>
<td></td>
</tr>
<tr>
<td>White tailed tropicbird <em>Phaethon lepturus</em></td>
<td></td>
<td>Breed in the natural forest (&lt;10 pairs)</td>
<td></td>
</tr>
<tr>
<td>Masked booby <em>Sula dactylatra</em></td>
<td></td>
<td>Present, but no proof of breeding</td>
<td>&quot;A couple of White tailed tropicbirds” cited by Fosberg (1972)</td>
</tr>
</tbody>
</table>
Seabird assemblages on Rapa include mostly Procellariiformes, with seven species recorded, which is the highest diversity on the Australs Islands. The bird assemblage of Marotiri seems to be very similar to Rapa, but the small surface of the three rocks that form the island is a limits population size (Gaskin 2007). An unidentified nocturnal petrel has been heard on Rurutu, and further investigation will be required to verify this (Te Manu vol. 39 2002). Few data are available for Maria atoll (Table 8). No large seabird colonies have been recorded, but the island has, until recently, been exploited for coprah and may provide a future-breeding site for Murphy's petrel.

Raivavae and Rapa-Marotiri are the most important islands for seabirds in the Austral Islands, in terms of species diversity, population densities and levels of endemcity (Tables 8-9). When compared with other eastern Polynesian archipelagos (Society, Tuamotus and Marquesas), we noticed an abundance of Procellariiformes species, a moderate number of boobies and the absence of important colonies of Sooty tern.

Among species breeding in Austral Islands, only three (the Red tailed tropic bird, the Brown noddy, and the Common fairy tern) are distributed on every island (Table 8). The presence of Newell's

<table>
<thead>
<tr>
<th>Species</th>
<th>Number</th>
<th>Breeding</th>
<th>Breeder</th>
<th>Common</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
<th>Breeder</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown booby (Sula leucogaster)</td>
<td>88</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Red footed booby (Sula sula)</td>
<td>397</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Great frigatebird (Fregata minor)</td>
<td>220</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Sooty tern (Sterna fuscata)</td>
<td></td>
<td>Present, but no proof of breeding</td>
<td></td>
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<tr>
<td>Spectacled tern (Sterna lunata)</td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Brown noddy (Anous stolidus)</td>
<td>72</td>
<td>Breeder (&lt;200 pairs)</td>
<td>Common breeder in coconut trees</td>
<td>Breeder on mainland (Tonarutu cliffs and islets (Motu, Tohena))</td>
<td>&lt;500 pairs on mainland and coral islets</td>
<td>&lt;500 pairs on mainland and coral islets</td>
<td>Breed on mainland and 7 islets (&gt;1000 &lt;10000 pairs)</td>
<td>&quot;Breeding most likely&quot; (13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black noddy (Anous minutus)</td>
<td>31</td>
<td>Probably breed, but number unknown</td>
<td>Breeder on Motu Tohena (several ten pairs)</td>
<td>580-720 pairs on islets</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Blue gray noddy (Procellsterna cerulea)</td>
<td></td>
<td>Present in small number in cliffs; recent breeder according to (4)</td>
<td>30-50 pairs in cliffs on mainland and Motu Hotuatau</td>
<td>Breed on mainland and 5-6 islets (&gt;1000 &lt;10000 pairs)</td>
<td>&quot;Breeding most likely&quot; (13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common fairy tern (Gygis alba)</td>
<td>265</td>
<td>Breeder (&lt;300 pairs)</td>
<td>Fairly common</td>
<td>Present (200 pairs on Toena and Roa islands in 1974) (5)</td>
<td>&lt;500 pairs on mainland and coral islets</td>
<td>Breeding on mainland and 3 islets (&lt;1000 pairs)</td>
<td>&quot;Breeding most likely&quot; (13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Number of species</th>
<th>7-9</th>
<th>5</th>
<th>6</th>
<th>7-9</th>
<th>12-14</th>
<th>11</th>
<th>c. 12</th>
</tr>
</thead>
</table>

Table 9: Population sizes of Sternidae on the mainland and islets off Raivavae (nb. pairs) observed in November-December 2002 (Thibault 2003).
The Birds: an Unbalanced but Unique Avifauna

The shearwater and White bellied storm petrel is due to the presence of cooler sub-tropical water currents. Great frigatebirds are only thought to breed on Maria atoll, but the two Pacific species visit the other islands regularly and in good numbers, except on Rapa (and Marotiri) where they are rare visitors.

**Seabird population sizes**

Most seabird species occur at low densities in the Austral Islands, most probably because of human pressure rather than any limitation of resources. For instance, all Procellariiformes populations are small, when compared with uninhabited islands in the Pitcairn archipelago (Brooke 1995b); most populations are restricted to very small areas (steep cliffs, mountain ridgetops and islets), because they were eliminated from more accessible areas by hunting, introduced predators and habitat destruction.

The uninhabited islet of Marotiri, while only rarely visited by humans, is not host to a large population of seabirds simply because of its small size (several hectares). There are significant populations of the Blue gray noddy on Rapa, with comparable population sizes to those found in the Marquesas.

**Introduced birds**

Five introduced bird species inhabit the Austral Islands (Table 10). Humans intentionally introduced three of these species. The early Polynesians brought Red junglefowl, Gallus gallus, and more recently in the 20th century Europeans introduced the domestic pigeon, Columbia livia and Common myna, Acridotheres tristis. It is unclear whether the Chestnut breasted manikin, Lonchura castaneothorax, recorded in the archipelago since the 1980s, was deliberately introduced or arrived from Tahiti by itself. The Silvereye (Zosterops lateralis) has been recorded on Tubuai, Raivavae and Rurutu since 1984 (Pratt et al. 1987), probably colonizing independently from Tahiti (Thibault & Monnet 1990). Curiously this species has not been yet reached or become established on Rimatara, although the distance from Tahiti is equivalent to the distance to Raivavae or Tubuai. Rapa is probably too remote to be colonized rapidly. It seems more probable that the Silvereye colonized each of the three islands separately from Tahiti, which constitutes an important source with several hundred thousand individuals, rather than by intra-island colonization within the Austral Islands, where numbers remained low during the 1980s (Thibault & Monnet 1990). On Raivavae, the Silvereye inhabits all woody areas: Hibiscus tiliaceus thickets, agricultural plantations (e.g. banana groves), Pinus caribaea (Pinaceae) and Casuarina equisetifolia (Casuarinaceae) forests, patches of native forests dominated by Metrosideros collina (Myrtaceae) and Hernandia moerenhoutiana (Hernandiaceae) on Mt Hiro. This species is common everywhere on the mainland with a mean density of several pairs per hectare where vegetation is above 4 m high. Population size was estimated to be more than one thousand pairs in 2002. The Silvereye also breeds on islets, but only in low densities (Thibault 1976).

**Landbird extinctions**

No historical extinctions have been recorded in Austral Islands since the WSSE. Scattered data indicates that several species were probably extirpated on the Austral Islands soon after the arrival

---

Table 10: Distribution of introduced birds on islands of the Austral Islands. (1) According to Paulay (1982) “a hawk-sized raptor was seen several times during my visit” suggesting that the Australian harrier (Circus approximans) introduced in the Society Islands might be an accidental visitor in the Austral Islands. Although, the Peregrine falcon, never recorded in Austral-Society Islands has been recorded in the Pitcairn Group (Brooke 1995a).

<table>
<thead>
<tr>
<th>Species</th>
<th>Rimatara</th>
<th>Rurutu</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>References</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red jungle fowl Gallus gallus</td>
<td>common (2004)</td>
<td>common</td>
</tr>
<tr>
<td>Chestnut breasted manikin Lonchura castaneothorax</td>
<td>2002 &lt;100 individuals (2004)</td>
<td>present</td>
</tr>
</tbody>
</table>
of the first Polynesian settlers (Steadman 2006; M. Prebble pers. comm.). Table 11 shows that several species of pigeons (*Ptilinopus* spp., *Ducula* spp., *Gallicolumba* spp.), rails (*Gallirallus* spp., *Rallus* spp.), Reed warblers (*Acrocephalus* spp.), one or several Lorikeets (*Vini* spp.), and a shorebird (*Prosobonia* sp.) occupied most of the southern Polynesian islands and we can hypothesize that species belonging to most of these genera also occupied the Austral Islands.

We don’t know to what extent some species which have a large range in Polynesia, also inhabited the Austral Islands in the past. The only example, Kuhl’s lorikeet, had a larger range formerly, extending into the Cook Islands as shown by subfossil records (Steadman 1985). However, Polynesians carried Lorikeets between islands, and it is difficult to know where the natural range was. A similar case is found in flying foxes, *Pteropus tonganus*, whose distribution in Central Polynesia may have been human-mediated (Flannery 1995). The natural or anthropogenic origin of the specimen for which bones were recently discovered on Rurutu remains unknown (Weisler et al. 2006).

### Seabird extinctions

Comparison with lists of extinct taxa from other southern Polynesian islands does not suggest an important rate of extinction (Table 12), compared with landbirds. On Rapa, we know that during the 20th century seabirds were actively hunted as a food source, sometimes on dangerous cliffs, whereas ducks and Fruit-doves were not (Paulay 1982); in the 1920s, Quayle (undated) found charred petrel bones. However, Thibault & Varney (1991a) noticed that while chicks of some petrels (*Pterodroma neglecta, P. ultima, Puffinus nativitatis*)...
Table 11: Comparison of landbird assemblages on Mangaia (Cook Islands), and the Austral Islands combined, Mangareva (Gambier) and Henderson (Pitcairn Group) from actual (X) and extinct birds [historic and sub-fossils data (†)].


<table>
<thead>
<tr>
<th>Species</th>
<th>Mangaia (21°55'S) (1)</th>
<th>Austral Is. (22°28'-27°26'S) (2)</th>
<th>Mangareva (23°S) (3), (4)</th>
<th>Henderson (24°22'S) (5), (6)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egretta sacra</td>
<td>X</td>
<td>X</td>
<td></td>
<td>visitor</td>
</tr>
<tr>
<td>Anas superciliosa</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porzana tabuensis</td>
<td>X</td>
<td>X</td>
<td>†</td>
<td></td>
</tr>
<tr>
<td>Porzana atra</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porzana rua</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gallirallus ripleyi</td>
<td>†</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Prosobonia sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Prosobonia cancellata</td>
<td></td>
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</tr>
<tr>
<td>Gallicolumba erythroreta</td>
<td></td>
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<td></td>
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<tr>
<td>Gallicolumba nui</td>
<td>†</td>
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<td></td>
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<tr>
<td>Gallicolumba leonpascoi</td>
<td></td>
<td></td>
<td>†</td>
<td></td>
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<tr>
<td>Ptilinopus sp.</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Ptilinopus insularis</td>
<td></td>
<td></td>
<td>†</td>
<td>X</td>
</tr>
<tr>
<td>Ptilinopus rarotongensis</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ptilinopus buttoni</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ducula harrisoni</td>
<td>†</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Ducula cf. galeata</td>
<td>†</td>
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<td></td>
<td></td>
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<tr>
<td>Ducula sp.</td>
<td></td>
<td></td>
<td>†</td>
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<tr>
<td>Vini stepheni</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Vini kuhlii</td>
<td>†</td>
<td>X</td>
<td></td>
<td></td>
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<tr>
<td>Vini vidivici</td>
<td>†</td>
<td></td>
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<tr>
<td>Halcyon gambieri</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Halcyon mangaia</td>
<td>X</td>
<td></td>
<td>†</td>
<td></td>
</tr>
<tr>
<td>Hirundo tahitica</td>
<td></td>
<td></td>
<td>†</td>
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<tr>
<td>Acrocephalus sp.</td>
<td></td>
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<tr>
<td>Acrocephalus kerearako</td>
<td></td>
<td>X</td>
<td>†</td>
<td></td>
</tr>
<tr>
<td>Acrocephalus timidus</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Acrocephalus taiti</td>
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</tr>
</tbody>
</table>

| Number of species today | 6 | 6 | 1 | 4 |
| Number of known extinct species | 7 | 0 | 6 | 6-7 |

and eggs of the Tropicbird were collected until the 1970’s, they were no longer eaten in the 1990’s. Improvements in the standards of living have permitted a dietary switch from wild birds to frozen chicken, a change in human activities very beneficial to the petrel populations. Agricultural cultivation on Tarakoi islet in 1993 probably destroyed at least one third of the breeding habitat of a large colony of Storm petrels (A. Guillemont pers. comm.). Observations in 2002 confirm this (J.-Y. Meyer pers. comm.; B. Fontaine pers. comm.).

Causes of extinction

Three main causes of extinction have been identified. Firstly, habitat modification or destruction, especially the clearing of natural forests by non-woody vegetation (e.g. fern covered slopes). Secondly, hunting of wild birds as a food source or...
Table 12: Comparison of seabird assemblages from actual (X) and extinct birds (†) on Mangaia (Cook Islands), Austral Islands combined and Henderson (Pitcairn Group).


<table>
<thead>
<tr>
<th>Species</th>
<th>Mangaia (1)</th>
<th>Australs Is. (2)</th>
<th>Henderson (3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pterodroma ultima</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Pterodroma externa</td>
<td></td>
<td></td>
<td>†</td>
</tr>
<tr>
<td>Pterodroma alba</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pterodroma neglecta</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Pterodroma heraldica</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pterodroma atrata</td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Pterodroma nigripennis</td>
<td>†</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Unidentified small petrel</td>
<td></td>
<td></td>
<td>†</td>
</tr>
<tr>
<td>Pterodroma cf. leucoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudobulweria rostrata</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Puffinus nativitatis</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Puffinus pacificus</td>
<td></td>
<td>X</td>
<td>†</td>
</tr>
<tr>
<td>Puffinus bailloni</td>
<td>†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puffinus (newelli) myrtae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Puffinus «assimils/thermineri»</td>
<td></td>
<td></td>
<td>†</td>
</tr>
<tr>
<td>Fregetta (grallaria) titan</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Nesofretta fuliginosa</td>
<td>†</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Phaethon rubricauda</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Phaethon lepturus</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sula sula</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sula leucogaster</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sula dactylatra</td>
<td></td>
<td>?</td>
<td>X</td>
</tr>
<tr>
<td>Fregata minor</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Fregata ariel</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sterna fuscata</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Sterna lunata</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anous stolidus</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Anous minutus</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Procelsterna cerulea</td>
<td>X</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Gygis alba</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gygis microrhyncha</td>
<td></td>
<td>X</td>
<td>X</td>
</tr>
</tbody>
</table>

Adult White tailed tropicbird at nest (Phaethon lepturus), Raivavae (Photo J.-C. Thibault).

Chick of White tern (Gygis alba), Raivavae (Photo B. Fontaine).
The Birds: an Unbalanced but Unique Avifauna

... for the use of feathers for fishing or as ornamentation. Lastly, the advent of introduced species, as predators or competitors, has been an important cause of extinction on oceanic islands (Atkinson 1989), and is probably also the case in the Austral Islands. The presence of the domestic cat and Black rat still constitutes a significant threat to native bird species in French Polynesia.

CONSERVATION

The need for conservation of Austral Islands birds

Seven species which occur in the Austral Islands are recognized by the IUCN (2009) as threatened: three landbirds, Kühl’s lorikeet (Endangered), the Rapa fruit dove and Rimatara reed warbler (Vulnerable); and four seabirds, the Collared petrel and Polynesian storm petrel (Vulnerable), Tahiti petrel and Murphy’s petrel (Near Threatened). Recommendations are given for the conservation of these endangered taxa. As for plants and other animals, conservation of the last patches of natural forests is essential to maintain healthy populations of native landbirds on every island; this can be achieved by prohibiting forest clearing, fires and the planting of exotic trees, e.g. *Pinus caribaea* (Pinaceae).

Translocation of landbirds

Translocations can restore the historical avifauna of islands and increase the survival chances of birds only found on single islands (Franklin & Steadman 1991; Steadman & Martin 2003), although it is imperative that the carrying capacities of the habitat is assessed prior to translocation, as well as a thorough understanding of the causes of the historical and current distributions of the taxa, in order to ensure that the causes of extinction are managed and monitored at any given translocation site. For example, the translocation of the Marquesas lorikeet, *Vini ultramarina*, from Ua Huka to Fatu Hiva was initially successful (Lieberman et al. 1997), but the subsequent introduction of the Black rat has resulted in the near extinction of this new population (Thibault & Meyer 2000, pers. obs. 2009). In the Austral Islands 27 individuals of Kühl’s lorikeet from Rimatara have already been successfully translocated to Atiu in the Cook Islands (Gouni & Kape 2007; www.cookislands.bishopmuseum.org), but continued surveillance of the population is vital to its persistence. A second feasible project would be the translocation of the Rimatara reed warbler, which is the only known warbler in the Austral Islands. It is highly likely that specific forms inhabited all the other islands in the chain in the recent past, if we consider their colonization ability and the high rate of differentiation among Polynesian reed warblers (Cibois et al. 2007). Taking into account the presence of suitable habitat and the absence of the behaviorally dominant, introduced Common myna and Red vented bulbul, Raivavae is the only promising translocation site. The Seychelles warbler, *Acrocephalus sechellensis*, provides an encouraging example of a successful translocation habitat restoration on the islands of Cousine and Aride have allowed...
Landbird species have probably been affected by extinctions in the recent past as a result of human disturbances: hunting, introduction of alien species and habitat destruction. However, real data to support these hypothesized extinctions is elusive. It is, therefore, important to promote palaeontological and archaeological studies that might shed light on prehistoric extinctions. Seabird diversity is high in the Austral Islands, although population sizes are small. For both landbirds and seabirds, the presence of several endemic species, listed as threatened, highlights the importance of conserving the birds of the Austral Islands. It is essential that conservation priorities should be put into practice, along with the long-term monitoring of breeding populations.

**CONCLUSIONS**
Almost forgotten: 12 already extinct recently described endodontids species from Rurutu (Photos O. Gargominy).
Overview of the Terrestrial and Freshwater Molluscs

Olivier Gargominy & Benoit Fontaine

With some 557 species or subspecies of which 508 (91%) are endemic, the land snail fauna of French Polynesia is of high conservation value, but is highly threatened: 112 molluscs species from French Polynesia are recorded as extinct or threatened by the IUCN (2010). Recent fieldwork in the Gambier Islands (French Polynesia) showed that most of the native malacofauna is extinct: in Mangareva, 30 Endodontidae species, two Assimineidae species and two Euconulidae species are reported as being extinct (Abdou & Bouchet 2000; Bouchet & Abdou 2001, 2003). In this context, a malacological survey of the Austral Islands was undertaken between 2002 and 2004, in the framework of a terrestrial biodiversity inventory of this archipelago, funded by the French Polynesia government. The aims of this survey were to:

- Produce an inventory of the terrestrial and freshwater malacofauna of the archipelago, including distribution maps;
- Clarify the conservation status of endemic species;
- Identify key sites for mollusc conservation.

The earliest known collection of land snail from the Austral Islands dates from 1828 when H. Cuming visited Rurutu, Tubuai and Rapa (St. John 1940). In 1838, 15 species were recorded from Rapa (Beck 1837; Anton 1838), then a review of the fauna of Rurutu was published by Garrett (1879). In his compilation, Kobelt (1879) mentioned 11 species from Rapa but totally ignored the other Austral Islands. In 1921, M. Stokes collected in Rapa (32 species) and Raivavae (13 species) (Cooke in Gregory 1935). The first major malacological sampling in the Austral Islands was performed in 1934, during the Bishop Museum’s Mangarevan Expedition. This pluridisciplinary expedition visited 25 high islands and 31 atolls all over Southeastern Polynesia. Two of its members were malacologists (C.M. Cooke Jr., expedition leader, and D.W. Anderson). Rapa, where they stayed for 32 days, was the climax of the expedition, with 37593 specimens collected, followed by Mangareva in the Gambier (30695 specimens) and Raivavae (19227 specimens). All the other islands, including Rurutu, Tubuai and Rimatara, yielded less than 3000 specimens altogether (Gregory 1936). Despite the high quality of the sampling done in Rapa, C.M. Cooke considered their mission in Rapa as an exploration rather than a thorough investigation, and believed that the island should be revisited, as they “probably collected about half the species inhabiting this island” (Cooke in Gregory 1935). The Mangarevan Expedition material was deposited in the Bishop Museum collections in Honolulu (Hawaii), and led to the publications of major monographs covering the most speciose families: Euconulidae (Baker 1938, 1940, 1941), Achatinellidae (Cooke & Kondo 1961; Kondo 1962) and Endodontidae (Solem 1976). Other families were also covered: Hydrobiidae (Hubendick 1952), Partulidae (Crampton & Cooke 1953), Charopidae (Solem 1983) and Assimineidae (Cooke & Clench 1943). For several families, nothing has ever been published based on the Mangarevan Expedition material, including all the introduced species (Subulinidae, Streptaxidae, Bradybaenidae in particular), as well as some other important (either in number of species or in number of specimens) families such as Hydrocenidae, Helicinidae and Vertiginidae.

At the end of the 1960s, a marine malacologist, H. Rehder, took the opportunity of being in Rapa to sample terrestrial snails. He could not find any endodontids, and as the original vegetation was known to be severely damaged, A. Solem (1976) suggested that “it may well be that the Rapan radiation has joined the ranks of the extinct”. In 1980, G. Paulay opportunistically collected some land snails during his study of Rapan weevils. His collection is deposited at the Yale Peabody Museum.

This paper presents the main results of a 2002-2004 survey, listing all taxa, clarifying the status of endemic species, giving the first ever account of introduced snail species in the Austral Islands, and presenting a list of critical sites for the conservation of this unique malacofauna.

METHODS

... Collecting effort
Sampling took place in November and December 2002 (19 days in Raivavae, 10 days in Rapa), in November 2003 (7 days in Tubuai, 14 days in Rurutu) and in October and November 2004 (12 days in Rimatara). Because Rapa is isolated in the
south, we use the term "northern islands" hereafter to refer to Raivavae, Tubuai, Rurutu and Rimatara.

Altogether, 80 stations (sampling localities) were sampled in Raivavae, 69 in Rurutu, 49 in Rapa, 46 in Tubuai and 42 in Rimatara (Fig. 9). We believe all islands were reasonably well sampled, except for Rapa, where the field trip was too short. The survey focused on sampling remnants of natural vegetation on ridges, upraised limestones or other remote areas. Agricultural areas were opportunistically sampled but appeared to be very poor in native molluscs. Fossil or subfossil shells were also collected in limestone areas in Rurutu and Rimatara.

In the northern Austral Islands, type localities of every species described from these islands, as given in the relevant literature (Baker 1938, 1940, 1941; Cooke & Clench 1943; Crampton & Cooke 1953; Cooke & Kondo 1961; Kondo 1962; Solem 1976, 1983), were systematically visited. As the northern islands were well sampled, we suggest that species for which we did not find live specimens or fresh shells could be extinct. We do not make this assumption for species from Rapa, which was less well sampled.

A station is defined as a collecting locality, spread over 5-10 m² at most, in a single habitat. At each station, c. 30 minutes was spent searching at ground level for live snails, then leaf-litter and a few millimeters of topsoil were collected. This sample was processed at the collecting location with a Winkler sieve (1 cm mesh), the coarse material being checked for shells (empty shells and live animals) and discarded. The remaining material was bagged and sun-dried as soon as possible. The molluscs collected alive were drowned overnight and fixed in 70% ethanol, for future dissection.

Once dried, the bagged leaf-litter material was passed through 5 mm, 2 mm and 0.6 mm sieves. The two larger fractions were thoroughly searched with the naked eye, the third one sorted under a dissecting microscope. Material passing through the 0.6 mm sieve was checked, but as it contained no molluscs, as was the case in earlier studies (e.g. Tattersfield 1996; De Winter & Gittenberger 1998), it was subsequently discarded.

For each station, we recorded geographical coordinates using a GPS GARMIN 12CX, as well as the habitat, microhabitat, exposure, altitude as given by the GPS and date.

Almost all species for which live specimens were collected were photographed on the spot, to supplement shell drawings of original descriptions that were the only existing illustrations for these species.

![Figure 9: Sampling localities in the Austral islands. Islets on the barrier reef, which were sampled in Raivavae and Tubuai, are not represented.](image)

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**Taxonomic processing and data analysis**

All specimens were sorted to morphospecies, or Recognizable Taxonomic Units (New 1999), according to shell characters, assigned to a family and, when possible, to a described genus or species. Most of our RTUs are equivalent to species as generally understood by mollusc taxonomists, and in the Results and Discussion sections, "RTUs" and "species" refer to the same concept. In the many instances where we did not allocate a specific name to our morphospecies, they were identified by a number.

In our analyses, we combined animals collected live and those collected dead, for two reasons:

- we collected more dead shells than live animals, and did not want to exclude the bulk of our data from the analyses,
Terrestrial Biodiversity of the Austral Islands, French Polynesia

... species richness
A total of 218 species or subspecies are known from the archipelago, including 181 islands endemics, 9 archipelago endemics and 22 introduced species. This fauna is thus characterised by very high speciation level. Species diversity and endemism per island and for the archipelago are summarized in Table 13. No freshwater bivalves were recorded. Most of the material collected during our surveys was sorted to species level, except for the family Achatinellidae.

A well-known island biogeography phenomenon is that island faunas are depauperate when compared with adjacent continents. Indeed, many families of land and freshwater snails have not reached the remote Austral Islands. Families with the highest number of species are Achatinellidae, Endodontidae and Euconulidae, and to a lesser extent Helicinidae, Assimineidae and Hydrobiidae. These families are dominated by single island endemic species, i.e. in situ speciation after rare colonisation events is the main source of diversity. Rapa culminates both in terms of diversity and endemism, and is the only Austral Island with generic speciation: 16 of the 26 endemic genera from French Polynesia are restricted to Rapa, and another genus is endemic from the Australs (Rapa, Raivavae).

Several taxa are new records for the Austral Islands, including introduced species (Subulinidae, Achatina fulica, Euglandina rosea, Streptaxidae, Carychium sp., Bradybaena similaris), as well as some species in the families Hydrocenidae, Assimineidae and Vertiginidae. The common species were probably also collected by the Mangarevan Expedition, though the material has not yet been studied.

In this study we follow the higher classification of Mollusca proposed by Bouchet & Rocroi (2005). Voucher material collected during this collecting trip is deposited at the Muséum national d’Histoire naturelle, Paris (France).

RESULTS

Species richness
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<table>
<thead>
<tr>
<th></th>
<th>Rimatara</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Raivavae</th>
<th>Rapa</th>
<th>TOTAL</th>
</tr>
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<tr>
<td>Indigenous</td>
<td>25</td>
<td>62</td>
<td>26</td>
<td>44</td>
<td>108</td>
<td>217</td>
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<tr>
<td>Indigenous / km²</td>
<td>2.9</td>
<td>1.9</td>
<td>0.6</td>
<td>2.5</td>
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<td>33</td>
<td>13</td>
<td>29</td>
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<tr>
<td>Archipelago endemics</td>
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<td>3</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>5</td>
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<tr>
<td>Endemism</td>
<td>37.5%</td>
<td>59%</td>
<td>56%</td>
<td>77%</td>
<td>93.5%</td>
<td>87%</td>
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<tr>
<td>Endemism /km²</td>
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<td>1.2</td>
<td>0.3</td>
<td>1.8</td>
<td>2.45</td>
<td>1.0</td>
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<tr>
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<td>0</td>
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<td>0</td>
<td>16</td>
<td>16</td>
</tr>
<tr>
<td>Extinct</td>
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<td>14</td>
<td>7</td>
<td>8</td>
<td>2</td>
<td>38</td>
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<tr>
<td>Extinction ratio of endemic fauna</td>
<td>78%</td>
<td>39%</td>
<td>50%</td>
<td>24%</td>
<td>2%</td>
<td>20%</td>
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<tr>
<td>Threatened</td>
<td>0</td>
<td>6</td>
<td>3</td>
<td>10</td>
<td>94</td>
<td>114</td>
</tr>
<tr>
<td>Threat ratio of extant endemic fauna</td>
<td>-</td>
<td>25%</td>
<td>43%</td>
<td>37%</td>
<td>93%</td>
<td>61%</td>
</tr>
<tr>
<td>Threat and extinction ratio of endemic fauna</td>
<td>78%</td>
<td>64%</td>
<td>93%</td>
<td>61%</td>
<td>95%</td>
<td>81%</td>
</tr>
<tr>
<td>Introduced</td>
<td>14</td>
<td>18</td>
<td>15</td>
<td>13</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>Ratio of introduced taxa on current fauna</td>
<td>44%</td>
<td>27%</td>
<td>44%</td>
<td>27%</td>
<td>9%</td>
<td>11%</td>
</tr>
</tbody>
</table>

Table 13: Austral Islands diversity, endemism, extinction and threats of terrestrial and freshwater molluscs in terms of terminal taxa (species or subspecies). Indigenous includes cryptogenic (sensu Carlton 1996). Morphospecies recognized as new species still to be described are included.
Family records and checklists of species

Superfamily HELICINOIDEA Férussac, 1822
Family HELICINIDAE Férussac, 1822
At least five different Helicinae species were collected live in the Austral Islands. On each island except Rapa, *Helicina pacifica* was found to be abundant from sea level to the highest ridges. It was one of most common species on Rimatara and Rurutu "mato" (limestone rock faces). Generic assignation of Pacific Helicinae is not yet stabilized (Richling 2009, 2011; Richling & Bouchet 2013) and needs the female genital apparatus anatomy to be reviewed. Meanwhile, we keep here original names except for species treated by Richling & Bouchet (2013).

It is questionable that Garrett (1879) did not mention neither *Nesiocina solidula* nor *Helicina aff. trochlea* but only *minuta* as "very abundant", while these two species are by far the most abundant nowadays.

*Helicina* Lamarck, 1799

*Helicina minuta* G.B. Sowerby II, 1842
Status unclear: Rurutu (Garrett 1879), Tahiti and Moorea (Garrett 1884).

*Helicina pacifica* Pease, 1865
Remarks: Cited from the Australs by Brook (2010), this species may belong to the *Nesiocina solidula* species complex mentionned by Richling & Bouchet (2013).

*Helicina aff. trochlea* A.A. Gould, 1847
Austral Islands endemic?: Rimatara*. Rurutu*.
Remark: Very abundant on rocks in limestone areas in Rurutu and Rimatara. It probably represents a species new to science (I. Richling pers. comm.). *Helicina trochlea* is currently only known from Makatea in the Tuamotus (Gould 1847; Cooke 1934).

*Helicina villosa* Anton, 1839
Island endemic?: Rapa.

*Nesiocina* Richling & Bouchet, 2013

*Nesiocina cf. villosa* (Anton, 1839)
Range in the Australs: Raivavae (Richling & Bouchet 2013)

*Nesiocina solidula* (G.B. Sowerby I in J.E. Gray, 1839)
Range in the Australs: Rurutu* (Richling & Bouchet 2013).

Superfamily HYDROCENOIDEA Troschel, 1857
Family HYDROCENIDAE Troschel, 1857

*Georissa* species were found on all islands, and were abundant on rocks and on dead leaves. At least two species were found in Rurutu, and *Chondrella striata* Pease, 1871 was recorded on Rurutu by Garrett (1879). All were found live. *Georissa* species were less abundant on Tubuai.

*Georissa* Blanford, 1864

*Georissa (Chondrella) striata* (Pease, 1871)
Widespread in eastern Polynesia.
Range in the Australs: Rurutu.

*Georissa sp.*

Superfamily CERITHIOIDEA Fleming, 1822
Family THIARIDAE Gill, 1871 (1823)

*Melanoides* Olivier, 1804

*Melanoides tuberculata* (O.F. Müller, 1774)
Introduced species.
Remarks: A widespread introduced species, found on each island, abundant in streams, even when polluted.

* Represents a new island record issued from this fieldwork.
Superfamily RISSOIDEA Gray, 1847
Family ASSIMINEIDAE H. Adams & A. Adams, 1856
Nine taxa were known from the archipelago, of which we found five, all live: Rapanella andersoni, Assiminea pupoides, Omphalotropis dubia (all from Rapa), as well as Assiminea nitida and Omphalotropis subimperforata from Rurutu and Rimatara. In addition, two unidentified Omphalotropis species (one from Rurutu and one from Rapa) were found live, as well as one Rapanella species (Rapa). Omphalotropis curta (Rurutu) and Omphalotropis albescens (Rapa) were not found, but no precise type locality was given with the description. Electrina succinea was known from Rapa with two subspecies. We went to the type localities of both, and did not find them. Consequently, we consider that this species could be extinct.

Subfamily ASSIMINEINAE H. Adams & A. Adams, 1856
Assiminea Flemming, 1828
Assiminea parvula (Mousson, 1865)
= Assiminea nitida (Pease, 1865)
Cryptogenic.
Assiminea lucida Pease, 1869
Range in the Australs: Rurutu.

Electrina Baird, 1850
Island endemic: Rapa.
Electrina succinea succinea (Sowerby, 1846)
Island endemic: Rapa.
Electrina succinea orites Cooke & Clench, 1943
Island endemic: Rapa.

Subfamily OMPHALOTROPIDINAE Thiele, 1927
Omphalotropis L. Pfeiffer, 1851
Omphalotropis albescens (L. Pfeiffer, 1855)
Island endemic: Rapa.
Omphalotropis curta Garrett, 1879
Island endemic: Rurutu.
Omphalotropis dubia (L. Pfeiffer, 1846) comb. nov.
Island endemic: Rapa.
Omphalotropis papoides (Anton, 1839)
= Hydrocena oparica L. Pfeiffer, 1848
Island endemic: Rapa.
Omphalotropis subimperforata C. Boettger, 1916
Austral Islands endemic: Rimatara, Rurutu*.

Rapanella Cooke & Clench, 1943
Island endemic: Rapa.
Rapanella andersoni Cooke & Clench, 1943
Island endemic: Rapa.
Rapanella sp.
Island endemic: Rapa*.

Family HYDROBIIDAE Stimpson, 1865
Two species of Fluviopupa were known, one from Rapa, the other from Rapa and Rurutu. We found Fluviopupa on each island except Rimatara, and there appear to be different species on each island: two from Rapa (previously described), two from Raivavae, one each from Tubuai and Rurutu, all new to science and described elsewhere (Haase et al. 2005). Where present, these species are abundant on rocks and submerged dead leaves. Rimatara, being the oldest and westernmost (i.e. closest to western source populations) island in the group, was also probably host to Fluviopupa spp. However, the island no longer has any permanent flowing water, all the springs
having been diverted, and thus any *Fluviopupa* species from this island must now be extinct.

*Fluviopupa* Pilsby, 1911
- *Fluviopupa crassiiscula* Frauenfeld, 1863
  - Island endemic: Rapa.
- *Fluviopupa deflexa* Frauenfeld, 1863
  - Island endemic: Rapa.
- *Fluviopupa jeanyvesi* Haase, Gargominy & Fontaine, 2005
  - Island endemic: Raivavae*.
- *Fluviopupa raivavaensis* Haase, Gargominy & Fontaine, 2005
  - Island endemic: Raivavae*.
- *Fluviopupa rurutua* Haase, Gargominy & Fontaine, 2005
  - Island endemic: Rurutu*.
- *Fluviopupa tubuaia* Haase, Gargominy & Fontaine, 2005
  - Island endemic: Tubuaï*.

Superfamily LYMNAEOIDEA Rafinesque, 1815
Family LYMNAEIDAE Rafinesque, 1815

*Pseudosuccinea* E.C. Baker, 1908
- *Pseudosuccinea columella* (Say, 1817)
  - Introduced species.
  - Remarks: Found in low altitude streams.

Superfamily PLANORBOIDEA Rafinesque, 1815
Family PHYSIDAE Fitzinger, 1823

*Physella* Haldeman, 1843
- *Physella acuta* (Draparnaud, 1805)
  - Introduced species.
  - Remarks: Species known from Rurutu and Tubuai (Marquet 1993). We did not find it on Rurutu, but it was present at low altitude on Tubuai and Rimatara.

Family PLANORBIDAE Rafinesque, 1815

One species was found in a ditch on a roadside in Rurutu. It probably belongs to *Ferrissia noumeensis*, an introduced species on other Pacific islands (New Caledonia, Fiji, American Samoa - Haynes 2001). Pointier & Marquet (1990) mentioned the presence of this species from Tahiti only.

*Ferrissia* Walker, 1903
- *Ferrissia noumeensis* (Crosse, 1871)
  - Introduced species.
  - Range in the Australs: Rurutu*.

Superfamily ELLOBIOIDEA L. Pfeiffer, 1854 (1822)
Family ELLOBIDAE L. Pfeiffer, 1854 (1822)
Subfamily CARYCHINAE Jeffreys, 1830

This is the first record of this European subfamily in French Polynesia.

*Carychium* O.F. Müller, 1773
- *Carychium* sp.
  - Introduced species.
Range in the Australs: Rimatara*
Remarks: Three shells of Carychium sp. were found in degraded vegetation at sea level in Rimatara.

Superfamily VERONICELLOIDEA Gray, 1840
Family VERONICELLIDAE Gray, 1840

Laevicaulis Simroth, 1913
Laevicaulis alte (Férussac, 1822)
Introduced species.
Remarks: Always present at low altitude, as well as on mountains in Raivavae and Rurutu.
Superfamily SUCCINEOIDEA Beck, 1837
Family SUCCINEIDAE Beck, 1837

Historically, a single species was recorded in Rurutu, *Succinea degagei* Garrett, 1879, which was thereafter synonymised with *Succinea pudorina* A.A. Gould, 1846 (Garrett, 1884: 86). Later on, *Quickia concisa* (Morelet, 1868) has been shown to have spread over Polynesia recently, including Rimatara in the Australs (Brook 2010).

*Quickia* Ohdner, 1950

*Quickia concisa* (Morelet, 1868)
- Introduced species.
- Range in the Australs: Rimatara.

*Succinea* Draparnaud, 1801

*Succinea pudorina* A.A. Gould, 1846
- *Succinea degagei* Garrett, 1879
- French Polynesia endemic.
- Range in the Australs: Rurutu.
- Remarks: This species was not found during our survey.
Terrestrial Biodiversity of the Austral Islands, French Polynesia

Subclade Orthurethra

Superfamily PARTULIDOIDEA Pilsbr, 1900
Family PARTULIDAE Pilsbr, 1900

Partula hyalina is common at sea level, sometime very abundant locally. In Raivavae and Tubuai, it is also found in altitude, as well as on one islet on the barrier reef in Tubuai. It was present in 42% to 47% of our stations in Raivavae, Rurutu and Rimatara, but only in 19% of the stations in Tubuai. This might be due to the presence of the predatory Euglandina rosea in Tubuai.

In Rimatara, another partulid species, now extinct, was found in subfossil cave deposits. In Rapa, Samoana margaritae is not rare in forests, even if slightly degraded. The species was found on several tree species: Celtis, Zanthoxylum, Merita, Nesoluma, and even on invasive Psidium. In Raivavae, three Samoana species have been described (Crampton & Cooke 1953). Samoana dryas was found alive at its type locality, unlike S. oreas or S. hamadryas for which only old shells were found. A previously unknown population of a live Samoana sp. was discovered on the southern slope of the western peninsula. All these localities are among the last remnants of native forests, reduced in size, and the persistence of these endemic species is entirely dependent on conservation measures, such as fencing against goats.

Partula Férussac, 1821
Partula hyalina Broderip, 1832
Originally endemic from Tahiti.
Remarks: Introduced in the Australs (Lee et al. 2007).

Samoana Pilsbr, 1909
Samoana dryas (Crampton & Cooke, 1953)
Island endemic: Raivavae.
Samoana hamadryas (Crampton & Cooke 1953)
Island endemic: Raivavae.
Samoana oreas (Crampton & Cooke, 1953)
Island endemic: Raivavae.
Samoana sp.
Island endemic? Subfossil material.
Range in the Australs: Rimatara*.
Samoana margaritae (Crampton & Cooke, 1953)
Island endemic: Rapa.

Superfamily ACHATINELLOIDEA Gulick, 1873
Family ACHATINELLIDAE Gulick, 1873

The family is represented by 92 described species in the Austral Islands, including 58 restricted to Rapa. As mentioned above, the Achatinellidae were not fully sorted. Cryptogenic species such as Elasmias aper-tum, Tornatellides oblongus and Lamellidea oblonga were found in abundance in the northern Australs. The endemic Strobilus acicularis raphis was found under the only known Rapan specimen of the highly threatened tree Zanthoxylum tahitense (Meyer 2003), in a remnant patch of mesophilic forest. The snails were abundant under the tree, but completely absent in the surrounding vegetation. In Rimatara, the endemic Tubuaia voyana oromanaensis was only known from its type locality, the "Oromana hills" (Kondo 1962), at 80 m. This area is now completely degraded and transformed into agricultural fields, no snails (even introduced species) were found. We consider this subspecies extinct.

In addition to the following list, several undescribed taxa are mentioned in the literature: Tubuaia sp.? from Rurutu (Kondo 1962: 17) and Celticola (Meryticola) arborea ssp.? from Rapa (Cooke & Kondo 1961: 140).

Subfamily LAMELLIDEINAE Cooke & Kondo, 1961

Lamellidea Pilsbr, 1910
Lamellidea (Lamellidea) oblonga (Pease, 1865)
Large range in the Pacific.
Lamellidea (Lamellidea) pusilla (A.A. Gould, 1847)
Large range in the Pacific.
Range in the Australs: Rurutu.
A Global Overview of the Terrestrial and Freshwater Molluscs

Partula hyalina, Rimatara

Partula hyalina, Tubuai

Samoana margaritae, Rapa

Samoana dryas, Raivavae
Pacificella Odhner, 1921  
Pacificella variabilis Odhner, 1921  
Large range in the Pacific.  
Range in the Australs: Rapa.

Tornatellinops Pilsbry & Cooke, 1915  
Tornatellinops concolorans Cooke & Kondo, 1961  
Island endemic: Rapa.  
Tornatellinops philippus (L. Pfeiffer, 1850)  
Large range in the Pacific.  

Subfamily PITYSINAE Cooke & Kondo, 1961

Antonella Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella pfeifferi Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella tenuis Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella trochlearis fusiforma Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella trochlearis nesiotica Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella trochlearis radicula Cooke & Kondo, 1961  
Island endemic: Rapa.  
Antonella trochlearis trochlearis (L. Pfeiffer, 1842)  
Island endemic: Rapa.

Apopitys Cooke & Kondo, 1961  
Island endemic: Rapa.  
Apopitys andersoni Cooke & Kondo, 1961  
Island endemic: Rapa.

Celticola Cooke & Kondo, 1961  
Austral Islands endemic: Raivavae. Rapa.  
Celticola (Celticola) pilsbryi incerta Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Celticola) pilsbryi latior Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Celticola) pilsbryi pilsbryi Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Celticola) pilsbryi proxima Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Meryticola) arborea arborea Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Meryticola) arborea sororcula Cooke & Kondo, 1961  
Island endemic: Rapa.  
Celticola (Nesonoica) anatoniensis Cooke & Kondo, 1961  
Island endemic: Raivavae.  
Celticola (Nesonoica) conoides Cooke & Kondo, 1961  
Island endemic: Rapa.

Lamellovum Pilsbry, 1910  
Island endemic: Rapa.  
Lamellovum (Lamellovum) globosum (Petit de la Saussaye, 1843)  
Island endemic: Rapa.  
Lamellovum (Maitua) auricullea Cooke & Kondo, 1961  
Island endemic: Rapa.  
Lamellovum (Maitua) costata Cooke & Kondo, 1961  
Island endemic: Rapa.
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Achatinellidae

Antonella sp., Rapa

Raivavae

Lamellidea oblonga, Rimatara

Tornatellides oblongus, Rimatara

Elasmias apertum, Tubuai

Lamellidea sp., Rimatara
Lamellovum (Maitua) leptospira Cooke & Kondo, 1961
Island endemic: Rapa.
Lamellovum (Maitua) solitaria Cooke & Kondo, 1961
Island endemic: Rapa.

Mangaoa Cooke & Kondo, 1961
Island endemic: Rapa.
Mangaoa perissa Cooke & Kondo, 1961
Island endemic: Rapa.

Mitiperua Cooke & Kondo, 1961
Island endemic: Rapa.
Mitiperua simplex convexior Cooke & Kondo, 1961
Island endemic: Rapa.
Mitiperua simplex simplex Cooke & Kondo, 1961
Island endemic: Rapa.
Mitiperua simplex subcostata Cooke & Kondo, 1961
Island endemic: Rapa.

Perahua Cooke & Kondo, 1961
Island endemic: Rapa.
Perahua bakeri Cooke & Kondo, 1961
Island endemic: Rapa.
Perahua grandis Cooke & Kondo, 1961
Island endemic: Rapa.

Pitys Mörch, 1852
Pitys alpestris Cooke & Kondo, 1961
Island endemic: Rapa.
Pitys pagodiformis (E.A. Smith, 1892)
Island endemic: Rapa.
Pitys scalaris Cooke & Kondo, 1961
Island endemic: Rapa.

Pukunia Cooke & Kondo, 1961
Pukunia acuta Cooke & Kondo, 1961
Island endemic: Rapa.
Pukunia margaritae Cooke & Kondo, 1961
Island endemic: Rapa.
Pukunia pellucida Cooke & Kondo, 1961
Island endemic: Rapa.

Strobilus Anton, 1839
Island endemic: Rapa.
Strobilus (Strobilus) acicularis acicularis Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) acicularis raphis Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) opeas intermedius Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) opeas opeas Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) subtilis similaris Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) subtilis subtilis Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) turritus basalis Cooke & Kondo, 1961
Island endemic: Rapa.
Strobilus (Strobilus) turritus turritus Anton, 1839
Island endemic: Rapa.
Strobilus (Tanga) brevis brevis Cooke & Kondo, 1961
Island endemic: Rapa.

Strobilus (Tanga) brevis pumilus Cooke & Kondo, 1961
Island endemic: Rapa.

Strobilus (Tanga) brevis subsimilis Cooke & Kondo, 1961
Island endemic: Rapa.

Strobilus (Tautautua) perfragilis Cooke & Kondo, 1961
Island endemic: Rapa.

Taitaa Cooke & Kondo, 1961
Taitaa (Taitaa) arauana Cooke & Kondo, 1961
Island endemic: Tubuai.

Taitaa (Taitaa) dacryma Cooke & Kondo, 1961
Island endemic: Tubuai.

Taitaa (Taireva) striatula Cooke & Kondo, 1961
Island endemic: Rurutu.

Taitaa (Taireva) zimmermani Cooke & Kondo, 1961
Island endemic: Rurutu.

Taitaa (Taireva) neanica Cooke & Kondo, 1961
Island endemic: Raivavae.

Taitaa (Taireva) terebriformis Cooke & Kondo, 1961
Island endemic: Raivavae.

Tubuaia Cooke & Kondo, 1961
Tubuaia affinis (Garrett, 1879)
Island endemic: Rurutu.

Tubuaia amoebodonta Kondo, 1962
Island endemic: Rurutu.

Tubuaia bakerorum Kondo, 1962
Island endemic: Rurutu.

Tubuaia coprophora coprophora Kondo, 1962
Island endemic: Raivavae.

Tubuaia coprophora diminuta Kondo, 1962
Island endemic: Raivavae.

Tubuaia cremnobates Cooke & Kondo, 1961
Island endemic: Rapa.

Tubuaia cylindrata cylindrata Cooke & Kondo, 1961
Island endemic: Rapa.

Tubuaia cylindrata philolichen Cooke & Kondo, 1961
Island endemic: Rapa.

Tubuaia hygrobia Kondo, 1962
Island endemic: Raivavae.

Tubuaia inconstans Cooke & Kondo, 1961
Island endemic: Rapa.

Tubuaia myojinae Kondo, 1962
Island endemic: Raivavae.

Tubuaia perplexa (Garrett, 1879)
Large range in the Pacific
Range in the Australs: Rimatara. Rurutu.

Tubuaia saintjohni Kondo, 1962
Island endemic: Raivavae.

Tubuaia voyana manurevae Kondo, 1962
Island endemic: Rurutu.

Tubuaia voyana matonaeensis Kondo, 1962
Island endemic: Rurutu.

Tubuaia voyana oromanaensis Kondo, 1962
Island endemic: Rimatara.

Tubuaia voyana rapaensis Cooke & Kondo, 1961
Island endemic: Rapa.

Tubuaia voyana teutuensis Kondo, 1962
Island endemic: Rapa.
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Tubuaia voyana turivaoensis Kondo, 1962
Island endemic: Raivavae.  
Tubuaia voyana vaiaunanae Kondo, 1962
Island endemic: Raivavae.  

Subfamily TORNATELLIDINAE Cooke & Kondo, 1961

Tornatellides Pilsbry, 1910
Tornatellides (Tornatellides) oblongus oblongus (Anton, 1839)
Large range in the Pacific.

Subfamily TORNATELLININAE Sykes, 1900

Elasmias Pilsbry, 1910
Elasmias amphodon Cooke & Kondo, 1943
Island endemic: Rurutu.  
Elasmias apertum (Pease, 1865)
Cryptogenic.  
Elasmias ovatum exiguum Cooke & Kondo, 1961
Island endemic: Rapa.  
Elasmias ovatum ovatum (Anton, 1839)
Island endemic: Rapa.  
Elasmias simplicinum Cooke & Kondo, 1961
Austral Islands endemic: Raivavae. Rapa.  

Tornatellina L. Pfeiffer, 1842
Tornatellina bilamellata (Anton, 1839)
Island endemic: Rapa.  

Superfamily PUPILLOIDEA Turton, 1831
Family Valloniidae Morse, 1864

Pupisoma Stoliczka, 1873
Pupisoma orcula (Benson, 1850)
Cryptogenic.  
Remarks: Species not known previously from the Austral Islands, but found to be common in the northern islands. It lives on tree trunks and is often found at the base of pinnae, on the rachis of Angiopteris fronds.

Family Gastrocoptidae Pilsbry, 1918
Subfamily Gastrocoptinae Pilsbry, 1918

Gastrocopta Wollaston, 1878
Gastrocopta servilis (A.A. Gould, 1843)
Cryptogenic.  
Gastrocopta pediculus (Shuttleworth, 1852)
Cryptogenic  

Subfamily Nesopupiniae Steenberg, 1925
Several species of Nesopupa are present: at least two species in Raivavae, two in Tubuai, four in Rurutu and three in Rimatara. Here we mention Costigo saparuana for the first time in French Polynesia. Pronesopupa is represented by one species in each of the following islands: Rapa, Raivavae and Rurutu.
Family VERTIGINIDAE Pilsbry, 1918
Subfamily NESOPUPINAE Steenberg, 1925

Nesopupa Pilsbry, 1900

*Nesopupa* (*Nesopupa*) *pleurophora* (Shuttleworth, 1852)
Large range in the eastern Pacific.
Range in the Australs: Rurutu*, Raivavae*.

*Nesopupa* (*Nesopupa*) cf. *armata* (Pease, 1871)
Range in the Australs: Rurutu*.

*Nesopupa* (*Nesopupa*) cf. *paivae* (Crosse, 1865)
Range in the Australs: Rurutu*.

*Nesopupa* (*Nesopupa*) cf. *tongana* (Boettger, 1881)
Range in the Australs: Rurutu*.

*Nesopupa* (*Nesopupa*) sp.

Costigo O. Boettger, 1891

*Costigo* *saparuana* (O. Boettger, 1891)
Brook (2010) was the first to report this Indonesian species from Pacific islands with populations from Cook Islands and Niue inferred to be of anthropogenic origin in prehistoric time. This species is always found at low density and mixed together with much more abundant *Nesopupa* spp., so is difficult to record. Its range extends much further East: we have also recorded it from Moorea (Society — sequenced in the framework of the Moorea Biocode Project) and Makatea (Tuamotus).

Pronesopupa Iredale, 1913

*Pronesopupa* sp.1
Island endemic?: Rapa*.

*Pronesopupa* sp.2
Island endemic?: Raivavae*.

*Pronesopupa* sp.3
Island endemic?: Rurutu*.
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Superfamily ACHATINOIDEA Swainson, 1840
Family ACHATINIDAE Swainson, 1840

Achatina Lamarck, 1799
Achatina fulica Bowdich, 1822
Introduced species.
Range in the Australs: Tubuai*.
Remarks: The giant African snail Achatina fulica was found in Tubuai. According to local people, it was introduced in 1984 by a nurse near Mataura health center. The snails became invasive, and staff of the Service du Développement Rural tried to eradicate them (manual eradication and introduction of Euglandina rosea) without success. After an initial explosion, the populations dropped (P. Paccou pers. comm.). It was not abundant when we were in Tubuai, but several live individuals were collected. Shells were only found at low altitude.
Family FERUSSACIIDAE Bourguignat, 1883
Subfamily FERUSSACIINAE Bourguignat, 1883
This is the first record of this family in French Polynesia.

Geostilbia Crosse, 1867
Geostilbia aperta (Swainson, 1840)
Found in almost all tropical regions.
Range in the Australs: Rurutu*, Tubuai*.

Family SUBULINIDAE P. Fischer & Crosse, 1877
Subulinidae are now one of the main components of the malacofauna in French Polynesia, both in terms of abundance and ubiquity. Several species were found in all the northern islands, where they are common, especially at low altitude and in degraded areas: Subulina octona, Opeas hannense, Paropeas achatinaceum, Allopeas gracile, Allopeas oparanum and Allopeas clavulinum. Leptinaria unilamellata was only found in Rurutu and Raivavae, and is much less common than the other Subulinidae. In Rapa, the subtropical climate is probably less suitable for Subulinidae which are less abundant. Allopeas gracile is widespread and very abundant in the Austral Islands, a fact supporting the idea that it was spread throughout the Pacific islands by early polynesians (Christensen & Kirch 1981). The type locality of Bulimus beckianus L. Pfeiffer, 1846 is "Opara?" (=Rapa), which must be an error since Beckianum beckianum is now known to occur in tropical America (Massemín et al. 2009), and has never actually been collected in Polynesia. It is not included here.

Allopeas H.B. Baker, 1935
Allopeas clavulinum (Potiez & Michaud, 1838)
Introduced species.
Allopeas gracile (Hutton, 1834)
Introduced species.
Allopeas oparanum (L. Pfeiffer, 1846)
Cryptogenic.

Leptinaria Beck, 1837
Leptinaria unilamellata (d'Orbigny, 1837)
Introduced species.
Range in the Australs: Rurutu*. Raivavae*.

Opeas Albert, 1850
Opeas hannense (Rang, 1831)
= O. pumilum (L. Pfeiffer, 1840)
Introduced species.

Paropeas Pilsbry, 1906
Paropeas achatinaceum (L. Pfeiffer, 1846)
Introduced species.

Subulina Beck, 1837
Subulina octona (Bruguière, 1792)
Introduced species.

Superfamily TESTACELLOIDEA J. Gray, 1840
Family OLEACINIDAE H. Adams & A. Adams, 1855

Euglandina Crosse & P. Fischer, 1870
Euglandina rosea (Férrussac, 1821)
Introduced species.
Range in the Australs: Tubuai*.
Remarks: *Euglandina rosea* was introduced in Tubuai in 1985 (P. Paccou pers. comm.) to eradicate *Achatina fulica*, without success. It is present in all habitats, from sea-level to the highest ridges.

**Superfamily STREPTAXOIDEA J. Gray, 1860**

**Family STREPTAXIDAE J. Gray, 1860**

Two introduced species are present in the northern islands: *Streptostele musaeccola* is common in all four islands while *Huttonella bicolor* is much rarer and was only found in Rurutu and Raivavae. The impact of these carnivorous species on the native invertebrate fauna is unknown.

*Huttonella L. Pfeiffer, 1856*

*Huttonella bicolor* (Hutton, 1834)

Introduced species.

Range in the Australs: Rurutu*. Raivavae*.

*Streptostele Dohrn, 1866*

*Streptostele (Tomostele) musaeccola* (Morelet, 1860)

Introduced species.


**Superfamily PUNCTOIDEA Morse, 1864**

**Family PUNCTIDAE Morse, 1864**

*Punctum Morse, 1864*

*Punctum polynesicum* Solem, 1983

Austral Islands endemic: Tubuai. Raivavae.

**Family CHAROPIDAE Hutton, 1884**

*Discocharopa Iredale, 1913*

*Discocharopa aperta* (Mollendorff, 1888)

Cryptogenic.

Range in the Australs: Rurutu.

*Sinployea Solem, 1983*

*Sinployea? sp.*

Island endemic: Raivavae*.

**Family ENDODONTIDAE Pilsbry, 1895**

In Rapa, we found *Opanara bitridentata*, *Oranga cooki montana*, *Rhysocochia variumbilicata* and several other as yet undetermined species. A species found on the coast, at the base of a cliff, only accessible by boat, is a species new to science, illustrating the fact that coastal habitats once harboured a unique fauna that has been wiped out, possibly when early Polynesians settled there. Apart from this case, all extant Endodontidae in Rapa were found in high elevation native forest, or in remnants of native vegetation protected from fire and introduced herbivores (such as crevices in cliffs).

In Raivavae, three genera (one archipelago endemic, *Australodonata*) and eight species (all endemic) were previously known (Solem 1976). In particular, northeastern side of the island (east of Anatounu village) was very rich, with six sympatric species (Solem 1976), possibly due to the presence of a restricted limestone outcrop. However, the area was completely degraded by the encroachment of the village, and no live Endodontidae was found. In consequence, we suggest that the following species, only known from this area, could be extinct: *Minidonta micraconica* (one locality with old shells near the type locality); *Minidonta anatomana* (type locality visited without success, one very old shell could belong to this species), *Minidonta gravacosta*, *Minidonta sulcata*, *Minidonta planulata*, *Mautodontha ceuthma*, *Australodonata ectopia* (type localities visited without success). Considering the condition of the holotype, *Australodonata ectopia* may have been already extinct in 1934. Another species of *Minidonta*, new to science, was found near Anatounu, but it is also probably extinct, as we only found old shells. By contrast, *Australodonata raivavaeana* was found in several localities in the island, always above 80 m a.s.l. (live individuals), but not necessarily in native forest. Live individuals were found at the base of cliffs in herbaceous vegetation at the base of grass stems.

In Tubuai, two species and one subspecies were known, all endemic. We found *Australodonata radiella radiella* in abundance, with fresh shells. *Australodonata tubuiana* was found in two localities in the western part of the island, including the type locality, but only old shells were found. Only one fragment of *Australodonata*...
*pharcata* was found, not in the type locality. The type locality, now in Taahuaia village, could not be found. We suggest that *Australdonta tubuaiana* and *A. pharcata* should be classified as extinct.

Two genera and seven species were known from Rurutu prior to our survey. Litter sieving and thorough surveying of limestone areas revealed 12 other species new for science which have been described elsewhere (Zimmermann *et al.* 2009; Sartori *et al.* 2013). Up to 11 species were found in syntopy, north of Hauti village. However, no live specimen or very fresh shell was found. In consequence, we believe that a large part of the Endodontidae radiation in Rurutu is extinct. However, *Australdonta pseudoplanulata*, *Australondonta magnasulcata*, *Australondonta yoshii*, *Australondonta radiella rurutuensis*, *Australondonta tapina*, *Australondonta degagei* could still be extant, as we found some shells, which could be recent (though it is hard to be certain). If they live in rock crevices, we could have missed them. Three species were very abundant and widespread: we found 2,687 shells in 38 localities for *A. pseudplanulata*, 3,472 shells in 40 localities for *A. tapina*, 7,948 shells in 39 localities for *A. degagei*.

The east coast of Rurutu, and in particular between cape Arei and cape Toarepe, seems to be a micro-center of endemism for this island, eight of the 12 new species being restricted to this area. On the other hand, a few species had a wide distribution on the island, from sea-level to the mountain tops (*A. degagei*, *A. pseudplanulata*, *A. tapina*); these three species are the most widespread and abundant Endodontidae collected.

Two species were known from Rimatara (*Australondonta rimatarana*, *A. degagei*), which were found in 2004, but no live individuals were observed. We suppose they are extinct. *Libera fratercula rarotongensis* was found in huge quantities on the northeastern coast, but only old shells were found. This species previously only known from the Cook Islands (Solem 1969) is obviously extinct today on Rimatara on which it might represent an ancient introduction by early Polynesians. Three other species, new to science, were found as subfossils in a cave deposit. These are considered to be extinct species.

### Australdonta Solem, 1976

<table>
<thead>
<tr>
<th>Species</th>
<th>Author, Year</th>
<th>Endemism</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Australondonta annaeae</em></td>
<td>Sartori, Gargominy &amp; Fontaine, 2013</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta collicella</em></td>
<td>Zimmermann, Gargominy &amp; Fontaine, 2009</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta degagei</em></td>
<td>(Garrett, 1879)</td>
<td>Rurutu, Rimatara, Rurutu, Cook Islands: Mauke.</td>
</tr>
<tr>
<td><em>Australondonta ectopia</em></td>
<td>Solem, 1976</td>
<td>Raivavae</td>
</tr>
<tr>
<td><em>Australondonta florencei</em></td>
<td>Sartori, Gargominy &amp; Fontaine, 2013</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta magnasulcata</em></td>
<td>Solem, 1976</td>
<td>Rurutu</td>
</tr>
<tr>
<td><em>Australondonta magnasulcatissima</em></td>
<td>Zimmermann, Gargominy &amp; Fontaine, 2009</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta microspiralis</em></td>
<td>Zimmermann, Gargominy &amp; Fontaine, 2009</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta oheatora</em></td>
<td>Sartori, Gargominy &amp; Fontaine, 2013</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta pakalolo</em></td>
<td>Sartori, Gargominy &amp; Fontaine, 2013</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta pharcata</em></td>
<td>Solem, 1976</td>
<td>Tubuai</td>
</tr>
<tr>
<td><em>Australondonta pseudplanulata</em></td>
<td>Solem, 1976</td>
<td>Rurutu</td>
</tr>
<tr>
<td><em>Australondonta radiella radiella</em></td>
<td>(L. Pfeiffer, 1846)</td>
<td>Tubuai</td>
</tr>
<tr>
<td><em>Australondonta radiella rurutuensis</em></td>
<td>(Garrett, 1879)</td>
<td>Rurutu</td>
</tr>
<tr>
<td><em>Australondonta raivavaecana</em></td>
<td>Solem, 1976</td>
<td>Raivavae</td>
</tr>
<tr>
<td><em>Australondonta rimatarana</em></td>
<td>Solem, 1976</td>
<td>Rimatara</td>
</tr>
<tr>
<td><em>Australondonta sibleti</em></td>
<td>Sartori, Gargominy &amp; Fontaine, 2013</td>
<td>Rurutu*</td>
</tr>
<tr>
<td><em>Australondonta sulcata</em></td>
<td>Zimmermann, Gargominy &amp; Fontaine, 2009</td>
<td>Rurutu*</td>
</tr>
</tbody>
</table>
Australdonta tapina Solem, 1976
Island endemic: Rurutu.

Australdonta teae Sartori, Gargominy & Fontaine, 2013
Island endemic: Rurutu*.

Australdonta tubuiana Solem, 1976
Island endemic: Tubuai.

Australdonta yoshii Solem, 1976
Island endemic: Rurutu.

Australdonta sp.1
Island endemic: Rimatara*.

Australdonta sp.2
Island endemic: Rimatara*.

Australdonta ? sp.3
Island endemic: Rimatara*.

Kondoconcha Solem, 1976
Island endemic: Rapa.

Kondoconcha othnius Solem, 1976
Island endemic: Rapa.

Libera Garrett, 1881
Libera fratercula rarotongensis Solem, 1976
Australs: Rimatara*. Cook Islands: Rarotonga.

Mautodontha Solem, 1976
Mautodontha (Mautodontha) ceuthma Solem, 1976
Island endemic: Raivavae.

Minidonta Solem, 1976

Minidonta anatonuana Solem, 1976
Island endemic: Raivavae.

Minidonta bieleri Sartori, Gargominy & Fontaine, 2013
Island endemic: Rurutu.

Minidonta boucheti Sartori, Gargominy & Fontaine, 2013
Island endemic: Rurutu.

Minidonta gravacosta Solem, 1976
Island endemic: Raivavae.

Minidonta haplaenopla Solem, 1976
Island endemic: Rurutu.

Minidonta microaconica Solem, 1976
Island endemic: Raivavae.

Minidonta planulata Solem, 1976
Island endemic: Raivavae.

Minidonta sulcata Solem, 1976
Island endemic: Raivavae.

Minidonta sp.
Island endemic: Rimatara*.

Opanara Solem, 1976
Island endemic: Rapa.

Opanara altiapica Solem, 1976
Island endemic: Rapa.

Opanara arecaensis arecaensis Solem, 1976
Island endemic: Rapa.

Opanara arecaensis densa Solem, 1976
Island endemic: Rapa.

Opanara arecaensis microtorma Solem, 1976
Island endemic: Rapa.

Opanara bitridentata Solem, 1976
Island endemic: Rapa.

Opanara caliculata Solem, 1976
Island endemic: Rapa.

Opanara depasoapicata Solem, 1976
Island endemic: Rapa.
Opanara duplicidentata Solem, 1976  
Island endemic: Rapa.
Opanara fosbergi Solem, 1976  
Island endemic: Rapa.
Opanara megomphala megomphala Solem, 1976  
Island endemic: Rapa.
Opanara megomphala tepiahuensis Solem, 1976  
Island endemic: Rapa.
Opanara perahuensis Solem, 1976  
Island endemic: Rapa.

Orangia Solem, 1976  
Island endemic: Rapa.
Orangia cookei cookei Solem, 1976  
Island endemic: Rapa.
Orangia cookei montana Solem, 1976  
Island endemic: Rapa.
Orangia cookei tautautuensis Solem, 1976  
Island endemic: Rapa.
Orangia maituatensis Solem, 1976  
Island endemic: Rapa.
Orangia sporadica Solem, 1976  
Island endemic: Rapa.

Rhysocconcha Solem, 1976  
Island endemic: Rapa.
Rhysocconcha atanuensis Solem, 1976  
Island endemic: Rapa.
Rhysocconcha variumbilicata Solem, 1976  
Island endemic: Rapa.
Ruatara Solem, 1976
Island endemic: Rapa.
  
  Ruatara koarana Solem, 1976
  Island endemic: Rapa.
  
  Ruatara oparica normalis Solem, 1976
  Island endemic: Rapa.
  
  Ruatara oparica oparica (Anton, 1839)
  Island endemic: Rapa.
  
  Ruatara oparica reductidenta Solem, 1976
  Island endemic: Rapa.

Superfamily GASTRODONTOIDEA Tryon, 1866
Family EUCONULIDAE H.B. Baker, 1928

Several species were found alive in Rapa in native forests, including Philonesia tenuior, P. zimmermani zimmermani and Hiona orbis.

In all the northern islands, several species have probably been introduced by early inhabitants and are widespread: Lamprocystis cf. vitrinella, Liadertia discordiae (except in Rimatara), Diastole conula (except in Rimatara). In Raivavae, where four endemic species were known, Microcystis lenticula and M. aspera are still often encountered alive on the leaves in relict forests and Hibiscus tiliaceous forests.

In Tubuai, six endemic species were previously known. We found Microcystis saintjohni at the type locality, "north-east slope of Mt Pane" (Baker 1938), despite the fact that this area is now a pine plantation, with a Psidium understorey. M. saintjohni lives on Psidium leaves. However, its distribution seems to be very restricted, and it qualifies to be classified as Critically Endangered. The five other endemic species are believed to be extinct, as we did not find them anywhere, including the type locality: Cookeana vindex, Cookeana anathesis, Microcystis adusta, Microcystis andersoni (an old shell was found near Mataura) and Microcystis kondoi.

In Rurutu, Lamprocystis rurutuana was not found at the type locality, which is degraded by invasive Kalanchoe sp., and we suggest it could be extinct.

No Euconulidae species was known from Rimatara, though there is no reason they should not be there, like in the other Austral Islands. We found an arboreal species in the northern "mato", on epiphytic ferns on Pisonia grandis, probably new to science.

Subfamily MICROCYSTINAE Thiele, 1931

Cookeana H.B. Baker, 1938
  Cookeana anathesis H.B. Baker, 1938
  Island endemic: Tubuai.
  
  Cookeana vindex H.B. Baker, 1938
  Island endemic: Tubuai.

Diastole Gude, 1913
  Diastole (Diastole) conula (Pease, 1861)
  Cryptogenic.
  Range in the Australs: Rurutu. Tubuai*.
  
  Diastole (Diastole) rurutui H.B. Baker, 1938
  Austral Islands endemic: Rurutu. Raivavae.

Coneuplecta Möllendorf, 1893
  Coneuplecta calculosa (A.A. Gould,1852)
  Cryptogenic.
  Range in the Australs: Rimatara*.

Hiona Cooke in H.B. Baker, 1940
  Hiona (Opara) orbis (Beck, 1837)
  Island endemic: Rapa.

Lamprocystis Pfeffer, 1883
  Lamprocystis (Kerakyx) punctifera (Garrett, 1879)
  Island endemic: Rurutu.
  
  Lamprocystis (Kerakyx?) vitrinella rapana H.B. Baker, 1938
  Island endemic: Rapa.
  
  Lamprocystis (Kerakyx?) vitrinella vitrinella (Beck, 1837)
  Island endemic: Rurutu.
  
  Lamprocystis (Manureva) rurutuana H.B. Baker, 1938
  Island endemic: Rurutu.
Liardetia Gude, 1913
Liardetia (Oceanesia) discordiae (Garrett, 1881)
Cryptogenic.
Range in the Australs: Rurutu.

**Microcystis** Beck, 1837
**Microcystis** (Cnesticystis) aspera H.B. Baker, 1938
Island endemic: Raivavae.
**Microcystis** (Cnesticystis) kondoi H.B. Baker, 1938
Island endemic: Tubuai.
**Microcystis** (Facorhina) adusta H.B. Baker, 1938
Island endemic: Tubuai.
**Microcystis** (Facorhina) andersoni H.B. Baker, 1938
Island endemic: Tubuai.
**Microcystis** (Facorhina) lenticula H.B. Baker, 1938
Island endemic: Raivavae.
**Microcystis** (Facorhina) benesculpta H.B. Baker, 1938
Island endemic: Tubuai.
**Microcystis** (Facorhina) fosbergi fosbergi H.B. Baker, 1938
Island endemic: Raipavae.
**Microcystis** (Facorhina) fosbergi taraiae H.B. Baker, 1938
Island endemic: Raipavae.
**Microcystis** (Facorhina) ornatella ornatella (Beck, 1837)
Island endemic: Rapa.
**Microcystis** (Facorhina) ornatella parva H.B. Baker, 1938
Island endemic: Rapa.
**Microcystis** (Facorhina) perahui H.B. Baker, 1938
Island endemic: Rapa.

**Philonesia** Sykes, 1900
**Philonesia** (Rapafila) tenuior karaporahi H.B. Baker, 1940
Island endemic: Rapa.
**Philonesia** (Rapafila) tenuior tenuior H.B. Baker, 1940
Island endemic: Rapa.
**Philonesia** (Rapafila) zimmermani tautautui H.B. Baker, 1940
Island endemic: Rapa.
**Philonesia** (Rapafila) zimmermani zimmermani H.B. Baker, 1940
Island endemic: Rapa.

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**Superfamily LIMACOIDEA** Lamarck, 1801
**Family AGRIOLIMACIDAE** H. Wagner, 1935

**Deroceras** Rafinesque, 1820
**Deroceras laeve** (O.F. Müller, 1774)
Introduced species.
Range in the Australs: Rurutu*, Raivavae*, Rapa*.

**Bradybaena** Beck, 1837
**Bradybaena similaris** (Férussac, 1821)
Introduced species.
Remarks: Common in all the Austral Islands. In Rapa, it is very abundant around Haurei village, and in Raivavae, it is one of the most abundant snails, everywhere even on ridges, in forests and in degraded areas.

Because the family Achatinellidae was not sorted to species level, all the results and analyses hereafter exclude this family.
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*Philonesia zimmermani zimmermani*, Rapa

*Microcystis lenticula*, Raivavae

*Microcystis fosbergi fosbergi*, Raivavae

*Diestole rurutui*, Raivavae

*Lamprocystis sp.*, Tubuai

*Microcystis saintjohni*, Tubuai

*Microcystis aspera*, Raivavae
Introduced species and extinctions

No data has been published on introduced snail species in the Austral Islands. However, the collections of the Bishop Museum reveal that previous collectors had already found them, some data dating from more than a century ago (Table 14). Several nowadays common species that would not have been mistaken for something else, nor missed by experienced collectors, seem to be recent introduction (at least after 1934), since they were not collected by the Mangarevan Expedition. These include: *Pseudosuccinea columella*, *Physella acuta*, *Laevicaulis alte*, *Achatina fulica*, *Euglandina rosea*, *Paropeas achatinaceum*, *Allopeas clavulinum*, *Streptostele musaecola*, *Huttonella bicolor*, *Bradybaena similaris*. Even if some of these species are small, they are now widespread on at least one of the Austral Islands, and an expert collector such as J.M. Cooke would have found them. *Streptostele musaecola* can be mistaken for a subulind: *Luntia insignis* Smith, 1898 has been described from Trinidad and until very recently thought to be a Subulinidae. It has now been placed in the synonymy of *Streptostele musaecola* which has thus been recognized as a tramp species (Hausdorf & Bermudez 2003).

The Bishop Museum collections, however, do not contain unsorted Subulinidae (R. Cowie pers. comm.). As alcohol material was not checked, we do not know whether slugs were collected in the early 20th century. Nothing is known of the impact of *Euglandina rosea* on native species in Tubuai, but it could have an impact on *Partula hyalina*, has we found this species to be less abundant than in other islands without *Euglandina* (Fig. 10). Its impact on smaller species is known but not quantified (Gargominy 2007). Worth being noted, alien species have had various rate of success in the different islands (Fig. 11), but no single explanation is evident. Introduction date could simply explain this, but we have no indication about it, except that it was after 1934 (Table 14).

### Table 14: List of first recordings of introduced species in the Austral Islands, ordered by date.

<table>
<thead>
<tr>
<th>species</th>
<th>Raivavae</th>
<th>Tubuai</th>
<th>Rurutu</th>
<th>Rimataru</th>
<th>Rapa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allopeas gracile</td>
<td>1934</td>
<td>1934</td>
<td>1879</td>
<td>1921</td>
<td>1828</td>
</tr>
<tr>
<td>Gastrocopta pediculus*</td>
<td>1934</td>
<td>1902</td>
<td>1879</td>
<td>1934</td>
<td>1934</td>
</tr>
<tr>
<td>Gastrocopta servilis*</td>
<td>1934</td>
<td>1902</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
</tr>
<tr>
<td>Melanoideas tuberculata</td>
<td>2002</td>
<td>1902</td>
<td>1934</td>
<td>2004</td>
<td>1934</td>
</tr>
<tr>
<td>Pupisoma sp.*</td>
<td>1934</td>
<td>1902</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
</tr>
<tr>
<td>Allopeas clavulinum</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
<td>2004</td>
<td>1921</td>
</tr>
<tr>
<td>Opeas hannense</td>
<td>1921</td>
<td>1934</td>
<td>1921</td>
<td>1934</td>
<td>1921</td>
</tr>
<tr>
<td>Subulina octana</td>
<td>1921</td>
<td>1934</td>
<td>1921</td>
<td>1921</td>
<td>1934</td>
</tr>
<tr>
<td>Lamellidea oblonga</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
</tr>
<tr>
<td>Physella acuta</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
<td>1934</td>
<td>2004</td>
</tr>
<tr>
<td>Achatina fulica</td>
<td>1984</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euglandina rosea</td>
<td>1985</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gastrocopta sp.</td>
<td>1934</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lamellidea sp.</td>
<td>1934</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pseudosuccinea columella</td>
<td>2003</td>
<td>2003</td>
<td>2002</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Streptostele musaecola</td>
<td>2002</td>
<td>2003</td>
<td>2003</td>
<td></td>
<td>2004</td>
</tr>
</tbody>
</table>

Figure 10: Percentage of stations with *Partula hyalina* in the northern Austral Islands. Tubuai, the only island with *Euglandina rosea* has the lowest abundance of *Partula hyalina*.

Figure 11: Percentage of stations with introduced *Bradybaena similaris* in the Austral Islands. Results from Makatea (Tuamotu Islands) and Tahiti (Society Islands) are included for comparison.
could play a role, but Rapa with its subtropical climate has a similar rate of abundance for Bradybaena similis than tropical Tubuai and Rurutu, but much more than Rimatara and much less than Raivavae, where the climate is also tropical. The dominance of non-endemic species in the current fauna is demonstrated if we consider the number of live individuals collected of all mollusc species, according to their status (endemic, introduced and so on - Fig. 12). Introduced species account for 43% of the collected material, cryptogenic/large range species for 13%. Endemic species represent less than one-fourth of the data. If we consider the northern Austral Islands only, as Rapa was less thoroughly sampled, and excluding the whole Achatinellidae, 66 species were found either alive or recently dead (fresh shells), including 25 endemic. We consider the other endemic species to be extinct, representing a loss of 17 to 60% of the native fauna depending the island. Among species found alive or freshly dead, 16 were found only in one or two stations, or only in natural vegetation, and as such are candidate for a not-too-distant extinction: we might have a future fauna made of 50 indigenous taxa, only one fourth of them being endemics (Fig. 13). This percentage is conservative, as it implies that the number of introduced species does not increase, which is unlikely, as observations in Hawaii have shown (R. Cowie pers. comm.).

Our results show that biodiversity inventories with adapted extensive methods can yield new data, even in areas where focussed sampling has already been performed. The Mangarevan Expedition spent 11 days in Rurutu (we stayed 14 days on this island), but collected less than in other islands: 2 353 specimens, vs 19 227 in Raivavae or 37 593 in Rapa (Gregory 1936). Cooke (in Gregory 1935) considered "that [their] landshell collections are nearly complete from most of the islands and that these need not be revisited […] For further collecting in the southern islands, Raivavae comes second in importance to Rapa and Tubuai third." He thought that the forest was so degraded in Rurutu, Mangareva and Rimatara that very few new species could be found there. However, eight species new to science were described following fieldwork in Mangareva in 1997 (Abdou & Bouchet 2000; Bouchet & Abdou 2001), and we added 12 new endodontid species to the fauna of Rurutu: Cooke and his colleagues were very good collectors, but our advantage certainly lies in the fact that we used a very efficient collecting method, namely litter-sieving, whereas they only collected specimens found with the naked eye, and missed several rare and/or minute species. In Rurutu, several new species are large, but they are very localised, and were found in the "matos" where shells of common species are extremely abundant: finding them directly in this mass of shells is a matter of luck without the systematic searching of sieved litter in the lab. We observed that mollusc populations can survive in tiny pockets of remaining habitats (one or two square meters can be enough), and this is confirmed by other authors (Solem 1988): in this context, we may have missed some living populations of endemic species. However, the northern Australs have been well covered (Fig. 9) and after the 2002-2004 field trips their fauna can be considered as reasonably well known. Rapa, on the other hand,
has not been thoroughly surveyed for lack of time. A longer period would have allowed to survey more areas. In particular, Mts Pukutakatake and Koara, visited by the Mangarevan Expedition, were not surveyed this time, nor most of the north of the island (Mts Pukunia, Taga, Vairu and Ruatara). Some islets have never been prospected to our knowledge, and could be interesting (the last sandalwoods from Rapa are on one of these islets, J.F. Butaud pers. comm.). Nevertheless, the major known mollusc hotspots discovered in Rapa by the Mangarevan Expedition (Mt Perau and Maitua/Peupeu valley) were visited.

**The Austral Endodontidae: contrasting situations among islands**

In Rapa, according to the Mangarevan Expedition samples, eight taxa were restricted to the highest summit ridge (Mt Perau), between 400 m and 600 m a.s.l.; one species was restricted to the Mangaoa ridge (350-400 m); two were found between 150 m and 600 m a.s.l. and 10 were collected at mid-altitudes, between 100 m et 250 m a.s.l. Only one taxon has been collected from sea level to the summit of Perau. The endodontid fauna was mostly found at mid to high altitudes in 1934. Our collections were inadequate to confirm whether these species survive. However, the lack of species at low altitude can be explained in two ways: most of the low altitude areas are highly degraded, and this was already the case in 1934 (Cooke in Gregory 1935), thus the native fauna has disappeared; secondly, most of the native vegetation is restricted to high altitude ridges and gulleys, collectors (both the Mangarevan Expedition and ourselves) concentrated their efforts on these areas, and the absence of data from low altitude could be a sampling bias. This hypothesis is supported by the fact that we found a new species of Endodontidae at sea level, at the base of a cliff only accessible by boat, and a population of a still unidentified Endodontidae was found in a ferny cliff crack, out of reach from goats, at 260 m. The amount of suitable habitat (ferns) was much reduced, a few square meters only, but Endodontidae were abundant there. There must be several tiny pockets of remnant habitats spread all over the island, acting as refugia for native snails, but we did not stay long enough to have a better idea of the true distribution of Endodontidae on Rapa.

On Raivavae, one species survives (*Australodontia rai-vavacana*), and is found living from 40 m to 300 m. It was present at sea level, but only empty shells were found in that locality. All the other species found by the Mangarevan Expedition lived at low altitude (up to 40 m), except *Minidonta anatonuana*, which had been collected from 30 m to 100 m. All these species seem to be extinct today. In particular, the very rich localities of the Mangarevan Expedition around Anatonu village, with up to six co-existing species, are now degraded being part of the village. This rich fauna probably lived in dry coastal forests, which were destroyed when man settled there.

In Tubuai, only coastal species are known, and no species has ever been found in high altitude forests. In 1934, *A. radiella radiella* was already the commonest species, and *A. pharcata* the rarest (Solem 1976). *A. radiella radiella* seems to have survived human disturbance, as it is still abundant in coastal areas, though we never found any live individuals. However, the presence of many fresh shells suggests the species still survives. This coastal distribution is similar to the situation in Mangareva, where the richest localities are close to the sea on sand (Abdou & Bouchez 2000).

In Rurutu, the Endodontidae fauna is extremely rich, even more so than Rapa: 17 species are known from Rapa, 19 in Rurutu. This must be due to the abundance of the upraised coral reef outcrops, which act as micro-centers of endemism, especially the eastern ones. Except for three widespread species, most species are found on limestone, at low altitude. It is remarkable that the Mangarevan Expedition did not notice this amazing radiation. They stayed 11 days in Rurutu and visited the "matos", where they noticed that "*landshells were exceedingly abundant alive" (Cooke in Gregory 1935) but probably concentrated their efforts on the mountains. However, the main difference probably resides in the way they sampled: litter sieving is never mentioned in their reports, and it is most probable that they collected only by hand. They collected 602 endodontid specimens in Rurutu and only collected three of the most abundant species. By litter-sieving we collected 16908 individuals. Given that many species are rare, a large amount of material is necessary to find them. It is notable that the Mangarevan Expedition failed to collect eight of the rarer species.

Biological rarity sensu Bouchez et al. (2002) is the total number of specimens found of a given species, while ecological rarity is given by the number of stations where a species has been collected. It was estimated for Rurutu Endodontidae (Fig. 14) (Zimmermann 2006), which show a typical pattern (Gaston 1994), with a few abundant species and many rare ones.

In Rimatara, both previously known species were abundant in the "matos", but they seem to be extinct now. Another species, *Libera fratercula ratotongensis*, previously only known from the Cook Islands, was found to be extremely abundant in northeastern coastal areas where the soil was removed for road building. Dredging off Rimatara by the research vessel *Alis* (campagne BENTHAUS) at 900 m depth in 2002 also found some shells. This is consistent with the high densities of this species recorded from Rarotonga; in 1965 a single site had 429 individuals per square meter, i.e. "*a total population of the colony [...] estimated at about 43000000 living snails*" (Solem 1976). This figure covers a fraction of Rarotonga population, which could be "*several times the 43000000 estimated for part of one colony*" (Solem 1969). Today, the species is extinct in
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but this figure is probably higher and could reach over two thirds.

Fluvipupa rurutuana, found in five localities in the northern half of the island, qualifies to be classified as Vulnerable, as it has a very restricted distribution (less than 20 km²). Fluvipupa raivavaeensis, found in six localities in the main mountain range of Raivavae, qualifies to be classified as Vulnerable, as it has a very restricted distribution (less than 20 km²). Fluvipupa tubuaia and Fluvipupa jeanyvesi, known from a single locality, should be classified as Critically Endangered.

Australdonta magnasulcata occurs in several dispersed locations, isolated from each other, on Rurutu. The species has a distribution of less than 10 km², its populations are severely fragmented, and there is a continuing decline in habitat quality. It should then be classified as Critically Endangered. However, as we did not actually find live individuals, it could already be extinct.

Australdonta yoshii occurring on several sites distant from each other, on Rurutu. The species has a distribution of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should then be classified as Critically Endangered. However, as we did not find live individuals, it could already be extinct.

Australdonta pseudplanulata occurring only on the northern part of Rurutu, this species has a very restricted area of occupancy (typically less than 20 km²), and thus is classified as Vulnerable. However, this is a conservative classification, as we did not find live individuals, and this species could be extinct. If it survives, it does not meet the criteria to be classified as Critically Endangered.

Rimatara, probably because of coastal habitat degradation. Three new Endodontidae species found in a cave as subfossils in the northern “mato” demonstrate that the original fauna used to be richer. The “matos” are now without soil, the only remaining large trees being huge cryptogenic *Barringtonia asiatica* (Lecythidaceae). We hypothesize that the “mato” used to be covered with forest, with a real soil. The forest cover would have been destroyed (fires, plantations), and the soil was subsequently eroded leading to the extinction of litter species.

On Rurutu and Rimatara, the karstic relief is good for the preservation of shells, which get washed into subfossil remains in caves, these deposits provide a valuable insight into the historical diversity of these islands. There are no limestone caves on Rapa, Raivavae and Tubuai, thus we cannot be sure what has been lost from these islands.

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**IUCN Red List status**

Data collected during these surveys lead us to update the global conservation status of endemic (restricted to Austral Islands) species, according to Red List criteria (IUCN 2001). Status are summarized in Table 15, while figures of threatened and extinct species per island and for the whole archipelago are given in Table 13.

Thirty-two species or subspecies, all endemic, are considered Extinct (EX), as they were actively searched for in their type localities, without success (Sartori et al. 2013). While it is impossible to prove that a species is extinct, as we could simply have missed live individuals, it seems unlikely in this instance, due to thorough and targeted collection methods. If there were some surviving individuals, they represent relictual populations on the brink of extinction. Around 100 other endemic species have not been found alive, but were not the subject of a focused search in their type locality. We give them the benefit of the doubt and suggest they might still be extant and should be classified as Critically Endangered (see below).

A conservative estimate of extinction in the Austral would be 20% of the endemic fauna being extinct, but this figure is probably higher and could reach over two thirds.

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Australdonta yoshii occurring on several sites distant from each other, on Rurutu. The species has a distribution of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should then be classified as Critically Endangered. However, as we did not find live individuals, it could already be extinct.

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Australdonta radiella rurutuensis, occurring on several sites distant from each other in Rurutu, has an area of occupancy of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should then be classified as Critically Endangered. However, as we did not find live individuals, it could already be extinct.

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Australdonta magnasulcata occurs in several dispersed locations, isolated from each other, on Rurutu. The species has a distribution of less than 10 km², its populations are severely fragmented, and there is a continuing decline in habitat quality. It should then be classified as Critically Endangered. However, as we did not actually find live individuals, it could already be extinct.

Australdonta yoshii occurring on several sites distant from each other, on Rurutu. The species has a distribution of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should then be classified as Critically Endangered. However, as we did not find live individuals, it could already be extinct.

Australdonta pseudplanulata occurring only on the northern part of Rurutu, this species has a very restricted area of occupancy (typically less than 20 km²), and thus is classified as Vulnerable. However, this is a conservative classification, as we did not find live individuals, and this species could be extinct. If it survives, it does not meet the criteria to be classified as Critically Endangered.

Australdonta radiella rurutuensis, occurring on several sites distant from each other in Rurutu, has an area of occupancy of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should then be classified as Critically Endangered. However, as we did not find live individuals, it could already be extinct.
Australdonta radiella radiella only occurs along the coast in Tubuai. It has a very restricted area of occupancy (typically less than 20 km²), and thus is classified as Vulnerable. However, this is a conservative classification, as we did not find live individuals, and this species could be extinct. If it survives, it does not meet the criteria to be classified as Critically Endangered (population does not seem to be fragmented).

Australdonta raivavaeana, endemic from Raivavae, is Critically Endangered as it extent of occurrence is less than 100 km², severely fragmented and shows a continuing projected decline. Libera fratercula raortongensis is extinct in Rimatara. It is still extant in Rarotonga, but the population has suffered a severe (though not quantified) decline since the 1960's (Brook 2010). It should be listed as Data Deficient. Lamprocystis vitrinella, occurring on three sites distant from each other in Rurutu, has an area of occupancy of less than 10 km², its populations are severely fragmented, and there is a continuing observed decline in the quality of habitat. It should be classified as Critically Endangered. Microcystis saintjohni has a very restricted distribution, probably less than one square kilometer on Tubuai. There is only one population, and its habitat could be destroyed, if the pine plantation where it occurs is either logged or burnt. Microcystis saintjohni should be classified as Critically Endangered. Microcystis lenticula, still widespread in Raivavae, occurs on a 17.9 km² island; this species has a distribution of less than 20 km², and thus is classified as Vulnerable. Microcystis aspera, still widespread in Raivavae, occurs in a 17.9 km² island; this species has an area of occupancy less than 20 km², and thus is classified as Vulnerable.

Rapa endemics all qualify to be classified as CR, according to the IUCN criteria, as their distributions are less than 100 km², the populations are severely fragmented (most of the island is covered by grassland, and native vegetation is restricted to small patches), and habitat degradation continues. Considering the perilous state of the island's natural habitats, this classification is a conservative one: several of these species, undoubtedly, are extinct.

**Conservation areas**

Austral Islands native forests are among the most interesting areas for molluscs, insects (E. Claridge, R. Englund, D. Percy pers. comm.) and plants (J.-Y. Meyer pers. comm.). As such, they need protection against cattle, goats and fires, which are the main cause of degradation and fragmentation. Degraded areas can sometime harbour indigenous species, such as Vertiginidae on marae (early Polynesian religious sites) stones, but they are usually very poor habitats (the worst being pine plantations, agricultural areas and gardens). In lowlands, where human impact has been the most intense (plantations and settlements), native habitats have almost completely disappeared, along with any species they supported.

As is the case everywhere, people in the Austral Islands are not aware of most of the mollusc species which surround them. They only know the large partulid species, often considered as pests, and Omphalotropis spp. and Helicinidae (collectively called "pupu"), which are used to make necklaces. Small species are completely unknown to them. For this reason, mollusc species cannot be used as flagship species, and their conservation must be done through the conservation of sites. Actions focussing on single species are not suitable, because species are too numerous, and their requirements are unknown. The only exception in the Australs is probably Microcystis saintjohni. In Tubuai, this large and colourful species is highly threatened, and it could be used to highlight the fate of invertebrate native fauna among local people. The same may be true of Samoana spp. on Raivavae. Ex situ conservation, which has been done for Society Islands partulids (Coote & Loeve 2003; IUCN 2010), is not a solution either, as threatened species are too numerous. On the other hand, site protection aiming at mollusc conservation could be quite easy, as tiny pockets of relict habitat, which would be considered as lost in a vertebrate conservation perspective, can still harbour viable populations of endemic species and thus deserve targeted actions. Fencing against introduced herbivores and fire prevention would be necessary to protect these sites.

Another obvious conservation measure is the public awareness and the enforcement of strict controls at the harbours/airport to prevent the introduction of Euglandina rosea and Achatina fulica, which currently are only known from Tubuai in the Austral Islands. Raivavae's Samoana would certainly not survive the introduction of Euglandina on this island. Public education campaigns are essential to inform the local populations about the disastrous impact this could have on indigenous.

Figure 15 shows important areas for molluscan conservation deserving protection:

**Raivavae**

1. Gulley with natural forest (Metrosideros, Hernandia, Psychotria) south of pass between Mt Araua and Mt Hiro, type locality of Samoana aurata (23.85902°S, 147.6568°W).
2. Degraded forest (Thespesia, Celtis, Psidium, Citrus) at the base of the cliff south of Anotonu, type locality of Samoana hamadryas (23.85631°S, 147.64443°W).
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should protect it against grazing by horses, goats and cattle (27.58104° S, 144.36634° W).

8 - Mt Perau, with its exceptional cloud forest.

9 - Cliff bottom of the Puoro bay still harbours a littoral fauna, in particular with hydrobiids in small resurgences.

Rapa

6 - Endemic live species were found in a rocky area in Peupeu valley, which is otherwise very degraded and covered with invasive species such as Hedychium flavescens (Zingiberaceae) and pine plantations. This particular location should be protected (27.6264° S, 144.34257° W).

7 - C. one hectare of semi-xerophilous forest remnants above Pariati bay, NE of Mt Pukumape still has very localized live endemic species. Fencing should protect it against grazing by horses, goats and cattle (27.58104° S, 144.36634° W).

Tubuai

10 - The type locality of Microcystis saintjohni, NE of Mt Pane. Very degraded (pine plantation with a Psidium understorey), it still harbours the only known population of this beautiful large species. However, a single fire could wipe out the species which managed to survive a drastic environmental change (23.37405° S, 149.4776° W).

11 - River harbouring island endemic species of hydrobiid, Fluviopupa tubuaia.
Rurutu
12 - East coast "matos" (Mato Naa, and from Mato Arei to Mato Toarutu) appear to be micro-centers of endemism, with several Endodontidae species restricted to these areas. They should be protected. Moreover, Paparai area, in the south-east part of the island, is an area of outstanding beauty, rich in molluscs, which should be protected even if only for tourism purposes.

Rimatara
13 - Rimatara native fauna has almost completely disappeared. The northern "mato", where the airstrip was recently built, is the only area where a patch of native vegetation remains (Meyer et al. 2005). It is also there that we have found fresh shells of an unknown Euconulidae, probably native. Last but not least, a cave in this "mato" (22.63776° S, 152.80036° W) revealed several extinct species: it represents a unique opportunity to study Rimatara former fauna, which was much richer than today (at least three endemic Endodontidae species new to science and a Partulidae different from Partula hyalina have been found in cave deposits). For these reasons, the areas south of the airstrip that have escaped destruction should be given a protection status.

Table 15: Proposed or current IUCN status for Austral Island endemic mollusc species.

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Terrestrial Biodiversity of the Austral Islands, French Polynesia

Elin M. Claridge, Jessica E. Garb, Rosemary G. Gillespie & Diana M. Percy

Here we examine patterns of terrestrial arthropod diversity in the Austral Islands. This group of isolated volcanic islands, in the southeastern Pacific, represents one of the most remote archipelagos in the world. The islands formed as the result of midplate volcanism and have no historical connections with continental landmasses, thus all elements of the fauna must have colonized these islands by long distance dispersal from one of the neighboring island chains or continental regions.

Such extreme isolation means that the rate of immigration is frequently much lower than the rate of species generation by evolutionary processes, this effect, combined with the availability of ecological space on these islands can promote adaptive radiation. Despite this apparent potential for adaptive radiation, the Austral Islands are not widely regarded as a crucible of biodiversity and evolutionary novelty, as compared with the Hawaiian Islands, for instance. There are several reasons why this may be the case:

- The Austral Islands are much smaller and have a lower relief than the Hawaiian chain — the collective area of the archipelago is just 146.8 km², less than one seventieth of the area of the Big Island of Hawaii alone; the highest peak is Mt Perau on Rapa which is just 650 m, Mauna Kea on Hawaii is a lofty 4169 m, by comparison. Both area and elevation have long been understood to limit the absolute diversity of organisms that can occur on any given landmass (Macarthur & Wilson 1963; Peck et al. 1999).
- The Austral Islands have been little studied in comparison to the Hawaiian Islands. Collecting expeditions and systematic studies on terrestrial arthropods are patchy. The Pacific Entomology Survey, sponsored by the Bernice P. Bishop Museum, Hawaii, the California Academy of Sciences, San Francisco and the University of California, Berkeley, visited the Austral Islands in 1934 and the St. George Expedition sponsored by the British Museum, London, also visited the island of Rapa in the Australs during its time in French Polynesia in 1925. These expeditions did collect a substantial number of insects and spiders, but were by no means exhaustive and it is clear that some taxonomic groups were largely overlooked. The major systematic works on Austral Islands taxa all focus largely on the island of Rapa and include those of Zimmerman (1938) and later Paulay (1985)’s work on cryptorhychine weevils, Clarke (1971)’s extensive study of the Lepidoptera, and Berland (1934, 1942) and more recently Ledoux & Hallé (1995)’s work on the spider fauna.
- Lastly, the islands have been profoundly impacted by human-disturbance. Despite the fact that early Polynesians only colonized these islands within the last several hundred years, this has been sufficient time for their vegetation to be radically modified by habitat destruction for agriculture, grazing and the introduction of non-indigenous species. Anthropogenic impacts may be particularly pronounced in this archipelago due to its small size and low elevation.

Each of these factors likely contributes to the apparent depauperacy of the Austral Islands terrestrial arthropod fauna.

Terrestrial arthropod groups from the Austral Islands can be categorized as indigenous and non-indigenous. The latter represents introduced species that were transported to the islands by humans, intentionally or otherwise, and includes several notable agricultural pests. Undoubtedly there are other species that were introduced by early Polynesian settlers, but these may not be as easily identified as recently introduced species. Within the indigenous species category there are widespread species, which occur more broadly across the Pacific and endemic species, which may be endemic to island groups, a single island or even just a single mountain-top or valley. This latter category, termed narrow endemics hereafter, is of greatest interest to evolutionary biologists, as their study allows insights into the processes driving lineage diversification on these islands.

INTRODUCED SPECIES

The Austral Islands are host to a suite of non-indigenous, recently introduced species that are agricultural pests or are highly invasive. Introduced species may pose a significant threat to indigenous species in the Austral Islands: many prefer disturbed habitats, and occupy these in preference
to indigenous species; some may even displace natives directly through competition or predation as has been found in Hawaii (Krushelnycky et al. 2005). The following is not an exhaustive list of introduced species which occur in the Austral Islands, but it does outline some of the major groups of concern that were found to have reached significant densities and therefore are considered to be potentially problematic.

**Homalodisca vitripennis (Hemiptera, Cicadellidae)**

The Glassy-winged sharpshooter, *Homalodisca vitripennis* (senior synonym of *Homalodisca coagulata*, Takiya et al. 2006) is among one of the most recent documented introductions to the Austral Islands. It was first recorded in French Polynesia in July 1999 (SPC 2002) and more recently arrived in both Rurutu and Tubuai (official records date from January 2005, but population densities suggest that the species has been present in Rurutu for longer, Petit et al. 2008). In continental America the species poses a serious economic threat to wine-growing regions because it is a vector of Pierce’s disease (*Xylella fastidiosa*) a pathogen of grapevines. In French Polynesia, it is unclear that *H. vitripennis* is anything more than a nuisance due to the quantities of “honeydew” that it produces and its remarkably high population densities (Grandgirard et al. 2006). There is no evidence, as yet, to suggest that it is a vector of plant disease in French Polynesia nor that it is able to displace indigenous cicadellids, though there is some suggestion that the species may be toxic to spiders (Suttle & Hoddle 2006). A recent biocontrol program has been extremely efficient at controlling population densities in the Society Islands, with as much as 95% reduction in population densities in the Australs, Societies and Marquesas (Grandgirard et al. 2009). The biocontrol agent *Gonatocerus ashmeadi*, an egg parasitoid, is present in the Austral Islands, and it seems likely that this will effectively control the sharpshooter population there.

**Pantomorus cervinus (Coleoptera, Curculionidae)**

Fuller’s rose weevil, *Pantomorus cervinus* (also widely known by its junior synonym *Asynonychus godmani*) was collected from Rapa in the Austral Islands, the only other records from French Polynesia being from Mt Marau in Tahiti. This weevil species, which originates from South America, is an economic pest of citrus in continental America. It was first recorded as a pest in California in 1879 and has subsequently spread throughout Europe, Africa, Asia and Australasia (Chadwick 1965). In the Pacific it has been recorded from Hawaii and Easter Island (Woodruff & Bullock 1979). It may have been introduced to French Polynesia on the root-stocks of domestic roses or more likely citrus — oranges are grown both on Rapa and in the Punaruu valley below Mt Marau, Tahiti.

**Bactrocera xanthodes (Diptera, Tephritidae)**

In French Polynesia there are four introduced species of tephritid fruit flies that are of economic importance. One of these, the Pacific fruit fly *Bactrocera xanthodes*, is restricted to the Austral Islands (SPC 2002). Its presence has had an impact on the local economy because of the restriction of untreated citrus fruit exports from infested islands to Tahiti. Eradication programs are in place to control this pest as well as the other *Bactrocera* species found in French Polynesia, but as yet, they have been unsuccessful in achieving complete eradication (SPC 2000, 2002).
Terrestrial Biodiversity of the Austral Islands, French Polynesia

R. Englund recorded the species from Rurutu in 2003, but not elsewhere in the Australs. It does not appear to be a major threat to the local agroeconomy, but it should be treated as a species of concern. Biocontrol measures targeted at this species should only be approached with care as it has been demonstrated that parasitoids introduced to control Nezara viridula in Hawaii have also been targeting an endemic species, Coletichus blackburniae, the Koa bug (Hemiptera, Scutellaridae) (Johnson & Follett 2005). This is particularly pertinent as R. Englund also collected specimens of a new endemic species of Coletichus from Rurutu and Raivavae, further endemic species are also known to occur in Tahiti and the Marquesas.

Cheiracanthium mordax (Araneae, Miturgidae)
The Long-legged sac spider Cheiracanthium mordax, a native of Australia (Dondale 1966) was found to occur throughout the Austral Islands and is also known to have recently invaded Hawaii (Nishida 2002), and much of the insular Pacific. It is considered to be an agricultural pest when it infests agricultural crops in high densities in the US, primarily because it limits the export value of these crops. The species has also been shown to feed on indigenous arthropod species in Hawaii (Louda et al. 2003; R. Gillespie unpublished data).

Heteropsylla cubana (Hemiptera, Psyllidae)
The Leucaena psyllid, Heteropsylla cubana, native to Central and South America, occurs throughout the Pacific where it is found on the introduced legume, Leucaena leucocephala (Mimosoidea). In the Austral Islands both introduced legume and psyllid are present, and the psyllid reaches high densities in some locations. Of some concern on Rurutu is that the Leucaena psyllid can also be found on a native legume closely related to Leucaena, Schleinitzia insularum, and where this native legume grows in proximity to Leucaena numbers of H. cubana were found to be high (D. Percy pers. obs. 2003). The presence of this species is considered problematic where Leucaena is valued for agroforestry (e.g. Indonesia, and Africa), but in areas where the host plant is considered invasive, H. cubana may be effective as a biological control agent. The Leucaena psyllid can cause severe damage to the host plant, but initially the extent of the infestation may not be apparent because during early stages young shoots rather than mature leaves are worst affected.

Kallitaxila sinica (Hemiptera, Tropiduchidae)
The tropiduchid planthopper, Kallitaxila sinica, was recorded from Tubuai, Rurutu and Rimatara at high densities feeding on a wide variety of host plants including taro (Araceae) and Hibiscus tiliaceus (Malvaceae).

Sophonia orientalis (Hemiptera, Cicadellidae)
The Two-spotted leafhopper Sophonia orientalis (also widely known by its synonym Sophonia rufofascia, Webb & Viraktamath 2004) is an agricultural pest that occurs in the Society, Marquesas and Australs. It was collected in Rurutu, Tubuai and Rimatara during the survey. The species is highly polyphagous and in Hawaii feeds on a wide range of agriculturally important and indigenous plant species. Feeding damage can cause chlorosis, browning and has been implicated in the dieback of Metrosideros polymorpha (Myrtaceae) in Hawaii (Lenz & Taylor 2001).

Nezara viridula (Hemiptera, Pentatomidae)
The Southern green stinkbug Nezara viridula is a highly polyphagous agricultural pest that is broadly distributed across the globe, including Hawaii, New Zealand and Australia in the Pacific. The species is believed to have originated in Ethiopia and it is a major pest of crops such as cotton and soybean. In Hawaii, it is estimated that this species causes more than US$6 million of damage to Macadamia nut crops annually (Golden et al. 2006). Consequently, the species is a focus of numerous biocontrol programs.
Insects and Spiders

• constraints maintaining morphological stasis,
• recent colonization.

Each of these scenarios is testable, given some molecular phylogenetic data. In the first case, populations on islands should show genetic variation that is shared between islands, so there should be genetic variation but no geographic structure. In the second case we would expect to see variation and geographic structure in genetic data. In the third case there may have been insufficient time for diversification, in which case there should be no or very little genetic variation between populations. Here we present three examples of widespread species, for which some molecular data exists.

Tangaroa tahitiensis (Araneae, Uloboridae)

This species is endemic to the Austral and Society Islands. Other species in the genus Tangaroa are T. dissimilis from New Caledonia and Vanuatu and T. beattyi from the Caroline Islands (Opell 1983). The affinities of Tangaroa species outside the Pacific region (or between the islands of the Pacific) are unknown. However, Tangaroa species each occur broadly across islands within the region where they are found. Molecular analysis using mitochondrial COI gene sequences demonstrates that specimens of T. tahitiensis from three different islands in the Australs group are highly differentiated genetically from each other, populations from Rapa being separated by large distance

Table 16: Pairwise genetic distances between islands of the Australs for Tangaroa tahitiensis based on COI mtDNA sequence data.

<table>
<thead>
<tr>
<th></th>
<th>Moorea</th>
<th>Rurutu</th>
<th>Raivavae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moorea</td>
<td>7%</td>
<td>8-9%</td>
<td>8%</td>
</tr>
<tr>
<td>Rurutu</td>
<td>7%</td>
<td>5-6%</td>
<td></td>
</tr>
<tr>
<td>Raivavae</td>
<td>4%</td>
<td></td>
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Figure 16: Molecular phylogenetic tree for Tangaroa tahitiensis. See Table 16 for distance estimates.

Figure 17: Phylogenetic analysis of Misumenops rapaensis.

A - Strict consensus of 36 equally parsimonious trees retained from a parsimony tree search based on additional COI data (738 base pairs). Numbers above nodes refer to bootstrap support values from 1000 replicates, numbers below nodes refer to decay index values.

B - One of three trees retained from ML analysis of COI data, numbers above branches refer bootstrap values from 100 replicates.
from those on Rurutu and Raivavae (Fig. 16, Table 17). There appears to have been a geographic progression in how the islands have been colonized, from the oldest island of Rurutu, to the youngest island of Rapa (Fig. 16). However, divergence times between different island lineages estimated using the universal rate of arthropod mtDNA pairwise divergence, 2.3% per million years (Brower 1994), suggests that this progression does not fit the geological ages of the islands and implies a more recent colonization of the islands from west to east. Lack of morphological diversification here does not appear to be a result of continued gene flow or a recent colonization of the Austral Islands.

**Misumenops rapaensis (Araneae: Thomisidae)**

Thomisids in the Austral Islands are also represented by a single endemic, but widespread, species, *Misumenops rapaensis*. This species occurs throughout the archipelago (Berland 1934, 1942) and, despite the separation of the islands, Berland (1942) stated that across the different islands, *M. rapaensis* possesses no discernable morphological differences. A more recent taxonomic treatment by Ledoux & Hallé (1995) concluded that the species represented an endemic element of the archipelago with no differentiation between the islands, possibly due to inter-island migration. In addition to occurring widely across the islands, *M. rapaensis* appears common at both low and high elevation collecting sites. Molecular analysis of mitochondrial sequence data (Garb & Gillespie 2006) indicate that despite their lack of observable morphological differentiation, populations of *M. rapaensis* occurring on different islands are genetically distinct and likely represent an indigenous component of each island's terrestrial fauna (Fig. 17). Again scaling the level of genetic distance exhibited between these two islands to Brower's (1994) rate of arthropod mitochondrial pairwise sequence divergence (2.3% per million years), would suggest that the lineages restricted to Rurutu and Tubuai diverged approximately 3.7 million years ago. Thus, rather than current gene flow or recent colonization, the apparent lack of morphological differences between these two islands could be attributed to constraints maintaining morphological stasis across these islands, or simply lack of ecological opportunity for diversification.

In the examples above, there is evidence of geographic structure between different islands, which is a little unexpected in taxa that do not exhibit any notable morphological differentiation. It would be interesting to extend the study of broad endemics to include highly dispersive taxa, such as the dragonfly *Pantala flavescens* (Odonata: family), which has a very broad distribution and is an active flier, to establish whether some species undergo significant gene flow between islands in the Pacific. Another interesting example of a broadly dispersed species is the psyllid, *Mesohomotoma hibisci* (Carsidaridae). This species occurs throughout the Pacific, including the Austral Islands, on its host plant *Hibiscus tiliaceus*. There is some debate about whether *H. tiliaceus* is naturally widespread — it is a common element of low elevation forests in the Austral and other Pacific islands — or whether Polynesians introduced or augmented the distribution range of this plant and thereby in the process increased the distribution of the psyllid. Analysis of molecular divergence in *M. hibisci* could be used to test these scenarios.

## Narrow Endemics

The Austral Islands have been less studied than many other Pacific archipelagos thus far, and because of their small size and the heavy impacts of human modification, they might not be expected to host a substantial endemic arthropod fauna. Nevertheless, levels of endemcity are extremely high if the small island area is taken into account. Here we discuss several groups that appear to exhibit high levels of endemcity. Further groups of interest that require further study and more rigorous collections are also identified.

**Miocalles spp. (Coleoptera, Curculionidae, Cryptorrhynchinae)**

The cryptorrhynchine genus *Miocalles* occurs throughout French Polynesia and across the western Pacific to New Zealand and Australia. Astonishingly, however, the centre of diversity for this genus lies on the island of Rapa, where there are currently 67 described species (Paulay 1985) occurring on an island that is a mere 40 km$^2$, that is a species density of 1.67 species/km$^2$ (as compared with 0.06 species/km$^2$ for the celebratedly diverse Hawaiian Drosophilidae, of which there are an estimated 1000 species in the Hawaiian archipelago). *Miocalles* from Rapa was even proposed to be a possible example of adaptive radiation, though preliminary molecular work appears to support Paulay's (1985)'s assertion that the group could represent multiple independent colonizations of the island (E. Claridge unpublished data). Nevertheless, there is evidence that each of the lineages on Rapa has undergone dramatic morphological and ecological shifts associated with adaptation to host-plant preference and oviposition site. Collectively, the genus feeds on 24 genera of indigenous plants on the island, which represents the vast majority of the indigenous
vegetation. There are also a further nine endemic species that have been described from other islands in the Australs (Zimmerman 1938), not including a previously undescribed species collected on *Allophyllus rhomboidalis* (Sapindaceae) by Elin Claridge during the Austral Islands Biodiversity Survey of Rimatara in 2004 (Claridge 2006).

**Rhyncogonus spp. (Coleoptera, Curculionidae, Entiminae)**

The Broad-nosed weevil genus *Rhyncogonus* has also undergone considerable diversification in the Austral Islands. There are a total of 20 species described from the Australs (Van Dyke 1937), with a further three new species collected on the island of Raivavae in 2002 and another species collected from Rapa by G. Paulay in 1980. The distribution and density of species diversity across the Australs is shown in figure 18. Rapa is host to the highest species diversity in the archipelago, with 11 of the described species endemic to the island and a further two collected from Marotiri, a nearby uninhabited islet. Molecular phylogenetic work demonstrates that the Rapan species of *Rhyncogonus* form a monophyletic unit with an age consistent with the geological age of Rapa, suggesting that it represents an island radiation, though the cause of this radiation is not clear, it does not appear to be ecological (Claridge 2006). These Broad-nosed weevils are not host-specific to the same degree as *Miocalles*. Molecular work also suggests that the Austral Islands lineage has been present in the

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![Image of *Rhyncogonus nigerrimus*](https://example.com/ri.y.meyer.jpg)

Terrestrial Biodiversity of the Austral Islands, French Polynesia

region for the last 10 Myr, at least. This is consistent with the known geological age of the Austral Islands (Dickinson 1998).

Paro spp. (Araneae: Linyphiidae)
The linyphiid spider genus *Paro* (which has been proposed as a junior synonym of *Laetesia*, G. Hormiga pers. comm.) is confined to the summit area of Mt Perau on Rapa, where it builds flimsy sheet webs low down in the vegetation. To date, the only described species from Rapa has been *P. simoni* (Ledoux & Halle 1995). However, comparison of the male palp among the specimens collected in the field in 2002 show that there are only a few specimens that match the morphology of *P. simoni*. Others are quite distinct in palpal morphology, coloration and leg spination. This may represent a previously unknown case of radiation on the island of Rapa. Little is known of the ecological habits of these different morphotypes, but it will be the subject of future research.

A number of other groups have endemic species that occur in the Australs, but in most cases the group is not yet sufficiently well known, the systematic work has not yet been carried out, or they may be represented by just a small number of species. These groups include hemipteran groups, such as nabids, reduviids, scutellerids, and fulgoroid hoppers in the Delphacidae and Issidae. Members of the psyllid genus *Trioza* (Hemiptera: Triozidae) that feed on the plant genus *Metrosideros*, which is widely distributed in the Pacific, have undergone endemic island radiations in the Society and Marquesas Islands, but only one endemic member of this group, *T. zimmermani*, is currently known from the Austral Islands, and it is only known from Tubuai. Three other psyllid genera found in the Australs are also each represented by a single endemic species found on one island only, including a monotypic genus, *Anomocephala*, endemic to Rapa (Tuthill 1942).

Narrow endemic species are also a conservation priority, by definition, because of their uniqueness and their narrow distribution — they are readily threatened by habitat loss or by competition with, or predation by, introduced species.

**DISCUSSION**

Having outlined some of the terrestrial groups that are present in the Australs we will now discuss some of the common biogeographic patterns shown by the indigenous species that occur there.

**Western origins**

A prevailing view concerning the biogeographic origins of Polynesian biotas is that the vast majority of taxa have colonized these remote islands from the west, using intermediate islands as stepping-stones (Gressitt 1956; Miller 1996). For the Uloboridae, origins cannot be determined: The small genus *Tangaroa* (three species) which was established based on morphological criteria has — outside French Polynesia — been found only in New Caledonia and New Hebrides, and the Caroline Islands (Opell 1983), suggesting origination from the west; however its relationships to other genera in the family are unknown. For the Thomisidae, Lehtinen (1993) argued that the Polynesian fauna originated from two opposing directions, one being from the New World, giving rise to the *Misumenops* and *Mecaphesa* spiders of Hawaii, the Society Islands, and the Marquesas, and the other direction being from Melanesia, giving rise to the widespread *Diaea* found in Tonga, Samoa and Fiji. Molecular work on the Pacific Thomisidae (Fig. 19) shows that the Hawaiian and Society Islands Thomisidae in the genus *Misumenops* are allied, while *Misumenops rapaensis* is nested within the genus *Diaea* (Garb & Gillespie 2006). Thus, an eastern origin is inferred for the single (monophyletic) lineage found from Hawaii to the Marquesas and Societies, while a western origin is inferred for the widespread representative, *M. rapaensis*, in the Austral Islands. Interestingly,
Insects and Spiders

the lineages do not overlap; rather, their ranges abut between the Australs and Societies. In a similar manner, molecular data for the Pacific psyllids show that the Austral member of the genus Triozia, together with members from the Societies and Marquesas, have a western origin initiating from Australasia. However, two other monotypic psyllid species found in the Australs appear to have sister taxa in either the Hawaiian Islands or the neotropics (D. Percy unpublished data). For Rhyncogonus weevils, both molecular and morphological work suggest that the genus is nested within a sister tribe which occurs throughout the western Pacific and appears to represent the ancestral lineage that pre-dates the origin of Rhyncogonus (Claridge 2006). The distribution of diversity in Miocalles is also consistent with western affinities, though the centre of diversity is in fact on Rapa in the Australs. The hypothesized western origins of the Pacific biota appear to hold true for the Australs as far as we know at this point, though it has become increasingly apparent that the Hawaiian Islands have received colonists from continental America and that the same is probably true — though to a much lesser extent — of the Marquesas and the Societies.

### Sequential colonization of islands

Colonization in the direction of younger islands has been documented repeatedly in the Hawaiian Islands, and is a general pattern seen in hotspot island chains. It is explained as a consequence of the increased success of establishment on younger islands, where ecological opportunity is likely to be more readily available.
available (Gillespie 2002). For the Austral Islands, the progression rule and absolute geological ages of islands would predict a pattern of phylogenetic progression in the following order: Rimatara, Rurutu, Tubuai, Raivavae, then Rapa. The topology of the phylogenetic pattern consistent with this prediction is (Rurutu (Tubuai (Raivavae (Rapa)))), with older islands appearing in successively more basal positions relative to younger islands. However, geological evidence suggests that both Rimatara and Rurutu have been secondarily uplifted within the last 1-2 Myr (see chapter by Maury et al., this volume), and that the volcanic islands may in fact have been entirely submerged prior to this secondary uplift (Paulay & McEdward 1990). Thus, these two islands may be home to younger lineages, than predicted by absolute geological age. The results from molecular phylogenetic of Rhynoconus largely supports the second scenario, with evidence for back-colonization of Rurutu and Rimatara from the younger Australs, then a sequential colonization pattern down the chain (Claridge 2006). The pattern seen in Misumenops rapaensis is consistent with the first pattern, though it is important to note that the island of Rimatara was not sampled and that the estimated age of this species is considerably younger than that expected for a species which was shadowing the geological formation of islands, versus a more recent eastward expansion across the Pacific, using the islands available.

**The uniqueness of Rapa**

There appear to be a few groups of arthropods that form small radiations of endemic species in the Austral Islands, more particularly on the island of Rapa. In each case, there is plenty of scope for further investigation of these systems. Establishing a robust phylogenetic framework for Miocalles, in French Polynesia, in particular, would allow valuable insights into the geographic and geological timing of the radiation on Rapa.

The unique and unusual nature of the terrestrial biota of Rapa appears to be a recurring theme in this book. It is unclear exactly why Rapa is so unusual, though several hypotheses can be put forward.

- **Isolation** - Rapa is the most inaccessible island in French Polynesia, and one of the most isolated landmasses in the world.
- **Climate and topography** - Rapa has a cool wet subtropical climate, thus both wet and cloud forest occur at lower elevations here than in the Society Islands. It is also the only island in the Austral group that has sufficient elevation to generate its own climate and thus to support cloud forest. Cloud forest is known to harbor a high diversity of endemic species, elsewhere in the Pacific.
- **Human Impact** - Rapa is the most recently colonized island in French Polynesia, the inaccessibility of this island may have saved it from excessive human impact, and the island remains fairly isolated, lacking an airport. However, introduced ungulates have had a profound impact on mid to low elevation habitats. This may be less than that seen in the other Austral Islands, but islands in the Societies, by grace of their high elevation and rarely accessible ridges are definitely more intact.
- **Inherited diversity** - The region near the MacDonald seamount is geologically complex. Rapa sits on a large shallow plateau, and Pleistocene sea-levels fluctuated by up to 120 m over the past 1-2 Myr (Dickinson 1998), probably doubling the area of the island; G. Paulay (1985) suggested that such sea-level changes may have played a significant role in generating species diversity in Miocalles.

**CONCLUSIONS**

The terrestrial arthropod fauna of the Austral Islands is clearly a mosaic of indigenous and introduced species. Despite the small size, low elevation and intense human modification of the Austral Islands there is still an important endemic element present that represents a rich tapestry of diversity, with the low islands in the north showing strong biotic affinities, and in some cases the histories of the biota parallel the geological histories of the islands. The island of Rapa stands out as a diversity hotspot in the region. The distinctive history of the island may be related to a number of factors including its isolation, topographical diversity, and history (both geological and recent). Endemic groups should be the focus of conservation efforts as well as continued scientific study. The Austral Islands Biodiversity Surveys, organized by the Délegation à la Recherche (French Polynesia Government) in collaboration with the Institut Louis Malardé (Tahiti), identified a number of previously undescribed terrestrial arthropod species, primarily associated with the remnant patches of native vegetation found on the islands, which serves to emphasize the importance of conserving these remaining habitat patches. Research is critical at this point:

- To understand the histories of the different components of the biota in the region, in order to assess its future trajectory in the face of sustained or intensified habitat modification and climate change.
- To distinguish between native and introduced elements of the biota, and thus examine the interactions between these elements.
Ischnura aurora, female and male (Photo R. Englund).
Little was known about the aquatic insect fauna of the Austral Islands, prior to the 2002-2004 scientific expeditions, particularly the Odonata (dragonflies and damselflies). Early insect collecting expeditions to French Polynesia focused more on the Society and Marquesas Islands (Kimmins 1929; Needham 1932, 1933, 1935a, 1935b; Mumford 1942), with few known historical collections from the smaller and more isolated Austral Islands. The St. George Expedition, which stayed on Rapa from April 10-25, 1925, was probably the earliest insect collecting expedition in the Austral Islands (Lief tinck 1966). Likely, because of the steep topography of Rapa and the specialized nature of making these collections, aquatic insect collections from Rapa are unknown from the 1925 St. George Expedition. The 1934 Mangarevan Expedition was the next major expedition to visit the Austral Islands, with E.C. Zimmerman making extensive collections of a wide range of terrestrial beetles in the main Austral Islands, and also in many of the smaller offshore islands as well (Zimmerman 1936). Once again, aquatic insects were not a focus of collections during this expedition. The first collections of aquatic insects (a new damselfly species) were made in Rapa, by J.F. Gates Clarke in 1963 and even this was an incidental collection, as Clarke was conducting a Microlepidoptera study (Lief tinck 1966). This almost complete lack of knowledge of the aquatic insect fauna of these islands led to the current investigation. 

Extremely isolated and consisting of a series of small islands, yet older geologically than the Society Islands, the Austral Islands were found to have a rich and diverse aquatic insect fauna, despite their small size and mostly disturbed land areas. This paper covers the results of the 2002-2004 biodiversity surveys, with particular emphasis on the Odonata and the location and type of aquatic habitats found. Threats facing aquatic insects in the Austral Islands will be examined and suggestions will be provided to assist in the conservation of the diverse native aquatic insect fauna remaining in the Austral Islands.

All three widely recognized types of tropical island types (Mueller-Dombois & Fosberg 1998) were sampled during the Austral Islands surveys: atoll and reef islands, such as the outlying "motu" found on Tubuai, the elevated limestone or "makatea" island portions of Rurutu and the high volcanic inner portions of Rurutu and Tubuai. The diversity of geological island types sampled during these surveys allowed a variety of ecological areas and varying plant and aquatic systems to be assessed. Excluding the marine insects, dragonflies were the only aquatic insects observed in the makatea and "motu" (sandy or rocky islet) areas. The Austral Islands have been heavily inhabited and extensively disturbed for nearly a thousand years, with only remnant native forest vegetation remaining.

**AQUATIC INSECT SAMPLING**

The aquatic surveys concentrated on Odonata (damselflies and dragonflies), as they have been found to be sensitive to disturbance and are found in a wide range of aquatic habitats, thus they are good indicator species of environmental quality (Englund et al. 2007; Allison & Englund 2008). In the tropical insular Pacific, damselflies (Zygoptera) (Polhemus & Asquith 1996) and certain aquatic Heteroptera such as Veliidae (Polhemus & Polhemus 2004) or Saldidae (Cobben 1980) are also obvious indicator groups. Damselflies are also charismatic enough to be easily observed and collected by amateurs, they are often known and appreciated by indigenous peoples, making these insects good "flagship species".
Yellow pan traps, aerial nets, dip nets, selective fogging of aquatic habitats with pyrethrins, and benthic kick samples were used to collect larval and mature stages of aquatic insects. Benthic sampling was conducted at aquatic sampling stations by holding an aquatic dip net, while disturbing the rock substrate upstream of the net. Immature aquatic insects were collected from rocks found in riffles by using a toothbrush and fine-point tweezers to extricate larvae from algae covering the rocks. Visual observations of aquatic insects, especially of larger taxa such as Odonata (dragonflies and damselflies), were made whilst hiking along streambeds and in terrestrial habitats as well. Sampling effort was focused on habitat suitable for native aquatic insects such as splash-zones around riffles and cascades, wet rock faces associated with springs and seeps, waterfalls and wetland areas near and along the stream corridor. General collecting was conducted in prime native aquatic insect habitats with numerous aerial net sweeps taken around riffle splash-zones, cascades, seeps, and waterfall areas.

**AUSTRAL ISLANDS AQUATIC HABITATS**

**Rapa**
The second largest of the Austral Islands has a wetter climate regime, especially in the summit areas and a much greater quantity of stream habitats than the other Austral Islands. In contrast to Raivavae and Rurutu, almost all streams on Rapa are fully flowing, and not interrupted by a captage or diversion. A large water storage tank exists along the stream flowing into the main Haurei village, but it was uncertain if this tank is fed by a surface water diversion or groundwater wells, and municipal water in Haurei village is available only intermittently. However, the Haurei village stream flows uninterrupted from its headwaters to the ocean, where it is channelized. All streams in the other currently uninhabited valleys on Rapa flow uninterrupted to the ocean, although small and occasional water diversions for taro (*Colocasia esculenta*, Araceae) still occur in many valleys. Extensive taro wetlands can be found both above Haurei village, along the shores of Haurei bay, and in the many currently uninhabited valleys such as Hiri bay and elsewhere. Stream habitats can be separated into two distinct classes in Rapa:

- Areas containing and lacking overtopping riparian vegetation, with grazed areas containing...
only low grasses along the stream corridor. Most lowland stream habitats have been severely overgrazed by cattle, goats, and horses, with the resultant effect of a complete loss of stream vegetation.

- The second major type of stream habitat is a very small percentage of streams containing riparian vegetation. An example is the stark contrast between heavily overgrazed areas such as that above Tumu waterfall, and a portion of the stream flowing to Hiri bay where feral ungulates have been excluded because taro is still cultivated. These fenced areas exist to keep out grazing animals where taro is currently still grown, and some of the fenced riparian areas include a mixture of introduced Strawberry guava (Psidium cattleianum, Myrtaceae), native ferns and plants, with the alien plants appearing to have little negative impacts on native aquatic biota such as the large endemic Rapa damselfly. This includes areas around Haurei village where a large wooden fence extends far out into Haurei bay to keep cattle out of the village; this fence also has the effect of keeping cattle out of mountainous areas behind the village, and parts of Hiri valley where taro is still grown.

### Raivavae

Drainages on Raivavae are short, and all drainages on the island are interrupted by a concrete captage (drinking water diversion). The largest flowing drainage on the island was an apparently unnamed stream that drained into the extensive taro fields between Mahanatoa and Rairua villages, and was easily accessed at the concrete bridge crossing the stream. Above the captage this stream was 1-2 m wide, and contained some pools up to nearly 1.0 m in depth, although most areas were much shallower and consisted of 3-10 cm shallow riffles and runs. Many of the riffles were flowing over tree roots, although this stream did contain a small amount of gravel riffles. Vaipa stream, located above Vaiuru village, one valley away from Tuarani, was extensively sampled and was nearly as large as the Tuarani stream, but was quite different in character. Vaipa stream, and the streams draining into the Tuarani taro fields contained little to no loose gravel or cobble substrate, and flowed through bedrock chutes and pools. Vaipa stream was accessed by hiking above the water catchment at approximately 50 m elevation, and then hiking through thick Hibiscus tiliaceus (Malvaceae).
At 122 m elevation the stream corridor opens up into a series of spectacular cascades where taro is semi-cultivated on a long series of vertical cascades. Vaipa stream was then sampled until the stream became completely overgrown by Dicranopteris linearis (Gleicheniaceae) at 207 m elevation.

One important observation is that virtually all Raivavae streams still contained extensive riparian or streamside vegetation throughout most of their lengths. Riparian vegetation in the lowland areas consisted of secondary growths of Hibiscus tiliaceus and other species, but became increasingly more native as elevations increased. For example, water flow first appeared in a drainage of Mt Araua at 164 m elevation, in an area of relatively intact native vegetation. Mt Hiro is the highest peak on Raivavae, and water flow first appeared in the main gulch here at 213 m elevation, in an area of native ferns and plants. The highest permanent waterbody on Raivavae was at 262 m elevation and started as a perched spring and wetland that turns into a small trickle, on the Anatonu village side of Mt Hiro. The two largest taro-growing areas on Raivavae were the Tuarani taro fields located north of Vaiuru village, and the region between Mahanatoa and Rairua. These areas were extensively sampled for native and non-native aquatic biota.

**Tubuai**
The watersheds of Tubuai are relatively short and radiate out in a spoke-like arrangement from the central spine of the caldera. One of the most prominent features of Tubuai is the large wetland complex of Matavahi and Mihiura marshes, found on the western side of the island. These two wetlands are undoubtedly the largest in the Austral Island chain, and one of the larger wetland areas in all of French Polynesia. Small taro fields within the Matavahi marsh, near Piton Pahatu were sampled for aquatic insects, and the adjacent marsh was also briefly sampled. The two major watershed areas sampled included an unnamed stream sampled from 18-150 m elevation and an unnamed tributary at the highest reaches of the Vaiapu watershed, below the summit of Mt Panee. Tamatoa Stream was accessed near the Tamatoa cemetery and the stream was surveyed by hiking upstream. The stream was covered with a thick growth of Hibiscus tiliaceus and Pandanus tectorius (Pandanaceae) in the lowest reaches of this stream and had scattered cobbles and larger rocks, but mostly the stream flowed through soil and finer substrates. At 20 m elevation the stream channel started to pick up gradient and cobbles became more common, and small tributaries started to empty into Tamatoa Stream. Stream flow was somewhat high and the water was turbid from heavy rains the day before. At the end of the survey at around 150 m elevation a few 1-2 m high
plunge pools were observed, and stream gradient began to pick up significantly. The other major aquatic system surveyed was the area below the Mt Panee summit, and at 250 m elevation was the highest elevation at which flowing water was found on Tubuai. Water started flowing here from a perched spring in a mixed Pandanus tectorius and Strawberry guava (Psidium cattleianum) forest, flowing downstream over the smooth rock face into a large pool, estimated at 10 x 12 m in size, at around 170 m elevation. Several samples were collected while climbing down the steep madicolous rock wall. Madicolous or hygropetric habitat is defined as an area of vertical rock faces, over which a thin film of water flows permanently. As this is probably the largest permanently wetted rock face area on Tubuai the area was of great biological interest for aquatic insects, and should be sampled more thoroughly in the future as a number of aquatic taxa, not collected during the brief sampling period on Tubuai, could potentially be found here. This large wetted rock wall and downstream cascade chutes contradicts the observation by Craig (2003) that Tubuai lacks stream chute habitat. Stream sampling on Tubuai was hindered by poor water clarity resulting from very heavy rains during the collection period.

**Rurutu**

Aquatic wetland habitats are reduced in comparison to the vast wetlands found on Tubuai, even so, Rurutu contains small but significant stream systems with extensive aquatic habitats. Wetland areas, mainly taro fields are not uncommon, and those sampled included the Peva Iti marsh and wetland area that was being used as pastureland, several large taro fields near Moerai Village, and in the Plateau Paparai limestone plateau basin. Rurutu has a complex geological history and has undergone submergence and also emerged from the ocean Craig (2003). The streams in Rurutu appear geomorphologically older as they mainly flow over smooth chutes into shallow hard rock pools with cascades having mostly been eroded away, confirming Craig’s (2003) observations. Puputa stream, flowing behind the main village of Moerai was the largest stream on Rurutu and was diverted for domestic supplies (as were all streams on Rurutu) at an elevation of 64 m. Water temperature above the diversion was recorded at a cool 20.5°C. The stream flowed for an estimated 400-500 m above the captage before the largest waterfall observed on Rurutu was encountered at 82 m elevation. The free-flowing Puputa stream in this area was heavily shaded, mainly by Hibiscus tiliaceus and Pandanus tectorius and was relatively high gradient with ample riffle habitats and excellent water clarity. Puputa stream was sampled intensively for aquatic biota on November 2003. Other high quality stream habitats sampled on Rurutu included the smaller Uatoa Stream that fed the taro fields of Narui Village. Above the taro fields this beautiful stream flowed through a grove of Tahitian chestnut (Inocarpus fagifer, Leguminosae) trees and has a series of clear pools with very little vegetation growing underneath these large trees.

One of the most unusual hydrogeological features in French Polynesia was observed on Rurutu, just south of the village of 'Auti, with a freshwater stream disappearing directly into a makatea cliff. This stream originated in a bowl-shaped depression that supported taro fields in the Paparai limestone plateau, and flowed in an easterly direction before disappearing into the base of a 100 m tall makatea cliff. The stream then discharges underground into the ocean through the makatea somewhere along the coast around Toarepe point. Native migratory stream organisms are apparently able to penetrate these underground caverns as crustaceans and fish were observed in the stream prior to its disappearance into the makatea cliffs.

**Rimatara**

At only 9 km² this low-lying island has a highest elevation of only 106 m, and is circular in shape.
This island was sampled in October-November 2004, prior to the completion of the airport runway, when the island was only accessible by the Tuha'a Pae cargo boat. Found at 22°S, Rimatara is the smallest of the Austral Islands containing permanent freshwater habitats (Maria atoll and Marotiri islets lack permanent freshwater habitats). Only one small permanent stream (<150 m in length) was observed, but relatively large amounts of wetlands were found on Rimatara. Aquatic habitats sampled included several taro fields, the large Maunutu wetlands near Anapoto village, the Mururau taro fields and wetlands, and the Haretii wetlands. Much of the islands "mato" (raised limestone) habitat was destroyed during the construction of the airport in 2004, with this area containing some of the best native forest habitat. The Maunutu wetland complex near Anapoto was bound on the north where the karst walls form the wetland boundary. Taro is grown in small sections of this wetland, but dominant plant is the giant bulrush (Schoenoplectus subulatus subsp. subulatus, Cyperaceae). Freshwater eels (Anguilla marmorata) and eleotrid (Eleotris sp.) fish access the wetland through the karst surrounding the Maunutu wetland. The Mururau wetland and taro field area appeared to have been reduced in size by c. half, due to the construction of the municipal stadium, of the remaining wetland 60% was covered with taro and 40% was covered with Schoenoplectus rush. The only apparent flowing water on Rimatara was observed at an unused water catchment that was diverted at the Haretii wetland area. The stream was small and flowed where an abandoned water catchment no longer diverted the water. The stream started at the head of a small valley growing taro and bananas, but flowed for only 150 m in a muddy, shallow, 0.5 m wide channel, less than 3-5 cm deep, until disappearing into alluvium. No fish were observed in this small stream.

ODONATA AND AQUATIC INSECTS OF THE AUSTRAL ISLANDS

These were the first comprehensive aquatic insect surveys of the Austral Islands, and have provided much useful information, recording many new insect species. The native aquatic species found in the Austral Islands are internationally important, and preservation of this biodiversity is critical for preserving the rich Polynesian culture, found here. It is also necessary to preserve biodiversity to allow a greater understanding of the natural biological processes of dispersal and colonization of the fauna to these remote and isolated island areas.

A total of 10 Odonata species were collected or observed in the Austral Islands, with two new single-island endemic damselfly species collected from Raivavae and Rurutu (Table 17). Voucher specimens were collected for all species to verify their identifications, except for the large and fast Anax species observed on Tubuai — from its coloration and size this species appears to be Anax guttatus.
The total number of Odonata species on each island ranged from a four on Rimatara to a six on Tubuai and Rurutu. Rapa, Raivavae, and Rurutu had one endemic damselfly, while the other Odonata species found throughout the Australs were widespread indigenous species. With the exception of Tubuai, the Odonata species listed from the surveyed Austral Islands should be considered fairly comprehensive, due to the good survey conditions and adequate sampling time. Tubuai has the distinction of being the only island with flowing water in French Polynesia sampled since 1999 to not have an endemic damselfly species found on it, and this may result from a very short visit and very poor sampling conditions during our stay on Tubuai (rain and high water levels). Further sampling is clearly warranted on Tubuai and initial observations indicate that an endemic upland damselfly could potentially be found in the Mt Panee summit waterfall area, because this section of stream lacks invasive fish species (see "invasive species" section below).
<table>
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<tr>
<th>Taxon</th>
<th>Rapa</th>
<th>Raivavae</th>
<th>Tubuai</th>
<th>Rurutu</th>
<th>Rimatara</th>
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<td><strong>Heteroptera (True Bugs)</strong></td>
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<td></td>
<td></td>
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<tr>
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</tr>
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</tr>
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</tr>
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<td></td>
<td></td>
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<td>X</td>
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</table>

Table 17: Odonata and selected aquatic insect taxa found in the Austral Islands.
X = native but Indigenous and naturally found on other islands. E = island endemic. New species = discovered during these Austral Island expeditions and already described in literature.
Single-island endemic damselflies were found on Rapa, Raivavae, and Rurutu, and are noteworthy in that they are the largest and perhaps some of the rarest species found in the worldwide genus *Ischnura* (Englund & Polhemus 2010). Threats to these species include water diversions and invasive fish species. Virtually all the streams on Raivavae and Rurutu are diverted for agricultural or domestic use, and streams are quite small (<1 m wide, 3-15 cm deep in most cases) and abbreviated on these islands. On the island of Raivavae *Ischnura jeanyvesmeyeri* was collected at a wide range of elevations, from just above sea level at two locations, the Tuarani River (6 m elevation), and 1 m elevation at an unnamed stream, between Mahanatoa and Rairua villages. Both of these lower elevation locations were heavily vegetated forested areas, connecting taro fields. In low elevation areas *I. jeanyvesmeyeri* preferred areas of the stream around exposed rootwads, in the stream along the main part of a forested stream channel. None of the endemic Austral Islands damselflies were observed in or around the large lowland taro fields.
or wetland areas where *Ischnura aurora* and other dragonflies were abundant. The large endemic Austral damselflies are unusual in that they appear to be obligate forest-dwelling species. Although both introduced and native plant species inhabit these riparian areas, *I. thelmae*, *I. jeanyvesmeyeri*, and *I. rurutana* have been only found around riparian areas in forested stream habitats, usually in a mixed canopy of lowland plants of *Hibiscus tiliaceus*, guava (*Psidium guajava*), ferns, Tahitian chestnut, and other plants. While the damselfly species on Rapa (*Ischnura thelmae*) was described in 1966 (Lieftinck 1966), new species were found on Rurutu (*Ischnura rurutan*) and Raivavae (*Ischnura jeanyvesmeyeri*) during these expeditions. The endemic Austral Islands damselflies are unique as they represent the largest known species of the widespread *Ischnura* genus, of which members are normally quite small.

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**Other aquatic insect species of interest**

Although this chapter is focused on Odonata from the Austral Islands, some of the other aquatic insects collected during the surveys are also of great interest. Because very little has been published on the fauna of these islands, most of the groups shown in Table 17 and discussed below were new archipelago records for the Austral Islands. For example, a new species of aquatic beetle diving beetle in the family Dytiscidae was found on Tubuai (*Rhantus englundi*) (Balke & Ramsdale, 2006). Three species of *Rhantus* have been found in the Society Islands, but this was the first record of an aquatic beetle from the Austral Islands. *Rhantus englundi* was collected in slow-moving water at the lower elevations of Tamatoa stream, in an area that was heavily shaded by *Hibiscus tiliaceus* (Englund 2003).

An undescribed species of Microvelia, an aquatic heteroptera (true bug), was collected on Rapa. The Rapa *Microvelia* was quite distinct from other species in the *Microvelia prompta* group that is found elsewhere in the Austral Islands and in the Society Islands (J.T. Polhemus pers. comm.); this new species awaits description. On Rapa, two undescribed species of water skater flies (*Campsicnemus*) and a third closely related undescribed species (*Teuchophorus*) were found in aquatic habitats (N.L. Evenhuis pers. comm.). The record for *Campsicnemus* is the most southerly yet for this genus, and combined with the finding of the new species of *Teuchophorus* flies, are of great biogeographic interest due to Rapa being at the extreme ends of the known range of these genera (N.L. Evenhuis pers. comm.). Ephydrid flies were also quite common in many of the Austral Island stream habitats, and were particularly abundant in Rapa streams. Further work is needed on these flies, and it is unknown whether any new ephydrid species were collected.

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**CONCLUSIONS**

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**Conservation of native species in Austral Islands aquatic habitats**

Extensive research in Hawaii has shown the devastating impacts of alien fish species on the native stream fauna (Englund 1999; Englund & Eldredge 2001). So far, the Hawaii findings seem applicable to French Polynesia as well; island endemic damselflies have never been found in the presence of invasive fish species on the island of Tahiti (R. Englund unpublished data) or Tubuai. Every effort should be made to avoid additional introductions of any non-native aquatic species to the Austral Islands.

Significant findings of these surveys include a pristine native freshwater fauna lacking introductions of nonindigenous fish, amphibians, or aquatic reptiles in Rapa, Raivavae, Rurutu, and Rimatara. Tubuai was the only island currently having two harmful invasive fish species: guppies (*Poecilia reticulata*) and tilapia (*Tilapia* spp.). Invasive fishes were found in all aquatic habitats sampled on Tubuai, particularly the large wetland complex of Matavahi and Mihiuara marshes. The only area lacking invasive fish species on Tubuai was the large waterfall area below the Mt Panee summit, which contained the highest known elevation area on the island with flowing water. This waterfall flowed into a series of stair-step pools and chutes that were too steep and high gradient for introduced fish to access, and this area is a potential refuge area for native species, such as endemic damselflies, that could be negatively impacted by introduced fish.

It is quite possible that invasive fish species have eliminated the native damselfly from low-elevation stream areas, as none were observed during sampling. In contrast, endemic or native stream damselflies have recently been collected throughout areas of French Polynesia lacking these alien fish species. Endemic species were collected at low elevations on Raivavae (3-4 m above sea level), and at elevations just above sea level in the Marquesas and in Hawaii (Englund 2008). The widespread indigenous Odonata found throughout the Austral Islands appear to be more resistant to alien fish species, on Tubuai the common species of native damselfly, *Ischnura aurora*, was found in taro patches and wetland areas, along with five widespread species of dragonflies.
Future research prospects
The findings in this paper should be considered preliminary, due to the rapid nature of the biological assessments conducted during this study. These brief surveys found a rich taxonomic diversity in aquatic habitats, and the findings illustrate the need for additional research and monitoring of this highly endemic fauna. Future surveys should focus more effort on Tubuai because brief preliminary surveys found endemic insects aquatic insects such as Rhantus englundi and Tubuaivelia michaili, while more extensive surveys may find an even greater diversity of endemic species. Tubuai could provide a test case for the impacts of alien species on freshwater ecosystems, as this was the only island with two widely dispersed invasive fish species. Collaborations with paleoecologists have uncovered the remains of aquatic insects such as black flies (Simuliidae) in pre-human contact core samples (see chapter by Prebble, this volume) and will likely lead to many new exciting findings. We have only just started to examine the structure, function and biodiversity of freshwater habitats in these remote and isolated islands of French Polynesia.
Vegetation
Cyrtandra elizabethae (Gesneriaceae), an endangered shrub endemic to Raivavae and Rurutu (Photo J.-Y. Meyer).
General Traits and Main Threats

Jean-Yves Meyer, Hervé Chevillotte & Timothy J. Motley *

The Austral Islands remained for a long time outside shipping routes and were ignored by naturalists despite their proximity with the Society Islands, in particular Tahiti where the first plant collections were made by J. Banks & D. Solander in 1769 during J. Cook's first voyage. H. Cuming performed the first collections on the Austral Islands in 1828, representing about 20 samples from Rurutu, Rapa, and Tubuai that were deposited in Kew (K). At the end of the 19th century, E.F. Raoul spent some time in Rapa and the few specimens he collected were deposited at the herbarium of the Muséum national d'Histoire naturelle in Paris (P). It was only in the beginning of the 20th century that the Bernice P. Bishop Museum of Honolulu (BISH), alone or in association with other institutions, organized two expeditions between 1921 and 1923 covering almost the entire French Polynesia and resulting in the first significant collections on the Austral Islands. During the Bayard Dominick Expedition between 1921 and 1922, ethnobotanists such as R.T. Aitken in Tubuai and A.M. Stokes & J.F.G. Stokes collected across the Austral Islands. The Whitney South Seas Expedition took place between 1921 and 1923, with E.H. Quayle as the main collector on the Austral Islands. In 1934, the BISH organized the Mangarevan Expedition, the greatest scientific expedition of the century in Eastern Polynesia, with F.R. Fosberg & H. St John as the main collectors on the Austral Islands, the Gambier, the Pitcairn, and the majority of the Society Islands, adding over 5000 new specimens. About 40 years passed before the botanical surveys conducted by the Paris Muséum national d'Histoire naturelle (M.N.H.N.) in 1979 (Tubuai), 1981 (Rurutu), and 1984 (Rapa). The results were published by Hallé (1980, 1983), Hallé & Florence (1986), and Florence & Hallé (1986). The Bishop Museum harbors some plants from the Austral Islands collected by J.P. Chapin in 1934, W. Hambuechen in 1960, J.F.G. Clarke in 1963, S.H. Sohmer in 1971, N.L.H. Krauss in 1977, and G. Paulay in 1979. The M.N.H.N. and the Musée de Tahiti et des îles (PAP) hosts some collections done during the inventory of the flora of French Polynesia by J. Florence in 1983 and 1991 (in particular with W.R. Sykes in Raivavae, CHR, P and PAP). The present study includes some samples from R. Graffe and A. Varney, collected between 1982 and 1990 as well as specimens accumulated between 2001 and 2004, including collections on Rapa by T.J. Motley, S.P. Perlman & K.R.Wood funded by a National Geographic grant, and by J.-F. Butaud, J. Florence, J.-Y. Meyer during the program "Inventory of the biodiversity of the Austral Islands" undertaken by the government of French Polynesia in all islands.

Balgooy (1971) considered Eastern Polynesia (comprising the Cook Islands, French Polynesia, and the Pitcairn Islands) as the province of Southeastern Polynesia belonging to the Eastern Malaysia region. Its geographic location places it at the extreme part of the South Pacific islands characterized by an impoverishment in a west-east gradient: there are over 3000 species in New Caledonia and about 900 species in Eastern Polynesia, which has however a rate of endemism of about 50%.

In the vicinity of the Tropic of Capricorn for the northern group (Maria, Raivavae, Rimatara, Rurutu, and Tubuai, near 23°S) and well beyond for the Rapa group (Rapa and Marotiri, 27-28°S), the flora of the Austral Islands presents some tropical to subtropical or sub-temperate characteristics. In addition to the geographic similarities among themselves or with the Cook Islands (the nearest group), the islands of the northern group present some similarities with some tropical islands such as the Society Islands (500 km away, at 15-17°S) while the Rapa group is relatively isolated at over 1200 km from Tahiti.

To determine the floristic affinities, the Krober similarity index (Sk) will be applied. This index reduces the impacts of number disparity compared to an index such as the Sörensen. The Krober similarity index is computed as follows:

$$Sk = \left[ \frac{(A+B) \times C}{2A \times B} \right] \times 100$$

- $A =$ number of species from the first archipelago
- $B =$ number of species from the second archipelago
- $C =$ number of species common to both archipelagos.

* This paper was originally written in French with Jacques Florence (IRD, Paris) who declined co-authorship on this revised English version.
The index will help characterize the floristic similarities among the various archipelagos and island groups of Eastern Polynesia and indicate the status of the Austral Islands within Eastern Polynesia. Tables 18 and 19 summarize the data on vascular plants (Angiosperms and Pteridophytes), of the Angiosperms alone, and the values of the Kröber index.

To characterize the floristic affinities of Eastern Polynesia, a grouping can be made within an Austral-Cook-Society-Tuamotu-Gambier (ACSTG) polygon, with indices close to or higher than 50 (Fig. 20). The Pitcairn group is similar to the Gambier while the archipelagos or islands located far from this set present the lowest similarities first among themselves, then with the ACSTG polygon. Based on Table 18, Rapa and the Marquesas, with a distance of 2000 km between them have the lowest Sk index (Sk = 24). Among the other pairs including the Marquesas, the value is higher than 30 only with the Society Islands (Sk = 35) followed by the Austral Islands (Sk = 33). Globally, the floristic affinities are the exact reflection of the relative geographic location of the archipelagos: the greater the distance, the lower the floristic affinities. The most extreme examples are the Marquesas-Rapa Group or Marquesas-Pitcairn pairs. Brown (1935) ranked each archipelago (Austral, Rapa, Society, Marquesas, and Tuamotu) as a district, with the exception of the Gambier and the Pitcairn, which were grouped in one district. The Gambier Islands are virtually as similar with the Tuamotu than the Pitcairn. The Pitcairn, located further to the others except the Tuamotu, could be integrated in the ACSTGP polygon on one hand and opposed to the Marquesas and the Rapa Group on the other hand. However, such in-depth discussion is beyond the framework of this study. For the islands included in the biogeographical focus area, the highest Sk value corresponds to the Austral-Cook pair. The Austral Islands present just slightly lower affinities with the Gambier, the Society, and the Tuamotu, followed by the

<table>
<thead>
<tr>
<th>Archipelago</th>
<th>Austral</th>
<th>Gambier</th>
<th>Rapa</th>
<th>Marquesas</th>
<th>Society</th>
<th>Tuamotu</th>
<th>Cook</th>
<th>Pitcairn</th>
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Table 18: Floristic affinities (Angiosperms and Pteridophytes) among the archipelagos or the island groups of Eastern Polynesia. The numbers of common species are above the diagonal and the values of the Sk index below. The highest Sk values involving the Austral Islands and the Rapa Group are in bold, the lowest in bold italics. The floristic data were obtained from the botanical database "Nadeaud" under ™Access, updated in September 2006.

Figure 20: Graphical representation of floristic affinities for vascular plants among the archipelagos or island groups of Eastern Polynesia, based on the Sk index values from Table 18; the highest area values are in red for the northern group of the Austral Islands and in blue for the Rapa group.
Pitcairn (48%) and the Rapa Group (47%). The Rapa Group presents the highest index with the Cook, the Pitcairn, and the Society, and the lowest index with the Marquesas, then the Tuamotu (mainly due to very limited common coastal plants with the former and few common inland plants with the latter). These results highlight the remoteness of the Rapa Group, which justified its ranking as a district of the Eastern Polynesia province by Balgooy (op. cit.).

For Angiosperms only (Table 19), index values are globally lower since ferns, including numerous wide-ranging species found almost everywhere, increase the values of indices exceeding 70. The lowest affinities are with Rapa, for which the highest indices are with the same islands. The similarity index values for Angiosperms only (Table 21), except for Maria (with very few ferns) with Rapa, are still slightly lower than for the global flora.

**INTER-ISLAND AFFINITIES WITHIN THE AUSTRAL ARCHIPELAGO**

Table 19: Floristic affinities for Angiosperms among the archipelagos or island groups of Eastern Polynesia. The numbers of common species are above the diagonal and the values of the Sk index below. The highest Sk values involving the Austral Islands and the Rapa Group are in bold, the lowest in bold italics. The floristic data were obtained from the botanical database “Nadeaud” under ™Access, updated in September 2006.

<table>
<thead>
<tr>
<th>Archipelago</th>
<th>Austral</th>
<th>Gambier</th>
<th>Rapa</th>
<th>Marquesas</th>
<th>Society</th>
<th>Tuamotu</th>
<th>Cook</th>
<th>Pitcairn</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Austral</td>
<td>45</td>
<td>55</td>
<td>51</td>
<td>104</td>
<td>60</td>
<td>88</td>
<td>48</td>
<td>156</td>
<td></td>
</tr>
<tr>
<td>Gambier</td>
<td>51</td>
<td>24</td>
<td>30</td>
<td>48</td>
<td>40</td>
<td>38</td>
<td>34</td>
<td>62</td>
<td></td>
</tr>
<tr>
<td>Rapa</td>
<td>40</td>
<td>29</td>
<td>32</td>
<td>46</td>
<td>24</td>
<td>45</td>
<td>29</td>
<td>125</td>
<td></td>
</tr>
<tr>
<td>Marquesas</td>
<td>28</td>
<td>31</td>
<td>20</td>
<td>73</td>
<td>34</td>
<td>46</td>
<td>28</td>
<td>224</td>
<td></td>
</tr>
<tr>
<td>Society</td>
<td>47</td>
<td>45</td>
<td>25</td>
<td>26</td>
<td>71</td>
<td>93</td>
<td>43</td>
<td>372</td>
<td></td>
</tr>
<tr>
<td>Tuamotu</td>
<td>54</td>
<td>56</td>
<td>24</td>
<td>28</td>
<td>51</td>
<td>60</td>
<td>37</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td>Cook</td>
<td>57</td>
<td>43</td>
<td>33</td>
<td>25</td>
<td>43</td>
<td>55</td>
<td>38</td>
<td>151</td>
<td></td>
</tr>
<tr>
<td>Pitcairn</td>
<td>46</td>
<td>49</td>
<td>30</td>
<td>24</td>
<td>33</td>
<td>45</td>
<td>37</td>
<td>78</td>
<td></td>
</tr>
</tbody>
</table>

Table 20: Floristic affinities for vascular plants (Pteridophytes and Angiosperms) on the Austral Islands. The floristic data were obtained from the botanical database “Nadeaud” under ™Access, updated in September 2006.

<table>
<thead>
<tr>
<th>Islands</th>
<th>Maria</th>
<th>Raivavae</th>
<th>Rimataka</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Rapa</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maria</td>
<td>21</td>
<td>18</td>
<td>19</td>
<td>19</td>
<td>5</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Raivavae</td>
<td>52</td>
<td>65</td>
<td>116</td>
<td>124</td>
<td>76</td>
<td>162</td>
<td></td>
</tr>
<tr>
<td>Rimataka</td>
<td>50</td>
<td>59</td>
<td>71</td>
<td>66</td>
<td>36</td>
<td>84</td>
<td></td>
</tr>
<tr>
<td>Rurutu</td>
<td>48</td>
<td><strong>74</strong></td>
<td>66</td>
<td>120</td>
<td>71</td>
<td>152</td>
<td></td>
</tr>
<tr>
<td>Tubuai</td>
<td>47</td>
<td><strong>74</strong></td>
<td>58</td>
<td><strong>74</strong></td>
<td>82</td>
<td>172</td>
<td></td>
</tr>
<tr>
<td>Rapa</td>
<td><strong>12</strong></td>
<td>43</td>
<td>33</td>
<td>42</td>
<td>45</td>
<td>191</td>
<td></td>
</tr>
</tbody>
</table>

Similarly to the archipelagos, Tables 20 and 21 present the floristic affinities for all plants and Angiosperms only for each of the Austral Islands.

In Table 20, the values of the similarity index correspond to the geographic location and physiographic factors of the main islands (Raivavae, Tubuai, and Rurutu) of the northern group, which present the strongest affinities among themselves with

Table 21: Floristic affinities for Angiosperms on the Austral Islands. The floristic data were obtained from the botanical database “Nadeaud” under ™Access, updated in September 2006.

<table>
<thead>
<tr>
<th>Islands</th>
<th>Maria</th>
<th>Raivavae</th>
<th>Rimataka</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Rapa</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maria</td>
<td>17</td>
<td>14</td>
<td>15</td>
<td>15</td>
<td>1</td>
<td>19</td>
<td></td>
</tr>
<tr>
<td>Raivavae</td>
<td>52</td>
<td>49</td>
<td>77</td>
<td>82</td>
<td>44</td>
<td>113</td>
<td></td>
</tr>
<tr>
<td>Rimataka</td>
<td>48</td>
<td>61</td>
<td>52</td>
<td>48</td>
<td>24</td>
<td>63</td>
<td></td>
</tr>
<tr>
<td>Rurutu</td>
<td>47</td>
<td><strong>73</strong></td>
<td>68</td>
<td>75</td>
<td>39</td>
<td>99</td>
<td></td>
</tr>
<tr>
<td>Tubuai</td>
<td>46</td>
<td><strong>73</strong></td>
<td>60</td>
<td>72</td>
<td>45</td>
<td>111</td>
<td></td>
</tr>
<tr>
<td>Rapa</td>
<td>3</td>
<td>37</td>
<td>29</td>
<td>35</td>
<td>37</td>
<td>125</td>
<td></td>
</tr>
</tbody>
</table>
Vascular Flora, General Traits and Main Threats

Floristic data for the Austral Islands are the most recent in the botanical history of Polynesia. The islands remained long unexplored and were not included in the first inventory of the flora of the region (Drake del Castillo 1893), which covered the Society Islands and secondarily the Marquesas, the Gambier, and the Tuamotu, as well as Wallis. It was only in the 20th century with the works of Brown (1931, 1935) and Brown & Brown (1931) that the first collections and descriptions of new species from these islands were published. About one hundred taxa, considered to be endemic to these islands, were described, only half of which is maintained or combined to date. The works of Copeland (1938) on ferns, of Hallé & Florence (1986), and Florence (1997, 2004) on flowering plants have added 25 new taxa. Endemism will be presented at the genus and species levels, with an overview of the native flora of French Polynesia and the biogeographical focus area.

Genus-level endemism

While endemic families are the exception for the Pacific biome (five endemic families in New Caledonia, Jaffré et al. 2004, only one in Fiji, Balgooy op. cit.), genera that are endemic to an archipelago characterize insular flora (104 endemic genera in New Caledonia for example, Jaffré et al. op. cit.). Table 22 provides the figures of genus-level endemism for each archipelago in Polynesia, from the island level to the scale of Eastern Polynesia. While genus-level endemism appears marginal, the peculiar status of Rapa is again confirmed as it harbors seven genera endemic to the Eastern Polynesia province, representing about 5% of all genera on the island, way ahead of the Marquesas with about 2.5%.

Table 23 presents the taxonomic distribution of these genera, the genera with the wide distribution in the Pacific or those restricted to specific archipelagos or islands and found in the biogeographical focus area.

Table 22: Genus-level endemism in French Polynesia. El: endemic to an island. EA: endemic to an archipelago. EPF: endemic to French Polynesia. EPO: endemic to Eastern Polynesia. GE: endemic genera. The floristic data were obtained from the botanical database "Nadeaud" under "Access, updated in September 2006.

<table>
<thead>
<tr>
<th></th>
<th>Austral</th>
<th>Rapa</th>
<th>Gambier</th>
<th>Marquesas</th>
<th>Society</th>
<th>Tuamotu</th>
<th>French Polynesia</th>
</tr>
</thead>
<tbody>
<tr>
<td>El</td>
<td>-</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>EA</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>2</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>EPF</td>
<td>1</td>
<td>3</td>
<td>-</td>
<td>2</td>
<td>1</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>EPO</td>
<td>-</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>3</td>
<td>-</td>
<td>3</td>
</tr>
<tr>
<td>Total GE</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>11</td>
</tr>
</tbody>
</table>
Terrestrial Biodiversity of the Austral Islands, French Polynesia

Table 23: Distribution of several endemic genera of Polynesia or the Pacific (west to east). The extra-tropical islands of Lord Howe and Norfolk are included for Australia. For distribution types: EI = island endemic. EA = endemic to the Austral archipelago. EPA = endemic to the Pacific. EPAS = endemic to the South Pacific. EPF = endemic to French Polynesia. EPO = endemic to Eastern Polynesia. EPT = endemic to trans-equatorial Polynesia. The most restricted distributions are in bold.

<table>
<thead>
<tr>
<th>Genera</th>
<th>Austral</th>
<th>Rapa</th>
<th>Marquesas</th>
<th>Society</th>
<th>Cook</th>
<th>Hawaii</th>
<th>New-Zealand</th>
<th>Australia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Charpentiera (Amaranthaceae)</td>
<td>EPT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meryta (Araliaceae)</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
<td>EPA</td>
</tr>
<tr>
<td>Apostates (Asteraceae)</td>
<td>EI</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fitchia (Asteraceae)</td>
<td>EPO</td>
<td></td>
<td>EPO</td>
<td>EPO</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oparanthus (Asteraceae)</td>
<td>EPF</td>
<td></td>
<td>EPF</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacifigeron (Asteraceae)</td>
<td>EI</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Apetahia (Campanulaceae)</td>
<td>EPF</td>
<td></td>
<td>EPF</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corokia (Escalloniaceae)</td>
<td>EPAS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exocarpos (Santalaceae)</td>
<td>EPA</td>
<td></td>
<td>EPA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nesoluma (Sapotaceae)</td>
<td>EPT</td>
<td></td>
<td>EPT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hebe (Scrophulariaceae)</td>
<td>EPAS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haroldiella (Urticaceae)</td>
<td>EA</td>
<td></td>
<td>EA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Metatrophis (Urticaceae)</td>
<td>EI</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Nesoluma polynesicum (Sapotaceae), a small tree endemic to Raivavae, Rapa, and the Cook and Hawaiian Islands (Photo J.-Y. Meyer).

Haroldiella rapaensis (Urticaceae), an erect herb endemic to Rapa, only found on Mt Perau (Photo J.-Y. Meyer).
Vascular Flora, General Traits and Main Threats

Corokia (Escalloniaceae) is found in New Zealand and the extra-tropical islands of Australia (Lord Howe and Norfolk) and is represented by one species in Rapa. Hebe (Scrophulariaceae) is centered on New Zealand and has one endemic species in Rapa. Exocarpos (Santalaceae) ranges from Southeast Asia, through Malaysia and the South Pacific to Rapa (with one endemic species) and Hawaii to the north. Other genera not cited here, such as Eurya (Theaceae), an Asia-Pacific genus, has a range that finds its Australian-Eastern limit in Rapa; Astelia (Asteliaceae) is distributed from New Guinea, New Zealand, through the summits of the Pacific to Chile and has one endemic to Rapa.

Rapa clearly appears as the island harboring the largest number of endemics: three genera endemic to the island and virtually all the other endemic genera to Eastern Polynesia and French Polynesia, with the exception of Lebronnecia (Malvaceae) and Plakothira (Loasaceae) known from the Marquesas or Sclerotheca (Campanulaceae) from the Cook and Society Islands.

### Primary flora of French Polynesia

Table 24 presents the rate of endemic and native flora at species level, for vascular plants on all archipelagos of French Polynesia. The endemism rate is computed as followst:

\[
TE = 100 \times \frac{FE}{FEI}
\]

- **FE** is the number of endemic taxa
- **FEI** the sum of endemic taxa and non-endemic native taxa, i.e. the primary flora.

Only the island-level and archipelago-level endemics are taken into account; the higher-level endemics are considered native.

An impoverished flora in this region of the Pacific is the main result of the various physiographic and biogeographical factors since the emergence of volcanoes. French Polynesia harbors 884 species of vascular plants, a far lower number than on other archipelagos or islands: New Caledonia has over 4000, the Fiji about 1300, (Smith 1979-1991) and the Hawaii Islands about 1100 species (Wagner et al. 1990). These low numbers conceal a real diversity of endemic flora, with 477 endemic species or 54%.

---

**Table 24: Native and endemic vascular flora on the French Polynesia archipelagos.**

<table>
<thead>
<tr>
<th>FE</th>
<th>Austral</th>
<th>Rapa</th>
<th>Gambier</th>
<th>Marquesas</th>
<th>Society</th>
<th>Tuamotu</th>
<th>French Polynesia</th>
</tr>
</thead>
<tbody>
<tr>
<td>FI</td>
<td>205</td>
<td>131</td>
<td>76</td>
<td>166</td>
<td>329</td>
<td>92</td>
<td>407</td>
</tr>
<tr>
<td>FEI</td>
<td>230</td>
<td>191</td>
<td>83</td>
<td>321</td>
<td>553</td>
<td>98</td>
<td>884</td>
</tr>
<tr>
<td>TE</td>
<td>11%</td>
<td>31%</td>
<td>9%</td>
<td>48%</td>
<td>40%</td>
<td>6%</td>
<td>54%</td>
</tr>
</tbody>
</table>

---

*austral rapa Gambier Marquesas society tuamotu french polynesia*

---

*Paciﬁgeron rapensis (Asteraceae), a subshrub endemic to Rapa, restricted to the highest ridges of Mt Perau (Photo J.-Y. Meyer).*
For native flora, the total for the archipelagos is higher than the combined total for Polynesia as many species are common to two or more archipelagos. The Marquesas have the highest rate of endemism due to their isolation in the Pacific: they are the most distant from the landmasses, at over 5000 km from Central America or 7000 km from Australia, presenting an active speciation. The Society Islands benefit from the mass effect and the diversity of the ecological niches in Tahiti, the largest island at 1050 km² with the highest summit at 2241 m in Mt Orohena. Tahiti harbors 161 native species out of the 224 found in the archipelago, or 72%. Rapa ranks first in the biogeographical focus area with an endemism rate of 31%.

### Primary flora of the Austral Islands

Table 25 presents the numbers for endemic flora on the Austral Islands, at the (infra) species level. Only island endemic species are included, the higher-level endemics being considered native. The main islands of the northern group have comparable rates even if Raivavae is the only one with a rate reaching 4%, due to comparable physiographic and anthropogenic conditions. The rate does not exceed 5% at Rimatara, the smallest island with a maximum altitude of 100 m. Maria has a “motu” flora including only coastal species and no endemics.

### Specific status of Rapa

Data on species endemism also confirm the distinctiveness of Rapa (Table 26). The limited floristic
affinities with the neighboring archipelagos and the moderate endemism at genus-level (still the highest in the sub-region) highlight the isolation of this island in Eastern Polynesia. With an endemism rate of 31% at the level of species, Rapa has the highest rate in French Polynesia and Eastern Polynesia.

Table 25: Distribution of native and endemic flora at island-level on the Austral Islands. FE: endemic flora. FI: indigenous or native flora. FEI: endemic and native flora. TE: rate of endemism. The floristic data were obtained from the botanical database “Nadeaud” under ™Access, updated in September 2006.

<table>
<thead>
<tr>
<th>Islands</th>
<th>Maria</th>
<th>Raivavae</th>
<th>Rimatara</th>
<th>Rurutu</th>
<th>Tubuai</th>
<th>Rapa</th>
</tr>
</thead>
<tbody>
<tr>
<td>FE</td>
<td>–</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>59</td>
</tr>
<tr>
<td>FI</td>
<td>23</td>
<td>145</td>
<td>79</td>
<td>143</td>
<td>158</td>
<td>135</td>
</tr>
<tr>
<td>FEI</td>
<td>23</td>
<td>162</td>
<td>84</td>
<td>152</td>
<td>172</td>
<td>191</td>
</tr>
<tr>
<td>TE</td>
<td>–</td>
<td>4 %</td>
<td>2 %</td>
<td>1 %</td>
<td>1 %</td>
<td>31 %</td>
</tr>
</tbody>
</table>

Table 26: Comparison of endemism rates for the floristically richest islands of French Polynesia. The floristic data were obtained from the botanical database “Nadeaud” under ™Access, updated in September 2006.

<table>
<thead>
<tr>
<th>Islands</th>
<th>Hiva Oa</th>
<th>Nuku Hiva</th>
<th>Rurutu</th>
<th>Tahiti</th>
<th>Rapa</th>
</tr>
</thead>
<tbody>
<tr>
<td>% island endemism</td>
<td>9</td>
<td>14</td>
<td>14</td>
<td>18</td>
<td>31</td>
</tr>
<tr>
<td>Surface (km²)</td>
<td>315</td>
<td>340</td>
<td>1045</td>
<td>40</td>
<td></td>
</tr>
<tr>
<td>Max. elevation</td>
<td>1276</td>
<td>1224</td>
<td>2241</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Sophora* sp. (Fabaceae), a small shrub discovered on ridges below Mt Taitaa in Rurutu (Photo J-Y. Meyer).
TAXONOMIC DISHARMONY OF FLORA IN FRENCH POLYNESIA AND THE AUSTRAL ISLANDS

The distance between the volcanic islands and the continental landmasses or the nearest archipelagos, which are potential reservoirs of diaspores, contributes to the selection of living organisms based on their means of dispersal: among fauna, large carnivores or herbivores are absent; among plants, groups with voluminous fruits or seeds that cannot be transported through a natural means of dispersion or by ocean currents, air, or animals cannot be found. Entire families such as Meliaceae, Annonaceae or Ebenaceae are absent or poorly represented in Eastern Polynesia while they can be found in the Fijis. Conversely, some families benefited from this first filter and are overrepresented compared to the continental masses. Ferns, with spores that are easily dispersed by wind, are the most vivid example: the Society Islands harbor the highest rate of ferns among the oceanic islands (Florence 1993).

Tables 27 and 28 present the data on the Austral Islands and the Rapa group. As the flora is less significant and the relevant families (eight in total) less represented, the threshold was set at six species.

For the Austral Islands, the figures are heterogeneous but low: two families are overrepresented, the Urticaceae and the Convolvulaceae. While the former is found at a comparable rate in French Polynesia, the latter is absent at the Polynesian level. Its presence might be due to the relative significance of open and coastal habitats compared to forests but mainly to the low representation of large families: the Convolvulaceae of the Austral Islands for instance represent almost all those found in Polynesia. For the others, surpluses or deficits are milder than for the entire Polynesia, which reflects a more balanced flora for subtropical islands. It should be noted that due to the low numbers, a more rigorous interpretation is difficult.

The Rapa Group has partly the same elements as the Austral Islands, with less heterogeneous numbers. Urticaceae are overrepresented but in low

Table 27: Importance of the eight most abundant families in the Austral Islands compared to worldwide abundance. The highest surpluses are in bold, the highest deficits in bold italics. The Fabaceae family includes here the Caesalpiniaeae, Mimosaceae, and Fabaceae sensu stricto. The Malvaceae includes Bombacaceae, Malvaceae sensu stricto, Sterculiaceae and Tiliaceae.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>% (1)</th>
<th>Surplus/Deficit</th>
<th>Species</th>
<th>% (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fabaceae</td>
<td>14</td>
<td>6,1%</td>
<td>0,8% (1)/(2)</td>
<td>18 000</td>
<td>7,5%</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>14</td>
<td>6,1%</td>
<td>1,4%</td>
<td>10 200</td>
<td>4,2%</td>
</tr>
<tr>
<td>Orchidaceae</td>
<td>12</td>
<td>5,2%</td>
<td>0,7%</td>
<td>18 500</td>
<td>7,7%</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>7</td>
<td>3%</td>
<td>1,7%</td>
<td>4 350</td>
<td>1,8%</td>
</tr>
<tr>
<td>Convolvulaceae</td>
<td>6</td>
<td>2,6%</td>
<td>3,7%</td>
<td>1 600</td>
<td>0,7%</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>6</td>
<td>2,6%</td>
<td>0,8%</td>
<td>8 100</td>
<td>3,4%</td>
</tr>
<tr>
<td>Malvaceae</td>
<td>6</td>
<td>2,6%</td>
<td>1,3%</td>
<td>4 800</td>
<td>2%</td>
</tr>
<tr>
<td>Urticaceae</td>
<td>6</td>
<td>2,6%</td>
<td>6,5%</td>
<td>1 050</td>
<td>0,4%</td>
</tr>
<tr>
<td>All families</td>
<td>230</td>
<td></td>
<td></td>
<td>240 000</td>
<td></td>
</tr>
</tbody>
</table>
numbers; Cyperaceae are the other only family in excess, with a factor higher than 2. Other families such as Euphorbiaceae, Poaceae, and Rubiaceae are roughly balanced while Asteraceae, Fabaceae or Orchidaceae present the same deficit as on the global level.

*Cirrhopetalum umbellatum* (syn. *Bulbophyllum longiflorum*, Orchidaceae), a small epiphytic native orchid often growing on mossy branches in Tubuai and Rurutu (Photo J.-Y. Meyer).

*Parapteroceras papuanum* (syn. *Tuberolabium papuanum*, *Trachoma societatis*, Orchidaceae), a rare native epiphytic orchid found in Tubuai and Rapa (Photo J.-Y. Meyer).

*Pilea bisepala* (Urticaceae), an erect herb endemic to Raivavae, Rapa and extirpated in Rarotonga (Cook Islands) (Photo J.-Y. Meyer).

*Cladium mariscus* (Cyperaceae), a large erect native sedge commonly found in wetlands of Rimatara, Raivavae and Tubuai (Photo J.-Y. Meyer).
Due to the human presence since the arrival of the Polynesians, around 500 AD and the settlement of Europeans at the end of the 18th century, the indigenous flora had to compete with species introduced accidentally or intentionally with the different waves of human colonization in the Pacific. Species introduced by the Polynesians came mainly from the West while those brought by the Europeans are more cosmopolitan. Table 29 presents the breakdown of secondary flora for each archipelago. The secondarization index IS is computed as follows:

\[ IS = 100 \times \frac{FP}{FS} \]

- \( FP \): primary flora
- \( FS \): secondary flora.

This table highlights some general traits of the secondary flora:

- The Polynesian contribution is always inferior to the European contribution, which is about five-fold. European introductions were constant at first, centralized on the Society Islands and Tahiti, the unavoidable points of passage in the 19th century, then spread to the other archipelagos in the 20th century due to the increase of sea, then air trade. The European introduction ratio, in terms of area, is about 3.5 for the Austral Islands while it is about 2 for Rapa, located further from the air and sea routes and where the penetration of European species is less significant.

- Islands or archipelagos with an IS < 100 harbor more introduced species than native species, in descending order, the Tuamotu, the Gambier, and the Austral Islands. The converse ranking includes the Marquesas, the Society, and Rapa. In the former case, a pool of trivial secondary species rapidly invades the "coastal" islands where floristic diversity is low; conversely, high flora richness counterbalances its importance. Finally, Rapa continues to benefit from its isolation.

### Table 28: Importance of the eight most abundant families in the Rapa group compared to worldwide abundance. The highest surpluses are in bold, the highest deficits are in bold italics.

<table>
<thead>
<tr>
<th>Family</th>
<th>Rapa Group</th>
<th>Surplus/Deficit</th>
<th>Worldwide</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family</td>
<td>Species</td>
<td>% (1)</td>
<td>(1)/(2)</td>
</tr>
<tr>
<td>Asteraceae</td>
<td>9</td>
<td>4.7%</td>
<td>0.5</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>9</td>
<td>4.7%</td>
<td>2.6</td>
</tr>
<tr>
<td>Poaceae</td>
<td>7</td>
<td>3.7%</td>
<td>0.9</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>7</td>
<td>3.7%</td>
<td>0.9</td>
</tr>
<tr>
<td>Urticaceae</td>
<td>7</td>
<td>3.7%</td>
<td>9.2</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>6</td>
<td>3.1%</td>
<td>0.9</td>
</tr>
<tr>
<td>Fabaceae</td>
<td>6</td>
<td>3.1%</td>
<td>0.4</td>
</tr>
<tr>
<td>Orchidaceae</td>
<td>6</td>
<td>3.1%</td>
<td>0.4</td>
</tr>
<tr>
<td>All families</td>
<td>191</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Invasive species on the Austral Islands

Raivavae

The main invasive alien plants on Raivavae include, in order of importance: the thimbleberry Rubus rosifolius (Rosaceae), forming dense thorny scrubs in the understory of remnant altitude rainforests; the shrub Eugenia uniflora (Myrtaceae) forming almost impenetrable dense scrubs in low and medium altitude mesophilous communities; the grass Melinis minutiflora (Poaceae) forming dense mats in open areas following fires and overgrazing; the small tree or shrub Psidium guajava (Myrtaceae) found on dry ridges up to higher elevations; the plant Kalanchoe pinnata (Crassulaceae) forming dense colonies in the understory of low altitude mesophilous and hygrophilous forests; the sub-shrub Ocimum gratissimum (Lamiaceae) and the tall grass Miscanthus floridulus (Poaceae) in dry and open areas; the vine Passiflora maliformis (Passifloraceae) entirely covering some areas of secondary mesophilous vegetation; and the herbaceous plant Commelina diffusa (Commelinaceae) particularly abundant in low to high altitude wetlands, mixed with the small herbaceous vine Pilea microphylla (Urticaceae). Naturalized alien plants that are potentially invasive include Leucaena leucocephala (Fabaceae), Tecoma stans (Bignoniaceae), Hedychium flavescens (Zingiberaceae), still relatively uncommon, but also recently planted trees such as Falcataria moluccana (syn. Parasieranthus falcataria, Fabaceae) and Pinus caribaea (Pinaceae), quickly naturalizing in open areas. The vine Solanum seaforthianum (Solanaceae) observed in low altitude secondary vegetation, and Psidium cattleianum (Myrtaceae) planted in some gardens in Anatou are not yet naturalized. Lantana camara (Verbenaceae) is still absent on Raivavae.

Rapa

The vegetation on Rapa is highly threatened by repeated fires, accidental or voluntary, (for cultivation or to facilitate the hunting of wild pigs), overgrazing by herbivores (feral goats, cows, horses, pigs), and invasive plants (including Psidium cattleianum, Rubus rosifolius, and Hedychium flavescens). There are many potentially invasive species such as Falcataria moluccana or Syzygium cumini, and ornamentals such as Passiflora ligularis, Sambucus sp. that should be carefully monitored or even controlled.

Contrary to what Hallé (1987: 102) wrote following the 1986 mission that the altitude forest was not under the threats of fires, men, or goats, we observed signs and damages by goats up to the summit of Mt Perau at an altitude of about 600 m, and signs of fires on summits higher than 450 m (at Mt Karere). Already in 1934, it was reported that the people of Rapa burnt their lands, that only some areas of undisturbed natural forest remained and "hardly a quarter of the original forest cover now exists" (Zimmerman 1938: 6). Paulay estimated in 1980 that "only one-fifth of Rapa is covered by native forest" (1985: 99). Altitude rainforests remain the most preserved habitat on the island due to their relative remoteness.
Among the first recommendations, the rapid eradication of goats on Karapoo Rahi and the elimination of rats would protect one of the last remnants of semi-dry forests on Rapa and one of the last two populations of the endemic variety of sandalwood (*Santalum insulare* var. *margaretae*). Building fences would also protect some fragments of semi-dry forests of floristic (presence of rare endemic species) and faunal (presence of endemic *Samoana* snails) interest, such as those located above Pariati bay under Mt Erepa and above Anarua bay under Mt Motu. These conservation measures must be combined with a strict ban of fires, a limitation of the wandering of horses and cows, already recommended in 1986 during a public meeting at the village of Haurei and potentially done by building exclosures.

**Rimatara**

Deforestation and clearing of the coastal plains, valleys, hills, and interior plateaus for cultivation and plantation (coconut, pandanus, coffee, banana, citrus, potato, nono, etc.) resulted in the near-extinction of native plant formations, with the exception of limestone plateaus or "mato" that are difficult to reach (due to the sharp edges of "feo" and crevasses) and poorly suited to cultivation, even if dolines are cultivated or serve as pens for pigs or plantations for *Cannabis sativa*. Repeated fires to clear the understory of plantations (including *Pandanus tectorius*, pers. obs. 2004) also contributed to the local loss of native plants, particularly ferns. Construction on beaches (concrete benches and tables) and plantations of strands of "riri" (*Crinum asiaticum*) or "aito" (*Casuarina equisetifolia*) had a significant impact on the native coastal vegetation. Natural vegetation on some islets such as Motu Ura and Motu Rama south of the island (facing the village of Mutuaura) has been almost entirely destroyed by fires and wandering pigs. The impact of free-roaming pigs and feral goats has been observed in the "mato" and swamp areas: grazed native plants, destroyed ferns, churned-up earth, and dissemination of invasive introduced plants.

The construction of 1500 m-long and 150 m-wide airplane runway (started in 2000) on the largest limestone plateau in the north to accommodate ATR 72 planes was done without a proper environmental impacts assessment (Meyer *et al.* 2004) and caused severe damage on the natural forest of this limestone plateau (deforestation, fires, filling of caves with stumps of native trees, weed colonization). The deforested area represents 65 ha (a 2250 m-long strip of 400 m at its widest part) or about 40% of the limestone plateau area of the island.
**Rurutu**

Hallé and lower island compared to Tubuai and where the main crests are more accessible due to their soft terrain, suffered from a strong degradation of its primitive flora (Hallé 1983: 147). The natural forests of Rurutu are now restricted to small fragments of vegetation and their surface gradually decreases due to the impacts of past and current human activities, the growing threats of invasive introduced plants (including Melinis minutiflora, Tecoma stans, Lantana camara) and overgrazing by large herbivores (semi-feral goats and horses). Several endemic plants such as Cyrtandra elizabethae (Gesneriaceae) or Coprosma velutina (Rubiaceae) which are restricted to these forest remnants are now critically endangered (Meyer 2004).

With the presence of herbivores, voluntary or accidental fires constitute one of the main factors of
disturbance and change for the natural vegetation. They contribute to the destruction of the forest cover and the understory (rich in native and endemic ferns), its replacement by heaths dominated by "anu’e" Dicranopteris linearis (Gleicheniaceae) ferns or invasive grasses such as Melinis minutiflora, "ae’o" Miscanthus floridulus, Poaceae) savannas or "miri" Ocimum gratissimum (Lamiaceae) bushes, leading to soil depletion, intensification of erosion on steep slopes, and reduction of water resources for the island and its inhabitants.

**Tubuai**

Natural vegetation is reduced to small fragments of rainforests between 300 and 420 m on the crests and slopes of Mts Taitaa and Panee in the northeast and on the crest between Mts Mareura, Hanareho, Tavaetu, and Tonarotu in the south. The main threats on these vegetation formations include clearing and deforestation for cultivation and plantation, as well as quarries, accidental or voluntary fires, and invasion by the Strawberry guava Psidium cattleianum. According to Hallé (1983), the choice of natural areas to be protected corresponds to the richest areas in orchids. We believe that the loss of native orchids is directly linked to the massive invasion of Strawberry guava, closing completely the canopy and causing the disappearance of terrestrial orchids and support plants for epiphyte orchids. In a letter dated February 3, 1997 (pers. comm.), G. Paulay of Guam University suggested that "an intense manual eradication effort could probably stop this advance and save the numerous endemic species threatened". Given the current extent of the invasion, we believe that a complete eradication of this "plant pest" is impossible in Tubuai. Only a manual control, by uprooting the seedlings and cutting the trees, associated with chemical efforts to treat cut stumps on small areas of floristic interest (fragments of natural forests) seems feasible and would protect the most threatened and legally protected endemic species in French Polynesia such as Acalypha rai-vavensis (Euphorbiaceae), Charpentiera australis (Polygonaceae), Meryta brachypoda (Araliaceae), or Psychotria tubuaiensis (Rubiaceae).

**CONCLUSION**

Despite levels of species diversity and endemism that are lower than on the Society and Marquesas archipelagos, the primary vascular flora on the Austral Islands, and particularly on the remote island of Rapa, represents an exceptional natural heritage in French Polynesia. Given the intensification of anthropogenic threats (overgrazing by herbivore ungulates, accidental or intentional fires, invasive alien plants, construction of airfields), conservation efforts combined with an increased awareness of local authorities and populations constitute a priority.
Haurei village and bay from Mt Perau, Rapa (Photo R. Englund).
Oceanic islands are fragile ecosystems that are easily modified by human disturbance (Carlquist 1965; Kirch & Hunt 1997; Greimler et al. 2002). Islands make up more than one third (36%) of the World’s biological hotspots (Myers et al. 2000) and Polynesia/Micronesia (which also includes Hawaii and the western part of Melanesia) is categorized as one of the 34 world biodiversity hotspots (www.biodiversityhotspots.org). The flora and fauna of each island or archipelago are highly susceptible to degradation and extinction (Sakai et al. 2002); however, by continuing research efforts and examining biological and geological patterns we can perhaps focus conservation efforts. The criteria for determining biodiversity hotspots include the size of the area, degree of isolation, levels of species endemism, habitat loss, future threats to habitat, and number of extinct or threatened species.

Rapa, a small high volcanic island (Fig. 21) fits the hotspot criteria very well. Until recently, little current botanical information was available for the island, other than the specimens and data collected on short exploratory excursions during the Whitney South Seas Expedition in 1921 by E.H. Quayle, the Bayard Dominick Expedition in 1921-1922 by A.M. Stokes, the St. George Expedition by L.A.M. Riley in 1925, the Mangarevan Expedition in 1934 by F.R. Fosberg and H. St. John, and the Flore de la Polynésie Française project in 1983-1984 by J. Florence (IRD) and N. Hallé (Muséum national d’Histoire naturelle, Paris). Vascular plant endemism

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Family</th>
<th>Estimated Population Size (Nb. individuals)</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apostates rapae</td>
<td>Asteraceae</td>
<td>2</td>
<td>endemic genus</td>
</tr>
<tr>
<td>Astelia rapensis</td>
<td>Asteliaceae</td>
<td>5-10</td>
<td>endemic species</td>
</tr>
<tr>
<td>Bidens meyeri</td>
<td>Asteraceae</td>
<td>20</td>
<td>endemic species</td>
</tr>
<tr>
<td>Coprosma cookei</td>
<td>Rubiaceae</td>
<td>10-20</td>
<td>endemic species</td>
</tr>
<tr>
<td>Horologis stokesii</td>
<td>Haloragaceae</td>
<td>5-10</td>
<td>endemic species</td>
</tr>
<tr>
<td>Hernandia ovigera subsp. stokesii</td>
<td>Hernandiaceae</td>
<td>5</td>
<td>endemic subspecies</td>
</tr>
<tr>
<td>Liparis clypeolum</td>
<td>Orchidaceae</td>
<td>9</td>
<td>indigenous species</td>
</tr>
<tr>
<td>Malaxis resupinata</td>
<td>Orchidaceae</td>
<td>20</td>
<td>indigenous species</td>
</tr>
<tr>
<td>Marattia stokesii</td>
<td>Marratiaceae</td>
<td>3-10</td>
<td>endemic species</td>
</tr>
<tr>
<td>Metatrophis margaretae</td>
<td>Urticaceae</td>
<td>1</td>
<td>endemic genus</td>
</tr>
<tr>
<td>Pacifigeron rapensis</td>
<td>Asteraceae</td>
<td>10-20</td>
<td>endemic species</td>
</tr>
<tr>
<td>Pilea bisepala</td>
<td>Urticaceae</td>
<td>10-15</td>
<td>indigenous species</td>
</tr>
<tr>
<td>Pilea occulta</td>
<td>Urticaceae</td>
<td>3</td>
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<tr>
<td>Pisonia coronata</td>
<td>Nyctaginaceae</td>
<td>21</td>
<td>endemic species</td>
</tr>
<tr>
<td>Santalum insulare var. margaretae</td>
<td>Santalaceae</td>
<td>9</td>
<td>endemic variety</td>
</tr>
<tr>
<td>Zanthoxylum nadeaudii</td>
<td>Rutaceae</td>
<td>5</td>
<td>indigenous species</td>
</tr>
</tbody>
</table>

Table 30: The 16 extremely rare vascular plant species occurring on Rapa. Population size estimated in 2002.
is its location at 27°37’S latitude. Due to this southern position, temperatures can reach lows of 8.5°C and many species like coconuts, mangos, and breadfruit which are common on the other tropical islands do not thrive, or are absent (Brousse & Gelugne 1986). Mueller-Dombois & Fosberg (1998) described the vegetation of Rapa as moist to wet, broadleaf, evergreen forest. In the phytogeographic analyses of Rapa based on shared geographic affinities of genera from each Pacific island or continent, Van Balgooy (1971) found Rapa a difficult island to classify. Rapa not only shared affinities with Southeastern Polynesia like the other Austral Islands, but it also had strong affinities with New Zealand, Lord Howe, Norfolk, and Chatham islands in the southern hemisphere and with the Hawaiian islands to the north. Van Balgooy (1971) considered in fact Rapa as difficult to classify as New Caledonia, and in the end he resolved to place it in the Southeastern Polynesian Province, but as an anomalous district.

Humans have most likely inhabited Rapa since the 14th or 15th century. Goats were introduced by Europeans, after the discovery of the island by George Vancouver, captain of the HMS Discovery in 1791. Human impacts on the flora of Rapa were profound, even prior to European contact, and this human modification was only accelerated by the introduction of feral animals such as goats, cats, rats, horses, cattle, and rabbits (Zimmerman 1938), which are still present on Rapa today. Many early accounts of the islands mention the Polynesian-introduced *Aleurites moluccana* (Candlenut tree) as a common component of the lowland forest (Riley 1926; Collenette 1926; Mueller-Dombois & Fosberg 1998). It is no longer such a common tree; we observed only occasional individuals of this species during our surveys. Furthermore, large ferns such as *Marattia* (Mueller-Dombois & Fosberg 1998) are mentioned as being a common native component of the rain forest, but only a single individual was discovered during the recent botanical explorations. The Hawaiian species of *Marattia* are highly susceptible to feral pig disturbance (Palmer 2003) and this may explain its decline in Rapa.

Because the vegetation of Rapa Island is unique, threatened and dynamic, we have strived to document and delineate the present vegetation with an emphasis on the native components. Vegetation mapping, using satellite imaging with GIS technology, has allowed us to get a better estimate of the types and extent of the vegetation of Rapa. The vegetation map is used here to define broad vegetation classes and types, to calculate area and cover values of vegetation categories, to map distribution (GPS localities) and habitats of rare species, as a benchmark to study vegetation change over time, and to aid in making conservation decisions and policies.

on Rapa was estimated to be 59% by F.B.H. Brown (1935), Florence (1987) calculated 37.8% endemism on Rapa and the Marotiri islet, and Motley et al. (2002) estimated between 38-40% endemism for Rapa. These are relatively high levels of endemism for such a small island. The island is also host to three monospecific endemic genera; *Apostates*, *Pacifigeron*, (Asteraceae) and *Metatrophis* (Urticaceae). Each of these endemic genera is threatened. *Apostates rapae* is known from only two individuals, *Metatrophis margaretae* is known from a single individual and *Pacifigeron rapensis* is known from less than 20 individuals in two populations in the cloud forest. Thirteen other taxa of vascular plants on Rapa have been reduced to less than 25 individuals (Table 30).
A vascular plant checklist of Rapa was compiled from existing floras (Riley 1926; Brown 1931, 1935; Brown & Brown 1931; Copeland 1932; Florence 1997, 2004), botanical literature (Florence & Hallé 1986; Hallé & Florence 1986), the field notes of H. St. John and R. Fosberg (deposited at the B. P. Bishop Museum, Botany Department Archives), the B. P. Bishop Museum Herbarium type collection and herbarium specimens (BISH, NY, PAP, UC) and updated. Species were categorized as native or non-native. Native species were divided into indigenous (species naturally occurring on Rapa, but also occurring elsewhere) or endemic (species occurring only on Rapa). The non-native species category was divided into Polynesian introductions (species brought by Polynesians) and modern introductions (species that arrived after European contact).

The island vegetation was divided into three broad classes (Table 31):

- Native;
- Introduced (both modern and Polynesian);
- Mixed.

An area of vegetation was considered native if ≥ 60% of the vegetation cover was composed of native species. An area was placed in the introduced class if ≤ 10% of the vegetation was composed of native species. The mixed class applies to areas where the native component of the vegetation was approximately < 60% and > 10% (in most cases dominated by introduced species with small patches of scattered native species) or if the satellite resolution made the delineation among these categories unclear. Each vegetation class was then subdivided into vegetation types. The types were designated to reflect species composition using indicator species to define boundaries. In addition to species composition, climate, geography, elevation, and human land use were also factored into type classifications.

Field surveys carried out during March 18-May 11, 2002 sampled and vouchered vegetation (NY, P, PTBG, PAP, BISH, US) across 88.2% the island’s surface (leaving 11.8% unexplored). Supplementary field surveys were conducted by the third author in December 2002 (Meyer 2002b). During these surveys detailed notes and records of forest species and composition were recorded along with elevation and GPS coordinates in most situations. The extent and ranges of vegetation types were delineated on a topological map with the aid of an aerial photograph. Subsequent to the field survey a geo-referenced IKONOS natural color Satellite image (0.82 m resolution) was obtained of Rapa. By using the satellite image and ArcView GIS 3.2 software (ESRI, Redlands, CA, USA) we were able to delineate boundaries of vegetation types accurately. Once the vegetation layer was complete the resulting map could be used to visualize the extent of vegetation and calculate land area of different vegetation classes and types. Using GPS co-ordinates, rare species (species with fewer than 20 individuals or known from a single population) were overlaid on the vegetation map to identify locations of conservation interest.

### MATERIALS AND METHODS

### VEGETATION TYPES

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**Introduced vegetation**

**Pine plantation**

Dating from approximately 1980 (J.-F. Butaud, *Service du Développement rural*, pers. comm.), the evergreen coniferous species were planted in rows on the slopes near the villages and above Anatakuri bay. Presently the pine plantations have a closed canopy 10-15 m in height. The dominant planting is *Pinus caribaea* var. *hondurensis* with *P. caribaea* var. *caribaea* (Caribbean pines) and *Agathis lanceolata*. There is little ground cover beneath the canopy, but some native remnants (e.g. *Metrosideros collina*, *Vaccinium rapae*, *Glochidion longfieldiae*, *Boehmeria virgata* and *Dicranopteris linearis*) remain on the plantation periphery and in gulches and gaps at higher elevations. *Pinus caribaea* is becoming naturalized in the *Dicranopteris* heath fernlands of the island.
Active agriculture
This vegetation type refers mainly to the flooded taro (*Colocasia esculenta*) patches. These areas are often surrounded by other cultivated fruits and vegetables like banana, oranges, yams, guava, coffee, or carrots.

Inactive agriculture
This vegetation type consists of inactive taro fields and the surrounding vegetation that often still contains fruit trees and other cultivated species found in the active agricultural sites. Taro cultivation was once quite extensive on the islands with historic human populations estimated at over 2000 individuals (estimate of the Missionary Davies in 1826; Buck 1938) as compared to the 470 residents in 2002 (*Institut de la Statistique de Polynésie française*, www.ispf.pf).

Vancouver noted the extensive taro fields in the lowland areas during his visit to Rapa (Vancouver 1798; Beck 1922), many of which are now abandoned.

Human habitation
All permanent habitation presently exists along the coast of Haurei bay. There are two villages situated across from one another near the mouth of the bay. Area, the smaller of the two villages, is on the north shore and Haurei (Ahurei) village is on the south. There are also a few homes near the back of the bay, which do not appear in this vegetation type; these isolated homesteads are included in the active or inactive agricultural types. Additionally, the 14 archeological sites consisting of terraced fort-like structures (*“pa”*), which are on the summits of fourteen of the high peaks, and may also have been areas of human habitation, are not included in this vegetation type. These sites make up only 0.03 km² of the land area of the island and are included in the introduced grass-shrub vegetation type, which now envelops these abandoned structures.

Alien grass/shrub
This vegetation type is most common in the drier to mesic areas of the island, it is found from just above sea level to nearly 400 m elevation. In most of these savanna-like areas the dominant component is the grass *Miscanthus floridulus* accompanied by secondary grass species, such as *Melinis minutiflora* (Molasses grass), *Paspalum* spp., *Sporobolus* spp. and *Panicum maximum*. *Miscanthus floridulus* can grow up to 3 m in height and forms dense, almost impenetrable stands due to the buildup of plant material from the previous years of growth. When dry, this tangle of old growth makes excellent fodder for natural and anthropogenic fires which maintain this habitat and help it encroach on native vegetation.
Terrestrial Biodiversity of the Austral Islands,
French Polynesia

Burning has been practiced on the island for a long time (Zimmerman 1938), for clearing land and easing human movement, it also encourages new growth of grasses as forage for the feral goat, cattle, and horse populations. In burnt and grazed areas broadleaf herbs such as Emilia fosbergii, E. sonchifolia, Conyza bonariensis, Gnaphalium luteo-album, Pseudelyphantopus spicatus, and Verbena litoralis are common. The shrub component is made up almost entirely of stunted Strawberry guava (Psidium cattleianum). Lantana camara and Leucaena leucocephala, two invasive species in this type of habitat on other Pacific Islands, are not currently a problem on Rapa. Only a single individual of Leucaena leucocephala, which forms pure stands below 200 m in some of the Society Islands (Fosberg 1992) and the Marquesas, was seen next to the road west of Area village, and was destroyed.

Secondary forest
Secondary forest on Rapa is primarily composed of Strawberry guava (Psidium cattleianum) which grows from sea level up to >600 m in elevation. In places this species forms dense monospecific thickets, with stems <40 cm apart, shading out the entire understory. The canopy of these thickets can be as...
low as 1 m or up to 5 m, depending on the topology and habitat. Other invasive myrtaceous trees on Rapa include *Psidium guajava*, *Syzygium cumini* (Java plum), and *S. jambos* (Rose apple). A thicket of *Syzygium jambos* was seen growing near the summit of Mt Perau near 600 m. The other two species (Common guava and Java plum) are presently found only in the lower elevations and valleys near areas of human habitation or cultivation. Other trees making up the secondary forest type include *Citrus aurantium* (orange tree), *Coffea arabica* (coffee), *Melia azedarach*, *Erythrina variegata*, *Ficus tinto*ria, *Aleurites moluccana* (Candlenut), and *Casuarina equisetifolia*. In forest gaps and gulches the vine and shrub species *Ipomoea* spp., *Ricinus communis*, *Triumfetta rhomboidea*, *Musa* spp. (banana trees), *Rubus rosifolius*, *Hedychium flavescens*, and *Zingiber zerumbet* commonly occur.

### Native vegetation

**Cloud forest**

Cloud forest vegetation is found at elevations of 590-650 m, the summit regions of Mt Perau. As its name implies, this region is draped in clouds on most days. Mt Pukumaru (605 m), and the summits behind Haurei village are also often under cloud cover, but this region was not designated cloud forest because of the absence of some characteristic species. Indicator species for this vegetation type include *Carex stokesii*, *Geniostoma rapense*, *Pilea occulta*, *Pacificogon rapensis*, *Plantago rupicola*, *Elaphoglossum rapense*, and *Blechnum venosum*. Cloud forest vegetation consists of stunted *Metrosideros collina*, *Corokia collenettei*, *Oparanthus coriaceus*, *O. rapensis*, *Eurya japonica* and *Weinmannia rapensis* trees (2-3 m in height), and thick tangles of *Freyquinetia rapensis*. The trees and ground are covered with a heavy growth of bryophytes, small epiphytic filmy ferns, and large foliose lichens. Understory and/or epiphytic species which are only found here or in higher elevation rain forest vegetation include *Haroldiella rapensis*, *Marattia stokesii*, *Astelia rapensis*, and *Liparis clypeolum*.

**Rain forest**

This vegetation type is restricted to higher elevations on Rapa, found in hanging valleys, on steep slopes and ridges. There are remnant patches of this vegetation type in lower elevation areas, suggesting that this vegetation type may once have extended from near sea level up to around 600 m elevation. On the lower slopes and in valleys and
gulches between 150-400 m the dominant forest species is Metrosideros collina. Other canopy species are Corokia collenettei and Weinmannia rapensis. Secondary canopy species include Eurya japonica, Meryta brachypoda, Fitchia rapensis, Celtis pacifica, Oparanthus rapensis, Homalanthus stokesii, Sophora rapaensis, Fagraea berteroana, Melicope margaretae, the large ferns Angiopteris rapensis and several tree fern species (Sphaeropteris (Cyathea) tahitensis, Cyathea medullaris, and C. stokesii). Common understory species include Freycinetia rapensis, Streblus anthropophagorum, Apetahia margaretae, Acalypha polynesiaca, Claoxylon collenettei and Macropiper puberulum. Metrosideros, Fitchia, Boehmeria virgata and the tree ferns are the common component in the hanging valleys. On the drier, exposed ridge tops, dense tangles of Freycinetia give way to Dicranopteris, and other fern species such as Dodonaea viscosa, Vaccinium rapae, Glochidion spp., Myrsine rapensis, Styphelia rapae, Alyxia stellata, Dianella intermedia, Coprosma rapensis, Hedyotis rapensis, and Pipturus australium. On the higher, wetter slopes from 400-600 m, the pteridophyte flora becomes richer, as does the epiphyte cover on the branches of the canopy trees. Metrosideros is still the dominant tree species in the high elevation rain forest and Freycinetia forms thick stands between the trees. Other species restricted to or more common in this high moist rainforest include Geniostoma rapense, Meryta chlorisantha, Coriaria ruscifolia, Haloragis stokesii, Astelia rapensis, Plantago rapensis, Peperomia spp., Coprosma cookei, Psychotria rapensis, Hebe rapensis, Haroldiella rapensis, Pittosporum rapense, Hedyotis rapensis var. taverana and several fern species in the genera Blechnum, Elaphoglossum, Asplenium, Davallia and Trichomanes. Hebe and Hedyotis are usually on the windswept cliffs. Much of the native rainforest remains here only because it is on inaccessible, almost vertical slopes and because Freycinetia forms dense thickets, which act as a barrier to feral ungulates.

Dry-Mesic forest
Dry-mesic forest is becoming rare due to the heavy impact of fires and invasive animals (cattle, goats). Remnants of this forest type occur from 40-400 m. The forest canopy can reach heights of 7-8 m, with a semi-open canopy. One remaining remnant of this forest type occurs on Karapoo Rahi islet and is the location of species uncommon on the main island. Endemic indicator species include: Santalum insulare var. margaretae, Pisonia coronata, Nesoluma polynesiicum, Hernandia ovigera, and Zanthoxylum tahitense. Dominant trees include Metrosideros collina, Corokia collenettei, associated with Allophyllus rapensis, Celtis pacifica, Maytenus pertinax, Pittosporum rapense, Psydrax odorata, Melicope margaretae, Sophora rapaensis, and Streblus pendulinus (on boulders). The understory
Vegetation Types and Map of Rapa

consists of *Dicranopteris* fern heath with scattered shrub species *Glochidion longfieldiae*, *G. rapaense*, *Dodonaea viscosa*, and *Coprosma rapensis* and *Macropiper puberulum*. A remnant of native shrub land, untouched by grazing mammals, was found on the summit of Mt Tepiahu, with a dense cover of *Metrosideros collina*, *Hedyotis rapensis*, and the native vines *Cocculus orbiculatus* and *Morinda myrtifolia* (Meyer 2002b).

Coastal forest

Coastal forest is principally composed of *Pandanus tectorius* with *Myoporum rapense* and *Tournefortia argentea* and occurs on rocky beaches and coastal shelves. In the swampy interior coast of Haurei bay are areas of *Hibiscus tiliaceus* forest. These forest types exist from sea level to 20 m in elevation and have canopies 4-6 m in height. The understory is composed of salt-tolerant grasses, sedges, and a few herbs and vines. Species of special interest in these areas include the rare species *Hibiscus australensis*, which is found in wet seeps and ditches and is also known from Raivavae, Rurutu, Tubuai (Meyer 2002a,b), the Cook Islands (http://cookislands.bishopmuseum.org/species.asp?id=6228) and Pitcairn Island (Waldren et al. 1998), as well as the recently discovered (Florence & Hallé 1986), though widely distributed species, *Triglochin striatum*, a tiny herb (3 cm) that grows in seeps where fresh water meets the sea.

Strand vegetation

On Rapa this low vegetation type occurs on rocky shores, or more rarely on sandy shores along the coast and in bays, with *Pandanus tectorius*, *Myoporum rapense* and rare *Heliotropium foertherianum*.
Terrestrial Biodiversity of the Austral Islands, French Polynesia

Vegetation analysis and percent cover

Vegetation classes
Analysis of the vegetation classes (Fig. 22, Table 31) revealed that only 13% of intact native vegetation remains on Rapa. Most of these areas are steep cliffs or ridges, over one-third of the remaining native vegetation is in the form of coastal strand that clings to vertical sea-cliffs. Introduced vegetation makes up 64% of the island vegetation. This figure is likely an under-estimate as the remaining 23% of the vegetation is classified as either "mixed" or "unexplored". As noted above, the mixed forest and mixed grass/shrub vegetation are

Mixed vegetation

Introduced and native grass-shrub
This vegetation type is principally made up of the alien grass/shrub vegetation, but contains small patches of native vegetation. The resolution of the satellite image was not high enough to separate the small areas of native vegetation from the introduced vegetation in some areas. The native patches consist of *Dicranopteris* fern heath with scattered *Lycopodiella cernua* and the shrub species *Dodonaea viscosa*, *Vaccinium rapae* and *Glochidion longfieldiae*. More than 80% of the area designated with this vegetation type is introduced alien species. Continued burning of the grasslands favors the introduced vegetation occurring in these areas.

Introduced and native forest
Ninety-five percent of this vegetation type is composed of *Psidium cattleianum*. The 5% made up of native rain forest occurs in transition zones between delineations of native rain forest and introduced forest regions and in gulches or on steep cliffs and in valleys where our notes were not detailed enough and the satellite resolution was too low to distinguish the myrtaceous forests of the native *Metrosideros* patches from the *P. cattleianum* dominated introduced vegetation.

Syn. *Tournefortia argentea*, and most often on cliff faces. It can occur from sea level to up to 200 m elevation. It is a mixed community of species consisting of *Lycium sandwicense*, *Sesuvium portulacastum*, *Plantago rapensis*, *Portulaca lutea*, *Melanthera* (*Wollastonia*) *biflora*, *Apium prostratum*, *Peperomia* spp., and *Ischaemum byrone*. Other less common species associated with this vegetation type include on sea-cliffs *Capparis cordifolia*, *Chamaesyce sparrmanni*, *Lobelia anceps*, *Eugenia reinwardtiana*, *Hedyotis rapensis*, and *Tetragonia tetragonioides*.

Vegetation of the Austral Islands, French Polynesia...
Vegetation Types and Map of Rapa

predominantly composed of introduced vegetation. In no area that was surveyed in 2002 did we see any evidence that native vegetation was encroaching on introduced vegetation. Indeed, it was quite the opposite. *Freycinetia* thickets seem to be some deterrent to feral unugulates, acting as a protective barrier for the rainforest vegetation; however, there are areas where the goat populations are even consuming the tough *Freycinetia* thickets.

**Native vegetation**
The native vegetation was divided into five types (Fig. 23, Table 32). Rain forest accounts for just over half of the native vegetation. The coastal strand, which occurs primarily on the sea cliffs, comprises 35% of the native vegetation. The other three vegetation types (cloud, dry-mesic and coastal forests) make up less than 2% of the total island cover. The coastal forest still exists in bays along the periphery of the island. It was likely more extensive in these areas and also present in Haurei bay, where it no longer exists. This vegetation type is composed mostly of common widespread Pacific Island species, with the exception of the endemic species *Myoporum rapense*. On the other hand, the cloud and the dry-mesic forests contain much higher levels of endemism. Based on
the 1934 notes of St. John and Forsberg, it is likely that the dry-mesic forest was much more extensive in the recent past. Dry-mesic forest is heavily impacted by anthropogenic burning and grazing by feral ungulates. The cloud forest region may always have been restricted to the highest peaks of Mt Perau, although some peaks such as Mt Pukumaru may have in the past been high enough to support cloud forest habitat.

**Introduced vegetation**

The introduced vegetation was divided into six types (Fig. 24, Table 33). Grass/shrub vegetation makes up 75% of the introduced vegetation and covers nearly half of the entire island. This vegetation type is very susceptible to erosion. During the heavy rains which are common on Rapa the soil runoff containing the iron-rich volcanic soil is very apparent in the ocean and bays. Nine percent of the

<table>
<thead>
<tr>
<th>Type</th>
<th>Area (km²)</th>
<th>Percent of vegetation class (%)</th>
<th>Percent cover of island (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cloud forest</td>
<td>0.06</td>
<td>1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Rain forest</td>
<td>2.68</td>
<td>54</td>
<td>7</td>
</tr>
<tr>
<td>Dry-Mesic forest</td>
<td>0.37</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Coastal forest</td>
<td>0.16</td>
<td>3</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Coastal strand</td>
<td>1.73</td>
<td>35</td>
<td>5.0</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>5.00</strong></td>
<td><strong>100</strong></td>
<td><strong>13</strong></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Type</th>
<th>Area (km²)</th>
<th>Percent of vegetation class (%)</th>
<th>Percent cover of island (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>3.4</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>Grass-Shrub</td>
<td>18.4</td>
<td>75</td>
<td>48</td>
</tr>
<tr>
<td>Pine plantation</td>
<td>0.8</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Active agriculture</td>
<td>0.3</td>
<td>1</td>
<td>&lt;0.5</td>
</tr>
<tr>
<td>Inactive agriculture</td>
<td>0.6</td>
<td>3</td>
<td>1.5</td>
</tr>
<tr>
<td>Human habitation</td>
<td>1.0</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>24.5</strong></td>
<td><strong>100</strong></td>
<td><strong>64</strong></td>
</tr>
</tbody>
</table>
island is comprised of introduced forest and 2% is planted in pines. The remaining 5% of the island is used for human habitation and agriculture (either active or inactive taro fields).

### Table 34: Types of mixed vegetation.

<table>
<thead>
<tr>
<th>Type</th>
<th>Area (km²)</th>
<th>Percent of vegetation class (%)</th>
<th>Percent cover of island (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>2.4</td>
<td>60</td>
<td>6.5</td>
</tr>
<tr>
<td>Grass-Shrub</td>
<td>1.6</td>
<td>40</td>
<td>4.5</td>
</tr>
<tr>
<td>TOTAL</td>
<td>4.00</td>
<td>100</td>
<td>11</td>
</tr>
</tbody>
</table>

### Mixed and unexplored vegetation

The mixed vegetation is divided into two types (Table 34). This vegetation is a 60-40% split of forest and grass/shrub habitat, respectively. The unexplored vegetation (Table 35), which covers 12% of the island, is 80% forest and 20% grass/shrub vegetation.

<table>
<thead>
<tr>
<th>Type</th>
<th>Area (km²)</th>
<th>Percent of vegetation class (%)</th>
<th>Percent cover of island (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>3.7</td>
<td>80</td>
<td>10</td>
</tr>
<tr>
<td>Grass-Shrub</td>
<td>0.9</td>
<td>20</td>
<td>2.0</td>
</tr>
<tr>
<td>TOTAL</td>
<td>4.6</td>
<td>100</td>
<td>12</td>
</tr>
</tbody>
</table>

### CONSERVATION

Insular populations and fragmented ecosystems make the unique species on islands vulnerable to extinction (Paulay 1994; Laurance & Bierregaard 1997). Rapa, with only 13% of its intact native vegetation remaining, has many endemic species and habitats that need protection.

The cloud forest and dry-mesic forest types are obvious candidates for conservation, based on the small proportion of the island they now occupy (<2%) and the high number of endemics they harbor, however, their transitions to threatened habitats have taken very different pathways. Cloud forest (<1% of...
Terrestrial Biodiversity of the Austral Islands, French Polynesia

...this volume) were able to locate Rapan sandalwood (*Santalum insulare* var. *marginatae*) in only two of the remaining dry forest regions. Based on reports from local residents, sandalwood was once more widespread, occurring in additional populations. Therefore, choosing the appropriate regions for conservation are most critical for the dry-mesic forest, than for the intact cloud forest example.

One approach for selecting habitats and areas to preserve is to use the vegetation map with GPS coordinates of the rare and endemic species of a vegetation type to focus conservation efforts and select sites (Fig. 25). Using the vegetation map and satellite image it is also possible to monitor changes in the extent of native vegetation over time, using the present map as a benchmark. This approach has been used in the past in other islands using historical aerial photos and satellite images (e.g. Hawaiian Islands: University of Hawaii Department of Geography 1983).
Vegetation Types and Map of Rapa

The vegetation map of Rapa was created as a best estimate of the native and introduced vegetation present on the island in 2002. Creating an interactive vegetation map was not the primary goal of our field surveys so the delineations and descriptions of the vegetation types were done based on field observations and in conjunction with close examination of satellite imagery. The map is subjective because no plots were sampled or relevés made, and therefore no statistical calculations of coverage and abundance are available. In spite of these limitations, this is the best data that exists regarding the current vegetation of Rapa, and it can be improved upon in later studies by vegetation ecologists using more statistically rigorous methods. Because the map was made using GIS technology and overlaying the satellite image with data layers, we were able to make more precise calculations of the existing vegetation types. The remaining 13% intact native vegetation calculated here is less than the estimates (15-20%) made by the botanist visiting the island in 2002, and also those of previous scientists (20%: Paulay 1985). This map was made to produce a better understanding of the vegetation of Rapa and the remaining native plant component, to locate regions where rare and vulnerable forest remnants and species exist, to better direct and focus future biological surveys on Rapa, and to provide information for future conservation efforts by the French Polynesian Government.

We have established that Rapa fits all the criteria for a biological hotspot and contains one of the most unusual floras in the islands of Southeastern Polynesia, sharing affinities with other regions of the southern hemisphere (New Zealand, Pitcairn Islands and Juan Fernandez Islands) and with the Hawaiian Islands to the north (perhaps due to their shared subtropical climates). Phylogenetic studies are now being conducted on several plant lineages that confirm Rapa as a unique flora, important for understanding Pacific biogeography (Hoggard et al. 2003; Dempewolf et al. 2005; Motley 2005a,b; Rouhan et al. 2005; Tronchet et al. 2005). In our discussions of conservation we focused on the two rarest native vegetation types; however, this does not diminish the value of more intact areas like the native rain forest. Rain forest is an important component of the watershed of any island group (Wood 1982), it can also help reduce erosion, particularly since the loss of dry-mesic forest at low elevations. Presently, after heavy rains the iron-rich volcanic soil turns the ocean and Haurei bay red. This is detrimental...
to the coral growth and to fishing in the region, which is the protein staple for the human population of Rapa. It is our hope that conservation of the native vegetation will be a consideration in future construction and developments on Rapa (e.g. airports and roads), with a focus on preventing further fragmentation of the forests and protecting the unique species and ecosystem of Rapa.
Haurei village and bay from Mt Perau, Rapa (Photo R. Englund).
Record of Rapa: Indications for the Phytogeography
Matthew Prebble

The most enduring subject of interest in the phytogeography of the Pacific region is the process of speciation, specifically the timing of island radiations and the ecological controls on speciation (e.g. Carlquist 1974). The pattern of floral diversity on islands is thought to be determined by the timing of island orogeny, the vagility (dispersal ability) of species and the propensity for increased genetic isolation and/or divergence from parent populations after establishment on an island (Carlquist 1974, 1996; Grant 1981). Along geological timescales (over millions of years), it is thought that centres of geological diversity and tectonic activity may provide a good indication of floral diversity and rates of endemism. Balgooy et al. (1996) examined a limited phytogeographical dataset of the Malesian flora (a continental island), comparing the distribution of endemic plants with regional geological variation, and found that a correlation exists between areas of Miocene plate tectonic activity and the proportion of endemic taxa in that area. They suggest that the collision of more than thirty tectonic plates in northern New Guinea probably initiated intensive speciation. The geologically diverse islands of New Caledonia, as another example, have the most (~100) endemic genera and the highest rate of endemcity anywhere in the Pacific (Jaffré 1993; Morat 1993). By comparison, the relatively uniform geology of the neighbouring Vanuatu and the Santa Cruz Islands (Solomon Islands) is represented by only one endemic genus (Balgooy et al. 1996).

Current explanations for the endemic character of island floras that have developed since the Miocene are often based on the assumption of a stable geological, biological and climatic environment (Hope 1996). On the contrary, palaeoenvironmental data for the Pleistocene and Holocene suggest disturbance processes prior to human arrival were more pronounced on oceanic Pacific islands, than on the adjacent continents (Enright & Gosden 1992). Exposure to tectonic activity, fluctuating sea levels, tsunamis, cyclones and volcanic ash fallout have produced an uneven array of geomorphic signatures across many islands, some indicating entire removal of habitats suitable for particular vegetation types. The relationship between disturbance processes and endemism, however, remains uncertain.

Within geological timescales, one of the most critical forms of evidence that attest to the endemic character of island floras is the fossil record. MacPhail (1997) has outlined some compelling cases as to why endemism in island floras at the generic or family level is not necessarily evidence for long-term isolation or local speciation. Lactoris fernandeziana is the sole representative of the Lactoridaceae and is a shrub confined to cloud forest above 500 m on Masatierra island (33°50'S-80°00'E) in the Juan Fernandez archipelago of Chile (Sampson 1995). The location of fossil pollen of Lactoridaceae (Lactoripollenites) in Cretaceous deposits of Southern Africa (Zevada & Benson 1987), India, Australia and Antarctica (M.K. Macphail pers. comm.) suggests that this family may have been a common element in the Cretaceous Gondwana flora. Only L. fernandeziana has survived, as one of many highly restricted endemics on this volcanic oceanic island formed ~4 Ma (Stuessy et al. 1984). Other cases include the Norfolk Island (28°58'S-168°03'E) endemic and monospecific tree genus Ungenia floribunda (Malvaceae) in the Sterculiaceae. This species is partially synonymous with the extant Asian genus Reevesia (Malvaceae) known from Cretaceous deposits from Australia and New Zealand as the fossil pollen type Reevesiapollis reticulatus (Couper) Krutzsch. Norfolk Island formed between 3 and 2.3 Ma (Jones & McDougall 1973) pinpointing the maximum time at which the genus became extinct in Australia and New Zealand.

What can be gathered from first-time appearances in Cretaceous fossil pollen records, as Pole (1994, after Martin (1982) and MacPhail (1997) have suggested for the flora of New Zealand, is that the endemic character of Pacific Island floras probably owes much to selective extinctions of formerly more widespread lineages, but little to physical barriers to dispersal, as proposed by Carlquist (1996). MacPhail (1997) suggests that the New Zealand flora, as is the case for the oceanic islands of the Pacific, is entirely derived from long distance dispersal and the key to understanding the importance of endemic taxa is identifying the timing of extinction of parent populations.
Another key interest for phytogeography of the Pacific has been the extent of environmental change following human arrival on islands during the Holocene. Colonisation of the Austral Islands formed part of a wider oceanic movement of Austronesian speaking people that came out of the Western Pacific around 3 500 cal. yr B.P. culminating in the settlement of Easter Island (e.g. Hunt & Lipo 2006) and New Zealand (Anderson 2003; Wilmshurst et al. 2008) by 850 cal. yr B.P. Relevant to this paper are radiocarbon ages from archaeological sites on Rurutu (Vérin 1969; Bollt 2005; Weisler et al. 2006) and Tubuai (R. Bollt unpublished data) indicating that the Austral Islands was first colonised within this same period. Based on the largest, best-preserved and earliest archaeological sequence located on Rapa, colonisation of the Austral Islands was probably complete by around cal. yr B.P. (Kennett et al. 2006). Palaeoecological records from lowland swamp deposits from Rimatara (Prebble & Wilmshurst 2009), Tubuai and Raivavae (M. Prebble & Porch unpublished data) reveal that ecological impacts were initiated synchronously with human colonisation.

Late Holocene palaeobotanical records from many Pacific Islands indicate that vegetation change has primarily been a consequence of human activity. Indications of extensive ecological impacts come from evidence of human-induced terrestrial avifauna and snail extinctions from the fossil record (e.g. Solem 1991; Steadman 1995; Tennyson & Anderson 2012; see chapter by Gargominy & Fontaine, this volume). Abrupt changes in vegetation during the Pleistocene and Holocene have been defined from palaeoenvironmental research undertaken on several Pacific islands (e.g. Flenley et al. 1991; Athens & Ward 1995, 2001; Stevenson et al. 2001; Haberle 2003; Fall 2005; Prebble & Dowe 2008). For many of these islands, human impact has been inferred from palynological signatures, but the timing and processes of the respective changes have been contested given the uncertainties involved with absolute chronometric controls on dated archaeological material (e.g. Spriggs & Anderson 1993; Kirch & Ellison 1994; Anderson 1995), or with the influence of climate and sea-level change (e.g. Flenley et al. 1991; Hunter-Anderson 1993; Nunn 1997; Dickinson 2001).

In this paper, palaeobotanical records from Rapa are examined in the context of the modern flora of Rapa and phytogeography of the Austral Islands. An overview is provided of the phytogeography of the late Miocene-Pliocene (12-1.8 Ma) and Pleistocene (between 1.8 Ma and 10 000 years), examining the different plant lineages that migrated into Oceania following extensive island formation. The maximum first-time appearance of fossil pollen on Rapa is delimited by the island’s Pliocene orogeny (< 4.8 Ma). The Pleistocene is examined in the context of the available palaeobotanical records and environmental proxies for processes (e.g. glaciation and sea level fluctuation) that may influence vegetation change and plant migration to the islands and the propensity for speciation. I also examine the phylogeographic (the study of the distribution of genetic diversity) evidence for the derivation of oceanic floras based on the recent research on taxa represented in the Austral Islands flora.

Secondly, I present a summary of Holocene-aged (< 10 000 cal. yr B.P.) palaeobotanical records from the coastal lowlands of Rapa, providing an outline of vegetation change and differing floral representation of indigenous taxa during the three major regional environmental transitions: the post-glacial marine transgression, the mid-Holocene sea-level highstand and the late Holocene human impact period.

**PHYTOGEOGRAPHIC IMPLICATIONS OF THE PALAEOBOTANICAL RECORD**

**Late Miocene and Pliocene (~12-1.8 Ma) phytogeography of the Pacific**

For a prolonged period during the Miocene, the largest southern Pacific-rim continents (South America, Australia and New Zealand) moved northwards. New Zealand entered the warm-temperate zone shifting over 20° C northwards while Australia had moved into the warm-temperate and tropical climatic zones by the mid-Miocene (Markgraf et al. 1995). This northward drift allowed for the expansion of warm-temperate and tropical floras from the north. Fossil evidence for Australian genera such as *Eucalyptus* in New Zealand during early to mid-Miocene attests to this warm-temperate expansion (Pole 1993). The northward drift also provided a greater floral source area of potential colonists for the mid-Miocene-aged or older Pacific Islands (e.g. Fijian archipelago).
The climate of the late Miocene (~12-5.3 Ma) was characteristically cooler and more variable than the early-middle Miocene as a function of the increasing periodicity of sea level fluctuations driven by an intensified succession of glacial periods extending the polar ice shelves. These fluctuations are thought to have altered species distributions by hindering or enhancing speciation or ultimately causing extinction (Macphail et al. 1993). Winkworth et al. (2002) suggest that this environmental instability led to the development of more open habitats that allowed more opportunities for the establishment of a number of Pacific plant lineages. Unlike in New Zealand, where debate over the origin of the flora has involved long-distance dispersal mechanisms (Pole 1994) and the widely discredited panbiogeography theory (McGlone et al. 2001), the indigenous floras of the Austral Islands had to arrive across the Pacific Ocean by long-distance dispersal (Carlquist 1974, 1996). The 40K/40Ar chronologies for island orogeny reviewed by Maury et al. (see chapter by Maury et al., this volume) support the hypothesis that the original floral colonists probably migrated from adjacent, older seamount islands “downstream”. Given that all islands in the Austral Islands are of late Miocene to Pliocene age but derived from two different hotspots, the direction of plant dispersal is unclear but can generally be assumed to follow a northwest (Rimatara and Rurutu are the oldest islands) to southeast direction (Rapa and Marotiri are the youngest islands). If this interpretation holds, island orogeny and age may only have minor consequences for phyogeography, except that these islands have had, at a minimum, only 3.8 Ma (based on the 40K/40Ar ages of Marotiri) of above sea-level terrestrial exposure to accumulate and evolve endemic floras. The question remains whether the Austral Islands flora, including endemic species, arose during the late Miocene or later epochs.

**Palaeobotanical evidence and late Miocene-Pliocene phytoogeography**

Fossil data that provide an unambiguous signal of marine transgressions and regressions are difficult to obtain given the paucity of coastal or marine fossil records from the late Miocene-Pliocene (Jablonski 1980), especially in the Pacific region. The only probable Pliocene (<4.8 Ma) deposit of value for a palaeobotanical interpretation on the Austral Islands is a shallow (<2 m thick) lignite seam located at Arahu at the northeast head of Haurei harbour on Rapa at around 180 m in elevation (Fig. 29). As Maury et al. (see chapter by Maury et al., this volume) have discussed, the presence of palagonite suggests the lignite was deposited into a small lake or swamp, possibly within a previous lava lake (Brousse & Gelugne 1986). This lignite represents one of only two deposits in the remote island Pacific, the other located at Babeldaoib in Palau (Federated States of Micronesia). The Arahu deposit formed prior to the erosional dissection of a former lake caldera that now forms the harbour on the southeast side of the island.

### Table 36: List of taxa identified from the Arahu lignite deposit, Rapa, French Polynesia.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Biogeographic affinity</th>
<th>Palynologist</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arecales/Liliaceae</td>
<td>unknown</td>
<td>Wind dispersed exotic from the Western Pacific</td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Cupressaceae</td>
<td>Dacrydium sp.</td>
<td></td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Cyatheaceae</td>
<td>Cyathea spp.</td>
<td>Pacific</td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Cyperaceae</td>
<td>unknown</td>
<td>Cosmopolitan</td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Piperaceae</td>
<td>unknown</td>
<td>Pacific</td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Myrtaceae</td>
<td>unknown</td>
<td></td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>cf. Coprosma rapensis</td>
<td>New Zealand/Pacific</td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Sapindaceae</td>
<td>cf. Dodonea viscosa</td>
<td>Pacific</td>
<td>M. Prebble</td>
</tr>
<tr>
<td>Taccaceae</td>
<td>unknown</td>
<td></td>
<td>L. Cranwell</td>
</tr>
<tr>
<td>Zingiberaceae</td>
<td>unknown</td>
<td></td>
<td>L. Cranwell</td>
</tr>
</tbody>
</table>

1 - The earliest description of this deposit dates to 1865 when John Vine Hall on the S.S. Ruahine travelling from New Zealand to Panama stopped on the island in light of it being a suitable prospect for a steam ship depot. Hall (1869: 132-133) noted that “Coal of a very inferior quality, has been found in the interior, the natives use it occasionally for cooking etc., but it is useless for steam [ship] purposes”.

![Dodonea viscosa (Sapindaceae) (Photo J.-Y. Meyer).](image)
Chubb (1927) collected some material whilst on the St. George Pacific Expedition of 1924-25 and submitted some samples to the Natural History Museum (London). He described the deposit as lignite, ‘intercalated between lava flows’ and at points a few metres thick. He found an outcrop immediately below Mt Taga overlying parent rock consisting of clays interbedded with fine laminae of lignite. In 1939, Cranwell (1964) examined some Arahu lignite collected by Raymond Fosberg in 1934 as part of the Bernice P. Bishop Museum Mangareva Expedition. She suggests from J.F.G. Stokes earlier description of the lignite outcrop that ‘it can be inferred that the deposit lay partly in a calderon which was emptied when later breached by the sea’ (Cranwell 1964: 45-46).

A list of pollen and spore types identified from the Arahu deposit is presented in Table 36. Cranwell located Cyathea tree fern type and other ferns spores, algal (e.g. Phycopeltis) and fungal (Microthryriaceae) fruiting bodies and a range of pollen types. Characteristic of the pollen assemblages examined are high proportions of sedges (Cyperaceae) indicative of “nutrient-rich waters”. Other Monocotyledon taxa include: Zingiberaceae, Taccaceae and some "palmoid" grains (probably of Arecaceae or Liliaceae type). Of the Dicotyledon taxa identified, the following are represented: Myrtaceae, Piperaceae, Sapindaceae, and Rubiaceae of a type comparable to the endemic species Coprosma rapensis. Cranwell also identified a few grains of the Gymnosperm genus Dacrydium, distinct from the New Zealand species D. cupressinum initially considered to be a contaminant. This could also have been derived from a wind blown dispersal during the late Miocene following the pacific expansion of Dacrydium into areas such as New Zealand (Pole 2001) and potentially the Fijian archipelago or islands further west (M.K. Macphail pers. comm.).

The presence of a Coprosma type pollen grain within the pollen sample examined by Cranwell (1964) suggests that the floral affinity of Rapa with New Zealand ascribed for the modern flora of the island may have a late Miocene/Pliocene origin. Coprosma is regarded as one of a number of New Zealand genera that make up the flora of Rapa including Veronica (Scrophulariaceae), Olea (Asteraceae) and Corokia (Corokiaeae), not found on any of the other islands in the Austral Islands or in the tropical Pacific.

In August of 2002, the author collected some material from the Arahu lignite deposit with the intention of processing some material for pollen analysis. The site is heavily eroded across the whole outcrop and is only exposed in a few places below the Taga ridgeline. In a number of places the lignite is overlain by recently eroded clay. The banded clay that Chubb described was not located. Some lignite was processed at the Australian National University for palynomorphs with a similar, but less diverse assemblage consisting of Cyperaceae, Poaceae, Cyathea tree fern type and monolete fern spores, Dodonaea (Sapindaceae) and Rubiaceae type grains (see Table 36 for list). Like Cranwell, Macphail (pers. comm.) and the author did not identify any pre-Pleistocene fossil taxa, that may specify further the likely age of the deposit, although the 40K/40Ar ages provided in Maury et al. (see chapter by Maury et al., this volume) confine the age of this deposit to < 4.8 Ma or younger.

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**Phylogeographic evidence and late Miocene-Pliocene phytogeography**

Fossil data only provide a partial representation of the palaeoflora and thus do not always allow for a precise or complete interpretation of phyto-geographical patterns. The preserved pollen and fern spore assemblages of the Arahu lignite deposit, from Rapa, tend to be biased towards wind pollinated and swamp species. Previously, the absence of late Miocene-Pliocene sub-fossil deposits from Oceania has limited phyto-geographical interpretation to molecular evidence. The recent application of phylogenetic and phylogeographic methods allows the inference of the timing of genetic differentiation. These inferences are established on the basis that the geological age of island orogeny provides the upper boundary on the time available for a newly established population to become genetically isolated from their parent populations (Avise 2000). For many Pacific plant lineages, phylogenetic studies have confirmed the importance of an eastward dispersal route in which western Pacific species are basal to eastern species.
The timing of dispersal events can also be inferred from phylogenetic data using the first fossil appearance of a taxon as an upper boundary. There are, however, a number of problems that may arise in interpreting molecular evidence, including the genetic influence of multiple colonisation events, hybridisation and polyphyly. Despite these pitfalls, molecular data from many Austral Islands floral lineages suggests that most dispersal events took place during the late Miocene-Pliocene with extant island taxa derived from this diversification. Most taxa are derived from the tropical west-east dispersal routes (see examples below) with some taxa following a southerly route from New Zealand (e.g. *Sophora tomentosa* and *Veronica rapensis*) and American lineages (e.g. two *Plantago* species (Plantaginaceae) from Rapa after Hoggard et al. 2003 and T. Motley (unpublished data). Tronchet et al. (2005; T. Motley unpublished data) used two nuclear-encoder spacer regions from ribosomal RNA sequences to resolve the genetic relationships between the Pacific populations of the Araliaceae genus *Meryta*, of which two extant species (*M. chloristantha* and *M. brachypoda*) are found in the Austral Islands. The spacer region data showed that the Austral Islands populations are derived from the diverse New Caledonian lineages. The ancestral New Caledonian species may be derived from populations from either Fiji (*M. tenuifolia*) or New Zealand (*M. sinclairii*), although this relationship remains unclear. Tronchet et al. (2005) suggest that the east Pacific populations, including those from the Austral Islands would have arisen after the late Miocene-Pliocene island orogeny, from long-distance dispersal events. The phylogenetic relationship of some Austral Islands taxa to late Miocene-Pliocene dispersals from New Zealand has received more attention. Using sequences from an intergene region (atpB-rbcL) of chloroplast DNA, Hurr et al. (1999) found that the *Edwardsia* section of the genus *Sophora*, found across the southern Pacific from New Zealand to Chile, is monophyletic but from a distant non-*Edwardsia* lineage from the northwest Pacific. These data suggest that this section of *Sophora* initially dispersed to New Zealand from the northwest Pacific along an Antarctic route by the late Miocene, then dispersed across the South Pacific and to the Austral Islands. Based on molecular clock estimates and fossil pollen dates from ancestral New Zealand species, the derived *S. tomentosa*, represented on all islands in the Austral Islands (J.-Y. Meyer unpublished data) and *S. toromiro*, found only on Easter Island (Zizka 1991), are late Miocene to Pliocene in age. Dispersal of the buoyant *Sophora* seeds to these islands from New Zealand is seen as the most likely explanation for this distribution. Nuclear ribosomal internal transcribed spacers (nrITS) from species in the genus *Hebe*, represented on Rapa by *V. rapensis*, indicate dispersal eastward from New Zealand to South America probably during the late Miocene (Wagstaff & Garnock-Jones 2000; Winkworth et al. 2002; M. Bayly and P. Garnock-Jones unpublished data). Winkworth et al. (2002) suggest that the Sub-Antarctic Islands and the Antarctic may have provided a stepping-stone for dispersal from New Zealand to South
America. It is possible that Rapa may have also served as a stepping-stone for dispersal. Few other high-resolution phyleogeographic studies have been completed for representatives of the Austral Islands flora. Florence (1997) analysed the floral affinities the flora of subtropical Rapa with respect to that of other Pacific regions, and found that over 45% of the genera present were shared with the tropical Western Pacific. The other islands in the Austral Islands showed a higher affinity, unsurprising given their more tropical position.

Limited phyleogeographic studies are also available for a number of pan-tropical genera including Scaevola (Goodeniaceae; *S. taccada* is found on most of the islands in the Austral Islands; Howarth et al. 2003), Hibiscus (Malvaceae: Hibisceae; including *Talipariti tiliaceum* syn. *Hibiscus tiliaceus* represented on most islands; Pfeil et al. 2002) and Erythrina (Fabaceae represented by *E. variegata* on most of the islands; Bruneau 1996) each known to display some long-distance dispersal capacities. These phylogenetic analyses suggest that most pantropical taxa had arrived in the Pacific region prior to the orogeny of the Austral Islands.

**Pleistocene (last 1.8 Ma - 10 000 yr B.P.) phytogeography of the Australs**

Little is known of the dynamics of Pleistocene vegetation change for Pacific Islands. The configuration of islands in the Pacific Basin was essentially the same as today and the geology has remained tectonically stable throughout this period, compared to the regions lying along the continental plate boundaries to the west. Few terrestrial catchments in the region have accumulated Pleistocene-aged sediment deposits. The lack of large sedimentary basins in this region dictates that continuous terrestrial records of an age exceeding the Holocene will remain elusive (Hope 1996). Inferences of vegetation change for the Pleistocene in Oceania tend to rely on indirect proxies such as glacial or sea level signatures to determine constraints on vegetation.

The influence of Pleistocene sea level fluctuations on vegetation change in the Pacific can be inferred from sea-level proxies found in marine (e.g. coral reefs and marine sediments) and coastal sedimentary deposits (e.g. mangrove sediments) and other geomorphological indicators (e.g. coastal caves and uplifted coral terraces). Eustatic sea levels in the last 1.8 Ma have fluctuated by up to 140 m on a time scale of about 100000 years. The time spent at the lowest levels is similar to that spent at their highest, about 10-15000 years or 10% of the time with intermediate levels achieved at other times (Shackleton 2000).

Bathymetric data from much of the Pacific indicates that almost all existing island groups remained separated during glacial lowstand sea levels.

Estimates of interglacial and glacial sea levels are known for the late Pleistocene Pacific from a series of dated uplifted-coral terraces in the Huon Peninsula, Papua New Guinea (Chappell & Polach 1991). The closest series of uplifted terraces to the Austral Islands that provide any indication of Pleistocene sea levels come from the Fijian archipelago (e.g. Nunn & Omura 1999). Uplifted Pleistocene reefs are found on Rurutu (Stoddart & Spencer 1987; Pirazzoli & Salvat 1992) and Tubuai (Pirazzoli & Salvat 1992) where emergence by volcanic loading of the Arago Seamount (Bonneville et al. 2002) has left Last Interglacial shoreline signatures from a time when sea level was approximately 5 m above present level (e.g. Chappell & Shackleton 1986).

Lower sea levels during glacial periods had the effect of increasing land area and therefore reducing migration distances between islands. For the Austral Islands this would have resulted in a marginal reduction in the distances between islands. Based on limited bathymetric data and with the estimated sea level decline for the Last Glacial period, Rapa potentially expanded its terrestrial area up to around 200 km². The ocean floor immediately surrounding these islands lies at a depth varying between 2 and 4.7 km. All of the surrounding satellite islets off the coast would have been joined with the main island allowed continuous tracts of vegetation to form between them. Given the rise in altitude of the island with lowering sea-level, orographic precipitation concentrated on windward flanks of the island may have increased leading to increasing valley dissection and sediment erosion, as has been proposed for most Pacific high islands (e.g. Gavenda 1992). Paulay (1985) suggests that the montane cloud forest of Rapa would have extended down in elevation to encompass a greater area, potentially connecting the previously disjunct forest tracts.

Lower sea levels also had the effect of creating erosion dominated fluvial systems by increasing river gradients. This increased valley incision and sediment mobilisation limiting accommodation space for sediment deposition and organic accumulation and subsequently sub-fossil preservation. Vegetation development particular at the outlets of rivers and in coastal areas was likely to have been greatly restricted. Coastal swamp forest or mangrove environments would have been restricted to small refugia, or, were entirely absent during these periods.

**Palaeobotanical evidence and Pleistocene phytogeography**

Lyon (1930) identified Pleistocene-aged macrobotanical remains of fifteen tree species from a tuff deposited in a salt lake at Moanalua, Oahu in the Hawaiian Islands. Amongst the species identified were the endemic *Pritchardia* spp. (Areaceae), *Metroseros polymorpha* (Myrtaceae) and *Acacia koa* (Fabaceae), all indicative of a mesic interglacial environment (Ruhe 1964 in Gavenda 1992).

By contrast, Hay & Iijima (1968 in Gavenda 1992) later examined the geomorphology of the site and
interpreted the deposit to be from a glacial period at ~350 000 yr B.P. providing evidence for the long-term presence of at least three endemic species. Some near-continuous Pleistocene palynological records are available from continental sites in Oceania including the Grande Terre, New Caledonia (Stevenson et al. 2001; Stevenson & Hope 2005) and in New Zealand where there are numerous records (Vandergoes et al. 2005). Only one record has been located from the Fijian archipelago at Lake Tagimaucia on Taveuni (Southern 1986; Hope 1996). Discrete Pleistocene units have also been located along the Plaine des Lacs, New Caledonia (Hope & Pask 1998), Nadrau Plateau on Viti Levu, Fiji (Southern 1986) and from several sites in New Zealand (e.g. Moar & Suggate 1996). Only three island groups in Oceania have provided palynological records extending back to the Pleistocene, including Easter Island (Rano Kao, Rano Raraku and Rano Aroi in Flennley et al. 1991), Oahu, Hawaiian Islands (Selling 1948; Athens 1997; Hotchkiss & Juvik 1999) and San Cristobal, Galápagos Islands (Colinvaux 1972; Colinvaux & Schofield 1976). All of these sites are located in either high elevation bogs (Hawaiian sites) or remnant volcanic caldera lakes, but are rare in the region. Most interpretations of these records imply cooler and drier conditions during glacial periods with an increase in montane and herbaceous taxa in lowland areas in response to a decrease in forested environments. Pleistocene-aged palaeobotanical material may be retrievable from the moat-swamp deposits of Rimatara. Maunutu moat-swamp on the north-east side of Rimatara has been cored to a depth of 14.5 m in two different locations both not reaching basal parent rock. Material has yet to be submitted for radiocarbon dating, but it is anticipated that this material may yield late glacial ages. It has been found that such moat swamp deposits on other “makatea” islands in the Cook Islands may reach depths of more than 16 m below the sedimentary surface, but the depths of these deposits may be much greater, potentially below 20 m in depth.

Phylogeographic evidence for Pleistocene phytogeography

From phyllogenetic evidence it seems probable that most plant dispersals to the Austral Islands took place soon after island orogeny in the late Miocene/ Pliocene. Additional plant migration to the archipelago probably occurred via long-distance dispersal mechanisms, including avian dispersal and floating propagules, but most of these recent arrivals were probably taxa already established on the islands. Little evidence, molecular or otherwise, has been made available confirming any Pleistocene plant arrivals of taxa new to the Austral Islands. Wright et al. (2000) examined the nuclear ribosomal DNA of the Metrosideros subgenus Metrosideros that includes ~26 anemophilous (wind-dispersed pollen) species found throughout the Pacific. They identified three monophyletic clades, two of Miocene age with one thought to be derived from a Pleistocene dispersal of a species identical to the New Zealand species Metrosideros excelsa, only separated by a single nucleotide change. Wright et al. (2000) attribute this late dispersal to a change in late Pleistocene wind patterns, namely an intensification of the southeast trades. Using several molecular calibration methods, Percy et al. (2008) estimate the colonization of the Hawaiian Islands by Metrosideros to be potentially as old as 3.9 Myr with an ancestral position on Kauai. This clearly represents a more ancient arrival of Metrosideros to the islands than suggested by Wright et al. (2000). Percy et al. (2008) do agree with the direction of dispersal from New Zealand indicated by Wright et al. (2000) and suggest that the Austral Islands was probably the first stepping-stone.

Two varieties of M. collina are now found throughout Oceania and are found on all of the populated islands of the Austral Islands, except Rimatara, although fossil pollen has recently been identified from that island (M. Prebble unpublished data). Metrosideros may also have been extirpated on Easter Island since human colonisation as indicated by fossil Myrtaceae pollen characteristic of Metrosideros (Flennley et al. 1991).

Holocene phytogeography of the Austral Islands

Compared to Pleistocene phytogeography, the Holocene is relatively well understood from numerous records (Hope et al. 1999). Holocene...
phytogeography, prior to human colonization, is primarily controlled by geodynamic processes, influenced by eustatic and hydro-isostatic sea-level fluctuations. The post-glacial marine transgression of the early Holocene had the regional effect of enhancing the sediment budget, especially behind accreting river levees, boulder beachridges, and coral reef systems. This increase in sediment accumulation allowed formerly restricted coastal vegetation to establish. On most islands in the Pacific this usually did not take place until eustatic sea level reached near modern levels by ~8000 cal. yr B.P. When coastal sediment accumulation reached its peak behind reef bound lagoons that restricted wave-induced sediment erosion. Palynological sequences obtained from anaerobic, organic rich depositional contexts, that have accumulated since the post-glacial marine transgression in the early Holocene are available in most Pacific island archipelagos, including the Austral Islands. Suitable contexts for pollen preservation, such as large closed lake basins or *Sphagnum* peat deposits, are rare in the Pacific Islands and are absent in the Austral Islands. The lack of closed volcanic lake calderas and peat bogs in the Austral Islands has meant that most sedimentary catchments preserving Holocene palaeobotanical remains are located on levee-backed marshlands (Rapa and Raivavae), beach-backed swamps (Rapa, Raivavae, Tubuai, Rurutu) and "makatea" moat swamps (Rurutu and Rimatara). Deep upland sedimentary deposits are absent from the Austral Islands, although some shallow deposits have been located with cores retrieved, but these have yet to be analysed.

Coastal marshland deposits on the islands can be characterised on the basis of sedimentary basin size and morphology, structure of the alluvial/marine interface and the morphology of offshore reefs. The largest coastal sedimentary catchments in the Austral Islands with organic rich marshland deposits, are found on Tubuai. Cores retrieved from these sites have yet to be analysed, but preliminary results from Mihiu swamp reveal a substantial coastal swamp forest dominated by *Pandanus* and palm trees including *Pritchardia* and *Cocos nucifera* (Prebble & Dowe 2008). Other trees growing in abundance within or adjacent to these swamp forests included a number of extirpated (e.g. *Macaranga*) or rare (e.g. *Charpentiera*) tree or shrub taxa. Similar records have been retrieved from Raivavae at Rairua, the largest coastal sedimentary catchment on the island. The largest coastal sedimentary catchment on Rapa is found at the head of Haurie (see below). Smaller sedimentary catchments are located at the base of windward boulder and leeward sandy beach embayments of the island (Fig. 26). The more deeply incised windward embayments are characterised by higher energy fluvial/alluvial systems, but highly organic fine-grained sediment deposits preserving botanical

![Figure 26: Satellite image of Rapa showing the main windward boulder beach and leeward sandy beach embayments. The position of Tukou and the highest mountain peak are also indicated.](image-url)
remains tend to be of late Holocene age and often directly associated with human-induced sedimentation following agricultural expansion (Kennett et al. 2006; Prebble & Dowe 2008).

A unique characteristic of "makatea" islands, like Rimatara and Rurutu is the extensive sediment-filled and waterlogged depressions that extend out like a moat, between the inner rim of the annular limestone and the base of the inland volcanic core. Most of these "moat deposits" are covered with swamp vegetation. Small ponds are also found in some locations on Rimatara, lying adjacent to the "makatea" cliff edge. A series of palaeobotanical records have been retrieved from the most intact moat-swamp deposits located on Rimatara, described by Prebble and Wilmshurst (2009). The pre-human record from Maunutu Swamp is dominated by Pandanus and palm swamp forest with an understorey of Acrostichum fern. Other trees growing in abundance within or adjacent to these swamp forests included a number of extirpated (e.g. Terminalia) or rare (e.g. Homalium) tree or shrub taxa. This swamp forest was rapidly cleared after around 800 yr BP during human colonisation at which time Colocasia esculenta raised fields were established.

The moat deposits located on Rurutu may yield significant palaeoecological information, but now appear to be buried under thick layers of sterile overburden. Estuarine or lagoon deposits on the south side of the island may reveal some fossil material, but this has yet to be established.

**PALAEOBOTANICAL EXAMINATION OF TUKOU MARSH, RAPA**

...Study site: geography, climate and vegetation...

Haurei harbour on Rapa represents the remnant of one of the original volcanic calderas formed during island orogeny and opened to the sea sometime in the Pliocene. The shallow bathymetry of the harbour suggests that the entire area was exposed during glacial lowstand sea levels. The exposed reef at the harbour entrance, backed by calcareous reef shoals along the interior, currently restricts wave-action from the sea, to the degree that the harbour can be described as a lagoon. At low tide fine-grained sediments of a mixture of alluvial sediments, shell and coral detritus are exposed to reveal three prominent birds-foot river deltas and tidal flats extending out from the high-tide shoreline. Water depth surrounding the Tapuki ("Tapui") basaltic islet in the centre of harbour is no more than 1.5 m below low tide level.

Figure 27: Section of a sketched map of the head of Haurei harbour, Rapa by John Vine Hall (1869a) showing the location of the main marsh systems ("Taro patches") including Tukou.
Shoreward of the exposed deltaic sediments are a series of levee-backed marshes positioned at Tukou, Matataa and Aitoke (Fig. 27). All of these sites have been heavily modified by human activity and grazing by cattle, horses and goats. A map of Haurei harbour sketched in 1864 by Captain John Vine Hall (1869) shows the position of a number of coastal pondfield systems that were used for Colocasia esculenta cultivation (Fig. 27). Remnant dry stonewall terrace features are now interspersed within many of the levee-backed marshes, along the margins of riverbeds or situated along the present shoreline. At certain points, these marshlands extend over 100 m inland and rise to an elevation of over 3 m above sea-level. On the most inland side, these marshes are bound either by river levees or steeply rising embankments of the surrounding hill slopes that appear to have been cut by a previous, probably mid-Holocene, sea-level highstand (Fig. 28).

Tukou marsh lies on the south side of the broadest river delta and associated tidal flats of Haurei harbour. The marsh is banked and divided by two smaller prograding river channels forming two waterlogged depressions. The central most marsh depression was chosen for palaeoenvironmental analysis (Fig. 29) and sediment cores were taken in 2002 (June-August). The modern marsh appears to have developed behind the southern levee of the main river and the northern levee of the smaller river bounded the marsh to the south. The marsh extends from the estuarine shoreline, marked at high tide (~0.4 m above mean sea level) by driftwood and estuarine detritus, ~135 m to the embankment of the surrounding hill slope. Below the embankment the marsh reaches a maximum elevation, based on laser transit measurements, of 3 m above the high tide mark. The topography of the remnant agricultural terrace features lie an additional 50 cm or more above the marsh surface.

Tukou receives around 2500-3000 mm annual rainfall based on measurements taken from Haurei village, also at sea-level (Rapa Meteo unpublished data). Tukou is fed by two permanent streams that drain the eastern catchment of the Perau-Namuere range with water flow gradients averaging above 30° C. Hydrological data are unavailable for this catchment. From readings taken in 2002, both rainfall and wind are greatest from June to August with the average temperature minimums fluctuating around 15° C reaching as low as 10° C in August 2002 (Rapa Meteo unpublished data). Thunder and lightning occur infrequently at any time of the year with only two storms recorded from February to March 2002.
The vegetation of the waterlogged marsh surface is currently dominated by introduced agricultural grasses (e.g. *Paspalum subjugatum*) and adventive herbs (e.g. *Commelina diffusa* and *Ludwigia octovalvis*) with some indigenous sedges (e.g. *Carex spp.*) and rushes (e.g. *Schoenoplectus subulatus* subsp. *subulatus*; some authors suggest that this may have been introduced to French Polynesia). The embankment on the periphery of the marsh is largely open grass with some naturalised *Syzygium jambos* and *Psidium* spp. trees (both in the Myrtaceae). Some indigenous tree taxa are found at the site including *Talipariti tiliae* (Malvaceae) and *Metrosideros collina* (Myrtaceae). Hall's (1868) sketch of the site indicates that stone-wall terraces lined the upper portion of the marsh and were focused along the banks of the adjacent river channels. Some of these terrace features remain but in a degraded state. Only one feral *C. esculenta* specimen was located at Tukou with no other cultigens identified. The marsh is currently left for cattle grazing.

**Field methodology**

The vegetation history of Rapa, as inferred from Tukou marsh, was examined for three main purposes. Firstly, to outline the extent of Holocene vegetation on Rapa; secondly to assess the influence of fluctuating Holocene sea levels on vegetation and coastal sedimentation; and lastly the site was
examined for human impact signatures as discussed in Kennett et al. (2006). In order to assess changes in vegetation throughout the Holocene, an attempt was made to obtain the oldest and most continuous section from the marsh. Cores were attempted in the Haurei lagoon at different intervals between Tukou marsh and Tapuki islet, using both Russian D-Section and Livingston corers. The texture of sediments in the lagoon was such that no core was retained with sufficient integrity for palynological analysis. After initial probing, the longest profile was located at the marsh/lagoon interface (Tukou Core 1, Fig. 29). This 6.5 m sediment profile was taken 5 m inland of the shoreline using a 30 mm Russian D-Section corer down to 5 m below the marsh surface, with the remaining 1.5 m extracted using a 35 mm diameter Livingston piston corer.

**Laboratory and numerical methods**

Each extracted core was taken back to the laboratory for further analyses including radiocarbon dating, sedimentary, faunal and palynological analyses. Five samples were submitted for Accelerator Mass Spectrometry (AMS) radiocarbon dating, listed in Table 37. The calibrations provided were calculated using the OxCal program version 3.10 with the IntCal04 calibration data set (Bronk Ramsey 2005). Of these radiocarbon samples, one leaf sample was submitted along with three macro-charcoal particles. The remaining sample was submitted as a pre-treated pollen concentrate, processed using standard pollen protocols without the addition of carbon-based acids. One cubic centimetre (cm$^3$) samples in volume were taken at approximately 0.10 m intervals throughout each core. Pollen analysis of sediment samples was conducted using the standard preparation techniques. To enable the calculation of pollen concentrations, *Lycopodium clavatum* marker spores of a known number were added. Palynomorph counts generally amounted to 300. Microscopic charcoal fragments were also counted for each sample using the point count method (Clark 1982). Foraminifera (rotalids indicative of estuarine/intertidal conditions; J. Reeves pers. comm.) and calcareous dinoflagellates (indicative of estuarine conditions; M. Young pers. comm. 2004) within the pollen concentrates were counted as broad indicators of estuarine/intertidal environments, but were not identified to taxa due to dissolution during pollen processing.

Pollen and spore identification was assisted by reference material collected in the field by the author and regional reference collections held at the Australian National University. All pollen taxa names refer to the family or genera of extant plant taxa, with the exception of the fossil classification Arecaceae: Iguanurinae type (Prebble & Dowe 2008) derived from an extinct palm of that sub-tribe. Mineral magnetic susceptibility analysis was used to detect coarse changes in mineralogy down the cores. Each core was scanned using a MS/2 Bartington Susceptibility Meter and core loop at 2 cm intervals, in order to identify peaks in magnetic mineral concentration.

All pollen and spores were counted as a ratio to added exotic *Lycopodium* spores (per cm$^3$). The concentration (per cm$^3$) data for pollen, spores and microcharcoal particles, foraminifera and dinoflagellate counts as well as percentage pollen and spore data were placed into stratigraphic diagrams (Figs 30A,B) using the program C2 Data Analysis version 1.4 (Juggins 2005). Radiocarbon ages, linear age models and magnetic susceptibility data were also placed in these diagrams. This program was also used to numerically examine the relationship between samples using correspondence analysis (CA).
Table 37: List of AMS radiocarbon dates obtained from the Tukou Core 1 sediment profiles. Presented are the sample depths, radiocarbon laboratory (ANU = Australian National University. California = University of California, Irvine. ANSTO = Australian Nuclear Science and Technology Organisation), material dated, pollen concentrations/cc, laboratory sample codes, uncalibrated determinations and calibrated ages to 2σ and 2σ central point estimates. Dates from two samples were replicated at 240-242 cm (Core 3) and 210-212 cm (Core 6) and calibrated using the combine algorithm in the OxCal program version 3.10.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Material dated</th>
<th>Pollen conc/cc</th>
<th>Lab Code</th>
<th>C14 Age (uncal.)</th>
<th>Error</th>
<th>2 σ</th>
<th>2 σ central point estimates</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>180-182 cm (California)</td>
<td>Leaf</td>
<td>UCIAMS 2196</td>
<td>1845</td>
<td>30</td>
<td>1870-1700</td>
<td>1785</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td>232-234 cm (ANU)</td>
<td>Pollen</td>
<td>39556</td>
<td>ANU 11921</td>
<td>3650</td>
<td>4550-3450</td>
<td>4000</td>
<td>550</td>
<td></td>
</tr>
<tr>
<td>516-518 cm (California)</td>
<td>Charcoal</td>
<td>UCIAMS 2283</td>
<td>5150</td>
<td>25</td>
<td>5990-5760</td>
<td>5875</td>
<td>115</td>
<td></td>
</tr>
<tr>
<td>562-564 cm (California)</td>
<td>Charcoal</td>
<td>UCIAMS 2195</td>
<td>6700</td>
<td>45</td>
<td>7670-7470</td>
<td>7570</td>
<td>100</td>
<td></td>
</tr>
<tr>
<td>582-584 cm (ANU)</td>
<td>Charcoal</td>
<td>ANU 11928</td>
<td>6520</td>
<td>190</td>
<td>7750-6950</td>
<td>7350</td>
<td>400</td>
<td></td>
</tr>
<tr>
<td>624-626 cm (ANU)</td>
<td>Pollen</td>
<td>14240</td>
<td>ANU 11922</td>
<td>7020</td>
<td>8300-7450</td>
<td>7875</td>
<td>425</td>
<td></td>
</tr>
</tbody>
</table>

**PALAEOBOTANICAL RESULTS**

**Core stratigraphy, chronology and eustatic sea levels**

The basal sediments (650-600 cm) of the core consist primarily of compacted reddish-brown basaltic clays with minimal organic content (< 10%). Above these clays, a large unit (600-120 cm) encompassing much of the core consists of fine to coarse estuarine sands, silts and differing proportions of shell and coral debris and other calcareous material. Magnetic susceptibility measurements (K units) correspond to increasing proportions of inorganic (basaltic) mineral sands. Above this unit lies a predominantly organic unit (120-0 cm) with differing degrees of silt and clay, but lacking any calcareous material. The upper 22 cm of the core lie above the high-tide line and consist of sedge (Cyperaceae) and grass (Paspalum conjugatum) roots.

Five AMS dates were obtained for Tukou Core 1 at different intervals throughout the core (Table 37) and these are presented as linear-age models in stratigraphic diagrams (Figs 30A,B). The most basal sample submitted for dating located at 624 cm in depth obtained an age of 8300-7450 cal. yr B.P. (Table 37). Dated from pollen concentrates this sample represents the most basal age for the Tukou deposit, but may as discussed below stem from reworked material. The estuarine sedimentary unit with calcareous material was dated to between ~8000 and 2000 cal. yr B.P. No radiocarbon dates were obtained from the upper organic unit, thus the chronology remains uncertain and is discussed below in the context of palynological markers.

The most detailed chronological measurements for eustatic sea level change in OIRO come from an analysis of barrier reef coral cores from coastal Tahiti (Bard et al. 1996). These have provided comparable rates of sea level change for the late Glacial-Holocene period and a linear age model of the Tukou Core 1 sequence (Figs 30A,B). The three most basal ages dating from 7450-8300 cal. yr B.P. are all situated at depths deemed to lie above eustatic sea level at that time. All of these ages have been taken from depths associated with counts of foraminifera and dinoflagellates representative of intertidal or estuarine conditions. From the Tahiti coral record, Bard et al. (1996) estimates the level of eustatic sea level to lie at this time between around -20 and -12 m below current mean sea level, at least 6 m below the Tukou levels. Either sea level rose more rapidly on Rapa, or older organic material at the base of Tukou Core 1 have been reworked. The later explanation is followed here. By 6500 cal. yr B.P., the Tahiti record indicates that sea levels reached levels represented at the Tukou Core 1 site. Ages obtained from this core that are younger than 6500 cal. yr B.P. are assumed to be consistent with the timing of sediment deposition and not a product of post-depositional processes. Direct indications of estuarine or littoral conditions are available from the shell macro-remains of bivalves, gastropods and other fauna (e.g. crabs). The highest concentrations (10-15%) of shell remains are found at differing depths between 250-150 cm along with whole pieces of coral debris. Taxa recorded in this section of the core include bivalves in the Veneridae (Galtararium pectinatum; Clypeomorus sp.) and Mytilidae (Saccostrea sp.), Tellinidae (Tellina cf. staurella) families (K. Szabo pers. comm.). In the basal sediments of the core between 540-250 cm shell concentrations lie below 5% with all of the above taxa recorded in different sections. Saccostrea sp. and crab remains were recorded throughout this section. Until further analyses of these bivalve remains including isotopic analyses are undertaken, no definitive interpretation of the littoral or estuarine environment can be made.
<table>
<thead>
<tr>
<th>Pollen taxa</th>
<th>Family</th>
<th>Present in Tertiary</th>
<th>Present in early – mid Holocene</th>
<th>Present in last 2000 years</th>
<th>Indigenous representatives in modern flora</th>
<th>Biogeographic affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acalypha¹</td>
<td>Euphorbiaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Acalypha spp. Possible extinct species</td>
<td>Indo-Pacific/Endemic?</td>
</tr>
<tr>
<td>Angiopteris</td>
<td>Angiopteridaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Angiopteris rapensis, A. longifolia</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td>Arecaeae: Iguanurinae Type</td>
<td>Arecaeae, Subfamily Arecoideae, Tribe Iguanurinae</td>
<td>Y?</td>
<td>Y</td>
<td>Y</td>
<td>Extinct</td>
<td>?</td>
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<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Asteraceae-Liguliflorae</td>
<td>Asteraceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Casuarina²</td>
<td>Casuarinaceae</td>
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<td>Y</td>
<td>Y</td>
<td>Casuarina equisetifolia</td>
<td>Indo-Pacific, probably exotic/contamination</td>
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<tr>
<td>Celtis</td>
<td>Ulmaceae</td>
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<td>Y</td>
<td>Y</td>
<td>Celtis pacifica</td>
<td>Indo-Pacific</td>
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<tr>
<td>Coprosma</td>
<td>Rubiaceae</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Coprosma cookei, C. rapensis</td>
<td>Pacific/Endemic</td>
</tr>
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<td>Cyathea</td>
<td>Cyatheaceae</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Cyathea affinis, C. medullaris, C. rapensis, C. stokesi</td>
<td>Indo-Pacific/Endemic</td>
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<td>Cyperaceae</td>
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<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>Pan-tropical, cosmopolitan</td>
</tr>
<tr>
<td>Davallia/Histiopteris</td>
<td>Davalliaeae/Dennstaedtiaeae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>Pan-tropical, cosmopolitan</td>
</tr>
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<td>Dryopteridaceae</td>
<td>Dryopteridaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>Pan-tropical</td>
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<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Freycinetia</td>
<td>Pandanaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Freycinetia arborea</td>
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<tr>
<td>Glochidion</td>
<td>Euphorbiaceae</td>
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<td>Y</td>
<td>Y</td>
<td>Glochidion longfieldiae, G. rapaense, G. societatis</td>
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</tr>
<tr>
<td>Haloragaceae</td>
<td>Haloragaceae</td>
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<td>Y</td>
<td>N</td>
<td>Haloragis stokesi</td>
<td>Indo-Pacific/Endemic</td>
</tr>
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<td>Hebe rapensis</td>
<td>Scrophulariaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Hebe rapensis</td>
<td>New Zealand/Endemic</td>
</tr>
<tr>
<td>Hibiscus tiliaceus</td>
<td>Malvaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Hibiscus tiliaceus</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Hypolepis</td>
<td>Dennstaedtiaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Hypolepis punctata, H. tenifolia</td>
<td>Indo-Pacific/Pan-tropical</td>
</tr>
<tr>
<td>Lycopodium sp.</td>
<td>Lycopodiaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
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<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Meryta</td>
<td>Araliaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>M. chloristantha, M. brachyypoda</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Monolete Psilate</td>
<td>?</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Monolete undiff.</td>
<td>?</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Myrtaeae undiff.</td>
<td>Myrtaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Omalanthus</td>
<td>Euphorbiaceae</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>Omalanthus nutans, O. stokesii</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td>Pandanus cf. tectorius</td>
<td>Pandanus</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Pandanus tectorius</td>
<td>Indo-Pacific/Endemic?</td>
</tr>
<tr>
<td>Poaceae</td>
<td>Poaceae</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Pteris</td>
<td>Pteridaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Polypodiaceae</td>
<td>Polypodiaceae</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>Rubiaceae</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Sophora</td>
<td>Fabaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Sophora tomentosa</td>
<td>Pacific</td>
</tr>
<tr>
<td>Trilete Psilate</td>
<td>?</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Trilete undiff.</td>
<td>?</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
<tr>
<td>Triumfetta comp.</td>
<td>Malvaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Triumfetta procumbens</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Urticaceae/Moraceae</td>
<td>Urticaceae/Moraceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Numerous species</td>
<td>?</td>
</tr>
</tbody>
</table>
Table 38: Palynomorphs from Tukou Core 1. Listed are the presence or absence of palynomorphs in Tertiary and mid-Holocene sediments or from sediments <2000 cal. yr B.P. in age. Also listed are the possible representatives of the palynomorphs found in the modern flora and the biogeographic affinity of taxa.

1Pollen or spore type wind blown. 2Pollen or spore type capable of long distance dispersal (after Close et al. 1978).

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**Palynological analysis**

The different palynomorphs identified from Tukou Core 1 are listed in Table 38, along with their presence or absence in Tertiary, mid-Holocene and <2000 cal. yr B.P. aged sediments and their biogeographic affinity. Proportional palynological data are also presented in stratigraphic diagrams according to the occurrence of taxa throughout the core in proportions of either >5% (Fig. 30A) or <5% (Fig. 30B). Taxa are grouped from left to right according to trees and shrub, herb, fern and fern ally groups. Taxa are sorted within these groups in stratigraphic succession using the sort function in C2 Data Analysis program (Juggins 2005). The core is divided into four palynological zones on the basis of major vegetation changes.

**Zone I (650 to 245 cm; ~6 500 - 4 000 cal. yr B.P.)**

Trilete fern spores including *Cyathea* tree fern and *Angiopteris* types dominate this Zone. Palynomorph concentrations remain low until ~6 500 cal. yr B.P. after which time concentrations reach their highest in the early Holocene until 5000 cal. yr B.P. Tree and shrub taxa are only preserved in low percentages or trace counts or percentages. *Pandanus* cf. *tectorius* type pollen does not enter the record in percentages >5% until after 6 000 cal. yr B.P. *Triumfetta* (probably *T. procumbens*), Euphorbiaceae and Myrtaceae pollen are the most consistently represented tree and shrub taxa found in this Zone. Both foraminifera and dinoflagellates are found in trace counts at the base of this Zone but were not located after around 5 000 cal. yr B.P. From 6 500 cal. yr B.P. the Arecaceae: Iguanurinae type pollen appears in the record.

**Zone II (255 to 145 cm; ~4 000-1 500 cal. yr B.P.)**

Fern spores continue to dominate the early part of this Zone but in fluctuating proportions and decrease by 3 000 cal. yr B.P. in response to increasing *Pandanus* cf. *tectorius* and Cyperaceae pollen. Palynomorph concentrations decline from the base of this Zone to the lowest recorded concentrations at the top of the zone from 3 000-2 000 cal. yr B.P. Both foraminifera and dinoflagellates reappear in the early part of this Zone from ~4 000 to 3 000 cal. yr B.P.

**Zone III (145 to 85 cm; ~1 500-1 000 cal. yr B.P.)**

*Pandanus* cf. *tectorius* pollen along with palynomorph concentrations increase from the base of this Zone. Trilete fern spores including *Cyathea* tree fern and *Angiopteris* types decline in this Zone. *Celtis* (probably *C. pacifica*) and Arecaceae: Iguanurinae type pollen become more consistently represented in this Zone.

**Zone IV (85 to 0 cm; ~1 000 cal. yr B.P. to present)**

Apart from Myrtaceae (undifferentiated to species) pollen, all tree and shrub taxa and trilete type fern spores decline or are absent in this Zone. Charcoal particles first appear in high concentrations at the base of this zone. *Pandanus* cf. *tectorius* type peaks to its highest recorded levels at the base of this Zone. Charcoal concentrations and *Pandanus* proportions decline to low levels in association with a sedimentary change at around 50 cm below the marsh surface. Cyperaceae and Poaceae (both <40 µm and >40 µm size classes) and palynomorph concentrations increase to their highest levels at the top of this Zone.

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**Correspondence analysis (CA)**

Correspondence analysis was performed on the percentage data all pollen and spore taxa identified in Tukou Core 1. Eigenvalues (Axis 1) generated for each sample are presented as proportions of the total variation in the dataset in each of the two stratigraphic diagrams (Fig. 30A and 30B). These values account for 36% of the variation in the entire dataset. These values are primarily controlled by the proportions of *Pandanus* cf. *tectorius* type pollen within each sample. The greatest variation that exhibited in this core occurs in the basal section of Zone I from ~6 500-6 000 µm cal. yr B.P. and in Zones II and IV.

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*Pandanus tectorius* (Photo J.-Y. Meyer).
The Paleobotanical Record of Rapa: Indications for the Phytogeography

The following are presented in the diagram from left to right: Core lithology (>0 = increasingly coarse), magnetic susceptibility values (k), calibrated radiocarbon ages (line and ticks with the Tahitian sea-level curved overlaid in green after Bard et al. 1996), taxa (pollen and spores: taxa with ≥ 5% of total palynomorph sum are presented as colour coded bars; samples with proportions <5% are presented as triangle symbols) and total palynomorph concentrations (per cm$^3$), microcharcoal particle concentrations (per cm$^3$), foraminifera and dinoflagellate counts, palynomorph richness (number of taxa), Correspondence Analysis scores (CA score 1) and palynological zones. Four palynological zones (Early Holocene Marine Transgression Zone I; Mid-Holocene highstand Zone II; Late Holocene swamp forest Zone III; Human impact Zone IV) are presented. The dashed black line indicates the position of the high tide line. The horizontal transparent red bar indicates the section of the core where the sedimentary unit associated with palynological signatures of human impact (namely micro-charcoal particles) are poorly constrained by radiocarbon ages.
Terrestrial Biodiversity of the Austral Islands, French Polynesia

Figure 30B: Percentage pollen diagram for Tukou Core 1 (total of 6.55 m).

The following are presented in the diagram from left to right: Core lithology (>0 = increasingly coarse), magnetic susceptibility values (k), calibrated radiocarbon ages (line and ticks with the Tahitian sea-level curved overlaid in green after Bard et al. 1996), (pollen and spores: taxa with <5% are presented as coloured triangle symbols) and total palynomorph concentrations (per cm³), microcharcoal particle concentrations (per cm³), foraminifera and dinoflagellate counts, palynomorph richness (number of taxa), Correspondence Analysis scores (CA score 1) and palynological zones. Four palynological zones (Early Holocene Marine Transgression Zone I; Mid-Holocene highstand Zone II; Late Holocene swamp forest Zone III; Human impact Zone IV) are presented. The dashed black line indicates the position of the high tide line. The horizontal transparent red bar indicates the section of the core where the sedimentary unit associated with palynological signatures of human impact (namely micro-charcoal particles) are poorly constrained by radiocarbon ages as shown in Figure 30A.
Early Holocene marine transgression Zone I (~6500 - 4000 cal. yr B.P.)
The dominance of ferns (e.g. Angiopteris) and Cyathea tree ferns from ~6500 cal. yr B.P. indicate a waterlogged swamp setting characterised by prominent alluvial sedimentation infilling an intertidal embayment indicated by the presence of foraminifera, dinoflagellates and litoral/intertidal shell remains. Some tree and shrubs including Pandanus and Triumfetta (a coastal strand taxon) were located along the coastal surrounding the throughout this Zone. The extinct Arecaceae: Iguanurinae type palm became prominent on the coastline after around 6500 cal. yr B.P.

Mid-Holocene highstand Zone II (~4000 - 1500 cal. yr B.P.)
Fluctuation in the estuarine hydrology of the waterlogged fern swamp from 4000-3000 cal. yr B.P. is indicated by traces of both foraminifera and dinoflagellates as well as differing proportions of litoral/intertidal shell remains at irregular depths. A coastal Pandanus forest with a sedge (Cyperaceae) understorey is represented but is restricted to the brackish/freshwater periphery of the fern swamp and estuary after 3000 cal. yr B.P. This swamp forest is restricted from expanding by high sediment mobility from both transgressive and regressive hydrological influences inferred from extremely low palynomorph concentrations (see below for further discussion).

Late Holocene swamp forest Zone III (~1500 to 1000 cal. yr B.P.)
After around 1500 cal. yr B.P. the Pandanus coastal forest expanded behind a prograding tidal-river levee indicated by a magnetic susceptibility peak (high mineral sedimentation) and the absence of calcareous shell remains. This restricted any tidal influence on the site and allowed the predominantly freshwater swamp to develop. Other taxa including Celtis and the Arecaceae: Iguanurinae type palm became established within this developing swamp forest.

Human impact Zone IV (<1000 cal. yr B.P. to present)
This Zone, divided into two parts, is characterised by palaeoenvironmental human impact signatures including swamp forest decline in response to burning indicated by peaks in microcharcoal particles. From the presence of charcoal particles radiocarbon dated from Zone I it is clear that burning was part of the pre-human island ecosystem. An interpretation of charcoal particles present in Zone IV may therefore remain equivocal in the absence of other human impact indicators. This problem is illustrated by the peaks in charcoal particles in the first part of this Zone (highlighted in Figs 30A,B) that are followed by an increase in Pandanus cf. tectorius representation. Peaks in Pandanus pollen may be representative of one of the following: sediment compaction in the early part of this Zone allowing for pollen to accumulate and become more concentrated with depth; the opening of forest conditions allowing for more pollen deposition; or the possibility that Pandanus responds to burning by increased flowering and pollen production. The abrupt decline in Pandanus in the later part of this Zone (above 50 cm below marsh surface) appears to represent a more precise indication of human activity. This palynological signature of coastal swamp forest clearance appears similar in extent to that represented by the modern marsh at Tukou. The decline in charcoal signals in this later part may represent a decreased in the amount of available fuel available for burning at Tukou after an initial peak in human-induced fires.

EARLY HOLOCENE MARINE TRANSGRESSION AND VEGETATION CHANGE

The prominence of long-dispersal ability, as a feature of the Austral Islands flora (see chapter by Meyer et al., this volume), has led to selective immigration, and is responsible for many characteristic features of tropical/sub-tropical island floras, particularly during periods of lowered sea-level and consequent land expansion. The early Holocene sea-level transgression must have restricted the retention of coastal taxa, but its effect on the range of endemic taxa remains difficult to assess. Disjunct patterns of representation of endemic taxa in the Austral Islands may be directly caused by repeated sea-transgressions/inundation. As Paulay (1985) has suggested, on the highest islands montane cloud forests may have extended down in elevation to encompass a greater area during sea-level low stands. However, during the post-glacial marine transgression, genetically isolated populations may have been created within each of the main valleys, that were formerly connected along the now inundated coastal margins. Some tree and shrubs including Pandanus and Triumfetta may have been more prominent on the coast of Rapa prior to inundation.

Mid-Holocene sea-level and vegetation change
The most pronounced feature of the mid-Holocene record at Tukou is the development of coastal...
swamp forest vegetation. Records of swamp forest development elsewhere in the Pacific following mid-Holocene sea level change are available from mangrove pollen studies in Micronesia (e.g. Ward 1988; Kawana et al. 1995) and Tonga (Ellison 1989, 1991). No "true" mangrove taxa are presently known from the Austral Islands or in the sub-fossil record, but some of the specialised growth forms and life-histories that characterises the mangrove habit, namely aerial prop or stilt root growth phases, are found in a few coastal strand species (e.g. *Ficus* and *Pandanus* species). Prop roots are found in many species of *Pandanus* (Pandanaceae), notably on the most widespread species, *P. tectorius* (Stone 1976, 1988; St. John 1979). Tomlinson (1986) regards them as a stabilising feature of older trunked trees. *P. tectorius* is found throughout the tropical and subtropical Indian and Pacific Oceans in substrates ranging from freshwater swamps to coastal rocky beaches and seasonally brackish periphery of the tidal zone. For their ability to establish on these wide-ranging environments some *Pandanus* species have been described as "freshwater mangroves".

*Pandanus tectorius* is a common swamp and dry land forest tree found throughout the Austral Islands and on other islands in the region, it commonly forms monospecific stands with a sedge/herb dominated understorey (Ash & Ash 1984). As no "true" mangrove species occur in the Austral Islands, *P. tectorius* appears to assume the role of the mangrove type habit, forming dense stands along the few margins of tidal flats where human activity has not been prominent. Other *Pandanus* species may be indigenous to the Austral Islands, for example Harold St. John recorded 13 species of *Pandanus* on Rapa in 1934 and made a similar number of *Pandanus* species determinations for many Pacific Islands (e.g. Fiji, St. John 1976). Stone (1988) and Smith (1981) suggest many of these are simply varieties of *P. tectorius*. In examining the genus on Tahiti, Stone (1988) could not discount the human introduction of additional of *Pandanus* species or *P. tectorius* varieties.

The tree has an unusual life history rarely found in perennial plants (Halle et al. 1978) that may be an adaptation to coastal strand environments. From a study of Fijian populations, Ash (1987) found that *P. tectorius* prop roots usually do not develop until 5-12 years after a semi-prostrate growth and trunk growth phase. Prop root growths coincide with a flowering phase that may last for up to 40 years. Like "true" mangrove species this growth form allows these trees to adjust to mobile sediment regimes, but also to accrete sediment immediately behind the prop roots, creating an autogenic environment suitable for *P. tectorius* but also pollen preservation.

*P. tectorius* is a species which produces vast amounts of pollen, a strategy not often exhibited in perennial dioecious taxa. *Pandanus* pollen grains are generally dispersed by wind (anemophily) or small invertebrates (entomophily) (Meilleur et al. 1997). Modern pollen studies of *Pandanus* suggest it is only locally dispersed, though one case of long distance dispersal, presumably by river transport, to deep-sea sediments has been recorded by Van der Kaars (1991). One study from a series of lowland swamp forest sites in

Table 39: Additional palynomorphs recorded from Tukou Cores 2-6 not recorded in Core 1. Listed are the presence or absence of palynomorphs in Tertiary sediment (after Cranwell 1964), early to mid-Holocene sediments (Zones II and III) and in Zone IV sediments aged <1000 cal. yr BP, the botanical status and biogeographic affinity of taxa.

<table>
<thead>
<tr>
<th>Pollen taxa</th>
<th>Family</th>
<th>Present in Tertiary</th>
<th>Present in Zone II</th>
<th>Present in Zone III</th>
<th>Present in Zone IV</th>
<th>Indigenous representatives in modern flora</th>
<th>Biogeographic affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amaranthaceae</td>
<td>Amaranthaceae</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Y</td>
<td>?</td>
<td>Pan-tropical/Endemic</td>
</tr>
<tr>
<td>Arecaceae/Liliaceae</td>
<td>Arecaceae/Liliaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>Canavalia</td>
<td>Fabaceae</td>
<td>N</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>Canavalia sericea</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Canavalia spp.</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Possible extinct species</td>
<td></td>
</tr>
<tr>
<td>cf. Psychotria</td>
<td>Rubiaceae</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Psychotria rapensis</td>
<td>Endemic</td>
</tr>
<tr>
<td>Dicranopteris</td>
<td>Gleichenaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Dicranopteris linearis</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Dodonaea viscosa</td>
<td>Sapindaceae</td>
<td>Y?</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>Dodonaea viscosa</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>Geniostoma</td>
<td>Loganiaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>Y</td>
<td>G. quadrangularis, G. rapense, G. nepetra var. micranthum</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td>Myoporum</td>
<td>Myoporaceae</td>
<td>N</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td>Myoporum rapense</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td>Santalaceae</td>
<td>Santalaceae</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>N</td>
<td>Exocarpus psilitiformis, Santalum insulare var. margaretae</td>
<td>Indo-Pacific/Endemic</td>
</tr>
<tr>
<td>Scaevola taccada</td>
<td>Goodeniaceae</td>
<td>N</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>Scaevola taccada</td>
<td>Indo-Pacific</td>
</tr>
</tbody>
</table>
The Paleobotanical Record of Rapa: Indications for the Phytogeography

Southeast Asia (Anderson & Muller 1975) found that pollen representation may be poor from sites dominant in *Pandanus*, but this may be due to differential pollen production of species other than *P. tectorius*. It is likely that for this reason no other species will be discernable with any certainty. From Zone III of the Tukou Core 1 sequence I suggest that *Pandanus tectorius* swamp forest expanded behind a prograding tidal-river levee after around 2000 cal. yr B.P. This levee probably appeared due to accreting sediments built up behind developing *Pandanus* prop roots during a period of stable sea level. This autogenic process acted to restrict any tidal influence on the site and allowed the predominantly freshwater swamp to develop. Other taxa including *Celtis* and the Araceae: Iguanurinae type palm become established within this developing swamp forest. The mid-Holocene swamp forest expansion described may have allowed many plant taxa to establish on the island in a formerly restricted or unavailable environment.

Palynological data from five other mid-Holocene aged cores obtained from Tukou along a 100 m transect, extending inland from the Core 1 location, reveal a number of additional taxa not identified in Core 1 (Table 39). Important amongst these taxa are Santalaceae (either *Exocarpos psiliformis*, or *Santalum insulare* var. *margaretae*) discussed in regard to historical exploitation by Butaud et al. (2005) and Butaud et al. (see chapter by Butaud et al., this volume), *Myoporum* and *Geniostoma* which have endemic representatives in the modern flora. Macrobotanical remains identified from these same five other cores, mostly in the form of seeds (Table 40), provides evidence of local presence of *Celtis pacifica*, *Meryta* and *Pandanus tectorius* with some tentative identifications of *Astelia*, *Zanthoxylum*, Apocynaceae and possibly an extinct *Lepidium*.

Table 40: Macrobotanical remains recorded from Tukou Cores 1-6. Listed are the presence or absence of material in pre-human Holocene sediments (Zones I, II and III) and in Zone IV sediments aged <1000 cal. yr B.P., the botanical status and biogeographic affinity of taxa.

<table>
<thead>
<tr>
<th>Pollen taxa</th>
<th>Family</th>
<th>Material</th>
<th>Present in pre-human zones</th>
<th>Material present in human impact Zone IV</th>
<th>Indigenous representatives in modern flora</th>
<th>Biogeographic affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td>cf. Apocynaceae</td>
<td>Apocynaceae</td>
<td>seed</td>
<td>Y</td>
<td>N</td>
<td></td>
<td>Indo-Pacific?</td>
</tr>
<tr>
<td><em>Meryta</em></td>
<td>Araliaceae</td>
<td>seed</td>
<td>Y</td>
<td>N</td>
<td><em>M. chloristantha</em>, <em>M. brachypoda</em></td>
<td>Austral Islands endemic</td>
</tr>
<tr>
<td>cf. Lepidium</td>
<td>Brassicaceae</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td>EXTINCT</td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>cf. Astelia</td>
<td>Liliaceae</td>
<td>N</td>
<td>Y</td>
<td>N</td>
<td><em>A. rapensis</em></td>
<td>Endemic</td>
</tr>
<tr>
<td><em>Pandanus cf. tectorius</em></td>
<td>Pandanaceae</td>
<td>Y</td>
<td>Y</td>
<td>N</td>
<td><em>Pandanus cf. tectorius</em></td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td>cf. Zanthoxylum</td>
<td>Rutaceae</td>
<td>seed</td>
<td>Y</td>
<td>N</td>
<td><em>Zanthoxylum</em></td>
<td>Indo-Pacific</td>
</tr>
<tr>
<td><em>Celtis pacifica</em></td>
<td>Ulmaceae</td>
<td>seed</td>
<td>Y</td>
<td>N</td>
<td><em>Celtis pacifica</em></td>
<td>Indo-Pacific</td>
</tr>
</tbody>
</table>
HUMAN IMPACT AND VEGETATION CHANGE

Palaeoenvironmental research in the Pacific Islands has focused on the issue of whether vegetation change in late Holocene records can be used as a proxy of human impact and initial colonization, especially in situations where the archaeological record remains ambiguous (Flenley et al. 1991; Spriggs & Anderson 1993; Kirch & Ellison 1994; Parkes 1997; Dodson & Intoh 1999; Stevenson et al. 2001; Athens et al. 2002; Anderson 2003). Palaeobotanical records now provide a robust proxy for human activity, particularly in remote archipelagos like the Austral Islands, as human colonisation was late on these islands. Palaeobotanical research conducted on Rapa (Kennett et al. 2006) by the author on Haurei sediments recorded the introduction of agriculture signaled by the appearance in sedimentary sequences of introduced plant cultigen pollen (e.g. *Colocasia esculenta*). Such evidence provides an unequivocal human introduction and its appearance parallels evidence for burning as indicated by increasing charcoal concentrations in the same records and the decline in arboreal pollen types. The rise of pollen and spores of seral taxa are also found to increase in conjunction with more colluvial sedimentation. The human colonisation sequence on Rapa, evident in the palaeobotanical record and familiar to most remote Pacific islands settled within the last 1500 cal. yr B.P., involved the substantial alteration of the environment in the form of lowland deforestation and the establishment of extensive agricultural systems. The decline of a *Pandanus* palm tree swamp forest is a feature of this record, although several other taxa identified in pre-human aged sediments are not found after 800 cal. yr B.P. (*Omalanthus*, *Myoporum*, *Santalaceae*, *Lepidium*, *Amaranthaceae* and *Haloragis*). Decline in these taxa may reflect a direct response to human-induced forest clearance, but may also represent the environmental impact of rat (*Rattus exulans*) introduction, or a response to the extinction of key bird dispersers including cf. *Ducula*, *Gallirallus* and *Cyanoramphus* (Tennyson & Anderson 2012).

CONCLUSIONS

From the palaeobotanical research conducted on Rapa, the diversity and endemic character of the flora, with its high representation of sub-tropical Pacific lineages, is a fragmented relict of a formerly more diverse flora. Many of the endemic genera represented on the island probably did not evolve as endemics in situ but became extinct on other island groups either from preceding climatic or geological events (namely sea-level fluctuations) or through extensive environmental impact associated with human impact. The relative floral richness of Rapa compared with the other islands in the Austral Islands, discussed by Meyer et al. (see chapter by Meyer et al., this volume) is intriguing. I suggest that the island’s elevation and geographic/geomorphic diversity, including the size of the eroded volcanic calderas and disjunct valley systems, may have maintained greater habitat heterogeneity, allowing endemic species to survive despite the intense and continuing environmental degradation, following human settlement evident on the Austral Islands.
Sandalwood (*Santalum insulare*) formerly planted on Tubuai Island, May 2012 (Photo J.-F. Butaud).
Sandalwood

Sandalwood is a small, root hemi-parasitic tree, prized worldwide for the distinctive fragrance of its heartwood (its sapwood has no scent). Sandalwood essential oil, extracted by distillation of the wood, is used in perfumery and aromatherapy. In India and China, sandalwood has been used in religious ceremonies for thousands of years, particularly as temple incense (Ehrhart & Nasi1996).

There are 16 species of sandalwood, exclusively distributed in the Indo-Pacific region (Barrett & Fox 1995). The most commonly known species, the white sandalwood (due to the pale color of its heartwood) or Indian sandalwood (*Santalum album*), grows naturally and is cultivated in India, Indonesia, and Australia, but has also been introduced into many countries including French Polynesia. Other known species are the yellow sandalwoods (with a yellowish heartwood) from New Caledonia (*Santalum austrocaledonicum*) and Fiji (*Santalum yasi*).

### The sandalwood in French Polynesia

There is only one native species of sandalwood in French Polynesia, the eastern Polynesian sandalwood (*Santalum insulare*). This species is also found on the Cook Islands (Mitiaro only) and on the Pitcairn Islands (Henderson only), hence it is endemic to eastern Polynesia. In contrast, the Indian, New Caledonian, and Fijian sandalwoods were introduced relatively recently to French Polynesia for timber. Among these three species, the Indian sandalwood is now a naturalized species on the semi-dry hills of the northwestern coast of Tahiti, on Moorea and Hiva Oa (Butaud & Defranoux 2007). Botanists have divided *Santalum insulare* into nine varieties restricted to the different archipelagos, based on their anatomy (flowers, fruits, and leaves) (Fosberg & Sachet 1985). Of these nine varieties, two are found on the Austral Islands: the first is endemic to Raivavae (var. *raivavense*) and the second to Rapa (var. *margaretae*). Botanists and foresters have never been able to demonstrate the presence of sandalwood on the other Austral Islands (Maria, Rimatara, Rurutu, Tubuai, and Marotiri), despite several indications on Tubuai (Aitken 1930; Sam Tahuhuterani pers. comm. 2002). Furthermore, surveys done under the present scientific program did not identify any introduced species of sandalwoods. However, it is likely that the Indian sandalwood is present in gardens on Tubuai and Rurutu, the most populated islands.

### History of the discovery and exploitation of sandalwood from the Austral Islands

In 1896, Jean Nadeaud was the first botanist to obtain the information on the Austral Islands sandalwood, in this case that of Raivavae (Nadeaud 1896). However, these sandalwood populations had been made known to the western world some 70 years earlier, at the time of the sandalwood traders and the triangular trade between the Anglo-Saxon sailors, China, and the Pacific islanders. The latter supplied wood to the sailors in exchange for metal objects, fabric, whaleboats, weapons and liquor. Sandalwood traders used the wood as an exchange currency with China, mainly for tea (Shineberg 1967; Dening 1980). The stock of sandalwoods on the two (or three) islands must have been low compared to Fiji, the Marquesas, Hawaii, or New Caledonia as there are very few traces left of this exploitation.

### Raivavae

According to Edwards (2003, partially quoting Maude 1968): "Sandalwood traders were coming to Raivavae in the 19th century. Captain Fodger convinced the locals to supply 1.5 tons of sandalwood in 1812 (Maude 1968: 196) and in 1819, Captain Lewis agreed with the Tahitian King Pomare II to take him to Tubuai and Raivavae in exchange of sandalwood from Raivavae. There are very few records of visits of sandalwood traders on Raivavae but sandalwood was as at the time the main commodity in eastern Polynesia. It is therefore likely that other traders came. Oral tradition confirms this allegation as the top of the Taamoa peninsula (probably Taamora, the summit of Vaianaua peninsula) was allegedly covered with sandalwood forest. Today, it is mainly grasslands. (...) In 1817, sandalwood was the main commodity of the eastern Pacific but trade was declining due to the depletion of sandalwood resources on many islands. In addition, the Australian government imposed a tax..."
of 2.10 pounds per ton of sandalwood (and mother-of-pearl) (Maué 1968: 200). An important reserve of sandalwood remained on Raivavae and Tubuai, but high demographic pressure on limited resources caused frequent tribal wars which sidelined the trade and the flow of highly desirable European goods”.

Maué & Crocombe (1962) further mentioned that Captain Michael Fodger of the Daphne obtained 1.5 tons of sandalwood as ransom for the release of a Raivavae chief he held hostage. This is more proof of the brutality of sandalwood traders throughout Polynesia. Fodger was the first to mention the presence of sandalwoods on Raivavae. Captain Lewis of The Arab was persuaded by Pomare II to take him to the island in exchange for sandalwood, following the information provided by Fodger (Massal 1973).

Rapa

Hanson (1973) recounts: “In 1825, taking advantage of a stopover on Rapa, the galley Snapper loaded several tons of sandalwood. In 1826, an English trader settled on the island for the exploitation of resources, including sandalwood, a commodity highly-prized by the Chinese at the time”. Shineberg (1967) notes that sandalwood had been found on the Austral Islands in the 1820s: "Captain Ebrill brought back 40 tons from his 1826 voyage, and 28 tons in his 50-ton schooner the year after”. However, she questions the veracity of the statements made by sandalwood traders who might have wanted to conceal a more important source of sandalwood (New Hebrides).

Given that these two sources are concordant, it is highly likely that part of the sandalwood exploitation on Rapa (and, similarly, on Raivavae) occurred in the mid-1820s. These dates and information are reported in the Encyclopédie de la Polynésie (Toullelan 1986).

Based on an average weight of 50 kg of heartwood per tree, the 70 tons of sandalwood harvested on Rapa represented about 1750 individual trees.

Assessment

Sandalwood was occasionally exploited on the Austral Islands over two decades (from 1812 to 1827). This consisted of uprooting the trees, stripping them of their sapwood on the spot and transporting the logs to the seashore. Tree populations were thus overexploited. J. Nadeaud (1896) noted that sandalwood used to be abundant on Raivavae, but that the populations were plundered for sale (or bartering). However, Edwards (2003) indicated that tribal wars interrupted the sandalwood trade on Raivavae and that much wood remained during the first quarter of the 19th century. Nevertheless, it is possible that the remaining populations were exploited between 1830 and the end of the 19th century.

TRADITIONAL AND CONTEMPORARY USES OF SANDALWOOD ON THE AUSTRAL ISLANDS

The Polynesian name for sandalwood on the Austral Islands is the same on Raivavae and Rapa: "ahi". Early botanists sometimes spelled it "eahi", including the "e" meaning "the" or "this". In comparison, sandalwood is called "ahi" on the Society Islands, "puahi" on the Marquesas Islands, and "a'i" on the Cook Islands. As elsewhere in the Pacific (Brown 1933; Shineberg 1967), the inhabitants of the Austral Islands, in particular those of Raivavae (Nadeaud 1896), identified several varieties of sandalwood based on the qualities of the heartwood (scent, color, hardness). It appears that regardless of the species, there are roughly three varieties:

- • a high-quality dark sandalwood often called red,
- • a relatively high-quality sandalwood called yellow,
- • a low-quality sandalwood called white.

These names have led to some confusion between the high-quality Indian white sandalwood and the low-quality variety (white) of Polynesian red sandalwood. As far as Raivavae is concerned, J. Nadeaud noted in 1896, from the account of one of his acquaintances, a native of the island, the different varieties recognized by the islanders:

- • The "ahi mara aito" with hard and dark wood;
- • The "ahi popouru" with soft and very fragrant wood, the real "ahi";
- • The "ahi tiare", called "ahi marea" by the Tahitians, with a pale yellow wood.

While the inhabitants of Raivavae distinguished the different varieties, we have no record of any traditional use from the island even if it is likely that many uses existed. An ethnobotanical study of the island should help collect more information even if some knowledge has been lost.

On Rapa, sandalwood was only used as fuel wood due to its pleasant smell. It is likely that it was also appreciated for its insect repellent properties. Aitken, an ethnologist who studied life on Tubuai in the 1920s (Aitken 1930), reported several uses of sandalwood on the island. Unfortunately, it cannot be determined whether these applied to the local sandalwood or to that from Raivavae. Nor is it known whether the inhabitants practicing such uses were those who originally came from other islands. Indeed, Aitken’s inventory of the plants of the island does not include the sandalwood or "ahi/eahi/iahi".

The reported uses included the following:

- • Flowers and pieces of sandalwood or rosewood are placed in the box used to store clean laundry.
- • Sandalwood was used to perfume the tapa.
- • "Raau vari": cure for painful periods or lack of menstruation. Mix the water of four green coconuts with a handful of dried sandalwood pow-
There is clearly an imbalance of available information between Tubuai, where there is little or no sandalwood left, and Raivavae and Rapa, where natural populations remain. It suggests that some knowledge on the Raivavae and Rapa sandalwoods must have been overlooked or lost. Ethnobotanical studies of both islands are highly desirable in order to preserve any remaining knowledge.

During the past ten years or so, a demand for sandalwood has arisen on Raivavae (no commercial prospect for sandalwood exists on Rapa, where there are only relict populations). Sandalwood is transformed and sold as hairpins, powder to perfume the monoi or even as raw wood on Raivavae or Tahiti.

BOTANICAL DESCRIPTION OF THE SANDALWOOD FROM THE AUSTRAL ISLANDS

Botanical history
The first samples of sandalwood from the Austral Islands were collected in 1921 by a couple of American ethnologists, the Stokes, who spent several months on both islands (mainly on Rapa). In 1935, the American botanist F.B.H. Brown used the two samples to describe two new taxa:

- *Santalum insulare* var. *raivavense* for the Raivavae sandalwood, considering the variety to be very close to the Tahitian one (*Santalum insulare* var. *insulare*).
- *Santalum margaretae* for the Rapa sandalwood, considering that the anatomical differences from the Tahitian variety were significant enough to describe it as a different species.

In 1938, C. Skottsberg, using the samples collected by H. St John and F.R. Fosberg during the 1934 Mangarevan Expedition, validated *Santalum insulare* var. *raivavense* and reduced the Rapa sandalwood to a simple variety of the Polynesian sandalwood, *Santalum insulare* var. *margarita*, considering that the observed variation did not justify its naming as a distinct species (Skottsberg 1938).

The latest study, by Fosberg & Sachet in 1985, maintained and repositioned both varieties within the nine botanical varieties of *Santalum insulare* of eastern Polynesia and considered the species as a variable complex.

Recent morphological data
The botanical descriptions by Fosberg & Sachet (1985) can be amended with our own observations and collections of fruits (N = 36), seeds (N = 206), and leaves (N = 520). While hundreds of measures of seeds and leaves were taken during the different missions, the former descriptions were based only on three collections for the Rapa variety and eight for the Raivavae variety. In addition, no description of the mature fruit was available for either variety; the fruit described from Rapa was clearly immature. The newly acquired data are presented in Tables 41 and 42.

Fruits and Seeds
During the various expeditions, fruits, seeds (shell and kernel), and shell pieces (endocarp) were collected from the various populations. Sometimes, the only parts available were leftover seeds gnawed by rats. The figures in Table 41 relate to mature fruits and fully developed seeds except the fruit collected on Rapa. Only one green fruit, shaped as a double pear (narrowed at the apex and base) was observed on Rapa on a tree in the Karapoo Rahi population. Three old nuts damaged by rats were found on the ground in Anatukuri Nako and a single one in Karapoo Rahi. The green fruit was close to maturity as its seed was well developed and hard. However, it is likely that a mature fruit would have been 1 or 2 mm bigger than the green fruit, making it 28 mm long and 19 mm wide. The dimensions and shapes of the fruits and seeds were recorded. Average, maximum, and minimum values for each population are noted in Table 41. Sandalwood seeds have a more or less pointed apex and a more or less developed excrescence at the base. These parameters were estimated, along with the roughness of the seeds. Seeds have lines of weakness or ridges where the shell cracks open upon germination; the number of ridges, mainly between two and four, was recorded. Raivavae fruits are round to oval, averaging about 25 mm in length and width while the only fruit from Rapa is more oval and slender, reaching an estimated length of 28 mm and an estimated width of 19 mm at maturity. Based on these unbalanced data, a net differentiating criterion would be the length/width ratio, which is higher than 1.4 on Rapa and lower than 1.2 on Raivavae.

On Raivavae, seeds are oval, obtuse, and rough. Most often, they have three dehiscence lines and very little excrescence at the base. They have an average length of 17.2 mm and an average width of 15.7 mm with a length/width ratio lower than 1.2. The limited data available from Rapa indicate a length of 19 mm and a width of 13.1 mm, with a ratio higher than 1.3. The length/width ratio is also a distinctive criterion between both varieties.
It should be noted that the dimensions of these apparently viable fruits and grains can vary by a factor of two within the same population. Seeds from “motus” on Raivavae appear to be slightly larger than those from the main island.

Leaves
The sample size was 10 adult leaves per tree. Table 42 presents the average, maximum, and minimum values for each population and each island of the length and width of the limb, the length of the petiole, the nervation, and the angles of the apex and limb base.

Measurements show that the leaves of Raivavae sandalwoods are elliptical to oval, with a petiole of (13)-8-(4) mm long. The limb is acute to obtuse, 79 mm long and 42 mm wide on average and has 6 to 14 pairs of veins. Leaves of Rapa sandalwoods have similar characteristics, but are more frequently oval, with an obtuse apex on the limb. On average, the limb is 66 mm long and 32 mm with 6 to 11 pairs of veins and the petiole is (10)-7.4-(5) mm. The limb is smaller on average on Rapa (which could be due to more restrictive weather...
Terrestrial Biodiversity of the Austral Islands,
French Polynesia

Table 42: Morphological data of leaves of *Santalum insulare* from the Austral Islands (dimensions in mm and angles in grads, max-average-min).

<table>
<thead>
<tr>
<th>Island</th>
<th>Population</th>
<th>Nb. trees</th>
<th>Shape (E = Elliptical, O = Oval)</th>
<th>Pétiole</th>
<th>Lenth</th>
<th>Width</th>
<th>Apex (A = Acute, O = Obtuse)</th>
<th>Nervation</th>
<th>Apex angle</th>
<th>Base angle</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Raivavae</strong></td>
<td>Anatonu-Mouatapu area</td>
<td>3</td>
<td>E &gt; O</td>
<td>7-5.8-5</td>
<td>88-71-60</td>
<td>50-40-31</td>
<td>A</td>
<td>11-9-7</td>
<td>130-95-70</td>
<td>150-120-100</td>
</tr>
<tr>
<td></td>
<td>Anotonu temple</td>
<td>3</td>
<td>E &gt; O</td>
<td>12-9.4-6</td>
<td>123-83-62</td>
<td>50-39-29</td>
<td>O &gt; A</td>
<td>12-9-6</td>
<td>100-75-60</td>
<td>150-110-70</td>
</tr>
<tr>
<td></td>
<td>Hotuatu islet</td>
<td>3</td>
<td>E = O</td>
<td>11-6.7-5</td>
<td>109-81-65</td>
<td>52-45-34</td>
<td>A</td>
<td>12-9.5-8</td>
<td>120-85-60</td>
<td>150-120-90</td>
</tr>
<tr>
<td></td>
<td>Mahanatoa-Pahonou area</td>
<td>1</td>
<td>E &gt; O</td>
<td>8-7-16</td>
<td>58-52-43</td>
<td>32-29-26</td>
<td>O &gt; A</td>
<td>9-7-5-6</td>
<td>130-90-70</td>
<td>150-100-90</td>
</tr>
<tr>
<td></td>
<td>Anotonu-Mahanatoa area</td>
<td>1</td>
<td>E</td>
<td>11-9-8-8</td>
<td>87-76-72</td>
<td>50-40-30</td>
<td>O</td>
<td>8-7-7</td>
<td>120-85-70</td>
<td>100-90-80</td>
</tr>
<tr>
<td></td>
<td>Moutapu</td>
<td>1</td>
<td>E = O</td>
<td>8-6-4-6</td>
<td>58-53-47</td>
<td>31-27-20</td>
<td>A</td>
<td>8-6-5-6</td>
<td>100-70-60</td>
<td>130-115-90</td>
</tr>
<tr>
<td></td>
<td>Tapioi</td>
<td>1</td>
<td>E</td>
<td>12-11.3-10</td>
<td>72-63-57</td>
<td>47-38-32</td>
<td>A</td>
<td>10-8-5-7</td>
<td>120-95-80</td>
<td>120-100-80</td>
</tr>
<tr>
<td></td>
<td>Vaiamau peninsula</td>
<td>8</td>
<td>E &gt; O</td>
<td>12-8-5</td>
<td>100-70-50</td>
<td>61-39-22</td>
<td>A &gt; O</td>
<td>12-9-6</td>
<td>160-105-60</td>
<td>160-105-70</td>
</tr>
<tr>
<td></td>
<td>Motu Haha</td>
<td>2</td>
<td>E = O</td>
<td>11-8-3-5</td>
<td>91-77-66</td>
<td>58-49-31</td>
<td>O &gt; A</td>
<td>11-9-7</td>
<td>120-90-70</td>
<td>150-125-80</td>
</tr>
<tr>
<td></td>
<td>Motu Mano Iti</td>
<td>3</td>
<td>E</td>
<td>9-7-6-4</td>
<td>94-83-40</td>
<td>63-44-35</td>
<td>O &gt; A</td>
<td>13-10-7</td>
<td>140-105-70</td>
<td>150-115-80</td>
</tr>
<tr>
<td></td>
<td>Motu Niupapa Rahi</td>
<td>1</td>
<td>E</td>
<td>9-7-3-5</td>
<td>94-84-72</td>
<td>45-38-31</td>
<td>A</td>
<td>10-9-8</td>
<td>100-80-70</td>
<td>160-120-100</td>
</tr>
<tr>
<td></td>
<td>Motu Numiri Rahi</td>
<td>3</td>
<td>E</td>
<td>11-7-7-4</td>
<td>99-83-66</td>
<td>57-45-30</td>
<td>O &gt; A</td>
<td>13-10-7</td>
<td>140-105-70</td>
<td>150-115-80</td>
</tr>
<tr>
<td></td>
<td>Motu Rani</td>
<td>3</td>
<td>E</td>
<td>11-8-5-5</td>
<td>113-87-66</td>
<td>54-47-30</td>
<td>O &gt; A</td>
<td>12-9-5-8</td>
<td>120-90-70</td>
<td>120-100-80</td>
</tr>
<tr>
<td></td>
<td>Motu Vaiaamu</td>
<td>5</td>
<td>E &gt; O</td>
<td>12-8-5-4</td>
<td>107-85-64</td>
<td>58-43-31</td>
<td>O &gt; A</td>
<td>14-10-5-8</td>
<td>130-85-50</td>
<td>140-110-80</td>
</tr>
<tr>
<td><strong>Rapa</strong></td>
<td>Karapoo Rahi</td>
<td>7</td>
<td>O &gt; E</td>
<td>8-6-5-5</td>
<td>91-67-46</td>
<td>50-33-22</td>
<td>O</td>
<td>11-8-6</td>
<td>100-65-40</td>
<td>150-95-70</td>
</tr>
<tr>
<td></td>
<td>Anatakuri Nako</td>
<td>2</td>
<td>O &gt; E</td>
<td>10-7-8-5</td>
<td>78-64-50</td>
<td>37-31-22</td>
<td>O</td>
<td>12-8-5-6</td>
<td>80-60-50</td>
<td>120-90-60</td>
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<tr>
<td><strong>Total</strong></td>
<td></td>
<td>9</td>
<td>O &gt; E</td>
<td>10-7-4-5</td>
<td>91-66-46</td>
<td>50-32-22</td>
<td>O</td>
<td>11-8-6</td>
<td>100-65-40</td>
<td>130-95-60</td>
</tr>
</tbody>
</table>

There was no significant variation between the populations of the high island and those of the "motus" on Raivavae. However, the leaves from the low-altitude sheltered populations appear to be larger than those from the exposed populations at higher altitude. Thus populations at Moutapu (high altitude cliff), Mahanatoa Pahonu (exposed rocky area at medium altitude), and Tapioi (boulder at mid-altitude) have smaller limbs. These observations indicate the existence of ecotypes by adaptation to site-specific conditions.

**Assessment**

More information is now available, allowing a better characterization of these two varieties. Differentiating criteria are clearer for seeds and leaves but there is an important variability within each variety and population. In addition, these variations could be correlated with ecological conditions such as altitude and climate, showing that the sandalwood adapts to its habitat.
This assessment is based on information from herbarium samples, inhabitants of the islands of Tubuai, Rapa, and Raivavae, and recent surveys.

**Tubuai**

As mentioned above, no botanist has ever found any sandalwood on Tubuai. The locals simply recall that "previously", sandalwood was present on the island (Butaud 2006). Recently, only one person could attest the presence of sandalwood ten years earlier on Tubuai (S. Tahuhuterani pers. comm. 2002). It seems reasonable to assume that sandalwood still exists on the island based on this account and the configuration of the island. The area mentioned includes Mt Tavaetu and Mt Hanareho, their western slopes, and their eastern foothills where a tree supposedly used to be exploited near the old "tou" (*Cordia subcordata*) or "miro" (*Thespesia populnea*). In 2003, a one-day survey focused on the area but there was no sign of sandalwood. If there are any sandalwoods remaining on Tubuai, it is likely that there are fewer than ten relict individuals. However, it is likely that a few trees were recently introduced from Raivavae and grow on Tubuai near settlements.

**Rapa**

Before our surveys, sandalwood populations on Rapa Island were known to botanists from two sites: the historical site of Mt Tanga, where the first two samples were collected in 1921 and 1934, and Anatakuri Nako bay, near the pass leading to Akao bay, discovered in 1984. Our surveys focused on these sites, as well as on two other sites mentioned by islanders, in particular by Benjamin Pukoki, the local SDR manager. The latter sites are located respectively on the left side of Anarua valley and on Karapoo Rahi islet. The findings of the surveys are presented in Figure 31 and in the following paragraphs (Butaud 2006).

The summit of Mt Tepiahu to Mt Tanga east of Haurei (Ahurei) was surveyed, as well as the slopes northwest of the pass between these two mounts. No sandalwood tree was found. The vegetation is very degraded today, consisting only of a bush of Cattley guavas (*Psidium cattleianum*), ferns (*Dicranopteris linearis*), and "reeds" (*Miscanthus floridulus*). This degradation is probably due to fires and overgrazing by goats. In addition, the site is relatively visible and accessible from the current quay from which the inhabitants or possibly visitors could have easily spotted any sandalwood. Another Mt Tanga exists north of Area and was visited. The vegetation there is very low and again no sandalwood tree was observed.

**Anatakuri Nako bay**

The islanders, in particular B. Pukoki, know this sandalwood site. The botanists J. Florence and N. Hallé also visited the site in 1984. According to J. Florence, it contained about 30 trees in 1984; 10 years ago (around 1992), only about 15 trees were known from the site, according to B. Pukoki. The survey shows that this historical population now includes only three live trees and 13 dead trees, still standing or washed away by a landslide. The site is exposed to the north and has a slope of 70%. This stand is located in Anatakuri Nako bay, under the pass to Akao bay. The main tree was found at an altitude of 205 m and had a diameter at breast height of 13 cm (stump diameter of 24 cm) for a height of 4.5 m. The two other trees had a stump diameter of respectively 13 and 26 cm. On the observation date, March 26, 2002, the leaves just came out, with a pale to soft green color and were visible from far away. Only a few flower buds were observed. No fruit was found. Three old nuts damaged by rats were found on the ground: the width of the shells was measured and was close to 12.5 mm.

The surrounding vegetation was very poor as *Freycinetia* and *Macropiper* were the only semi-woody plants directly found near the sandalwoods. What appeared to be a *Sophora* had been dead for several years and a little further, a few *Cyathea* and *Metrosideros* were observed. Several assumptions can be made to explain the extremely rapid decline of this population. First, no regeneration is possible due to the presence of...
rangers and their predation on fruits, as well as the presence of goats and their predation on any plantlets and suckers. Mature trees are constantly under the attack of goats (and maybe cows) that eat the leaves. This is obvious as no leaf was found below one meter fifty from the ground. Furthermore, goats are causing the disappearance of host plants, leading to a nutritional stress for the sandalwoods. And last, it can be reasonably assumed that soil compaction due to the presence of herbivores has a negative impact on sandalwoods (root asphyxia) and that, associated with the loss of neighboring trees, contributes to landslides on steep slopes as observed for this population. The landslide has washed at least three sandalwoods and four other live or dead trees are located at its edge. It is remarkable that anthropogenic exploitation of sandalwood has played no role in the decline of this population. There was no sign of exploitation on this site well known by the islanders. A potential conservation effort for this very precarious stand would be to build a fence impassable to herbivores and to plant native trees near the sandalwoods and the landslide.

**Anarua bay**

Thirty years ago, B. Pukoki noticed at least three sandalwoods on the southern side of Anarua bay, above Akaeke point. The survey area is located at an altitude of 150 m, with a northern exposure and an average slope of 80%. This site is a relict semi-dry forest including the following woody species: *Metrosideros collina*, *Nesoluma polynesicum*, *Streblus anthropophagorum*, *Psyludax odorata*, *Cyclophyllum barbatum*, *Myrsine* sp., *Meryta* sp., *Myoporum rapense*, *Boehmeria virgata*, *Celtis pacifica*, *Myoporum pertinax*, *Allophyllus rapensis*, *Scirpus* sp., and *Freyacineta* sp. No sandalwood, dead or live, was found. The forest was highly degraded due to overgrazing by goats and cows. Several trees were observed, particularly on the lower part. The sandalwoods observed 30 years ago might have been exploited and thrown to the ocean from the neighboring cliff.

**Karapoo Rahi islet**

B. Pukoki and several other inhabitants knew this population of sandalwoods. It is found on an islet located south of the island, separated by a stretch of shallow water of about thirty meters wide. The side where the sandalwoods are found has a western and northwestern exposure, an altitude of 80 to 110 m and a slope of 80%.

This population comprised 11 distinct adult trees and four dead trees. There was no sign of regeneration and no indication of exploitation by man. The sapwood was still intact on the dry trees, which means that they died not long ago. Dry leaves were even present on one of the dead trees. Goats (about thirty) have devastated this islet. Rats were also present as indicated by an old eaten nut on the ground.

On March 26, 2002, the trees had recent leaves of light to soft green color. Some trees seemed to have been affected by the sea spray. The phenological stage was more advanced than on Anatakuri Nako as most trees were in full bloom. A single fruit was observed; a large double-pear shaped green fruit of a length of 26 mm and a width of 18 mm, with a 19 mm long and 14 mm wide seed. The nut found on the ground had the same dimensions. The largest tree was 4 m tall with a diameter at breast height of 17 cm.

The surrounding vegetation was very degraded and poor due to overgrazing by goats. It was primarily herbaceous layer including *Paspalum conjugatum*, *Commelina diffusa*, *Bident pilosa*, *Ageratum conyzoides*, *Macropiper* sp., and *Gahnia* sp. There were several scattered shrubs and trees, including *Cyathea medullaris* (many dead individuals), *Pandanus* sp., *Xylosma* sp., and *Celtis pacifica*.

This population is likely the most important on Rapa and apparently the only hope for safeguarding this endemic variety if conservation measures are taken. It is crucial to eradicate the goats from this island of high value for flora (J.-F. Butaud pers. obs.) and fauna. The second step would be to eradicate the rats for the benefit of birds, insects, and the regeneration of some plant species.

**Assessment**

There are very few data available on the original range of the Rapa sandalwood. Therefore, it is difficult to assess the extent of the populations of sandalwood before the arrival of sandalwood traders or herbivores about 200 years ago. However, several assumptions can be made:
The exposure is significantly similar for the four sites visited: west, northwest to north. It appears that the sandalwoods on Rapa prefer the sites most exposed to the sun and heat, with the driest conditions. This confirms the observations made on the Society Islands (Butaud 2004). The altitude range is also relatively restricted for the various sites (between 80 and 250 m). The sandalwood seems to grow at a lower altitude, with a lower level of precipitations.

Sandalwood populations were observed on steep slopes (70 to 80%), which are common on Rapa. This does not preclude the growth of sandalwoods on gentler slopes (< 50%). However, populations on gentle slopes are easier to access and exploit, which might have led to their loss on such sites and their restriction to steeper slopes today.

Finally, while highly degraded, the vegetation on these sites could be considered as a low altitude mesophilous vegetation, but not supralittoral. Most tree species found on these sites do not grow at higher altitudes (above 300 m) where the vegetation varies from hygrophilous to ombrophilous.

It is highly likely that the original range of the Rapa sandalwood covered areas of mesophilous vegetation, at an altitude between 10 and 300 m, with a slope higher than 50%, and facing west, northwest and north. Potential surveys should focus on this type of habitat to search for new populations of sandalwood. The chances are very small as neither the local inhabitants, nor the Hawaiian botanists who visited the area for a month during the first half of 2002 were able to find other trees. The 14 trees found in 2002 should be compared to the estimated 1 750 trees exploited by sandalwood traders in the beginning of the 19th century. This clearly shows that exploitation by man was the main factor leading to the depletion of sandalwood on the island of Rapa.

**Raivavae**

Before our various surveys, seven populations of sandalwood were known through herbarium samples. Three populations were from coral "motus" (Vaiamanu, Tahaupaetoru, and Haamu), one from a volcanic islet (Hotuatua), and the three others from the high island itself (Vaianaua, northern slopes of Mt Hiro and south side of Mt Hiro). Samples highlighted one of the characteristics of the Raivavae sandalwood: it grows both on limestone on "motus" and on the volcanic soils of the high island. Among the seven populations, six were found during our recent surveys. The population on the southern side of Mt Hiro was not located but is not necessarily lost as the survey in the area was limited. In addition, 13 new populations were found. All sites were surveyed and studied (Fig. 32) with the exception of Anatou stadium — the population was observed through binoculars —, the south side of Mt Hiro, and Motu Haamu, which was not surveyed during the expeditions but still has many sandalwoods (W. Tetuanui, SDR pers. comm.). Table 43 presents the altitude and population size for each site.
In addition to the "motus" in the aforementioned table, the Papararuu, Ruahune, Arae, Ruahota Rahi, Ruahota Iti, Opunui, Numiri Iti, Tou, Otaha 4, and Otaha 3 "motus" were visited but no sandalwood was observed. It appears that the size of the "motu" might affect the presence or absence of sandalwood. Below a certain surface threshold, sandalwoods are not present. Small "motus" are often submerged by the sea, which could impede the growth or germination of sandalwoods. Larger "motus" are higher and often protected against sea rise. The originality of Raivavae compared to the other islands where sandalwood can be found in French Polynesia lies in the diversity of its soils. The Raivavae sandalwood can be found both on the "motu" coral soils and on the volcanic soils of the high island. Sandalwoods on "motus" are peculiar, as are some other plant species (Myoporum stokesii, Nesoluma polynesicum) unusual for this type of habitat. Precipitations might be a factor as they are well distributed throughout the year and might wash out the salt from the sols (150 mm per month on average with a minimum of 108 mm in September). Therefore, there are two main types of populations (Butaud 2006).

### Populations on "motus"

"Motus" are flat limestone areas, varying from sand to gravel with more or less organic matter. The surrounding vegetation is rather sparse with a grass cover. The main trees found near sandalwoods include the "tafano" (Guettarda speciosa), the "fara" (Pandanus tectorius), the coconut tree (Cocos nucifera), the "pu'atea" (Pisonia grandis), and the "aito" (Casuarina equisetifolia). It should be noted that no other species, including the sandalwood, is found on the pure stands of "aito", "pu'atea", and "fara". The shrub layer can contain the "pohotura'aua" (Sophora tomentosa), the "nanie" (Suriana maritima), the "ouru" (Scaevola sericea), Hedyotis romanzoffiensis and the "miki miki" (Pemphis acidula). The herbaceous layer includes the "naveoveo" (Lepturus repens), the "tonene" (Cassytha filiformis), Psilotum nudum, Chamaesyce fosbergii, Boerhavia tetrandra, the
"metuapua’a" (*Microsorum grossum*), *Achyranthes aspera* var. *velutina*, the "pia" (*Tacca leontopetaloides*), *Davallia solida*, and *Nephrolepis* sp. Regenerated sandalwoods were only observed on the Motu Rani. Most trees are from root or stump suckers, following harvest but mainly due to accidental or deliberate (clearing) fires that regularly devastate some islets such as Motu Mano Rahi. The biggest sandalwoods are 6 m tall with a diameter of 15 cm at the base. On average, they are about 3 m tall with a diameter of 8 cm. The heartwood is only formed in the roots when they are not unearthed for sale or for monoi.

**Populations on the high island**

They are found mainly on dry crests with a northern exposure (populations from Anatonu to Mahanatoua) as well as near rocky areas (Tapioi, Mouatapu, Vaianau Peninsula, and Hotuatua islet). These topographical conditions match those of the sandalwoods found on the other islands of French Polynesia. The slope is not necessarily steep and some trees can even be found on a flat terrain (Mt Taamora on the Vaianau peninsula). The surrounding vegetation is usually low (less than 5 m), open, and degraded by fires or feral goats. The tree and shrub layers include "purau" (*Hibiscus tiliaceus*), "fara" (*Pandanus tectorius*), *Xylosma suaveolens*, *Celtis pacifica*, *Premna obtusifolia*, *Glochidion raivavense*, *Psidium guajava*, and even *Serianthes rurutensis*. The herbaceous layer consists of *Microsorum grossum*, *Ocimum gratissimum*, *Miscanthus floridulus*, *Elephantopus mollis*, *Dianella intermedia*, *Nephrolepis* sp., *Dioscorea* sp., *Davallia solida*, and *Dicranopteris linearis*. The lower
part of the "Anatonu temple" stand is located on an unusual raised limestone area, where some more calcicolous species such as the "tafano" (Guettarda speciosa) are found. The sandalwoods on the high island are generally shorter than 5 m, including the numerous suckers from the Anatonu populations.

Assessment
The original range of the Raivavae sandalwood was very broad. Given its good dynamics (suckers and natural regenerations) on coral "motus", it is certain that its presence is natural and not due to man. The original range was likely restricted to the edge of the "motu", on the seaside, on rocky sols among Scaevola or on the lagoon side on sandy soils among Sophora, as well as in areas cleared by storms. The extension of the range was due to the presence of men and the anthropogenic clearing on the "motus" since the Polynesian period. Today, recurrent fires contribute to its vegetative propagation through root and stump suckers. On the northern coast of the high island, sandalwoods probably grew on most medium-to-steep slopes of ridges and sides, on rocky soils or scree, with the driest exposure, from sea level to the summit. Its presence on the more humid southern coast must have been limited to the steepest slopes. It was likely absent from the coastal plains and the large valleys with gentler slopes.

DYNAMICS AND THREATS

The sandalwood from the Austral Islands is faced with a contrasting situation on the two islands where it is still found. On Rapa, the remaining populations are relict, quite old, in a moderately anthropized environment. On Raivavae, the populations consist essentially of numerous young trees surviving in a highly anthropized and modified habitat. Regeneration, both seed-propagated and vegetative, has not happened for dozens of years on Rapa. On Raivavae, vegetative propagation through root and stump suckers is intense and seed-propagated reproduction, although marginal, still exists. These dynamics are related to relatively similar but slightly different ecological and anthropogenic conditions among the islands. These conditions are presented below and are not fundamentally different from the other archipelagos (Butaud & Tetuanui 2005).

Poaching
While direct human impact is not the main cause for the diminishing numbers of sandalwoods in the Austral Islands today, it was in the case in the past and some populations did not recover from the abusive harvests of the past centuries. Poaching is still effective today and continues to decrease the populations and to limit the growth of large fruit-bearing trees. Focusing on the best trees, the harvest contributes to a negative selection among varieties and limits the enhancement opportunities under a production plantation program. Human exploitation is particularly visible on Raivavae due to a recent demand for sandalwood, arising partly from the regular meetings in Tahiti, during craft shows, of craftsmen from all over French Polynesia. On these occasions, Marquesans, who are large users of sandalwoods, were able to engage with the Raivavae and buy sandalwood at a lower price than in the Marquesas Islands. The Raivavae realized the importance of the available resource and the potential revenues. In "handicraft fare" from Rairua to Raivavae, several sandalwood objects can be found including hairpins (between 1 000 XPF and 1 300 XPF), pieces of sandalwood more or less stripped of sapwood (2 000 XPF for a 60 cm long by 5 cm wide branch or 3 000 XPF for a hollow branch of 80 cm in length and 10 in width), and sandalwood powder (2 000 XPF for a 150 ml jar), which is often of low quality as it includes the sapwood or is mixed with "ngaio" (Myoporum stokesii), another fragrant wood. In Tahiti, the "craftsmen' Heiva" offered in 2001 some sandalwood powder at 1 100 XPF per bag (20 cm long, 5 cm wide) and in 2002 a non-carved piece of sandalwood from Raivavae (30 cm by 12 cm) at 50 000 XPF. At the 2005 agricultural fair in Tahiti, a 35 cm piece with a 10 cm diameter was offered at 3 000 XPF and a 35 cm piece with an 8 cm diameter was sold at 2 500 XPF. Due to the growing demand, we have observed many trees stripped of their branches (particularly on "motus") and others that are totally uprooted and exploited (Anatonu, Vaianaua). While the sandalwood variety from Raivavae is not protected through the regulations on nature protection, harvesting is regulated under the Polynesian Forest Code, which requires felling permits.

Fire-induced degradation
Fire represents the second major threat on Raivavae. Burning is deliberate on "motus" for clearing and accidental on the heights of Anatonu. Land clearing by fire is forbidden by the Polynesian forest regulations but is still practiced. It leads to the loss of populations of fruit-bearing sandalwoods, creating, in the best cases, numerous suckers from the scars on the roots.

Predation of seeds by rats
The main limiting factor of the seed-propagated reproduction on both islands is the predation of most seeds by rats feasting on their kernel. Caused by the Polynesian rat (Rattus exulans) on both islands and by the Black rat (Rattus rattus) on Rapa, many
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gnawed and open shells were found. Unlike in the Society Islands and the Marquesas Islands (except in Tahuata), predation is not absolute on Raivavae where several dozens of mature seeds were found. This could be explained by the absence or scarcity of Black rats on Raivavae (J.-C. Thiabault pers. comm. 2002). The Polynesian rat is less arboreal and only eats a portion of the seeds, probably the most accessible ones. The near lack of seed reproduction is mainly due to the successive introductions (Polynesian and modern) of rats on the islands.

Extinction of disseminators
In the same vein, the likely extinction of several avian disseminators such as the Imperial pigeons and Fruit doves (except the "koko" Ptilinopus huttoni on Rapa) on the Austral Islands (Steadman 1997) would have also limited the chances of germination of sandalwood seeds. The uneaten ripe fruits fall and rot quickly on the ground, resulting in the rotting of the kernel (J.-F. Butaud pers. obs.).

Overgrazing by herbivores
The current main threat on the Rapa sandalwood is overgrazing by introduced herbivores, principally goats but also cows. The feral goat populations on Rapa are only restricted by the available food. Their size is increasing every year, as they are not hunted enough, leading to the loss of natural forest. Goats are highly present on both populations of sandalwoods on Rapa. Leaves are only found at the top of trees and no sucker bigger than 20 cm was found. The surrounding vegetation has been grazed and replaced by unpalatable weeds. Therefore, very few host plants remain, soils are compacted due to grazing, and sandalwoods decline at an accelerated rate. Both seed-propagated and vegetative regenerations are impossible due to the pressure from herbivores. While there are other reasons for the scarcity of the Rapa sandalwood, goats will hasten its loss. Goats are less abundant on Raivavae but still present on the altitude stands and on Vaianau Peninsula where the absence of suckers is the first impact of their presence.

Growth of invasive plants
Natural habitat changes due to more or less invasive naturalized plants are also a concern on both islands. Currently, there is no plant considered as invasive in the sandalwood populations on both islands but it is likely that in a near future, Psidium cattleianum (Myrtaceae) on Rapa and Leucaena leucocephala (Mimosaceae) on Raivavae will grow and suffocate the mature trees, the suckers, and the potential plantlets. In addition, many naturalized grasses form the understory of sandalwoods and certainly impair the germination of falling seeds. The dynamics of sandalwood on the Austral Islands has largely diverged from its natural path. While on Raivavae the sandalwood seems to adapt to changing conditions through a significant vegetative propagation, it might disappear soon from Rapa without any voluntary effort. Threats are varied and accumulative. Sandalwood is a good example of the challenges faced by most natural habitats in French Polynesia.

CHEMICAL CHARACTERISTICS OF THE SANDALWOOD FROM THE AUSTRAL ISLANDS

Background, sampling and methods
The chemical study was based on a 37 samples of wood (Table 44). Dead trees were sampled on both islands. Therefore, the total number of samples can be higher than the number of known individuals (in particular for Anatakuri Nako on Rapa). The data presented below were produced by Gaydou (2004) in addition to new samples in 2005. The chemical studies aim at characterizing the essential oil of the Austral Islands sandalwood and estimating its variability based on geographic (islands, populations) and site-specific (type of soil) criteria (Butaud et al. 2004).

Wood samples were collected mainly on dead wood to prevent any injury to the rare trees remaining in some populations. As most individuals, in particular on Raivavae, are small, the high quality heartwood could not be collected. Often, only false heartwood (duraminization due to injury) or wood with many impurities were collected. While experience has shown that in most cases the composition of false heartwood is very similar to actual
duramen, the nature and the state of the wood were taken into account in the result. Wood extracts were analyzed by gas chromatography. Concrete was obtained through solvent extraction from a small quantity of wood and the essential oil or essence by hydrodistillation of a larger quantity. In practice, solvent extracts less volatile (heavier) molecules compared to hydrodistillation: the heavy fraction of the concrete will not be found (and no traces either) in the essence. The proportion of key molecules in the concrete will be lower than in the essence. Therefore, it is not possible to accurately calculate the yield of essential oil as well as the proportion of the most important essence molecules on an olfactory point of view.

The identification of molecules represented by chromatogram peaks was based on the calculation of Kovats indices (using retention times) and on the coupling with the mass spectrometry and comparison with the existing spectra database. Twenty-six peaks or groups of peaks could be individualized. Some peaks were grouped, as they could not be separated in a sufficient number of individuals. They generally included one majority compound and several minority compounds.

### Chemical composition of the concrete

Table 45 presents the results of the chemical analyses of the Austral Islands sandalwood. For each island, data are presented for all samples and for samples of heartwood with no or few impurities (false heartwoods and impure duramens were removed).

The molecules producing the characteristic smell of sandalwood are mainly the (+)-(Z)-α-santalol (α-santalol) and the (-)-(Z)-β-santalol (β-santalol), on the dark green of the table. They form the main compounds of the Austral Islands sandalwood concrete, ranging from over 35% on average for all samples from Raivavae to about 60% for quality samples from Rapa. Important variations were observed among the various samples but most variations seemed to be explained by the poor quality of the heartwood collected. When only the purest samples are considered (duramens with no or few impurities), the proportion of both molecules is about 49% on Raivavae and 59% on Rapa.

The Rapa sandalwood appears to be of better quality than on Raivavae with a higher content in α- and β-santalol. This needs to be put into perspective as the number of samples is relatively low, in particular from Rapa, and the structure of sandalwoods on Rapa is significantly different than on Raivavae. Sampled trees on Rapa had a

![Table 44: Sampling of *Santalum insulare* on the Austral Islands for chemical and genetic studies.](image-url)
well-developed trunk, with an average diameter of 10 to 20 cm, and formed heartwood in branches, trunks, and roots. On Raivavae, most individuals were stump and root suckers, with a shrub or bush structure, reaching less than 10 cm in diameter and with heartwood formation only near the stump or the root. The difference of quality should be related to the age as well as to the location of the sampled trees. Also, the difference of climate between both islands (chillier and more humid on Rapa) has certainly an impact.

Compared to the Indian sandalwood (Santalum album), the world reference in terms of heartwood quality, the Austral Islands sandalwood is of good quality. Standards for the essential oil of Indian sandalwood indicated α- and β-santalol contents respectively between 41 and 55% and between 16 and 24% (ISO 2002). As the data available are only for the concrete in the case of the Austral Islands sandalwood (between 35 and 41% for the α-santalol and between 14 and 18% for the β-santalol), the proportion in the essential oil can only be roughly estimated at 38-43% for the α-santalol and 16-19% for the β-santalol. At first sight, the quality of the essential oil from the Austral Islands sandalwood seems to be slightly lower than the Indian sandalwood. For the latter, extraction is done from trunks, branches, and roots of large trees. On the contrary, for the Austral Islands sandalwood, only small pieces of wood from branches or trunks could be used. There is presumably a high potential for the local varieties.

The extraction yield by hydrodistillation for the essence of Indian sandalwood reaches 3 to 6% (Alpha 1997) and about 2.5% for the New Caledonian sandalwood (Butaud 2006). The laboratory extraction protocol using solvent has a yield of 8 to 10% of concrete for the Austral Islands sandalwood. The solvent extraction technique produces a higher yield in α- and β-santalol compared to hydrodistillation. Furthermore, several molecules (heavy fraction) not extracted by hydrodistillation are only present in the concrete. The yields obtained are not directly comparable but suggest a good yield (likely to be higher than 4%) of essential oil under a long-term enhancement program (from plantations) of the Austral Islands sandalwood.

**Variability of the concrete**

To assess the chemical composition variability of the concrete of Austral Islands sandalwood, a Discriminant Factor Analysis (DFA) was performed on all samples grouped in four populations (the two from "Rapa" and a group each for the "high island" and the "motu" on Raivavae), based on the 12 molecules presented in Table 45. The analysis maximizes the differences among groups. Figure 33 illustrates the DFA. The DFA highlights group segregation for α-, β- and epi-β-santalol (positive F1 axis) and bergamotene (negative F2 axis) and α-santaldiol (positive F2 axis). The Rapa populations are relatively distinct with higher concentrations of α- and β-santalol. There is an apparent distinction between the two groups from Raivavae, mainly based on the type of soil. Individuals growing on the coral "motu" have lower concentrations of α- and β-santalol compared to trees on the volcanic high island. The tree marked with an arrow on the graph also illustrates this statement: the
Figure 33: Graphical representation of the Discriminant Factor Analysis of the chemical composition of the concrete of *Santalum insulare* from the Austral Islands, by population group.

Tree is from the high island but its profile corresponds more to the "motu" as it grows on raised coral on the main island (Anatonu temple population). The various surveyed populations present variable chemical characteristics, some considered to be an adaptation to the habitat, as demonstrated by the slight differences in composition according to the type of soil for the same botanical variety.

**GENETIC CHARACTERISTICS OF THE AUSTRAL ISLANDS SANDALWOOD**

Two genetic studies were successively carried out based on leaf samples collected on islands where sandalwoods grow, in French Polynesia and on the Cook Islands (Mitiaro). The studies used chloroplast microsatellite (Butaud *et al.* 2005) and nuclear (Lhuillier *et al.* 2006) markers and were performed in the laboratory of genetics of CIRAD-Forêt in Montpellier. The results from these studies for the Austral Islands are summarized here.

Table 44 describes the sampling for both studies. In addition to the samples collected in the Austral Archipelago, two samples from Mitiaro, Cook Islands (collected by Lex Thomson, CSIRO) were added to the analysis using chloroplast microsatellites.

The evaluation of genetic diversity was only done at the level of the archipelago and the islands, but note at the population level to assess population dynamics. Exhaustive sampling of a population (except for the two relict populations on Rapa) was not possible and priority was given to cover a maximum number of populations.

**Chloroplast microsatellites**

Throughout French Polynesia, 17 different chlorotypes were found on about 500 collected samples from 10 islands where sandalwoods are found, in addition to Mitiaro, Cook Islands. No chlorotype was shared among the archipelagos. In the Cook-Austral Archipelago, only three chlorotypes were identified: one specific to Rapa, one specific to Raivavae, and one shared between Raivavae and Mitiaro. There is no diversity on Rapa and Mitiaro and an average diversity on Raivavae (Table 46), compared to the existing data from the other Polynesian islands. Values can be explained by the small size of the islands and the associated small number of habitats but also by the relict nature of sandalwood populations due to exploitation, fires, and introduced animals. In addition, the archipelago has a strong genetic structure (69% of the total molecular variation observed among islands and 31% within the islands) due to the high differentiation between Raivavae and Rapa from the absence of a shared chlorotype. Differentiation is likely due to the distance (over 500 km) between the two islands, which restricts the exchange of seeds. The main finding is the notable differentiation among the sandalwoods of each archipelago, with distinctive chlorotypes. Within the Cook-Austral archipelago, Rapa is well isolated by its specific
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chlorotype, corroborating its botanical (several endemic genera) and geological (very old age of the islets neighboring Marotiri) characteristics (Florence 1997; Clouard & Bonneville 2001). The fact that the Mitiaro chlorotype is shared with Raivavae might suggest a same origin as well as preferential movements within a same geological archipelago rather than between two islands that are close but belong to two different archipelagos. In order to refine the recently developed conservation strategy for the Mitiaro sandalwood (Tangianau et al. 2004), a last resort hybridization, with the introduction of seeds from the genetically closer Raivavae sandalwood, should be considered rather than from the geographically closer Raiatea (as initially planned).

However, as shown by the minimum dissimilarity network among the chlorotypes (Fig. 34), one of the two populations studied at Raiatea (black solid circle under Society) has a chlorotype that is relatively close to the one from Mitiaro and Raivavae, which suggests a past gene flow in the archipelago that does not seem to exist anymore. The network reveals three series of chlorotypes, the ones from the Cook-Austral archipelago falling between the Marquesas and the Society chlorotypes. This is surprising from a geographic point of view (as the Marquesas are closer to the Society than the Austral Islands) but is a reflection of the important influence of geology and the distinct ages and histories of the various archipelagos on sandalwood colonization. The likely routes of colonization are established but neither the direction (Marquesas-Austral-Society or the opposite, or Austral-Marquesas and Austral-Society) nor the origin (even if the Hawaiian Archipelago is the most likely from a taxonomic point of view (Fosberg & Sachet 1985; Harbaugh & Baldwin 2005)).

At the population level, the distribution of chlorotypes is not very structured on Raivavae. The two chlorotypes are rather mixed on the “motu” and only one seems to be present on the high island. The lack of structure might be due to the small size of the island and to the good dynamics of sandalwood, probably due to the scarcity or absence of Black rats and the high number of individuals.

### Nuclear microsatellites

Nuclear microsatellites are more polymorphic than chloroplast microsatellites as they are subject to random recombination of the genome during sexual reproduction. Nuclear microsatellites help detect diversity at a finer scale, down to the subpopulation level, if used in sufficient numbers. In the present case, eight markers were applied and were able to define multilocus genotypes (allele combination of 8 locus or 16 alleles). Considering the significant multiplication in situ of sandalwoods through suckers, trees sampled as distinct individuals (“ramets”), but with the same multilocus genotype, are presumed to be from the same genetic individual (“ortet”) and form a clone. Diversity is calculated based on allele frequencies as well as genetic structure indices. Genetic distances between genotypes are calculated based on allele composition.

It appears from the study that a little over 50% of sampled sandalwood trees are clones, with the same genetic heritage as all tested microsatellites (Table 47). This is particularly surprising as care was taken during sampling at Raivavae to focus on scattered trees in order to limit the selection of root suckers from the same parent plant. This means that the actual number of individuals (genetic individuals) is at maximum half of the estimated trees or a little less than 1,200 on Raivavae. On Rapa, the same genetic individual (“genet”) constitutes both known populations in which all trees were sampled. The situation appears to be more critical than what was assumed by conservationists. The situation on Raivavae is relatively stable.
...different as there are not many clones (less than 40%) on the big "motus" and more frequent ones (over 50%) in the more concentrated populations of the high island or the small "motus". The dynamics of the sandalwood is therefore likely to be important on the "motu" than on the high island. This clonality is due to the capacity of the sandalwood to grow some suckers from stumps (after exploitation) or roots (after a fire), all the more so because of the slow or inexistent seed reproduction caused by predation by rats and the extinction of avian disseminators, thwarting all chances of seed germination and dissemination.

<table>
<thead>
<tr>
<th>Populations</th>
<th>Samples</th>
<th>Nb. génotypes</th>
<th>% of clones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anatonu East</td>
<td>7</td>
<td>3</td>
<td>57</td>
</tr>
<tr>
<td>Anatonu West</td>
<td>13</td>
<td>5</td>
<td>62</td>
</tr>
<tr>
<td>Motu East</td>
<td>8</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td>Motu South-West</td>
<td>8</td>
<td>5</td>
<td>38</td>
</tr>
<tr>
<td>Motu Vaianamu</td>
<td>8</td>
<td>5</td>
<td>37</td>
</tr>
<tr>
<td>Petits Motu</td>
<td>10</td>
<td>5</td>
<td>50</td>
</tr>
<tr>
<td>Vaianaua</td>
<td>8</td>
<td>4</td>
<td>50</td>
</tr>
<tr>
<td><strong>Total Raivavae</strong></td>
<td><strong>62</strong></td>
<td><strong>34</strong></td>
<td><strong>42</strong></td>
</tr>
<tr>
<td>Anatakuri Nako</td>
<td>3</td>
<td>1</td>
<td>67</td>
</tr>
<tr>
<td>Karapoo Rahi</td>
<td>11</td>
<td>1</td>
<td>91</td>
</tr>
<tr>
<td><strong>Total Rapa</strong></td>
<td><strong>14</strong></td>
<td><strong>2</strong></td>
<td><strong>86</strong></td>
</tr>
<tr>
<td><strong>Total Austral</strong></td>
<td><strong>76</strong></td>
<td><strong>36</strong></td>
<td><strong>53</strong></td>
</tr>
</tbody>
</table>

Genetic structure is very important among the various archipelagos (Fst of 0.4 between the Marquesas and the Austral Islands and 0.5 between the Society and the Austral Islands), which corresponds to the results of the precedent study. Within the archipelagos, the most important differentiation among islands is between Raivavae and Rapa (Fst = 0.648), confirming the recognition of the two botanical varieties even if the markers used only measure neutral diversity (Fig. 35). The Rapa genotypes are very clearly distinguished from those of Raivavae (100% bootstrap). Furthermore, the populations of Raivavae present a significant differentiation (Fst = 0.162; P < 0.001). This corroborates the grouping of the population genotypes from Vaianaua and the South West Motu observed in figure 35.

Figure 36 indicates that the Austral Archipelago has an intermediate position compared to the other archipelagos in terms of variability of nuclear microsatellites, confirming the findings of chloroplast microsatellites. Bootstrap values (the probability of observing a branch at a given spot on a tree) are low due to the small sampling on Rapa and other islands outside of the archipelago but the structure of the tree is well established.

**Assesement**

The situation is contrasted between both islands with a significant differentiation between the two varieties. Diversity is very limited on Rapa with...
only two "genets" and richer on Raivavae where many populations do not have a defined structure. Diversity indices for the Austral archipelago are significantly lower than on other archipelagos (Expected heterozygosis (He) of 0.33 compared to 0.51 on the Society and 0.55 on the Marquesas, average number of alleles per locus (nA) of 3.25 compared to 6.50 on the Society and 6.13 on the Marquesas). This means that diversity is lower due to the degradation of the natural environment and the populations as well as the small size of the islands compared to the other archipelagos. Therefore, the sandalwood populations on the Austral Islands are more sensitive to new disturbances and require preferred and early conservation efforts.

On the biogeographical level, the Austral Islands sandalwood could constitute a link between the Marquesas and the Society sandalwoods.

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**Reproduction efforts**

**Rapa**

On Rapa, the only known experiment on the germination of the Rapa sandalwood by local SDR agents used very few seeds and was a relative failure: two seeds sprouted, then quickly rotted. However, this demonstrates the possibility of collecting viable seeds and getting to the germination stage.

**Raivavae**

In May 1985, seeds of Raivavae sandalwoods were sent to Tahiti by the Rural Economy Services (SER) but we do not have any subsequent information. In March and April 2002, an SDR agent sent about 200 sandalwood fruits from Raivavae, from Motu Rani to the 3rd agricultural sector on Tubuai. The fruits were pulped upon arrival on Tubuai. They were put to germinate at the Mataura nursery after scarification (complete removal of the shell). No preliminary treatment using gibberellic acid was performed as advised by the management technique for the production of sandalwood plants in nurseries (Butaud 2001). The results of this germination were deceiving: some seeds sprouted but no seedling was produced due to a lack of monitoring at the nursery (rotten kernels and damping-off). The local staff performed a similar germination, which produced several seedlings, scattered here and there on Tubuai. None of these seedlings was recently found. It seems that some inhabitants on Raivavae succeeded in reproducing the local sandalwood as several trees observed in private homes or in the SDR nurseries on Tahiti and Raiatea presumably came from Raivavae. A pastor on the island was presumed to have developed his own germination technique, applied today by the SDR agents in Moorea (non scarified seeds are put to germinate in moss collected from trees and the kernel is manually released from the shell after germination). While no private plantations of sandalwoods were found on Raivavae, this information shows that the population is willing to cultivate and plant sandalwoods and that the seeds can be easily accessed. The lack of a real nursery on the island also hinders the efforts to develop this species.

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**Conservation and enhancement strategies**

**Rapa**

The situation of the Rapa sandalwood is very simple. There are only two populations left, in visible decline, composed of a unique clone each and presenting therefore major risks of inbreeding and genetic depression. Trees bear very few fruits and are directly threatened by grazing by feral goats. Wood from this variety seems to of very high quality. The Rapa sandalwood variety is very differentiated from the varieties from Raivavae and other Polynesian islands. Conservation of *Santalum insulare var. margaretae* is therefore a priority as it has an original part of the genetic diversity of the species, is at the verge of extinction, and constitutes a high quality natural resource for the future.

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The proposed strategy would be to start with the mandatory preservation of both populations (at least one tree for each population) and the search of new populations on favorable sites.

The Anatakuri Nako population should be fenced (wire fence) in order to mitigate the impacts of grazing by goats and to restore the surrounding vegetation. The minimal area to be fenced should be 2 500 m² (or a 50 m by 50 m square and 200 m of wire fence), centered on the three remaining trees and including the higher and lower parts of the population. This technique could help restore the adult trees and obtain root suckers. The genetic diversity would not be enhanced but the clone will have better chances of preservation. In a second phase, local shrubs or trees could be planted in the enclosure to restore the stock of host plants. The trunk could be wrapped (without any nails or perforating devices) with metal bands (as used on coconuts) to prevent the destruction of seeds by rats. This would allow the harvest of potential fruits and germination experiments ex situ.

Goats should be eradicated (culling or capture) on the islet of Karapoo Rahi. This eradication would benefit both the sandalwoods and the overgrazed vegetation of interest. The sandalwood population could be restored in a similar way than in Anatakuri Nako. Host plants can also be replanted. Regarding rats (probably Black rats), metal bands could be used but it seems more interesting to perform a complete eradication of rats on the islet to restore the entire ecosystem (seabirds, endemic insects, vegetation).

In both populations, the seed harvest should be done on a regular basis (every two weeks) so that the mature fruits do not fall on the ground (and risk rat predation or rot). The maturation duration is between five and six months (J.-F. Butaud pers. obs.). The maturity stage of the fruit should be estimated to determine when to visit the populations that are far from the main village.

If the production and germination of seeds prove successful, the seedlings can be used first to enhance the existing populations and mainly to diversify the gene pool. One tree from Anatakuri Nako could be planted in Karapoo Rahi and vice versa. In this way, tree fertility (reduction of consanguinity) could be enhanced in case of a self-incompatibility system.

Raivavae

The Raivavae sandalwood is not threatened by extinction in the short run. The number of genetic or apparent individuals is still important and genetic diversity is relatively high. The priority is to establish a conservation plantation (seed orchard) and to conserve in situ isolated or original populations. There are two of the latter: the population of the Vaianaua peninsula, which only has old trees and is grazed by goats, and the altitude population(s) near Mt Moutapu and Mt Hiro, comprising very isolated trees in areas inaccessible to goats. The strategy is the same for these populations and involves eradication or control of the goat populations. On the Vaianaua peninsula, sandalwoods are easy to access and subject to poaching. Awareness should be raised among the population or at least the owner(s) of the area.

A conservation plantation requires the establishment of an equipped nursery (fridge, automatic watering system, protected germination area) and the training of future nursery workers. This project is being developed by SDR for fruit-bearing species. Sandalwood could be included. The second step is to collect seeds from the maximum number of different populations, as genetic studies did not highlight any significant differentiation among the various areas. Collections could be done without using rat poison, in particular on "motus" where rats are not abundant. Otherwise, rat eradication could be performed on some small "motus", well-developed trees could be wrapped with metal bands, or rats could be eliminated in some populations (use of rat poison every two weeks at least). Harvested fruits can be pulped, separated by origin, and stored in a cold place. Germination could follow the protocol developed for the Marquesas (Butaud 2001). The conservation plantation will include at least 200 individuals from a dozen of origins, or twenty some trees for each population. In situ enrichment planting can be derived eventually from the ex situ conservation plantation.
Tukou marsh and taro pondfields, Rapa (Photo R. Englund).
Rapa, or Oparo as it was originally named, is the southernmost inhabited island of the Austral Islands ("Tuha'a pae"). Rapa is isolated, being about a day and a half by boat away (550 km) from its closest neighbor, Raivavae. Scientific estimates date Polynesian habitation beginning in the 14th or 15th centuries (Kirch & Hunt 1997). Captain George Vancouver was the first European to discover Rapa in December 1791. Due to its isolation, missionaries from Tahiti did not arrive to stay until 1826 (Davies & Newberry 1961).

At 27°S latitude, Rapa is outside the tropics. The resulting near-temperate climate must have presented particular challenges to its original Polynesian settlers, because many of their common food staples don’t flourish this far south. For instance, breadfruit (Artocarpus altilis, Moraceae) doesn’t grow, and while coconut palms (Cocos nucifera, Arecaeae) grow, they do not set fruit. Bananas (Musa spp., Musaceae), or "tautau", grow either as dooryard plants, as scattered garden plantings, or in small groves in damp forest areas, but they do not flourish with enough luxuriance to become a staple. As in many places in the Pacific, sweet potatoes (Ipomea batatas, Convolvulaceae), or "kumara", do grow, but are not generally relished.

In Rapa, taro (Colocasia esculenta, Araceae), or "mikaka", is the staple crop. It is grown either dry or wet, in extensive systems of shallow ponds called "roki", reminiscent of bygone taro culture in Hawaii, where taro also once grew in extensive systems of ponds, or "lo'i". Even though dry taro cultivated on Rapa can grow shoulder high, most taro is cultivated wet, and most wetland taro grows only knee high. The most common taros found in "roki" are by far, the "'ara'ara" and "ma'areva" cultivars. It is remarkable how many of Rapa’s taro cultivars are the branching type, with corms that branch at the apex.

As elsewhere, taro is vegetatively propagated using slips or cuttings, termed "'uli" in Rapa. Farmers prepare slips by nicking a taro corm with their thumbnail at the very base of the stalk, then smartly snapping the stalk from the corm. The slip is deliberately separated as closely as possible to the corm, to insure none of the starchy corm is left
on the "uli" to cause rot. The slips are immediately replanted in the "roki". Leaves are left on, but folded over under the water. This is done so newly planted "uli" are not felled easily by the wind. As with "ploi" in Hawaii, in Rapa taro is pounded into a paste called "popoi". The consistency of Rapa's "popoi" however, is stiffer than "ploi" is in Hawaii. It corresponds to Hawaiian "pa'i'ai", or the stage after taro is pounded smooth, but before enough water is added to make "ploi". In Rapa, when asked about diluting "popoi" to as thin as Hawaiian "ploi" an informant (T. Flores) made the humorous remark, "kapke te popoi", which invokes Kapeke, a Marquesan, who preferred his "popoi" much too thin for Rapan sensibility!

The process of pounding taro into paste differs in other notable ways between Rapa and Hawaii. In Rapa, women work in the "roki", cook the taro, and pound the "popoi", though this may not have been the case in ancient times. Alternatively, in Hawaii, men usually did the cultivating, cooking, and pounding of taro. For a good description of taro culture in Hawaii, see Pukui's article (1967) Poi Making in Hawaii.

Once a week in Rapa, usually on Saturdays, women gather to prepare the coming weeks' "popoi", while the men go fishing. Before, taro was cooked in the "ko'otu", or underground oven, but presently, boiling is the preferred method. Once cooked, the taro is peeled, "oni", and pounded on a large flat stone, the "tuki", using another stone, the "karä", that evokes the size and shape of half a red brick. Once the corms are pounded smooth, the whole mass of "popoi" is then repeatedly tossed forward on the "tuki" with a resounding "whump", in a process called "nane". This is done to both aerate the large mass of "popoi" and to mix in a small packet of sour "popoi" saved over from the previous week. This packet, called "te āñoi", is intentionally added to the freshly made "popoi" so it ferments quickly, because of the preference for the pleasant, tangy taste of sour "popoi" at mealtimes. Both of these terms, "nane" and "te āñoi", are Tahitian, the original Rapan terms are "taviri" and "akama'u", respectively. Like souring enhances its taste according to the Rapan palate, aerating the "popoi" enhances its consistency. This process of aeration is a uniquely Rapan invention.

The next step is to take appropriately sized portions (c.1-2 liters) of just-made "popoi" and transfer them to "ti" (Cordyline fruticosa, Asparagaceae), or "karakaro", leaf parcels for storage. These parcels are tied at the top, to form tear-drop-shaped bundles called "penu", that are hung up, away from harm or nowadays, put in the ubiquitous covered plastic bowl, and left to ferment. At mealtime, "penu" are opened, their contents partially consumed, and then wrapped up again for future meals.

Besides "popoi", another unique way taro is consumed in Rapa is in "takae" or "takai". "Takae" is made by wrapping small, cooked taros tightly together and then heating or pressing the bundle with enough force to exclude air, so that the individual small taros consolidate into one large loaf. This resulting loaf is then sliced and eaten as is, like a single large slice. Another taro dish in Rapa, a preparation of taro leaves and pork called "fafapuaka", is only eaten on special occasions. This uncommon use of taro leaves in the daily diet of Rapa is quite in contrast with their ubiquity in Hawaiian culinary tradition. Also, in contrast with Hawaii, in Rapa there are no particular taro cultivars especially identified as being grown for their leaves.

The above description of how taro is used in Rapa at present differs markedly from historical practice as recounted by Stokes (1930), who did extensive fieldwork on Rapa from 14 April 1921 to 25 January 1922 (Stokes 1923). In an unpublished manuscript housed at the Bishop Museum, Stokes (1930) reported that the ancient way in Rapa of using taro for food was not by making "popoi", but by storing it in a pit, or "rua", to ferment, and then, usually baking it before eating. Taro treated in this way was termed "tio'o" or "ma'ā". Indeed, large pits that may have served this purpose can still be seen even today, beside the ancient hilltop forts, or "pa", for which Rapa is renowned.

The merchant Lucette's (1851) eyewitness account from Rapa in February 1843 describes "tio'o" taro preparation: "The tarro [sic] is first washed and scraped free of all fibres of the outer coating, and it is laid up in pits lined with leaves and grass, and well covered with stones. In this manner it becomes consolidated into a paste-like mass and will keep for a year or two. It has to me a sour and very unpleasant flavour, being something like that of turned cream cheese, and its smell is like that of a strong cheese. The natives are passionately fond of it, and will eat three or four pounds weight of it at a meal if they can get it". Although the "tio'o" method of preparing taro was abandoned by about the middle of the nineteenth century, Stokes reported that it was still commonly remembered in the early 1920's. Storing seasonal crops underground to ferment was a common practice in other Pacific islands like the Marquesas, Mangareva, Samoa, Fiji, etc. In fact, according to Teiura Henry of Tahiti, breadfruit fermented in this manner was also actually called "tio'o" or "ma'ā" (Henry 1928). The unique aspect about this underground storage method being used so extensively on Rapa is that taro is not a seasonal crop, but can be harvested all year round. Stokes concludes from this that in Rapa there is a strong cultural preference for the taste of fermented food. This preference is self-evident even today, because the universal
staple of every meal is deliberately soured "popoi". Stokes (1930) makes a convincing case that "popoi" was actually introduced from Tahiti, around the time when Tahitian missionaries first permanently came to Rapa in 1826. He points out that the word "popoi" (written sometimes as "poipoi") is a Tahitian word imported to Rapa, and he speculates that by the mid-1870s it had completely supplanted the original Rapan term, "poi". Stokes (1930) records another remarkable observation about the evolving use of taro in Rapa: "The commonly related account of the introduction of the "taviri" (aeration process) describes it as an accident, resulting from the play of two young girls. The survivor of these, when interviewed in Mangareva, stated that she and her companion were making "poi" at "Tupuaki" (a village on Rapa) about 1870 or 1875 and (as may frequently be observed today) they began to play. One of them kneaded the "poi"; lifted and dropped it. The resulting drum-like noise probably amused her companion, who imitated her, and the play continued until they were tired. The "poi" was found to have been much improved, and the process was subsequently repeated. Other people in "Tupuaki" took it up, and later those in "Aurei" and other parts of the island." Stokes noted that other parts of the taro, besides the corn, were used for food. In ancient times, taro stems, or "urū", were cooked and eaten, though by the time of Stokes' visit, stems were only an animal feed. Interestingly, he found a dish called "rū" was made with taro leaves, by cooking together pounded, unfurled taro leaves with the edible seaweed "limu papa" (Ulva fasciata, Ulvaceae).

During a two month period (March-May 2002) author Fenstemacher conducted interviews of local residents to compile Rapan taro cultivar names, morphological descriptors for the varieties, uses and cultivation methods. We compared these data with records and herbarium vouchers from earlier scientists, and with photos taken by author Motley during the interview process.

The Rapa Island taro cultivar descriptions, given below, are taken from field observations and interviews made between 18 March and 11 May 2002, and supplemented with unpublished and published material from Stokes (1930, 1935), his herbarium collections from 1921 (deposited at the B.P. Bishop Museum, Botany Department Herbarium), the 1934 field notebooks and herbarium collections of St. John (deposited at the B. P. Bishop Museum, Botany Department Archives and Herbarium), and a Rapa language word list compiled and housed in the administrative offices on Rapa (Anonymous 2001). Interview informants that provided significant data consisted of ten residents. Other people were interviewed, but said they did not know too much about the topic or told us to talk to the informants in this study (i.e., identified these individuals as the most knowledgeable about taro culture). They included three women and seven men. Their names and estimated age ranges at the time of study are:

- Women: Mama Fa'atu (mid-60s), Mama Luita (early 60s), and Mate Vahine (mid-40s);
- Men: Benjamin Pukoki (late 30s), Cerdan Faraire (mid-40s), Papa Fa’atu (mid-60s), Papa Teri'i (mid-late 60s), Papa Teura (early 50s), Raymond Barsinas (late 20s-early 30s), and Tetua Flores (mid-50s).

The cultivar descriptions that follow are admittedly open to criticism from many standpoints. Two month's worth of field observation is hardly sufficient to fully describe taro cultivars completely, since taro has a distinctly cyclic growth pattern. For instance, taro flowers are not described below because none were seen. Furthermore, the choice of color descriptors is somewhat subjective, no standard color chart was used as reference to determine them. However, color images were taken when possible. Some cultivars have several forms and no systematic attempts were made to describe each form. Some well-known cultivars from earlier times have disappeared and their descriptions are from what little could be recalled by informants or gleaned from the literature. Such regrettable imperfections are not just limited to descriptions of taro, but occur whenever one attempts to describe from observations limited by time, plants with a large number of cultivars and forms that have arisen through vegetative propagation. Many other plants fall into this category, most notably banana, sweet potato, kava, and sugar cane to name a few. Despite these obvious limitations of the present treatment, it is believed that the descriptions presented below are at least, a solid first step toward cataloging Rapa's different taro cultivars.

The following descriptions of each taro cultivar are arranged as follows: The nomenclature used in the descriptions maintains Rapan sensibility whenever possible. The most common cultivar names are in italics, parenthetically followed by alternate, less common names for the same taro cultivar. Listed subsequently are some general characteristics of
the cultivars and forms, consisting of the overall impressions and distinguishing features that one might summarily use to categorize a taro from field observations. The description details that follow include petiole, leaf blade, and corm characteristics as well as distribution, use, and additional remarks. The concluding remarks section includes any historical observations that were recorded for that particular cultivar by Stokes in 1930, by St. John in 1934, and by any information on the herbarium vouchers that were collected by Stokes in 1921 and by St. John in 1934. In the interests of presenting as complete and accurate record as possible of these largely unpublished results, these historical observations are presented as found, no attempts were made to correlate the occasional conflicts in the cultivar descriptions. Finally, although "'uo'uo", "'ere'ere", and "'ute'ute" are formally used in the descriptions below as white, black and red, respectively, it may be useful in the field to also consider them informally in terms of light, dark and bronzed, respectively. Two common Hawaiian terms are repeatedly used in the following cultivar descriptions: "'ohā" to mean taro suckers or lateral shoots, and "piko" to mean the spot on the upper surface of a peltate taro leaf, where the petiole is attached underneath.

**RAPA Taro NAMES AND DESCRIPTIONS**

***"'Apura" ("Matoe", "Matae")***

**General characteristics:** Wild (naturalized), self-green taro with long, slender rhizomes.
**Petiole:** Uniformly self-green (whitish green), occasionally may slightly darken right at apex, just below attachment to leaf blade; edges of petiole sinus reddish; base is light green to greenish white.
**Leaf Blade:** Green with a light green to occasionally pinkish "piko".
**Corm:** Small; white with yellow fibers; long, thin rhizomes.
**Distribution:** Not cultivated, but commonly found scattered along streams and seeps

**Uses:** None seen.

**Remarks:** Stokes (1921; Stokes 341 BISH, 1930, 1955) recorded "matoe" in 1921 as a two-foot tall "mountain taro", that grew "between ferns and under trees". In 1930 he records it was a wild taro "which grew on the cliff faces... now known by its Tahitian name "apura", is commonly referred to as ancestral food". Our informants in 2002 still recognized "matoe" or "matae" as synonyms for "apura", and as the original Rapan names for this cultivar. Both of these original names were recorded on the *Rapa language list* (Anonymous 2001).

This taro was not cultivated in 2002, yet it was still very common to find scattered along streams and seeps. It is one of the two cultivars commonly found in the wild, the other being "kapu'ue". The two are readily distinguished by their different coloration and different rhizome habit.

This cultivar is known in Hawaii as "'aweu", where it too is also the most commonly found wild taro (Whitney et al. 1939).


**General characteristics:** Light yellow, thin petioles that droop to give a widely spreading appearance; many "'ohā".

**Petiole:** Yellowish turning whitish at apex; edges of petiole sinus red; pink base.
In 1921, Stokes (1921; Stokes 433 BISH, 1930, 1955) collected this wetland cultivar originally under the name "poitere". In 1930 he recorded that this native cultivar was called either "araara" or "poitere". By 1955 he listed "araara" and "poitere" separately, without mentioning their synonymy. Informants from Rapa today confirm Stokes’ original 1930 record, by saying that "poitere" is definitely not its own taro cultivar per se, but rather describes any kind of taro with lots of "'ohā", a description that aptly fits this cultivar! Both "'ara'ara" and "poitere" appear as taro cultivars separately in the *Rapa language list* (2001) without explaining this relationship. The herbarium voucher from 1921 (Stokes 1921; Stokes 433 BISH) appears to have a light stem and a leaf with a dark line on its underside that runs from the base of the leaf sinus to the "piko".

St. John (1934; St. John 15753 BISH) records this cultivar as "ara ala" and that it was much cultivated, leaves pale green above, whitish green beneath, and petioles violet. Corm white and "popoi" whitish, and that this cultivar "makes one of the best "popoi".

*Hamoa*

**General characteristics:** Dark petiole with color going into veins beneath leaf blade, black "piko".

**Petiole:** White at base, then dusky blackish into maroon at apex, color goes into veins on underside of leaf; edge of petiole sinus is very narrowly a dusky reddish color.

**Leaf Blade:** Green, prominent black "piko".

**Corm:** White; 5-6 "'ohā".

**Distribution:** Only occasionally seen, planted dry.

**Use:** None seen

**Remarks:** Said to spread rapidly and cook fast. This name was recorded by Stokes (1930, 1955) and the *Rapa language list* (2001). Interestingly, Stokes identified this cultivar in 1930 as a "mountain taro" but in 1955 as a "cultivated variety of taro".

St. John (1934; St. John 15362 BISH) recorded finding this cultivar by a trail in the woods and identifies it as indigenous, with erect, purplish-red petioles.

*Kaupapa* ("Kopapa", "Ruri")

**General characteristics:** Very light color, almost white petioles striped midway with darker green; leaf has a distinct, red "piko".

**Petiole:** Bright red ring at base then pink above, grading into very light greenish-white with green stripes midway, into light pinkish just at apex; edge of petiole sinus red with dark blotches adjacent; young petioles light pinkish.

**Leaf Blade:** Green, long; distinct, red "piko".

*Kapu'ue* ("Kapue")

**General characteristics:** Wild (naturalized), reddish taro with short, thick rhizomes.
Corm: Pink; said to become dark when cooked and taste like "veo" cultivar.  
**Distribution:** Rare, only found growing wild in a stream above the renowned taro growing area, "Tukou". Not seen cultivated.  
**Use:** None seen.  
**Remarks:** Informants on Rapa in 2002 recognized "ruri" as a synonym for this cultivar and say it has three forms: "ute'ute" or red, "uo'uo" or white, and "toretore" or striped. The description above is taken from a wild-collected "toretore" form. The other two forms were not seen and may be lost. Informants said the "uo'uo" form has red sap and a petiole sinus with a dark red edge. Stokes (1921; Stokes 133 BISH, 1930, 1955) wrote on the herbarium sheet of this collection from 1921, that this cultivar was a "mountain taro" that grew two feet tall, with creamy white flowers and that both the leaves and corm were eaten. Interestingly, he identified it as a cultivated taro in 1930 but again called it a "mountain taro" in 1955. St. John (1934; St. John 15754 BISH) records this cultivar was a little-cultivated wet or dry taro of mediocre quality, leaves pale green above, paler green beneath, edge of leaf sheath brown, petiole base pinkish, and whitish above. Corm light rose. This cultivar is on the Rapa language list (Anonymous 2001).  

**"Kokura"**  
This cultivar was not found in 2002. It is recognized by informants as a name for a lost taro cultivar, but otherwise unknown. Stokes (1930, 1955) included this name in his 1930 cultivar list, saying that it was a wetland variety of taro that was "cultivated in early days", but that it had disappeared. This cultivar is on the Rapa language list (Anonymous 2001).  

**"Kororoinako" ("Kororoinaku", "Tororoinako")**  
**General characteristics:** In 2002, informants on Rapa say this cultivar only grows at the mouth of a cave near the ocean at a place called "Tegaire". It was not collected in 2002.  
**Remarks:** Said to have dark red petioles and a white corm. Stokes (1930, 1955) included this name in his 1930 cultivar list, saying that it was a wetland variety of taro that was "cultivated in early days", but that it had disappeared. This cultivar is on the Rapa language list (Anonymous 2001).  

**"Ma'areva" ("Mareva")**  
**General characteristics:** Dark leaf with a distinct, y-shaped "piko" (caused by pigment going into the leaf veins). Two forms of this cultivar were seen, "uo'uo" or white and "ere'ere" or black. These forms are quite similar; the only apparent difference between cultivar forms is that "uo'uo", is decidedly lighter overall than "ere'ere". Petiole: Base white in both forms, then transitions to a dusky, dark green in the "ere'ere" form or into just dark green in "uo'uo" form; both forms transition gradually to a reddish-maroon, beginning about halfway toward apex in "ere'ere" or nearer the apex, and about two-thirds of the way up in "uo'uo" form, both forms have an indistinctly whitish edge of the petiole sinus.  
**Leaf Blade:** Dark green; "piko" distinct and y-shaped, its reddish-maroon color goes into the leaf midrib and primary veins of the lobes or the leaf base; the lower leaf blade has a dark line running from base of sinus to "piko".  
**Corm:** White; branching, sometimes a lot (up to 7 times).  
**Distribution:** Very common, widely planted in "roki".  
**Use:** As "popoi".  
**Remarks:** One of the two most common taro cultivars on Rapa, the other being "'ara'ara". Both forms of this cultivar were seen in 2002, "uo'uo" or white and "ere'ere" or black. These forms are quite similar; their only apparent difference being that one was decidedly lighter than the other. Known as "ti'iti'i" on Raivavae, Rapa's nearest neighbor. An informant notes that when the purple "piko" of "ma'areva" yellows, that means it is ripe. St. John (1934; St. John 15752 BISH) noted this cultivar was "the taro of Mangareva", an ancient introduction to Rapa, a much-cultivated wet taro, leaf blades bluish green above and whitish beneath, and reddish purple at point of attachment to the green petiole. Its white corm makes brown "popoi" of good quality. Curiously, St. John makes no mention of this cultivar's distinctly y-shaped "piko" and the voucher specimen made from his collection "15752" has no evidence of this characteristic either.
Also quite curiously, and quite in contrast to St. John's identification of this cultivar as an ancient introduction to Rapa, Stokes (1930, 1955) definitely does not include this as a separate cultivar on lists from 1930 or 1955, nor did he collect a voucher of it in 1921. (See however, "maiapa mareva" discussion below.)

This cultivar name is on the Rapa language list (Anonymous 2001).

There are two cultivars from Hawaii that, although they lack corms that branch, nonetheless have very similar appearances to "ma'areva". These two Hawaiian cultivars are named "manapiko" and "Tahitian" (Whitney et al. 1939). While the first, "manapiko", is an ancient cultivar from Hawaii, the second, "Tahitian", was "introduced by Wilmer from Tahiti" early in the last century. Coincidentally, the main difference between these two Hawaiian cultivars parallels the main difference between the two forms of "ma'areva" as cataloged above, i.e. "manapiko" is decidedly darker than "Tahitian".

"Maiapa" ("Mai'iapu wowo", "Maiapa white", "Maiapa mareva", "Maiapa mangareva")

This cultivar was not found in our 2002 survey. Informants say that around 2000, this cultivar vanished in Rapa from an introduced disease. It was said to have a corm that branched and that it was "all white", similar to "'ara'ara" in appearance. Three forms of "maiapa" were recorded: "'uo'uo" or white, "'ere'ere" or black, and "mangareva".

Stokes (1921; Stokes 423["maiapa"], 434["maiapa white"], 435["maiapa mareva"] BISH, 1930, 1955) collected all three forms of this wetland cultivar in 1921 and noted in 1930 that while the "light and dark varieties" of "maiapa" were native, "maiapa mangareva", ("maiapa mareva") was a recent introduction.

He described "maiapa" ("maiapa dark") (Stokes 1921; Stokes 423 BISH) as a native wetland cultivar that was a foot and a half tall (46 cm), with yellow flowers, a red "piko", red leaf veins, and red on the upper part of the stems.

He described "maiapa white" ("maiapa 'uo'uo") (Stokes 1921; Stokes 434 BISH) also as a native wetland cultivar that was a foot and a half tall (46 cm), but that it had white stems and a branching corm, with "two or more tops to one root". On the herbarium sheet for this cultivar, it looks as though its leaves have a distinct but delicate, y-shaped "piko", with streaks of color going rather far along the leaf veins, almost reaching the edge of the leaf. Underneath the leaf, there appears to be a dark line running from the base of the leaf sinus to the "piko".

He described "maiapa mareva" ("maiapa mangareva") (Stokes 1921; Stokes 435 BISH) as a wetland cultivar that was two feet tall (61 cm), with dark purple stems, veins, and "piko", and that its yellow flowers also had purple stems. From the herbarium sheet, it looks as though this cultivar's y-shaped "piko" went along the leaf veins rather far, with streaks going almost to the edge of the leaf, akin to but darker and more robustly than the "maiapa white" form does. Underneath the leaf there also appears to be a dark line running from the base of the leaf sinus to the "piko", again somewhat akin to, but more robustly than "maiapa white" does. Unlike the "maiapa white" form however, this cultivar has some small dark purple area on the face of its leaf at the base of the leaf sinus.

St. John (1934; St. John 15748 BISH) listed "mai'iapa wowo" ("maiapa 'uo'uo") as indigenous and commonly cultivated, leaf blades pale green above, whitish green beneath, with whitish petioles, corm and "popoi" white. He noted this cultivar is "especially eaten as "takai" —steamed, pounded into a mass, sliced and eaten". This cultivar is on the Rapa language list (Anonymous 2001).

"Manaura"

General characteristics: Petiole is practically uniform green, leaf has no distinct "piko".

Petiole: Whitish green towards base transiting to uniformly plain, dark green that lightens again toward apex, light brown just under leaf blade; slightly whitish-green edge of petiole sinus.
Leaf Blade: green, slightly wavy edges; indistinct "piko".
Corm: pink; > 7 "'ohā".
Distribution: Uncommon, planted dry.
Use: None seen.
Remarks: This cultivar was only found once in 2002, growing dry. The grower, Benjamin Pukoki, said it was from Raivavae. It appears to be a quite recent introduction, as neither Stokes (1930, 1955) nor St. John (1934) mentions finding this cultivar on Rapa. In unpublished material about Raivavae however, Stokes (1930) listed "manaura" taro as an "ancient food" from Raivavae, Rapa's nearest island neighbor. This cultivar is not found on the Rapa language list (Anonymous 2001) either.

**"Matoro"**
This cultivar was not found in 2002. Informants describe it as having dark red petioles with a pink base and a red corm. There were two forms, "'uo'uo" or white and "'ere'ere" or black. In 1930, Stokes (1930, 1955) included this cultivar name on a list of taros that were being actively cultivated at the time of his visit in 1921, saying that it was a wetland variety of taro that was "cultivated in early days", but did not collect a voucher of it. This cultivar is not found on the Rapa language list (Anonymous 2001).

**"Matuku"**
General characteristics: Petioles slightly striped toward base then turn purple two-thirds of the way up towards leaf; distinct broad pink to white edge of petiole sinus.
Petiole: Dark red ring at base, then pink into dark green with a few light green stripes at base, grading into dusky purple two-thirds of the way to apex; broad pink to white edge of petiole sinus.
Leaf Blade: Green.
Corm: Pink; soft, easy to pound.
Distribution: Uncommon, planted dry.
Use: Not seen
Remarks: Informants say this cultivar has two forms, "'uo'uo" or white, and "'ute'ute" or red. Stokes (1921; Stokes 425, 432 BISH, 1930, 1955) described "matuku" in 1921 as a native wetland cultivar that was three feet tall (91 cm), with red stems and yellow flowers. He noted that it could grow to five to six feet tall (1.5 cm to 1.8 cm). Although Stokes makes no mention of this cultivar having different forms, he still collected it twice, Stokes 425 on 15 November 1921 and Stokes 432 on 1 December 1921. The herbarium sheet of the first field collection Stokes 425 however, only consists of a single flower, which although it lacks a tip, appears to have had a spathe ~ 38 cm long!
St. John on the other hand, collected two forms of this cultivar in 1934. He recorded "matuku" (1934; St. John 15750 BISH) as an indigenous, much cultivated, well-liked wet taro, leaf blades dull green above, pale green beneath, petioles violet at base, clear green above. Corm and "popoi" rose colored. "Matku 'uo'uo" (St. John 15746 BISH) he described as an indigenous, much cultivated, well-liked wet taro, leaf blades dull green above, pale green beneath, petioles white at base, violet at middle and upper parts. Corm and "popoi" white. (Note: The summary checklist for H. St. John's fieldwork in Rapa lists "'matuleu 'uo'uo" as the cultivar name for St. John 15746. However, from the actual field notes for St. John 15746, his handwriting reads "'matuku 'uo'uo". Thus, "'matuleu" is not considered to be a valid cultivar name). This cultivar is on the Rapa language list (Anonymous 2001).

**"Paka" ("Laupaka", "Raupaka")**
A taro by this name was not found during our survey in 2002 and local informants said that "paka" is definitely not a taro cultivar name, but instead means "the skin of a young taro" or "to skin a young taro". Thus, it appears that "paka" is not a valid cultivar name. Neither Stokes (1930) nor St. John (St. John 1934 BISH) reported finding a taro cultivar named "paka". "Paka" in fact, does not appear on any listing of taro cultivars until 1955, when Stokes includes it on his list of words from Rapa (1955). It was subsequently included on the Rapa language list (Anonymous 2001).

Just how "paka" became a cryptocultivar remains obscure, but it may be linked to the very first two taros that Stokes ever collected on Rapa (1921; Stokes 47 & 133 BISH). Having arrived on Rapa on 14 April 1921, he made his first collection of taro on 10 June. The herbarium sheet of this first...
collection (1921; Stokes 47 BISH) consists of just one large leaf with a dark purplish cast. On the sheet, Stokes originally recorded the name as “laupaka”, then crossed this out and wrote “raupaka”. The taro came from Maitua at 183 m elevation, where it grew three feet tall (91 cm). He noted that the leaves and blossom were cooked as greens, the root as food, and that its flowers were white. Two months later, on 15 August 1921, he collected his second taro, "kaupapa" (1921; Stokes 133 BISH), also from Maitua but at 168 m elevation. On its herbarium sheet, this cultivar’s leaves have a dark purplish cast too. Stokes recorded it was a "mountain taro", that it grew two feet tall (61 cm), that both the leaves and the corm were eaten, and that it had creamy white flowers. These two collections are similar enough that they appear to be the same cultivar. Their leaves both have a similar dark purplish cast, unlike any other taros from Rapa in the herbarium. Both have quite unusual white flowers; all other Rapa taros reportedly have yellow flowers. Both were collected just two months apart from the upland area Maitua within 15 m elevation of each other. Both are the only two taro cultivars noted whose leaves were eaten as greens. Most importantly, informants in Rapa today define "raupaka" as "taro leaf", not as the name of any particular taro cultivar. Putting all this information together, it may just be that in June 1921, when Stokes asked about the name of the taro whose large leaf he had just collected, informants simply told him that he had collected a "raupaka" or a taro leaf. Two months later, when he may have grown more adept at the language, he collected this cultivar once again from the same general area, and this time was able to get its proper cultivar name, "kaupapa". It is plausible that the name "laupaka" or "raupaka" was a case of mistaken identity in June 1921 and that thirty-four years later in 1955, Stokes imperfectly recalled it as "paka". In any event, Stokes himself left these three particular names off his 1930 listing of taro cultivars and St. John (St. John 1934 BISH) never collected any cultivars with these names either. Additionally, in 1955 even Stokes himself tentatively identified "raupaka" as "a leaf (of taro?)" in his list of words from Rapa (Stokes 1955). Since Stokes left "paka" off his original 1930 listing of taro cultivars and since it didn’t show up until 1955, 34 years after he left Rapa, and since informants today say that "paka" is definitely not a taro cultivar, it appears fair to conclude that "paka" is not a valid taro cultivar name. Likewise with "raupaka", Stokes did not put this name on any listing of taro cultivars and informants today define "raupaka" as "taro leaf", not as a taro cultivar, and so it appears fairly certain that "raupaka" is also not a valid taro cultivar name either.

"Rarotonga" ("Larotoa", "Raratoa")
This plant was not found, nor was any mention made of it in 2002 by local informants. It currently belongs in the genus Xanthosoma according to its herbarium specimens. Thus, it appears that "rarotonga" is not a valid taro cultivar.

In 1921, Stokes (1921; Stokes 136 BISH, 1930, 1955) recorded this plant was "an introduced taro now growing wild", in 1930 he wrote that it was recently introduced to Rapa, calling it "a dryland taro which is now growing without cultivation", and in 1955 he listed "taro rarotonga" as "an introduced variety of taro". On the herbarium sheet of his 1921 collection, Stokes included extensive explanatory notes. He originally labeled it "larotoa", but crossed this out and wrote "rarotonga". He recorded that it was known in Rurutu and Rapa as Rarotongan taro. It grew dryland, two to three feet high (61-91 cm) on Rapa in the high, sheltered valley of Maitua. Its primary stem was never eaten because it was too coarse, only the lateral stems (or tubers) were cooked underground and eaten, with the primary stem being left alone to reproduce. Although he noted that its tubers were very mealy when cooked and never used for "popoi", their advantage was that they would keep well for six months or more, whereas ordinary wetland taro rots within a week. He recorded that its leaves were eaten too. St. John however (1934; St. John 15756), identified "raratoa" as Alocasia macrorrhiza, which is most definitely not a taro. His field notes record it as introduced and cultivated dryland, leaves bright green above and pale green beneath and that its corms were baked in the "ko’otu", not made into "popoi", with only side sprouts eaten and the main one fed to pigs. In 1981, it was determined from herbarium collections (Stokes 1921; Stokes 136 BISH & St. John 1934; St. John 15756 BISH) that "rarotonga" is a species of Xanthosoma. This name does not appear on the Rapa language list (Anonymous 2001).

"Rotere"
A taro by this name was not found during our survey in 2002. In fact, "rotere" was tentatively identified as a possible taro cultivar only on the Rapa language list (Anonymous 2001) and not from any other reference. When presented with this name, informants would correct "rotere" to "rotea", and then hesitantly offer that it might be a lost taro, but otherwise it was unknown. Stokes (1930, 1955) does not identify "rotere" as a taro cultivar, but records that "rotea" was the name of "a fern". Brown & Brown (1931) documented "karotaa" ("ka rotea") was the name of bird’s-nest fern (Asplenium nidus) in Rapa. St. John (St. John 1934 BISH) did not collect any taro cultivar called either "rotere" or "rotea" during his 1934 visit. From this evidence, it appears likely that "rotere" is not a valid taro cultivar name.
"Taitika"

This cultivar was absent in 2002 and may be lost, though it was noted on the Rapa language list (Anonymous 2001). Informants describe it as having a white petiole, yellow corm, and lots of "ohā".

Stokes (1921; Stokes 424 BISH, 1930, 1955) recorded "taitika" in 1921 as a native wetland cultivar that grew a foot and a half tall (46 cm), with a red "piko" and a red root. In 1930 however, he labeled "taitika" a wild taro, "which grew on the cliff faces". By 1955, he listed "taitika" simply as "a variety of taro" with no further explanation.

St. John (1934; St. John 15749 BISH) reported "taitika" as indigenous and fairly commonly cultivated, leaf blades light green above with purplish margin, whitish green beneath. Corm and "popoi" are yellowish. His note that this cultivar has a "sweeter flavor than most kinds", may indicate that his sample was overripe.

"'Ue'ueine" ("Uue'eine", "Ulueine")

Informant Benjamin Pukoki called his taro "'uue'eine 'uo'uo", or the white form of this cultivar, while Mama Luita called her taro "'uue'eine 'ute'ute" or the red form of this cultivar.

**General characteristics:** Reddish-green petioles with light green stripes appearing towards base and apex, solid color between; indistinct "piko".

**Petiole:** The "'uo'uo", or white form, has a light reddish base with a few indistinct green stripes, grading into reddish-green with indistinct lighter green stripes for about the first third, then becoming more or less solid green-light reddish for the middle third, and changing to light reddish-green with indistinct green stripes, lighter than at base, for the top third; light reddish edge of petiole sinus. The "'ute'ute", or red form, has a bright red petiole base going into red with green stripes of the lower third, then more or less solid reddish-green on the middle third, and then back to red with green stripes, lighter than at base, for the top third, (an informant says, sometimes this form can be red with green stripes all along the petiole, lightening toward apex); edge of petiole sinus is red.

**Leaf Blade:** Green; indistinct "piko".

**Corm:** White; soft, easy to pound.

**Distribution:** Occasional.

**Use:** For "popoi".

**Remarks:** Two forms of this cultivar were seen, the "'uo'uo" or white and the "'ute'ute" or red. These forms are quite similar; their apparent difference is that the white form, "'uo'uo", is generally lighter red than the latter, with a light reddish petiole base, while the red form, "'ute'ute", is darker red overall, with a bright red petiole base.

Stokes (1930, 1955) does not list this cultivar name. St. John (1934; St. John 15751 BISH) recorded this was an indigenous taro, much cultivated wet or dry, leaf light green above with paler veins, whitish green beneath. Corm pulp and good quality "popoi" are both white.

This cultivar is on the Rapa language list (Anonymous 2001).

"Veo"

**General characteristics:** Broad to narrow dark green stripes on light green petiole; yellow corm.

**Petiole:** Base white, light green with broad to narrow dark green stripes on from bottom half, solid light green on top portion.

**Leaf Blade:** Green; indistinct "piko".

**Corm:** Yellow; c. 5 "'ohā".

**Distribution:** Occasionally seen planted dry.

**Use:** Not seen.
Remarks: Informants say there are two forms of this cultivar, “uo’uo” or white and “ute’ute” or red. Stokes (1930, 1955) does not list this cultivar name. St. John (1934; St. John 15747 BISH) listed a cultivar named "veevoeo" as indigenous, much cultivated and well liked, leaf blades dull green above and whitish green beneath, petioles purplish. Corm pulp and "popoi" white. This description however, does not match very well the taro presently called "veo". This cultivar is on the Rapa language list (Anonymous 2001). *Veo* appears to be very similar, if not identical, to a well-known cultivar in Hawaii, introduced from American Samoa and known as “fai fa'ausi” (Lyon Arboretum 1970).

**DISCUSSION AND CONCLUSIONS**

Taro is the staple starch source on Rapa. It has been estimated based on satellite imagery and GIS that 2% of the island has been under taro cultivation at some time (see chapter by Motley *et al.*, this volume). This includes all of the suitable arable lands, comprising most of the lower valleys and flat valley floors on the island. It has been hypothesized that the Rapan Forts or "pa" were built to protect limited food resources when the islands population was at a maximum capacity (Ferdon 1965). Because of the importance of taro in the Rapan diet over the past centuries, combined with the island’s isolation and the human selection pressures on the original cultivars brought to the island in colonizing canoes, over time many distinctive cultivars have been selected for that are endemic to Rapa.

Our study recorded 19 possible cultivar names of taro from Rapa. Three however, "Paka", "Rotorenga", and "Rotere", should not really be considered as valid names for taro and should be left off cultivar lists for the following reasons. None of these three putative cultivars were found during our survey in 2002. Historically, although Stokes (1930, 1955) identified the first, "Paka", as a taro cultivar in 1955, he did not do so in earlier work from 1930. He never collected any taro cultivar by this name during his 1921 visit. St. John also never collected any taro cultivar by this name during his 1934 visit. While "Paka" was included on the Rapa language list (Anonymous 2001) as a taro cultivar, informants from Rapa today definitely say this is not a taro cultivar, but instead that "Paka" means "the skin of a young taro" or "to skin a young taro". The second cultivar, "Rotorenga", is not a taro according to its herbarium specimens, but belongs in the genus Xanthosoma. The third questionable cultivar is "Rotere", which appears as a tentative taro cultivar only in the Rapa language list (Anonymous 2001) and not in any other previous references. When informants were presented with "Rotere", it was invariably corrected to "Rotea", which was then hesitantly recalled as maybe being a lost taro. Stokes (1930, 1955) did not record "Rotere" as the name of any taro cultivar however, but noted that "Rotea" was the name of "a fern" instead. Brown & Brown (1931) recorded "karotaa" ("ka rotea"?) as the name for bird’s-nest fern (*Asplenium nidus*) in Rapa. St. John never collected any taro cultivar by either name in 1934, in further support that "Rotere" is likely not a valid taro cultivar. Thus, it appears reasonable to believe that these three names, "Paka", "Rotorenga", and "Rotere", have been mistakenly identified as taro cultivars in the recent past and will be so treated here. These three invalid names will not be counted as *bona fide* taro cultivars from Rapa.

Of the remaining 16 authentic cultivars of taro from Rapa in Table 48, eight have several forms that are widely recognized by local residents. The cultivars "Kauipapa" and "Maiapa" each have three distinct forms and "Ara’ara", "Ma’areva", "Matoro", "Matuku", "Ue’ueine", and "Veo" each have two recognizable forms (Table 48). In total there are 26 distinct taros from Rapa, known either currently or in the past. Three of these cultivars and one form of a fourth cultivar are identified by informants or from records as "not Rapan." "Hamoa" is identified as a Samoan cultivar. "Ma’areva" and the "Mangareva" form of "Maiapa" are both introductions from Mangareva Island. "Manaura" was introduced via Raivavae.

The diversity of Rapan taro is impressive for a small island. Unfortunately, five cultivars and their various forms no longer exist (Table 48). These cultivars and their physical descriptions, although sometimes vague, are still alive in the memories of our informants. Therefore, some taro cultivars that we recorded above we did not see during out visit. Whether they still exist is unknown. For example, "Kororoinako" is a cultivar known to grow only at
we were unable to investigate this site. Many of the cultivars may have just disappeared because of preference for other taros and disuse. Because population levels have dropped on Rapa, so has cultivation. Only about one quarter of the taro fields identified by satellite imagery are still actively planted (see chapter by Motley et al., this volume). A more serious threat to taro comes from disease, which could destroy the unique germplasm resources that may exist in Rapan cultivars. An accidental introduction of taro leaf blight into Samoa in 1993 nearly wiped out most cultivars there (Caillon et al. 2006). The recent loss on Rapa (in c. 2000) of the three forms of "Maiapa" due to disease exemplifies the fragile nature of these resources.

The erosion of genetic diversity of crop species (Myers 1988) and cultural knowledge (Balick et al. 2001) was the driving force behind this study. When preparing to conduct this botanical expedition and research on Rapa it was apparent from literature (Beck 1922) and from accounts in historical expeditions, that tāro played an important role in the survival of the Rapan people and that they had developed unique culinary practices and cultivars. We have confirmed these historical accounts and have given our best account of tāro cultivars, traditions, and uses in 2002.

Future studies should study the genetic diversity that exists in the cultivars and forms of Rapan tāro, using molecular techniques. A germplasm collection should be established because these plants may harbor unique genetic material that could be used to enhance disease resistance or production. However, since tāro is typically clonally propagated, seed storage is not an option; long-term maintenance of such living collections is fraught with difficulties (Motley 2006). The best method is probably preservation through tissue culture. Tissue culture efforts are underway at Lyon Arboretum in Honolulu, Hawaii to preserve the remaining Hawaiian taro cultivars. Using their methods and facilities may be a way to start banking the germplasm resources of Rapa. We also strongly suggest that support, both financial and technical, be given to the people of Rapa to maintain a living collection of tāro cultivars in situ. Plans are underway to continue our studies to include a genetic assessment of diversity of Rapan tāro.

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Table 48: The 16 confirmed tāro cultivar names recorded on Rapa in 2002 and comparison with previous cultivar surveys. Numbers in parentheses represent number of forms of cultivar.

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<td>'Arara (2)</td>
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<td>Hamoa</td>
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<td>Kaupapa (3)</td>
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<td>Kororoinako</td>
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<td>Ma'areva (2)</td>
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<td>Mangareva</td>
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<td>Maiapa (3)</td>
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<td>Mangarevan form</td>
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<td>Manaura</td>
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<td>Raivavae</td>
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<td>Matoro (2)</td>
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<td>Matuku (2)</td>
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<td>Tatika</td>
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<td>'Ue'ueine (2)</td>
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<td>Veo (2)</td>
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</table>

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The mouth of a cave on the north side of the island;
GLOSSARY OF TARO TERMINOLOGY*

a'apo'i – to cover an oven with plant material.
'akama'u – to make sour; by extension, the small packet of sour popoi that’s pounded into freshly made popoi, in order to make it sour rapidly. Being replaced by Tahitian term ‘ano'i or te ‘ano'i.
'akarapu – to mix.
'akatika – to level ground in roki by using water.
'akotoki – to separate twinned stalks of young branching taro.
'aka'ui – sheaf of plants.
'anavai – river, large stream.
'ano'i – see te ‘ano'i.
eka – roots of taro plant.
'e're're – black, blackish, or dark-colored.
'e – to cook food in oven; considered to be a Tahitian word, Rapan term is tao.
fā – stem of taro plant.
fio – young taro spathe used by children as noisemaker; to whistle.
fā'arue'a kotae – small irrigation ditch between roki.
ha'apahura'a kotae – dam across watercourse that diverts water into ditch that irrigates roki.
kai – food, to eat.
kaikai – food, to eat.
ka'o – unfurled young taro leaf.
kara – a very hard kind of stone; a brick-shaped pounder made of such stone, pestle to pound popoi.
karakaro – Cordyline fruticosus, ti.
kauatu – oven.
kavake – taro suckers.
kavakevake – copiously suckering taro.
kō'a – general name for taro; cooked taro; taro food.
koki te veoveo – perfectly ripe taro, just ready to eat.
kokura – oven.
ko'ai te veoveo – dam across watercourse that diverts water into a loaf that is sliced and eaten as is, as if it were one large taro.
takai – see tākai.
tao – to place food in oven.
.tapau mikaka – taro sap.
tapiri – stage in pounding popoi; paste of taro; to glue.
tarua – starchy.
tauau – Musa spp., Musaceae, general Rapan term for banana.
taviri – to vigorously aerate popoi with a resounding “whump,” now replaced by Tahitian word, nane.
te ‘ano'i – small packet of sour popoi that’s pounded into freshly made popoi, in order to make it sour rapidly. Considered a Tahitian word, similar Rapan term is ‘akama'u.
teatea – white, whitish, light-colored.
tio'o – ancient way of using taro, by fermenting in a pit and then cooking (see ma'u above), abandoned by about the middle of the nineteenth century for popoi.
to'i – to separate leaves from the taro stem.
tuki – large, flat stone to pound popoi on; to pound food.
'uo'uo – white, whitish, light-colored; considered a loan word from Tahiti, Rapan term is teatea.
'uri – taro slip to plant; stem of taro.
uru – to clean.
'ute'ute – red, reddish, bronzed.
'uvai – ditch that directs water to the roki.
va'iva'i – soft rot of taro.
vāruravāruravā – to peel, to scrape.
veoveo – young taro flowers, which are edible.

* This glossary is a compilation of vocabulary words from Rapa that are associated with taro culture and use. Besides terms that were collected in 2002, other sources of words for this glossary are Stokes (1930, 1955) and Anonymous (2001).
Annexes
Taro pondfields, Rurutu (Photo J.-Y. Meyer).
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The success of these field expeditions is largely attributed to the skills, complementarity and humour of the teams lead by Jean-Yves Meyer (nicknamed "El Commandant") who would like to dedicate this book to Priscille Froger, head of the Délegation à la Recherche, and Ruth Leng-Tang, her secretary-accountant, for their indefatigable moral support during the past 12 years!


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