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The phytogeographical affinities of the Pitcairn Islands – a model for south-eastern Polynesia?

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Abstract

Aim To identify how the Pitcairn group relates biogeographically to the south-eastern Polynesian region and if, as a subset of the regions flora, it can then be used as a model for biogeographical analyses.

Location The Pitcairn group (25°4′ S, 130°06′ W) comprises four islands: Pitcairn, a relatively young, high volcanic Island; Henderson, an uplifted atoll, the uplift caused by the eruption of Pitcairn; and two atolls, Ducie and Oeno. The remote location, young age and range of island types found in the Pitcairn Island group makes the group ideal for the study of island biogeography and evolution.

Methods A detailed literature survey was carried out and several data sets were compiled. Dispersal method, propagule number and range data were collected for each of the 114 species that occurs in the Pitcairn group, and environmental data was also gathered for islands in Polynesia. Analyses were carried out using non-metric multidimensional scaling and clustering techniques.

Results The flora of the Pitcairn Islands is derived from the flora of other island groups in the south-eastern Polynesian region, notably those of the Austral, Society and Cook Islands. Species with a Pacific-wide distribution dominate the overall Pitcairn group flora. However, each of the islands show different patterns; Pitcairn is dominated by species with Pacific, Polynesian and endemic distributions, with anemochory as the dominant dispersal method (39.5%); Henderson is also dominated by species with Pacific, Polynesian and endemic distributions, but zoochory is the dominant dispersal method (59.4); Oeno and Ducie are dominated by Pantropic species with hydrochory as the most common dispersal method (52.9% and 100%, respectively).

Main conclusions
- Habitat availability is the most significant factor determining the composition and size of the flora.
- South-east Polynesia is a valid biogeographical unit, and should include the Cook, Austral, Society, Marquesas, Gambier, Tuamotu and Pitcairn Islands with Rapa, but should exclude Easter Island, Tonga and Samoa.
- Regionalization schemes should take island type into consideration.
- The Pitcairn Island group can serve as a useful model for Pacific biogeographical analyses.

Keywords
Colonization, dispersal, habitat diversity, island biogeography, insular biotas, NMDS, Pitcairn, Sorensen distance, south-eastern Polynesia, UPGMA.

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INTRODUCTION

Since Schouw (1823) first recognized the Polynesian region, numerous biogeographical schemes, using virtually all groups of organisms, have distinguished Polynesia as a subset of the Indomalayan (Oriental) Realm (Kay, 1979). Many schemes have also recognized south-eastern Polynesia as a further subdivision of the Polynesian region, although the position of the boundaries varies (van Balgooy, 1960, 1971; Gressit, 1963; van Balgooy *et al.*, 1996). The problems associated with dividing south-eastern Polynesia are best summarized by van Balgooy *et al.* (1996) who stated that as a result of the considerable overlap in provinces, the floristic provinces could not be classified into a hierarchical system. Stoddart (1992) considers that island type should be included in biogeographical schemes, as once the relatively homogeneous biotas of atolls and makatea islands are removed the problem resolves itself into the consideration of high islands.

Brown (1935) was the first to assess the flora of south-eastern Polynesian, dividing it into six regions: Marquesas, Society, Tuamotu, Austral, Rapa, Pitcairn and Gambier Islands. However, the information from which these divisions were derived was very limited, with only 251 species being known from the region at that time, mostly from the Society and Marquesas Islands (there are currently over 600 species known from the Society Islands alone; Florence, 1987). As many of the collections were very recent, and hence poorly understood, 87% of these species were thought to be confined to the Polynesian region, and only two species were assigned a pantropical distribution. Brown also suggested that 82% of the species were of American origin.

In terms of general patterns, there is a gradual reduction in the total number of species from west to east across the Pacific; islands in the eastern half of the Pacific have virtually nothing in common with the flora of the Americas; disjunct, discontinuous and patchy distributions are frequent phenomena; and distribution patterns are associated with island type (Kay, 1979). The biota of atolls are composed of few species, most of which are widely distributed on tropical strandlines, while even a slight elevation is accompanied by a substantial increase in the floristic diversity (Sachet, 1967; Fosberg, 1984; van Balgooy *et al.*, 1996). Differences in the flora based on island type relate to the fact that atolls are ephemeral structures, subject to constant change and having resulting 'weedy' native floras exhibiting little endemism, while high islands have significant species diversity where dynamic processes of speciation and extinction occur (Brownlie, 1965; Kay, 1979).

We studied the remote Pitcairn group (25°4′ S, 130°06′ W), which lies just south of the Tropic of Capricorn, about halfway between New Zealand and South America. The group comprises four islands: Pitcairn, a relatively young, high volcanic Island; Henderson, an uplifted atoll, the uplift caused by the eruption of Pitcairn; and two atolls, Ducie and Oeno. The remote location, relatively young age and range of island types found in the Pitcairn Island group makes the group ideal for the study of island biogeography and evolution. Henderson, Oeno and Ducie Islands are *c.* 16, 13 and 8 Myr old, respectively, although all have undergone cycles of submergence and re-emergence during that period (Spencer, 1989). Pitcairn Island itself is < 1 Myr old (Spencer, 1989).

The atolls of Oeno and Ducie have a limited range of available habitats for plant colonization, and as a result have a total flora of only 18 and three species, respectively (Florence *et al.*, 1995). Waldren *et al.* (1995) identified four distinct vegetation communities on Oeno; open littoral vegetation, *Argusia argentea* L.f. scrub, Closed forest and *Cocos nucifera* L. grove. Henderson, the largest island in the group has 65 species (Florence *et al.*, 1995), having not only strand habitats as on the atolls, but also cliff and inland forest communities on the uplifted makatea. Waldren *et al.* (1995) identified six main vegetation communities; beach-front communities, embayment forests, open limestone scrub, cliff and ledge communities, exposed cliff top communities and plateau forests. The nature of Pitcairn Island, as a high island, means that a more diverse array of habitats is available than on other islands in the group. Kingston & Waldren (2003) identified eight main vegetation communities; *Metrosideros collina* (J.R. Forst. & G. Forst.) A. Gray woodland, *Homalium taypau* H.St. John woodland, *Syzygium jambos* (L.) Alston woodland, Mixed woodland, weedy scrub, fernlands, coastal rock communities and coastal scrub communities. Unfortunately, as Pitcairn is the only inhabited island in the group, human induced habitat change has resulted in a reduction in the amount of native forest and significant reduction in the populations of the 81 native species. In addition over 250 species have been introduced to the island, several of which have become nuisance invasive species and dominate large tracts of land (Kingston & Waldren, 2003).

Aims

The aim of this study was to make a biogeographical assessment for the flora of the Pitcairn group, and to determine:

- Where the flora came from.
- How the species colonized the island.
- The factors which explain any distribution patterns found.

Using this information it could then be determined how the Pitcairn group relates biogeographically to the south-eastern Polynesian region and if, as a subset of the regions flora, it can then be used as a model for biogeographical analyses.

METHODS

Several separate but related data sets were compiled from many sources, listed at the end of this section. Only native plants were used as the natural processes of plant migration and dispersal were under study, rather than anthropological progression in the area, and only vascular plants were chosen for use in this study, as these are the groups for which information is most readily available. Finally, only the 114 indigenous species occurring on the Pitcairn group of islands were used (see Appendix), as the main aim of this study was to consider the origin and formation of the flora of the Pitcairn group, rather than a biogeographical analysis of plant distribution in Polynesia or the Pacific region.

Dispersal data

Species were also assigned one of five dispersal classes based on the dispersal mechanism employed as follows: 1 = Endozoochory (actively by an animal agent), 2 = Ectozoochory (passively by an animal agent), 3 = Hydrochory (water dispersal), 4 = Anemochory (wind dispersal), 5 = More than one of the dispersal mechanisms 1–4. The number of propagules in a single dispersed unit was also recorded to allow quantification of the number of potential colonizing individuals that could arise from a single dispersal event.

Distribution data

Species were assigned one of seven general distribution classes, based on their global distributions as follows: 1 = Pantropic/Transpacific, 2 = Old World, 3 = Indo-Malesian, 4 = Australian, 5 = Pacific, 6 = Polynesian, 7 = Endemic to Pitcairn group.

Range data

The world-wide range, as presence or absence in defined geographical units (Fig. 1), for each native vascular plant species and genus in the Pitcairn Island group was compiled. Species for which native synonymy or status was uncertain were included (e.g. *Hibiscus tiliaceus* L., *Thespesia populnea* (L.) Sol. ex Corrêa); in most cases these species were widespread pantropical Indo-Pacific species, and thus did not affect the resulting data analysis. For some endemic species, especially those for which the synonymy and status was uncertain, the distribution of closely related species was also compiled.

Environmental data

Environmental parameters for each island group in the Polynesian region were also collated, including: latitude and longitude, land area, altitude, maximum age (that the islands have been above sea level), island types (whether atolls, atoll and makatea, high volcanic islands or all island types), total species number, % endemism, ecosystem number (the number of broad terrestrial or marine ecosystem types, based where possible on an existing classification or estimated from the island description and structure, from Dahl, 1980; UNEP-Earthwatch, 1998) and invasive index (the threat represented by invasive introduced species rated on both on the number of such species and their aggressiveness in island situations, from Dahl, 1980; UNEP-Earthwatch, 1998).

Data collation

Data were sourced where possible from recently completed floras, but in other cases from taxonomic literature, websites and older floras. In addition, information was taken from various general books relating to the Pacific Islands. Field observations made on the Islands of Rimatara, Rurutu, Tubuai and Raivavae in the Austral Islands, Mangareva in the Gambier Islands, and Tahiti, Moorea, Huahine and Raiatea in the Society Islands, during 1997 and 2000 were also incorporated. A record was kept of all of the data sources, listed below:

Australian Biological Resources Study (1993)
Australian Biological Resources Study (1994)
Bridson (1985)
Brooke *et al.* (1996)
Brown & Brown (1931)
Brown (1931)
Brown (1935)
Brownlie (1961)
Brownlie (1965)
Brownsey (1977)
Cheesman (1903)
Christensen & Skottsberg (1920a)
Christensen & Skottsberg (1920b)
Clague (1996)
Copeland (1932)
Copeland (1938)
Copeland (1947)
Doty (1954)
Florence (1996)
Florence (1997a)
Florence (1987)
Florence (1997b)
Florence *et al.* (1995)
Fosberg & Renvoize (1980)
Fosberg & Sachet (1967)
Fosberg & Sachet (1981)
Fosberg (1973)
Fosberg *et al.* (1983)
Gothesson (1997)
Hallé (1980)
Heads (1996)
Heywood (1978)
Holttum (1964)
Holttum (1973)
Holttum (1976)
Holttum (1978)
Holttum (1985)
Huguenin (1974)
Hunt *et al.* (2000)
Lam (1938)
McCormack (2000)
Merrill (1947)
Mueller-Dombois & Fosberg (1998)
Oliver (1935)
Rougerie (1995)
Royal Botanic Gardens Kew (1906–1996)
Royal Botanic Gardens Kew (1993)
Sherff (1926)
Skottsberg (1920–1956)
Skottsberg (1922a)
Skottsberg (1922b)
Skottsberg (1951)
St. John & Philipson (1962)
St. John (1987)
Stoddart & Sachet (1969)
Stoddart (1975)
UNEP-Earthwatch (1998)
van Balgooy (1971)
van Balgooy (1975)
van Balgooy (1984)
van Balgooy (1993)
van Steenis & van Balgooy (1966)
van Steenis (1963)
Waldren *et al.* (1995)
Waldren *et al.* (1999)
Wheeler & Carillet (1997)
Wilder (1934)
Yuncker (1937)
Zizka (1991)

Data analysis

Exploratory analysis of the range data were carried out using cluster analyses with the Sørensen coefficient as a distance measure, and group averaging as the clustering procedure (an agglomerative clustering method, sometimes referred to as unweighted pair group method with arithmetic mean (UPGMA). The ordination technique of non-metric multi-dimensional scaling (NMDS) using the Sørensen coefficient was also carried out to further visualize the data set. In order to determine what environmental variables could explain the variation found in the NMDS dimensions, the final NMDS output for the regions was correlated with the environmental data set, using Spearman rank correlations. PC-ORD for windows ver. 3.2 (McCune & Mefford, 1997) was used for the data analysis. Maps were compiled using ArcView GIS ver. 3.1.

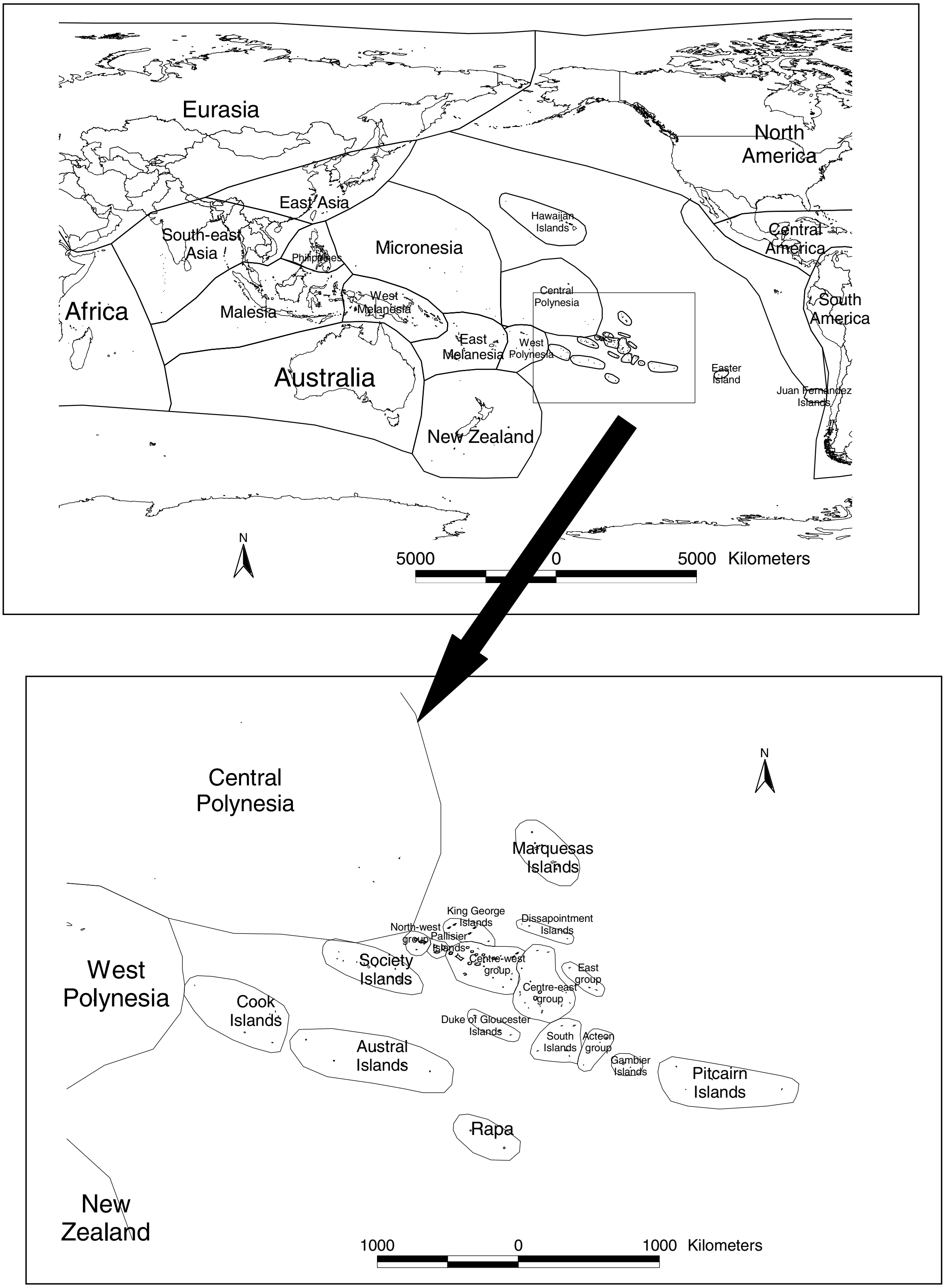

Figure 1 Geographical units to which species were assigned presence or absence in order to compile their world-wide ranges. The geographical units are delimited based on a combination of van Balgooy (1971) for the larger continents and landmasses, Mueller-Dombois & Fosberg (1998) for the Pacific islands, and UNEP-Earthwatch (1998) for the Tuamotu island subdivisions.

RESULTS & DISCUSSION

Colonization of the flora

An assessment of the dispersal mechanisms employed by the flora, found that of the four dispersal mechanisms assigned to the species, zoochory is the most frequent mechanism for dispersal, with active rather than passive methods prevailing (Table 1). Anemochory is also frequent but rarely found in the angiosperms. Zoochorous mechanisms involving a single propagule are by far the most frequent, being found 35 times in the data set (29.7% of cases). Both hydrochory and endozoochory are the mechanisms in which more than one colonizer may be dispersed in a single dispersal event, but in many cases of ectozoochory more than one propagule will attach to the dispersal agent. In theory a single propagule seems unlikely to result in successful dispersal events, however in practice some species are capable of self-fertilization, and many pteridophyte species can reproduce vegetatively by apogamy and apospory (Miller, 1968). Thus even if a single propagule reaches an island it may result in successful colonization.

Species with a Pacific-wide distribution dominate the Pitcairn flora (21.1%; see Table 2), with Old world, pantropic and endemic species also forming a large component. There were no species recorded with an American distribution. Pteridophytes tend to have more widespread distributions and the Pitcairn flora is typical, with eight of the 31 pteridophyte species having pantropic distributions.

Table 1 Occurrence of the four dispersal mechanism in the Pitcairn flora, and the number of propagules dispersed in each case

	Propagule number					
Mechanism*	1	2	3–6	7–10	10+	Total
Endozoochory	14	7	4	6	1	32
Ectozoochory	21	1	3	0	0	25
Hydrochory	14	8	3	1	1	27
Anemochory	34†	0	0	0	0	34
Total	83	16	10	7	2	

*Eleven species employ more than one mechanism.

†Thirty-one pteridophytes and three angiosperms (*Taeniophyllum fasciola*, *Metrosideros collina* and *Senecio stokesii*).

Table 2 shows the dispersal mechanism for species in each of the distribution classes, and some patterns can be established. Pantropic species are mostly water dispersed, with all the wind-dispersed species being pteridophytes. Old world species are also most likely to be water dispersed, but there are an increasing number of zoochorous species. Pacific, Polynesian and endemic species however, are more likely to be dispersed by an animal agent, in particular through bird ingestion. Dispersal using a single propagule dominates all distribution classes, but increasing numbers of species in the Pacific, Polynesian and Endemic classes contain more than one propagule in their dispersed unit. This explains the increased number of Pacific-wide species on Pitcairn, as dispersal is more likely to be successful when the distance is reduced, and a population is most likely to establish if more than one propagule arrives in a dispersal event.

As complete species lists are available for all of the islands in the Pitcairn group, it is possible to further analyse distribution and dispersal within the island group. Figure 2 shows the percentage of the total flora in each of the seven worldwide distribution classes. Pitcairn and Henderson show similar patterns, with over 45% of the species being distributed within the Pacific region (Pacific, Polynesian and endemic distribution categories). The atolls of Oeno and Ducie however differ in that the dominant element in their flora is Old World and pantropic. van Balgooy (1960) and Sachet (1967) also conclude that the highest percentages of widely distributed species are found on atolls.

Each of the islands in the Pitcairn group show differing patterns in terms of dispersal mechanisms (Fig. 3). The dominant dispersal mechanism for the Pitcairn flora is anemochory (39.5%), explained by the large number of pteridophyte species in the flora, as is typical for high islands. Zoochory is the most common method found in the Henderson flora (59.4%), and hydrochory the most common for both Oeno and Ducie (52.9% and 100% respectively). This pattern is expected due the nature of pantropic and Old World species being dispersed by hydrochory, and the fact that these atolls are dominated by species with such distributions. The smaller atoll floras are also more likely to contain species that can be dispersed in more than one way. This accounts for the success of these species in colonizing even the remotest island (i.e. Ducie), where 66.6% of the flora is dispersed in more than one

Table 2 The number of Pitcairn group species occurring in each distribution and dispersal class. The percentage of the total native flora is in parentheses after the species number

		Dispersal class			
Distribution class	Total species (%)	Endozoochory	Ectozoochory	Hydrochory	Anemochory
World-wide/ Transpacific	19 (16.7)	1	0	11	8
Old World	23 (20.2)	4	5	11	6
Indo-Malesian	8 (7.02)	2	0	1	5
Australian	6 (5.26)	2	1	0	3
Pacific	24 (21.1)	13	2	5	7
Polynesian	15 (13.1)	7	4	4	4
Endemic	19 (16.7)	10	6	1	2

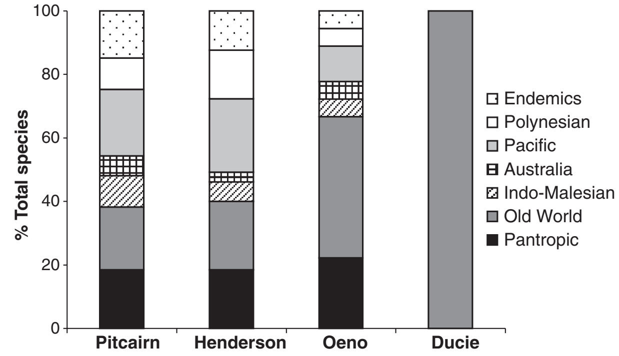

Figure 2 Percentage of species in each of the even distribution classes, calculated for each of the islands in the Pitcairn group.

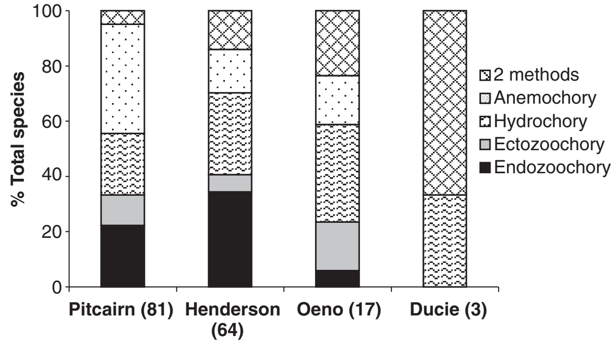

Figure 3 Percentage of species in each of the five dispersal classes, calculated for each of the islands in the Pitcairn group. Total number of species from each island is indicated in brackets.

way (the two species *Lepturus repens* (G.Forst.) R.Br. & *Argusia argentea*).

A cluster analysis of the Pitcairn flora using the range data set is shown in Fig. 4, with the dispersal mechanisms for each species overlaid. The species endemic to the Pitcairn group form cluster one, and these species are predominately dispersed by zoochory. The second cluster contains all species with narrow distributions in Polynesia, but with various dispersal methods. The third cluster contains a large proportion of water dispersed (hydrochorous) species that dominate the strand lines of all Polynesian islands and the low-lying wooded interiors of atolls. Cluster four contains species that are found in the interior of high islands, with some separation between the taxa found on both volcanic and makatea islands, from those confined to volcanic islands only in the lower part of the cluster. The cluster diagram thus shows putative ecological groupings, suggesting that the species occurring on an island strongly relate to the habitats available, and to a lesser extent to the dispersal ability of the species. It also suggests that species evolve a dispersal mechanism appropriate to habitat, with strand species being water dispersed, while inland and higher altitude species are wind and bird dispersed.

Geographical origins of the flora

A cluster analysis of the range data (Fig. 5) places the Cook, Society and Austral Islands together with East Melanesia, and West Polynesia, the Pitcairn, Marquesas and Gambier Islands and Rapa on branches from this. The atoll cluster grouped all of the Tuamotu islands together, and close to Central Polynesia. At the top of the cluster diagram is a group of the regions to the west of Polynesia, and below is a group of the islands and continents to the east of Polynesia. This shows that the Pitcairn group has the least similarities with Eurasia, which is not represented as it has no common species with the Pitcairn Island group, and America, and Pacific islands to the east of Pitcairn (i.e. Easter, Juan Fernandez and East Pacific Islands), and the highest similarities with the other south-east Polynesian island groups.

To further explore these relationships within south-eastern Polynesia, Venn diagrams were drawn to show the relationships between the floras of the Society, Austral and Cook Island groups based on the Pitcairnese element in their floras (Fig. 6a). Only seven species were not found on the Austral Islands, but six species are only found in the Austral group. This suggests that the flora of the Pitcairn group is most closely related to the flora of the Austral Islands. Figure 6b shows the comparable relationship for the Austral, Gambier Islands and Rapa, and while Rapa and the Gambier are geographically closer to Pitcairn, they are less closely associated to Pitcairn floristically than the Austral Islands.

The strongest associations with the Society, Austral and Cook Islands are because these island groups also contain all of the island types found in the Pitcairn islands and are found at comparable latitudes. However, they have larger floras as they are closer to the main floristic source (the Indo-Malesian region) and have a larger area. The relationship is, therefore, due the Pitcairn flora being essentially a subset of the larger flora of these island groups. This is supported by several species being endemic to the Austral Islands, Rapa and the Pitcairn Islands (e.g. *Hibiscus australense* Fosberg, *Peperomia rapensis* F.Br., *Senecio stokesii* F.Br.).

Within the Pitcairn group itself, Pitcairn and Oeno showed the lowest similarity, having only 10 shared species, while the highest similarity was between Henderson and Pitcairn with 33 common species (Fig. 6c). However, 17 species were common to Henderson and Oeno, which is over 90% of the Oeno flora. Ducie was not included here as only three widespread species have been ever recorded from the island, and in the most recent survey only two species (*Pemphis acidula* JR. & G.Forst. and *Argusia argentea*), both of which are recorded from Pitcairn and Henderson. The 23 species common to Henderson and Pitcairn, but not found on Oeno, are inland species, not supported on the low lying atoll habitats found on Oeno. The 48 species found only on Pitcairn are high volcanic island species found on the high slopes and volcanic soils of Pitcairn. These species would not be tolerant of the limestone and associated dry habitats found on Henderson (e.g. various pteridophytes which generally require a humid habitat). Similarly, the 25 species found only on Henderson are adapted to the dry

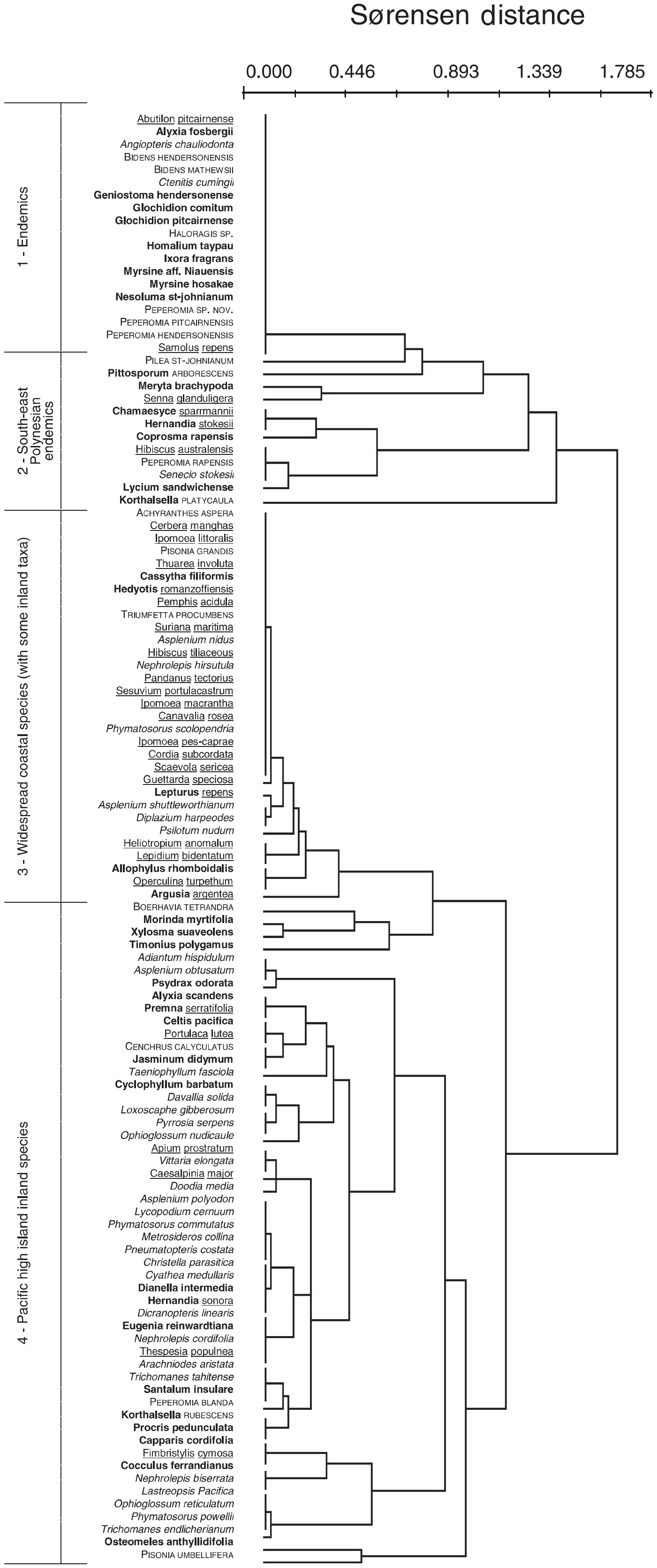

Figure 4 Cluster diagram of Pitcairn species based on their distribution in Polynesia. Differences in formatting relate to dispersal mechanism with: **Endozoochory** (bold); ECTOZOOCHORY (small caps); Hydrochory (underlined); *Anemochory* (italicized). For species dispersed by more then one mechanism the branch label is formatted twice. The clustering procedure uses Sørensen distance and the group average linkage method.

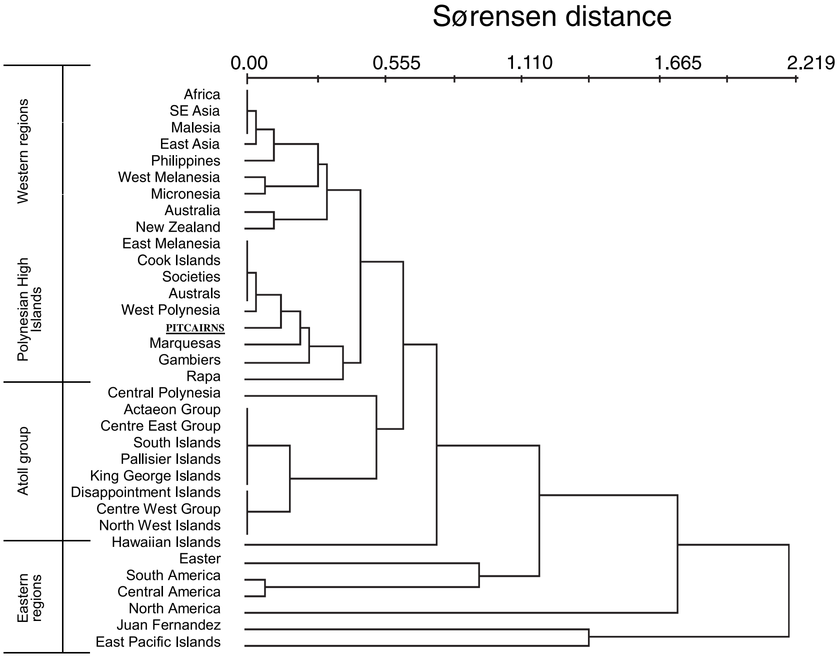

Figure 5 Cluster diagram of regions based on the distribution of Pitcairn species. The clustering procedure uses Sørensen distance and the group average linkage method.

limestone habitat and absent from the damper or more shaded high island habitats. In addition, several strand species are found on Henderson and not on Oeno, owing to the larger area of the island and the presence of coastal cliff habitats.

If the origins of the endemic flora of the Pitcairn group are also considered, the link with the Cook, Society, Austral chain is reinforced. Table 3 shows the island groups with species closely related to the Pitcairn endemics and thus islands from where these endemics may have originated. It should be noted that these relationships are largely speculative and have not been tested phylogenetically, being based both on generic distributions in the Pacific and reviews in the literature. The strongest floristic affinities are found with Rapa and the Austral Islands, as well as the Society and Cook Islands, thus reinforcing the other analyses. The close association with Rapa is unexpected based on the previous analyses, but there are actually only 12 species from the Pitcairn group not found on Rapa. Considering the strength of the association between the Austral and Pitcairn groups, however, the affinities with Rapa may not be due to a direct link, but rather both Pitcairn and Rapa may have been separately colonized by ancestral species from the Austral Islands, which in some cases then speciated separately. An example is demonstrated in the genus *Peperomia* which has a high degree of genetic plasticity, and thus an ability to radiate and speciate into different habitats. Molecular analyses have indicated that *P. pitcairnensis* (Lauterb.) C. DC is related to *P. rapensis*, a species also found in the Australs and Rapa. *Peperomia hendersonensis* Yuncker and an as yet undescribed species from Pitcairn are closely related to *P. pallida* (G.Forst.) A.Dietr. (distributed from Tonga in the west to French Polynesia in the east), and detailed molecular studies have revealed that *P. hendersonensis* and *P.* sp. *nov*. are most closely related to populations on *P. pallida* on the Austral Islands of Rurutu and Raivavae (Bradley, 2002). In addition, there are five other species common between Rapa and the Pitcairn group with closely related species in the Austral Islands, so there is undoubtedly a strong biogeographical link between the islands.

Causal factors of these distribution patterns

In order to determine if environmental gradients could account for the distribution patterns found, an NMDS ordination of the range data set for the Polynesian island groups was carried out, and the environmental data for each island group was correlated with the dimension scores. A five-dimensional solution gave the lowest stress values, with 23% of the variation explained by dimension 1, 66% by dimension 2, and $< 5\%$ by each of axes 3–5. A Monte Carlo test of 100 runs was carried out with the NMDS to test for robustness in the data set and showed $P < 0.01$ for all dimensions.

The Pitcairn group had a score of almost zero on dimension 1 and ordinates closely to all of the island groups with the exception of the Hawaiian group (Fig. 7). Longitude and total number of plants were the only environmental variables to correlate with dimension 1 ($P < 0.05$ in both cases; Table 4) and they would explain the separation of the Hawaiian islands, as they have a much higher total plant number and a higher longitude than the other island groups. Dimension 2 separated the Tuamotu islands with negative scores from the other island groups with positive scores, and correlated with altitude, island type, invasive index, % plant endemism ($P < 0.01$ in all cases) and total plants

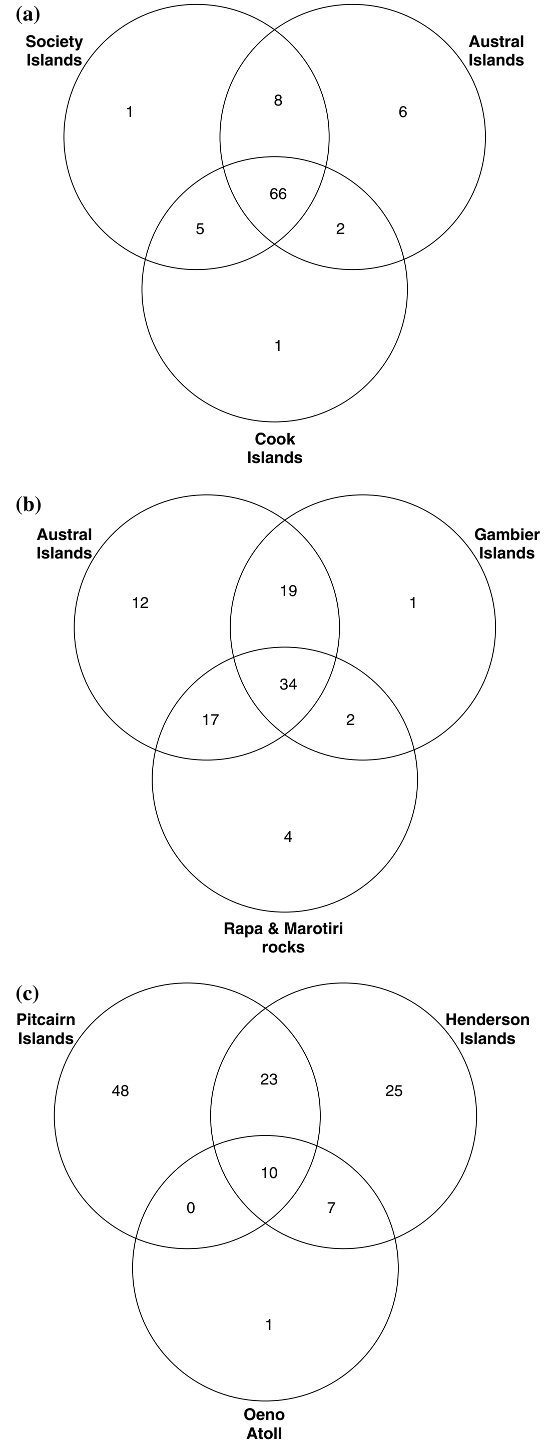

Figure 6 Venn diagrams to show the relationship between the Pitcairnese element in floras of: (a) the Society, Austral and Cook Islands; (b) the Austral and Gambier Islands and Rapa; (c) the islands in the Pitcairn group. Each circle represents the flora of the island group, with the overlap representing the number of common species in the floras of the islands.

($P < 0.05$). Much more of the variation is explained by dimension 2 (66%) and so this may explain why so many environmental factors correlate. This division would be expected as the Tuamotu islands only contains the island type of atolls which are by nature low in altitude and have few endemic species. In addition, they tend to be less inhabited and so have fewer invasive species.

As climatic factors, sea currents, sea levels and island geologies do not remain static, it is necessary to look at past environments in discussing the plant colonization of the Pitcairn group. In the period since the formation of the islands in the Pitcairn group, sea levels have probably not been lower than *c.* 150 m below current sea levels (Menard, 1964; Spencer, 1989; Pirazzoli, 1996). However, during periods of high sea levels before the formation of Pitcairn, Oeno, Ducie and Henderson (then an atoll) may have been totally submerged during certain periods, thus removing all of the terrestrial biota. Since the formation of Pitcairn and subsequent uplift of Henderson, there have been terrestrial habitats above water even during periods of high sea levels. During periods of low sea level there are several seamounts that may have been above water level and supported a terrestrial biota. Figure 8 shows the locations of seamounts and reefs that may have formed islands during such periods, and there would have been a number of emergent islands in the vicinity of Pitcairn, most notably to the west. There are also a number of seamounts and reefs around the Austral Islands, Rapa, the Cook Islands and across towards Fiji (in East Melanesia and the source of most of the Polynesian flora). Aside from a volcanic seamount close to Pitcairn, and another near Henderson, there are no seamounts or reefs between Pitcairn and Easter Island. The presence of these potential islands during cooler, windier and stormier periods would have allowed them to act as additional stepping stones for species to migrate to and colonize Pitcairn. Stepping stone islands are important to species whose propagules tend to be dispersed by zoochory, hydrochory or on floating rafts (e.g. reptiles, small mammals and arthropods can be carried on floating vegetation), and less important to anemochorous species (MacArthur & Wilson, 1967).

In van Balgooy's (1960, 1971) biogeographical regional analyses of the Pacific, Rapa is segregated into its own region, separate to the Polynesian region, to which it is geologically more associated. This division is based on the fact that the flora is more closely associated with that of Australia and New Zealand and forms a more southern element than that of Polynesia. It is interesting to note that there are several submerged reefs and banks to the south-west of Rapa towards New Zealand that could have acted as stepping stone islands for non-Polynesian species and genera to colonize Rapa (e.g. *Corokia* – found in New Zealand, Australia and Rapa; *Hebe* – found in New Zealand, Australia, Rapa and the Falklands). This theory might also account for some of the southern transpacific element found in the Pitcairn flora, notably *Samolus repens*, found in Australia, New Zealand, Pitcairn, Easter Island and South America, and *Asplenium obtusatum* G. Forst. found in Australia, New Zealand, Polynesia, Easter Island and South America.

Table 3 Locations of species that may be closely related to the endemic species found in the Pitcairn group

Genus	East Melanesia	New Zealand	West Polynesia	Cook Island	Society Island	Austral Island	Rapa	Marquesas Island	Tuamotu Island	Gambier Island	Hawaiian Island
Abutilon			✔					✔	✔	✔	
Alyxia	✔		✔		✔	✔	✔	✔	✔	✔	
Angiopteris				✔	✔	✔	✔	✔			
Bidens			✔		✔	✔	✔	✔	✔	✔	✔
Coprosma				✔	✔	✔	✔			✔	
Ctenitis			✔	✔	✔	✔	✔				✔
Geniostoma	✔			✔			✔	✔		✔	
Glochidion	✔			✔	✔	✔	✔	✔	✔	✔	
*Haloragis**		✔				✔	✔				
Homalium				✔		✔			✔		
Ixora	✔		✔	✔	✔	✔	✔	✔	✔		
Meryta				✔	✔	✔	✔	✔			
Myrsine				✔	✔	✔	✔				
Nesoluma				✔	✔	✔	✔				✔
Peperomia				✔	✔	✔	✔	✔	✔	✔	
Total	4	3	5	11	11	13	13	9	7	7	3

*Putative endemic, the taxonomy of the Pitcairn material is uncertain.

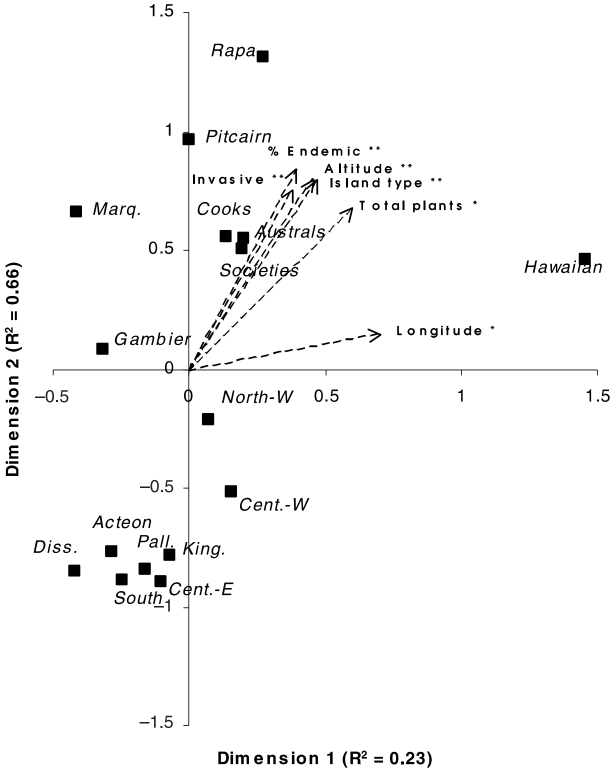

Figure 7 NMDS ordinations, with dimension 1 plotted against dimension 2, for Polynesian islands. Key: Cent.-E, Centre east group; Cent.-W, Centre west group; Diss., Disappointment islands; King, King George islands; Marq., Marquesas islands; Pall., Pallisier islands. Arrows indicate direction of environmental variables.

Table 4 Spearmans rank correlation for environmental variables with NMDS dimensions 1 and 2

	Dimension 1	Dimension 2
Latitude	$0.391^{\mathrm{n.s.}}$	$0.356^{\mathrm{n.s.}}$
Longitude	0.706^{*}	$0.150^{\mathrm{n.s.}}$
Area (km^2)	$0.418^{\mathrm{n.s.}}$	$0.153^{\mathrm{n.s.}}$
Altitude	$0.454^{\mathrm{n.s.}}$	0.798^{**}
Maximum age (Myr)	$0.248^{\mathrm{n.s.}}$	$-0.395^{\mathrm{n.s}}$
Island type	$0.470^{\mathrm{n.s.}}$	0.791^{**}
Ecosystem number	$0.195^{\mathrm{n.s.}}$	$0.332^{\mathrm{n.s.}}$
Invasive index	$0.387^{\mathrm{n.s.}}$	0.758^{**}
Total plants	0.602^{*}	0.679^{*}
% Plant endemism	$0.397^{\mathrm{n.s.}}$	0.839^{**}

n.s. > 0.05; $*P < 0.05$; $**P < 0.01$.

Approximately 40 birds have been recorded from either the islands of the Pitcairn group or crossing the ocean area between the islands, and at least four landbirds became extinct during the period of Polynesian habitation (Brooke, 1995; Wragg, 1995). Most of the sea birds and migrants are opportunists, feeding primarily on fish or squid, but the landbirds are commonly either omnivores or frugivores (Brooke & Jones, 1995; Imber *et al.*, 1995; Jones *et al.*, 1995; Trevelyan, 1995). Studies on the feeding biology of the Henderson fruit dove (*Ptilinopus insularis* North) show that it feeds on the fruits of 19 species (Brooke & Jones, 1995). Two extinct frugivores, a ground dove (*Gallicolumba* sp.) and a pigeon (*Ducula* sp.), would have browsed from a similar number of species, but also probably from species with larger fruits (e.g. *Santalum insulare* Bertero) (Brooke &

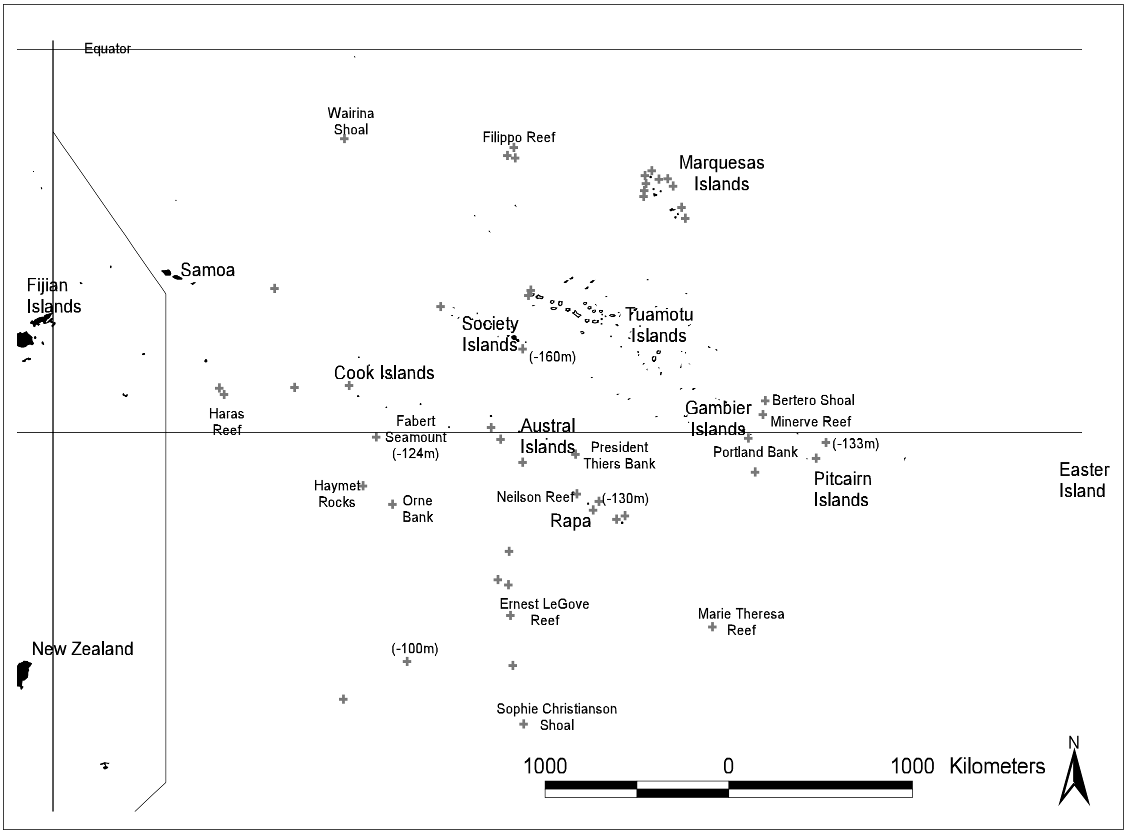

Figure 8 Locations of seamounts and reefs that may have emergent islands during periods of lowered sea levels (−150 m). Potential islands are marked with grey crosses. Figure is derived from charts 4607 and 4061 of the Admiralty series.

Jones, 1995). In addition, the migrant Bristle-thighed curlew (*Numenius tahitensis* Gmelin) and the Stephen's Lory (*Vini stepheni* North) have been observed feeding on fruits (Brooke & Jones, 1995). These frugivores would have acted as dispersers for the plant species through the Pitcairn islands and farther afield, and there are almost certainly other migrant and vagrant birds that feed on fruit, but have not been observed doing so in the Pitcairn group.

Discrepancies in the phytogeographical patterns

Looking at the distribution of species within the Pitcairn group also raises some questions as to why certain species are not more widely dispersed within the archipelago. *Homalium taypau* is an example of an endemic species that is confined to the volcanic interior slopes of Pitcairn Island. Closely related species occur in the Cook and Austral Islands, but in the Austral Islands a *Homalium* species is found growing on both volcanic and makatea substrates. *Homalium taypau* could in theory, therefore, occur on Henderson Island. It seems unusual that a species so dominant on Pitcairn does not occur on nearby Henderson, especially as the species is probably bird dispersed. The explanation may lie in the fact that many *Homalium* species require a disturbance event (such as a severe storm or cyclone) to flower and set seed (G. McCormack, pers. comm., 2000), and as such disturbances are not common on Pitcairn, this dispersal has not had a chance to occur. Other species that occur on Henderson, but could also occur on Pitcairn include *Senecio stokesii*, *Geniostoma hendersonensis* H.St. John and *Nesoluma st-johnianum* Lam & B. Meeuse (based on observations of these or closely related species occurring on volcanic substrates in the Austral Islands).

As well as considering species that could be more widespread within the archipelago, it is also necessary to examine the many species and genera that do not occur in the Pitcairn group but could do so based on their distributions and habitat requirements. *Cyrtandra* is one such genus occurring in Malesia and the Pacific islands including the Cook, Society, Austral and Marquesas Islands, and has speciated widely on these islands. It is a genus of herbs and shrubs that occur in forest undergrowth, and may be dispersed by both endozoochory and hydrochory (van Steenis & van Balgooy, 1966). It would be ideally suited to forest habitats on Pitcairn Island, but is not found there. *Colubrina asiatica* Brongn. is a pantropic species, found extensively in Polynesia, and typical of seashore, rocky and forest habitats at low elevations. It is dispersed by flotation and this mechanism has proved very successful in its widespread colonization of remote locations. It would be suited to all of the Pitcairn Islands, especially Oeno and Henderson. *Byttneria* is a genus made up mostly of American and Madagascan species. It has an unusual distribution in the Pacific, not being found in Melanesia or western Polynesia, but in the Society, Marquesas and Gambier Islands. It is thus one of the few species in Polynesia derived from recent American origin. It is a genus of forest shrubs and climbers that are dispersed by ectozoochory. As it has a limited distribution in the eastern Pacific, it is perhaps not surprising that *Byttneria* is not found in the Pitcairn group, but due to the proximity of the Gambier high islands to Pitcairn, it would seem reasonably likely that it would be dispersed there.

Because of its remoteness, the flora of the Pitcairn group is a subset of the larger flora of south-east Polynesia, notably the Austral, Cook and Society Islands. Therefore, the fact that these genera and species do not occur may be due to the simple fact that they have not yet colonized. The Pitcairn group is also out of the line of cyclones which affect the Cook, Society and Austral Islands, and thus aid dispersal between these groups. The most recent records found for the Pitcairn group are in many cases coastal species that occur in very small population numbers (e.g. *Samolus repens*, *Ipomoea littoralis* Blume, *Haloragis* sp.) which may be very recent colonizers, or may have been overlooked by previous surveys. This supports the idea that species such as *Colubrina asiatica* may either have not yet arrived in the group, or may have been overlooked. Similarly these species may have existed in the past on Pitcairn and become extinct due to the natural species turnover cycle which has been suggested for islands which are at equilibrium (MacArthur & Wilson, 1967).

Problems with the data set

There is a large potential for error in compiling and analysing data of this sort. In many cases, the floras are unknown or under collected, especially as many early collectors were mainly interested in useful and food plants and a full floristic survey has not been carried out for many of the Pacific islands. In addition many collections have incomplete location information, often simply citing an island group or region. These problems are discussed further in van Balgooy (1971), Fosberg (1984) and Chown *et al.* (1998). Misidentified specimens, and errors in the published record are all too common and seriously affect analyses of this sort (Spellerberg & Sawyer, 1999). This is less of a problem when dealing at the genus level, but may be a major source of error at the species level (van Balgooy, 1971). Examples of this include a record of a *Coprosma* sp. from Tubuai which was a *Psidium* sp. *Coprosma* spp. are some of the most biogeographically important in the Pacific, while *Psidium* spp. are introduced invasive species. Obsolete synonymy also causes confusion and many of the species from the Pacific region require taxonomic revisions.

Because of the nature of island floras containing narrow endemic species, there is also a danger that species may have become extinct since human occupation of the island, and so are not recorded. There are many examples of taxa, in particular useful plants, whose distribution would have a major affect on this analysis, and may have become extinct on many Pacific islands (e.g. *Santalum* spp. now extinct on Juan Fernandez, remaining in the Austral islands on only one motu). In this data set the presence/absence method has been used, but without accounting for pseudo-absences (taxon exists but has not yet been recorded) or reversal-absences (because of the extinction of the taxon from a geographical region). When compiling this data set it was often difficult to assign a species to a distribution class based on its current area of occupancy, and the low number of Australian and Indo-Malesian species may be due to misclassification.

Only vascular plants are considered in this analysis as it is the relationships and origins of the Pitcairn group vascular flora that are of interest here. Further studies should undoubtedly consider other taxonomic groups. However, Carson (1996) suggested that biogeography could not exist without considering plants, as their distributions are not only more stable than in animals, but also frequently serve as specific determinant substrates of various animal species.

van Balgooy (1971) argues strongly for the use of the genus as a working unit in biogeographical analyses, mainly because at the genus level one is less likely to encounter problems with synonymy or poorly defined species. He does, however, concede that the species distributions give a clearer and more detailed 'phytogeographical picture'. Tryon (1986) in his biogeographical analysis of fern species does not consider genera, as he considers the basic biogeographical features to be those of species. Using the genus as a working unit also means that widespread genera (e.g. *Asplenium*; *Peperomia*) will show no biogeographical patterns, but the same genera have many species which show biogeographically interesting and useful distributions in the Pacific and Polynesia. Thus studies at the level of genus may fail to pick up some biogeographical patterns at the large scale, the scale of interest in this study. Other disadvantages inherent to the generic method are that genera, whether large or small, are treated at the same level, and also genera are not uniformly known with some being the subject of recent revisions, and some not (van Balgooy, 1960).

Ideally a study at this scale would consider island by island distributions and thus be able to pick up more differences by island type, as recommended by Stoddart (1992). Unfortunately, however, as such island by island floristic data are not yet available, an analysis such as that would increase the effect of pseudo-absences in the data set. Steps are being taken to rectify this situation in initiatives such as the ongoing 'Flore de la Polynésie française' (J. Florence, pers. comm., 1997) and the 'Cook Island Natural Heritage Project' (G. McCormack & E. Saul, pers. comm., 2000). In contrast to Stoddart (1992), however, Whittaker (1998) argues that if island by island data are used there is a complicating effect of within-archipelago rather than island-mainland distance effects.

Implications of this analysis in terms of Pacific biogeography

Stoddart (1992) discusses the difficulties associated with existing biogeographical schemes, and suggests taking island type into consideration as the best solution. This study supports this idea, but finds that it is not island type alone, but also habitat availability that may be the most important factors affecting species distributions in the Pacific region. Thus the results here echo MacArthur & Wilson (1967) who also suggested that ultimately habitat availability would be found to be the dominant factor affecting the assembly of island biotas.

The results presented here show that as the Pitcairn group contains all of the island types, it provides a simplified model of species distribution patterns. Differences are clearly seen between the floristics of a species poor remote atoll (Ducie), a less remote and slightly more diverse atoll (Oeno), a makatea island (Henderson) and a high island (Pitcairn). The results also suggest that analyses in future should look at the distribution of habitats to explain floristic distributions. However, the same habitats on different islands do not necessarily contain the same species, as some islands have higher species diversity due to other factors. An example would be a comparison between *Metrosideros collina*-dominated cloud forest on Tahiti and Pitcairn. On Tahiti this forest type occurs at high altitudes (1000 m+; Mueller-Dombois & Fosberg, 1998), and with many diverse plant species in the community, while on Pitcairn it occurs at lower altitudes (200 m+) and with fewer plant species diversity. Direct comparison of the similarity between the habitat types, is difficult and would not explain phytogeographical relationships between the islands. However, the consideration of habitat types in conjunction with the actual species present, may prove to resolve many of the problems associated with phytogeographical regionalization systems.

CONCLUSIONS

The flora of the Pitcairn Islands is derived from the flora of the other island groups in the south-eastern Polynesian region, notably those of the Austral, Society and Cook Islands. The flora would seem to be predominantly derived from that of the Austral Islands. The Polynesian flora is in turn derived largely from the flora of the Indo-Malesian region. The migration methods of the flora are closely linked to the habitats in which the taxa occur, with strand species arriving through hydrochory, while taxa that occur farther inland arriving through zoochory and anemochory. Therefore, it is not simply dispersal of propagules to islands which limits their occurrence, but also the availability of a vacant niche in which they can establish a viable population before events that might lead to their extinction are experienced.

In terms of regionalization of the Pacific, the results of this analysis using Pitcairn group floristic data only suggest that south-east Polynesia is a valid biogeographical unit. This unit should contain the Cook, Austral, Society, Marquesas, Gambier, Tuamotu and Pitcairn Islands with Rapa, but exclude Easter Island, Tonga and Samoa. This disagrees with most biogeographical regionalizations published to date, notably in the inclusion of the Cook Islands and exclusion of Easter Island (see van Balgooy, 1971; Stoddart, 1992). However, the closeness of the association between the Pitcairn group and the Cook Islands found in this analysis, closer even than with the Marquesas Islands, suggests that this inclusion is valid.

The study presented here contradicts the conclusions of Brown (1935) that the flora of the region is of American origin; no features of the flora of Pitcairn are of American origin. In addition Brown describes the flora as being 87% confined to the Polynesian region, with only two pantropic species. This study also shows this not to be the case. Brown's (1935) research was based on limited knowledge of the Polynesian floras (his work was confined to the Marquesas Islands, and most of the other island groups had not yet been surveyed), and was at a time when new species were being described without proper comparisons between collections from other islands (Spellerberg & Sawyer, 1999). Even so, his was the first analysis to note both the high degree of endemism in the flora, and the floristic affinities between Rapa and New Zealand (van Balgooy, 1971).

Stoddart (1992) discussed the limitations of previous regional schemes, but did not carry out an analysis or add to the schemes already in place. He did however recommend that analysis should take island type into consideration when developing regional schemes, a factor taken into consideration in this study and indeed shown to have an effect. Having struggled with the problem of the phytogeographical regionalization of the Pacific (van Balgooy, 1960, 1971), van Balgooy *et al.* (1996) supports Stoddart's view that a hierarchical system of regions is impractical and classifications should be based on the patterns shown in analyses based on island type.

Although the flora of the Pitcairn group is essentially a subset of the flora of the Polynesian region, the results of this analyses still show the biogeographical relationships found when using a larger data set for the whole of Pacific. This demonstrates that although the Pitcairn Island group has a impoverished and disharmonic flora, due to its age and location, the fact that the group contains all of the oceanic island types found in the region, and thus a representative sample of the habitats available in the region, means it can serve as a useful model for Pacific biogeographical analyses.

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BIOSKETCHES

Naomi Kingston is currently a postdoctoral researcher in the Department of Botany of Trinity College Dublin working on disjunct phytogeographical patterns in the European flora. Her PhD (2001) involved research in a broad number of areas including floristics, vegetation analysis and mapping, conservation genetics and island biogeography, using the study site of the Pitcairn Islands.

Steve Waldren is Curator/Administrator of Trinity College Botanic Gardens. His current research interests include biogeography of the Irish and Polynesian floras, the physiological ecology of turlough (seasonal lakes) plants and plant conservation biology.

Una Bradley recently completed her PhD on biogeography and speciation of *Peperomia* in the islands of south-eastern Polynesia.

Appendix List of the native vascular plants species for the Pitcairn group of islands, which are the species used in this analysis. The range column relates to the range of the species within the Pitcairn group as follows: P, Pitcairn; H, Henderson; O, Oeno; D , Ducie

Family	Genus	Species	Authority	Range
Adiantaceae	*Adiantum*	*hispidulum*	Sw.	P
Aizoaceae	*Sesuvium*	*portulacastrum*	(L.) L.	P, H
Apiaceae	*Apium*	*prostratum*	Labill.	P
Apocynaceae	*Alyxia*	*fosbergii*	Florence	H,
Apocynaceae	*Alyxia*	*scandens*	Roem. aeiou Schult.	P
Apocynaceae	*Cerbera*	*manghas*	L.	P
Araliaceae	*Meryta*	*brachypoda*	Harms	H
Aspidiaceae	*Ctenitis*	*cumingii*	Holttum	P
Aspidiaceae	*Diplazium*	*harpeodes*	T.Moore	P
Aspleniaceae	*Arachniodes*	*aristata*	(G.Forst.) Tindale	P
Aspleniaceae	*Asplenium*	*nidus*	L.	P, H, O
Aspleniaceae	*Asplenium*	*obtusatum*	G.Forst.	P, H
Aspleniaceae	*Asplenium*	*polyodon*	G.Forst.	H
Aspleniaceae	*Asplenium*	*shuttleworthianum*	Kunze	P
Aspleniaceae	*Lastreopsis*	*pacifica*	Tindale	P
Aspleniaceae	*Loxoscaphe*	*gibberosum*	T.Moore	P
Asteraceae	*Bidens*	*hendersonensis*	Sherff	H, O
Asteraceae	*Bidens*	*mathewsii*	Sherff	P
Asteraceae	*Senecio*	*stokesii*	F.Br.	H
Blechnaceae	*Doodia*	*media*	R.Br.	P
Boraginaceae	*Argusia*	*argentea*	L. f.	P, H, O, D
Boraginaceae	*Cordia*	*subcordata*	Lam.	H
Boraginaceae	*Heliotropium*	*anomalum*	A.Gray	H
Brassicaceae	*Lepidium*	*bidentatum*	Montin	P, H, O
Capparidaceae	*Capparis*	*cordifolia*	Lam.	P, H
Convolvulaceae	*Ipomoea*	*littoralis*	Blume	P
Convolvulaceae	*Ipomoea*	*macrantha*	Roem. aeiou Schult.	P, H

Appendix *continued*

Family	Genus	Species	Authority	Range
Convolvulaceae	*Ipomoea*	*pes-caprae*	L.	P
Convolvulaceae	*Operculina*	*turpethum*	(L.) S. Manso	H
Cyatheaceae	*Cyathea*	*medullaris*	(G. Forst.) Sw.	P
Cyperaceae	*Fimbristylis*	*cymosa*	Hillebrand	H
Davalliaceae	*Davallia*	*solida*	(G. Forst.) Sw.	P, H
Davalliaceae	*Nephrolepis*	*biserrata*	(Sw.) Schott	P, H, O, D
Davalliaceae	*Nephrolepis*	*cordifolia*	(L.) C.Presl	P
Davalliaceae	*Nephrolepis*	*hirsutula*	(G. Forst.) C. Presl	P, H
Euphorbiaceae	*Chamaesyce*	*sparrmannii*	(Boiss.) Hurus.	P, H
Euphorbiaceae	*Glochidion*	*comitum*	Florence	P
Euphorbiaceae	*Glochidion*	*pitcairnense*	(F. Br.) H.St. John	P, H
Flacourtiaceae	*Homalium*	*taypau*	H.St. John	P
Flacourtiaceae	*Xylosma*	*suaveolens*	(J.R. Forst. aeiou G. Forst.) G.Forst.	P, H
Gleicheniaceae	*Dicranopteris*	*linearis*	(Burm.) Underw.	P, H
Goodeniaceae	*Scaevola*	*sericea*	Vahl	P, H, O
Gramineae	*Cenchrus*	*calyculatus*	Cav.	P
Haloragaceae	*Haloragis*	sp.	Indet.	P
Hernandiaceae	*Hernandia*	*sonora*	L.	P
Hernandiaceae	*Hernandia*	*stokesii*	(F.Br.) Kubitzki	H
Hymenophyllaceae	*Trichomanes*	*endlicherianum*	C.Presl	P
Hymenophyllaceae	*Trichomanes*	*tahitense*	Nadeaud	P
Lauraceae	*Cassytha*	*filiformis*	L.	H, O
Leguminosae	*Caesalpinia*	*major*	(Medik.) Dandy aeiou Exell	P, H
Leguminosae	*Canavalia*	*rosea*	(Sw.) DC.	H
Leguminosae	*Senna*	*glanduligera*	(H.St. John) A.C.Sm.	H
Liliaceae	*Dianella*	*intermedia*	Endl.	P, H
Loganiaceae	*Geniostoma*	*hendersonense*	H.St.John	H,
Lycopodiaceae	*Lycopodium*	*cernuum*	(L.) Pic.Serm.	P
Lythraceae	*Pemphis*	*acidula*	J.R. Forst. aeiou G. Forst.	P, H
Malvaceae	*Abutilon*	*pitcairnense*	Fosberg	P
Malvaceae	*Hibiscus*	*australense*	Fosberg	P
Malvaceae	*Hibiscus*	*tiliaceus*	L.	P, H, O
Malvaceae	*Thespesia*	*populnea*	(L.) Sol. ex Corrêa	P, H, O
Marattiaceae	*Angiopteris*	*chauliodonta*	Copel.	P
Menispermaceae	*Cocculus*	*ferrandianus*	Gaudich	P
Myrsinaceae	*Myrsine*	*hosakae*	H.St. John	H
Myrsinaceae	*Myrsine*	aff. *niauensis*		P
Myrtaceae	*Eugenia*	*reinwardtiana*	(Blume) DC	P, H
Myrtaceae	*Metrosideros*	*collina*	(J.R. Forst. aeiou G. Forst.) A.Gray	P
Nyctaginaceae	*Boerhavia*	*tetrandra*	G. Forst.	H, O
Nyctaginaceae	*Pisonia*	*grandis*	R.Br.	H, O
Nyctaginaceae	*Pisonia*	*umbellifera*	(J.R. Forst. aeiou G. Forst.) Seem.	P
Oleaceae	*Jasminum*	*didymum*	G. Forst.	P, H
Ophioglossaceae	*Ophioglossum*	*nudicaule*	L.	P
Ophioglossaceae	*Ophioglossum*	*reticulatum*	L.	P
Orchidaceae	*Taeniophyllum*	*fasciola*	(G. Forst.) Rchb.	P
Pandanaceae	*Pandanus*	*tectorius*	Parkinson ex Z	P, H, O
Piperaceae	*Peperomia*	*blanda*	Kunth.	P
Piperaceae	*Peperomia*	*hendersonensis*	Yuncker	H,
Piperaceae	*Peperomia*	*pitcairnensis*	(Lauterb.) C.DC	P
Piperaceae	*Peperomia*	*rapensis*	F.Br.	P
Piperaceae	*Peperomia*	sp.	Indet.	P
Pittosporaceae	*Pittosporum*	aff. *arborescens*	W. Rich ex A. Gray	H
Poaceae	*Lepturus*	*repens*	(G. Forst.) R.Br.	P, H, O, D
Poaceae	*Thuarea*	*involuta*	(G. Forst.) R.Br. ex Roem. aeiou Schult.	H
Polypodiaceae	*Phymatosorus*	*commutatus*	(Blume) Pic.Serm.	P
Polypodiaceae	*Phymatosorus*	*powellii*	(Baker) Pic.Serm.	P
Polypodiaceae	*Phymatosorus*	*scolopendria*	(Burm.) Pic.Serm.	P, H, O
Polypodiaceae	*Pyrrosia*	*serpens*	(G.Forst.) Ching	P, H

Appendix *continued*

Family	Genus	Species	Authority	Range
Portulacaceae	*Portulaca*	*lutea*	Sol. ex Seem.	P, H
Primulaceae	*Samolus*	*repens*	Pers.	P
Psilotaceae	*Psilotum*	*nudum*	(L.) Beauv.	P, H
Rosaceae	*Osteomeles*	*anthyllidifolia*	(Sm.) Lindl.	P
Rubiaceae	*Coprosma*	*benefica*	W.R.B.Oliver	P
Rubiaceae	*Cyclophyllum*	*barbatum*	(G.Forst.) N.Hallé aeiou Florence	P, H
Rubiaceae	*Guettarda*	*speciosa*	L.	P, H
Rubiaceae	*Hedyotis*	*romanzoffiensis*	(Cham. aeiou Schlech.) Fosberg	H, O
Rubiaceae	*Ixora*	*fragrans*	(Hook. aeiou Arn.) A.Gray	H
Rubiaceae	*Morinda*	*myrtifolia*	A.Gray	P, H
Rubiaceae	*Psydrax*	*odorata*	(G.Forst.) A.C.Sm. aeiou S.P. Darwin	P, H
Rubiaceae	*Timonius*	*polygamus*	(G.Forst.) Robinson	H
Santalaceae	*Santalum*	*insulare*	Skottsberg	H
Sapindaceae	*Allophylus*	*rhomboidalis*	(Nadeaud) Radlkofer	H
Sapotaceae	*Nesoluma*	*st-johnianum*	Lam. aeiou Meeuse	H
Solanaceae	*Lycium*	*sandwichense*	A.Gray	P, H
Surianaceae	*Suriana*	*maritima*	L.	H, O
Thelypteridaceae	*Christella*	*parasitica*	(L.) Lév.	P
Thelypteridaceae	*Macrothelypteris*	*torresiana*	(Gaudich) Ching.	P
Thelypteridaceae	*Pneumatopteris*	*costata*	Holttum	P
Tiliaceae	*Triumfetta*	*procumbens*	G.Forst.	H, O
Ulmaceae	*Celtis*	*pacifica*	G.Planch.	P, H
Urticaceae	*Pilea*	*sancti-johannis*	Florence	P
Urticaceae	*Procris*	*pedunculata*	(G.Forst.) Wedd.	H
Verbenaceae	*Premna*	*serratifolia*	L.	H
Viscaceae	*Korthalsella*	*platycaula*	(Tieghem) Engler	H
Viscaceae	*Korthalsella*	*rubescens*	(Tieghem) Lecomte	H
Vittariaceae	*Vittaria*	*elongata*	Sw.	P