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A comparison of the vegetation communities from the islands of the Pitcairn Group

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The vegetation of the raised coralline Henderson Island and Oeno Atoll (Pitcairn Group, south-central Pacific Ocean) is described from cover-abundance values of the vascular flora sampled in 10×10 m quadrats. Exploratory data analysis by detrended correspondence analysis and two-way indicator species analysis was used to summarize the resulting data matrices for each island, and to aid definition of vegetation types. For Henderson, six major vegetation communities are described, which are often closely linked to geomorphology: beachfront, embayment forests, open limestone scrub, cliff and ledge, exposed cliff top, and plateau forests. For Oeno, four main vegetation communities are described: open sandy littoral, *Argusia* scrub, closed forest, and coconut grove. For each island, the main vegetation types were further subdivided into a number of communities depending on the proportions of various taxa. Brief qualitative descriptions of the vegetation of Ducie and Pitcairn are also given. Anthropogenic communities, some of which are highly invasive, are widespread on Pitcairn. Adequate conservation measures must be given to all islands in the Pitcairn Group; this will protect not only the endemic-rich and possibly unique plateau forests of Henderson, but also the species-poor and scientifically important analogues of vegetation types which occur elsewhere in the Pacific islands.

ADDITIONAL KEY WORDS:—Henderson – Oeno – Ducie – Pitcairn – South-Central Pacific – vegetation communities – island conservation.

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INTRODUCTION

The floras of oceanic islands have been the subject of much biogeographic investigation. This interest has frequently been related to the occurrence of relict taxa and the evolutionary divergence of others (Wilson, 1988). The islands of the Pacific are no exception, and much effort has been put into determining the numbers of taxa on islands of different areas, and in particular, on different sized *motus* of atolls (Stoddart, 1975). A surprisingly large amount of floristic information is available on both high islands and atolls of the Pacific, despite the multitude of islands. However, most botanical studies of Pacific islands have simply described the floras; a few give qualitative descriptions of the vegetation communities, but there have been few quantitative analyses of vegetation. Notable exceptions include studies in the southern Cook Islands (Merlin, 1991; Franklin & Merlin, 1992), where ordination and classification techniques were used to describe forest communities. Most visits to remote island groups have been of short duration, providing little time for quantitative field work.

The flora of the Pitcairn Group is reasonably well known (St John & Philipson, 1960, 1962; Rehder & Randall, 1975; St John, 1987; Fosberg *et al.*, 1983, 1989; Florence Waldren & Chepstow-Lusty, 1995), but the only attempt to describe plant communities anywhere in the group was by Paulay & Spencer (1989), who qualitatively described communities from a limited part of the northern area of Henderson Island. The Sir Peter Scott Commemorative Expedition to the Pitcairn Islands 1991–1992 provided an opportunity to build on the efforts of Paulay and Spencer by allowing sufficient time for reasonably detailed quantitative studies to be made of the vegetation. The present paper describes the vegetation of Pitcairn, Henderson, Ducie and Oeno with a view to providing a synthesis that will be useful to other expedition research parties; more detailed investigations of the ecological factors responsible for the development of vegetation on Henderson Island and Oeno Atoll will appear elsewhere.

METHODS

Varying lengths of time were spent by the authors on Pitcairn Island (8 days), Henderson Island (68 days) and Oeno Atoll (7 days) between April and July 1991. We chose not to visit Ducie Atoll because of the very low diversity of vascular plants; our information for Ducie comes from aerial photographs and the comments of other expedition members, especially M. Brooke and P. Jones. Because of poor weather and the relatively little time spent on Pitcairn, no quantitative assessment of the vegetation was undertaken; instead we chose to visit and collect vouchers from as much of the island

as possible during our short stay. The vegetation accounts which are included here are culled from field notes taken during plant collecting forays.

For Henderson and Oeno, vascular plants were recorded from 10×10 m quadrats. No attempt was made to sample the various components of the vegetation using different sized quadrats, this allowed a unified analysis of all vegetation recorded. Quadrats were not placed randomly, but selected according to the following criteria, roughly in order of priority:

(1) Efforts were made to sample all habitats, and all qualitatively different communities within each island;
(2) Some quadrats were placed in transects along obvious gradients of vegetation change (e.g. from beach to plateau forest);
(3) As far as possible, all extant species were recorded from at least one quadrat—for rare species this meant deliberately placing quadrats over these species;
(4) Efforts were made to sample from as many parts of the island as possible: coverage was reasonably complete for Oeno, but this was not possible for Henderson.

The result was a partially stratified sampling procedure, but one which is likely to over-emphasize vegetation gradients and rare taxa. A total of 54 quadrats were recorded from Oeno and 220 from Henderson. The cover of individual taxa was recorded using the Domin scale (Kent & Coker, 1992). The approximate cover of tree canopies was projected vertically and estimated; in practice, the low stature of the vegetation of both islands made this relatively simple. The maximum height of the vegetation, and the cover of plant litter and bare sand, soil or rock were estimated.

The resulting data matrices of quadrats by taxa were analysed separately for each island. Exploratory analyses using detrended correspondence analysis (DCA; Hill, 1979a) and two way indicator species analysis (TWINSPAN; Hill, 1979b) were used as an aid in interpreting vegetation patterns. TWINSPAN divisions were continued until a point when further divisions were difficult to interpret, or separated similar quadrats. The number of pseudospecies (a combination of individual taxa at different cover values) cut levels applied was varied; nine pseudospecies, defined by the Domin scores of 0, 1, 2, 3, 4, 5, 6, 7 and 8, gave the most-readily interpretable results and also utilized the Domin values to better effect than fewer cuts used in default program runs. TWINSPAN and DCA are currently the most widely used methods for ordination and classification of vegetation data (Kent & Coker, 1992), although their methodology is somewhat obscure and arbitrary. However, results from these analyses were similar to those produced with principal components analysis (PCA) and Ward's error sum of squares clustering procedure.

The implementation of DCA was that used in CANOCO (ter Braak, 1988), while TWINSPAN was used as part of the VESPAN II suite of programs (Malloch, 1988). Further details of these techniques may be found in Kent & Coker (1992). TWINSPAN classifications were imposed on DCA ordinations and investigated using DataDesk (Data Description Inc., Ithaca, New York). PCA was also performed using DataDesk, while Ward's clustering procedure was run using SPSS. Nomenclature follows Florence *et al.* (1995) throughout.

RESULTS AND DISCUSSION

Henderson Island data analyses

TWINSPAN analysis of the 220 quadrats produced 19 terminal groups which could be interpreted; the resulting dendrogram is shown in Figure 1. DCA scores grouped by the six major vegetation types described later are shown in Figure 2, while mean DCA scores for all 18 communities subsequently described are given in Table 1.

The initial TWINSPAN division (uppermost in Figure 1) separated quadrats containing the indicator species *Pisonia grandis* and *Phymatosorus scolopendria* on the left side of the dendrogram from those containing the indicators *Heliotropium anomalum, Scaevola sericea* and *Chamaesyce sparrmannii* to the right. Groups 0000, 00010, 00011 (all on the left of Fig. 1) contained most of the quadrats recorded from beach fronts. Two East Beach quadrats with at least 5% cover of *Suriana maritima* growing with a low cover of *Cassytha filiformis* formed group 0000. Groups 00010 and 00011 were poorly separated; *Triumfetta procumbens* (cover to 33%), *Lepturus repens* (cover to 20%) and *Pemphis acidula* (with cover often over 33%, but often absent) occurred with higher frequency in 00010, while *Heliotropium anomalum* was more frequent in 00011 with cover values up to 20%. There was some separation of sandy beach front quadrats into 00011, with quadrats from coarser sediments and beachrock in 00010.

Two small groups of beachfront quadrats (groups 101 and 111) occurred to the right side of the dendrogram in Figure 1, well separated from other beach quadrats which have just been described. Group 111 consisted of two anomalous quadrats from the East Beach where *Pemphis acidula, Heliotropium anomalum* and little else were growing over isolated rocks. Group 101 contained beachfront quadrats from the North Beach with an abundance of *Scaevola sericea* (up to 50% cover) and *Argusia argentea* (25–50% cover). *Scaevola* and *Heliotropium* also occurred in communities from exposed cliff tops (groups 1001, 10000 and 10001) which are also on the right side of the dendrogram (Fig. 1), but *Argusia* was absent from these. The apparent anomaly in the TWINSPAN results is resolved by examining the DCA results (Fig. 2A), where all beach communities were given high scores (i.e. >2) on axis 2 (Table 1). None of the DCA axes were able to consistently separate the different beachfront communities.

Group 0010 was recorded from low dunes where cover of *Argusia argentea* and *Pandanus tectorius* was usually over 20–50%. Group 0011 contained a mixture of species-poor beach crest and beach embayment forest quadrats, in which *Cordia subcordata* and *Argusia argentea* were important components, often with cover values above 25%. This community is probably transitional between low dune communities of group 0010 and the more-diverse embayment forest quadrats grouped in 01100 described below. The third DCA axis (Fig. 2B, Table 1) separated the beachfront groups 0000, 00010, 00011 (DCA score <1.5) from the low dune and transitional groups 0010 and 0011 (DCA score >1.5). TWINSPAN results suggest that *Ipomoea macrantha* was an indicator species for this partition, with a cover of at least 5% in all but two of the quadrats in 0010 and 0011.

Groups 01000, 01001 and 0101 contain forest and thicket quadrats from

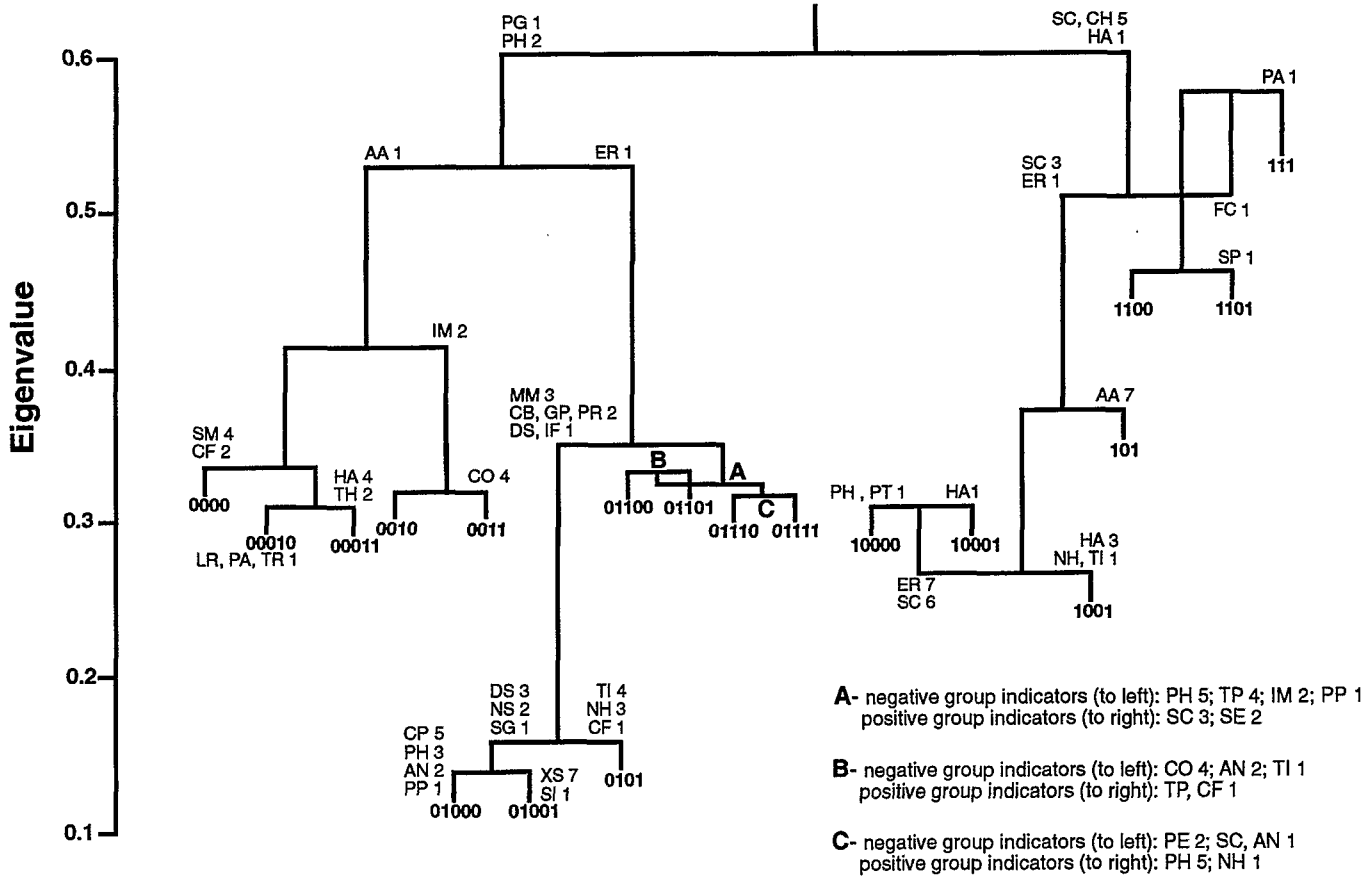

Figure 1. TWINSPAN dendrogram of 220 10 × 10 m quadrats from Henderson Island, plotted against eigenvalue at which division occurred. Number codes refer to the TWINSPAN groups described in the text. Indicator species and their pseudospecies cut level are indicated for each division by the following abbreviations: AA = *Argusia argentea*, AN = *Asplenium nidus*, CB = *Cyclophyllum barbatum*, CF = *Cassytha filiformis*, CH = *Chamaesyce sparrmannii*, CO = *Cordia subcordata*, CP = *Celtis pacifica*, DS = *Davallia solida*, ER = *Eugenia reinwardtiana*, FC = *Fimbristylis cymosa*, GP = *Glochidion pitcairnense*, HA = *Heliotropium anomalum*, IF = *Ixora fragrans*, IM = *Ipomoea macrantha*, LR = *Lepturus repens*, MM = *Morinda myrtifolia*, NH = *Nephrolepis hirsutula*, NS = *Nesoluma st-johnianum*, PA = *Pemphis acidula*, PE = *Peperomia hendersonensis*, PG = *Pisonia grandis*, PH = *Phymatosorus scolopendria*, PR = *Premna serratifolia*, PP = *Procris pedunculata*, PT = *Pandanus tectorius*, SC = *Scaevola sericea*, SE = *Senecio stokesii*, SG = *Senna glanduligera*, SI = *Santalum insulare* var *hendersonense*,

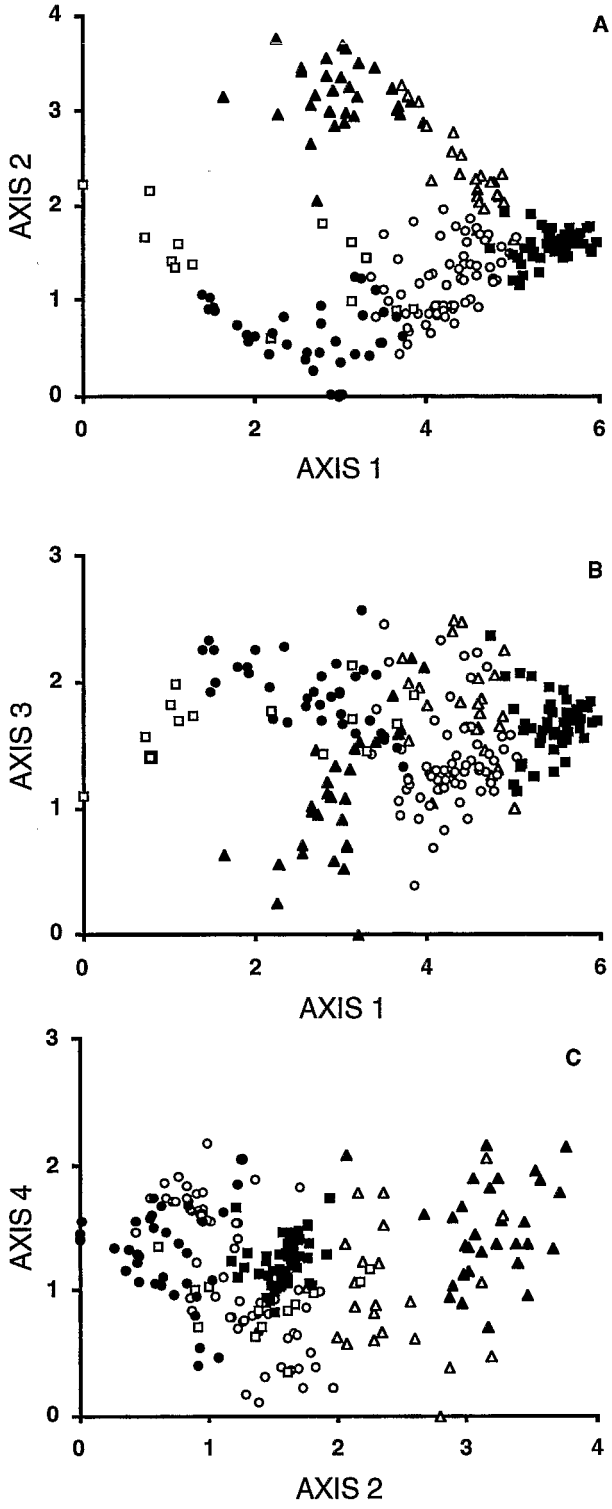

Figure 2. Scatterplots of DCA axes, A: 1 versus 2, B: 1 versus 3 and C: 2 versus 4 for 220 10×10 m quadrats from Henderson Island. Symbols indicate the six major vegetation communities: (▲) beachfront communities; (△) embayment forests; (○) open limestone scrub; (□) cliff and ledge communities; (●) exposed cliff top communities; (■) plateau forests.

TABLE 1. Means (minima–maxima) for Henderson Island vegetation communities for the first four DCA axes

Community	Axis 1	Axis 2	Axis 3	Axis 4
A1 Herbaceous beachfront	2.74 (2.25–3.09)	3.05 (2.06–3.65)	1.02 (0.56–1.47)	1.54 (0.95–2.09)
A2 *Suriana* beachfront	2.86 (2.54–3.18)	3.34 3.15–3.55)	0.62 (0.00–1.21)	1.33 (0.71–1.89)
A3 Shrubby beachfront	2.86 (1.62–3.67)	3.22 (2.89–3.75)	0.98 (0.25–1.59)	1.57 (0.90–2.17)
A4 Beach-ridge scrub	3.68 (3.39–3.96)	3.11 (2.89–3.45)	1.83 (1.53–2.19)	1.37 (0.97–1.90)
B1 Species-rich embayment forest	4.64 (3.77–5.00)	2.19 (1.65–3.15)	1.68 (1.01–2.26)	1.16 (0.58–2.06)
B2 Species-poor embayment forest	4.05 (3.69–4.41)	2.83 (2.28–3.26)	2.05 (1.05–2.50)	0.74 (0.00–1.60)
C1 *Timonius*-rich cliff slopes	4.60 (4.27–5.04)	1.57 (1.36–1.86)	1.75 (1.41–2.24)	0.69 (0.12–1.13)
C2 Fern-rich cliff slopes	4.19 (3.34–4.87)	1.40 (0.85–1.96)	1.12 (0.39–1.57)	0.65 (0.17–1.00)
C3 Limestone fissure community	4.14 (3.40–4.81)	0.96 (0.43–1.70)	1.38 (0.92–2.46)	1.57 (0.65–2.19)
D1 Spray zone community	1.13 (0.00–3.13)	1.67 (1.35–2.24)	1.68 (1.10–2.13)	0.81 (0.35–1.17)
D2 Sheltered ledge community	3.14 (2.17–3.85)	1.10 (0.59–1.81)	1.65 (1.43–1.89)	0.99 (0.71–1.34)
E1 Herb-rich cliff top community	2.75 (2.20–3.17)	0.44 (0.00–1.24)	1.84 (1.67–2.05)	1.44 (1.06–2.05)
E2 Shrub-rich cliff top community	3.34 (2.95–3.72)	0.70 (0.36–1.22)	1.78 (1.33–2.58)	1.45 (0.80–1.85)
E3 Sedge lawn	1.76 (1.38–2.32)	0.78 (0.44–1.06)	2.15 (1.92–2.34)	0.92 (0.40–1.29)
F1 Species-rich *Pisonia* forest	5.68 (5.44–5.85)	1.66 (1.59–1.76)	1.71 (1.51–1.86)	1.35 (1.19–1.51)
F2 Open *Pisonia/Hernandia* forest	5.43 (5.04–5.65)	1.54 (1.20–1.76)	1.37 (1.14–1.70)	1.52 (1.45–1.66)
F3 Species-poor *Pisonia/ Xylosma* forest	5.63 (5.13–5.96)	1.58 (1.30–1.91)	1.72 (1.51–2.05)	1.21 (0.98–1.40)
F4 *Timonius* thicket	5.27 (4.74–5.60)	1.53 (1.16–1.93)	1.65 (1.19–2.37)	1.14 (0.83–1.73)

the plateau; these groups formed a tight cluster on all DCA axes, and were given the highest scores (>4.5) on DCA axis 1 (Fig. 2A, Table 1). Group 01000 contained quadrats where *Xylosma suaveolens* was a co-dominant with *Pisonia grandis* (cover values for both species were usually greater than 33%), with very low cover of herbs and epiphytes. Quadrats in group 01001 were the most diverse on the island in terms of numbers of species present, with relatively well-developed ground and epiphyte floras. They were usually dominated by *Pisonia grandis*, with lower cover of *Xylosma* than 01000. Lower stature forests, thickets and more-open areas had quadrats which were grouped into 0101, indicator species for this group were *Timonius polygamus* (cover usually above 33%, but variable), *Nephrolepis hirsutula* and *Cassytha filiformis.*

The latter was almost always present, but its slender stems never resulted in high cover values.

Group 01100 contained quadrats from the embayment forests behind the low dunes at the top of the beaches. These embayment forest quadrats were more species-rich than groups 0011 and 0010 described above; *Thespesia populnea* (not on East Beach) and *Cordia subcordata* were common trees with high cover values in most quadrats, together with *Pisonia grandis*, *Celtis pacifica* and forest herb species. The embayment forest group (01100) formed a tight cluster on the DCA axes 1 and 2 (Fig. 2A, Table 1), linking plateau forest types and the taller beach crest quadrats dominated by *Cordia* and referred to above.

Group 01101 contained quadrats recorded on cliff slopes behind the North and East Beach embayments characterized by high cover values of *Timonius polygamus* (cover usually over 20%, often above 50%) with *Casdsytha filiformis* usually present but with low cover. *Phymatosorus scolopendria* was also usually present with at least 20% cover. Quadrats in group 01111 were also recorded mainly from cliff slopes but in this group *Timonius* was absent and the vegetation was mainly dominated by high cover (>20%) of the ferns *Phymatosorus scolopendria* and *Nephrolepis hirsutula*, with *Scaevola sericea* reaching 20% cover in about a quarter of the quadrats. Quadrats recorded from areas of pitted and dissected limestone on the plateau occurred mainly in group 01110, which had similar species to the fern-dominated cliff slopes of 01111, but with low cover (<5%) of *Asplenium nidus* and *Peperomia hendersonensis* in the limestone fissures while *Scaevola* was absent.

Although the beach embayment forest group (01100) was closely associated with the dissected limestone (group 01111) and cliff slope quadrats (groups 01101 and 01110) in the TWINSPAN analysis (Fig. 1), DCA separated these on axis 2 (Fig. 2A), the embayment forest quadrats having a higher score on this axis (>1.8, Table 1). Some of the cliff slope quadrats (in groups 01101 & 01111) were closely placed with the embayment forest quadrats by DCA, probably because the embayment forest graded into cliff slope at the North and East Beach. The cliff slope quadrats were closely associated with dissected limestone quadrats (mainly group 01110) by TWINSPAN and axes 1 and 2 of DCA (Figs 1, 2A; Table 1); however, cliff slope quadrats dominated by *Timonius polygamus* (01101) were separated from those dominated by ferns on axis 3 (Fig. 2B, Table 1). Axis 4 (Fig. 2C, Table 1) separated all cliff slope quadrats from these recorded on dissected limestones of the plateau (group 01110).

Groups 10000 and 10001 contained most of the quadrats recorded from cliff top communities at the southern end of the island. *Eugenia reinwardtiana* and *Scaevola sericea* were abundant (up to 50% cover) in these quadrats along with varying proportions of the plateau forest species, but these were always dwarfed and reached only 1 m in height. These distinct quadrats were recorded on the fairly level ground of fossil reef flats (Pandolfi, 1995) a short way inland from the cliff edge (the exact distance varied depending on exposure), but seaward of plateau forest margin or dissected limestone quadrats referred to above. Quadrats in group 10000 tended to be further from the cliff and contained more *Pandanus tectorius* (to 50% cover in some quadrats) and up to 20% cover of *Phymatosorus scolopendria*; the latter was

absent from quadrats in 10001 which tended to be more seaward or exposed than 10000. *Heliotropium anomalum* was more consistently present in 10001, together with occasional low cover of *Portulaca lutea* and *Lycium sandwicense.* This group graded into cliff top quadrats described below; however none of the four DCA axes examined effectively separated the groups 10000 and 10001 (Fig. 2A,B,C).

Quadrats from cliff tops and ledges, and also sparsely vegetated cliff slopes, were grouped by TWINSPAN into groups 1101 and 1001. Group 1001 contained mostly quadrats from the North and East Beach cliff slopes and tops, often containing *Timonius polygamus* (up to 33% cover) and *Phymatosorus scolopendria* (to 25% cover) along with *Heliotropium anomalum.* This community was associated with both the cliff slope and the *Eugenia reinwardtiana* cliff top groups (Fig. 2A). In contrast, 1101 was made up of quadrats from the exposed southern cliff tops and fairly bare ledges on the North Beach cliff, with up to 33% cover of *Sesuvium portulacastrum* and *Heliotropium,* 24% cover of *Lycium sandwicense* (but absent from North Beach); ferns and *Timonius polygamus* were absent. Quadrats in group 1101 were given the lowest score (<1.5) on axis 1 of DCA (Fig. 2A, Table 1).

TWINSPAN group 1100 was closely associated with the cliff top quadrats just described in Figure 1. Quadrats in this group were very distinct, being dominated (cover values often over 75%) by the sedge *Fimbristylis cymosa,* with occasional associated herbs and dwarf shrubs also found on cliff tops (*Heliotropium anomalum* and *Chamaesyce sparrmannii,* with *Lycium sandwicense* around rock outcrops). Quadrats in this group had DCA axis 1 scores intermediate between the 1101 and 1001 groups just described (Table 1).

The combination of DCA and TWINSPAN analyses described above aid the definition of six major vegetation types on Henderson, largely based on physiographical details, and often closely linked to the local geomorphology (Pandolfi, 1995). Species composition of these communities is shown in Table 2. Many of these communities have been qualitatively described by Paulay & Spencer (1989), but their classification of communities only referred to the north and north western parts of the island.

Vegetation communities of Henderson Island

A. Beachfront communities. These communities include all herbaceous and shrubby beach front and fore dune communities, and their transition to embayment forest. They were restricted to the beaches of the northern part of island.

B. Embayment forests. These were tall forests, with a canopy usually 8–12 m high, which occurred in the embayments between the shrubby dune communities and the cliff slope communities of the North, North-West and East Beaches. They have been influenced by earlier Polynesian colonists, and continue to be exploited by the Pitcairn Islanders.

C. Open limestone scrub. These were low (to 2 m), open shrub communities on dissected plateau limestone, and the thickly vegetated cliff slopes of the North and East Beaches.

TABLE 2. Abundance indices for Henderson taxa in various vegetation communities. Values are the total Domin scores for each taxon per community, divided by the total number of quadrats, and multiplied by 10. Community codes are described in the text

Taxon	Community																	
	A1	A2	A3	A4	B1	B2	C1	C2	C3	D1	D2	E1	E2	E3	F1	F2	F3	F4
Achyranthes aspera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.1	–	–	–
Allophyllus rhomboidalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.1	–	–	0.2
Alyxia sp. nov.	–	–	–	–	–	–	–	–	0.3	–	–	–	–	–	16.5	–	19.1	4.0
Argusia argentea	68.3	50.0	52.7	52.5	5.6	34.4	3.5	5.3	–	–	15.0	–	–	–	–	–	–	–
Asplenium nidus	–	–	–	–	20.6	–	5.4	–	11.8	–	–	–	3.3	–	30.0	30.0	5.9	14.4
Asplenium obtusatum	–	–	–	–	–	–	–	–	–	–	3.3	3.8	–	–	–	–	–	–
Asplenium polyodon	–	–	–	–	–	–	–	–	0.9	–	–	–	–	–	1.5	10.0	–	–
Bidens hendersonensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	5.0	2.7
Boerhavia tetrandra	17.8	16.3	12.7	11.7	–	–	–	–	0.1	1.3	–	–	–	–	–	–	–	0.8
Caesalpinia bonduc	–	–	–	–	15.6	–	3.5	2.9	–	–	–	–	–	–	1.5	–	0.5	10.8
Canavalia rosea	–	–	–	–	–	–	–	–	–	–	–	4.6	–	–	–	–	–	–
Capparis cordifolia	3.3	–	0.5	–	–	–	0.8	8.2	–	–	–	–	–	–	–	–	–	–
Cassytha filiformis	0.6	7.5	3.6	–	4.4	5.0	16.9	29.1	11.6	2.5	9.2	0.8	10.4	–	–	10.0	3.6	13.8
Celtis pacifica	–	–	–	–	13.4	2.5	6.5	–	–	–	–	–	–	–	33.5	26.3	14.5	19.6
Chamaesyce sparrmannii	–	–	0.5	–	–	–	12.7	13.5	2.4	33.6	55.0	53.5	46.3	65.0	–	–	–	–
Cocos nucifera	–	–	–	20.8	5.0	–	0.4	0.3	–	–	–	–	–	–	–	–	–	1.3
Cordia subcordata	–	–	–	–	37.8	51.9	1.5	–	–	–	–	–	–	–	–	–	–	–
Cordyline fruticosa	–	–	–	–	–	–	0.8	2.6	–	–	–	–	–	–	–	–	–	5.4
Cyclophyllum barbatum	–	–	–	–	11.6	2.5	26.9	14.4	2.9	–	3.3	–	2.9	–	41.9	18.8	40.5	34.2
Davallia solida	–	–	–	–	–	–	–	1.2	0.6	–	–	–	–	–	31.2	42.5	25.9	7.7
Dianella intermedia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8	–	–	2.5
Eugenia reinwardtiana	–	–	–	–	15.3	1.3	33.8	32.4	35.3	–	25.8	50.8	39.2	–	23.1	22.5	20.9	33.3
Fimbristylis cymosa	–	–	–	–	–	–	–	–	–	19.4	–	1.5	–	73.6	–	–	–	–
Geniostoma hendersonense	–	–	–	–	0.6	–	0.8	–	5.3	–	–	–	–	–	16.5	22.5	19.1	23.5
Guettarda speciosa	–	–	3.6	12.5	–	–	1.5	4.7	1.5	–	–	3.8	4.2	–	6.2	7.5	1.8	6.7
Glochidion pitcairnense	–	–	–	–	1.9	–	1.5	–	0.1	–	–	–	–	–	39.6	20.0	29.1	27.1
Heliotropium anomalum	28.9	15.0	25.0	–	–	–	–	2.4	–	45.0	43.3	31.2	–	54.1	–	–	–	–
Hernandia stokesii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	47.5	–	–

Ipomoea macrantha	0.6	–	–	18.3	15.6	32.5	16.9	4.7	0.6	3.8	–	–	–	–	–	–	–	1.3
Ixora fragrans	–	–	–	–	–	–	–	–	–	–	–	–	–	–	36.5	5.0	32.7	15.2
Korthalsella platycaula	–	–	–	–	–	–	0.8	–	–	–	–	–	–	–	0.8	–	0.5	–
Korthalsella rubescens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.8	10.0	0.5	0.4
Lepidium bidentatum	–	–	–	–	–	–	–	–	1.9	–	8.3	–	10.0	–	–	–	–	–
Lepturus repens	5.6	15.0	1.4	–	–	–	–	–	–	26.3	–	0.8	–	5.0	–	–	–	–
Lycium sandwicense	–	–	–	–	–	–	–	–	–	31.9	1.7	1.5	–	6.8	–	–	–	–
Meryta brachypoda	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3.5	–	–	–
Morinda myrtifolia	–	–	–	–	–	–	7.3	7.9	2.8	–	6.7	–	–	–	36.5	25.0	36.4	26.0
Myrsine hosakae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15.0	–	1.8	8.8
Nephrolepis hirsutula	–	–	–	1.7	17.5	5.0	26.5	46.5	2.8	–	18.3	–	–	–	–	–	–	16.9
Nesoluma st-johnianum	–	–	–	–	–	–	–	2.4	0.6	–	–	–	–	–	38.8	5.0	36.4	10.8
Operculina turpethum	–	–	–	–	–	–	–	–	0.3	–	–	–	3.3	–	–	–	–	–
Pandanus tectorius	11.7	13.8	11.8	48.3	35.0	30.6	6.5	2.4	4.9	–	–	6.9	16.3	4.5	39.6	15.0	19.5	18.5
Pemphis acidula	–	–	32.7	–	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–
Peperomia hendersonensis	–	–	–	–	23.1	–	14.6	0.3	17.6	–	–	–	3.3	–	20.0	30.0	6.4	16.0
Phymatosorus scolopendria	35.0	21.3	43.6	66.7	66.3	65.6	48.5	47.1	25.1	5.0	28.3	5.0	40.0	–	31.5	25.0	19.5	33.1
Pisonia grandis	–	–	5.5	11.7	45.0	30.0	45.4	45.3	43.7	–	21.7	–	11.7	–	59.2	52.5	58.6	55.6
Pittosporum arborescens	–	–	–	–	–	–	–	–	–	–	–	6.2	–	–	–	–	–	–
Portulaca lutea	2.2	–	0.5	–	–	–	–	1.2	–	14.4	8.3	5.4	–	4.5	–	–	–	–
Premna serratifolia	–	–	–	–	–	–	2.3	–	–	1.3	3.3	–	–	–	37.3	10.0	25.5	25.6
Procris pedunculata	–	–	–	–	21.6	–	11.5	–	1.9	–	–	–	–	–	23.1	27.5	1.8	25.4
Psilotum nudum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–
Psydrax odoratum	–	–	–	–	–	–	6.9	4.7	5.3	–	6.7	–	0.4	–	33.1	–	27.7	29.6
Pyrrosia serpens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	13.1	5.0	2.7	–
Santalum insulare	–	–	4.5	–	–	–	7.7	–	1.8	–	–	0.4	–	–	–	–	17.3	–
Scaevola sericea	15.6	–	–	–	1.3	–	4.2	15.3	34.9	–	39.2	64.6	57.1	40.0	–	–	6.4	5.4
Senecio stokesii	–	–	2.3	–	–	–	0.8	12.4	30.3	3.1	24.2	27.3	39.2	11.8	8.5	7.5	14.5	8.1
Senna glanduligera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	29.6	10.0	20.9	3.3
Sesuvium portulacastrum	–	–	–	–	–	–	–	–	–	47.5	–	–	–	–	–	–	–	–
Suriana maritima	5.6	43.8	–	5.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Thespesia populnea	–	1.3	–	–	39.1	–	1.5	–	–	–	–	–	–	–	–	–	–	–
Thuarea involuta	8.9	1.3	7.7	20.0	11.6	15.0	–	–	–	–	–	–	–	–	–	–	13.6	4.6
Timonius polygamus	–	–	0.5	3.3	10.0	0.6	58.1	2.4	7.8	2.5	28.3	–	–	–	8.5	–	–	34.2
Triumfetta procumbens	5.6	20.0	13.2	10.8	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Xylosma suaveolens	–	–	–	–	–	–	2.3	7.6	–	–	–	–	–	–	22.7	–	58.6	15.2

D. Cliff and ledge communities. These occurred on the edges of cliffs around the plateau margin that are too steep or exposed for limestone scrub (group C) development, and on cliff ledges mainly behind the North and East Beaches; elsewhere the vertical cliff faces supported virtually no vascular plant life.

E. Exposed cliff top communities. These low (~50 cm tall) communities occurred close to the exposed southern cliffs on fossil reef flats (Pandolfi, 1955), and in a limited area near the North East Point. None of these areas are protected by fringing reefs and the communities are probably maintained in a dwarf state by salt spray.

F. Plateau forests. These covered much of the elevated plateau area of the island and the fossil lagoon, dominated mainly by *Pisonia grandis*; *Pandanus tectorius* groves were common throughout.

These major groups can be subdivided as follows; the relevant TWINSPAN groups and the relationship to the communities of Paulay & Spencer (1989) are indicated:

A. Beachfront communities

A1. Herbaceous beachfront. This was the most seaward beach community on sand, and was dominated by either *Heliotropium anomalum* or *Scaevola sericea*, with *Lepturus repens* common. Group 101 and much of 00011. Part of the Strand Pioneer and Seaward Beachridge community of Paulay & Spencer.

A2. Suriana *beachfront.* Sandy substrates in the central areas of the North and East Beaches were dominated by *Suriana maritima* shrubs (to 1.5 m), which provided shelter for herbs such as *Boerhavia tetrandra* and *Phymatosorus scolopendria.* Group 0000 and part of 00010. Part of the Strand Pioneer and Seaward Beachridge community of Paulay & Spencer.

A3. Shrubby beachfront. A shrub community in which *Argusia argentea* and *Pandanus tectorius* were common, as was *Pemphis acidula* on beachrock and coarse pebbles. Herbaceous species (e.g. *Boerhavia tetrandra, Triumfetta procumbens*) were also present in the shelter of bushes. Shrubby beachfront graded into beach ridge scrub. Group 111 and much of 00010. Part of the Strand Pioneer and Seaward Beachridge and the Limestone Platform communities of Paulay & Spencer.

A4. Beach-ridge scrub. This occurred on the low dunes on the North and East Beaches, and was dominated by *Argusia argentea* bushes. *Ipomoea macrantha* was frequent and *Cordia subcordata* absent. Group 0010. Part of the Beachridge Crest and Backbarrier Swale community of Paulay & Spencer.

A5. Coconut groves. These occurred locally on the North and North-West Beaches, especially near the Pitcairner camps. They contained few other species and were not sampled in quadrats. This community was possibly invading the beach-ridge and species-rich embayment communities; there have been some recent attempts to plant coconuts on the East Beach by Pitcairners. Part of the Beachridge Crest and Backbarrier Swale community of Paulay & Spencer.

B. Embayment forests

B1. Species-rich embayment forest. This community occurred on the East, North and North West Beaches in the embayments behind the fore-dune community, and also extended up slopes at the North West Beach and at the eastern and western extremities of the North Beach. *Cordia subcordata* was a prominent feature at the East and North Beaches, with *Thespesia populnea* abundant at the North and North West Beaches. *Pisonia grandis* was very common, along with *Celtis pacifica* and a well-developed herb layer (especially *Phymatosorus scolopendria, Peperomia hendersonensis* and *Procis pedunculata*). Inland, this community graded to cliff slope scrub, usually dominated by *Timonius polygamus.* Mostly group 01100. Part of the Beachridge Crest and Backbarrier Swale, the Limestone Buttress and Cliff Face, and the 'Miro' Woodland communities of Paulay & Spencer.

B2. Species-poor embayment forest. This was dominated by taller *Argusia argentea* than A4, with which this community intergraded. *Cordia subcordata, Ipomoea macrantha, Pandanus tectorius* and *Pisonia grandis* also occurred, but there were fewer associated species than B1, and the herb layer was very poorly developed. Group 0011. Probably related to the Beachridge Crest and Backbarrier Swale community of Paulay & Spencer.

B3. Pandanus *grove. Pandanus tectorius* occurred throughout the island, usually in small groves. Parts of the North Beach *Thespesia populnea* forest were cut by American Naval personnel during an airfield survey to provide a gift of *Thespesia* timber for the Pitcairn Islanders (M. Fraser, personal communication), and the original forest has been replaced by dense, almost monospecific stands of *Pandanus*; with an incomplete herb layer of *Phymatosorus scolopendria.* Numerous cut stumps of *Thespesia* occurred beneath the dense *Pandanus* leaf litter. An anthropogenic community, not sampled in quadrats. Not mentioned by Paulay & Spencer.

C. Open limestone scrub

C1. Timonius*-rich cliff slopes.* This community consisted of low, tangled shrubs covering cliff slopes behind the main beaches, dominated by *Timonius polygamus* which formed very dense thickets. Other shrubs were present, notably small forms of *Santalum insulare* var. *hendersonense, Cyclophyllum barbatum* and dwarf *Pisonia grandis. Cassytha filiformis* and *Phymatosorus scolopendria* were common. Group 01101. Part of the Limestone Buttress and Cliff Face community of Paulay & Spencer.

C2. Fern-rich cliff slopes. These were cliff slopes dominated by *Nephrolepis hirsutula* and *Phymatosorus scolopendria*; a number of shrubs occurred, but *Timonius polygamus* was rare. *Senecio stokesii* was present on the East Beach, but absent at the North Beach. Group 01111. Part of the Limestone Buttress and Cliff Face community of Paulay & Spencer.

C3. Limestone fissure community. A variable community, but usually an open scrub up to 1.5 m high, in rather sparsely vegetated areas of pitted limestone. The limestone fissures were usually 1.5 m or less in depth (cf. F2 below). The community contained some of the plateau forest species such as *Pisonia grandis, Psydrax odoratum* and *Cyclophyllum barbatum* growing as low shrubs in

rock crevices. Ferns (*Phymatosorus scolopendria* and *Nephrolepis hirsutula*) were common, with *Peperomia hendersonensis* and *Asplenium nidus* in deeper fissures. *Scaevola sericea* and *Cassytha filiformis* were often also common. This community graded into the thicket woodland (F4), and the *Pisonia/Hernandia* forest (F2). Mostly group 01110. Not recorded by Paulay & Spencer.

D. Cliff and ledge communities

D1. Spray zone community. The spray zone community was mainly restricted to the cliff margins at the southern end where the vegetation was constantly salt-sprayed, and to exposed ledges behind the North Beach. Few species were present, and all were strongly halophytic. The community was dominated by *Heliotropium anomalum* and *Sesuvium portulacastrum*, with *Portulaca lutea* and *Lycium sandwichense* where low outcrops in fossil spur-and-groove features (Pandolfi, 1995) provided some shelter. Group 1101. Not recorded by Paulay & Spencer.

D2. Sheltered ledge community. This occurred mainly on the East and North Beach cliffs. *Heliotropium anomalum* was present with some of the non-halophytic cliff slope species such as *Senecio stokesii* (East Beach only), *Timonius polygamus* and *Nephrolepis hirsutula.* The community was much less prone to salt spray than D1, as evidenced by the presence of non-halophytes. Group 1001. Probably part of the Limestone Buttress and Cliff Face Community of Paulay & Spencer.

E. Exposed cliff top communities

These communities intergraded; E1 and E2 were perhaps the most extreme forms of a continuum. However, both types could be recognised at the southern end of the island inland from the cliffs. E3 also occurred near the North-East Point.

E1. Herb-rich cliff top community. The herb-rich community occurred closer to the cliff edge than E2, and was dominated by *Scaevola sericea. Heliotropium anomalum*, *Senecio stokesii* and *Chamasyce sparrmannii* were also common. Shrubs, mainly *Eugenia reinwardtiana* and *Lycium sandwicense*, were generally of very low stature. Group 10001. Not recorded by Paulay & Spencer.

E2. Shrub-rich cliff top community. Compared to E1, this consisted of more *Eugenia reinwardtiana* and occasionally other plateau species reduced to low shrubs (to 50 cm) by the harsh salt-sprayed conditions; these include *Pisonia grandis*, *Guettarda speciosa*, *Psydrax odorata* and *Santalum insulare* var. *hendersonense.* There was less *Scaevola sericea* than E1, and *Heliotropium anomalum* was absent. *Pandanus tectorius* groves are frequent, with *Phymatosorus scolopendria*, and *Asplenium nidus* in deeper fissures. *Timonius polygamus* was absent. Graded into C3 at the southern end. Group 10000. Not recorded by Paulay & Spencer.

E3. Sedge lawn. This was dominated by the sedge *Fimbristylis cymosa*, forming a dense low sward. A few associated herbs from D1 and E1 occurred, especially *Chamaesyce sparrmannii.* Sedge lawn was very distinctive and occurs locally at the South-West and North-East Points in exposed conditions. Group 1100. Not recorded by Paulay & Spencer.

F. Plateau forests

F1. Species-rich Pisonia *forest.* This closed-canopy forest was dominated by *Pisonia grandis*, but with a very wide range of associated species; *Nesoluma st-johnianum*, *Celtis pacifica*, *Xylosma suaveolens* and *Glochidion pitcairnensis* were all locally abundant. Many of the larger trees (especially *Pisonia*) were partially decumbent; the general canopy height was 7–10 m, with emergent *Guettarda speciosa* and *Pandanus tectorius.* Epiphytes (*Pyrrosia serpens* and *Davallia solida*), parasites (*Korthalsella* sp.) and lianas (*Alyxia* sp., *Morinda myrtifolia*) were common. A shrub layer of *Psydrax odorata*, *Cyclophyllum barbatum* and *Ixora fragrans* was often well developed. The herb layer was also usually well developed, consisting of *Peperomia hendersonensis*, *Procris pedunculata*, *Asplenium nidus* and *Phymatosorus scolopendria. Pisonia* forest was usually found on the best-developed rendoll soils of the island (S. Waldren & L. Scally, unpublished data). Mainly consists of group 01001. Part of the Limestone Glade Woodland community of Paulay & Spencer.

F2. Open Pisonia/Hernandia *forest.* A rather amorphous community which occurred on massively fissured and pinnacled limestone (fissures to 3 m; cf. C3 above) in the north-west. Generally a poorer version of F1 with *Hernandia stokesii*, and grading from F1 into open areas rather like community C3. *Asplenium polyodon* was locally common. The presence of *Hernandia* and *A. polyodon*, the extremely dissected local topography, and the features in common with F4 and C3 are the main criteria for separation of this community. Parts of 01001, 0101. The Pinnacle-pitted Limestone community of Paulay & Spencer.

F3. Species-poor Pisonia/Xylosma *forest.* This community was similar to F1, but contained fewer species, and *Xylosma suaveolens* was co-dominant with *Pisonia grandis.* Epiphytes and terrestrial herbs were rare. The canopy tended to be more open than F1, with *Bidens hendersonensis* and *Senecio stokesii* common in gaps. *Santalum insulare* and *Eugenia reinwardtiana* were more frequent than in F1. *Pisonia/Xylosma* forest graded into F1, and into F4 in the island centre; it is possibly a transitional form, and occurred on poorer soils than F1 (S. Waldren & L. Scally, unpublished data). Contains mainly group 01000. Part of the Limestone Glade Woodland community of Paulay & Spencer.

F4. Timonius *thicket.* Generally this was an open, lower stature (to 3 m) version of F1, with abundant *Timonius polygamus*, *Psydrax odorata* and *Cyclophyllum barbatum*; *Geniostoma hendersonense* and *Nephrolepis hirsutula* were also common. These thickets occurred around the plateau margin of the North and East Beaches, possibly in areas of Polynesian disturbance (Weisler, 1995), and inland from the fissured limestone in the south. The fossil patch reefs of coral rubble in the island centre were mostly covered by very open *Timonius* thicket. Thickets often occurred in areas with very poor soil development, as in the fossil lagoon (S. Waldren & L. Scally, unpublished data). Group 0101. Contains the Cliff Top and Plateau Margin, *Timonius* Scrub, and Lagoonal Patch Reef communities of Paulay & Spencer.

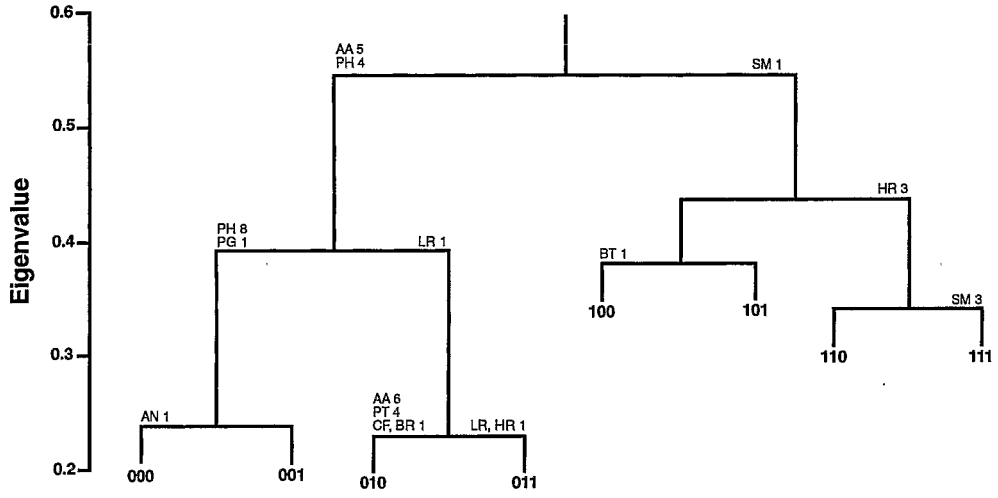

Figure 3. TWINSPAN dendrogram of 54 10 × 10 m quadrats from Oeno Atoll, plotted against eigenvalue at which division occurred. Number codes refer to the TWINSPAN groups described in the text. Indicator species and their pseudospecies cut level are indicated for each division by the following abbreviations: AA = *Argusia argentea*, BR = terrestrial bryophytes, BT = *Boerhavia tetrandra*, CF = *Cassytha filiformis*, HR = *Hedyotis romanzoffiensis*, LR = *Lepturus repens*, PH = *Phymatosorus scolopendria*, PT = *Pandanus tectorius*, SM = *Suriana maritima*.

Oeno Atoll data analyses

TWINSPAN analysis of the Oeno quadrats was terminated with eight end groups (Fig. 3). The major division was between sparsely vegetated communities on coastal sand (all groups beginning with 1, indicator species *Suriana maritima*) and more completely vegetated areas of scrub and forest (all groups beginning with 0, indicator species *Argusia argentea* and *Phymatosorus scolopendria*). This major division of open shore and inland communities was reflected by loadings on axis 1 of DCA; forest quadrats had scores of less than 1.5, and open coastal communities greater than 2 on this axis (Fig. 4, Table 3). Axes 3 and 4 of the DCA were not readily interpretable and failed to separate any of the groups described below; scatter diagrams are not presented for these axes.

Axis 2 of the DCA separated the open coastal communities (Fig. 4). Group 101 contained quadrats dominated by a dense scrub of *Suriana maritima* (cover 50–100%), these scored highly on axis 2 (>2.25). Quadrats in group 110 were from bare sandy areas with scattered *Hedyotis romanzoffiensis* (cover up to 5%) and occasional *Lepturus repens*, these scored less than 0.8 on axis 2. Quadrats from the open vegetation of the sand spit (group 100) were close to the *Hedyotis* sand flats, while group 111 consisted of mixed *Argusia argentea*, *Suriana maritima* and *Hedyotis* were closer to 101.

Group 011 consisted of quadrats from the coastal fringe, but with better vegetation development than the groups already described; *Argusia argentea* was the dominant species with between 5 and 50% cover, but *Cocos nucifera*, *Lepturus repens* and *Hedyotis romanzoffiensis* were also common components. Quadrats in this group had intermediate scores on axis 1, suggesting that they were intermediate between coastal sandy communities and the better developed forest and scrub described below.

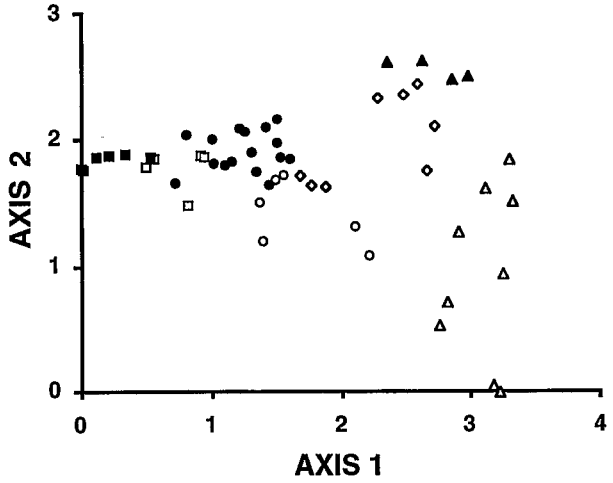

Figure 4. Scatterplot of DCA axes 1 versus 2 for 54 10 × 10 m quadrats from Oeno Atoll. Symbols indicate the vegetation communities: (▲) *Suriana* beachfront; (△) sandy flats; (◇) sand spit; (○) beachfront *Argusia* scrub; (●) inland *Argusia* scrub; (□) tall *Argusia* forest; (■) *Pisonia/Argusia* forest.

TABLE 3. Means (minima–maxima) for Oeno Atoll vegetation communities for the first four DCA axes

Community	Axis 1	Axis 2	Axis 3	Axis 4
A1 *Suriana* beachfront	2.70 (2.34–2.97)	2.57 (2.49–2.64)	0.58 (0.52–0.66)	0.87 (0.67–1.17)
A2 Sand flats	3.09 (2.75–3.32)	0.94 (0.00–1.85)	0.93 (0.57–1.43)	0.94 (0.23–1.82)
A3 Sand spit	2.25 (1.67–2.71)	2.00 (1.63–2.45)	1.09 (0.86–1.36)	0.60 (0.00–0.88)
B1 Beachfront *Argusia* scrub	1.68 (1.36–2.21)	1.42 (1.09–1.72)	0.80 (0.35–1.29)	1.32 (0.80–2.08)
B2 Inland *Argusia* scrub	1.24 (0.72–1.60)	1.90 (1.64–2.15)	1.00 (0.53–1.65)	1.34 (0.77–1.73)
C1 Tall *Argusia* forest	0.75 (0.50–0.94)	1.77 (1.48–1.87)	0.29 (0.00–0.56)	1.40 (0.93–1.60)
C2 *Pisonia/Argusia* forest	0.20 (0.00–0.53)	1.83 (1.75–1.88)	0.58 (0.41–0.84)	1.40 (1.24–1.52)

Group 010 contained quadrats which covered much of the interior of Oeno. These were dominated by bushes (to 2.5 m) of *Argusia argentea* (cover varied between 5 and 50%), with *Boerhavia tetrandra* (up to 5% cover) and *Phymatosorus scolopendria* (up to 33% cover) always present. *Pandanus tectorius*, *Lepturus repens*, *Lepidium bidentatum* and *Cassytha filiformis* also occurred in this community. The vegetation in these quadrats was generally open, with closed canopies of the dominant *Argusia* only in small patches.

Groups 000 and 001 contained quadrats where a closed canopy of *Argusia argentea* had developed, sometimes in association with *Pisonia grandis*. Quadrats from group 000 were distinct in containing abundant *Pisonia* (cover up to 75%), *Asplenium nidus* and *Achyranthes aspera*; the former two species only occurred at the south western end of the island. Quadrats dominated by tall

(to 9 m, cf. 010 above) *Argusia* occurred elsewhere, but always lacked *Asplenium* and *Pisonia*—these were grouped into TWINSPAN group 001, together with *Pisonia* forest quadrats from which *Asplenium* was absent.

From the TWINSPAN and DCA analyses, three major vegetation types can be discerned, each with a number of communities; species composition of these communities is given in Table 4.

Vegetation communities of Oeno Atoll

A. Open sandy littoral vegetation. These communities occurred around shorelines, particularly the northern part of the island, and consisted of scattered low shrubs and the grass *Lepturus repens.*

B. Argusia *scrub.* These were fairly low stature communities (3 m) dominated by *Argusia argentea.* They occurred inland over much of the island, and locally along shorelines.

C. Closed forest. Closed forest was usually much taller than *Argusia* scrub (canopy about 7–9 m), with fewer open habitat species present; it often occurred as a shoreline fringe in the southern part of the island, especially the south-eastern embayment, and as a well-developed forest at the southern end.

D. Coconut grove. Coconut groves occurred mainly at the northern end close to the sand spit. *Cocos nucifera* was dominant and few other species were present; the groves were probably planted by Pitcairners. These were not recorded in quadrats.

The following communities can be recognized within the first three of these

TABLE 4. Abundance indices for Oeno taxa in various vegetation communities. Values are the total Domin scores for each taxon per community, divided by the total number of quadrats, and multiplied by 10. Community codes are described in the text

Species	Community A1	A2	A3	B1	B2	C1	C2
Achyranthes aspera	—	—	—	12.5	8.4	10.0	10.0
Argusia argentea	25.0	2.2	30.0	47.5	63.4	68.0	78.3
Asplenium nidus	—	—	—	—	—	—	25.0
Boerhavia tetrandra	12.5	4.4	—	33.3	31.6	29.0	3.3
Bryophytes	2.5	2.2	—	3.3	10.0	—	—
Cassytha filiformis	—	—	—	8.3	15.6	—	—
Cocos nucifera	—	5.6	1.3	—	—	—	—
Hedyotis romanzoffiensis	5.0	28.3	—	21.7	0.6	—	—
Lepidium bidentatum	—	—	—	—	9.4	—	—
Lepturus repens	7.5	10.0	23.8	23.3	11.9	—	—
Pandanus tectorius	5.0	1.1	1.3	3.3	20.0		
Phymatosorus scolopendria	12.5	—	—	35.0	35.9	78.0	75.0
Pisonia grandis	—	—	—	—	—	14.0	53.3
Scaevola sericea	—	19.4	—	20.0	0.6	—	—
Setaria verticillata	—	—	—	—	0.6	—	—
Solanum viride	—	—	—	3.3	—	6.0	—
Suriana maritima	80.0	19.4	18.8	—	—	—	—
Triumfetta procumbens	—	—	7.5	—	—	—	—

main types; TWINSPAN groupings are again shown, and species occurrence shown in Table 3.

A1. Suriana *beachfront.* This was dominated by dense, tall (2–3 m) bushes of *Suriana maritima*, forming a narrow fringe along the upper shore. *Argusia argentea* was occasionally present; *Phymatosorus scolopendria* and *Boerhavia tetrandra* occurred amongst the shrubs. One area occurred well away from the shoreline in the north east, it may indicate the presence of a former shoreline. Group 101.

A2. Sand flats. This community covers bare sandy areas around the northern part of the coastline, but excluding the sand spit. *Hedyotis romanzoffiensis* and *Suriana maritima* were common, *Argusia argentea* was also present, with occasional *Phymatosorus scolopendria, Scaevola sericea, Lepturus repens* and *Boerhavia tetrandra.* We do not think it necessary to split the very open *Hedyotis* dominated areas (group 110) from those where *Suriana* and a wider range of species were present (group 111). Groups 110 and 111.

A3. Sand spit. This was a very open community, probably an early stage of the previous two. The sand spit was very species-poor, with only *Argusia argentea, Suriana maritima* and *Lepturus repens*, and the very rare *Triumfetta procumbens.* Some *Cocos nucifera* have obviously been planted by Pitcairners, often in rows. Group 100.

B1. Beachfront Argusia *scrub.* This was dominated by low *Argusia argentea* bushes, with *Lepturus repens, Boerhavia tetrandra* and *Phymatosorus scolopendria.* It may have developed from the more species-rich forms of A2, but *Suriana maritima* was notably absent. Mainly group 011.

B2. Inland Argusia *scrub.* Generally this was a low stature (to 3 m), open vegetation of shrubby *Argusia argentea*, with occasional large specimens of *Argusia* and *Pandanus tectorius.* A varied ground cover of *Lepturus repens, Lepidium bidentatum, Phymatosorus scolopendria* and *Cassytha filiformis* occurred, with terrestrial bryophytes in sandy areas. A very variable community, and the most species-rich community of the island. Most of group 010.

C1. Tall Argusia *forest.* Tall forest was dominated by tall (to 9 m) *Argusia argentea* trees, with a ground flora of *Phymatosorus scolopendria* and *Boerhavia tetrandra.* It was generally more coastal than B2, and was possibly formed where sand is accreting with consequent nutrient incorporation. It was well developed in the major embayments. In the south it graded into C2. Group 001.

C2. Pisonia/Argusia *forest.* This was a closed forest of *Pisonia grandis* and *Argusia argentea* with a canopy at 6–8 m. The ground flora was dominated by *Phymatosorus scolopendria, Achyranthes aspera* and *Asplenium nidus*, the only habitat for the latter on Oeno. This was the most specialised community, occurring only at the southern end on the best developed soil profiles of the island (S. Waldren & L. Scally, unpublished data). Group 000.

Vegetation of Ducie Atoll

We did not visit Ducie; only two species of higher plant were present in 1991–1992, one of which is rare and first recorded by the expedition (*Pemphis acidula*). The vegetated islands contained *Argusia argentea*, which grew to varying heights as on Oeno; early in 1991 it appeared severely storm-damaged with many of the larger *Argusia* regrowing from horizontal trunks (P. Jones, personal communication).

Vegetation of Pitcairn Island

The coastline of Pitcairn is generally steeply sloping, and as a result there was very little beach or strand vegetation. Many of the typical Pacific coastal species such as *Argusia argentea* and *Pemphis acidula* were rare, suggesting that coastal vegetation was either highly disturbed, or poorly developed. At the West Harbour, *Pandanus tectorius* grew about the strand line with *Mariscus javanicus*, and several weedy species, including *Solanum americanum* and *Plantago major*. Coastal cliffs contained several species found in similar habitats on Henderson, including *Sesuvium portulacastrum*, *Portulaca lutea*, *Asplenium obtusatum*, *A. shuttleworthianum* and *Apium prostratum*. Good examples of this community were found at Down Rope.

Lower altitude vegetation was often highly disturbed by the activities of the Pitcairn Islanders and by the earlier Polynesian inhabitants. Many exotic species occurred, some deliberately planted by both Polynesians and Pitcairners, and several species have escaped from cultivation, see Florence *et al.* (1995). The *Bounty* mutineers brought with them Polynesian women and men from Tahiti, and it is likely that some typical Polynesian introductions may have arrived on Pitcairn with the *Bounty*. The fern *Christella parasitica* was common in shady areas at lower altitude. Less disturbed valleys contained a forest dominated by the endemic *Homalium taypau*, with various exotic and native species associated, but none of them particularly common. *Cerbera manghas* occurred in drier *Homalium* forest at Tedside. The herb layer included *Phymatosorus scolopendria*, and *Peperomia* species. At least one steep sided valley contained a community of several rare ferns (*Angiopteris chauliodonta*, *Ctenitis cumingii*, and *Trichomanes endlicherianum*) amongst *Homalium* and a number of exotics, including mango. Roadsides through these shaded forests were rich in exotic species, but a number of native fern species were also present. The remoter valleys generally had the more varied tree floras, but many Polynesian introductions occurred throughout the *Homalium* forest. The dates of introduction remain uncertain as Polynesian occupation of Pitcairn covered a considerable period (see Weisler, 1995) and also because of the likelihood of at least some Polynesian plants being introduced at the time of the *Bounty*'s arrival.

Some of the valleys and middle slopes were dominated by dense monospecific stands of *Syzygium jambos*. Originally introduced for fuel wood but now rarely used, this has invaded native woodlands and now threatens much of the remaining native flora. Few other species were associated with this community.

Slopes on the eastern side of the island were covered by fern scrub

dominated by *Dicranopteris linearis* and *Nephrolepis hirsutula*, *Cordyline fruticosa* also occurred in scrub areas. This anthropogenic community seems to be spreading; St. John (1987) recorded *Dicranopteris* as rare and local during his visit in 1934, whereas we found it locally abundant at mid-altitudes. *Sorghum sudanense* was also invading this community, and *Lantana camara* was invasive at higher elevations; both may become serious pests. Numerous weedy species occurred in these relatively open areas, particularly along paths. These fern scrub areas graded into a shrub community of *Psidium guava*, *Citrus sinensis*, *C. aurantiifolia* and *Morinda citrifolia*, with *Glochidion* species occurring locally.

Steep eroded slopes on the main ridge were dominated by *Dicranopteris*, but on the more sheltered side a montane forest occurred dominated by *Metrosideros collina* (with abundant aerial roots) and *Homalium taypau*. The tree fern *Cyathea medullaris* was very locally frequent in this community, and the ground flora was rich in ferns, including *Phymatosorus scolopendria*, *P. powellii* and *Asplenium shuttleworthianum*. The trees were richly clothed in epiphytic lichens and bryophytes, and the only native orchid of the island group, *Taeniophyllum fasciola*, also occurred as an epiphyte.

CONCLUSIONS

Several distinct plant communities occur in the Pitcairn Group. Many of these have affinities with vegetation communities elsewhere in Polynesia, but the consistent feature of the Pitcairn Group is that the communities are impoverished, with some expected species absent. The beaches of Henderson Island contain typical low atoll communities (Papy, 1951–54; Fosberg, 1991), grading from *Lepturus repens* and other herbs, through *Suriana maritima* scrub on sand and *Pemphis acidula* scrub on beachrock, to beach-ridge and embayment forests dominated by *Argusia argentea*, *Pisonia grandis* and others. Similar communities occur on Oeno Atoll, but they are generally poorer in species compared to Henderson, while Ducie Atoll represents an even more extreme form of impoverishment. The lack of *Pemphis* communities on Oeno is especially notable, as this forms characteristic communities on beachrock and the upper lagoon fringe of atolls further west (Papy, 1951–54; Stoddart, 1975; Fosberg, 1991); suitable habitat seems to be present on Oeno. Other notable absentees from Oeno are *Guettarda speciosa* and *Heliotropium anomalum*, the latter is common on sandy beachfronts on Henderson and in the Tuamotu Islands. On Oeno both *Hedyotis romanzoffiensis* and *Argusia argentea* are characteristic features of vegetation of sandy areas; in the Tuamotus both species occur more typically on limestone gravel and coral rubble. The coastal vegetation of Pitcairn Island is rather different as there are only limited sand deposits; the coastal vegetation here bears closer resemblance to some of the cliff communities of Henderson.

Henderson beach communities grade through cliff slope scrub into a plateau forest that is never overwashed by seawater. This has allowed a much wider range of vegetation to develop, which includes several endemic species. This forest remains largely undisturbed; regeneration along old trails appears to always involve indigenous species which may naturally colonize gaps in the canopy. In addition, the scattering of helicopter-loads of *Thespesia* seeds and *Cocos* fruits over the plateau forest in 1966 (M. Fraser, personal

communication) seems (thankfully!) to have been an unsuccessful attempt to establish these species in plateau forest. We found a few obviously young *Cocos* palms on the plateau; these seem to have been deposited at the ends of trails (e.g. the Operation Raleigh trail), and all were destroyed. The Henderson plateau forests therefore differed considerably from the highly disturbed communities on Makatea Island, also a raised atoll (Wilder, 1934). Although the flora of Makatea is larger than Henderson, its communities seem poorly defined, and is notable that Wilder reported only a single endemic species (*Eupritchardia vuylstekeana*) and even this is generally considered conspecific with a palm native to Miti'aro in the southern Cook Islands. The *makatea* areas of raised limestone on Mangaia in the southern Cook Islands contain a similar low-stature mixed forest, although *Pisonia grandis* is absent and different species occur (Merlin, 1991). Henderson plateau communities may therefore represent a species-poor analogue of pre-European (and possibly pre-Polynesian, as the effects of the latter seem to be limited to the plateau margin) vegetation on raised atolls of the central and eastern Pacific. However, because of the widespread degradation of natural ecosystems on virtually all other raised atolls, it is not clear whether communities similar to those of the Henderson plateau still occur or have previously occurred elsewhere. Merlin (1991) also recorded dwarfed shrub communities from exposed windward parts of Mangaia; similar communities occur on Henderson, but on Mangaia these dwarfed communities contain several herbs and shrubs which are absent from the Henderson cliff top communities and only occur some distance from the plateau margin in the limestone fissure community. This may indicate that harsher conditions prevail on Henderson, possibly because the Mangaian *makatea* reaches 55–70 m above sea level (Merlin, 1991), compared to the 30 m of the Henderson plateau. Several of the Henderson communities appear to be absent or unsampled on Mangaia, while there is no equivalent on Henderson of the Mangaian *Barringtonia* forest (Merlin, 1991).

Pitcairn likewise contains vegetation types found elsewhere on Pacific high islands (Papy, 1951–54; Fosberg, 1991), but it is considerably poorer in species richness. The upper ridges of the island contain a very poor analogue of cloud forests on other high islands, including the Society (Papy, 1951–54) and Austral (Hallé, 1980) groups. The species impoverishment in this formation may be explained by the isolation, relatively low altitude (300 m on Pitcairn, cf. 2200 m on Tahiti), and southerly subtropical location of Pitcairn. The middle and lower valley slopes of mixed forest or anthropogenic *Dicranopteris* scrub are also found elsewhere; the latter is characteristic of disturbed ground and degraded forest on the lee side of high islands at moderate altitude (Papy, 1951–54), and is likely to be the result of Polynesian disturbance (Fosberg, 1991; Weisler, 1995); on Pitcairn they seem to have spread since 1934 (cf. St. John, 1987), certainly by the influence of the Pitcairners. Anthropogenic communities occur elsewhere throughout the islands; the coconut groves of Henderson and Oeno, disturbance of beach forest on Henderson by Polynesians and Pitcairners, Polynesian cultivation areas on Henderson (inland from Each Beach) and Pitcairn (Weisler, 1995), and the more recent disturbance to Pitcairn by the islander's gardens. The most problematic of these anthropogenic communities are the *Syzygium jambos*

thicket, *Lantana camara* scrub and *Lablab purpureus* scrub of Pitcairn. All appear to be spreading, and threatening other natural and semi-natural plant communities of the island (Waldren, Florence & Chepstow-Lusty, in press). *Ipomoea indica* and *Passiflora maliformis* are also spreading and may become pests as in the Austral, Gambier and Society Islands. Many of the more interesting areas of native Pitcairn vegetation contain endemic molluscs (Preece, 1995), so at least some animal communities are also threatened by invasive plants. There is an urgent need for a detailed vegetation survey of Pitcairn.

Despite the potential problems just mentioned for Pitcairn, the whole group provides an interesting diversity of vegetation types, typical of many Pacific islands. The communities of the group are, however, of great interest and scientific value for many reasons, not least because they are relatively species-poor. Thorough knowledge of the functioning of relatively simple communities can be an important aid in interpretation of more species-rich analogues elsewhere. Furthermore, Henderson may contain communities that are absent or have all but disappeared from other raised atolls, which have often been greatly disturbed by mineral extraction. For these reasons, it is essential that adequate conservation measures be applied to the whole of the Pitcairn Group.

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REFERENCES

Florence J, Waldren S, Chepstow-Lusty AJ. 1995. The flora of the Pitcairn Islands: a review. *Biological Journal of the Linnean Society* **56:** 79–119.

Fosberg FR. 1991. Polynesian plant environments. In. Cox PA, Banack SA, eds. *Islands, Plants and Polynesians: An Introduction to Polynesian Ethnobotany.* Portland, Oregon: Dioscoredes Press, 11–23.

Fosberg FR, Sachet M-H, Stoddart DR. 1983. Henderson Island (southeastern Polynesia): a summary of current knowledge. *Atoll Research Bulletin 272,* 47pp, 8 figs.

Fosberg FR, Paulay G, Spencer T, Oliver R. 1989. New collections and notes on the plants of Henderson, Pitcairn, Oeno, and Ducie Islands. *Atoll Research Bulletin 329,* 18 pp.

Franklin J, Merlin M. 1992. Species-environment patterns of forest vegetation on the uplifted reef limestone of Atiu, Mangaia, Ma'uke and Miti'aro, Cook Islands. *Journal of Vegetation Science* **3:** 3–14.

Kent M, Coker P. 1992. *Vegetation Description and Analysis.* London: Belhaven Press.

Hallé N. 1980. Les orchidées de Tubuaï (archipel des Australes, Sud Polynésie). *Cahiers de l'Indo-Pacifique* **2:** 69–130.

Hill MO. 1979a. *DECORANA—a FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging.* Cornell University, Department of Ecology and Systematics, Ithaca, New York.

Hill MO. 1979b. *TWINSPAN—a FORTRAN Program for Arranging Multivariate Data in an Ordered Two Way Table by Classification of Individuals and the Attributes.* Cornell University, Department of Ecology and Systematics, Ithaca, New York.

Malloch AJC. 1988. VESPAN II. A computer package to handle and analyse multivariate species data and handle and display species distribution data. Lancaster: University of Lancaster.

Merlin M. 1991. Woody vegetation on the raised coral limestone of Mangaia, southern Cook Islands. *Pacific Science* **45:** 131–151.

Pandolfi JM. 1995. Geomorphology of the uplifted Pleistocene atoll at Henderson Island, Pitcairn Group. *Biological Journal of the Linnean Society* **56:** 63–77.

Papy HR. 1951–54. Tahiti et les Iles voisines. La végétation des Iles de la Société et de Makatéa. *Travaux du Laboratoire Forestier de Toulouse, Tome V. Vol. I, Article III.* 386 pp.

Paulay G, Spencer T. 1989. Vegetation of Henderson Island. *Atoll Research Bulletin 328,* 1–13.

Preece RC. 1995. Systematic review of the land snails of the Pitcairn Islands. *Biological Journal of the Linnean Society* **56:** 273–307.

Rehder HA, Randall JE. 1975. Ducie Atoll: its history, physiography and biota. *Atoll Research Bulletin 183,* 40 pp.

St. John H. 1987. An account of the flora of Pitcairn Island with new *Pandanus* species. *Pacific Plant Studies 46;* Honolulu, Hawaii: privately published.

St. John H, Philipson WR. 1960. List of the flora of Oeno Atoll, Tuamotu archipelago, South-Central Pacific Ocean. *Transactions of the Royal Society of New Zealand* **88:** 401–403.

St. John H, Philipson WR. 1962. An account of the flora of Henderson Island, South Pacific Ocean. *Transactions of the Royal Society of New Zealand, Botany* **1:** 179–194.

Stoddart DR. 1975. Vegetation and floristics of the Aitutaki motus. *Atoll Research Bulletin 190:* 87–116.

ter Braak CJF. 1988. *CANOCO—a FORTRAN Program for Canonical Community Ordination by [Partial] [Detrended] [Canonical] Correspondence Analysis (Version 2.0).* Wageningen; TNO Institute of Applied Computer Science.

Waldren S, Florence J, Chepstow-Lusty AJ. In press. Rare and endemic vascular plants of the Pitcairn group, south-central Pacific Ocean: a conservation appraisal. *Biological Conservation.*

Weisler MI. 1995. Henderson Island prehistory: colonization and extinction on a remote Polynesian island. *Biological Journal of the Linnean Society* **56:** 377–404.

Wilder GP. 1934. The flora of Makatea. *B. P. Bishop Museum Bulletin 120:* 1–49.

Wilson EO. 1988. *Biodiversity.* Washington DC: National Academy Press.