

PUBLISHED VERSION

Carpenter, Raymond John; Read, Jennifer; Jaffre, Tanguy.

[Reproductive traits of tropical rain-forest trees in New Caledonia](#), Journal of Tropical Ecology, 2003; 19 (4):351-365.

Copyright © 2003 Cambridge University Press

PERMISSIONS

<http://journals.cambridge.org/action/stream?pageId=4088&level=2#4408>

The right to post the definitive version of the contribution as published at Cambridge Journals Online (in PDF or HTML form) in the Institutional Repository of the institution in which they worked at the time the paper was first submitted, or (for appropriate journals) in PubMed Central or UK PubMed Central, no sooner than one year after first publication of the paper in the journal, subject to file availability and provided the posting includes a prominent statement of the full bibliographical details, a copyright notice in the name of the copyright holder (Cambridge University Press or the sponsoring Society, as appropriate), and a link to the online edition of the journal at Cambridge Journals Online. Inclusion of this definitive version after one year in Institutional Repositories outside of the institution in which the contributor worked at the time the paper was first submitted will be subject to the additional permission of Cambridge University Press (not to be unreasonably withheld).

2nd May 2011

<http://hdl.handle.net/2440/48082>

Reproductive traits of tropical rain-forest trees in New Caledonia

Raymond J. Carpenter^{*1}, Jennifer Read^{*} and Tanguy Jaffré[†]

^{*}School of Biological Sciences, P.O. Box 18, Clayton Campus, Monash University, Victoria 3800, Australia

[†]IRD – Institut de recherche pour le développement, Centre de Nouméa, BP A5 Nouméa – 98848, New Caledonia

(Accepted 19 June 2002)

Abstract: Reproductive traits of 123 species of rain-forest tree from ultramafic regions of New Caledonia were assessed, mainly from herbarium specimens. Most species had extremely small, simple, pale-coloured flowers that are probably mainly pollinated by small insects, but not including bees. The seeds of most species were considered to be bird dispersed. However, wind is also important for pollination and seed dispersal. The phenological trend was for an increase in the number of species flowering and fruiting around the end of the warm dry season/start of the hot wet season, followed by a decline at the end of the wet season, and lower proportions during the cooler season. Seed size was significantly correlated with fruit size. Other correlations, between flower size and fruit size, and between seed size and seed number, were significant using species as independent observations, but did not hold following phylogenetic correction. Compared with non-dioecious species, dioecious species had significantly larger seeds, and a greater proportion of species with biotic dispersal, abiotic pollination and solitary (female) flowers. The long-term persistence of at least the larger-seeded tree species in New Caledonia is precarious, since the endemic giant pigeon, *Ducula goliath*, is probably their principal effective disperser, and this species is in decline.

Key Words: dispersers, flowers, fruits, pollinators, seeds

INTRODUCTION

The south-western Pacific island group of New Caledonia is recognized as a global biodiversity ‘hotspot’ (Myers 1988), containing nearly 3500 plant species in an area of only 19 170 km² (Veillon 1993). The flora includes a diverse rain-forest component, a rich, highly endemic, scrubby ‘maquis’ vegetation, and remnants of sclerophyll woodland (Jaffré *et al.* 2001, Morat 1993). New Caledonia formed part of the eastern margin of Gondwana, until about 90 million years BP, when the Tasman Sea formed (Wilford & Brown 1994). Volcanic islands associated with the Lord Howe Rise could have facilitated plant migration between Australia and the New Caledonian region during the Neogene (Wilford & Brown 1994), and island chains are also implicated along the Norfolk and Reinga Ridges toward New Zealand during this time (Herzer *et al.* 1997). Ophiolites associated with Eocene obduction cover most of the southern third of the present main island of New Caledonia. Soils derived from ultramafic substrates in these regions can not only be highly infertile, but may even be toxic for plant growth because of high concentrations of metals (Brooks 1987, Jaffré 1992).

Carlquist (1974) argued that the biota of New Cale-

donia is largely derived via long-distance dispersal, albeit over a long period of time. However, there is increasing evidence for the presence of archaic, poorly dispersible faunal elements, suggestive of Gondwanan heritage (Bickel 1999, Chazeau 1993, Diamond 1984, Holloway 1979). The present biota is probably best viewed as a mixture of ancient and recently immigrant taxa, with an evident post-Eocene radiation of certain groups such as Araucariaceae (Setoguchi *et al.* 1998). The presence of clearly relictual taxa such as *Acmopyle* (Hill & Carpenter 1991) is indicative of a continuously favourable moist climate, perhaps throughout the Cenozoic.

Ecological processes in New Caledonian rain forests are not well understood, and there are few published reports. These include papers on the ultramafic vegetation by Jaffré (1980) and Jaffré & Veillon (1991), and, with a focus on *Nothofagus*-dominated forest, by Read & Hope (1996) and Read *et al.* (1995, 2000). The recent fragmentation of forests into isolated patches as a result of burning (McCoy *et al.* 1999) has serious conservation implications, in part because the New Caledonian fauna is depauperate with respect to animals that may serve as pollinators or seed dispersers. Notable examples include very few species of native bee (Donovan 1983), and an absence of native land mammals (Diamond 1984, Holloway 1979).

Relationships and energetic trade-offs among plant

¹ Corresponding author. Present address: 3 Lorraine Ave, Port Lincoln, South Australia, 5606. Email: rcarpenter@ozemail.com.au

traits are undoubtedly complex, but it has been hypothesized that distinct sets of traits should have evolved in response to similar selective pressures (Primack 1987). Of the reproductive traits, seed size has perhaps received the greatest attention from ecologists (Foster 1986, Grubb 1996, 1998; Grubb & Metcalfe 1996, Hammond & Brown 1995, Harms & Dalling 1997, Metcalfe & Grubb 1997), but other tropical studies include those of phenology (Wright & Calderon 1995), fruit traits with respect to dispersers (Gautier-Hion *et al.* 1985, Mack 1993, Wheelwright 1985), and floral traits with respect to pollination vectors (Momose *et al.* 1998, and summaries by Bawa 1990, Endress 1994, Williams & Adam 1994).

Large-scale, multitrait studies are rare in tropical ecosystems, but include papers by Ibarra-Manríquez & Oyama (1992) on Mexican rain-forest trees, and by Osunkoya (1996) on North Queensland rain forest. The latter study is of particular interest to us because of the floristic similarity of the study forests to those of New Caledonia.

The aim of our research was to investigate reproductive traits of a large set of New Caledonian rain-forest trees that occur on ultramafic substrates. In particular, we predict that the extreme soil and faunal characteristics might lead to differences with respect to studies of forests elsewhere. In another paper we will relate plant traits to light requirements for regeneration.

STUDY SPECIES AND REGION

A total of 123 species from 85 genera and 39 families in 26 orders was assessed (Appendix 1). This group represents about 19% of the total rain-forest tree flora on ultramafic substrates. The species were all the trees with trunks of at least 10–15 cm diameter at breast height (75% were species attaining > 20 cm dbh) recorded from nine research plots totalling 4.6 ha in *Nothofagus*-dominated

and adjacent mixed rain forest, from 240–940 m asl (described in Read *et al.* 2000). We concentrated on larger tree species (not the understorey) in order to provide comparisons among species with theoretically more uniform selection pressures.

The climate in southern New Caledonia was discussed by Jaffré (1980), and briefly by Hope & Pask (1998) and Read *et al.* (1995, 2000). It can be described as moist subtropical, with four seasons. Tropical depressions tend to bring most rains in the hottest period from December to March. The prevalent south-east trade winds then assume more control from around April until December. April/May is regarded as a mini-dry season, followed by a cooler season with moderate precipitation until September, when a warm dry season ensues until the resumption of summer rains. However, there can be great variability in both the monthly distribution and amount of precipitation from year to year, and the duration of dry periods. Mean annual precipitation at each rain-forest study site is probably of the order of 2500–3000 mm, whilst mean annual temperatures range from minima of about 18 °C to maxima of about 25 °C.

METHODS

Specimens and collectors' notes lodged in the IRD Herbarium in Nouméa, New Caledonia, were used for assessment of the reproductive traits listed in Table 1. Results were supplemented by field observations and by reference to relevant literature, most notably the *Flore de la Nouvelle-Calédonie et Dépendances* (vols 1–23) published by the Muséum National d'Histoire Naturelle, Paris. Herbarium specimens provide vast and important resources for this type of ecological research. However, there are limitations associated with curatorial processes and possible collection biases.

Table 1. Characters and their categories measured or recorded for each species.

Character	Categories
Flower length and width	
Fruit length and width	
Seed length and width	
Number of seeds per fruit	
Flowering month(s)	
Fruiting month(s)	
Flower type:	(a) fig (b) flag (c) brush (d) salverform (e) small tube (f) dish
Inflorescence position:	(a) terminal (b) axillary (c) cauliflorous (d) other (not clearly terminal or axillary)
Inflorescence type:	(a) solitary (b) compound
Flower colour:	(a) red (+any red) (b) white only (c) yellow(ish) (d) dark brown (e) pale (f) green
Flower odour:	(a) present (b) absent
Pollinator syndrome:	(a) wind (b) insect (c) bird or bat
Fruit type:	(a) fig, drupe, berry (b) pod, follicle, capsule (c) achene, nut (d) samara or similar
Fruit/seed appendages:	(a) wings, hairs (b) fleshy; e.g. aril, arillode, caruncle (c) none
Fruit colour:	(a) red (+any red) (b) purple, black, blue (c) brown (d) green (e) orange, yellow
Dispersal syndrome:	(a) wind (b) bird, bat (c) other
Breeding system:	(a) dioecious (b) not dioecious

Quantitative characters

At least 10 separate specimens were used for measurements where possible. However, in order to obtain 10 measurements, it was sometimes necessary to measure several organs from the same specimen. Maximum dimensions of flowers, fruits and seeds were used as measures of size. In addition, we opted to include length \times width as another measurement of fruit size, since this variable reduces the bias caused by long, linear fruits. Many other papers have used mass as a measurement of fruit and seed size. We chose length and width (diameter) so that direct comparisons could be made with the work of Osunkoya (1996) (and others), because dimensions are of more obvious relevance to potential dispersers (Jordano 1995, Willson *et al.* 1989), and to minimize damage to herbarium specimens. If propagules had appendages such as papery wings that were readily separable from the body of the organ, these were not included in measurements. The Podocarpaceae used in this study had fertile scales partly or completely surrounding their seeds, and so these complexes were deemed to be fruits. In Moraceae, we treated the fleshy receptacles ('figs') that partially enclose the multiple flowers and achenes as single fruits. In *Nothofagus* the fruits are the rounded nuts held in cupules. The diameters of podocarp 'fruits', figs, drupes and berries were used in discussions concerning frugivory, in addition to those of seeds with arils or aril-like appendages, since these can be regarded as functionally fleshy (van der Pijl 1982). Herbarium fruit specimens are sometimes compressed or shrunken (especially fleshy layers) due to dehydration, and it is possible that some fruits examined were not fully mature. The true sizes of these organs are therefore likely to be slightly larger than that measurable. The fruits of some species also had very thin outer layers, which could not be separated from the seed. In these cases the fruit and seed were deemed to have the same dimensions.

Only what were interpreted to be fully opened, intact flowers were measured, although the larger flowers in particular were sometimes distorted by pressing. We generally followed Osunkoya (1996) in using maximum corolla dimension for flower size, but reasoned that the androecium of staminate flowers must be included for the true ecologically important measure. In the only other cases we could find of flower measurement in tropical floras, Ibarra-Manríquez & Oyama (1992) used flower length, but did not detail their methods. For clearly dioecious species, and for others in which male and female flowers could easily be distinguished, male and female flowers were assessed separately but only females were subsequently used in analyses. Conifers were not included in the analyses that required flower dimensions.

For phenology, collection dates were recorded from all

available (up to May 1999) herbarium specimens with apparently mature flowers and fruits, and from the literature. Again, it is possible that some of the organs were not fully mature, resulting in the interpretation that reproductive periods were longer than in reality. On the other hand, reproductive periods for some species could be interpreted as being shorter than in reality, because of such factors as rarity and difficulty in collection (e.g. tall trees). With such limitations in mind, a frequency plot was made of the number of species in flower and fruit each month, to illustrate general phenological trends only. *Ficus* species were deemed to be in flower and fruit simultaneously, as it was not possible to easily determine fruit maturity. For conifers, mature male cones only were used for flowering phenology.

Qualitative characters

Qualitative reproductive traits chosen for analysis are included in Table 1. Conifers were included where possible (i.e. 'inflorescence' position, 'fruit' colour, appendage type and pollination and dispersal syndromes). If present, propagule appendages were classified as either wings/hairs or fleshy (e.g. arils). For Podocarpaceae, cone bracts were treated as fleshy appendages in all except *Retrophyllum* (see de Laubenfels 1972). The category of 'other' for the principal seed/fruit dispersal syndrome includes species with propagules having no obvious specializations, and which do not seem to be dispersed other than by falling directly from the tree, and possibly moving downslope. The 'red' category for fruits and flowers was used regardless of whether this was the sole colour or not, as it sometimes appeared in combination with other colours. Blue-coloured fruits were combined with black and purple, following Willson *et al.* (1989).

The flower types recognized were essentially those widely acknowledged in the field of floral morphology (see Endress 1994). For instance, 'brush flowers' were defined as flowers or inflorescences in which the appearance of the stamens tended to dominate that of the other organs. These included spherical inflorescences, brush-like flowers and the stamiferous open forms typical of Myrtaceae. Two categories contained those flowers in which the corolla or perianth was at least partly fused into a tube. The first was those with 'salverform' flowers (e.g. Apocynaceae), and the second those with various 'small tubes' – small flowers having the shape of a very short tube (we included *Cryptocarya* here) or bell or intermediate form. 'Dish' flowers ranged in size from inconspicuous to large and showy, but typically had an open form with obvious, free petals and/or sepals. The open female flowers of *Balanops*, *Nothofagus* and *Gymnostoma* lack conspicuous perianth segments but were included as dish flowers. Flowers of *Stenocarpus trinervis* (Proteaceae)

were not readily classifiable, but were included as dishes, having an open form when mature. Dioecious species were taken to be those stated as dioecious in the literature or in herbarium notes. Species were recorded as cauliflorous if collectors had noted that flowers occur on old wood. Inflorescences were treated as either compound (e.g. panicles, racemes) or typically solitary flowers. The pollination biology of New Caledonian trees is very poorly known. Species were thus initially classified following Faegri & van der Pijl (1979) and Endress (1994), as being either wind or animal pollinated. We regarded the latter group to be composed only of insect- and bird-pollinated species, where all the mainly red flowers were classified as bird pollinated, as well as the large, showy flowers of *Crossostylis grandiflora* and *Deplanchea speciosa*.

Data analysis

The data were first analysed using each species as an independent observation (TIPs analysis). The *G*-test for goodness of fit was used to test for differences in species frequencies among qualitative character traits. Continuous data could not always be transformed appropriately for parametric statistics and therefore ANOVA and *t*-tests were undertaken on ranks of continuous variables. Nested ANOVA was used to detect how variation was distributed among taxonomic levels. Since a diverse set of species was used, across a wide range of genera and families, the differences among genera and families account for a relatively large proportion of the total variation in all traits (Table 2). Spearman rank correlation was used to test for associations among continuous variables, with probabilities unadjusted for multiple comparisons following Stewart-Oaten (1995). Correlations at the higher taxonomic levels (family and genus) generally exhibited similar trends as for species, and the results are not presented here. SYSTAT® V. 10.0 for Windows® was used for all analyses except the *G*-test. A critical value of $\alpha = 0.05$ was used in hypothesis testing.

The data were then reanalysed using phylogenetically independent contrasts (PICs) computed by CAIC V. 2.0.0 (Purvis & Rambaut 1995). A phylogenetic tree was derived for the 123 species using the *rbcL*-based phylogeny of Nandi *et al.* (1998), chosen because it allowed

placement of families not included in previous phylogenies. The tree was modified according to Bradford & Barnes (2001), Conran *et al.* (2000), Gadek *et al.* (1996), Kårehed (2001), Plunkett & Lowry (2001), Schwarzbach & Ricklefs (2000) and Wilson *et al.* (2001). Where insufficient information was available regarding relationships between or within genera, the taxa were inserted as polytomies. Twenty-six species were involved in 13 polytomies, with five polytomies among genera, and the remainder among species within genera. Branch lengths were not known for all relationships and were given unit length, which assumes a punctuational mode of change (Purvis & Rambaut 1995). Independent standardized contrasts for each continuous variable were computed by CAIC using the 'Crunch' option, and Spearman rank correlations calculated using SYSTAT. Differences between dioecious and non-dioecious taxa in the continuous traits were investigated using a one-sample *t*-test on the mean of contrasts calculated in the 'Brunch' option (11 contrasts). Under the null hypothesis of no significant difference, the mean value of the contrasts should be zero (Purvis & Rambaut 1995).

RESULTS

Phenology

The phenology of 120 flowering and 118 fruiting species followed a trend of a sharp increase, and highest frequencies, in the warm dry season/start of the hot wet season, contrasted with a decline in the late hot wet season, to fewest species in flower or fruit during the cooler seasons (mid-April to mid-September) influenced by the southeasterly trade winds (Figure 1a). The greatest number of flowering species occurred in October, and of fruiting species in December. The least number of species for both flowering and fruiting was recorded in May. Despite the presence of the trends it is clear that seasonal differences were not pronounced, since peaks amounted to only about 60% of species, and minima about 40% (Figure 1a). The observed trend in flowering was mainly attributable to species with small flowers (≤ 10 mm maximum dimension), since the number of species with large flowers (> 10 mm) showed little variation with respect to season but peaked in June (Figure 1b). There were no

Table 2. Taxonomic distribution of variance in quantitative reproductive traits. Each variance component has been expressed as a percentage of the total variance from nested ANOVA.

Among: Within:	Families Order	Genera Family	Species Genus
Flower maximum dimension	32	55	13
Fruit maximum dimension	46	33	21
Fruit length \times width	51	40	9
Seed maximum dimension	65	26	9
Seed number per fruit	35	61	4

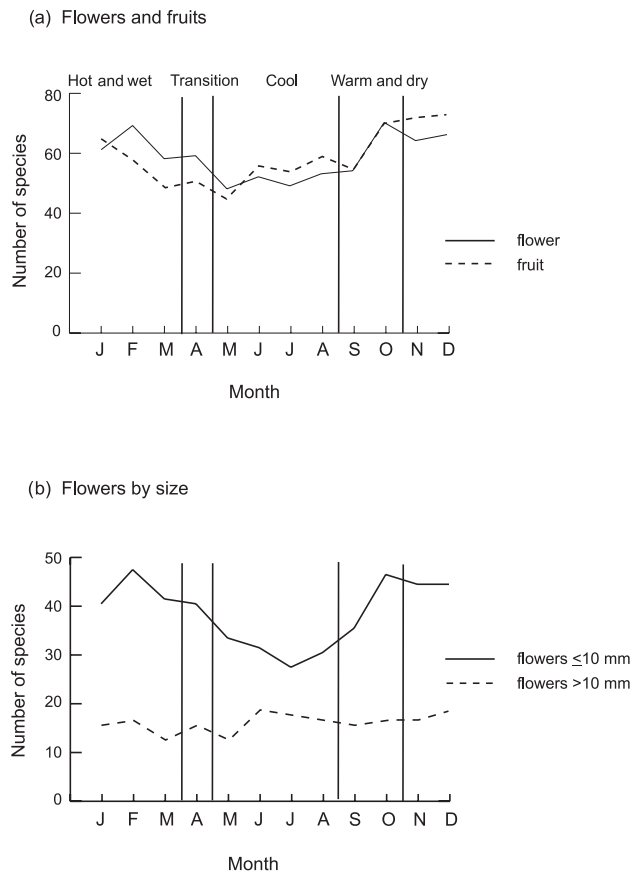


Figure 1. Timing of flowering and fruiting by month and by season. (a) Frequency of species with flowers and with fruits. (b) Frequency of species with large vs. small flowers.

other reproductive traits that clearly departed from the overall phenological trend.

Floral traits

Species differed significantly in flower size ($F = 178$, $P < 0.001$), with mean maximum dimensions (Figure 2a) ranging from less than 2 mm in *Ficus* species and *Macaranga alchorneoides* to over 50 mm in *Deplanchea speciosa* and *Strasburgeria robusta*. Some 88% of taxa had flowers less than 20 mm for the maximum dimension. Mean maximum flower dimension for 111 species was 9.9 ± 1.1 mm.

By far the most common flower type (Figure 3a) was the dish (57% of species overall), ranging from abundant, small and often simple forms less than 10 mm (e.g. Araliaceae, Sapindaceae, Oleaceae) to relatively few, large, showy forms greater than 15 mm (e.g. Elaeocarpaceae and *Crossostylis grandiflora*). About 19% of species had brushes (mostly Myrtaceae and Cunoniaceae), whilst 15% had small tubular forms (e.g. *Cryptocarya*). The remainder comprised those with salverform flowers (Rubiaceae, Apocynaceae), specialized fig flowers and the flag flower of *Deplanchea speciosa*. Inflorescences were most com-

monly axillary (45% of species), whilst for 29% of species they were terminal, and for only about 7% cauliflorous (Figure 3b). Most inflorescences were compound, with only 17% of species recorded as having solitary flowers. Most flowers were white or very pale coloured (about 61% of species), whilst yellow flowers were recorded for 17% of species, and part-red and red flowers for 13% (Figure 3c). The flowers of about 27% of species were known to be fragrant, and 32% not fragrant.

Approximately 16% of the 123 species were dioecious, in 10 families. No significant difference in maximum flower dimension was recorded between non-dioecious species (10.6 ± 1.2 mm, $n = 95$) and dioecious species (5.8 ± 0.6 mm, $n = 16$), using either TIPs analysis ($t = 1.46$, $P = 0.15$) or PICs analysis ($t = 0.28$, $P = 0.78$).

In all, 81% of species were regarded as being principally pollinated by insects, 13% by wind and only 6% by birds (Figure 3d). For dioecious species, 30% were regarded as being abiotically pollinated, compared with only 9% for non-dioecious species. All of the biotically pollinated dioecious species were considered to be insect pollinated.

Fruit traits

There was significant variation among species in fruit size (maximum dimensions: $F = 160$, $P < 0.001$; fruit length \times width: $F = 170$, $P < 0.001$), with mean maximum dimensions (Figure 2b) ranging from less than 5 mm in *Codia discolor*, *Cunonia* spp., *Styphelia pancheri* and *Xanthomyrtus hienghenensis*, to over 85 mm long in the dry, dehiscent-fruited species *Stenocarpus trinervis*, *Alstonia lenormandii*, *Archidendropsis granulosa*, *Deplanchea speciosa* and *Pagiantha cerifera*. In terms of the other measure of size (length \times width) (Figure 2c), the species with the largest fruits were *Acropogon austrocaledonicus*, *Archidendropsis granulosa*, *Storckiella pancheri*, *Strasburgeria robusta* and *Montrouziera gabriellae*. Overall, the mean maximum fruit dimension was 24.9 ± 2.1 mm ($n = 115$). Mean maximum fruit dimension did not differ between dioecious (20.9 ± 2.1 mm) and non-dioecious species (25.0 ± 2.4 mm), using either TIPs analysis ($t = 0.78$, $P = 0.44$) or PICs analysis ($t = 1.61$, $P = 0.14$). *Montrouziera gabriellae* had the largest fleshy fruits of the New Caledonian trees examined, with a mean length of 60.0 ± 6.5 mm. The mean diameter of fleshy fruits (i.e. fleshy Podocarpaceae, drupes, berries and figs) was 15.7 ± 2.1 mm ($n = 69$). Some 16% of species, from nine families, had fleshy fruits greater than 2 cm in diameter. These included members of Lauraceae, Sapotaceae, Myrtaceae and Rubiaceae. The mean diameter of the combined fleshy and functionally fleshy fruits (i.e. those attractive to frugivores, including arillate seeds) was 13.8

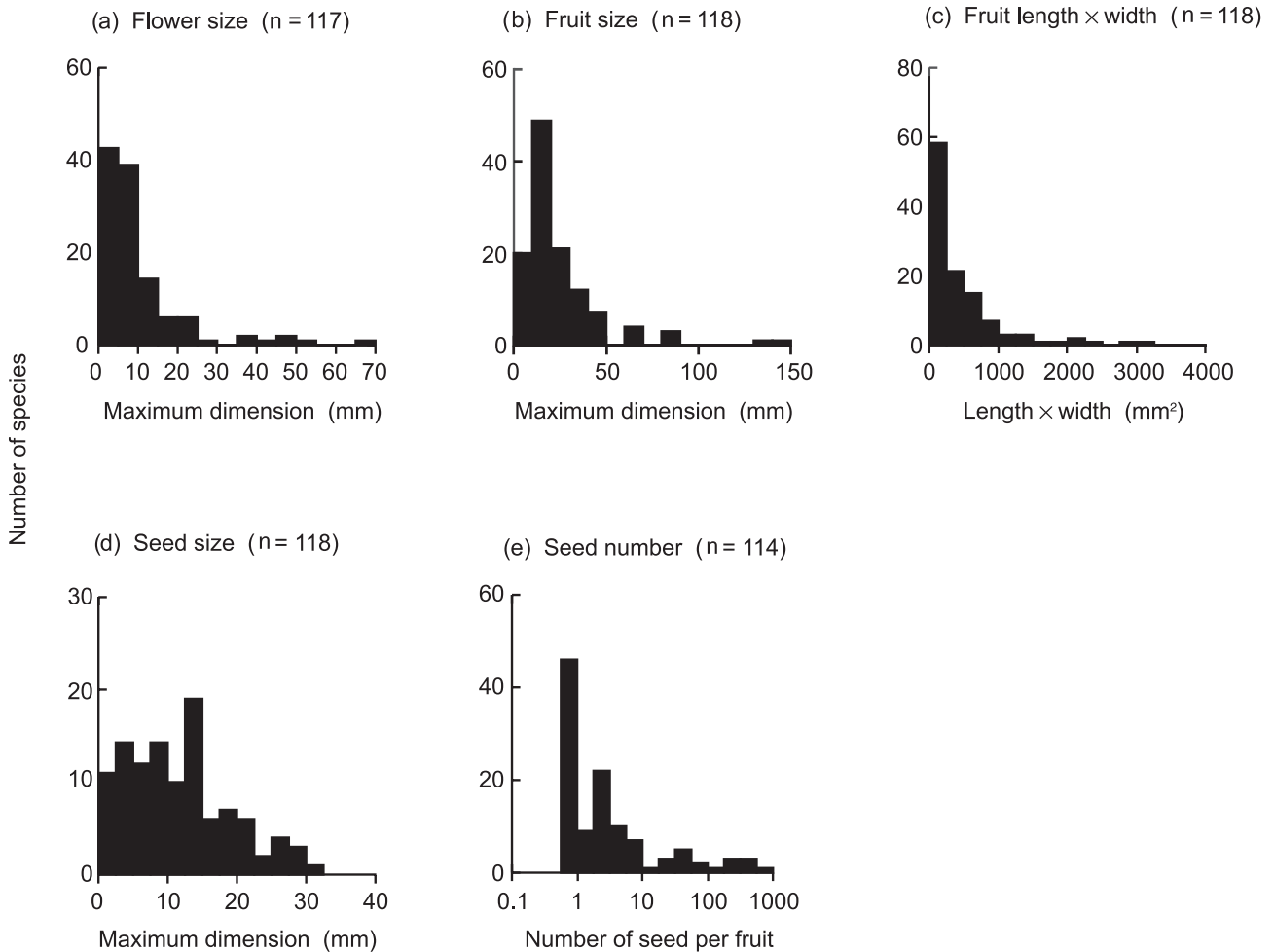


Figure 2. Frequency of species with respect to flower size (a), fruit size (b, c), seed size (d) and seed number per fruit (e).

± 1.0 mm ($n = 85$). The frequency distribution of the size of these fruits is shown in Figure 4.

About 59% of the 116 angiosperm species had figs, drupes or berries, 34% pods, follicles or capsules and the remaining 7% achenes, nuts and samaras or similar (Figure 3e). Appendages occurred on the fruits and/or seeds of about 41% of the 123 species, comprising 23% with wings or hairs and 18% with fleshy appendages (Figure 3f). Overall, 72% of species were considered to exhibit adaptations for dispersal by vertebrates (Figure 3g), being those with figs, drupes and berries, plus those which had seeds with fleshy appendages. Wind was regarded as the likely dispersal vector for 21% of species, with the remaining 7% dispersed by other processes (Figure 3g). Apart from the mostly brown dry fruits (39% of species), the most common colours were red (28%) and purple/black/blue (23%) (Figure 3h). Considering the combined fleshy and functionally fleshy fruits, for about 42% of species they were red, 31% purple/black/blue, 17% orange/yellow, 8% green/brown and 2% white. The fruits/seeds of about 90% of dioecious species were likely

to be biotically dispersed, compared with only 69% of non-dioecious species.

Seed traits

Species differed significantly in seed size ($F = 174$, $P < 0.001$). Seed size (Figure 2d) ranged from less than 2 mm in *Ficus* spp., *Cunonia* spp., *Pancheria sebertii*, *Codia discolor*, *Metrosideros dolichandra* and *Tristaniopsis reticulata* to over 25 mm in certain Sapotaceae and *Elaeocarpus* species, as well as *Diospyros macrocarpa*, *Semecarpus neocaledonica* and *Piliocalyx laurifolius*. Overall, mean seed size was 11.5 ± 0.7 mm ($n = 105$). Mean seed size of non-dioecious species (10.5 ± 0.8 mm, $n = 100$) was significantly less than that of dioecious species (13.2 ± 1.5 mm, $n = 18$) using both TIPs analysis ($t = 2.21$, $P = 0.035$) and PICs analysis ($t = 2.39$, $P = 0.038$).

The frequency distribution of the number of seeds per fruit is shown in Figure 2e. About 40% of species exhibited only one seed per fruit. Species with at least 50 seeds per fruit were *Ficus* spp., *Alstonia lenormandii*, *Gardenia*

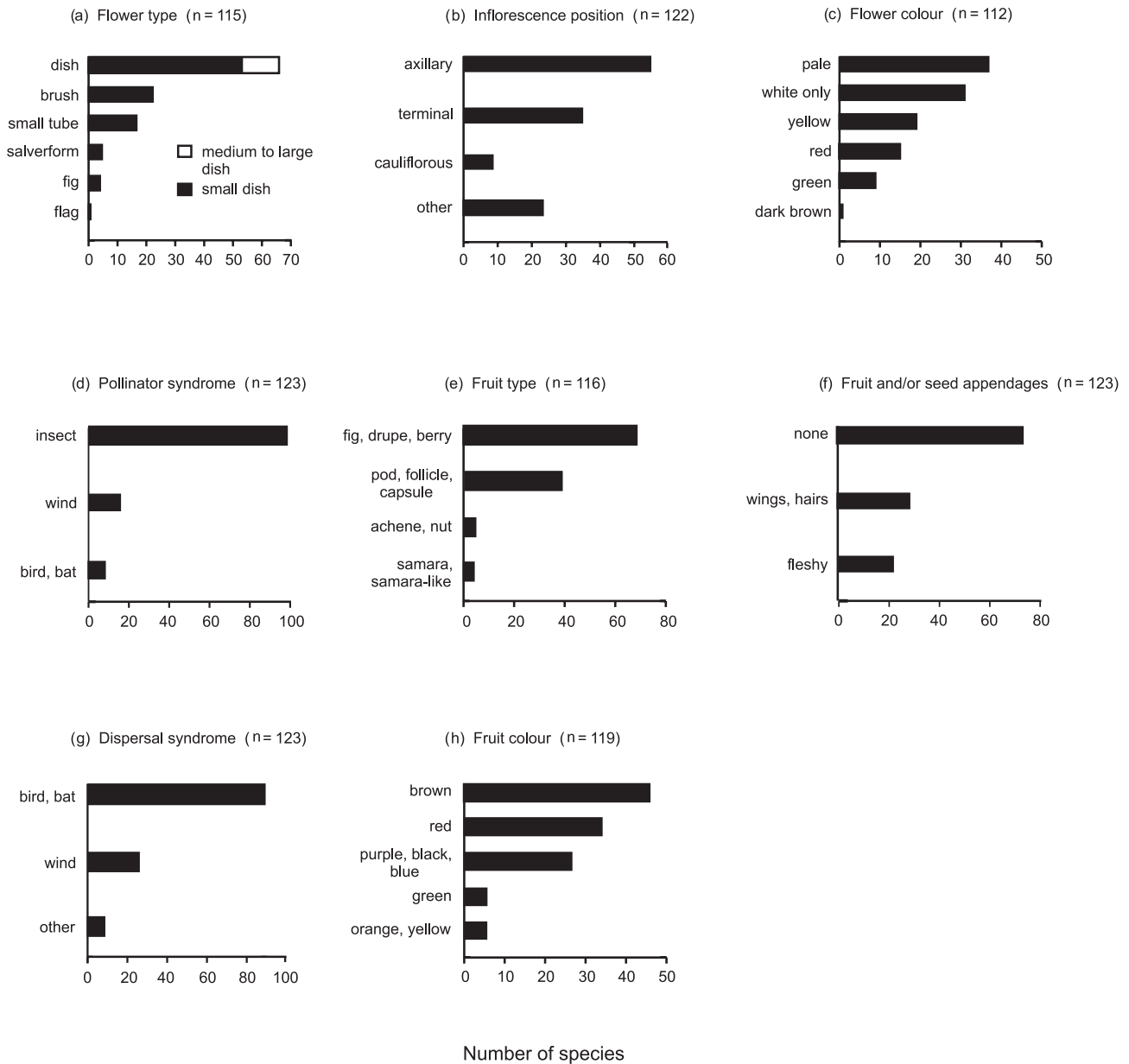


Figure 3. Frequency of species with respect to floral traits (a–d) and fruit and seed traits (e–h). The G-test indicated significant differences in species frequencies among categories for all character traits ($P < 0.05$).

aubryi, *Geissois hirsuta*, *Metrosideros dolichandra*, *Pancheria sebertii* and *Pleurocalyptus pancheri*. There was a significant difference in seed number per fruit among species ($F = 35.1$, $P < 0.001$). Particularly high variability within families in seed number per fruit was recorded in Apocynaceae (1– c. 400), Myrtaceae (1– c. 200) and Rubiaceae (8 and 500). The mean number of seeds per fruit for dioecious species was only 2.6 ± 0.5 ($n = 18$), considerably less than non-dioecious species, where it was 42.7 ± 14.4 ($n = 89$), although not significantly different using TIPs analysis ($t = 0.23$, $P = 0.82$) or PICs analysis ($t = 1.35$, $P = 0.21$). The main difference is that the dioecious species all had < 10 seeds per fruit.

Relationships between flowers, fruits and seeds

The Spearman correlation matrix is shown in Table 3. For the species for which data were available, a significant positive correlation existed between flower size and fruit size using TIPs analysis, but not PICs analysis, and between fruit size and seed size for both forms of analysis. Also, not unexpectedly, there was a very strong positive correlation between the two fruit size measures. There was a significant negative correlation between seed size and seed number per fruit using TIPs analysis, due to large seeds occurring only at low densities per fruit. No significant correlation was recorded using PICs analysis. Typical taxa with large, single seeds per fruit included

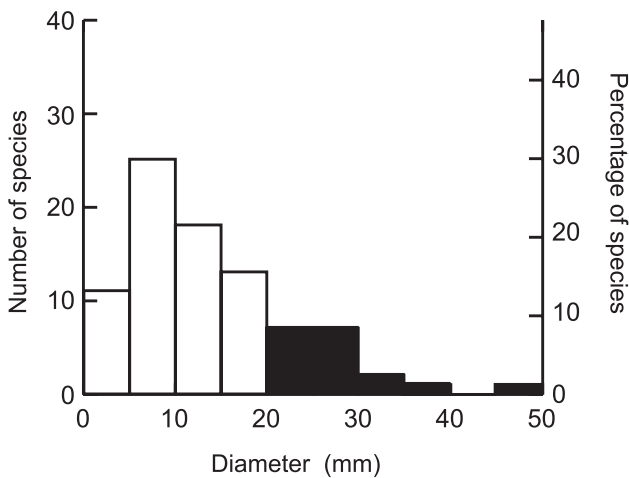


Figure 4. Size of functionally fleshy fruits (comprising figs, drupes, berries and seeds with colourful and/or fleshy appendages). The shaded bars indicate fruits of a size that could be eaten only by *Ducula goliath*.

Sapotaceae, *Elaeocarpus* spp. and Lauraceae, whilst typical taxa with multiple, small seeds per fruit included certain Cunoniaceae and capsular Myrtaceae.

DISCUSSION

Relationships between the quantitative aspects of the reproductive traits of New Caledonian trees generally supported previous predictions (Primack 1987) and observations elsewhere, although, as yet, there is a paucity of evidence obtained from analyses of tropical tree species using PICs. Similar correlations derived from the method of using taxonomic hierarchies have been found in other large data sets concerning rain-forest species from North Queensland (Osunkoya 1996) and Mexico (Ibarra-Manríquez & Oyama 1992). Thus, for instance, at the species and genus levels our data concur with Osunkoya (1996) that there are significant correlations between fruit size and seed and flower sizes, and at the species level a significant negative correlation between seed size and

seed number per fruit. However, our analysis demonstrated that of these, only the correlation between fruit size and seed size was evident when phylogenetic correction was applied. The proposal by Leishman (2001) that the trade-off between seed size and seed number holds true regardless of growth form or habitat may therefore not apply for tropical rain-forest trees. Clearly, however, generalizations concerning quantitative reproductive trait relationships among such species must await further studies. This will be explored in more detail in a subsequent paper dealing with light requirements and regeneration processes in New Caledonian rain forests.

Although data for comparisons are limited, there is evidence that there are some trends in the reproductive traits of rain-forest trees from New Caledonia that differ from elsewhere. For instance, the proportion of species with wind-dispersed propagules in our sample was 21%, with representatives from 12 families. By contrast, the available data shows that wind dispersal is rare in lowland rain-forest trees of North Queensland (Irvine & Armstrong 1990, Webb & Tracey 1981) and Costa Rica (Levey *et al.* 1994), although it does reach 16% for the large trees of Barro Colorado Island moist forest (Gentry 1982). The relatively high proportion of wind dispersal in New Caledonia may be related to nutrient-deficient soils and the low diversity of vertebrates. In particular, abiotically dispersed propagules require less energy for production than biotically dispersed ones, and more seeds can be produced per unit energy (see McKey 1975). Wind dispersal also tends to be more prevalent in regions of steep topography, such as are typical in the study region, and where more open forests occur. The upper canopy can be relatively open in *Nothofagus*-dominated rain forest in New Caledonia compared with rain forests elsewhere (Read & Hope 1996). The relative advantage of wind dispersal in New Caledonia is apparently expressed in the evolution of some unusual reproductive behaviours. Examples include *Araucaria* spp., which occur as towering canopy emergents, and two remarkable, endemic angiosperms, *Myodocarpus fraxinifolius* and *Cerberiopsis*

Table 3. Spearman rank correlations (r_s) of the continuous variables using TIPs analysis and PICs analysis. NSF, number of seeds per fruit. Asterisks indicate significant correlations (unadjusted for multiple comparisons): *, $0.01 \leq P < 0.05$; **, $0.001 \leq P < 0.01$; ***, $P < 0.001$. $n = 103$ for TIPs analysis; $n = 90$ contrasts for PICs analysis.

	FrMD	FLW	SMD	NSF
Flower maximum dimension (FMD)				
TIPs	0.27**	0.26**	0.13	0.14
PICs	-0.05	-0.10	-0.23	-0.04
Fruit maximum dimension (FrMD)				
TIPs		0.97***	0.69***	-0.03
PICs		0.96***	0.56***	0.11
Fruit length \times width (FLW)				
TIPs			0.69***	0.01
PICs			0.60***	0.01
Seed maximum dimension (SMD)				
TIPs				-0.54***
PICs				0.15

candelabra. *Myodocarpus* is novel among araliads for its dry, winged schizocarpic fruits (Plunkett & Lowry 2001), whilst *C. candelabra* is monocarpic and often occurs in populations that reproduce and die synchronously (Veillon 1971).

The proportion of species pollinated by wind also appears to be relatively high in New Caledonia, perhaps for similar reasons as for wind dispersal. In our sample it was around 13%. Future studies may demonstrate this proportion to be even higher, since many species in New Caledonia have the type of very small flowers that may in fact be wind-pollinated (Bullock 1994). By contrast, wind pollination is generally regarded to be rare in tropical lowland rain forest (Bawa 1990, Kress & Beach 1994), and ranges from only 0.3% to 7.9% in North Queensland (Irvine & Armstrong 1990).

There are also some interesting patterns regarding flower size and pollinators of New Caledonian rain-forest trees. Our sample was dominated by particularly small, actinomorphic (often dish-like), white or pale-coloured flowers. In Hawaii and New Zealand the predominance of similar unspecialized flowers has been partly attributed to an absence or scarcity of larger pollinating insects, notably long-tongued bees and large butterflies (Carlquist 1974, 1980; Lloyd 1985). The New Caledonian fauna appears to be similarly depauperate. For instance, Donovan (1983) recorded an absence of highly social bees, and of long-tongued, typically large-sized taxa, such as *Xylocopa*, *Amegilla* and Apidae. He concluded that a likely scenario is that bees are of little importance as pollinators in New Caledonia. This view is reinforced by reference to the lists of forest canopy arthropods collected by Guilbert (1997), who, for example, did not record a single representative of the bee superfamily Apoidea. By contrast, Kress & Beach (1994) concluded that as many as 60% of canopy and subcanopy tree species at La Selva, Costa Rica will prove to be bee-pollinated, predominantly by medium to large-sized, long-tongued species. Such bees have been associated with the relatively large, complex, often zygomorphic flowers that are common in the Neotropics (see review by Dafni *et al.* 1997). In a rain forest of Sarawak, South-East Asia, Momose *et al.* (1998) also found that bee pollination was the dominant syndrome, although larger, long-tongued species were not as important, particularly amongst canopy species. It is also interesting that long-tongued bees are poorly represented in the Australian tropics, where Irvine & Armstrong (1990) noted that small flowers that could only be utilized by micro-beetles, flies and thrips are very common. There is evidence that New Caledonian flowers are even smaller. Osunkoya (1996) used six size classes for North Queensland rain-forest flowers, so that the frequency distribution approached normality. Around 82% of our tree species fall into the first three of his classes (ranging up to only 16 mm), with the highest frequency being in the

second class (4–8 mm). Also, in New Caledonia, there are examples of very small-flowered endemic species from widely distributed genera, such as *Diospyros* (see White 1993).

Floral structures and nectar and pollen production also represent a significant energy cost to the plant, and there is evidence that small flowers are selected for when resources are limiting (Galen 1999). However, the fact that small flowers also predominate in Hawaii, where volcanic soils are presumably much more fertile than in New Caledonia, suggests that pollinators may have a greater influence on flower size than nutrient availability, although it would be of interest to investigate nectar quality and quantity. Also, although individual flowers may be very small, in many species they are aggregated into large, dense inflorescences (e.g. *Cerberiopsis*) that would be obvious to pollinators. In our sample, about 83% of species exhibited compound inflorescences, although it is not known how this compares to floras of other regions.

Overall, despite the apparent unimportance of bees, insect-pollinated species amounted to at least 81% of our sample. This is a similar figure to that recorded in rain forests of North Queensland (Irvine & Armstrong 1990) and Sarawak (Momose *et al.* 1998), and supports the notion that insect pollination is universally the dominant mode in tropical forests (Bawa 1990, Momose *et al.* 1998, Williams & Adam 1994). Also, more than a quarter of our species were known to have fragrant flowers, a trait probably related to attracting insects (Endress 1994). Only a few native bird species (see Hannecart & Letocart 1980) are likely to serve as effective pollinators. Notwithstanding this, the flowers of about 6% of the species may be bird pollinated, though it is unknown whether any are exclusively so. The proportions of species that are bird pollinated in Sarawak (Momose *et al.* 1998) and La Selva (Kress & Beach 1994) are very similar. These flowers usually include red coloration, sometimes combined with other bright colours. They are typically tubular or brush-like, robust, scentless and nectariferous (Endress 1994). Among our study species, they included a few Myrtaceae, *Geissois* spp. and probably *Deplanchea speciosa* and *Crossostylis grandiflora*. We found no evidence in the literature or herbarium collectors' notes for specialized bat-pollinated flowers. The most characteristic feature of such flowers is a powerful smell of fermented material (Endress 1994).

The phenological pattern for our sample showed an overall trend toward a concentration of flowering and fruiting in the late dry, and early wet seasons at the warmest time of the year. This conforms to that generally observed in the tropics, particularly where there is climatic seasonality (Borchert 1996, Bullock 1995, Floyd 1990, Newstrom *et al.* 1994, Richards 1996, van Schaik *et al.* 1993). However, even during the least favourable months of the year, around 40% of the New Caledonian

tree species were still recorded with mature flowers or fruits. This might be a consequence of marked irregularity in rainfall distribution and amount, which could be expected to lead to irregularity in flowering for certain species (Jaffré 1980). The development of ripe fruits at the beginning of the warm, wet season is likely to be adaptive in that germination and establishment can take place while water is plentiful (Osunkoya 1994, van Schaik *et al.* 1993). The first heavy rainfalls following a period of prolonged dry is also likely to be the principal cue for the initiation of flowering (Borchert 1996). Further, it has been suggested that the timing of flowering is linked to the increased abundance of potential pollinators at this time of year (Bawa *et al.* 1985). In the case of New Caledonia, there is little published entomological evidence with which to explore this hypothesis. However, the peak of large-flowered species we found in the cool season could be related to the energetic requirements of insects, particularly at higher altitudes. In cool conditions, it may be too cold for many small insects with high surface area to volume ratios to survive, and larger species have higher energy requirements than in warm conditions (Heinrich & Raven 1972). A scenario of lower overall insect diversity with a higher proportion of large insects would favour plants with larger, high-reward flowers (Cohen & Shmida 1993). Apart from the different trends for large vs. small flowers, there was no conclusive evidence for differences in pollination type, breeding system, seed size, fruit morphology or dispersal mode with respect to flowering or fruiting season. In New Caledonia, ripe fleshy fruits appear to be available for frugivores in all seasons of the year. Perhaps most notable are the three widespread *Diospyros* species examined in this study. Like the well-known example of figs, these might be regarded as keystone species (see Peres 2000). More detailed studies may shed further light on relationships between flowering periodicity, climate and soil fertility.

The 16% of tree species we recorded as being dioecious is similar to data from the floristically similar Manning Valley of New South Wales, where Williams & Adam (1994) found 18% of 142 rain-forest tree species to be dioecious. In addition, our finding that dioecious species tended to have few, large seeds per fruit and very small flowers, and to have biotic dispersal and abiotic pollination, is in accordance with the results of, for instance Bullock (1994), Ibarra-Manríquez & Oyama (1992) and Renner & Ricklefs (1995). We also confirmed the tendency for the female flowers to be solitary. This could be associated with wind pollination, and a high likelihood of fertilization without the need for investment in floral advertising. The incidence of dioecy has repeatedly been claimed to be disproportionately high on islands (Carlquist 1974, Lloyd 1985). However, it is clear that a remarkably similar proportion (around 20%) of subtropical to tropical tree species are dioecious, regardless of

rain-forest type and biogeographic history (Williams & Adam 1994; see also Bawa 1990, Ibarra-Manríquez & Oyama 1992, Kress & Beach 1994).

The preponderance of red and blue/purple/black fruits in our sample is undoubtedly a reflection of these colours being universally chosen by birds. The proportions of fruit colours appear to be similar to data from elsewhere in Australasia (Willson *et al.* 1989), but distinct from areas such as southern Africa, where there are higher proportions of green and brown fruits, a factor attributable to the importance of large mammals (Gautier-Hion *et al.* 1985, Knight & Siegfried 1983). The proportion of functionally fleshy fruits we recorded is similar to that observed in other tropical regions, and elsewhere in Australasia. For instance, it is almost identical to that of the rain forests of New South Wales and southern Queensland (Willson *et al.* 1989), and New Zealand (Clout & Hay 1989). Regarding the Neotropics, although some 90% of trees at La Selva produce fleshy fruits, most of these are only functionally fleshy, in being large, arillate seeds (Levey *et al.* 1994). Thus, this represents a contrast with New Caledonia (and elsewhere), where most are fleshy-walled figs, drupes and berries. The reasons for this are unclear, but may relate to different frugivore compositions.

Webb & Tracey (1981) and Willson *et al.* (1989) have used a fruit diameter of 2 cm as an upper threshold for effective dispersal by volant animals in Australia. In all, 16% of the New Caledonian tree species we examined had fleshy fruits (drupes, berries and figs) larger than this. We believe that although more research is required, effective dispersal of most of these species is probably dependent on the notou or giant pigeon, *Ducula goliath* G. R. Gray (see Figure 4). It seems that most New Caledonian fleshy fruits are not too large for consumption by these birds, since they eat the fruits of *Diospyros macrocarpa* (White 1993), which are about 2.6 cm in diameter. Of the species in our study, only *Piliocalyx laurifolius*, *Montrouzieria gabriellae* and *Gardenia aubryi* had fleshy fruits much larger than *D. macrocarpa*, and the latter two species have multiple-seeded soft fruits, which could be eaten piecemeal. *Ducula* species swallow fruit whole without the seeds being ground in the gizzard (Crome 1975), and can be very important seed dispersers over relatively large distances (Corlett 1998, Steadman 1997, Whitaker 1997). Other frugivorous birds in New Caledonia (see Hannecart & Letocart 1980) are much smaller and/or would destroy seeds in their gizzards. The relatively high diversity of smaller frugivorous birds (with small gape widths) in New Caledonia can also be related to the frequency distribution of fleshy-fruit diameters, where most species have fruits in the smallest third of the size range. Wheelwright (1985) obtained a similar distribution for fleshy fruits from Costa Rican rain forest. The only other animals in New Caledonia capable of effectively dispersing propagules are probably limited to mega-

chiropteran bats, and perhaps certain lizards. Long-distance dispersal via fruit bats can occur, but is probably mainly limited to that of small seeds (e.g. *Ficus*) by the larger species (Marshall 1985, Shilton *et al.* 1999). However, the feeding behaviour, which usually involves the voiding of solids near the source plants, could be important for the local dispersal and germination of such taxa as Sapotaceae and Myrtaceae (see Banack 1999).

The evidently important role of the notou is perhaps paralleled in New Zealand, where Clout & Hay (1989) stressed the precarious situation for the larger-fruited tree species, since their seed dispersal depends almost entirely on the New Zealand pigeon (*Hemiphaga novaeseelandiae* Gmelin). The situation in New Caledonia is precarious since the 1996 IUCN Red List of Threatened Animals lists *Ducula goliath* as vulnerable. This species is apparently largely restricted to upland forests where it is in decline as a result of hunting. It is also likely that the fragmentation of rain-forest into small patches is highly deleterious for *D. goliath* populations, as it evidently is for *D. bicolor* Scopoli in the monsoon tropics of Australia (Price *et al.* 1999).

The Holocene fossil record offers evidence for the past occurrence of very large frugivorous birds and reptiles in New Caledonia (see Balouet 1991, Balouet & Olson 1989), that could easily have consumed fruits of all the species in our sample. Also, at least one extant plant species, *Strasburgeria robusta*, has fruits which are reminiscent of the type now consumed and dispersed by large mammals, as described by for instance Gautier-Hion *et al.* (1985). Its fruits are very large (over 60 mm wide), indehiscent, green, fibrous, have very hard-coated seeds (Dickison 1981), and smell of apples. Although there are as yet no fossil records of non-volant New Caledonian mammals, perhaps this species had a mammalian disperser that became extinct (see Janzen & Martin 1982). If there has been relatively recent extinction (or at least decline) of potential dispersers, it would be expected that plant species which depend on these will have unusually low colonization of new areas, as has been observed on La Reunion by Thébaud & Strasberg (1997), and in the Philippines by Hamann & Curio (1999). Current rain-forest dynamics research (Read, Jaffré, unpubl. data) in New Caledonia will provide further evidence with which to evaluate dispersal success. New Caledonia also has a complement of introduced vertebrates (Gargominy *et al.* 1996) that are undoubtedly affecting plant regeneration through consumption of fruits, seeds, and seedlings, or predation on native creatures. The effects of forest fragmentation and the introduction of exotic species on pollination processes also require investigation.

ACKNOWLEDGEMENTS

This study could not have been done without the contributions of plant collectors to the IRD herbarium in Nouméa.

We thank the IRD for continued support, particularly the herbarium staff. Gordon Sanson provided invaluable assistance with the CAIC analysis. This study was supported by an Australian Research Council Small Grant.

LITERATURE CITED

- BALOUET, J. C. 1991. The fossil vertebrate record of New Caledonia. Pp. 1383–1409 in Vickers-Rich, P., Monaghan, J. M., Baird, R. F. & Rich, T. H. (eds). *Vertebrate palaeontology of Australasia*. Pioneer Design Studio/Monash University Publications Committee, Melbourne.
- BALOUET, J. C. & OLSON, S. L. 1989. Fossil birds from late Quaternary deposits in New Caledonia. *Smithsonian Contributions to Zoology* 469:1–38.
- BANACK, S. A. 1999. Diet selection and resource use by flying foxes (genus *Pteropus*). *Ecology* 79:1949–1967.
- BAWA, K. S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21:399–422.
- BAWA, K. S., BULLOCK, S. H., PERRY, D. R., COVILLE, R. E. & GRAYUM, M. H. 1985. Reproductive biology of tropical lowland rain forest trees. II. Pollination systems. *American Journal of Botany* 72:346–356.
- BICKEL, D. J. 1999. *Antyx* (Diptera) in eastern Australia and New Caledonia. *Australian Journal of Entomology* 38:168–175.
- BORCHERT, R. 1996. Phenology and flowering periodicity of Neotropical dry forest species: evidence from herbarium collections. *Journal of Tropical Ecology* 12:65–80.
- BRADFORD, J. C. & BARNES, R. W. 2001. Phylogenetics and classification of Cunoniaceae (Oxalidales) using chloroplast DNA sequences and morphology. *Systematic Botany* 26:354–385.
- BROOKS, R. R. 1987. *Serpentine and its vegetation*. Dioscorides Press, Portland. 454 pp.
- BULLOCK, S. H. 1994. Wind pollination of Neotropical dioecious trees. *Biotropica* 26:172–179.
- BULLOCK, S. H. 1995. Plant reproduction in neotropical dry forests. Pp. 277–303 in Bullock, S. H., Mooney, H. A. & Medina, E. (eds). *Seasonally dry tropical forests*. Cambridge University Press, Cambridge.
- CARLQUIST, S. 1974. *Island biology*. Columbia University Press, New York. 660 pp.
- CARLQUIST, S. 1980. *Hawaii. A natural history*. Pacific Tropical Botanical Garden, Hawaii. 463 pp.
- CHAZEAU, J. 1993. Research on New Caledonian terrestrial fauna: achievements and prospects. *Biodiversity Letters* 1:123–129.
- CLOUT, M. N. & HAY, J. R. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. *New Zealand Journal of Ecology* 12 (suppl.):27–33.
- COHEN, D. & SHMIDA, A. 1993. The evolution of floral display and reward. *Evolutionary Biology* 27:197–244.
- CONRAN, J. G., WOOD, G. M., MARTIN, P. G., DOWD, J. M., QUINN, C. J., GADEK, P. A. & PRICE, R. A. 2000. Generic relationships within and between the gymnosperm families Podocarpaceae and Phyllocladaceae based on an analysis of the chloroplast gene *rbcl*. *Australian Journal of Botany* 48:715–724.

- CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73:413–448.
- CROME, F. H. J. 1975. The ecology of fruit pigeons in tropical northern Queensland. *Australian Wildlife Research* 2:155–185.
- DAFNI, A., LEHRER, M. & KEVAN, P. G. 1997. Spatial flower parameters and insect spatial vision. *Biological Reviews* 72:239–282.
- DE LAUBENFELS, D. J. 1972. Gymnospermes. In Aubréville, A. (ed.). *Flore de la Nouvelle-Calédonie et Dépendances* 4. Muséum National d'Histoire Naturelle, Paris. 167 pp.
- DIAMOND, J. 1984. Biogeographic mosaics in the Pacific. Pp. 1–13 in Radovsky, F. J., Raven, P. H. & Sohmer, S. H. (eds). *Biogeography of the tropical Pacific*. Bishop Museum Special Publication 72.
- DICKISON, W. C. 1981. Contributions to the morphology and anatomy of *Strasburgeria* and a discussion of the taxonomic position of the Strasburgeriaceae. *Brittonia* 33:564–580.
- DONOVAN, B. J. 1983. Comparative biogeography of native Apoidea of New Zealand and New Caledonia. *GeoJournal* 7:511–516.
- ENDRESS, P. K. 1994. *Diversity and evolutionary biology of tropical flowers*. Cambridge University Press, Cambridge. 511 pp.
- FAEGRI, K. & VAN DER PIJL, L. 1979. *Principles of pollination ecology*. (Third edition). Pergamon Press, Oxford. 244 pp.
- FLOYD, A. G. 1990. *Australian rainforests in New South Wales*. Vol. 1. Surrey Beatty, Sydney. 136 pp.
- FOSTER, S. A. 1986. On the adaptive value of large seeds for tropical moist forest trees: review and synthesis. *Botanical Review* 52:260–299.
- GADEK, P. A., FERNANDO, E. S., QUINN, C. J., HOOT, S. B., TERRAZAS, T., SHEAHAN, M. C. & CHASE, M. W. 1996. Sapindales: molecular delimitation and infraordinal groups. *American Journal of Botany* 83:802–811.
- GALEN, C. 1999. Why do flowers vary? *Bioscience* 49:631–640.
- GARGOMINY, O., BOUCHET, P., PASCAL, M., JAFFRÉ, T. & TOURNEUR, J. C. 1996. Consequences for biodiversity of plant and animal species introductions in New Caledonia. *Revue d'Ecologie (Terre et Vie)* 51:375–402.
- GAUTIER-HION, A., DUPLANTIER, J.-M., QURIS, R., FEER, F., SOURD, C., DECOUX, J.-P., DUBOST, G., EMMONS, L., ERARD, C., HECKETSWEILER, P., MOUNGAZI, A., ROUSSILHON, C. & THIOLLAY, J.-M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65:324–337.
- GENTRY, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15:1–84.
- GRUBB, P. J. 1996. Rainforest dynamics: the need for new paradigms. Pp. 215–233 in Edwards, D. S., Booth, W. E. & Choy, S. C. (eds). *Tropical rainforest research: current issues*. Kluwer, Dordrecht.
- GRUBB, P. J. 1998. Seeds and fruits of tropical rainforest plants: interpretation of the range in seed size, degree of defence and flesh/seed quotients. Pp. 1–24 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds). *Dynamics of tropical communities*. Blackwell, Oxford.
- GRUBB, P. J. & METCALFE, D. J. 1996. Adaptation and inertia in the Australian tropical lowland rain-forest flora: contradictory trends in intergeneric and intrageneric comparisons of seed size in relation to light demand. *Functional Ecology* 10:512–520.
- GUILBERT, E. 1997. Arthropod biodiversity in the canopy of New Caledonian forests. Pp. 265–277 in Stork, N. E., Adis, J. & Didham, R. K. (eds). *Canopy arthropods*. Chapman & Hall, London.
- HAMANN, A. & CURIO, E. 1999. Interactions among frugivores and fleshy fruit trees in a Philippine submontane rainforest. *Conservation Biology* 13:766–773.
- HAMMOND, D. S. & BROWN, V. K. 1995. Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forests. *Ecology* 76:2544–2561.
- HANNECART, F. & LETOCART, Y. 1980. *New Caledonian birds*. Vol. 1. Les Editions Cardinalis, Nouméa. 150 pp.
- HARMS, K. E. & DALLING, J. W. 1997. Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology* 13:617–621.
- HEINRICH, B. & RAVEN, P. H. 1972. Energetics and pollination ecology. *Science* 176:597–602.
- HERZER, R. H., CHAPRONIERE, G. C. H., EDWARDS, A. R., HOLLIS, C. J., PELLETIER, B., RAINE, J. I., SCOTT, G. H., STAGPOOLE, V., STRONG, C. P., SYMONDS, P., WILSON, G. J. & ZHU, H. 1997. Seismic stratigraphy and structural history of the Reinga Basin and its margins, southern Norfolk Ridge system. *New Zealand Journal of Geology and Geophysics* 40:425–451.
- HILL, R. S. & CARPENTER, R. J. 1991. Evolution of *Acmopyle* and *Dacrycarpus* (Podocarpaceae) foliage as inferred from macrofossils in south-eastern Australia. *Australian Systematic Botany* 4:449–479.
- HOLLOWAY, J. D. 1979. *A survey of the Lepidoptera, biogeography and ecology of New Caledonia*. *Series Entomologica* 15. Dr W. Junk, The Hague. 588 pp.
- HOPE, G. S. & PASK, J. 1998. Tropical vegetational change in the late Pleistocene of New Caledonia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 142:1–21.
- IBARRA-MANRÍQUEZ, G. & OYAMA, K. 1992. Ecological correlates of reproductive traits of Mexican rain forest trees. *American Journal of Botany* 79:383–394.
- IRVINE, A. K. & ARMSTRONG, J. E. 1990. Beetle pollination in tropical forests of Australia. Pp. 135–148 in Bawa, K. S. & Hadley, M. (eds). *Reproductive ecology of tropical forest plants*. Unesco, Parthenon, Carnforth.
- JAFFRÉ, T. 1980. *Etude écologique du peuplement végétal des sols dérivés de roches ultrabasiqes en Nouvelle-Calédonie*. Collection Travaux et Documents de l'ORSTOM no. 124, ORSTOM, Paris. 273 pp.
- JAFFRÉ, T. 1992. Floristic and ecological diversity of the vegetation on ultramafic rocks in New Caledonia. Pp. 101–107 in Baker, A. J. M., Proctor, J. & Reeves, R. D. (eds). *The vegetation of ultramafic (serpentine) soils*. Intercept Ltd, Andover.
- JAFFRÉ, T. & VEILLON, J.-M. 1991. Etude floristique et structurale de deux forêts denses humides sur roches ultrabasiqes en Nouvelle-Calédonie. *Adansonia ser.* 4 12: 243–273.
- JAFFRÉ, T., MORAT, P., VEILLON, J.-M., RIGAUD, F. & DAGOSTINI, G. 2001. *Composition et caractéristiques de la flore indigène de la Nouvelle-Calédonie*. Document Scientifique et Technique II 4. IRD, Nouméa. 121 pp.
- JANZEN, D. H. & MARTIN, P. S. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215:19–27.
- JORDANO, P. 1995. Angiosperm fleshy fruits and seed dispersers: a

- comparative analysis of adaptation and constraints in plant-animal interactions. *American Naturalist* 145:163–191.
- KÅREHED, J. 2001. Multiple origin of the tropical forest tree family Icacinaceae. *American Journal of Botany* 88:2259–2274.
- KNIGHT, R. S. & SIEGFRIED, W. R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia* 56:405–412.
- KRESS, W. J. & BEACH, J. H. 1994. Flowering plant reproductive systems. Pp. 161–176 in McDade, L. A., Bawa, K. S., Hespeneheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a tropical rainforest*. University of Chicago Press, Chicago.
- LEISHMAN, M. R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93:294–302.
- LEVEY, D. L., MOERMOND, T. C. & DENSLow, J. S. 1994. Frugivory: an overview. Pp. 282–294 in McDade, L. A., Bawa, K. S., Hespeneheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a tropical rainforest*. University of Chicago Press, Chicago.
- LLOYD, D. G. 1985. Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany* 23:707–722.
- MACK, A. L. 1993. The sizes of vertebrate-dispersed fruits: a neotropical-paleotropical comparison. *American Naturalist* 142:840–856.
- MARSHALL, A. G. 1985. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zoological Journal of the Linnean Society* 83:351–369.
- MCCOY, S., JAFFRÉ, T., RIGAUULT, F. & ASH, J. E. 1999. Fire and succession in the ultramafic maquis of New Caledonia. *Journal of Biogeography* 26:579–594.
- McKEY, D. 1975. The ecology of coevolved seed dispersal systems. Pp. 159–191 in Gilbert, L. E. & Raven, P. H. (eds). *Coevolution of animals and plants*. University of Texas Press, Austin.
- METCALFE, D. J. & GRUBB, P. J. 1997. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forest in Singapore. *Functional Ecology* 11:215–221.
- MOMOSE, K., YUMOTO, T., NAGAMITSU, T., KATO, M., NAGAMASU, H., SAKAI, S., HARRISON, R. D., ITIOKA, T., HAMID, A. A. & INOUE, T. 1998. Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. *American Journal of Botany* 85:1477–1501.
- MORAT, P. 1993. Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. *Biodiversity Letters* 1:72–81.
- MYERS, N. 1988. Threatened biotas: 'hotspots' in tropical forests. *The Environmentalist* 8:1–20.
- NANDI, O. I., CHASE, M. W. & ENDRESS, P. K. 1998. A combined cladistic analysis of angiosperms using *rbcL* and non-molecular data sets. *Annals of the Missouri Botanical Garden* 85:137–212.
- NEWSTROM, L. E., FRANKIE, G. W., BAKER, H. G. & COLWELL, R. K. 1994. Diversity of long-term flowering patterns. Pp. 142–177 in McDade, L. A., Bawa, K. S., Hespeneheide, H. A. & Hartshorn, G. S. (eds). *La Selva: ecology and natural history of a tropical rainforest*. University of Chicago Press, Chicago.
- OSUNKOYA, O. O. 1994. Postdispersal survivorship of north Queensland rainforest seeds and fruits: effects of forest, habitat and species. *Australian Journal of Ecology* 19:52–64.
- OSUNKOYA, O. O. 1996. Light requirements for regeneration in tropical forest plants: taxon-level and ecological attribute effects. *Australian Journal of Ecology* 21:429–441.
- PERES, C. A. 2000. Identifying keystone plant resources in tropical forests: the case of gums from *Parkia* pods. *Journal of Tropical Ecology* 16:287–317.
- PLUNKETT, G. M. & LOWRY, P. P. 2001. Relationships among "ancient araliads" and their significance for the systematics of Apiales. *Molecular Phylogenetics and Evolution* 19:259–276.
- PRICE, O. F., WOINARSKI, J. C. Z. & ROBINSON, D. 1999. Very large area requirements for frugivorous birds in monsoon rainforests of the Northern Territory, Australia. *Biological Conservation* 91:169–180.
- PRIMACK, R. B. 1987. Relationships among flowers, fruits, and seeds. *Annual Review of Ecology and Systematics* 18:409–430.
- PURVIS, A. & RAMBAUT, A. 1995. Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in the Biosciences* 11:247–251.
- READ, J. & HOPE, G. S. 1996. Ecology of *Nothofagus* forests of New Guinea and New Caledonia. Pp. 200–256 in Veblen, T. T., Hill, R. S. & Read, J. (eds). *The ecology and biogeography of Nothofagus forests*. Yale University Press, New Haven.
- READ, J., HALLAM, P. & CHERRIER, J.-F. 1995. The anomaly of monodominant tropical rainforests: some preliminary observations in the *Nothofagus*-dominated rainforests of New Caledonia. *Journal of Tropical Ecology* 11:359–389.
- READ, J., JAFFRÉ, T., GODRIE, E., HOPE, G. S. & VEILLON, J.-M. 2000. Structural and floristic characteristics of some monodominant and adjacent mixed rainforests in New Caledonia. *Journal of Biogeography* 27:233–250.
- RENNER, S. S. & RICKLEFS, R. E. 1995. Dioecy and its correlates in the flowering plants. *American Journal of Botany* 82:596–606.
- RICHARDS, P. W. 1996. *The tropical rainforest*. (Second edition). Cambridge University Press, Cambridge. 575 pp.
- SCHWARZBACH, A. E. & RICKLEFS, R. E. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. *American Journal of Botany* 87:547–564.
- SETOGUCHI, H., OSAWA, T. A., PINTAUD, J.-C., JAFFRÉ, T. & VEILLON, J.-M. 1998. Phylogenetic relationships within Araucariaceae based on *rbcL* gene sequences. *American Journal of Botany* 85:1507–1516.
- SHILTON, L. A., ALTRINGHAM, J. D., COMPTON, S. G. & WHITAKER, R. J. 1999. Old World fruit bats can be long-distance seed dispersers through extended retention of viable seeds in the gut. *Proceedings of the Royal Society of London: Biological Sciences* 266: 219–223.
- STEADMAN, D. W. 1997. The historic biogeography and community ecology of Polynesian pigeons and doves. *Journal of Biogeography* 24:737–753.

- STEWART-OATEN, A. 1995. Rules and judgments in statistics: three examples. *Ecology* 76:2001–2009.
- THÉBAUD, C. & STRASBERG, D. 1997. Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene Archipelago. Pp. 321–332 in Laurance, W. F. & Bierregaard, R. O. (eds). *Tropical forest remnants*. University of Chicago Press, Chicago.
- VAN DER PIJL, L. 1982. *Principles of dispersal in higher plants*. (Third edition). Springer-Verlag, Berlin. 214 pp.
- VAN SCHAIK, C. P., TERBORGH, J. W. & WRIGHT, S. J. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- VEILLON, J.-M. 1971. Une Apocynacée monocarpique de Nouvelle-Calédonie *Cerberiopsis candelabrum* Vieill. *Adansonia*, ser. 2 11:625–639.
- VEILLON, J.-M. 1993. Protection of floristic diversity in New Caledonia. *Biodiversity Letters* 1:88–91.
- WEBB, L. J. & TRACEY, J. G. 1981. Australian rainforests: patterns and change. Pp. 607–694 in Keast, A. (ed.). *Ecological biogeography of Australia*. Vol. 1. Dr W. Junk, The Hague.
- WHEELWRIGHT, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. *Ecology* 66:808–818.
- WHITAKER, R. J. 1997. The rebuilding of an isolated rainforest assemblage: how disharmonic is the flora of Krakatau? *Biodiversity and Conservation* 6:1671–1696.
- WHITE, F. 1993. Ébénacées. Pp. 3–89 in Aubréville, A. & Leroy, J.-F. (eds). *Flore de la Nouvelle-Calédonie et Dépendances* 19. Muséum National d'Histoire Naturelle, Paris.
- WILFORD, G. E. & BROWN, P. J. 1994. Maps of late Mesozoic-Cenozoic Gondwana break-up: some palaeogeographical implications. Pp. 5–13 in Hill, R. S. (ed.). *History of the Australian vegetation: Cretaceous to Recent*. Cambridge University Press, Cambridge.
- WILLIAMS, G. & ADAM, P. 1994. A review of rainforest pollination and plant-pollinator interactions with particular reference to Australian subtropical rainforests. *Australian Zoologist* 29:177–212.
- WILLSON, M. F., IRVINE, A. K. & WALSH, N. G. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21:133–147.
- WILSON, P. G., O'BRIEN, M. M., GADEK, P. A. & QUINN, C. J. 2001. Myrtaceae revisited: a reassessment of infrafamilial groups. *American Journal of Botany* 88:2013–2025.
- WRIGHT, S. J. & CALDERON, O. 1995. Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology* 83:937–948.

Appendix 1. Species used in this study. Nomenclature follows Jaffré *et al.* (2001).

GYMNOSPERMS

Araucariaceae

Agathis lanceolata
Agathis ovata
Araucaria subulata

Podocarpaceae

Acmopyle pancheri
Falcatifolium taxoides
Podocarpus lucienii
Retrophyllum comptonii

ANGIOSPERMS

Anacardiaceae

Euroschinus verrucosus
Euroschinus rubromarginatus
Semecarpus neocaledonica

Apocynaceae

Alstonia lenormandii
Cerberiopsis candelabra var. *candelabra*
Pagiantha cerifera

Araliaceae

Arthrophyllum otopyrenum
*Myodocarpus fraxinifolius*¹
Schefflera sp. (group *Caracoschefflera*)
Schefflera sp. (group *Gabriellae*)

Atherospermataceae

Nemuaron vieillardii

Balanopaceae

Balanops pachyphylla
Balanops vieillardii

Bignoniaceae

Deplanchea speciosa

Burseraceae

Canarium oleiferum

Caesalpiniaceae

Storckiella pancheri

Casuarinaceae

Gymnostoma deplancheanum
Gymnostoma intermedium

Chrysobalanaceae

Hunga rhamnoides

Clusiaceae

Calophyllum caledonicum
Garcinia balansae
Garcinia neglecta
Montrouzieria gabriellae

Cunoniaceae

Codia discolor
Cunonia balansae
Cunonia montana
Geissois hirsuta
Geissois montana
Geissois velutina
Pancheria sebertii

Dilleniaceae

Hibbertia lucens
Hibbertia pancheri

Ebenaceae

Diospyros macrocarpa
Diospyros olen
Diospyros parviflora

Elaeocarpaceae

Elaeocarpus castanaefolius

Elaeocarpus speciosus
Elaeocarpus weibelianus
Elaeocarpus yateensis
Sloanea haplopoda

Epacridaceae
Styphelia pancheri

Euphorbiaceae
Austrobuxus pauciflorus
Austrobuxus rubiginosus
Cleistanthus stipitatus
Macaranga alchorneoides
Neoguillauminia cleopatra

Fagaceae
Nothofagus aequilateralis
Nothofagus balansae
Nothofagus codonandra
Nothofagus discoidea

Flindersiaceae
Flindersia fourneri

Icacinaceae
Apodytes clusiifolia
*Gastrolepia austrocaledonica*¹

Lauraceae
Cryptocarya guillauminii
Cryptocarya mackeei
Cryptocarya odorata
Cryptocarya transversa
Endiandra sebertii

Meliaceae
Dysoxylum minutiflorum
Dysoxylum roseum

Mimosaceae
Archidendropsis granulosa

Monimiaceae
Hedycarya parvifolia

Moraceae
Ficus asperula
Ficus austrocaledonica
Ficus nitidifolia
Ficus vieillardiana
Sparattosyce dioica

Myrtaceae
Arillastrum gummiferum
Austromyrtus vieillardii
Eugenia paludosa
Metrosideros dolichandra
Ptilocalyx laurifolius
Pleurocalyptus pancheri
Rhodamnia andromedoides
Stereocaryum rubiginosum
Syzygium austrocaledonicum

Syzygium baladense
Syzygium macranthum
Syzygium multipetalum
Tristaniopsis reticulata
Xanthomyrtus hienghenensis
Xanthostemon ruber

Oleaceae
Chionanthus brachystachys
Osmanthus austrocaledonicus subsp. *collinus*

Proteaceae
Beauprea asplenioides
Beauprea filipes
Stenocarpus trinervis

Rhamnaceae
Alphitonia neocaledonica
Alphitonia xerocarpa

Rhizophoraceae
Crossostylis grandiflora

Rubiaceae
Gardenia aubryi
Guettarda eximia
Guettarda trimera

Sapindaceae
Arytera lepidota
Cupaniopsis oedipoda
Elattostachys apetala
Gongrodiscus bilocularis
Guioa villosa
Storthocalyx chryseus
Storthocalyx pancheri

Sapotaceae
Beccariella sebertii
Bureavella endlicheri
Bureavella wakere
Niemeyera balansae
Ochrothallus gordoniaefolius
Ochrothallus multipetalus
Ochrothallus sessilifolius
Planchonella kuebiniensis
Planchonella thiensis
Pycnandra fastuosa
Sebertia acuminata

Sphenostemonaceae
Sphenostemon pachycladus

Sterculiaceae
Acropogon austro-caledonicus
Acropogon dzumacensis

Strasburgeriaceae
Strasburgeria robusta

Winteraceae
Zygogynum pancheri ssp. *pancheri*

¹ For phylogenetic corrections, *Myodocarpus fraxinifolius* was placed in its own family, Myodocarpaceae (Plunkett & Lowry 2001), and *Gastrolepia austrocaledonica* was placed in Stemonuraceae (Kårehed 2001).

