# Dry zone forests of Fiji: species composition, life history traits, and conservation

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Abstract Species composition and life history traits of trees in native forests in the dry zone of Fiji were investigated. Areas receiving less than 2500 mm yr<sup>-1</sup> of rain and covered with native forest

were identified using maps, aerial photographs, estimated climate (WorldClim) and field reconaissance.

4 Ten forest remnants were identified and species lists and data on natural history, and disturbance were

compiled. Cluster analysis and DECORANA identified two principal forest types, moist forest (MF)

and tropical dry forest (TDF), each defined by unique climate, species composition, and tree life history

characteristics. TDF (reported for the first time from Fiji) has a pronounced dry season (5 months with

< 100mm rainfall each) and several deciduous canopy species. MF lack a pronounced dry season and

have few deciduous species. The amount and variability of rainfall seem to influence the type of forest

in a particular location and disturbance is negatively correlated with precipitation. TDF are probably

Fiji's most endangered ecosystems.

14 **Keywords** climate; deciduous; mesic forest; moist forest; natural history; sclerophyll; talasiga

15 grasslands; tropical dry forest

#### INTRODUCTION

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Tropical forests may occur in a broad scale of climatic conditions, ranging from high to low precipitation and no to strong seasonality. Many different schemes to classify these forests have been proposed (Beard 1955; Webb 1959; Holdridge 1971; Gagné & Cuddihy 1990). Here we use the following definitions for the different types of tropical forest. Tropical dry forest (TDF) are at least partially deciduous and have an annual rainfall from 500 to 2000 mm with a dry season of several months of rainfall near or below 60 mm (Mooney et al. 1998). Tropical rain forests are evergreen, have

- few sclerophyllous leaves, and have an annual rainfall of more than 2000 mm with no dry periods
- 2 (more than one month with an average rainfall of less than 100 mm) (Walsh 1996). Sclerophyllous
- 3 leaves are tough and can resist drought and insect attack through thick cell walls and relatively low
- 4 nitrogen content (Eamus 1999). The term moist forest (MF, after Holdridge 1971) is used for evergreen
- 5 forests with a strong sclerophyllous component and an annual rainfall of more than 1700 mm with a
- dry period of up to 4 months and, hence, corresponding to the evergreen seasonal rain forest of Walsh
- 7 (1996).
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- 9 Tropical dry forests (TDF) have a more or less closed and deciduous canopy that is lower and less
- complex than in lowland tropical rainforests. Species diversity and biomass are also lower and lianas
- may be common (Murphy & Lugo 1986; Martínez-Yrízar 1998; Menaut et al. 1998). Clumping of tree
- species is a common phenomenon (Hubbell 1979), as has been found in some rainforest trees (Chave et
- al. 2003; Hardy & Sonke 2004; Svenning et al. 2004).
- On a global scale, TDF is probably the most endangered tropical forest type but has relatively little
- protection. This threat is the result of centuries of logging, burning, farming, and grazing. Currently
- only small fragments of dry forests remain and the existence of pristine patches is very unlikely (Janzen
- 18 1988; Lerdau et al. 1991; Trejo & Dirzo 2000). The situation is similar in the insular Pacific where
- protection is generally inadequate or non-existent (Gillespie & Jaffré 2003) and dry zone ecosystems
- are extremely vulnerable (Rolett & Diamond 2004).
- The Fiji archipelago includes about 500 named islands, between 177°W to 177°E and 15° to 22°S in
- 23 the subtropical Pacific Ocean. The two largest islands are relatively high (to 1323 m) and large (10388
- 24 km<sup>2</sup>) (Fig. 1) and intercept the prevailing south-east tradewinds, creating rain shadows on the leeward
- side. As a result, a great variety of rainfall regimes exist in Fiji, ranging from about 1800 mm in the

- coastal regions of the western sides to 3000 mm and more on the south-eastern side (Mataki et al.
- 2 2006). The wet, windward, south-eastern sides are covered with rainforest, while most of the dry,
- 3 leeward, western sites are presently covered with grasslands, called "talasiga" ("sunburnt land") in the
- 4 native vernacular, and small forest remnants (Parham 1972; Mueller-Dombois & Fosberg 1998). On
- 5 the drier, leeward side droughts regularly occur. Mean annual rainfall is lowest in the coastal regions
- and increases inland (Mataki et al. 2006).

- 8 Palynological evidence suggests that, before the arrival of people some 3000 years ago, much of the
- 9 present day talasiga grasslands on Fiji's largest island, Viti Levu, was covered with forests. Herbaceous
- vegetation composed of grasses, sedges, and ferns may, however, have occurred in some of the driest
- places, especially during glacial periods (Southern 1986). The present persistence of fire-resistant
- species, such as *Cycas seemannii*, in some talasiga grasslands attests to the original woody vegetation
- 13 (Keppel 2002).

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- Rain forest and "dry forest" have been reported to occur in Fiji's lowlands (Mueller-Dombois &
- Fosberg 1998). However, the reported "dry forest" is evergreen and dominated by the conifer
- 17 Dacrydium nidulum and the angiosperm Fagraea gracilepes, with Gymnostoma vitiensis, Myristica
- 18 castaneifolia, Dysoxylum richii, Parinari insularum, Intsia bijuga, Casuarina eqiusetfolia, species of
- 19 Syzygium, and the conifer *Podocarpus neriifolius* being other locally common species (Twyford et al.
- 20 1965; Berry & Howard 1973). As suggested by Mueller-Dombois & Fosberg (1998), this is better
- referred to as MF. No other native forest type has been reported from the lowland of the leeward site of
- 22 Fiji.

- In this paper we report the existence of true TDF in Fiji. We then compare it with MF to 1) identify the
- 25 different species and families that are characteristic of each forest type; 2) delimit the climatic

- boundaries of both forest types, 3) determine differences in life history traits of tree species in these
- 2 forests, and 4) assess the anthropogenic impact on TDF and MF.

#### **METHODS**

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#### Climate

- 8 The climates of the Suva (18.09° S, 178.27° E) and Nadi (17.75° S, 177.45° E; see Fig. 1) weather
- 9 stations reflect the climates of rainforests and TDF, with Suva in the wet, south-eastern rain forest zone
- and Nadi in the drier, western dry forest zone. The climatological observations of these two stations
- between 1961 and 2003 were detailed by Mataki et al. (2006). While the annual average surface
- temperature is similar at both stations, Nadi receives considerably less average annual total rainfall
- 13 (1810 mm) than Suva (3040 mm). In addition, Nadi has a distinct dry season of five consecutive
- months (May to September), each with less than 100 mm rainfall. Mataki et al. (2006) also pointed out
- that moderate to strong ENSO events lead to more severe drought conditions.

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- 17 Unfortunately, such a long and consistent record does not exist for Fiji's other weather stations. The
- station at Udu Point (16.13° S, 179.98° E; see Fig. 1), Vanua Levu, is located in the MF zone. It has
- been recording climatological observations since 1973, but has few years where rainfall records exist
- for every day. However, the average annual rainfall is about 2400 mm and the average temperature is
- about 26°C (Keppel et al. 2006).

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### **Selection of sample sites**

- To identify forest remnants in Fiji's dry zone, we used climatic information (Fitzpatrick et al. 1966;
- 25 Krishna 1980) to find zones with an average annual rainfall of less than 2500 mm, which should

- include TDF and MF. We then used aerial photographs (Fiji Lands Department survey in 1996) to
- 2 identify the areas that still have forest cover (rather than talasiga grassland), and eliminated areas that
- 3 were composed of commercial plantations of *Pinus carribae* using the maps of Chandra & Mason
- 4 (1998). Having identified places with potentially native vegetation, we visited 21 potential sites and
- 5 eliminated those that were almost completely covered with the invasive legumes Samanea saman,
- 6 Albizia lebbeck, and Leucaena leucocephala. We found 12 locations that still had several native
- species, but two of these, Mali Island and Yanuca Island, had only tiny fragments (less than 50 m<sup>2</sup>) of
- 8 native trees remaining and were excluded from subsequent analyses. This left us with 10 study sites
- 9 (Fig. 1), which showed a diversity of rainfall regimes (Table 1). The average rainfall for each study site
- was estimated using the data available on WorldClim (2006). Unfortunately it is based on an algorithm
- with high uncertainities on isolated islands, such as those of the Fiji group (Hijmans et al. 2005).
- However, it provides the only available information about the climate of the study sites.

#### **Data collection**

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- 15 Between May 2002 and July 2004 we prepared a list of all species encountered in each location by
- walking through the forest for at least 10 person hours. The surveyors (GK & MT) were the same for
- all localities to ensure comparability of results. We collected specimens of all species that we were not
- able to identify in the field for identification at the South Pacific Regional Herbarium (SUVA). For all
- species, forest type (MF or TDF) and life form (climber, epiphyte, herb, shrub/small tree, tree fern, and
- tree) were recorded (Appendix 1). For a subset of the data, which included only indigenous canopy and
- subcanopy tree species associated with mature-stage forests (Appendix 2), we determined whether or
- 22 not a species was annually deciduous (pers. obs. in different TDF during the dry season) or
- 23 sclerophyllous. Published literature was used to assign floral sexuality (monoecious, dioecious or
- 24 hermaphrodite; Smith 1979, 1981, 1985, 1988, 1991, 1996) and likely dispersal agents (Guppy 1906;
- Leenhouts 1956; Carlquist 1974; Wodzicki & Felten 1975; Lock & Marshall 1976; Fujita & Tuttle

- 1 1991; Mishra & Gautam 1992; Hamann et al. 1999; Setoguchi et al. 1999; Prider & Christophel 2000;
- 2 Ghazanfar et al. 2001; Webb & Peart 2001; Hodgskison et al. 2003; González-Astorga & Castillo-
- 3 Campos 2004; McConkey et al. 2004; Thapliyal & Phartyal 2005) for these tree species.

- 5 Species were classified as deciduous or sclerophyllous using broad concepts. Deciduous species
- 6 included "true" deciduous species that loose their leaves at regular seasonal intervals and drought-
- 7 deciduous species, which only loose their leaves during prolonged dry periods. We did not distinguish
- 8 between those and other types of deciduousness (Eamus 1999), because long-term phonological data
- 9 does not exist for most species. Sclerophylly lacks a precise definition, although sclerophyllous leaves
- are easily recognised by their small size and relatively thick leaves. These traits are associated with
- thick cuticles, abundant sclerification, low concentration of nutrients, and high longevity (Turner 1994;
- 12 Vendramini et al. 2002). Here we considered leaves or leaflets as sclerophyllous if they were less than
- about 7 cm long and more than about 0.5 mm thick.

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- We quantified disturbance by developing an index of anthropogenic disturbance similar to that of
- Gillespie et al. (2000) to determine the most affected sites. Grazing was ranked as (1) sites with no
- evidence of goat grazing, (2) sites that previously had goat populations but no recent grazing, (3) sites
- with frequent and current goat browsing, and (4) sites with extremely high goat browsing that has
- eliminated all or most of the native understorey. Fire was ranked as (1) sites with no signs or reports of
- recent fires, (2) sites with recent fires, (3) sites with frequent and recent fires. The effect of invasive
- species was ranked as (1) sites with no or few invasive species with negligible ecological effect, (2)
- sites with moderate effect by invasive species, and (3) sites that are dominated by invasive species. The
- index of anthropogenic disturbance is the sum of all ranks for each site.

#### Data analysis

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We excluded species that were sometimes found at the coastal fringes of the forest systems studied but 2 are generally associated with coastal locations (Abrus prectorius, Colubrina asiatica, Lumnitzera 3 littorea, Pandanus tectorius, Premna serratifolia, Terminalia catappa, Terminalia littoralis, Thespesia 4 populnea) and species that are non-native and invasive (e.g., Albizia lebbeck, Leucaena leucocephala, 5 Rivina humilis, Samanea saman) or generally restricted to disturbed or regenerating sites sites (e.g. 6 7 Commersonia bartramia, Culcuita straminea, Merremia peltata, Nephrolepis hirsutula, Pureria 8 lobata, Sphaerostephanos invisus) from our analysis. This was done to reduce noise by species not genuinely associated with particular vegetation types. Some of the sites had experienced goat grazing 9 for several years, which can be detrimental to the vegetation of island forests (Spatz & Mueller-10 Dombois 1973; Scowcroft & Hobdy 1987). The island of Monuriki was extremely affected, having 11 12 almost been entirely denuded of its undergrowth and, as a result, is experiencing severe erosion. To account for this effect, we removed from the analysis all climbers, herbs, shrubs, and small trees (those 13 14 that do not normally exceed a dbh 5 cm), which are the most vulnerable to grazing (Daubenmire 1972; 15 Gillespie et al. 2000). Vegetation data (species presence/absence; Appendix 2) was analysed using agglomerative clustering with average linkage based on the Jaccard coefficient of the Community 16 17 Analysis Package (CAP; Henderson & Seaby 2002) to determine the presence of different native forest 18 types. Two distinct clusters, corresponding to MF and TDF, were produced. 19 We tested the significance of the two clusters (forest types) by analysis of similarity (ANOSIM) using 20 21 PRIMER 5 (Clarke & Gorley 2001). One group was three MF sites, the other was seven TDF sites. The hypothesis that there is no difference between MF and TDF was tested by creating a square-root 22 transformed Bray-Curtis similarity matrix and doing an ANOSIM between the samples using all 23 possible (120) permutations. We then tested which species were associated with TDF and MF using 24

- Detrended Correspondence Analysis (DCA) for correlation between the sites and plant species (CAP;
- 2 Henderson & Seaby 2002).

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#### RESULTS

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#### Vegetation

- 8 Two distinct forest types with low similarity are found in Fiji's dry zone (Fig. 2). One comprises all the
- 9 sites with an estimated annual precipitation less than 2400 mm, has many tree species that are
- deciduous, such as Garuga floribunda, Gyrocarpus americanus, Koelreuteria elegans, and Pongamia
- pinnata (Appendix 2), and therefore is best referred to as tropical dry forest (TDF). The other is
- dominated by Gymnostoma vitiense, Dacrydium nidulum, Fagraea gracilipes, and Myristica
- 13 gillespieana, has mostly evergreen trees (several of which are sclerophyllous), is composed of sites
- with higher rainfall, and is best classified as moist forest (MF). Gau (estimated total annual rainfall =
- 15 2439 mm yr<sup>-1</sup>) is an exception to this pattern, clustering with TDF sites. ANOSIM showed that the two
- vegetation types are significantly different (Global R: 0.984, level of significance: 0.8%). Within the
- 17 MF, Nautuutu is very different from Lekutu and Nabourewa, the former having several taxa and
- physiognomic features characteristic of tropical rain forest, the highest rainfall (2458 mm), and has
- been described as a transitional forest between MF and rainforests (Keppel et al. 2006).
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- 21 Several tree species, including *Racosperma richii*, *Buchanania richii*, *Dacrydium nidulum*,
- 22 Decaspermum vitiense, Fagraea gracilipes, Gymnostoma vitiense, Palaquium fidjiense, Rapanea
- 23 myrtifolia, Sarcomelicope petiolaris were clearly associated with MF in the DECORANA plot (Fig. 3).
- 24 This also included several tree species that are also common in lowland rain forests, such as *Amaroria*
- 25 soulemanoides, Dillenia biflora, Garcinia pseudoguttifera, Myristica spp., Parinari insularum, and

- 1 Syzygium fijiense (cf. Keppel et al. 2005). Trees such as Antirhea inconspicua, Arytera brackendridgei,
- 2 Cynometra falcata, Diospyros elliptica, Diospyros phlebodes, Drypetes vitiensis, Excoecaria
- 3 acuminata, Gyrocarpus americanus, Kingidendron platycarpum, Mallotus tiliifolius, Pouteria grayana
- 4 and *Premna protusa*, show strong affinity to TDF. Some species generally considered to be coastal,
- 5 such as Cordia subcordata, Erythrina variegata and Millettia pinnata (cf. Ghazanfar et al. 2001), were
- 6 also part of this group. Species associated with both forest types, MF and TDF, were *Cerbera manghas*,
- 7 Cynometra insularis, Dysoxylum richii, Intsia bijuga, Maniltoa spp., Pittosporum arborescens,
- 8 Pleiogynium timoriense and Vavaea amicorum.

# 10 Flora of dry zone forests

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- A total of 310 native (and 14 common invasive) species were recorded in forests of the dry zone (Table
- 12 2). Fern and fern allies represent 12% (19 families, 31 genera, 38 species), gymnosperms 2% (4
- families, 5 genera, 5 species), dicots 73% (62 families, 160 genera, 227 species), and monocots 13%
- 14 (12 families, 32 genera, 40 species) of the native flora.
- Plants that are native to Fiji's dry zone represent 96% of the flora. Of this 33% (102 species) are
- endemic to Fiji (Table 2). MF is richer in species than TDF and has greater percentage endemism (38%)
- 18 cf. 18% of indigenous species). Invasive and/or naturalised taxa comprise 4% of species encountered
- within the forest and include Mikania micrantha, Spathodea campanulata, Coccinea grandis, Clidemia
- 20 hirta, Albizia labbeck, Samanea saman, Leucaena leucocephala, Passiflora foetida, and Lantana
- 21 camara.

- Overall, about 45% of the indigenous species were trees, 19% shrubs and small trees, 14% herbs, 13%
- climbers, 7% epiphytes and less than 1% (2 species) tree ferns, the latter being restricted to MF (Table
- 25 2). Climbing plants were more diverse in TDF, comprising almost 21% of all indigenous species (cf.

- 1 11% in MF). Epiphytes and herbaceous plants were more diverse in MF, comprising 9% (cf. 3% in
- 2 TDF) and 16% (cf. 9% in TDF), respectively.

- 4 Rubiaceae is the most diverse family with 15 genera and 26 species of the native flora, followed by
- 5 Euphorbiaceae with 14 genera and 24 species and Orchidaceae with 10 genera and 14 species.
- 6 Legumes (Caesalpinaceae, Fabaceae, and Mimosaceae) account for 14 native genera and 16 species.
- 7 These four groups comprise about 26% of Fiji's indigenous dry zone forest flora. Ficus (Moraceae) is
- 8 the largest genus comprising 8 species of the native flora, followed by Syzygium (7 spp.; Myrtaceae),
- 9 Psychotria (6 spp.; Rubiaceae), Glochidion (5 species; Euphorbiaceae), and Garcinia (4 spp.;
- 10 Clusiaceae) and *Maesa* (4 spp., Myrsinaceae). These six genera contribute about 11% of the indigenous
- 11 dry zone flora.

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- 13 The diversity within plant families differed greatly between forest types (Table 3). Orchids
- 14 (Orchidaceae), sedges (Cyperaceae), Myrtaceae, Sapotaceae, grasses (Poaceae), and the Sapotaceae are
- 15 the most diverse families in MF, while legumes (Caesalpinaceae, Fabaceae, Mimosaceae),
- 16 Flacourtiaceae, and Sapindaceae were most diverse in TDF. In addition, several families that are
- usually associated with rain forests and are found in MF were absent from TDF: tree ferns
- 18 (Cyatheaeceae), filmy ferns (Hymenophyllaceae), gingers (Alpiniaceae), Elaeocarpaceae,
- 19 Melastomataceae, and Urticaceae.

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#### Life history characteristics of trees

- Sclerophyllous species make up almost 30% of species in MF and TDF (Table 4). A fifth of the trees in
- TDF are deciduous, while few trees are deciduous in MF. If only canopy species are considered, more
- 24 than 30% of the species are deciduous. TDF also differs by having a lower percentage of species
- 25 dispersed by vertebrates (70% cf. 82%). Both forest types, however, are similar with regard to floral

- 1 sexuality, having a similar ratio of hermaphroditic:monoecious:dioecious and more than 30% of the
- species being monoecious. 2

**Disturbance** 

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- Almost all the TDF sites have higher disturbance indices than the MF sites studied (Table 1). There is a 5
- strong negative correlation between average rainfall and the disturbance index (r = 0.87). Six of the 6
- 7 seven TDF sites showed signs of recent fires, and recent grazing had affected five of those. The
- Monuriki and Navo forests suffered from extensive goat grazing that prevent regeneration of native 8
- species and the Navo and Vatia forests were dominated by invasive species in most locations. 9

**DISCUSSION** 

Fiji's TDF and MF are two fundamentally different forest types that differ in species composition and 14

life history traits. Total annual rainfall and seasonality of rainfall seem to be major factors determining

the type of forest present and the degree of deciduousness, but existing climate data are not sufficiently

precise to determine the exact effect of climate. Generally, areas with an average total precipitation of

2400 mm or less and several successive months with less than 100 mm of rain between May and

September support TDF (Fig. 2). This is considerably more than the maximum of 2000 mm proposed

elsewhere (Holdridge 1971; Mooney et al. 1998). Although the WorldClim values probably

overestimate rainfall because of high uncertainities in the underlying algorithm on isolated Pacific

Islands (Hijmans et al. 2005), rainfall is likely to be higher than 2000 mm. This could be caused by

occasional extreme weather events associated with cyclonic systems pushing the annual rainfall

average up. 24

Macuata (2337 mm), Naicobocobo (2362 mm), and, especially, Gau (2439 mm) have relatively high rainfall but cluster with TDF sites. These sites are on small offshore islands or peninsulas on the

probably not well estimated by World Clim, as the numerous leafless deciduous trees during the dry

leeward side of high and relatively large islands. The strong rainshadow effect on the leeward site is

season attest to the water stress trees experience (Borchert et al. 2002). The frequent winds in coastal

locations may exert a "drying effect", reducing the soil moisture. In addition, soil drainage needs to be

considered, as well-drained soils may support "low-rainfall" vegetation in areas of high rainfall. In

addition type, depth and water-holding capacities of the soils potentially play a major role determining

the type of forest present at a particular rainfall regime, although TDF sites generally had shallow soils

(few cm deep and rock outcrops present). Unfortunately, information on the above is not readily

available and our study did not investigate these aspects. Setting up rainfall gauges at different TDF

sites and recording basic soil properties should be considered a priority and is the only way to

determine actual water stress.

The two forest types differ in structure, composition and life history. While the canopy of MF is to 30m tall and closed, that of TDF usually doesn't exceed 20cm and is more open, with several of the tallest trees being deciduous. Overall MF are more diverse and have much higher endemism. Lianas, however, are diverse and common in TDF, a common phenomenon (Lott et al. 1987, Sussman & Rakotozafy 1994). Probably because of the prolonged droughts in TDF, epiphytes are uncommon and tree ferns and other rain forest taxa are absent (Table 2). These trends are reflected in the diversity within families. The mostly epiphytic Orchidaceae and the rain forest families Myrtaceae and Clusiaceae are more diverse in MF, while the Rhamnaceae and Passifloraceae (which have many species of climbers) are more diverse in TDF (Table 3). Nitrogen-fixing legumes are also more diverse in TDF than in MF, possibly because of the shallower soils.

The clear compositional distinction between the two forest types is reflected in the DCA plot (Fig. 3),
with TDF & MF sites forming two distinct clusters. Several species are resticted to each forest type and

3 some are shared. Other than this, the DCA plot is difficult to interpret. While the first axis is obviously

related to precipitation to some degree, factors effecting the second axis are less clear. The wedge-

5 shaped distibution of the species and study sites on the DCA plot is interesting but possibly simply

6 caused by the fact that the MF cluster consists of only three sites, compared to the seven TDF sites.

8 In Fiji, MF seems to be associated with climates with moderate annual rainfall (2400 mm or more)

9 lacking a distinctive dry season, although monthly rainfall may be less than 100 mm per month

between June and August. MF appears to be very heterogenous with species composition varying

considerably, which has been noted by Berry & Howard (1973) and Keppel et al. (2006). This could be

caused by variation in climatic and edaphic features. The presence of tree ferns, filmy ferns, ginger,

Elaeocarpaceae, and Melastomataceae and the relatively high diversity of orchids are elements

normally associated with tropical rain forest and attest to the moist conditions of this forest type. The

site with the highest rainfall (Naiutuutu; 2458 mm) is most similar to rain forest. Also, the percentage

of vertebrate-dispersed species (82%) is similar to that of lowland tropical rainforest (cf. 85% in

Bornean rainforest; Webb & Peart 2001).

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TDF is here reported for the first time in Fiji. It is characterized by a distinct species assemblage and more than 20% of its tree species being deciduous. While some species loose all their leaves on a yearly basis (deciduous), others only lose their leaves during extremely dry spells (drought-deciduous). The moderate number of deciduous species and comparatively high annual rainfall, place Fiji's TDF as semi-deciduous TDF on the spectrum from evergreen MF to deciduous TDF, in which more than half the canopy species are deciduous (Bullock et al. 1998). Although MF and TDF differ considerably in the composition of taxa, natural history, and climate, they should not be considered clearly delimited

- forest types but rather as extremes of varying degrees deciduousness and other features (Lerdau et al.
- 2 1991; Medina 1998). Unfortunately, zones where the two forest types intergrade have been largely
- destroyed. Only at Naicobocobo did we observe such a transition, which was an abrupt change from
- 4 TDF to MF dominated by *Gymnostoma vitiense*.

- 6 In the Pacific region, TDF has been recorded from Australia (Fensham 1995), New Guinea (Paijmans
- 7 1976, p.66; Heylingers 1982), the Solomon Islands (Whitmore 1969), Vanuatu (Mueller-Dombois &
- 8 Fosberg 1998), New Caledonia (Gillespie & Jaffré 2003), and Hawaii (Hatheway 1952). Except for
- 9 Hawaii, they seem to share the presence of *Gyrocarpus americanus*, *Garuga floribunda*, and *Intsia*
- bijuga. The percentage of genera shared with Fiji is 21% for Hawaii, 25% for New Caledonia, and 33%
- for Australia. High similarity with Australia and relative low endemism in Fiji (compared Fijian MF
- and rain forest; Keppel et al. 2003, 2006) suggest that plant species of Pacific TDF are good dispersers.

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- High similarity with Australia may also help to explain the high percentage (30-35%) of monoecious
- tree species in Fijian dry zone vegetation, which is higher than that reported in other tropical vegetation
- 16 (5-20%; Gross 2005; Machado et al. 2006). Only in Australia have similar percentages of monoecy
- 17 (20-35%) been reported and New Guinea is suggested to have similar levels of monoecy (Gross 2006).
- As New Guinea is believed to be the major source area for the Melanesian flora, close phylogeographic
- relationships could be the reason for the high percentage of monoecious species in Fiji.

- 21 Most TDFs surveyed were highly disturbed (Table 1), and the strong negative correlation between
- disturbance and rainfall (r = 0.87) in this study suggests that the driest forests are likely to be most
- vulnerable to disturbance. This corresponds well with findings that dry zones on Pacific islands are
- especially vulnerable to anthropogenic effects (Rolett & Diamond 2004). It can also explain the failure
- by earlier botanists and naturalists (Mead 1928; Smith 1951; Berry & Howard 1973) to discover TDF.

An increase in the frequency of fire since the arrival of people some 3000 years ago (Austin 1999)

2 probably decimated TDF so that it was already rare in the early 20th century. The global apathy

towards TDF that was prevalent until recently may have also contributed to Fijian TDF being

4 overlooked.

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6 Currently only small fragments of TDF remain in Fiji, with only that on Yadua Taba having some

7 protection. This makes TDF one of (if not the) most endangered ecosystems in Fiji. It is essential that

the dry forests on Yadua Taba and Macuata islands be treated as conservation priorities, not only

9 because they harbour the last viable populations of the endemic crested iguana (*Brachylophus* 

vitiensis), but also because of relatively good and extensive TDF stands. In addition, both forests are

located on islands, which eases their protection from fires and other human effects. The TDF of Vatia

and Naicobocobo are the biggest remaining fragments of TDF on Fiji's two biggest islands and as such

should be protected and rehabilitated where necessary. The latter may be the only location in Fiji,

where the transition between TDF and MF can still be observed. Extensive stands of MF, though

threatened by logging, remain only on Vanua Levu, and concrete protective measures are urgently

needed (Keppel et al. 2006). Small remnants may also still be found on Viti Levu, Kadavu and other

islands (Berry & Howard 1973). A corollary of the importance of climate (especially rainfall regime) is

that climate change will change the boundaries of forest types, as has occured in the past (Southern

1986; Stevenson & Hope 2005). Conservation programmes therefore need to take into account global

warming and its effect on local climates during reserve system design.

22 As TDF is here reported for the first time, the need and opportunities for further research are immense.

Virtually nothing is known about the ecology of this ecosystem and its resident flora and fauna, which

underlines that the leeward sides of high Pacific islands require immediate and thorough attention by

scientists and conservationists. This is underlined by the discovery of new taxa and records for Fiji

- from the TDF within the last 10 years (Gardner 1997; this study). There is an urgent need to identify,
- 2 map and assess the conservation status of all remaining TDF fragments to ensure that the best
- 3 remaining fragments of Fiji's TDF are preserved. This needs to be coupled with a quantitative study
- 4 of TDF vegetation, investigation of prevalent climatic and soil conditions, and a detailed evaluation of
- 5 the conservation status of the rare and potentially highly endangered plant species that are endemic to
- 6 this forest type in Fiji, such as Cynometra falcata and Guettarda wayaensis. Finally, there is an urgent
- 7 need to gain an understanding about the dynamics of Fijian TDF and the influence of various
- 8 environmental factors have. This should facilitate predicting the response of TDF to long-term stresses,
- 9 which is likely scenario under climate change.

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#### REFERENCES

- 24 Austin CC 1999. Lizards took the express train to Polynesia. Nature 397: 113-114.
- 25 Beard JS 1955. The classification of tropical American vegetation types. Ecology 36: 89-100.

- Berry MJ, Howard WJ 1973. Fiji Forest Inventory. Volume 1. The Environment and Forest Types.
- 2 Land Resource Study No. 12. Land Resource Division, Surbiton, Surrey, England.
- 3 Borchert R, Rivera G, Hagnauer W 2002. Modification of vegetative phenology in a tropical semi-
- deciduous forest by abnormal drought and rain. Biotropica 34: 27-39.
- 5 Brownlie G 1977. The Pteridophyte Flora of Fiji. (Beihefte zur Nova Hedwigia, Heft 55). Vaduz,
- 6 Liechtenstein, J. Cramer.
- 7 Bullock SP, Mooney HA, Medina E (eds.) 1998. Seasonally Dry Tropical Forest. Cambridge, UK,
- 8 Cambridge University Press.
- 9 Carlquist S 1974. Island Biology. New York, USA, University of Colombia Press.
- 10 Chandra R, Mason A ed. 1998. An atlas of Fiji. Suva, Fiji, Geography Department, University of Fiji.
- 11 Chave J, Condit R, Lao S, Caspersen JP, Foster RB, Hubbell SP 2003. Spatial and temporal variation
- of biomass in a tropical forest: results from a large census plot in Panama. Journal of Ecology 91:
- 13 240-252.
- 14 Clarke KR, Gorley RN 2001. PRIMER v5 User Manual/ Tutorial. Plymouth Routines in Multivariate
- Ecological Research. Plymouth Marine Laboratories, Plymouth, UK, Primer-E Ltd.
- Daubenmire R 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-
- western Costa Rica. Journal of Ecology 60: 147-170.
- Eamus D 1999: Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry
- tropics. Trends in Ecology and Evolution 14: 11-16.
- 20 Fensham RJ 1995. Floristics and environmental relations of inland dry rainforest in North Queensland.
- Journal of Biogeography 22: 1047-1063.
- 22 Fitzpatrick EA, Hart D, Brookfield HC 1966. Rainfall seasonality in the tropical Southwest Pacific.
- 23 Erdkunde 20: 181-194.
- Fujita M, Tuttle MD 1991. Flying foxes (Chiroptera: Pteropodidae): threatened animals of key
- ecological and economic importance. Conservation Biology 5: 455-463.

- Gardner RO 1997. New and noteworthy plants from Fiji. New Zealand Journal of Botany 35: 487-492.
- 2 Gagné W, Cuddihy, LW 1990. Classification of Hawaiian plant communities. In: Wagner W, Herbst D,
- 3 Sohmer S ed. Manual of flowering plants of Hawaii. Honolulu, Hawaii, Bishop Museum. Pp. 45-
- 4 114.
- 5 Ghazanfar SA, Keppel G, Khan S 2001. Coastal vegetation of small islands near Viti Levu and Ovalau,
- 6 Fiji. New Zealand Journal of Botany 39: 587-600.
- 7 Gillespie TW, Jaffré T 2003. Tropical dry forest in New Caledonia. Biodiversity and Conservation 12:
- 8 1687-1697.
- 9 Gillespie TW, Grijalva A, Farris CN 2000. Diversity, composition, and structure of tropical dry forest
- in Central America. Plant Ecology 147: 37-47.
- González-Astorga J, Castillo-Campos G 2004. Genetic variability of the narrow endemic Antirhea
- *aromatica* Castillo-Campos & Lorence, (Rubiaceae, Guettardeae) in a tropical forest of Mexico.
- 13 Annals of Botany 93: 521-528.
- Gross CL 2005. A comparison of the sexual systems in the trees from the Australian tropics with other
- tropical biomes more monoecy but why? American Journal of Botany 92: 907-919.
- Guppy HB 1906. Observations of a naturalist in the Pacific between 1896 and 1899. London, UK,
- 17 Macmillan & Co. Ltd.
- Hamann A, Barbon EB, Curio E, Madulid DA 1999. A botanical inventory of a submontane tropical
- rainforest on Negros Island, Philippines. Biodiversity and Conservation 8: 1017-1031.
- 20 Hardy OJ, Sonke B 2004. Spatial pattern analysis of tree species distribution in a tropical rain forest of
- Cameroon: assessing the role of limited dispersal and niches differentiation. Forest Ecology and
- 22 Management 197: 191-202.
- Hatheway WH 1952. Composition of certain native dry forests: Mokuleia, Oahu, T.H. Ecological
- 24 Monographs 22: 153-168.

- 1 Henderson PA, Seaby RMH 2002. Community Analysis Package. Version 2.15. Pennington,
- 2 Lymington, Hants, UK, PISCES Conservation Ltd.
- 3 Heylingers PC 1982. Semi-deciduous scrub and forest and eucalypt woodland in the Port Moresby
- area. In: Gressitt JL ed. Biogeography and Ecology of New Guinea. The Hague, Netherlands, Dr W.
- 5 Junk Publishers. Pp. 437-457.
- 6 Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A 2005. Very high resolution interpolated climate
- 7 surfaces for global land areas. International Journal of Climatology 25: 1965-1978.
- 8 Hodgskison R, Balding ST, Zubaid A, Kunz TH 2003. Fruit bats (Chiroptera: Pteropodidae) as seed
- 9 dispersers and pollinators in a lowland Malaysian rain forest. Biotropica 35: 491-502.
- Holdridge LR 1971. Forest Environments in Tropical Life Zones. A Pilot Study. Oxford, UK,
- 11 Pergamon Press.
- Hubbell SP 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299-
- 13 1309.
- 14 IPNI. 2007. The International Plant Names Index. http://www.ipni.org/index.html [accessed July
- 15 2007].
- Janzen DH 1988. Tropical Dry Forest The most endangered major tropical ecosystem. In: Wilson
- EO, Peter FM ed. Biodiversity. Washington, USA, National Academy Press. Pp. 130-137.
- 18 Keppel G 2002. Low genetic variation in a Pacific cycad: Conservation concerns for Cycas seemannii
- 19 (Cycadaceae). Oryx 36: 41-49.
- 20 Keppel G, Navuso JC, Naikatini A, Thomas NT, Rounds IA, Osborne TA, Batinamu N, Senivasa E
- 2005. Botanical diversity at Savura, a lowland rainforest site along the PABITRA gateway
- transect, Viti levu, Fiji. Pacific Science 59: 175-191.
- 23 Keppel G, Rounds IA, Thomas NT 2006. The flora, vegetation, and conservation value of the mesic
- forest at Dogotuki, Vanua Levu, Fiji Islands. New Zealand Journal of Botany 44: 273-292.

- Krishna R 1980. Rainfall maps of Viti Levu, Vanua Levu and Taveuni. Nadi, Fiji, Fiji Meterological
- 2 Service, Publication No. 1.
- 3 Leenhouts PW 1956. Burseraceae. Flora Melanesiana, Series 1, 5. 1: 209-296.
- 4 Lerdau M, Whitbeck J, Holbrook NM 1991. Tropical deciduous forest: Death of a biome. Trends in
- 5 Ecology and Evolution 6: 201-202.
- 6 Lock JM, Marshall AG 1976. Possible pollination of *Parinari polyandra* by bats. The Nigerian Field
- 7 41: 89-92.
- 8 Lott EL, Bullock SH, Solis-Magallanes JA 1987. Floristic diversity and structure of upland and Arroyo
- 9 forests of coastal Jalisco. Biotropica 19: 228-235.
- Machado IC, Lopes AV, Sazima M 2006. Plant sexual systems and a review of breeding system studies
- in the Caatinga, a Brazilian tropical dry forest. Annals of Botany 97: 277-287.
- Martínez-Yrízar A 1998. Biomass distribution and primary productivity of tropical dry forests. In:
- Bullock SP, Mooney HA, Medina E ed. Seasonally Dry Tropical Forest. Cambridge, UK,
- 14 Cambridge University Press. Pp. 326-345.
- 15 Mataki M, Koshy KC, Lal M 2006. Baseline climatology of Viti Levu (Fiji) and current climatic
- trends. Pacific Science 60: 49-68.
- McConkey KR, Meehan HJ, Drake DR 2004. Seed dispersal by Pacific Pigeons (*Ducula pacifica*) in
- Tonga, Western Polynesia. Emu 104: 369-376.
- Mead JP 1928. The forests of the Fiji Islands. Council Papers of Fiji 4: 47-54.
- 20 Medina E 1998. Diversity of life forms of higher plants in neotropical dry forests. In: Bullock SP,
- Mooney HA, Medina E ed. Seasonally Dry Tropical Forest. Cambridge, UK, Cambridge University
- 22 Press. Pp. 221-242.
- 23 Menaut J-C, Lepage M, Abbadie L 1998. Savannas, woodlands and dry forests in Africa. In: Bullock,
- SP, Mooney HA, Medina E ed. Seasonally Dry Tropical Forest. Cambridge, UK, Cambridge
- University Press. Pp. 64-92.

- 1 Mishra RM, Gautam P 1992. Dispersal ecology of *Alangium lamarckii* Lamk. Geobios 19: 94-99.
- 2 Mooney HA, Bullock SP, Medina E 1998. Introduction. In: Bullock SP, Mooney HA, Medina E eds.
- 3 Seasonally Dry Tropical Forest. Cambridge University Press, Cambridge, UK. Pp. 1-8.
- 4 Mueller-Dombois D, Fosberg RF 1998. Vegetation of the Tropical Pacific Islands. Berlin, Germany,
- 5 Springer Verlag.
- 6 Murphy PG, Lugo AE 1986. Ecology of tropical dry forest. Annual Review of Ecology and
- 7 Systematics 17: 67-88.
- 8 Paijmans K 1976. New Guinea Vegetation. Australian National University, Canberra, Australia.
- 9 Parham JW 1972. Plants of the Fiji Islands. Government Printer, Suva, Fiji.
- Prider JN, Christophel DC 2000. Distributional ecology of *Gymnostoma australianum* (Casurinaceae),
- a putative palaeoendemic of Australian wet tropic forest. Australian Journal of Botany 48: 427-434.
- Rolett B, Diamond J 2004. Environmental predicors of pre-European deforestation on Pacific Islands.
- 13 Nature 431: 443-446.
- Scowcroft PG, Hobdy R 1987. Recovery of goat-damaged vegetation in an insular tropical montane
- 15 forest. Biotropica 19: 208-215.
- Setoguchi H, Kosuge K, Tobe H 1999. Molecular Phylogeny of Rhizophoraceae Based on rbcL Gene
- 17 Sequences. Journal of Plant Research 112: 443-455.
- Smith AC 1951. The vegetation and flora of Fiji. Scientific Monthly 73: 3-15.
- Smith AC 1979. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only). Vol. 1. Lawai, Kauai,
- 20 Hawaii, USA, Pacific Tropical Botanical Garden.
- 21 Smith AC 1981. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only). Vol. 2. Lawai, Kauai,
- Hawaii, USA, Pacific Tropical Botanical Garden.
- 23 Smith AC 1985. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only). Vol. 3. Lawai, Kauai,
- 24 Hawaii, USA, Pacific Tropical Botanical Garden.
- 25 Smith AC 1988. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only). Vol. 4. Lawai, Kauai,

- 1 Hawaii, USA, Pacific Tropical Botanical Garden.
- 2 Smith AC 1991. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only). Vol. 5. Lawai, Kauai, Hawaii,
- 3 USA, Pacific Tropical Botanical Garden.
- 4 Smith AC 1996. Flora Vitiensis nova: A new flora of Fiji (spermatophytes only): Comprehensive indices. Lawai,
- 5 Kauai, Hawaii, USA, Pacific Tropical Botanical Garden.
- 6 Southern W 1986. The Late Quartenary environmental history of Fiji. Unpublished PhD thesis,
- 7 Australian National University, Canberra, Australia.
- 8 Spatz G, Mueller-Dombois D 1973. The influence of feral goats on koa tree reproduction in Hawaii
- 9 Volcanoes National Park. Ecology 54: 870-876.
- Stevenson J, Hope G 2005. A comparison of late Quartenary forest changes in New Caledonia and
- northeastern Australia. Quartenary Research 64: 372-383.
- Sussmann RW, Rakotozafy A 1994. Plant diversity and structural analysis of a tropical dry forest in
- Southwestern Madagascar. Biotropica 26: 241-254.
- Svenning J-C, Kinner DA, Stallard RF, Engelbrecht BMJ, Wright SJ 2004. Ecological determinism in
- plant community structure across a tropical forest landscape. Ecology 85: 2526-2538.
- Thapliyal RC, Phartyal SS 2005. Dispersal and germnation syndromes of tree seeds in a monsoonal
- forest in northern India. Seed Science Research 15: 29-42.
- 18 Trejo I, Dirzo R 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in
- Mexico. Biological Conservation 94: 133-142.
- Turner IM 1994. Sclerophylly: primarily protective? Functional Ecology 8: 669-675.
- Twyford IT, Wright ACS, Parham JW, Loweth N 1965. Plant Cover. In: Twyford IT, Wright ACS ed.
- The soil resources of the Fiji Islands. Volume 1. Suva, Fiji, Government Printers. Pp.19-86.
- Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG 2002. Leaf traits as
- indicators of resource-use strategies in floras with succulent species. New Phytologist 154: 147-
- 25 157.

- Walsh RPD 1996. Climate. In: Richards PW ed. The Tropical rain forest: an ecological study.
- 2 Cambridge, UK, Cambridge University Press. Pp. 159-205.
- Webb CO, Peart DR 2001. High seed dispersal rates in faunally intact tropical rainforest: theoretical
- and conservation implications. Ecology Letters 4: 491-499.
- 5 Webb LJ 1959. A general classification of Australian rainforests. Journal of Ecology 41: 551-570.
- 6 Whitmore TC 1969. The vegetation of the Solomon Islands. Philosophical Transactions of the Royal
- 7 Society, London, Series B 255: 259-270.
- 8 Wodzicki K, Felten H 1975. The peka, or fruit bat (Pteropus tonganus tonganus) (Mammalia,
- 9 Chiroptera), of Niue Island, South Pacific. Pacific Science 29: 131-138.
- WorldClim 2006. http://www.worldclim.org [accessed September 2006]

**Table 1** Location, substrate, rainfall, and disturbance regimes for the 10 study sites. Study sites are sorted by disturbance index. TDF, tropical dry forest; MF, moist forest. \* Data estimates obtained from the WorldClim webpage (Hijmans et al. 2005). ^ Dry months are months with less than 100 mm rainfall, the number in brackets gives the number of months with less than 120 mm of rainfall.

Site	Elevation	Latitude,	Substrate,	Mean annual	Number of		Distu	ırbance	
	(m a.s.l.)	longitude	topography	rainfall	dry months	Grazing	Fire	Invasive	Index
				(mm)*	per year*^				
Monuriki	5-50	17°36'34 S,	Volcanic, steep	1780	6 (6)	4	3	2	9
(TDF)		177°02'07 W	slopes						
Navo (TDF)	5-10	18°06'40 S,	Limestone,	2031	3 (6)	4	2	3	9
		177°19'07 W	mostly flat						
Vatia (TDF)	20-40	17°23'10 S,	Volcanic,	2092	3 (5)	3	3	3	9
		177°49'14 W	moderate slopes						
Macuata	5-30	17°21'14 S,	Volcanic,	2337	2 (3)	2	3	2	7
(TDF)		178°01'60 W	moderate slopes						
Yadua Taba	5-200	16°50'06 S,	Volcanic, steep	2248	2 (4)	2	2	2	6
(TDF)		178°16'40 W	slopes						

Gau (TDF)	5-20	18°00'14 S,	Volcanic,	2439	0 (3)	1	2	1	4
		179°14'47 W	moderate slopes						
Dogotuki	40-70	16°13'55 S,	Volcanic,	2400	2 (3)	1	2	1	4
(MF)		179°46'32 W	mostly flat						
Naicobocobo	5-50	16°49'00 S,	Volcanic,	2362	2 (2)	1	2	1	3
(TDF)		178°29'45 W	moderate slopes						
Lekutu (MF)	220-230	16°38'04 S,	Volcanic,	2411	2 (3)	1	1	1	3
		178°50'07 W	mostly flat						
Nautuutu	30-40	16°13'55 S,	Volcanic,	2458	2 (3)	1	1	1	3
(MF)		179°49'27 W	mostly flat						

Table 2 Summary of the species origin in the dry zone forests of Fiji with regard to major taxonomic group and life form (italics). Numbers for moist forest (M) and tropical dry forest (T) are given in brackets. \*, includes endemic species.

Taxonomic Group/	Endemic	Indigenous*	Invasive and/or	Total	
Life Form			naturalised		
Ferns & Allies	4 (M:4,T:0)	38 (M:36,T:10)	0	38 (M:36,T:10)	
Gymnosperms	0	5 (M:5,T:1)	0	5 (M:5,T:1)	
Dicotyledon	91 (M:80,T:28)	227 (M:172,T:128)	14 (M:11,T:12)	241 (M:183,T:140)	
Monocotyledons	8 (M:8,T:0)	40 (M:37,T:15)	0	40 (M:37,T:15)	
Epiphytes	4 (M:4, T:0)	23 (M:22, T:5)	0	23 (M:22, T:5)	
Climbers	5 (M:5, T:2)	41 (M:28, T:32)	4 (M:4, T:4)	45 (M:31, T:36)	
Herbs	6 (M:6, T:0)	44 (M:41, T:14)	3 (M:2, T:1)	47 (M:44, T:15)	
Shrubs/Small Trees	25 (M:23, T:7)	60 (M:48, T:36)	3 (M:3, T:3)	63 (M:51, T:39)	
Tree Ferns	1 (M:1, T:0)	2 (M:2, T:0)	0	2 (M:2, T:0)	
Trees	62 (M:53, T:18)	140 (M:109; T:67)	4 (M:2, T:4)	144 (M:111, T:71)	
Totals	103 (M:92,T:27)	310 (M:250,T:154)	14 (M:11,T:12)	324 (M:261,T:166)	

Table 3 Most diverse families in TDF and MF. First value give total number of species, number
 of species endemic to Fiji are given in brackets.

Tropical D	ry Forest	Moist Forest			
Euphorbiaceae	Euphorbiaceae 12 (2) spp.		20 (13) spp.		
Rubiaceae	12 (3) spp.	Euphorbiaceae	15 (11) spp.		
Moraceae	9 (2) spp.	Orchidaceae	12 ( 3) spp.		
Caesalpinaceae	7 (4) spp.	Moraceae	10 ( 4) spp.		
Mimosaceae	7 (1) spp.	Cyperaceae	8 ( 0) spp.		
Apocynaceae	7 (1) spp.	Myrtaceae	8 ( 6) spp.		
Fabaceae	6 (0) spp.	Sapotaceae	7 ( 3) spp.		
Flacourtiaceae	6 (2) spp.	Apocynaceae	6 ( 1) spp.		
Sapindaceae	5 (0) spp.	Clusiaceae	6 (2) spp.		
Passifloraceae	4 (0) spp.	Poaceae	6 ( 2) spp.		
Rhamnaceae	4 (0) spp.	Caesalpinaceae	5 ( 1) spp.		
		Meliaceae	5 ( 4) spp.		
		Mimosaceae	5 ( 1) spp.		

Table 4 Percentages of large tree species recorded in leaf type, dispersal, and floral sexuality categories. TDF, tropical dry forest (n = 43),

2 MF, moist forest (n = 60).

Forest	Leaf T	ype <sup>1</sup>	Dispersal <sup>2</sup>		Floral Sexuality			
Type	% Decidu-	% Sclero-	Vertebrate	Wind	Other	Hermorphrodite	Dioecious	Monoecious
	ousness	phyll						
TDF	20.9	27.9	69.8	7.0	23.3	40.5	26.2	33.3
MF	3.3	28.3	81.7	5.0	13.3	36.5	27.0	36.5

- Fig. 1 Location of study sites and weather stations (both indicated by arrows) and approximate 2000
- 2 mm (dotted line) and 2500 mm (dashed line) rainfall boundaries (after Fitzpatrick (1966) and
- Krishna (1980)) in the Fiji group. Study sites named; weather stations mentioned in text: A, Suva; B,
- 4 Nadi; C, Udu Point.

- 6 Fig. 2 Results of agglomerative clustering using average linkage and the Jaccard coefficient. The
- 7 average annual rainfall is given in brackets below each study location.

8

- 9 Fig. 3 DCA plot of tree species. Circles, study sites; squares, species. Species affinities are shown in
- 10 Appendix 1 and the input data set in Appendix 2.

- 1 Appendix 1 Plants collected or recorded in the forests of Fiji's dry zone. E, endemic to Fiji; var. E,
- 2 variety endemic to Fiji; \*, introduced; <sup>T</sup>, plants recorded in tropical dry forest; <sup>M</sup>, plant recorded in
- moist forest. Values in brackets state life form. C, climber; E, epiphyte; H, herb; S, shrub/small tree;
- 4 TF, tree fern, ST, strangler; T, tree. Nomenclature follows Brownlie (1977), Smith (1979, 1981, 1985,
- 5 1988, 1991, 1996) and IPNI (2007).

1	PTERIDOPHYTA (Ferns and Fern Allies)	30	СУАТНАСЕАЕ
2		31	Cyathea lunulata Copel. <sup>M</sup> (TF)
3	LYCOPSIDA	32	Cyathea propinqua Mett. E, M(TF)
4		33	
5	LYCOPODIACEAE	34	DAVALLIACEAE
	Lycopodiella cernua (L.) Pic.Serm. M(H)	35	Davallia solida var. fejeensis (Hook.) Noot. (var. E), M(E)
6		36	Davallia solida (G.Forst.) Sw. <sup>M, T</sup> (E)
7	Huperzia phlegmaria (L.) Rothm. M(E)	37	Humata heterophylla (Sm.) Desv. <sup>M</sup> (E)
8	<i>Huperzia squarrosa</i> (G.Forst.) Trevis. <sup>M</sup> (E)	38	
9		39	DENNSTAEDTIACEAE
10	SELAGINELLACEAE	40	Pteridium esculentum (G.Forst.) Cockayne <sup>M</sup> (H)
11	Selaginella breynioides Baker <sup>E, M</sup> (H)	41	Tapeinidium melanesicum Kramer <sup>M</sup> (H)
12	Selaginella laxa Spring M(H)	42	
13	Selaginella viridangula Spring <sup>E, M</sup> (H)	43	DICKSONIACEAE
14		44	Calochlaena straminea (Labill.) M.D.Turner & R.A.White <sup>M</sup> (H)
15		45	
16	FILICOPSIDA	46	DRYOPTERIDACEAE
17	ADIANTACEAE	47	Tectaria latifolia (G.Forst.) Copel. <sup>M</sup> (H)
18	Adiantum hispidulum Sw. <sup>T</sup> (H)	48	Teetaria tangona (G.1 olst.) copei. (11)
19	Cheilanthes nudiuscula (R.Br.) T.Moore $^{T}(H)$	49	GLEICHENIACEAE
20	Doryopteris concolor (Langsd. & Fisch.) Kuhn <sup>T</sup> (H)	50	Gleichenia oceanica Kuhn <sup>M</sup> (H)
21	Taenitis pinnata (J.Sm.) Holttum <sup>M</sup> (H)		Gietchenia oceanica Kuini (11)
22		51	INVMENORINA I A CE A E
23	ASPLENIACEAE	52	HYMENOPHYLLACEAE
24	Asplenium australasicum Hook. <sup>M</sup> (E)	53	Abrodictyum dentatum (Bosch) Ebihara & K.Iwats. M(H)
25	Asplenium polyodon G.Forst. <sup>M</sup> (E)	54	Cephalomanes atrovirens C.Presl. M(H)
26		55	Crepidomanes intermedia (Bosch) Ebihara & K.Iwats. <sup>M</sup> (H)
27	BLECHNACEAE	56	
28	Blechnum orientale L. <sup>M</sup> (H)	57	
29	· <i>'</i>	58	LOMARIOPSIDACEAE
		59	Lomagramma polyphylla Brack. <sup>M</sup> (C/E)

1		30	
2	MARATTIACEAE	31	CYCADALES
3	Angiopteris evecta (G.Forst.) Hoffm. <sup>M</sup> (H)	32	
4		33	CYCADACEAE
5	OLEANDRACEAE	34	Cycas seemannii A.Braun M, T(T)
6	Nephrolepis biserrata (Sw.) Schott M, T(H)	35	
7	<i>Nephrolepis hirsutula</i> (G.Forst.) C.Presl <sup>M</sup> (H)	36	
8		37	CONIFERALES
9	POLYPODIACEAE	38	
10	<i>Drynaria rigidula</i> (Sw.) Bedd. <sup>M, T</sup> (E)	39	ARAUCARIACEAE
11	Pyrrosia lanceolata (L.) Farwl <sup>M, T</sup> (E/C)	40	Agathis macrophylla (Lindl.) Mast. <sup>M</sup> (T)
12		41	rigamis macrophyma (Email) wast. (1)
13	PTERIDACEAE	42	PODOCARPACEAE
14	Pteris ensiformis Burm.f. M, T(H)		
15	Pteris pacifica Hieron. <sup>M</sup> (H)	43	Dacrydium nidulum de Laub. M(T)
16		44	Podocarpus neriifolius D.Don <sup>M</sup> (T)
17	SCHIZAEACEAE	45	
18	Lygodium reticulatum Schkuhr <sup>M</sup> (C)	46	
19	Schizaea dichotoma (L.) Sm. <sup>M, T</sup> (H)	47	GNETALES
20	(2)	48	
21	THELYPTERIDACEAE	49	GNETACEAE
22	Sphaerostephanos invisus (G.Forst.) Holttum <sup>M, T</sup> (H)	50	Gnetum gnemon L. M(T)
23	Spinerosiepinnos nivisus (G.Poist.) Holium (H)	51	
	VIETADIACEAE	52	
24	VITTARIACEAE	53	ANGIOSPERMAE (Angiosperms)
25	Haplopteris elongata (Sw.) E.H.Crane <sup>M</sup> (E)	51	
26	Monogramma acrocarpa (Holttum) D.L.Jones <sup>E, M</sup> (E)	54	
27		55	DICOTYLEDONAE (Dicotyledons)
28		56	
29	GYMNOSPERMAE (Gymnosperms)	57	ACANTHACEAE

1 Graptophyllum insularum (A.Gray) A.C.Sm. M(S) 31 **ASCLEPIADACEAE** 2 Pseuderanthemum laxiflorum (A.Gray) C.E.Hubb. ex 32 L.H.Bailey E, M(S) Hoya australis R.Br. ex J.Traill M, T(C) 3 33 Tylophora brackenridgei A.Gray M, T(C) 4 34 ANACARDIACEAE 35 Buchanania attenuata A.C.Sm. E, M, T(T) **ASTERACEAE** 36 Buchanania vitiensis Engl. E, M(T) \*Mikania micrantha H.B. & K. M, T(C) 37 *Pleiogynium timoriense* (DC.) Leenh. M, T(T) 38 Rhus taitensis Guill. M, T(T) **BIGNONIACEAE** 39 Semecarpus vitiense (A.Gray) Engl. M(T) \*Spathodea campanulata P.Beauv. M, T(T) 10 40 41 11 **BORAGINACEAE ANNONACEAE** 12 42 Cyathocalyx cf. vitiensis A.C.Sm. E, M(T) Cordia subcordata Lam. <sup>T</sup>(T) 13 43 Polyalthia laddiana A.C.Sm. <sup>T</sup>(T) 44 15 BURSERACEAE 45 Canarium cf. vitiense A.Gray M(T) **APOCYNACEAE** 16 46 Alstonia pacifica (Seem.) A.C.Sm. M(T) Garuga floribunda Decne. <sup>T</sup>(T) 17 47 Alstonia costata (G.Forst.) R.Br. M(T) Haplolobus floribundus subsp. salomonensis (C.T.White) 18 48 Alyxia bracteolosa Rich. ex. A.Gray T(C/S) 19 49 Leenh. M(T) Alyxia stellata (J.R.Forst. & G.Forst.) Roem. & Schult. M, T 50 20 (C/S)21 **CAESALPINIACEAE** 51 Cerbera manghas L. M, T(T) Caesalpinia major (Medik.) Dandy & Exell <sup>T</sup>(C) 22 52 Cynometra falcata A.Gray E, T(T) Ochrosia vitiensis (Markgr.) Pichon <sup>T</sup>(T) 53 23 Cynometra insularis A.C.Sm. E, M, T(T) Parsonsia laevis (A.Gray) Markgr. M, T(C) 24 54 Parsonsia smithii Markgr. E, T(C) *Intsia bijuga* (Colebr.) Kuntze M, T(T) 25 55 *Tabernaemontana pandacaqui* Lam. M, T(S/T) Kingiodendron platycarpum B.L.Burtt E, M, T(T) 26 56 Maniltoa grandiflora (A.Gray) Scheff. M, T(T) 27 57 Maniltoa vestita A.C.Sm. E, M, T(T) **ARALIACEAE** 58 28 Plerandra vitiensis (Seem.) Baill. E, M(T) 29

Polyscias multijuga (A.Gray) Harms M, T(S/T)

1		30	CONNARACEAE
2	CAPPARACEAE	31	Connarus pickeringii A.Gray <sup>E, M</sup> (C)
3	Capparis quiniflora DC. <sup>T</sup> (C)	32	
4		33	CONVOLVULACEAE
5	CARICACEAE	34	Ipomoea macrantha Roem. & Schult. M, T(C)
6	*Carica papaya L. <sup>M, T</sup> (S/T)	35	Merremia peltata (L.) Merr. M, T(C)
7		36	
8	CASUARINACEAE	37	CUNNONIACEAE
9	$\textit{Gymnostoma vitiense} \text{ L.A.S.Johnson}^{\text{ E, M}}(T)$	38	Geissois ternata A.Gray <sup>E, M</sup> (T)
10		39	
11	CELASTRACEAE	40	CURCUBITACEAE
12	Celastrus richii A.Gray <sup>T</sup> (C)	41	*Coccinia grandis (L.) Voigt M, T (C)
13	Maytenus vitiensis (A.Gray) Ding Hou <sup>T</sup> (S/T)	42	
14		43	DICHAPETALACEAE
15	CHRYSOBALANACEAE	44	Dichapetalum vitiense (Seem.) Engl. M, T (S/C)
16	Parinari insularum A.Gray <sup>M</sup> (T)	45	
17		46	DILLENIACEAE
18	CLUSIACEAE	47	$\emph{Dillenia biflora}$ (A.Gray) Martelli ex Durand & Jacks. $^{M}\!(T)$
19	Calophyllum cerasiferum $Vesque^{E, M}(T)$	48	Hibbertia lucens Brongn. & Gris ex Sébert & Pancher $^{M}(S)$
20	Calophyllum vitiense Turrill $^{E, M}(T)$	49	
21	Garcinia adiantha A.C.Sm. & S.P.Darwin E, M(T)	50	EBENACEAE
22	Garcinia myrtifolia (A.Gray) Seem. M(T)	51	Diospyros elliptica (J.R.Forst. & G.Forst.) P.S.Green $^{T}(T)$
23	Garcinia pseudoguttifera Seem. M(T)	52	Diospyros major (G.Forst.) Bakh. M, T(T)
24	Garcinia sessilis (G.Forst.) Seem. M, T (T)	53	Diospyros phlebodes (A.C.Sm) A.C.Sm. $^{E, T}(T)$
25		54	
26	COMBRETACEAE	55	ELAEOCARPACEAE
27	$Terminalia\ catappa\ L.\ ^{T}(T)$	56	Elaeocarpus storckii Seem. E, M(T)
28	Terminalia littoralis Pancher ex Guillaumin <sup>T</sup> (T)	57	
29		58	EUPHORBIACEAE
		59	Acalypha insulana Müll.Arg. <sup>M, T</sup> (S/T)

1	Acalypha repanda Müll.Arg. <sup>E, M, T</sup> (S/T)	31	Mucuna gigantea (Willd.) D.C. <sup>T</sup> (C)
2	Aleurites moluccana (L.) Willd. M, T(T)	32	
3	Baccaurea stylaris Müll.Arg. <sup>E, M</sup> (T)	33	FLACOURTIACEAE
4	Claoxylon echinospermum Müll.Arg. <sup>E, M</sup> (S/T)	34	Casearia richii A.Gray <sup>T</sup> (S)
5	Claoxylon fallax Müll.Arg. <sup>E, M</sup> (S/T)	35	Erythrospermum accuminatissimum (A.Gray) A.C.Sm. M,
6	Croton metallicus Müll.Arg. <sup>T</sup> (S)	36	$^{\mathrm{T}}(\mathrm{T})$
7	Croton microtiglium Burkill <sup>T</sup> (T)	37	Flacourtia subintegra A.C.Sm. E, M, T(T)
8	Drypetes vitiensis Croizat <sup>T</sup> (T)	38	Homalium laurifolium A.C.Sm. <sup>M, T</sup> (T)
9	Endospermum macrophyllum (Müll.Arg.) Pax & K.Hoffm	n. <del>§</del> 9	Homalium vitiense Benth. E, M, T(T)
10	M(T)	40	
11	Excoecaria acuminata Gillespie <sup>T</sup> (T)	41	GYROCARPACEAE
12	Glochidion amentuligerum (Müll.Arg) Croizat <sup>E, M</sup> (S/T)	42	Gyrocarpus americanus Jacq. M, T(T)
13	Glochidion cordatum Seem. E, M(S/T)	43	
14	Glochidion ramiflorum J.R.Forst. & G.Forst. M, T (S/T)	44	LAURACEAE
15	Glochidion seemannii Müll.Arg. <sup>E, M, T</sup> (S/T)	45	Cinnamomum Schaeffer sp. <sup>T</sup> (T)
16	Glochidion vitiense (Müll.Arg.) Gillespie $^{T}(S/T)$	46	Cryptocarya hornei Gillespie <sup>M</sup> (T)
17	Homalanthus nutans (G.Forst.) Guill. <sup>M</sup> (T)	47	
18	$\it Macaranga\ membranaceae\ M\"{u}ll.Arg.\ ^{E,\ M}(T)$	48	LECYTHIDACEAE
19	Macaranga seemannii (Müll.Arg.) Müll.Arg. <sup>M</sup> (T)	49	Barringtonia edulis Seem. E, T(T)
20	Macaranga vitiensis Pax & K.Hoffm. E, M(T)	50	
21	Mallotus tiliifolius (Blume) Müll.Arg. <sup>T</sup> (T)	51	LOGANIACEAE
22	Phyllanthus heterodoxus Müll.Arg. <sup>E, M</sup> (S)	52	Fagraea berteroana A.Gray ex Benth. M(T/E)
23	Stillingia pacifica Müll.Arg <sup>T</sup> (T)	53	Fagraea gracilipes A.Gray <sup>M</sup> (T)
24		54	<i>Geniostoma rupestre</i> J.R.Forst. & G. Forst. <sup>M</sup> (S)
25	FABACEAE	55	<i>Neuburgia</i> cf. <i>corynocarpa</i> (A.Gray) Leenh. <sup>M</sup> (T)
26	Abrus precatorius L. <sup>T</sup> (C)	56	
27	Derris trifoliata Lour. M, T(C)	57	LORANTHACEAE
28	Erythrina variegata L. <sup>T</sup> (T)	58	Decaisnina forsterana (Schult. & Schult.f.) Barlow <sup>M</sup> (E/HP)
29	Inocarpus fagifer (Parkinson) Fosberg M, T(T)	59	
30	Millettia pinnata (L.) Panigrahi <sup>T</sup> (T)		

1	MALPHIGIACEAE	31	Serianthes melanesica Fosberg M, T(T)
2	Hiptage myrtifolia A.Gray <sup>E, M, T</sup> (C)	32	Serianthes vitiensis A.Gray <sup>E, T</sup> (T)
3		33	
4	MALVACEAE	34	MORACEAE
5	Hibiscus tiliaceus L. <sup>T</sup> (S/T)	35	Ficus barclayana (Miq.) Summerh. E, M, T (S/T)
6	<i>Thespesia populnea</i> (L.) Sol. ex Correa <sup>T</sup> (T)	36	Ficus fulvo-pilosa Summerh. E, M, T (S/T)
7		37	Ficus greenwoodii Summerh. <sup>E, M</sup> (S/T)
8	MELASTOMATACEAE	38	Ficus obliqua G.Forst. M, T (T/ST)
9	Astronidium cf. parviflorum A.Gray $^{E, M}(T)$	39	Ficus prolixa G.Forst. M, T(T/ST)
10	*Clidemia hirta (L.) D.Don <sup>M</sup> (H)	40	Ficus storckii Seem. M, T (S/T)
11	Melastoma denticulatum Labill. <sup>M</sup> (S)	41	Ficus theophrastoides Seem. E, M(S/T)
12	Memecylon vitiense A.Gray <sup>M</sup> (T)	42	Ficus tinctoria G.Forst. <sup>T</sup> (S/T)
13		43	Ficus vitiensis Seem. E, M(T)
14	MELIACEAE	44	Malaisia scandens (Lour.) Planch. M, T(C)
15	Aglaia basiphylla A.Gray <sup>E, M, T</sup> (T)	45	Streblus anthropophagorum (Seem.) Corner M, T (S/T)
16	Dysoxylum richii (A.Gray) C.DC. <sup>E, M, T</sup> (T)	46	Streblus pendulinus (Endl.) F.Muell. M, T(S/T)
17	Dysoxylum tenuiflorum A.C.Sm. $^{E, M}(T)$	47	
18	Vavaea amicorum Benth. M, T(T)	48	MYRISTICACEAE
19	Vavaea harveyi Seem. E, M(T)	49	Myristica castaneifolia A.Gray <sup>E, M</sup> (T)
20		50	Myristica gillespieana A.C.Sm. <sup>E, M</sup> (T)
21	MENISPERMACEAE	51	
22	Pachygone vitiensis Diels <sup>T</sup> (C)	52	MYRSINACEAE
23		53	Maesa corylifolia A.Gray <sup>E, M</sup> (S)
24	MIMOSACEAE	54	Maesa insularis Gillespie E, M(S)
25	*Adenanthera pavonina L. M, T(T)	55	Maesa persicifolia A.Gray <sup>E, M, T</sup> (S)
26	*Albizia lebbeck (L.) Benth. T(T)	56	Maesa pickeringii A.Gray <sup>E, T</sup> (S)
27	Entada phaseoloides (L.) Merr. M, T(C)	57	Maesa tabacifolia Mez M, T(S)
28	*Leucaena leucocephala (Lam.) de Wit $^{M, T}(S/T)$	58	Rapanea myricifolia (A.Gray) Mez M, T(T/S)
29	Racosperma richii (A.Gray) Pedley <sup>E, M</sup> (T)	59	Tapeinosperma grande (Seem.) Mez <sup>E, M</sup> (S)
30	*Samanea saman (Jacq.) Merr. <sup>T</sup> (T)	60	

1	MYRTACEAE (Myrtle Family)	31	
2	Decaspermum vitiense J.R.Forst. & G.Forst. <sup>E, M</sup> (T/S)	32	PHYTOLACCACEAE
3	Eugenia reinwardtiana (Blume) DC. <sup>T</sup> (S/T)	33	*Rivina humilis L. <sup>T</sup> (H)
4	Syzygium curvistylum (Gillespie) Merr. & L.M.Perry M(T)	34	
5	Syzygium decussatum (A.C.Sm.) Biffin & Craven <sup>E, M</sup> (T)	35	PIPERACEAE
6	Syzygium effusum (A.Gray) C.Muell. M(T)	36	Macropiper puberulum f. glabrum (C.DC.) A.C.Sm. <sup>M</sup> (S)
7	Syzygium eugenioides (Merr. & L.M.Perry) Biffin & Craven	<sup>™</sup> 37	
8	$^{\mathbf{E}}(\mathbf{T})$	38	PITTOSPORACEAE
9	Syzygium fijiense L.M.Perry <sup>E, M</sup> (T)	39	Pittosporum arborescens A.Gray <sup>M, T</sup> (T)
10	Syzygium rubescens (A.Gray) C.Muell. <sup>E, M</sup> (T)	40	Pittosporum brackenridgei A.Gray <sup>T</sup> (T)
11	Syzygium simillimum Merr. & L.M.Perry <sup>E, M</sup> (S/T)	41	Pittosporum rhytidocarpum A.Gray $^{E, M}(T)$
12		42	
13	NYCTGINACEAE	43	RHAMNACEAE
14	Pisonia grandis R.Br. <sup>T</sup> (T)	44	Alphitonia franguloides A.Gray <sup>E, M</sup> (T)
15		45	Alphitonia zizyphoides (Spreng.) A.Gray <sup>M, T</sup> (T)
16	OCHNACEAE	46	Colubrina asiatica (L.) Brongn. <sup>T</sup> (C)
17	Brackenridgea nitida A.Gray <sup>M, T</sup> (S/T)	47	Gouania richii A.Gray <sup>E, M</sup> (C)
18		48	Rhamnella vitiensis (Benth.) A.C.Sm. <sup>T</sup> (C)
19	OLACEAE	49	Ventilago vitiensis A.Gray <sup>M, T</sup> (C)
20	Anacolosa lutea Gillespie <sup>M</sup> (T)	50	
21		51	RHIZOPHORACEAE
22	OLEACEAE	52	Crossostylis pachyantha A.C.Sm. <sup>E, M</sup> (T)
23	Jasminum didymum G.Forst. M, T(C)	53	Crossostylis richii (A.Gray) A.C.Sm. <sup>E, M</sup> (T)
24	Jasminum simplicifolium G.Forst. M, T(C)	54	
25		55	RUBIACEAE
26	PASSIFLORACEAE	56	Airosperma vanuense S.P.Darwin <sup>E, M, T</sup> (T)
27	Passiflora aurantia G.Forst. <sup>T</sup> (C)	57	Antirhea incospicua (Seem.) Christoph. M, T(T)
28	*Passiflora foetida L. <sup>M, T</sup> (C)	58	Antirhea smithii (Fosberg) Merr. & L.M.Perry <sup>M</sup> (T)
29	Passiflora laurifolia L. <sup>T</sup> (C)	59	Coprosma persicifolia A.Gray <sup>T</sup> (S/T)
30	*Passiflora suberosa L. <sup>M, T</sup> (C)	60	Cyclophyllum sessilifolium (A.Gray) A.C.Sm. & S.P.Darwin

1	<sup>T</sup> (S/T)	31	SANTALACEAE
2	Gardenia gordoni Baker <sup>E, M</sup> (T)	32	Exocarpos vitiensis A.C.Sm. E, M(S/T)
3	Gardenia hillii Horne ex Baker <sup>E, M</sup> (T)	33	
4	Guettarda wayaensis R.O.Gardner E, T(T)	34	SAPINDACEAE
5	Guettarda speciosa L. <sup>T</sup> (T)	35	$Arytera\ brackenridgei\ (A.Gray)\ Radlk.\ ^{T}\!(T)$
6	Gynochthodes epiphytica (Rech.) A.C.Sm. & S.P.Darwin	36	Dodonaea viscosa (L.) Jacq. M, T(S)
7	$^{\mathrm{M}}(\mathrm{C})$	37	Elattostachys falcata (A.Gray) Radlk. <sup>M, T</sup> (T)
8	Ixora elegans Gillespie E, M(S/T)	38	Koelreuteria elegans (Seem.) A.C.Sm. M, T(T)
9	Ixora cf. myrtifolia A.C.Sm. <sup>E, M</sup> (S/T)	39	Unknown genus <sup>T</sup> (T)
10	Mastixidendron flavidum (Seem.) A.C.Sm. E, M(T)	40	
11	Morinda citrifolia L. <sup>M, T</sup> (S/T)	41	SAPOTACEAE
12	Morinda mollis A.Gray <sup>T</sup> (C)	42	Burckella richii (A.Gray) H.J.Lam. <sup>M</sup> (T)
13	Morinda myrtifolia A.Gray <sup>E, M, T</sup> (C)	43	Manilkara dissecta (L.f.) Dubard M, T(T)
14	Ophiorrhiza leptantha A.Gray <sup>M</sup> (H)	44	Manilkara smithiana H.J.Lam & Mass Geester. E, M(T)
15	Pelagodendron vitiense Seem. E, M(T)	45	Palaquium fidjiense Pierre ex Dubard <sup>E, M</sup> (T)
16	Psychotria amoena A.C.Sm. <sup>M, T</sup> (S/T)	46	Palaquium porphyreum A.C.Sm. & S.P.Darwin <sup>E, M</sup> (T)
17	Psychotria argantha A.C.Sm. <sup>E, M</sup> (S/T)	47	Pouteria cf. garberi (Christophers.) Baehni <sup>M</sup> (T)
18	Psychotria gibbsiae S.Moore <sup>E, M</sup> (S/T)	48	Pouteria grayana (H.St.John) Fosberg M, T(T)
19	Psychotria hypargyraea A.Gray <sup>E, M</sup> (S/T)	49	Pouteria membranacea (H.J.Lam) Baehni $^{\rm M}({\rm T})$
20	Psychotria tephrosantha A.Gray <sup>E, M</sup> (C)	50	
21	Psychotria volii R.O.Gardner <sup>E, T</sup> (S/T)	51	SIMAROUBACEAE
22	Psydrax odorata (G.Forst.) A.C.Sm. & S.P.Darwin M, T (S/	T <b>5</b> 2	Amaroria soulameoides A.Gray $^{E, M}(T)$
23	*Spermacoce remota Lam. M(H)	53	
24	Tarenna seemanniana A.C.Sm. & S.P.Darwin E, M(T)	54	SOLANACEAE
25		55	Capsicum frutescens L. <sup>T</sup> (S)
26	RUTACEAE	56	
27	Melicope cucullata (Gillespie) A.C.Sm. E, T(T)	57	STERCULIACEAE
28	Micromelum minutum (G.Forst.) Wight & Arn. M, T (S/T)	58	Commersonia bartramia (L.) Merr. <sup>M</sup> (T)
29	Sarcomelicope petiolaris (A.Gray) A.C.Sm. <sup>E, M</sup> (T)	59	Firmiana diversifolia A.Gray <sup>E, M</sup> (T)
30		60	Heritiera ornithocephala Kosterm. <sup>M</sup> (T)

1	Kleinhovia hospita L. <sup>T</sup> (T)	30	
2	Melochia degeneriana A.C.Sm. $^{E, T}(T)$	31	AGAVACEAE
3	Melochia grayana A.C.Sm. <sup>E, M</sup> (T/S)	32	Cordyline fruticosa (L.) A.Chev. M, T (S/T)
4		33	
5	THYMELAEACEAE	34	ARACEAE
6	Phaleria glabra (Turrill) Domke <sup>M</sup> (S)	35	Epipremnum pinnatum (L.) Engl. M, T (C)
7	Wikstroemia foetida (L.f.) A.Gray <sup>M, T</sup> (S)	36	
8		37	ARECACEAE
9	TILIACEAE	38	Veitchia filifera (H.Wendl.) H.E.Moore <sup>E, M</sup> (T)
10	Grewia crenata (J.R.Forst. & G.Forst.) Schinz & Guillaumi	n 39	
11	$^{\mathrm{T}}(\mathrm{T})$	40	CYPERACEAE
12	Trichospermum richii (A.Gray) Seem. <sup>M</sup> (T)	41	Carex dietrichiae Boeckeler <sup>M</sup> (H)
13		42	Fimbristylis dichotoma (L.) Vahl. $^{\rm M}({\rm H})$
14	ULMACEAE	43	Gahnia aspera (R.Br.) Spreng. <sup>M</sup> (H)
15	Gironniera celtidifolia Gaudich. <sup>M</sup> (T)	44	Hypolytrum nemorum subsp. vitiense (C.B.Clarke)
16	Trema cannabina L. <sup>T</sup> (T)	45	Koyama <sup>M</sup> (H)
16 17	Trema cannabina L. <sup>T</sup> (T)		Koyama <sup>M</sup> (H)  Machaerina falcata (Nees) Koyama <sup>M</sup> (H)
	Trema cannabina L. <sup>T</sup> (T)  URTICACEAE		
17 18		46	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)
17 18	URTICACEAE	46 47 48	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)
17 18 19	URTICACEAE	46 47 48	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)
17 18 19 20	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)	46 47 48 49	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)
17 18 19 20 21	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE	46 47 48 49 50 51	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)
17 18 19 20 21 22	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)	46 47 48 49 50 51	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE
17 18 19 20 21 22 23	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)  Faradaya ovalifolia (A.Gray) Seem. E, M(C)	46 47 48 49 50 51 52 53	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE  Dioscorea alata L. <sup>M, T</sup> (C)
17 18 19 20 21 22 23 24	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)  Faradaya ovalifolia (A.Gray) Seem. E, M(C)  Gmelina vitiensis (Seem.) A.C.Sm. E, M(T)	46 47 48 49 50 51 52 53	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE  Dioscorea alata L. <sup>M, T</sup> (C)
17 18 19 20 21 22 23 24 25	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)  Faradaya ovalifolia (A.Gray) Seem. E, M(C)  Gmelina vitiensis (Seem.) A.C.Sm. E, M(T)  *Lantana camara L. var. aculeata (L.) Moldemke M, T(S/C)	46 47 48 49 50 51 52 53 C)54 55	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE  Dioscorea alata L. <sup>M, T</sup> (C)
17 18 19 20 21 22 23 24 25 26	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)  Faradaya ovalifolia (A.Gray) Seem. E, M(C)  Gmelina vitiensis (Seem.) A.C.Sm. E, M(T)  *Lantana camara L. var. aculeata (L.) Moldemke M, T(S/C)	46 47 48 49 50 51 52 53 C)54 55	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE  Dioscorea alata L. <sup>M, T</sup> (C)  FLAGELLARIACEAE  Flagellaria gigantea Hook.f. <sup>M, T</sup> (C)
17 18 19 20 21 22 23 24 25 26 27	URTICACEAE  Leucosyke corymbulosa (Wedd.) Wedd. M(S)  VERBENACEAE  Clerodendrum inerme (L.) Gaertn. T(C)  Faradaya ovalifolia (A.Gray) Seem. E, M(C)  Gmelina vitiensis (Seem.) A.C.Sm. E, M(T)  *Lantana camara L. var. aculeata (L.) Moldemke M, T(S/C)	46 47 48 49 50 51 52 53 \$\infty\$\inft	Machaerina falcata (Nees) Koyama <sup>M</sup> (H)  Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf <sup>M</sup> (H)  Scleria lithosperma (L.) Sw. <sup>M, T</sup> (H)  Scleria polycarpa Boeckeler <sup>M, T</sup> (H)  DIOSCOREACEAE  Dioscorea alata L. <sup>M, T</sup> (C)  FLAGELLARIACEAE  Flagellaria gigantea Hook.f. <sup>M, T</sup> (C)

1 Bulbophyllum gracillimum (Rolfe) Rolfe <sup>M</sup>(E) 31 Tacca leontopetaloides (L.) Kuntze <sup>T</sup>(H) Bulbophyllum cf. hassallii P.J.Kores E, M(E) 32 Bulbophyllum rostriceps Rchb.f. M(E) 33 ZINGIBERACEAE Alpinia boia Seem. E, M(H) Corymborkis veratrifolia (Reinw.) Blume <sup>T</sup>(H) 34 Dendrobium catillare Rchb.f. E, M(E) Alpinia vitiensis Seem. E, M(H) 35 Dendrobium platygastrium Rchb.f. M(E) 36 Dendrobium tokai Rchb.f. ex Seem. M(E) 37 Luisia teretifolia Gaudich. M(E/C) Malaxis Sol. spp. M(H) Oberonia heliophila Benth. & Hook.f. ex Drake M(E) 10 Pseuderia smithiana C.Schweinf. E, M(E) 11 Taeniophyllum fasciola (Sw.) Seem. M, T(E) 12 Trachoma Garay spp. <sup>T</sup>(E) 13 14 **PANDANACEAE** Freycinetia cf. impavida (Gaudich. ex Hombr.) Stone M(C) 16 Pandanus tectorius Parkinson M, T (S/T) 17 18 **POACEAE** 19 Centosteca lappacea (L.) Desv. M, T(H) 20 Digitaria setigera Roth ex Roem. & Schult. M(H) 21 Garnotia linearis Swallen <sup>E, M</sup>(H) 22 Leptaspis angustifolia Summerh. & C.E.Hubb. E, M(H) 23 Oplismenus compositus (L.) P.Beauv. M, T(H) 24 Oplismenus hirtellus (L.) P.Beauv. M, T(H) 25 26 **SMILACEAE** 27 Smilax vitiensis (Seem.) A.DC. M, T(C) 28

TACCACEAE

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- Appendix 2. Tree species data set used for cluster analysis. Only canopy and subcanopy trees
- 2 genuinely associated with mature-stage forest were included. The major dispersal mechanism and
- 3 floral sexuality are indicated for tree species: DE, species deciduous; SC, species sclerophyllous; V,
- 4 vertebrate dispersed; W, wind dispersed; O, dispersed by other means (water, gravity, self-dispersed);
- 5 He, hermaphrodite; Di, dioecious; Mo, monoecious.

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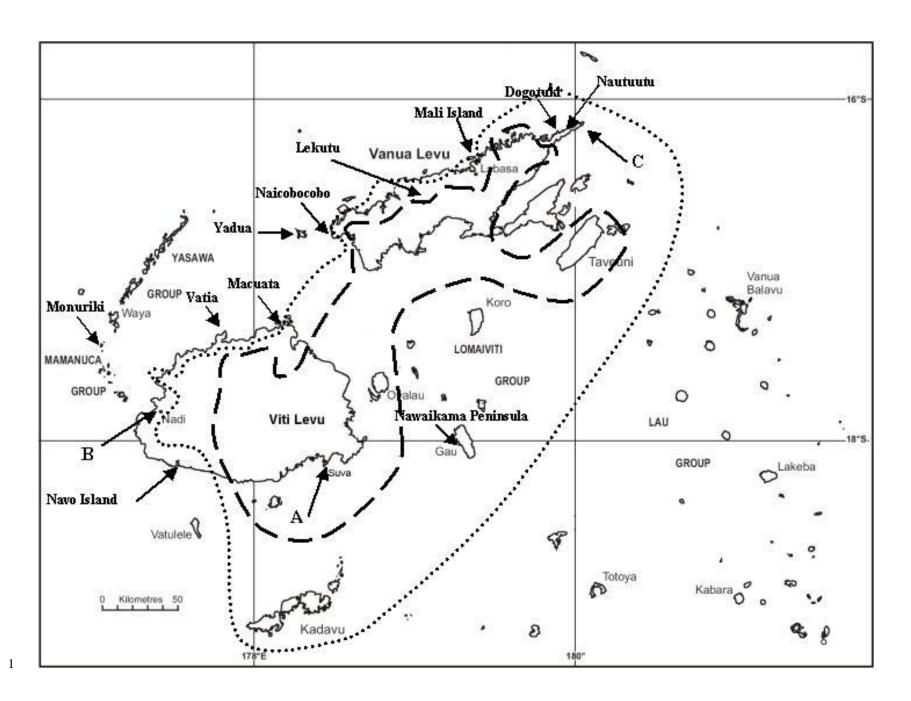
	Nautu-	Dogo-				Yadua	Naicobo-	Monu-		Macua-
	utu	tuki	Lekutu	Navo	Vatia	Taba	cobo	riki	Gau	ta
Agathis macrophylla SC, W, Mo	0	1	0	0	0	0	0	0	0	0
Amaroria soulameoides <sup>V, Di</sup>	1	1	1	0	0	0	0	0	0	0
Antirhea inconspicua DE, V, Di	0	0	0	1	0	1	1	0	1	1
Arytera brackenridgei <sup>SC, O, Mo</sup>	0	0	0	0	0	0	1	1	0	1
Buchanania attenuata <sup>V, He</sup>	0	1	1	0	0	0	1	0	0	0
Buchanania vitiensis <sup>V, He</sup>	1	1	0	0	0	0	0	0	0	0
Burckella richii <sup>SC, V, Mo</sup>	0	0	0	0	0	0	0	1	0	0
Calophyllum cerasiferum SC, V, He	0	1	0	0	0	0	0	0	0	0
Calophyllum vitiense V, He	0	1	0	0	0	0	0	0	0	0
Canarium vitiense <sup>V, Di</sup>	0	1	1	0	0	0	0	0	0	0
Cerbera manghas <sup>O, M</sup>	1	0	0	0	1	1	0	0	0	1
Cordia subcordata V, He	0	0	0	1	0	1	0	0	0	1
Crossostylis pachyantha V, He	0	1	0	0	0	0	0	0	0	0
Croton microtiglium V, Mo	0	0	0	0	0	1	0	0	0	1
Cryptocarya hornei <sup>V, He</sup>	0	0	1	0	0	0	0	0	0	0
Cyathocalyx cf. vitiensis V, He	0	1	1	0	0	0	0	0	0	0
Cycas seemannii <sup>SC, V, Di</sup>	0	0	1	0	0	0	0	0	1	0
Cynometra falcata SC, V, He	0	0	0	0	1	1	1	0	0	1

Cynometra insularis <sup>V, He</sup>	0	1	0	1	0	0	0	0	1	1
Dacrydium nidulum SC, V, Di	0	1	1	0	0	0	0	0	0	0
Decaspermum vitiense SC, V, He	0	1	1	0	0	0	0	0	0	0
Dillenia biflora <sup>V, Mo</sup>	1	1	0	0	0	0	0	0	0	0
Diospyros elliptica <sup>V, Di</sup>	0	0	0	1	1	0	1	1	1	1
Diospyros phlebodes SC, V, Di	0	0	0	0	1	1	0	1	1	1
Drypetes vitiensis <sup>V, Di</sup>	0	0	0	0	0	1	0	1	0	0
Dysoxylum richii <sup>V, Di</sup>	0	1	0	1	1	0	1	0	0	0
Dysoxylum tenuiflorum <sup>V, He</sup>	0	1	0	0	0	0	0	0	0	0
Elattostachys falcate SC, V, Mo	0	0	0	1	1	0	0	0	0	0
Erythrina variegata DE, O, Mo	0	0	0	1	1	1	1	0	0	0
Excoecaria acuminata <sup>V, Di</sup>	0	0	0	1	0	1	1	1	0	1
Fagraea gracilipes <sup>V, He</sup>	0	1	1	0	0	0	0	0	0	0
Ficus obliqua <sup>SC, V, Mo</sup>	0	0	0	1	0	1	1	0	0	0
Ficus prolixa SC, V, Mo	0	0	0	1	0	1	1	0	0	0
Garcinia pseudoguttifera <sup>V, Di</sup>	1	1	0	0	0	0	0	0	0	0
Garcinia sessilis <sup>SC, V, Di</sup>	0	0	0	0	0	0	1	0	0	0
Garuga floribunda <sup>DE, V, He</sup>	0	0	0	0	1	0	1	0	0	0
Gmelina vitiensis <sup>O, He</sup>	0	1	0	0	0	0	0	0	0	0
Gnetum gnemon V, Di	0	1	1	0	0	0	0	0	0	0
Guettarda wayaense DE, V, He	0	0	0	0	0	0	1	1	0	0
Gymnostoma vitiense SC, W, Mo	1	1	0	0	0	0	0	0	0	0
Gyrocarpus americanus DE, W, Mo	0	0	0	1	1	1	1	1	1	1
Haplolobus floribundus <sup>V, Di</sup>	0	1	1	0	0	0	0	0	0	0
Homalium laurifolium <sup>V, He</sup>	0	0	1	0	0	0	0	0	0	0
Homalium vitiense V, He	0	0	0	1	0	1	1	1	0	0
Intsia bijuga <sup>O, Mo</sup>	1	1	0	1	1	0	0	1	0	0

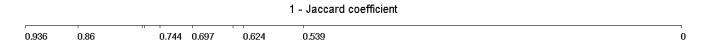
Kingiodendron platycarpum <sup>O, He</sup>	0	0	0	1	0	1	1	1	0	0
Koelreuteria elegans DE, W, Mo	0	0	0	0	1	0	1	0	0	0
Macaranga membranaceae <sup>V, Mo</sup>	0	1	0	0	0	0	0	0	0	0
Macaranga vitiensis <sup>V, Mo</sup>	0	1	0	0	0	0	0	0	0	0
Mallotus tiliifolius <sup>V, Di</sup>	0	0	0	0	1	1	1	1	1	1
Manilkara dissecta <sup>SC, V, Mo</sup>	0	1	0	1	0	1	1	0	0	0
Maniltoa grandiflora <sup>O, Mo</sup>	0	1	0	0	0	0	1	0	0	0
Maniltoa vestita <sup>SC, O, Mo</sup>	1	0	0	0	1	0	0	1	0	1
Mastixiodendron flavidum <sup>V, He</sup>	0	0	1	0	0	0	0	0	0	0
Millettia pinnata DE, O, He	0	0	0	0	1	1	0	1	1	0
Myristica castaneifolia <sup>V, Di</sup>	0	1	0	0	0	0	0	0	0	0
Myristica gillespieana <sup>V, Di</sup>	1	1	1	0	0	0	0	0	0	0
Palaquium fidjiense <sup>V, He</sup>	1	1	1	0	0	0	0	0	0	0
Parinari insularum <sup>V, He</sup>	0	1	1	0	0	0	0	0	0	0
Pittosporum arborescens <sup>V, He</sup>	0	1	0	1	0	0	1	0	0	0
Pittosporum brackenridgei <sup>V, He</sup>	0	0	0	0	0	1	1	0	0	0
Pleiogynium timoriense DE, V, Di	0	1	0	0	1	0	1	0	0	1
Podocarpus nerifolius <sup>SC, V, Di</sup>	0	1	1	0	0	0	0	0	0	0
Polyalthia laddiana <sup>V, He</sup>	0	0	0	1	0	0	1	0	0	0
Pouteria garberi <sup>V, He</sup>	0	1	1	0	0	0	0	0	0	0
Pouteria grayana <sup>V, He</sup>	0	0	0	1	1	1	1	1	1	1
Premna protusa <sup>V, He</sup>	0	0	0	0	0	1	1	0	0	1
Racosperma richii <sup>SC, O, Mo</sup>	0	1	1	0	0	0	0	0	0	0
Rapanea myrtifolia SC, V, Di	0	1	1	0	0	0	0	0	0	0
Sarcomelicope petiolaris <sup>V, Di</sup>	0	1	1	0	0	0	0	0	0	0
Semecarpus vitiensis <sup>V, Di</sup>	0	1	0	0	0	0	0	0	0	0
Serianthes melanesica <sup>O, He</sup>	0	0	0	0	0	0	0	0	0	1

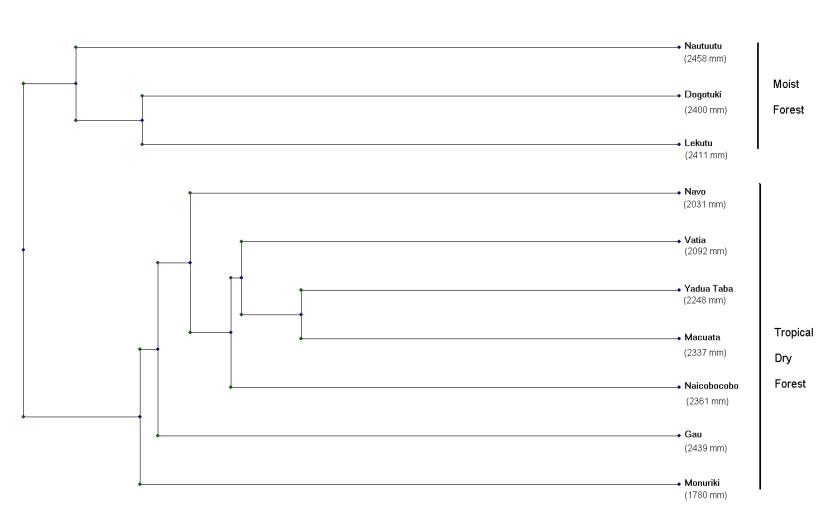
Stillinga pacifica SC, O, Mo	0	0	0	0	0	0	0	0	1	0
Syzygium decussatum V, Mo	0	1	0	0	0	0	0	0	0	0
Syzygium eugenoides SC, V, Mo	0	1	1	0	0	0	0	0	0	0
Syzygium fijiensis <sup>SC, V, Mo</sup>	0	1	1	0	0	0	0	0	0	0
Syzygium rubescens V, Mo	0	1	1	0	0	0	0	0	0	0
Sapindaceae DE, V, He	0	0	0	1	1	0	1	0	0	0
Vavaea amicorum <sup>V, He</sup>	1	1	0	1	1	1	1	1	1	1
Veitchia filifera <sup>V, Mo</sup>	1	1	0	0	0	0	0	0	0	0

**Fig. 1** 



## 1 Fig. 2





## **Fig. 3**

