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^{-1} of rain and covered with native forest were identified using maps, aerial photographs, estimated climate (WorldClim) and field reconaissance. 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.

Keywords climate; deciduous; mesic forest; moist forest; natural history; sclerophyll; talasiga grasslands; tropical dry forest

INTRODUCTION

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 (more than one month with an average rainfall of less than 100 mm) (Walsh 1996). Sclerophyllous leaves are tough and can resist drought and insect attack through thick cell walls and relatively low nitrogen content (Eamus 1999). The term moist forest (MF, after Holdridge 1971) is used for evergreen 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 (1996).

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 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 the subtropical Pacific Ocean. The two largest islands are relatively high (to 1323 m) and large (10388 km^2) (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. 2006). The wet, windward, south-eastern sides are covered with rainforest, while most of the dry, leeward, western sites are presently covered with grasslands, called “talasiga” (“sunburnt land”) in the native vernacular, and small forest remnants (Parham 1972; Mueller-Dombois & Fosberg 1998). On the drier, leeward side droughts regularly occur. Mean annual rainfall is lowest in the coastal regions and increases inland (Mataki et al. 2006).

Palynological evidence suggests that, before the arrival of people some 3000 years ago, much of the 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 (Keppel 2002).

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 *Dacrydium nidulum* and the angiosperm *Fagraea gracilepes*, with *Gymnostoma vitiensis, Myristica castaneifolia*, *Dysoxylum richii*, *Parinari insularum*, *Intsia bijuga*, *Casuarina eqiusetfolia*, species of *Syzygium*, and the conifer *Podocarpus neriifolius* being other locally common species (Twyford et al. 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 Fiji.

In this paper we report the existence of true TDF in Fiji. We then compare it with MF to 1) identify the 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 forests, and 4) assess the anthropogenic impact on TDF and MF.

METHODS

Climate

The climates of the Suva (18.09˚ S, 178.27˚ E) and Nadi (17.75˚ S, 177.45˚ E; see Fig. 1) weather 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 (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.

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).

Selection of sample sites

To identify forest remnants in Fiji's dry zone, we used climatic information (Fitzpatrick et al. 1966; 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 identify the areas that still have forest cover (rather than talasiga grassland), and eliminated areas that were composed of commercial plantations of *Pinus carribae* using the maps of Chandra & Mason (1998). Having identified places with potentially native vegetation, we visited 21 potential sites and eliminated those that were almost completely covered with the invasive legumes *Samanea saman*, *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^2) of native trees remaining and were excluded from subsequent analyses. This left us with 10 study sites (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

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 not a species was annually deciduous (pers. obs. in different TDF during the dry season) or sclerophyllous. Published literature was used to assign floral sexuality (monoecious, dioecious or 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

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

Species were classified as deciduous or sclerophyllous using broad concepts. Deciduous species included "true" deciduous species that loose their leaves at regular seasonal intervals and drought-deciduous species, which only loose their leaves during prolonged dry periods. We did not distinguish between those and other types of deciduousness (Eamus 1999), because long-term phonological data 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; 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.

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

We excluded species that were sometimes found at the coastal fringes of the forest systems studied but are generally associated with coastal locations (*Abrus prectorius*, *Colubrina asiatica*, *Lumnitzera littorea*, *Pandanus tectorius*, *Premna serratifolia*, *Terminalia catappa*, *Terminalia littoralis*, *Thespesia populnea*) and species that are non-native and invasive (e.g., *Albizia lebbeck*, *Leucaena leucocephala*, *Rivina humilis*, *Samanea saman*) or generally restricted to disturbed or regenerating sites sites (e.g. *Commersonia bartramia*, *Culcuita straminea*, *Merremia peltata*, *Nephrolepis hirsutula*, *Pureria 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 for several years, which can be detrimental to the vegetation of island forests (Spatz & Mueller-Dombois 1973; Scowcroft & Hobdy 1987). The island of Monuriki was extremely affected, having 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 that do not normally exceed a dbh 5 cm), which are the most vulnerable to grazing (Daubenmire 1972; 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 Analysis Package (CAP; Henderson & Seaby 2002) to determine the presence of different native forest types. Two distinct clusters, corresponding to MF and TDF, were produced.

We tested the significance of the two clusters (forest types) by analysis of similarity (ANOSIM) using 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 transformed Bray-Curtis similarity matrix and doing an ANOSIM between the samples using all possible (120) permutations. We then tested which species were associated with TDF and MF using

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

RESULTS

Vegetation

Two distinct forest types with low similarity are found in Fiji's dry zone (Fig. 2). One comprises all the 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 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 = 2439 mm yr^{-1}) 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 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).

Several tree species, including *Racosperma richii*, *Buchanania richii*, *Dacrydium nidulum*, *Decaspermum vitiense*, *Fagraea gracilipes*, *Gymnostoma vitiense*, *Palaquium fidjiense*, *Rapanea myrtifolia*, *Sarcomelicope petiolaris* were clearly associated with MF in the DECORANA plot (Fig. 3). This also included several tree species that are also common in lowland rain forests, such as *Amaroria soulemanoides*, *Dillenia biflora*, *Garcinia pseudoguttifera*, *Myristica* spp., *Parinari insularum*, and

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

Flora of dry zone forests

A total of 310 native (and 14 common invasive) species were recorded in forests of the dry zone (Table 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% (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% 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 hirta*, *Albizia labbeck*, *Samanea saman*, *Leucaena leucocephala*, *Passiflora foetida*, and *Lantana 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 2). Climbing plants were more diverse in TDF, comprising almost 21% of all indigenous species (cf.

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

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

The diversity within plant families differed greatly between forest types (Table 3). Orchids (Orchidaceae), sedges (Cyperaceae), Myrtaceae, Sapotaceae, grasses (Poaceae), and the Sapotaceae are the most diverse families in MF, while legumes (Caesalpinaceae, Fabaceae, Mimosaceae), 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 (Cyatheaeceae), filmy ferns (Hymenophyllaceae), gingers (Alpiniaceae), Elaeocarpaceae, Melastomataceae, and Urticaceae.

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 than 30% of the species are deciduous. TDF also differs by having a lower percentage of species dispersed by vertebrates (70% cf. 82%). Both forest types, however, are similar with regard to floral sexuality, having a similar ratio of hermaphroditic:monoecious:dioecious and more than 30% of the species being monoecious.

Disturbance

Almost all the TDF sites have higher disturbance indices than the MF sites studied (Table 1). There is a strong negative correlation between average rainfall and the disturbance index (r = 0.87). Six of the 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 species and the Navo and Vatia forests were dominated by invasive species in most locations.

DISCUSSION

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

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 leeward side of high and relatively large islands. The strong rainshadow effect on the leeward site is probably not well estimated by World Clim, as the numerous leafless deciduous trees during the dry 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 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-shaped distibution of the species and study sites on the DCA plot is interesting but possibly simply caused by the fact that the MF cluster consists of only three sites, compared to the seven TDF sites.

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

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. 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 TDF to MF dominated by *Gymnostoma vitiense*.

In the Pacific region, TDF has been recorded from Australia (Fensham 1995), New Guinea (Paijmans 1976, p.66; Heylingers 1982), the Solomon Islands (Whitmore 1969), Vanuatu (Mueller-Dombois & Fosberg 1998), New Caledonia (Gillespie & Jaffré 2003), and Hawaii (Hatheway 1952). Except for 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.

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 (5-20%; Gross 2005; Machado et al. 2006). Only in Australia have similar percentages of monoecy (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.

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) 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 overlooked.

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

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, map and assess the conservation status of all remaining TDF fragments to ensure that the best remainining fragments of Fiji's TDF are preserved. This needs to be coupled with a quantitative study of TDF vegetation, investigation of prevalent climatic and soil conditions, and a detailed evaluation of the conservation status of the rare and potentially highly endangered plant species that are endemic to this forest type in Fiji, such as *Cynometra falcata* and *Guettarda wayaensis*. Finally, there is an urgent need to gain an understanding about the dynamics of Fijian TDF and the influence of various environmental factors have. This should facilitate predicting the response of TDF to long-term stresses, which is likely scenario under climate change.

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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 (m a.s.l.)	Latitude, longitude	Substrate, topography	Mean annual rainfall (mm)*	Number of dry months per year*^	Disturbance			
						Grazing	Fire	Invasive	Index
Monuriki (TDF)	5-50	17º36’34 S, 177º02’07 W	Volcanic, steep slopes	1780	6 (6)	4	3	2	9
Navo (TDF)	5-10	18º06’40 S, 177º19’07 W	Limestone, mostly flat	2031	3 (6)	4	2	3	9
Vatia (TDF)	20-40	17º23’10 S, 177º49’14 W	Volcanic, moderate slopes	2092	3 (5)	3	3	3	9
Macuata (TDF)	5-30	17º21’14 S, 178º01’60 W	Volcanic, moderate slopes	2337	2 (3)	2	3	2	7
Yadua Taba (TDF)	5-200	16º50’06 S, 178º16’40 W	Volcanic, steep slopes	2248	2 (4)	2	2	2	6

Gau (TDF)	5-20	18º00’14 S, 179º14’47 W	Volcanic, moderate slopes	2439	0 (3)	1	2	1	4
Dogotuki (MF)	40-70	16º13’55 S, 179º46’32 W	Volcanic, mostly flat	2400	2 (3)	1	2	1	4
Naicobocobo (TDF)	5-50	16º49’00 S, 178º29’45 W	Volcanic, moderate slopes	2362	2 (2)	1	2	1	3
Lekutu (MF)	220-230	16º38’04 S, 178º50’07 W	Volcanic, mostly flat	2411	2 (3)	1	1	1	3
Nautuutu (MF)	30-40	16º13’55 S, 179º49’27 W	Volcanic, mostly flat	2458	2 (3)	1	1	1	3

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/ *Life Form*	Endemic	Indigenous*	Invasive and/or naturalised	Total
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 Dry Forest		Moist Forest	
Euphorbiaceae	12 (2) spp.	Rubiaceae	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), MF, moist forest (*n* = 60).

Forest Type	**Leaf Type**[1]		**Dispersal**[2]			**Floral Sexuality**		
	% Deciduousness	**% Sclerophyll**	**Vertebrate**	**Wind**	**Other**	**Hermorphrodite**	**Dioecious**	**Monoecious**
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 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, Nadi; C, Udu Point.

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

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

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

PTERIDOPHYTA (Ferns and Fern Allies)

LYCOPSIDA

LYCOPODIACEAE

Lycopodiella cernua (L.) Pic.Serm. [M](H)

Huperzia phlegmaria (L.) Rothm. [M](E)

Huperzia squarrosa (G.Forst.) Trevis. [M](E)

SELAGINELLACEAE

Selaginella breynioides Baker [**E**, M](H)

Selaginella laxa Spring [M](H)

Selaginella viridangula Spring [**E**, M](H)

FILICOPSIDA

ADIANTACEAE

Adiantum hispidulum Sw. [T](H)

Cheilanthes nudiuscula (R.Br.) T.Moore [T](H)

Doryopteris concolor (Langsd. & Fisch.) Kuhn [T](H)

Taenitis pinnata (J.Sm.) Holttum [M](H)

ASPLENIACEAE

Asplenium australasicum Hook. [M](E)

Asplenium polyodon G.Forst. [M](E)

BLECHNACEAE

Blechnum orientale L. [M](H)

CYATHACEAE

Cyathea lunulata Copel. [M](TF)

Cyathea propinqua Mett. [**E**, M](TF)

DAVALLIACEAE

Davallia solida var. *fejeensis* (Hook.) Noot. [(var. **E**), M](E)

Davallia solida (G.Forst.) Sw. [M, T](E)

Humata heterophylla (Sm.) Desv. [M](E)

DENNSTAEDTIACEAE

Pteridium esculentum (G.Forst.) Cockayne [M](H)

Tapeinidium melanesicum Kramer [M](H)

DICKSONIACEAE

Calochlaena straminea (Labill.) M.D.Turner & R.A.White [M](H)

DRYOPTERIDACEAE

Tectaria latifolia (G.Forst.) Copel. [M](H)

GLEICHENIACEAE

Gleichenia oceanica Kuhn [M](H)

HYMENOPHYLLACEAE

Abrodictyum dentatum (Bosch) Ebihara & K.Iwats. [M](H)

Cephalomanes atrovirens C.Presl. [M](H)

Crepidomanes intermedia (Bosch) Ebihara & K.Iwats. [M](H)

LOMARIOPSIDACEAE

Lomagramma polyphylla Brack. [M](C/E)

MARATTIACEAE

Angiopteris evecta (G.Forst.) Hoffm. [M](H)

OLEANDRACEAE

Nephrolepis biserrata (Sw.) Schott [M, T](H)

Nephrolepis hirsutula (G.Forst.) C.Presl [M](H)

POLYPODIACEAE

Drynaria rigidula (Sw.) Bedd. [M, T](E)

Pyrrosia lanceolata (L.) Farwl [M, T](E/C)

PTERIDACEAE

Pteris ensiformis Burm.f. [M, T](H)

Pteris pacifica Hieron. [M](H)

SCHIZAEACEAE

Lygodium reticulatum Schkuhr [M](C)

Schizaea dichotoma (L.) Sm. [M, T](H)

THELYPTERIDACEAE

Sphaerostephanos invisus (G.Forst.) Holttum [M, T](H)

VITTARIACEAE

Haplopteris elongata (Sw.) E.H.Crane [M](E)

Monogramma acrocarpa (Holttum) D.L.Jones [E, M](E)

GYMNOSPERMAE (Gymnosperms)

CYCADALES

CYCADACEAE

Cycas seemannii A.Braun [M, T](T)

CONIFERALES

ARAUCARIACEAE

Agathis macrophylla (Lindl.) Mast. [M](T)

PODOCARPACEAE

Dacrydium nidulum de Laub. [M](T)

Podocarpus neriifolius D.Don [M](T)

GNETALES

GNETACEAE

Gnetum gnemon L. [M](T)

ANGIOSPERMAE (Angiosperms)

DICOTYLEDONAE (Dicotyledons)

ACANTHACEAE

Graptophyllum insularum (A.Gray) A.C.Sm. [M](S)

Pseuderanthemum laxiflorum (A.Gray) C.E.Hubb. ex L.H.Bailey [**E**, M](S)

ANACARDIACEAE

Buchanania attenuata A.C.Sm. [**E**, M, T](T)

Buchanania vitiensis Engl. [**E**, M](T)

Pleiogynium timoriense (DC.) Leenh. [M, T](T)

Rhus taitensis Guill. [M, T](T)

Semecarpus vitiense (A.Gray) Engl. [M](T)

ANNONACEAE

Cyathocalyx cf. *vitiensis* A.C.Sm. [**E**, M](T)

Polyalthia laddiana A.C.Sm. [T](T)

APOCYNACEAE

Alstonia pacifica (Seem.) A.C.Sm. [M](T)

Alstonia costata (G.Forst.) R.Br. [M](T)

Alyxia bracteolosa Rich. ex. A.Gray [T](C/S)

Alyxia stellata (J.R.Forst. & G.Forst.) Roem. & Schult. [M, T](C/S)

Cerbera manghas L. [M, T](T)

Ochrosia vitiensis (Markgr.) Pichon [T](T)

Parsonsia laevis (A.Gray) Markgr. [M, T](C)

Parsonsia smithii Markgr. [**E**, T](C)

Tabernaemontana pandacaqui Lam. [M, T](S/T)

ARALIACEAE

Plerandra vitiensis (Seem.) Baill. [**E**, M](T)

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

ASCLEPIADACEAE

Hoya australis R.Br. ex J.Traill [M, T](C)

Tylophora brackenridgei A.Gray [M, T](C)

ASTERACEAE

**Mikania micrantha* H.B. & K. [M, T](C)

BIGNONIACEAE

**Spathodea campanulata* P.Beauv. [M, T](T)

BORAGINACEAE

Cordia subcordata Lam. [T](T)

BURSERACEAE

Canarium cf. *vitiense* A.Gray [M](T)

Garuga floribunda Decne. [T](T)

Haplolobus floribundus subsp. *salomonensis* (C.T.White) Leenh. [M](T)

CAESALPINIACEAE

Caesalpinia major (Medik.) Dandy & Exell [T](C)

Cynometra falcata A.Gray [**E**, T](T)

Cynometra insularis A.C.Sm. [**E**, M, T](T)

Intsia bijuga (Colebr.) Kuntze [M, T](T)

Kingiodendron platycarpum B.L.Burtt [**E**, M, T](T)

Maniltoa grandiflora (A.Gray) Scheff. [M, T](T)

Maniltoa vestita A.C.Sm. [**E**, M, T](T)

CAPPARACEAE

Capparis quiniflora DC. [T](C)

CARICACEAE

**Carica papaya* L. [M, T](S/T)

CASUARINACEAE

Gymnostoma vitiense L.A.S.Johnson [**E**, M](T)

CELASTRACEAE

Celastrus richii A.Gray [T](C)

Maytenus vitiensis (A.Gray) Ding Hou [T](S/T)

CHRYSOBALANACEAE

Parinari insularum A.Gray [M](T)

CLUSIACEAE

Calophyllum cerasiferum Vesque [**E**, M](T)

Calophyllum vitiense Turrill [**E**, M](T)

Garcinia adiantha A.C.Sm. & S.P.Darwin [**E**, M](T)

Garcinia myrtifolia (A.Gray) Seem. [M](T)

Garcinia pseudoguttifera Seem. [M](T)

Garcinia sessilis (G.Forst.) Seem.[M, T](T)

COMBRETACEAE

Terminalia catappa L. [T](T)

Terminalia littoralis Pancher ex Guillaumin [T](T)

CONNARACEAE

Connarus pickeringii A.Gray [**E**, M](C)

CONVOLVULACEAE

Ipomoea macrantha Roem. & Schult. [M, T](C)

Merremia peltata (L.) Merr. [M, T](C)

CUNNONIACEAE

Geissois ternata A.Gray [**E**, M](T)

CURCUBITACEAE

**Coccinia grandis* (L.) Voigt [M, T](C)

DICHAPETALACEAE

Dichapetalum vitiense (Seem.) Engl. [M, T](S/C)

DILLENIACEAE

Dillenia biflora (A.Gray) Martelli ex Durand & Jacks. [M](T)

Hibbertia lucens Brongn. & Gris ex Sébert & Pancher [M](S)

EBENACEAE

Diospyros elliptica (J.R.Forst. & G.Forst.) P.S.Green [T](T)

Diospyros major (G.Forst.) Bakh.[M, T](T)

Diospyros phlebodes (A.C.Sm) A.C.Sm. [**E**, T](T)

ELAEOCARPACEAE

Elaeocarpus storckii Seem. [**E**, M](T)

EUPHORBIACEAE

Acalypha insulana Müll.Arg. [M, T](S/T)

Acalypha repanda Müll.Arg. [E, M, T](S/T)

Aleurites moluccana (L.) Willd.[M, T](T)

Baccaurea stylaris Müll.Arg. [E, M](T)

Claoxylon echinospermum Müll.Arg. [E, M](S/T)

Claoxylon fallax Müll.Arg. [E, M](S/T)

Croton metallicus Müll.Arg. [T](S)

Croton microtiglium Burkill [T](T)

Drypetes vitiensis Croizat [T](T)

Endospermum macrophyllum (Müll.Arg.) Pax & K.Hoffm. [E, M](T)

Excoecaria acuminata Gillespie [T](T)

Glochidion amentuligerum (Müll.Arg) Croizat [E, M](S/T)

Glochidion cordatum Seem. [E, M](S/T)

Glochidion ramiflorum J.R.Forst. & G.Forst. [M, T](S/T)

Glochidion seemannii Müll.Arg. [E, M, T](S/T)

Glochidion vitiense (Müll.Arg.) Gillespie [T](S/T)

Homalanthus nutans (G.Forst.) Guill. [M](T)

Macaranga membranaceae Müll.Arg. [E, M](T)

Macaranga seemannii (Müll.Arg.) Müll.Arg. [M](T)

Macaranga vitiensis Pax & K.Hoffm. [E, M](T)

Mallotus tiliifolius (Blume) Müll.Arg. [T](T)

Phyllanthus heterodoxus Müll.Arg. [E, M](S)

Stillingia pacifica Müll.Arg [T](T)

FABACEAE

Abrus precatorius L. [T](C)

Derris trifoliata Lour. [M, T](C)

Erythrina variegata L. [T](T)

Inocarpus fagifer (Parkinson) Fosberg [M, T](T)

Millettia pinnata (L.) Panigrahi [T](T)

Mucuna gigantea (Willd.) D.C. [T](C)

FLACOURTIACEAE

Casearia richii A.Gray [T](S)

Erythrospermum accuminatissimum (A.Gray) A.C.Sm. [M, T](T)

Flacourtia subintegra A.C.Sm. [E, M, T](T)

Homalium laurifolium A.C.Sm. [M, T](T)

Homalium vitiense Benth. [E, M, T](T)

GYROCARPACEAE

Gyrocarpus americanus Jacq. [M, T](T)

LAURACEAE

Cinnamomum Schaeffer sp. [T](T)

Cryptocarya hornei Gillespie [M] (T)

LECYTHIDACEAE

Barringtonia edulis Seem. [E, T](T)

LOGANIACEAE

Fagraea berteroana A.Gray ex Benth. [M](T/E)

Fagraea gracilipes A.Gray [M](T)

Geniostoma rupestre J.R.Forst. & G. Forst. [M](S)

Neuburgia cf. *corynocarpa* (A.Gray) Leenh. [M](T)

LORANTHACEAE

Decaisnina forsterana (Schult. & Schult.f.) Barlow [M](E/HP)

MALPHIGIACEAE

Hiptage myrtifolia A.Gray [E, M, T](C)

MALVACEAE

Hibiscus tiliaceus L. [T](S/T)

Thespesia populnea (L.) Sol. ex Correa [T](T)

MELASTOMATACEAE

Astronidium cf. *parviflorum* A.Gray [E, M](T)

**Clidemia hirta* (L.) D.Don [M](H)

Melastoma denticulatum Labill. [M](S)

Memecylon vitiense A.Gray [M](T)

MELIACEAE

Aglaia basiphylla A.Gray [E, M, T](T)

Dysoxylum richii (A.Gray) C.DC. [E, M, T](T)

Dysoxylum tenuiflorum A.C.Sm. [E, M](T)

Vavaea amicorum Benth. [M, T](T)

Vavaea harveyi Seem. [E, M](T)

MENISPERMACEAE

Pachygone vitiensis Diels [T](C)

MIMOSACEAE

**Adenanthera pavonina* L.[M, T](T)

**Albizia lebbeck* (L.) Benth.[T](T)

Entada phaseoloides (L.) Merr. [M, T](C)

**Leucaena leucocephala* (Lam.) de Wit [M, T](S/T)

Racosperma richii (A.Gray) Pedley [E, M](T)

**Samanea saman* (Jacq.) Merr. [T](T)

Serianthes melanesica Fosberg [M, T](T)

Serianthes vitiensis A.Gray [E, T](T)

MORACEAE

Ficus barclayana (Miq.) Summerh. [E, M, T](S/T)

Ficus fulvo-pilosa Summerh. [E, M, T](S/T)

Ficus greenwoodii Summerh. [E, M](S/T)

Ficus obliqua G.Forst. [M, T](T/ST)

Ficus prolixa G.Forst. [M, T](T/ST)

Ficus storckii Seem. [M, T](S/T)

Ficus theophrastoides Seem. [E, M](S/T)

Ficus tinctoria G.Forst. [T](S/T)

Ficus vitiensis Seem. [E, M](T)

Malaisia scandens (Lour.) Planch. [M, T](C)

Streblus anthropophagorum (Seem.) Corner [M, T](S/T)

Streblus pendulinus (Endl.) F.Muell. [M, T](S/T)

MYRISTICACEAE

Myristica castaneifolia A.Gray [E, M](T)

Myristica gillespieana A.C.Sm. [E, M](T)

MYRSINACEAE

Maesa corylifolia A.Gray [E, M](S)

Maesa insularis Gillespie [E, M](S)

Maesa persicifolia A.Gray [E, M, T](S)

Maesa pickeringii A.Gray [E, T](S)

Maesa tabacifolia Mez [M, T](S)

Rapanea myricifolia (A.Gray) Mez [M, T](T/S)

Tapeinosperma grande (Seem.) Mez [E, M](S)

MYRTACEAE (Myrtle Family)

Decaspermum vitiense J.R.Forst. & G.Forst. [E, M](T/S)

Eugenia reinwardtiana (Blume) DC. [T](S/T)

Syzygium curvistylum (Gillespie) Merr. & L.M.Perry [M](T)

Syzygium decussatum (A.C.Sm.) Biffin & Craven [E, M](T)

Syzygium effusum (A.Gray) C.Muell. [M](T)

Syzygium eugenioides (Merr. & L.M.Perry) Biffin & Craven [M, E](T)

Syzygium fijiense L.M.Perry [E, M](T)

Syzygium rubescens (A.Gray) C.Muell. [E, M](T)

Syzygium simillimum Merr. & L.M.Perry [E, M](S/T)

NYCTGINACEAE

Pisonia grandis R.Br. [T](T)

OCHNACEAE

Brackenridgea nitida A.Gray [M, T](S/T)

OLACEAE

Anacolosa lutea Gillespie [M](T)

OLEACEAE

Jasminum didymum G.Forst. [M, T](C)

Jasminum simplicifolium G.Forst. [M, T](C)

PASSIFLORACEAE

Passiflora aurantia G.Forst. [T](C)

**Passiflora foetida* L. [M, T](C)

Passiflora laurifolia L. [T](C)

**Passiflora suberosa* L. [M, T](C)

PHYTOLACCACEAE

**Rivina humilis* L. [T](H)

PIPERACEAE

Macropiper puberulum f. *glabrum* (C.DC.) A.C.Sm. [M](S)

PITTOSPORACEAE

Pittosporum arborescens A.Gray [M, T](T)

Pittosporum brackenridgei A.Gray [T](T)

Pittosporum rhytidocarpum A.Gray [E, M](T)

RHAMNACEAE

Alphitonia franguloides A.Gray [E, M](T)

Alphitonia zizyphoides (Spreng.) A.Gray [M, T](T)

Colubrina asiatica (L.) Brongn. [T](C)

Gouania richii A.Gray [E, M](C)

Rhamnella vitiensis (Benth.) A.C.Sm. [T](C)

Ventilago vitiensis A.Gray [M, T](C)

RHIZOPHORACEAE

Crossostylis pachyantha A.C.Sm. [E, M](T)

Crossostylis richii (A.Gray) A.C.Sm. [E, M](T)

RUBIACEAE

Airosperma vanuense S.P.Darwin [E, M, T](T)

Antirhea incospicua (Seem.) Christoph. [M, T](T)

Antirhea smithii (Fosberg) Merr. & L.M.Perry [M](T)

Coprosma persicifolia A.Gray [T](S/T)

Cyclophyllum sessilifolium (A.Gray) A.C.Sm. & S.P.Darwin

[T](S/T)

Gardenia gordoni Baker [**E**, M](T)

Gardenia hillii Horne ex Baker [**E**, M](T)

Guettarda wayaensis R.O.Gardner [**E**, T](T)

Guettarda speciosa L. [T](T)

Gynochthodes epiphytica (Rech.) A.C.Sm. & S.P.Darwin [M](C)

Ixora elegans Gillespie [**E**, M](S/T)

Ixora cf. *myrtifolia* A.C.Sm. [**E**, M](S/T)

Mastixidendron flavidum (Seem.) A.C.Sm. [**E**, M](T)

Morinda citrifolia L. [M, T](S/T)

Morinda mollis A.Gray [T](C)

Morinda myrtifolia A.Gray [**E**, M, T](C)

Ophiorrhiza leptantha A.Gray [M](H)

Pelagodendron vitiense Seem. [**E**, M](T)

Psychotria amoena A.C.Sm. [M, T](S/T)

Psychotria argantha A.C.Sm. [**E**, M](S/T)

Psychotria gibbsiae S.Moore [**E**, M](S/T)

Psychotria hypargyraea A.Gray [**E**, M](S/T)

Psychotria tephrosantha A.Gray [**E**, M](C)

Psychotria volii R.O.Gardner [**E**, T](S/T)

Psydrax odorata (G.Forst.) A.C.Sm. & S.P.Darwin [M, T](S/T)

Spermacoce remota Lam. [M](H)

Tarenna seemanniana A.C.Sm. & S.P.Darwin [**E**, M](T)

RUTACEAE

Melicope cucullata (Gillespie) A.C.Sm. [**E**, T](T)

Micromelum minutum (G.Forst.) Wight & Arn. [M, T](S/T)

Sarcomelicope petiolaris (A.Gray) A.C.Sm. [**E**, M](T)

SANTALACEAE

Exocarpos vitiensis A.C.Sm. [**E**, M](S/T)

SAPINDACEAE

Arytera brackenridgei (A.Gray) Radlk. [T](T)

Dodonaea viscosa (L.) Jacq. [M, T](S)

Elattostachys falcata (A.Gray) Radlk. [M, T](T)

Koelreuteria elegans (Seem.) A.C.Sm. [M, T](T)

Unknown genus [T](T)

SAPOTACEAE

Burckella richii (A.Gray) H.J.Lam. [M](T)

Manilkara dissecta (L.f.) Dubard [M, T](T)

Manilkara smithiana H.J.Lam & Mass Geester. [**E**, M](T)

Palaquium fidjiense Pierre ex Dubard [**E**, M](T)

Palaquium porphyreum A.C.Sm. & S.P.Darwin [**E**, M](T)

Pouteria cf. *garberi* (Christophers.) Baehni [M](T)

Pouteria grayana (H.St.John) Fosberg [M, T](T)

Pouteria membranacea (H.J.Lam) Baehni [M](T)

SIMAROUBACEAE

Amaroria soulameoides A.Gray [**E**, M](T)

SOLANACEAE

Capsicum frutescens L. [T](S)

STERCULIACEAE

Commersonia bartramia (L.) Merr. [M](T)

Firmiana diversifolia A.Gray [**E**, M](T)

Heritiera ornithocephala Kosterm. [M](T)

Kleinhovia hospita L. [T](T)

Melochia degeneriana A.C.Sm. [**E**, T](T)

Melochia grayana A.C.Sm. [**E**, M](T/S)

THYMELAEACEAE

Phaleria glabra (Turrill) Domke [M](S)

Wikstroemia foetida (L.f.) A.Gray [M, T](S)

TILIACEAE

Grewia crenata (J.R.Forst. & G.Forst.) Schinz & Guillaumin [M, T](T)

Trichospermum richii (A.Gray) Seem. [M](T)

ULMACEAE

Gironniera celtidifolia Gaudich. [M](T)

Trema cannabina L. [T](T)

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)

Premna protrusa A.C.Sm. & S.P.Darwin [**E**, M, T](T)

MONOCOTYLEDONAE (Monocotyledons)

AGAVACEAE

Cordyline fruticosa (L.) A.Chev. [M, T](S/T)

ARACEAE

Epipremnum pinnatum (L.) Engl. [M, T](C)

ARECACEAE

Veitchia filifera (H.Wendl.) H.E.Moore [**E**, M](T)

CYPERACEAE

Carex dietrichiae Boeckeler[M](H)

Fimbristylis dichotoma (L.) Vahl. [M](H)

Gahnia aspera (R.Br.) Spreng. [M](H)

Hypolytrum nemorum subsp. *vitiense* (C.B.Clarke) Koyama [M](H)

Machaerina falcata (Nees) Koyama [M](H)

Mariscus javanicus (Houtt.) Merr. & F.P.Metcalf [M](H)

Scleria lithosperma (L.) Sw. [M, T](H)

Scleria polycarpa Boeckeler [M, T](H)

DIOSCOREACEAE

Dioscorea alata L. [M, T](C)

FLAGELLARIACEAE

Flagellaria gigantea Hook.f. [M, T](C)

Flagellaria indica L. [M](C)

ORCHIDACEAE

Appendicula reflexa Blume [M](E)

Bulbophyllum gracillimum (Rolfe) Rolfe [M](E)

Bulbophyllum cf. *hassallii* P.J.Kores [**E**, M](E)

Bulbophyllum rostriceps Rchb.f. [M](E)

Corymborkis veratrifolia (Reinw.) Blume [T](H)

Dendrobium catillare Rchb.f. [**E**, M](E)

Dendrobium platygastrium Rchb.f. [M](E)

Dendrobium tokai Rchb.f. ex Seem. [M](E)

Luisia teretifolia Gaudich. [M](E/C)

Malaxis Sol. spp. [M](H)

Oberonia heliophila Benth. & Hook.f. ex Drake [M](E)

Pseuderia smithiana C.Schweinf. [**E**, M](E)

Taeniophyllum fasciola (Sw.) Seem. [M, T](E)

Trachoma Garay spp. [T](E)

PANDANACEAE

Freycinetia cf. *impavida* (Gaudich. ex Hombr.) Stone [M](C)

Pandanus tectorius Parkinson [M, T](S/T)

POACEAE

Centosteca lappacea (L.) Desv. [M, T](H)

Digitaria setigera Roth ex Roem. & Schult. [M](H)

Garnotia linearis Swallen [**E**, M](H)

Leptaspis angustifolia Summerh. & C.E.Hubb. [**E**, M](H)

Oplismenus compositus (L.) P.Beauv. [M, T](H)

Oplismenus hirtellus (L.) P.Beauv. [M, T](H)

SMILACEAE

Smilax vitiensis (Seem.) A.DC. [M, T](C)

TACCACEAE

Tacca leontopetaloides (L.) Kuntze [T](H)

ZINGIBERACEAE

Alpinia boia Seem. [**E**, M](H)

Alpinia vitiensis Seem. [**E**, M](H)

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

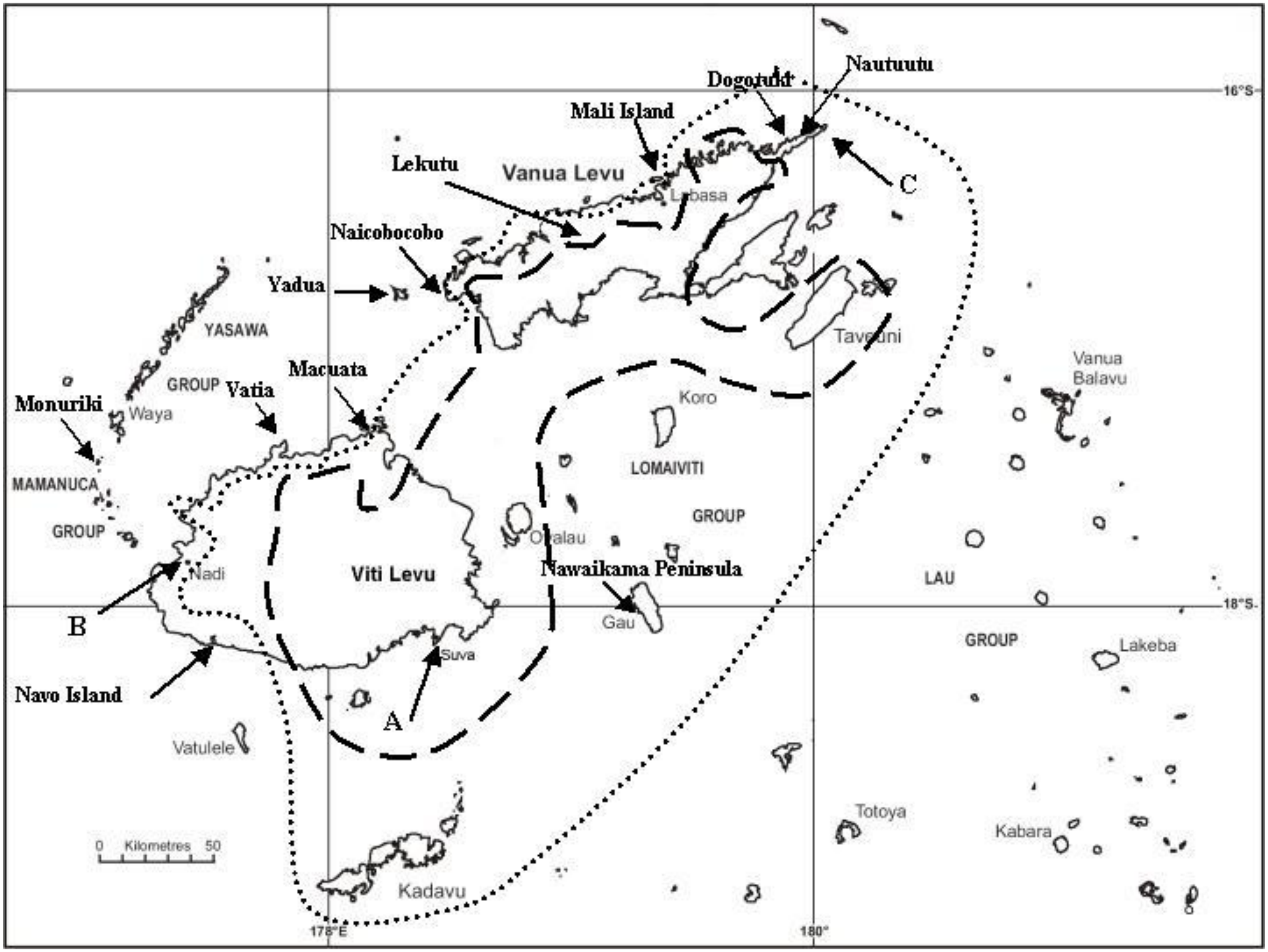
	Nautu-utu	Dogo-tuki	Lekutu	Navo	Vatia	Yadua Taba	Naicobo-cobo	Monu-riki	Gau	Macua-ta
Agathis macrophylla $^{\mathrm{SC, W, Mo}}$	0	1	0	0	0	0	0	0	0	0
Amaroria soulameoides $^{\mathrm{V, Di}}$	1	1	1	0	0	0	0	0	0	0
Antirhea inconspicua $^{\mathrm{DE, V, Di}}$	0	0	0	1	0	1	1	0	1	1
Arytera brackenridgei $^{\mathrm{SC,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

Cynometra insularis [V, He]	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 [V, Mo]	1	1	0	0	0	0	0	0	0	0
Diospyros elliptica [V, Di]	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 [V, Di]	0	0	0	0	0	1	0	1	0	0
Dysoxylum richii [V, Di]	0	1	0	1	1	0	1	0	0	0
Dysoxylum tenuiflorum [V, He]	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 [V, Di]	0	0	0	1	0	1	1	1	0	1
Fagraea gracilipes [V, He]	0	1	1	0	0	0	0	0	0	0
Ficus obliqua [SC, V, Mo]	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 [V, Di]	1	1	0	0	0	0	0	0	0	0
Garcinia sessilis [SC, V, Di]	0	0	0	0	0	0	1	0	0	0
Garuga floribunda [DE, V, He]	0	0	0	0	1	0	1	0	0	0
Gmelina vitiensis [O, He]	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 [V, Di]	0	1	1	0	0	0	0	0	0	0
Homalium laurifolium [V, He]	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 [O, Mo]	1	1	0	1	1	0	0	1	0	0

Kingiodendron platycarpum O, He	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 V, Mo	0	1	0	0	0	0	0	0	0	0
Macaranga vitiensis V, Mo	0	1	0	0	0	0	0	0	0	0
Mallotus tiliifolius V, Di	0	0	0	0	1	1	1	1	1	1
Manilkara dissecta SC, V, Mo	0	1	0	1	0	1	1	0	0	0
Maniltoa grandiflora O, Mo	0	1	0	0	0	0	1	0	0	0
Maniltoa vestita SC, O, Mo	1	0	0	0	1	0	0	1	0	1
Mastixiodendron flavidum V, He	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 V, Di	0	1	0	0	0	0	0	0	0	0
Myristica gillespieana V, Di	1	1	1	0	0	0	0	0	0	0
Palaquium fidjiense V, He	1	1	1	0	0	0	0	0	0	0
Parinari insularum V, He	0	1	1	0	0	0	0	0	0	0
Pittosporum arborescens V, He	0	1	0	1	0	0	1	0	0	0
Pittosporum brackenridgei V, He	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 SC, V, Di	0	1	1	0	0	0	0	0	0	0
Polyalthia laddiana V, He	0	0	0	1	0	0	1	0	0	0
Pouteria garberi V, He	0	1	1	0	0	0	0	0	0	0
Pouteria grayana V, He	0	0	0	1	1	1	1	1	1	1
Premna protusa V, He	0	0	0	0	0	1	1	0	0	1
Racosperma richii SC, O, Mo	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 V, Di	0	1	1	0	0	0	0	0	0	0
Semecarpus vitiensis V, Di	0	1	0	0	0	0	0	0	0	0
Serianthes melanesica O, He	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 [SC, V, Mo]	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 [V, He]	1	1	0	1	1	1	1	1	1	1
Veitchia filifera [V, Mo]	1	1	0	0	0	0	0	0	0	0

Fig. 1


Nautuutu
Mali Island
Lekutu
Vanua Levu
Labasa
C
Naicobocobo
Yadua
YASAWA
GROUP
Vatia
Macuata
Monuriki
Waya
MAMANUCA
GROUP
Taveuni
Vanua
Balavu
Koro
LOMAIVITI
GROUP
Ovalau
Nawaikama Peninsula
Nadi
Viti Levu
B
Gau
LAU
GROUP
Suva
Navo Island
A
Lakeba
Vatulele
Totoya
Kabara
0 Kilometres 50
Kadavu
16°S
18°S
178°E
180°

1

Fig. 2

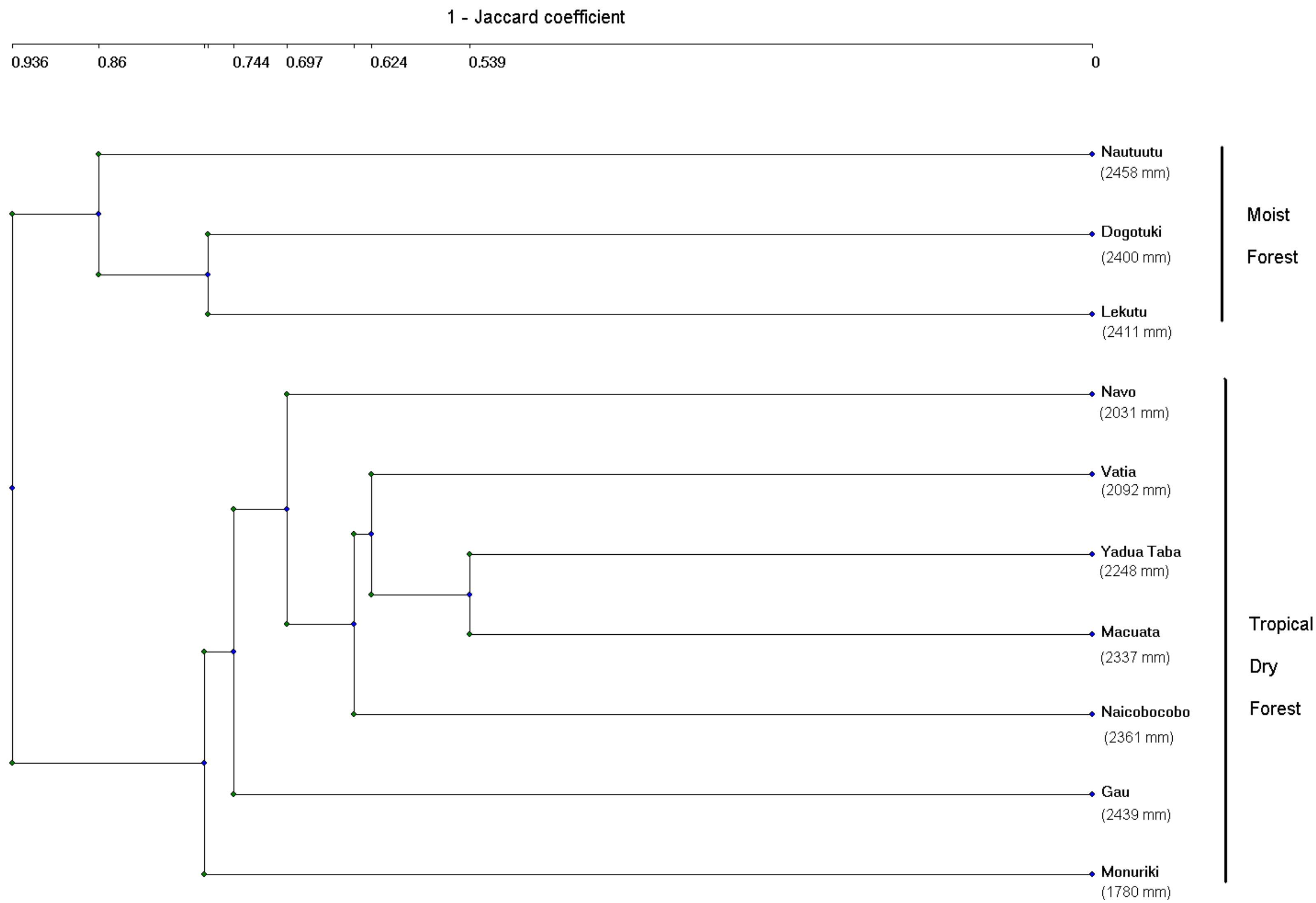
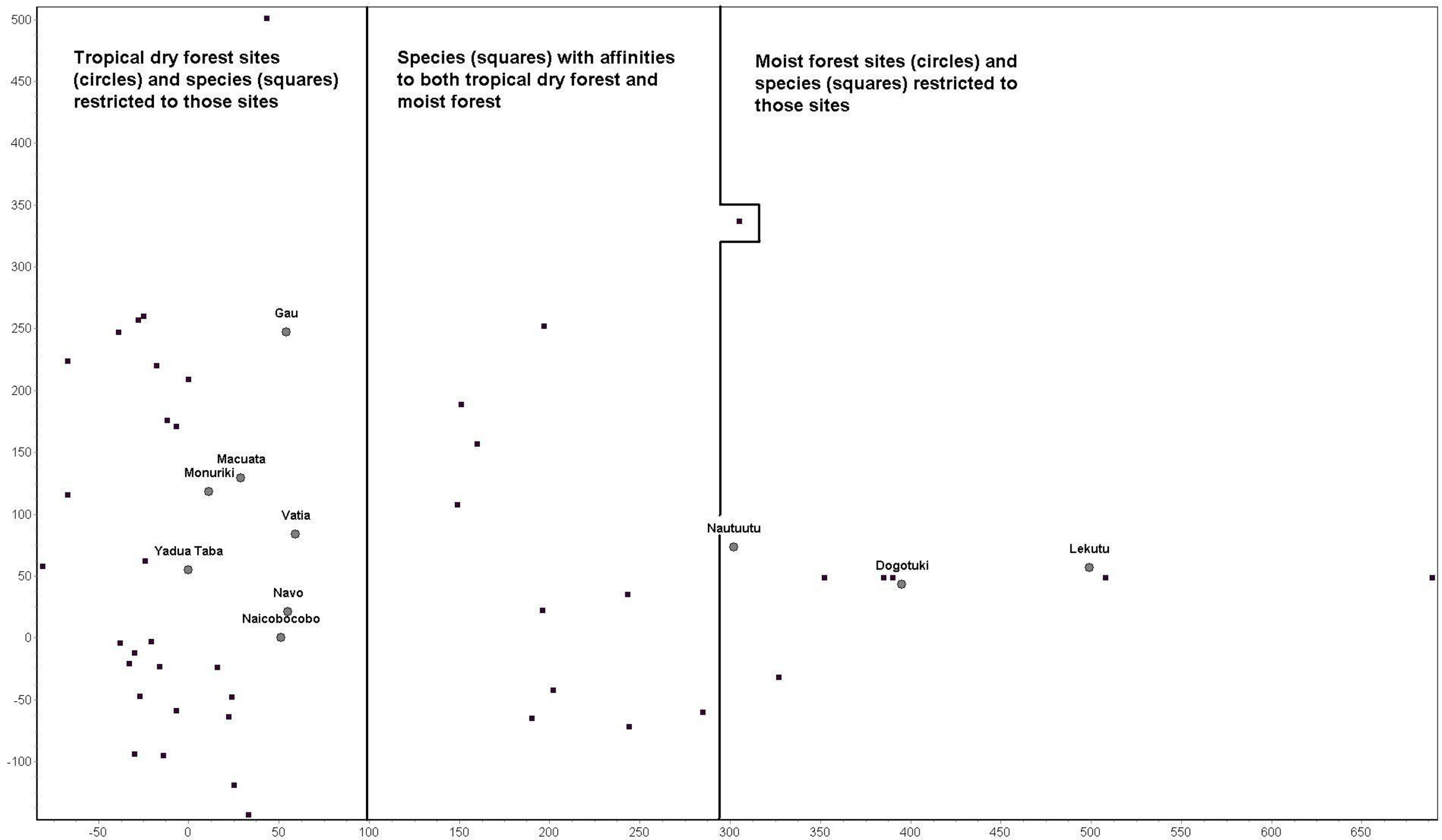

1 - Jaccard coefficient
0.936
0.86
0.744
0.697
0.624
0.539
0
Nautuutu
(2458 mm)
Dogotuki
(2400 mm)
Lekutu
(2411 mm)
Navo
(2031 mm)
Vatia
(2092 mm)
Yadua Taba
(2248 mm)
Macuata
(2337 mm)
Naicobocobo
(2361 mm)
Gau
(2439 mm)
Monuriki
(1780 mm)
Moist
Forest
Tropical
Dry
Forest

Fig. 3


Tropical dry forest sites (circles) and species (squares) restricted to those sites
Species (squares) with affinities to both tropical dry forest and moist forest
Moist forest sites (circles) and species (squares) restricted to those sites
Gau
Macuata
Monuriki
Vatia
Yadua Taba
Navo
Naicobocobo
Nautuutu
Dogotuki
Lekutu
500
450
400
350
300
250
200
150
100
50
0
-50
-100
-50
0
50
100
150
200
250
300
350
400
450
500
550
600
650