

Vegetation Ecology of Fiji: Past, Present, and Future Perspectives¹

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ABSTRACT: The Fiji Archipelago comprises a Tertiary island arc with several hundred small and a few large mountainous islands near the northeastern corner of the Australian tectonic plate, 3000 km from continental Australia–New Guinea. Despite contrary prevailing winds and ocean currents, the flora is very largely derived from that of Malesia, and the largest component was probably dispersed by frugivorous birds or bats, of which several taxa are established in Fiji. About 25% of the native vascular plant species are endemic and, with exceptions such as the relictual *Degeneria*, most have apparently diverged from overseas conspecifics. There are a few cases where speciation has occurred within Fiji but virtually none where reproductive isolation is established, permitting cohabitation. Until the arrival of humans, perhaps 4000 and certainly by 3000 yr B.P., the vegetation was predominately rainforests with stunted cloud forest at high altitude, though some more open communities might have occurred in drier areas. The forests have a mixed species composition, including most of the 1769 native species, and demographic observations indicate peak population fecundities after several hundred years for canopy trees and 80 years for several subcanopy taxa. Flowering phenology of forest species is seasonal with predominately synchronous annual or, in a few species, biennial frequency, while fruit maturation is spread throughout the year. Cyclones cause frequent minor damage and infrequent major damage, especially to coastal and ridge vegetation, and cause landslides. Insect-induced dieback has been recorded but there are no extensive single-species rainforests, except swamp forests, so the effects are diffuse. The impact of humans has been to convert much of the drier forest to frequently burned sedge-fern-grasslands, to create garden-forest successional mosaics around settlements in wetter areas, and, more recently, to selectively log much of the remaining accessible forest. Many plants have been introduced and established in cultivated or disturbed areas, increasing the flora by about 50% and largely excluding native taxa from those areas. Habitat conversion is thus the major threat to the conservation of Fijian native vegetation.

THE FIJI ARCHIPELAGO LIES in the seasonal tropics, with most islands between 16° and 19° S and 176° E to 178° W, about 3000 km east of continental Australia–New Guinea (Figure 1). The total land area of 18,376 km² is largely in the islands of Viti Levu (56%) and Vanua Levu (30%), with a further 300 islands exceeding 2.6 km², numerous smaller rocky islets, and sand cays on reefs. The surrounding ocean is 2–4 km deep, and all the islands have

a volcanic base. The larger, older islands have mountainous interiors rising to 1320 m, comprising dissected volcanic landforms, uplifted marine sediments, and limestones. Taveuni is the product of late Quaternary vulcanism and has a mountain range with scoria cones, craters, surface ash layers, and Holocene lava flows (most recently 2000 yr B.P.). Some islands in the eastern Lau group are raised coral reefs and have little or no surface exposure of the underlying volcanic rocks. Rotuma, a small island 500 km to the north, is not considered in this review. Alluvial coastal plains extend from valleys, and their shores

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have fine muddy sediments where there is offshore protection by coral barrier reefs. Coarser beaches occur where there is only a fringing reef to impede wave action, and cliffs and dunes (2 km²) are restricted to a few localities where deep water extends to the coast. During the last glacial period sea levels about 150 m below present levels would have exposed reefs and lagoonal sediments, especially around the larger islands (Figure 1). Sea level rose to slightly (45 cm) above present levels in the mid-Holocene, 5000 yr B.P. (Ash 1987a), a situation that may be repeated by current projected rises in sea level.

CLIMATE. The climate is oceanic, with sea-level temperatures averaging about 22°C in July and 26°C in January with a daily range

of only about 6°C. Rainfall and cloudiness is strongly influenced by the prevailing southeast winds, and annual rainfall typically rises from about 2000–3000 mm on southeast coasts and small islands up to 5000–10,000 mm on mountain ranges, declining to as low as 1500 mm on the northwest coasts of the larger islands. There is a marked seasonal pattern, and although localities with annual rainfalls exceeding about 5000 mm rarely experience prolonged soil water deficits, areas with less than about 2000 mm usually experience several months of soil water deficit within the June–November period. Cyclones, bringing high rainfall and high winds, occur every few years. During the last glacial period (20,000–14,000 yr B.P.) it is estimated that temperatures were 3–4°C lower in summer,

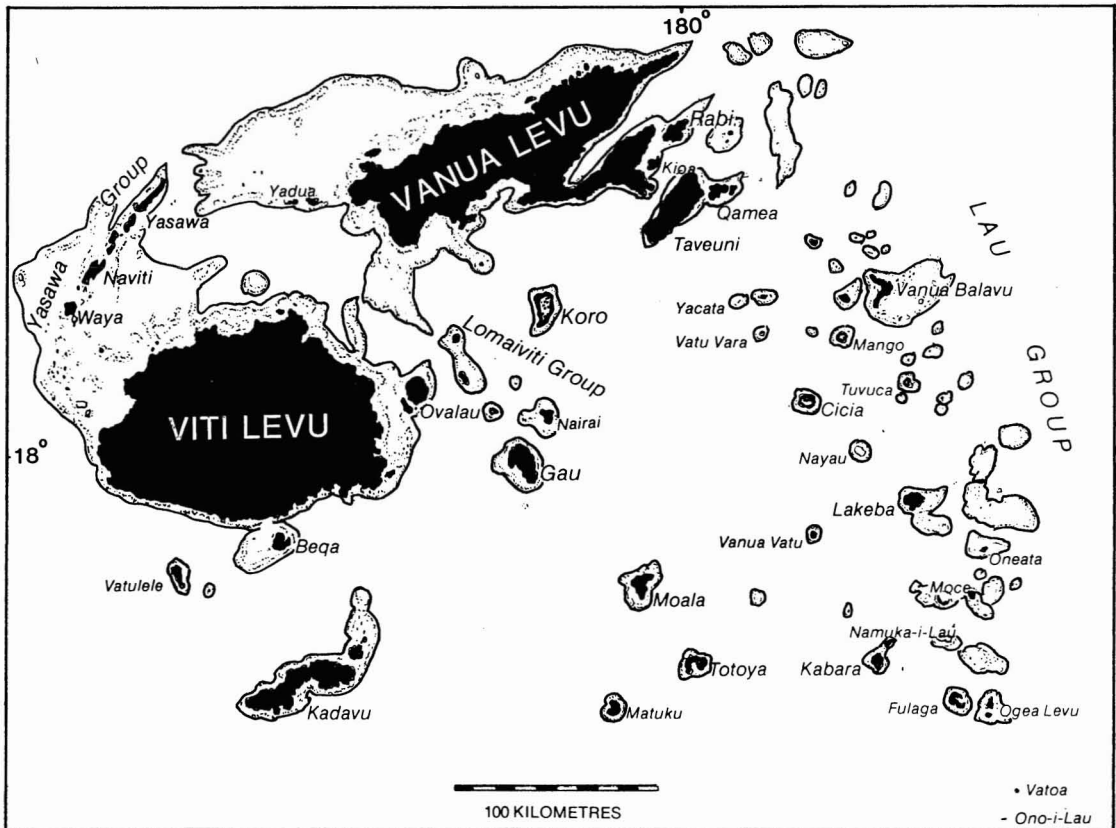


FIGURE 1. Map of the main Fiji islands (black) and reefs including the -150-m underwater contour delimiting islands at the lowest sea level in the glacial period, about 18,000 yr B.P.

the cloud base was reduced by 100–200 m, and rainfall was 30–50% reduced (Southern 1986), leading to increased periods of soil water deficit and fewer cyclones.

HUMAN POPULATION. Archaeological evidence suggests that humans first settled in Fiji at least 3300 and perhaps 4000 yr ago (Shaw 1975, Southern 1986, Allen et al. 1989), and genetic evidence (Serjeantson 1989) suggests that the founder populations were Polynesian with later immigration by Melanesians. Indirect evidence of population growth is available from geomorphic and palynological records, which indicate that forest clearance has occurred throughout this period (Southern 1986), with consequent erosion from hills and siltation of coastal habitats and nearshore coral reefs (Hughes et al. 1979, Ash 1987a). Forest clearance was occurring at the center of Viti Levu by 2000 yr B.P. (Southern 1986), close to the present eastern limit of such clearance and at similar dates in Lakeba (Hughes et al. 1979), and an early phase of expansion may have been followed by agricultural intensification. Undated prehistoric irrigation/drainage systems are evident on most alluvial flood plains (e.g., Rewa and Navua [Parry 1977, 1981]), probably associated with taro (*Colocasia esculenta*) cultivation. By the early nineteenth century the population was variously estimated as 110,000 to 200,000, mostly living around fortified villages and subsisting upon intensive horticulture supplemented by coastal marine foods (Derrick 1950, Frost 1974, Gibbons and Clunie 1986). Europeans introduced a cash economy and diversified agriculture, bringing about 60,000 indentured laborers, mostly from India, to tend plantations of sugarcane, coconuts, etc. High fecundity combined with reduced child mortality has since caused the population to grow rapidly, reaching about 730,000 in 1990 and increasing by $1.8\% \text{ yr}^{-1}$. Indian emigration, following recent racially discriminatory legislation, currently removes this increase, but it is anticipated that the population will double by about 2050 and, perhaps, stabilize at about 2 million. A quarter of the population is now urban and 80% is within Viti Levu, and these proportions are increasing.

Geological Origins of Fiji

The Fiji Archipelago is an emergent portion of the Tertiary Vitiav island arc-basin system (Green and Cullen 1973, Crook and Belbin 1978, Rodda and Kroenke 1984, Monger and Francheteau 1987) near the northeastern corner of the Australian tectonic plate. Fiji is about 800 km west of the Tonga Trench, where the Pacific Plate is being subducted at rates of about 8 cm yr^{-1} , and within the zone that has been subject to vulcanism, fracturing, westerly shearing, and clockwise rotation associated with the northerly contact between the two plates (Figure 2). Immediately west of the archipelago is an extensive submerged fragment of Gondwanic sialic rock, the Fiji Plateau, bounded by the Vanuatu and Vitiav trenches. The plateau is thought to have originated as part of the Norfolk Island–New Caledonia–d'Entrecasteaux Ridge, then adjacent to northeastern Queensland, and to have been carried northeastward by sea floor spreading during the past 80 million yr. These events are poorly defined and it is not known for how much, if any, of this period the plateau might have been emergent, nor how these developments relate to older Mesozoic Melanesian island arcs in the region. Evidence of vertical uplift is apparent from the exposure of early Tertiary marine pillow lavas and limestones in Viti Levu, but it is not evident that any substantial islands were created until the mid-Tertiary, perhaps 50 Ma and more certainly 30 Ma when the South Fiji Basin floor was spreading. Volcanic rocks of 7.5 million yr age are found in Vanua Levu (Rodda and Kroenke 1984). Uplift of the Lau Ridge may only date to the past 2.5 million yr, associated with sea floor spreading between the Lau and Tonga archipelagoes (Katz 1977).

Origins of the Flora

BIOGEOGRAPHIC PATTERN. There is little known of the fossil flora of Fiji before the past 23,000 yr (Southern 1986), so the development of the vegetation can only be inferred by interpretation of the current distribution of taxa. Balgooy's (1971) tabulation of the bio-

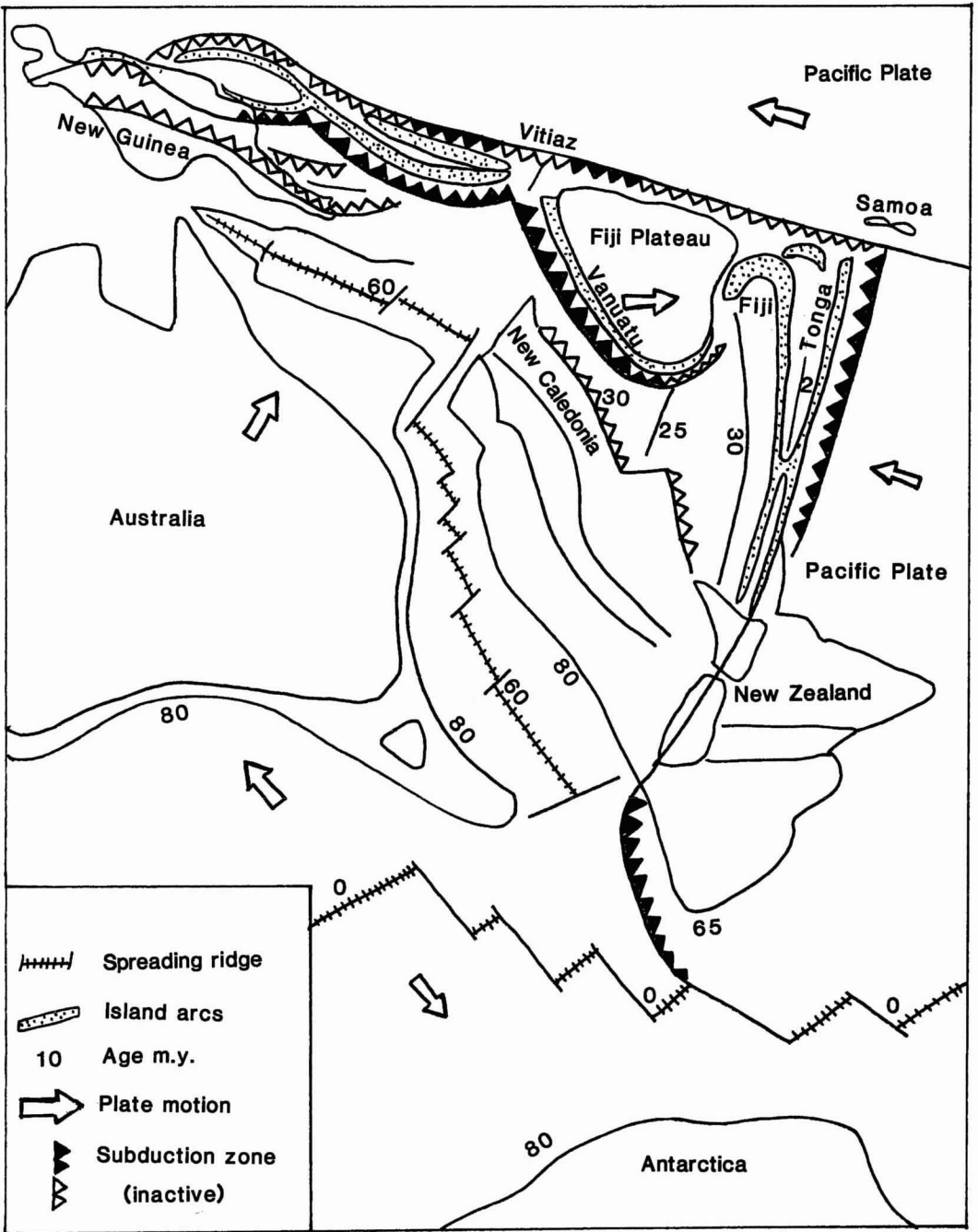


FIGURE 2. Simplified geological map of the southwestern Pacific showing the major tectonic features and dates of past ocean floor spreading (compiled from various sources listed in the text).

geography of Pacific seed plant genera provides a guide to such reconstructions, and it is evident that Fiji has very strong floristic links with Malesia–Asia. Of the 476 Fijian genera, 90% are present in New Guinea, with about 65–75% occurring in Australia, New Caledonia, and intervening archipelagoes. The geological history of Fiji suggests that the archipelago only emerged after it had reached close to its present location with respect to Australia–New Guinea, so the flora must have established by long-distance dispersal, including “stepping-stone” spread along the Melanesian island arcs. This view is supported by the absence in Fiji of some typical continental Gondwanic genera, notably *Nothofagus* and *Araucaria*, which were widespread on southern continents but seem unable to disperse long distances overseas (Ash 1982). There are, however, a number of better-dispersed genera with southern Gondwanic affinities such as *Citronella*, *Coriaria*, *Cordyline*, *Cryptocarya*, *Dacrydium*, *Dacrycarpus*, *Decussocarpus*, *Passiflora*, *Peperomia*, *Podocarpus*, and *Weinmannia* (Thorne 1978).

Passing eastward from New Guinea through the Solomon Islands and Vanuatu to Fiji, and on to Polynesia, there is a sharp

decline in the number of plant genera, consistent with a Malesian source. It is notable, however, that 70 Fijian plant genera are not recorded in the intervening archipelagoes, suggesting that either about 15% of colonization was by direct long-distance dispersal, or that both colonization and extinction have occurred on intervening islands. MacArthur and Wilson (1967) proposed that islands have a species diversity that results from the dynamic equilibrium between colonization and extinction and is strongly controlled by the area of the island, which limits their carrying capacity. A plot of the number of seed plant genera against archipelagic area for the southern Pacific (Figure 3) suggests such a relationship, but the pattern is confounded by a decline in area and habitat diversity with increasing distance from Malesia. There is little evidence to document plant extinctions on these islands except that Southern (1986) suggested that *Quintinia* became extinct in Fiji and *Dacrydium* and *Dacrycarpus* became extinct in Taveuni at the end of the last glacial period, though probably as a result of climatic change rather than reduced island area. It is not clear to what extent island species diversity is limited by extinctions, habitat areas, and

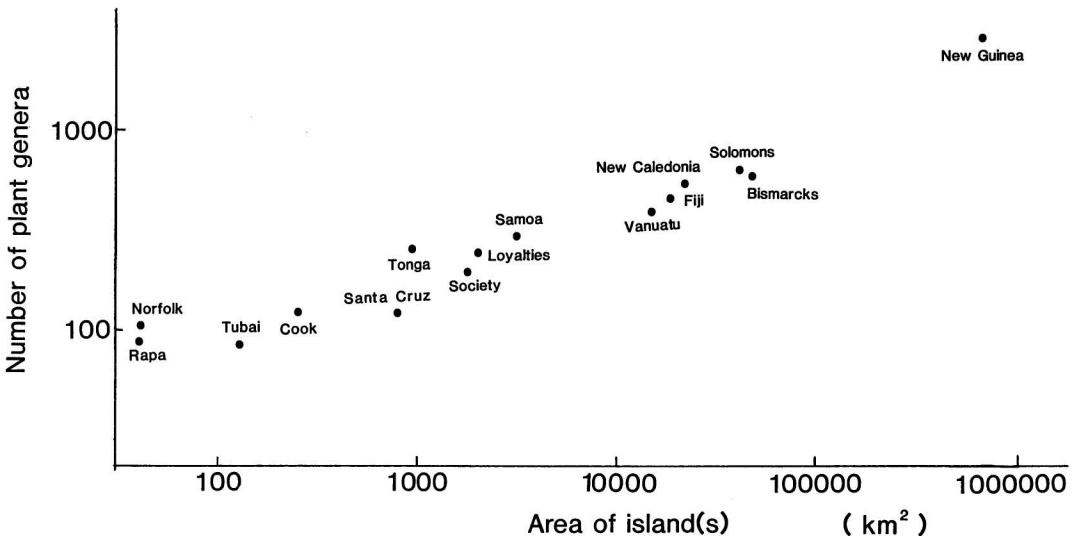


FIGURE 3. Relationship between the area of archipelagoes and islands in the southern Pacific Ocean and the number of native seed plant general (data from Balgooy 1971).

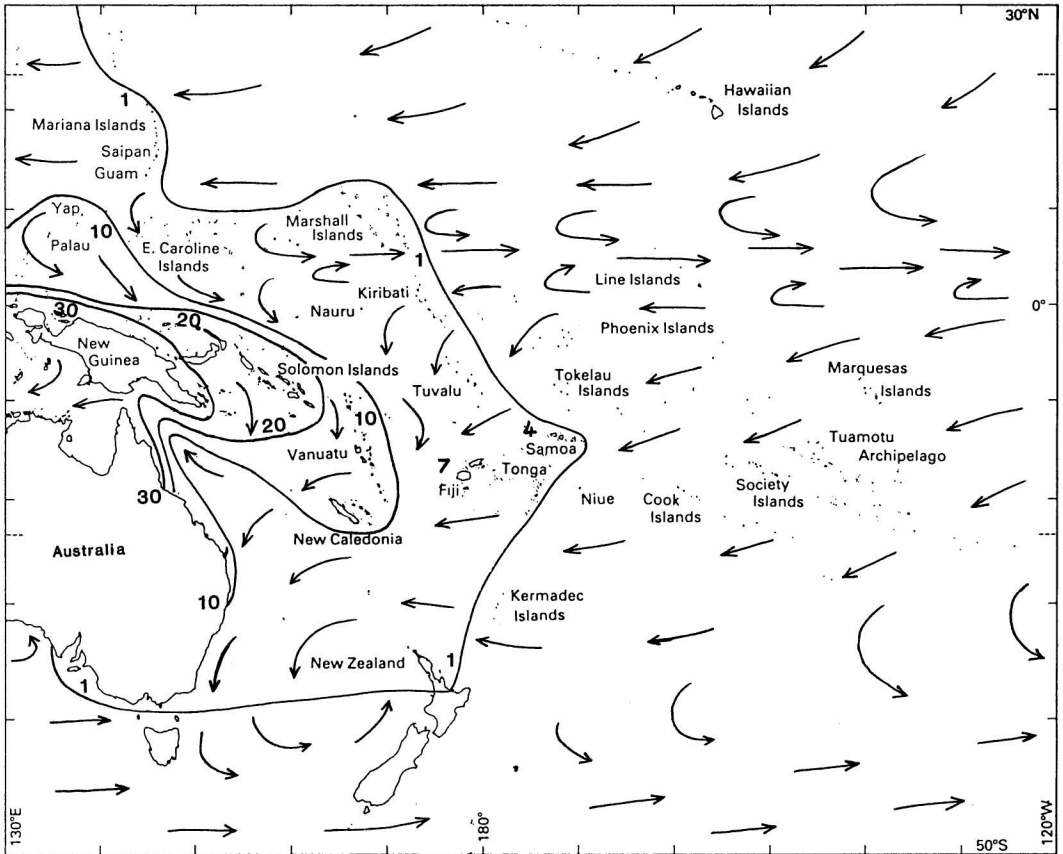


FIGURE 4. Map of the western Pacific Ocean showing the prevailing ocean currents in January and the number of naturally occurring water-dispersed mangrove species (partly after Woodroffe 1987).

competition, but disjunct distributions and the presence of primitive endemics such as *Degeneria* suggest that extinctions have modified island floras.

DISPERSAL VECTORS. Ocean currents now flow steadily in a westerly direction past Fiji, though midsummer southeasterly currents in the Solomon Islands region might occasionally penetrate nearer to Fiji (Figure 4). Mangroves are water dispersed and their distribution illustrates the probable influence of ocean currents. Of the approximately 30 mangrove species in New Guinea and Australia, 19 extend through the Solomon Islands, 7 reach Fiji, and 4 reach an eastern limit in Samoa (Woodroffe 1987). Evidently there is a reason-

able correlation with ocean currents, though a few species extend beyond the present normal range of easterly currents (Figure 4). Suitable habitats are less abundant in Polynesia but, with human aid, mangroves have been established on many previously uncolonized islands, and the pattern of mangrove distribution may be taken as a model for Malesian water-dispersed taxa with moderate seed longevity.

Fijian strandline and beach species are typically water dispersed and mostly show a wider distribution than mangroves through the tropical Pacific (Guppy 1906, A. C. Smith 1979, 1981, 1985, J. M. B. Smith 1990). These taxa apparently have more resistant and long-lived seeds than the precocious mangroves

and there are greater opportunities for their establishment in the central Pacific: the beach flora of one tropical Pacific island is much like that of another and about 80% of Fijian beach species occur throughout the region.

Overall only about 2.5% of the Fijian flora is primarily water dispersed but a further 20% may float and might be dispersed in this manner. Some taxa, such as *Cerbera* and *Barringtonia*, may have dispersed as strand-line species and since evolved inland forms and species.

Despite the prevailing southeasterly winds, occasional northwesterlies or cyclones could transport some seeds and spores from Malesia, and spore-dispersed pteridophyte species (Brownlie 1977) and bryophytes (Whittier 1975, Huerlimann 1978, Scott 1982) are widespread in suitable habitats in Fiji and neighboring archipelagoes. The small seeds of orchids and plumed seeds of *Alstonia* and *Asteraceae* are probably wind dispersed over long distances. Small seeds from capsules and small winged seeds, such as *Gymnostoma*, may also be blown over considerable distances, but it is unclear whether larger winged-seed taxa such as *Agathis* and *Gyrocarpus* experience significant long-distance wind dispersal. It is difficult to determine which seed plants could be transported long distances by wind but it is probably at least 10% of the flora.

The majority of Fijian seed plants are adapted for animal dispersal, mostly with fleshy fruits, and the occurrence of several fruit bat and frugivorous bird genera (Watling 1982), principally pigeons and doves, suggests that these were responsible for much overseas plant dispersal, especially for forest species adapted to inland habitats.

Ignoring probable speciation events within Fiji, there have been at least 1400 successful seed plant and 250 successful pteridophyte colonization events over a period of perhaps 10–30 million yr, suggesting a minimum rate of one successful colonization event every 6000–20,000 yr. Current rates of natural colonization are unknown and may have fluctuated in the past. Lower sea levels during glacial periods would have both increased island areas and created new island “stepping-stones” between Fiji and Malesia (Watling

1982, Gibbons and Clunie 1986). Certainly the prevailing patterns of ocean currents and winds are against dispersal from Malesia, and overseas frugivore dispersal has not been recorded, but it is evident that these events happen, probably much more frequently than the minimum rate given above. Perhaps more surprising is the minor contribution of American taxa to the flora, since water and wind both favor westerly dispersal and even iguanas have made this journey successfully (Balgooy 1971, Gibbons and Clunie 1986).

Polynesians and Melanesians evidently introduced a variety of crops and weeds, and probably established at least a hundred species, mostly in disturbed habitats associated with gardening (Kirch 1983). With increasing international traffic during the past 150 yr, several hundred new species have been established including many American and some African taxa. About two new weed species and three new cultivated species are introduced each year, such that the Fijian vascular plant flora has increased from about 1769 species before human arrival to at least 2600 species: a 50% increase (Parham 1972, Smith 1979, 1981, 1985). About 95% of introductions are herbaceous. It is observed that about 60% of introduced grasses, 40% of introduced herbs, but only 20% of introduced woody taxa establish outside cultivation. As yet, very few taxa have established in undisturbed native forests. In contrast, the floras of heavily disturbed sites, subject to cultivation, grazing, or fire, tend to be dominated by introduced species and natives are infrequent or absent (Parham 1959, Ash and Ash 1984).

Endemism and Speciation

Of the 1769 native vascular plant species in Fiji, about 75% are recorded from other archipelagoes, especially Samoa, Tonga, and Vanuatu, and many of the ca. 400 endemics have closely related species elsewhere, suggesting that rates of oceanic dispersal are high relative to rates of divergence and speciation. At the generic level, endemism through divergence is suggested in the Rubiaceae (*Gillespiea* [one sp.], *Hedstromia* [one sp.], *Readia* [one sp.], *Squamellaria* [three spp.], and *Sukumia*

[one sp.]), Arecaceae (*Neoveitchia* [one sp.: Gorman and Siwatibau 1975] and possibly *Goniocladus* [one sp.]), and Sterculiaceae (*Pimia* [one sp.]), though several of these taxa are not adequately known (Parham 1972, Smith 1979, 1981, 1985). The sole endemic family, Degeneriaceae (two spp., Miller 1988), represents a primitive form of angiosperm and is presumably a relict from a wider, earlier Malesian distribution.

Evidently most plant speciation in Fiji is at the level of primary divergence from taxa elsewhere, together with some taxa showing divergence on different Fijian islands (e.g., *Degeneria*, *Homalium*, *Pandanus*, and *Veitchia*) and some diverging in different altitude and climatic zones of the large islands (e.g., *Aglaia*, *Alpinia*, *Balaka*, *Cryptocarya*, *Excoecaria*, and *Peperomia*). Where an endemic species occurs sympatrically, cohabiting with a congener, their divergence generally appears to have occurred outside Fiji, but cladistic and chronistic analysis of Fijian taxa has yet to be undertaken to confirm these patterns. Several examples of cohabiting endemics from within a subsection of a genus (e.g., *Psychotria*) can be identified from Smith (1979, 1981, 1985), but mostly involve taxa that are poorly known, so the probable time, place, and degree of divergence is uncertain. These observations suggest that for most taxa there has been insufficient time, selection pressure, or opportunity for the evolution of reproductive isolating mechanisms between plant populations within Fiji. In only a few families (e.g., Arecaceae and Rubiaceae) does speciation appear to be relatively rapid.

Vegetation Structure and Dynamics

RAINFOREST (8300 km²). The native terrestrial vegetation of Fiji is predominantly rainforest, which varies principally in response to the climate (Berry and Howard 1973). On the wetter southeastern side of the large islands, the forests are diverse and mixed, including about 1350 vascular plant species (Smith 1979, 1981, 1985, Kirkpatrick and Hassall 1985, Ash and Vodanaivalu 1989), of which about 20% are notophyll-mesophyll trees forming a canopy at 20–30 m, 30% are small trees and

shrubs, 35% are epiphytes (including many ferns) and climbers, and the remainder are terrestrial ferns and herbs. Typically the single most common species may account for up to about 15% of a vegetation stratum in a particular habitat, and small clusters of each species are common but extensive stands are rare except in swamps (see below). In general the forests are taxonomically diverse, in keeping with most tropical rainforests.

On the drier northwest side of the large islands and on small islands (Garnock-Jones 1978), what remains of the lowland forests suggests that the species diversity, particularly of epiphytes, is lower and that species composition is different. There are, however, few examples of such forests, and these are mostly restricted to rocky sites and have been disturbed.

With increasing altitude there is a decline in species diversity of the forests and a gradual decline in canopy height. The cloud base is reached at about 600–800 m near southeastern coasts and at 900–1100 m inland, giving rise to cloud-shrouded mountain ridges supporting cloud forests that have low rates of photosynthesis, very low rates of transpiration (e.g., 2×10^{-7} g cm⁻² leaf s⁻¹), and, probably, low nutrient uptake (Ash 1987d). Under these conditions, the trees are stunted to 3–7 m height, climbing *Freycinetia* dominates in the canopy, and epiphytes, especially bryophytes, are abundant. Several endemics (e.g., *Ascarina swamyana*, *Medinilla spectabilis*, *M. waterhousei*, and *Paphia vitiensis*) are restricted to these conditions, each confined to a few adjacent mountaintops. At the generic level the cloud-forest flora has strong affinities to that on other neighboring Pacific archipelagoes, suggesting direct dispersal rather than evolution from local rainforest taxa (Ash 1987d).

FOREST DEMOGRAPHY. The population structures of several forest tree, palm, and tree-fern species have been examined (Ash 1985, 1986a, b, 1987b, c, 1988a). Although some species require the high light levels of tree-fall gaps and clearings (e.g., *Alpinia boia*, *Alstonia vitiensis*, *Erythrina variegata*, *Macaranga vitiensis*, *Parasponia andersonii*, and *Trema orien-*

talis), none seems to require extensive forest disturbance for regeneration to occur. Reproduction in canopy-tree species generally commences when they reach at least half their mature height coupled with high light levels, whereas subcanopy species mostly reproduce once a certain size is attained together with a moderate-to-fast growth rate. It appears that slow-growing individuals of subcanopy species (e.g., *Balaka microcarpa*) may never reproduce. Using radiocarbon dating and growth ring and growth rate analysis to estimate ages, coupled with information on seed production, the age-specific fecundity weighted by age-specific survivorship has been calculated for populations of several species (Figure 5). A relatively large emergent, *Agathis vitiensis*, reaches a peak in reproduction at about 300 yr; a smaller canopy tree, *Dacrydium nidulum*, reaches a peak at about 200 yr, and the subcanopy palm *Balaka microcarpa* and tree ferns *Cyathea hornei* and *Leptopteris wilkesiana* all have reproductive peaks at about 80 yr. Evidently the factors controlling fecundity and survival differ systematically in different forest strata, and subcanopy longevity may be limited by local canopy-tree longevity in addition to other factors. All these species, and others, appear to regenerate frequently, though some local fluctuations are apparent such that at a scale of 10^1 to 10^2 m² plants of similar age may occur together, probably reflecting the scales of canopy disturbance, while at scales of 10^3 to 10^4 m² such peaks in regeneration are obscured.

FOREST PHENOLOGY, POLLEN, AND SEED DISPERSAL. The phenology of Fijian forests is

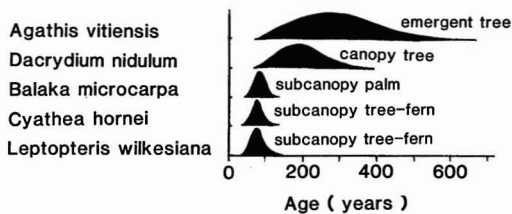


FIGURE 5. Graph showing the relative age-specific fecundity of various Fijian forest plants weighted by population survivorship, standardized so that each species has the same peak fecundity.

markedly seasonal, with some tree species being deciduous and many having a partial or complete annual leaf flush. Most individuals of a species flower synchronously within a period of a few weeks. *Endospermum macrophyllum* is exceptional in flowering twice in most years, and *Barringtonia petiolata* is exceptional in flowering at irregular asynchronous intervals 6–8 months apart. Most species, though not all canopy individuals, flower once each year, but a few, notably those with large slow-developing fruits, have a largely synchronous biennial pattern (e.g., *Goniocladus* and *Pandanus*). There do not appear to be any species that normally have longer than 2-yr intervals between flowering.

Generally, considering all forest species, there is a peak in leaf production near the start of the wetter season, about December–January, followed by a peak of flowering in about January–March; fruit maturation, which takes between 1 and 12 months in different species, is spread more evenly through the year with a peak in June–September (Figure 6). The majority of the tree species are apparently adapted for generalist insect pollination, coinciding with the hotter wetter season. The major seed vectors, the fruit bats and frugivorous birds, are dependent on the year-round supply of fruits, and their breeding seasons (Watling 1982) coincide with the peak in fruit abundance. This essential community-level coordination of plant phenology with vector populations may have arisen elsewhere in Malesia or it may have evolved within Fiji. At similar latitudes in Australia many fruit doves and pigeons are migratory, following local trends in fruit availability (Crome 1975) while related species in Fiji are relatively sedentary. Each major island has a different combination of frugivore species (Watling 1982), and there are typically only two to three fruit-bat species and three to five pigeon and dove species on each Fijian island—far fewer species than in the larger islands of Malesia and only a part of the fauna present in Fiji, suggesting that area-related competitive exclusion might be occurring between similar frugivores. This in turn suggests that the fruit resource is heavily exploited and limiting to the frugivores. There

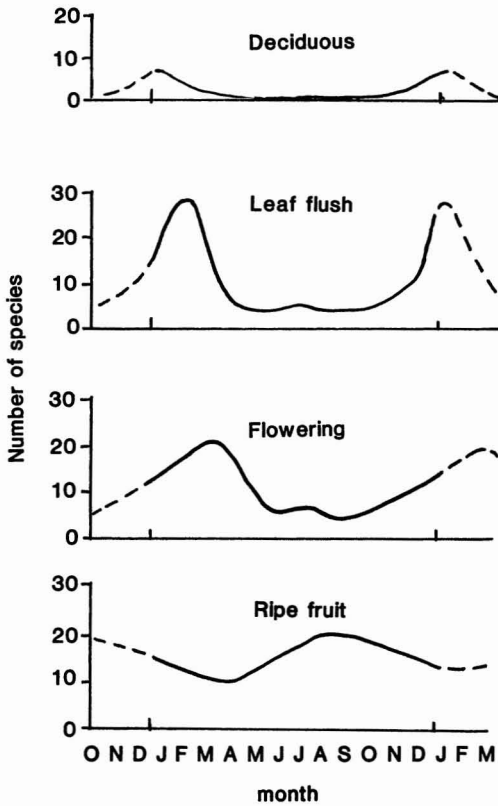


FIGURE 6. Graphs showing the average number of canopy-tree species deciduous, with leaf flushes, flowering, and bearing ripe fruit each month, in a forest plot of 81 species and 500 trees near Suva from 1982 to 1985.

does not appear to be much frugivore specialization, though some taxa feed primarily in the canopy and some near the ground, and most plant species of similar growth form probably experience similar patterns of vector dispersal. Excavations on Lakeba in the Lau group and Naigani (connected to eastern Viti Levu in glacial times) have revealed various extinct birds including large megapodes *Megapodius freycinet* and *Procura* sp. and a large pigeon (Best 1984), all of which probably dispersed fallen fruits and seeds. With these extinctions, coincident with human occupation, the dispersal of some large fruited and understory species may have been reduced. Introduced pigs and rats may have taken over some of the dispersal functions, though they are primarily seed predators.

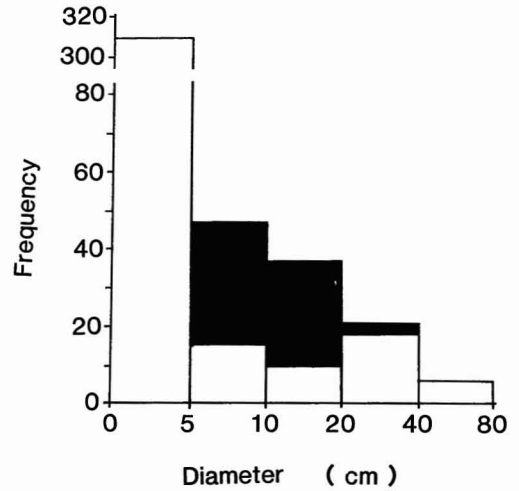


FIGURE 7. Histogram of the size-class frequency of the shade-tolerant forest canopy tree *Atuna racemosa* near Suva showing deaths (black) due to an epidemic of bark-boring beetles in 1983.

FOREST DIEBACK. There are no natural extensive single-species or single-genus stands of trees in well-drained Fijian forests (see swamps and mangroves discussed in following sections), and dieback is not obvious as an extensive forest-patch phenomenon, such as that in *Nothofagus* forests of New Guinea (Ash 1988b) and in *Metrosideros polymorpha* forests of Hawaii (Mueller-Dombois 1985). However, individual species within diverse forests are affected, and an epidemic of bark-boring beetles was noted in 1983 that caused mortality in subcanopy individuals of populations of *Atuna racemosa* (Figure 7), a common canopy tree notable for its large seeds that germinate and establish in clumps beneath and downslope of parent trees. Such dieback may explain why *Atuna racemosa* does not form extensive stands spreading from around parent trees.

CYCLONES AND FOREST DISTURBANCE. Cyclones, mostly coming from the northwest, are a frequent source of damage to Fijian forests, particularly near the coast and on ridges, where 150 km hr^{-1} gusts may be expected every 5–10 yr, 200 km hr^{-1} gusts every 30–50 yr, and 250 km hr^{-1} winds might occur every few centuries. Leaves, flowers, and fruits are

stripped off the trees every few years, and major branches are broken and trees uprooted every few decades. Certain emergents with spreading crowns are particularly susceptible to windthrow (e.g., *Serianthes melanesica*), but *Agathis vitiensis* is much more resilient and apparently has the lowest rate of cyclone-induced mortality for a canopy species. The subcanopy environment is relatively frequently subject to falling debris from canopy trees, and this damage accounts for part of the higher mortality of subcanopy plants and may explain the similar fecundity patterns in the three species that have been examined (Ash 1986b, 1987b, 1988a). Heavy rainfall, associated with cyclones, causes landslides on steep slopes, especially in the Serua hills of southern Viti Levu where they are a significant component of forest disturbance, creating bare patches of 10^2 – 10^4 m².

LOGGING OF RAINFOREST. Selective logging of old-growth rainforest, typically involving damage or destruction of 10–30% of the trees, with extraction of the larger trunks for local (93%) and export (7%) markets, is continuing at a rate of about 60 km² each year (yielding 200,000 m³ timber), and it is estimated that all of the accessible “production” forest will be logged by about 2020. This should leave about 2700 km² of unlogged, steep, catchment “protection” forest, and about 5100 km² of once-logged or low-yield forest (Berry and Howard 1973) that might provide a moderate sustained yield with a 50- to 70-yr logging cycle. Logging operations give easy access to disturbed forest and it is estimated that 5–10% of logged forest is subsequently gardened. A further 3–5% of logged forest is being planted with *Swietenia macrophylla* (mahogany) or *Pinus caribea* (Caribbean pine), and it is intended that plantations of exotic species should gradually replace native rainforests as the major source of timber.

SECONDARY VEGETATION (10,000 km²). Human disturbance of the forests traditionally involved felling and burning to create gardens, or, perhaps, simply burning of dry-zone forests. The fate of such disturbed sites depends very much upon subsequent disturbance and the presence of a local source of

seeds for secondary succession (Nicholson 1981). In higher-rainfall zones, cycles of gardening and forest regeneration have been long and widely established around alluvial valleys, forming a mosaic of seral stages in which species naturally favored by tree-fall gaps (see above) are abundant. In the dry zone, fires lit by man usually burn regenerating forest except in some fire-protected valleys and rocky areas, and sedge-fern-grasslands, known as *talasiqa*, now extend over most (3000 km²) of the drier half of the large islands and over most small islands. It is debatable whether there was any *talasiqa* land before humans arrived (Twyford and Wright 1965, Garnock-Jones 1978, Hughes and Hope 1979, Latham 1983, Southern 1986), though native taxa such as *Cycas rumphii*, *Allocasuarina*, and some grasses apparently require fairly open conditions. The 12 taxa Latham (1983) considered to be both native and restricted to *talasiqa* can, however, all be found in forest habitats, including rocky and coastal sites, in Viti Levu. Southern (1986) considered that during midglacial times the annual rainfall on the northwestern side of the larger islands may have been as low as 1000 mm, coupled with a temperature decline of a few degrees, which might have favored these more-open vegetation types. Subsequently, in the early Holocene, rainforests probably reoccupied much of these areas. Many introduced species have established in the *talasiqa*, and the flora typically includes *Dicanthium caricosum*, *Miscanthus floridulus*, *Panicum maximum*, *Pennisetum polystachyon*, *Sporobolus elongatus*, and the ferns *Dicranopteris linearis* and *Pteridium esculentum* (Brownlie 1977, Smith 1979). During the past century much of the more fertile alluvial land in the dry zones has been cultivated (Twyford and Wright 1965), especially for sugarcane, and 750 km² of *Pinus caribea* plantations are being established on the less fertile hills: to date about half this reforestation goal has been achieved. Currently (1990), Fijian pine production is about 300,000 m³ yr⁻¹, mostly from former *talasiqa* lands, and supplies about 30% of Fijian timber needs.

FRESHWATER SWAMPS (55 km²). Several of the craters on Taveuni, notably Tagimaucia

(Southern et al. 1986), contain lakes with sedge swamps dominated by *Lepironia articulata* growing around the margin on organic sediments and upon floating mats of algae and cyanobacteria (5 km²). With annual rainfalls of about 8000 mm, these swamps are rapidly flushed by the very high run-off, and some rain-fed surfaces support *Sphagnum cuspidatum* hummocks.

Frequently inundated areas of lowland floodplains apparently once supported stands of *Metroxylon vitiense*, a monocarpic "sago" palm, perhaps commencing about 4300 yr B.P. with the mid-Holocene stabilization and gradual fall in sea level (Southern 1986, Ash 1987a). *Metroxylon* was apparently not used as a source of sago in Fiji and stands do not seem to have been conserved or managed. Some remaining *Metroxylon* stands occupying several hectares near Deuba appear to be predominantly of even age, their regeneration perhaps linked to changes in drainage and flooding regimes.

Prehistoric human disturbance of poorly drained lowland areas with high rainfall appears frequently to have followed a sequence of events commencing with forest clearance for gardening, which, if abandoned, favored sedge colonization and peat development (0–2 m deep), and, combined with occasional burning by man, created extensive monocotyledon-dominated sedge–*Pandanus tectorius* swamps (50 km²; Ash and Ash 1984, Ash and Ash 1985, Southern 1986, Ash 1987c). Recently, drainage of such sites is leading to their use for agriculture and housing (e.g., Dreketi, Navua, and Rewa floodplains).

MANGROVE SWAMPS (194 km²) AND SEA GRASS BEDS. Mangrove species are present around most of the more wave-sheltered coastline growing both on fine silt and coarser rocky substrates including silted fringing coral reefs. With higher rainfall, on southeastern coasts and estuaries, the soil salinity is generally maintained at about marine concentrations. The trees (*Bruguiera gymnorhiza*, *Excoecaria agallocha*, *Lumnitzera coccinea*, *Rhizophora stylosa*, *R. samoensis* [plus infertile hybrids between the *Rhizophora* species], and

Xylocarpus granatum) reach heights of 7–15 m near the inland margins, declining in height to 3–6 m and changing to a *Rhizophora*-dominated seaward zone. On northwestern coastlines, with lower rainfall, soil salinities at the inland margin rise, through evaporation during dry periods, and a zone of highly saline bare mud is replaced seaward by stunted mangroves, principally *Rhizophora*, increasing in stature to 3–6 m height in the more frequently inundated seaward zone. Seeds and seedlings are generally abundant, frequently germinating but generally not surviving outside the zone of parental trees, except on the accreting mud flats of the estuaries where even aged stands are formed and extend several meters each decade.

The mid-Holocene marine transgression, to about +45 cm (Ash 1987a), extended mangrove distributions across some low-lying floodplains, and the subsequent fall in sea level induced a slow seaward successional trend in the mangrove zonation, which may now be reversed if sea levels rise.

Human impact on terrestrial ecosystems has tended to increase siltation of adjacent coastal regions, generally favoring mangroves (Ash 1987a). Siltation of fringing reefs, leading to death of the corals and establishment of mangroves, is apparently reflected in the changing composition of marine faunal remains in middens (Gifford 1951, 1955). Mangroves are one of the most intensively utilized natural ecosystems in Fiji, being a source of fuel and of foods such as crabs, prawns, and fish. Near towns mangroves are, however, frequently under threat as Crown Land available for infilling and redevelopment, while some rural mangrove stands have been enclosed by dikes and drained for cultivation (e.g., Dreketi Valley and near Labasa). Their acidic (sulfide-rich) soil has caused problems for crops, and some reclamation schemes have been abandoned. Such interference with drainage and siltation has locally led to mangrove dieback in adjacent areas.

Sea grass beds, principally comprising the widely dispersed *Halophila ovalis*, *Halodule pinifolia*, *H. uninervis*, and *Syringodium isoetifolium*, are found seaward of most mangroves and in shallow lagoonal areas. Although they

do not have a major direct role in marine herbivore food chains, they are an important food resource for turtles and act as a substrate for algae and provide protection for many marine invertebrates, especially at juvenile stages. Fiji has a rich marine benthic algal flora with, perhaps, 70–100 genera and 120–170 species, but it is not well known, nor are its dynamics and role in the marine food chain documented.

BEACH AND ROCKY SHORE VEGETATION. As indicated in the discussion of seed dispersal, the Fijian beach and coral cay vegetation is similar in floristics and dynamics to that of most tropical Pacific islands. Beaches and rocky shores are subject to continual wave action and infrequently to the huge swells induced by cyclones that periodically scour and reshape the beaches to considerable heights and distances inland. The seaward edge of most beach vegetation is, therefore, a successional community colonizing sand disturbed by the last storm: creeping vines such as *Ipomoea pes-caprae* and *Vigna marina* dominate this zone. On rocky substrates just above the normal wave range there is little soil material, drying winds, and salt spray, which together exclude most taxa except a few halophytic succulents (e.g., *Portulaca* sp., *Sesuvium portulacastrum*, the sedge *Fimbristylus cymosa*, and the grass *Lepturus repens*). Farther inland, out of the range of most waves, there is typically a zone of moderately salt spray-tolerant shrubs, such as *Clerodendrum inerme*, *Scaevola taccada*, *Wedelia biflora*, and *Sophora tomentosa*, frequently supporting the parasitic *Cassytha filiformis*. The shrub zone passes into a taller zone typified by *Pandanus tectorius* (Ash 1987c), and this passes into littoral forest vegetation often dominated by trees such as *Barringtonia asiatica*, *Calophyllum inophyllum*, *Cerbera mangas*, *Cocos nucifera*, *Cordia subcordata*, *Hernandia nymphaeifolia*, *Hibiscus tiliaceus*, *Tournefortia argentea*, *Terminalia catappa*, and *Thespesia populnea*. At Sigatoka on Viti Levu the beach vegetation extends into partially forested dunes (Kirkpatrick and Hassall 1981). These coastal forests and *Pandanus* are generally outside the zone of cyclone-induced wave damage but are sus-

ceptible to severe wind damage. Such disturbance apparently favors local dominance by particular species. These near-coastal forest habitats were often settled and cultivated by Fijians and, in the last century, developed as coconut plantations, such that littoral forests are generally fragmentary and disturbed. The species are, however, well adapted to disturbance and although the undisturbed vegetation type is scarce the flora appears to be reasonably widespread.

Future Developments

The human population of Fiji is expected to double or treble within the next century, accompanied by a greater rise in demand for goods and services. The consequences are both an intensification and extension of productive activities. The increased rate of natural biological resource utilization is likely to be met by raising the intensity and frequency of exploitation of native ecosystems, especially forests for timber products and coastal ecosystems for marine foods. In both instances the age-class structure of populations will be forced to change, and slow-maturing species are likely to be disadvantaged.

Natural populations of primary forest plants reach peak fecundities at 80–300 yr and, though their growth is accelerated by reductions in competition, faster maturing secondary species will be favored by the anticipated 20- to 40-yr logging cycles. This trend is expected for most of the 65% of forest area identified as production forest, though it may be several cycles before the floristic changes become overwhelming. As these changes occur, it is likely that interplanting or replanting with exotic tree species will become prevalent. The future of the remaining 35% of forest set aside for catchment protection is dependent upon political considerations since many of these forests do contain exploitable timber resources. Over the past few decades much of the interior of the large islands has been penetrated by a network of roads, some a consequence of logging activities, others built to villages and dams, all facilitating further logging initiatives. All-weather roads have generally attracted settlement and adjacent

forest clearance, a pattern that is expected to continue. The trend to urbanization is strong, however, so population growth in remote areas may be slight while nearer to towns, especially Suva, encroachment on the forests is likely to accelerate.

The more open habitats created by logging and clearance favor exotic weeds. With the establishment of a herbaceous vegetation cover, whether horticultural, arable, or pastoral, the switch from a native to an exotic flora and vegetation type is virtually complete. Similar changes are evident in the avifauna, with the remaining native birds virtually excluded from secondary vegetation (Clunie and Morse 1984), and similar changes probably occur in other animal taxa. Conservation of the Fijian native biota and vegetation is, therefore, largely synonymous with conserving the native forest habitats and maintaining a high proportion of long-lived trees. There are biological and aesthetic arguments for retaining old-growth forests intact as perpetual reserves and as standards by which to judge managed forest, but, at present, such reserves amount to only a few thousand hectares in a few localities: these would be totally inadequate as the sole forest reserves. Development of a representative system of protected reserves is highly desirable and has been proposed to the government (Secretary, National Trust for Fiji, pers. comm.).

Cloud forests, in particular, are of very limited extent and all should be placed in reserves: their biological, aesthetic, and tourism value greatly exceeds any value to be obtained from primary production (Ash 1987*d*). A threat to cloud forests is the development of mountaintop telecommunication facilities that, although of limited size, may inadvertently disturb much of this community. The upland lake and swamp catchments of Taveuni (Southern 1986, Southern et al. 1986) and representative sustainable areas of *Pandanus* swamp (Ash and Ash 1984, Ash 1987*c*), mangroves, dune (Kirkpatrick and Hassall 1981), beach, and dry zone forest are all habitats of limited extent or with a notable proportion currently disturbed and deserving of immediate conservation measures (Ash and Vodonaivalu 1989).

For most of the Fijian forest resource, conservation concerns must focus on the management of a forest that has been selectively logged once and is likely to be logged again. Logging procedures and management regimes span the range from disturbance analogous to the infrequent ravages of cyclones to much more frequent and intense practices that transform the primary forest to a secondary and exotic-dominated community. The future of the extensive production forests and perhaps that of some protection forest will depend on the type of logging that is practiced. A second major conservation concern is, therefore, to develop and implement silvicultural practices that will satisfy the financial demands of landowners and the timber needs of the community while conserving the native flora and fauna. Limited plantations of fast-growing exotic trees in already disturbed areas may achieve this goal provided there is a balance maintained between the two forest types, but ultimately sustainable timber and floristic management of these native forests is perhaps desirable, coupled with a system of permanent reserves.

Despite quarantine screening, accidental as well as deliberate introductions of exotic plants are likely to continue at a rate of several species a year. The existing trend for these species to establish and dominate open habitats is likely to continue, but it is also likely that more shade-tolerant species will establish and could invade native forests. Domesticated herbivore populations, notably cattle and goats, are increasing, and both goats and pigs have uncontrolled feral populations. These herbivores consume woody regrowth and favor open-habitat grasses, restricting the regrowth of native forests. Predatory mongooses, rats, dogs, and cats, as well as humans have already had a severe impact on ground-nesting birds and native lizards: their impact on the vegetation is indirect but could affect vectors of both pollen and seeds. Certain predators are absent from smaller islands (e.g., mongoose on Taveuni), and it is to be hoped that they are not introduced.

Global changes to the atmosphere and climate may increase temperatures, increase the frequency of cyclones, increase rainfall,

and cause sea levels to rise by 0.5–1.5 m in the next century (Pearman 1988). All these processes would affect Fiji, especially coastal areas, reefs, and cays, returning these to the situation of about 5000 yr ago. The littoral species are mostly capable of rapid migration and could track such sea-level changes inland, except on cays that might become totally submerged. Some loss of low-lying agricultural land is likely, increasing the need for more intensive land use. Compared with the impact on the atolls of Polynesia, Fijian ecosystems would be disturbed rather than destroyed, and there may be negotiations to resettle Polynesians on certain Fijian islands.

Conclusions

Though some endemic vertebrates have been lost through the impacts of man and most lowland dry zone and low island ecosystems are extensively disturbed, Fiji still retains a variety of more or less natural functioning ecosystems. With proper management these can be retained while production of timber and food in other areas is increased. In particular, attention should focus on preserving sustainable areas that include unusual or restricted habitats or contain rare species. A longer-term goal is to manage remaining forests to conserve species as well as to yield resources. Inevitably these goals will require government control and, probably, appropriation of some land: it should not be beyond the power of government to do these things.

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