

Microhabitat specialization of tropical rain-forest canopy trees in the Sovi Basin, Viti Levu, Fiji Islands

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(Accepted 16 May 2011)

Abstract: Island biotas often have lower species diversity and less intense competition has been hypothesized as a result. This should result in lower habitat specificity compared with mainland habitats due to larger realized niches. We investigate microhabitat associations of canopy trees with regard to differences in topography on an oceanic island (Viti Levu, Fiji) using twenty 10 × 60-m plots. We find high tree-species diversity (112 species with dbh ≥ 10 cm in a total of 1.08 ha) and high endemism (c. 60%), compared with other islands in Western Polynesia. Our sample plots aggregate into three distinct groups that are mostly defined by micro-topography: (1) ridges and steep slopes (well-drained sites), (2) moderate slopes and ridge flats (moderate drainage), and (3) flats (poor drainage). Associations with microhabitat are found for more than 50% of the 41 most common species but only one species is apparently restricted to a single habitat. These findings are similar to other rain forests and demonstrate considerable niche differentiation among island rain-forest tree species.

Key Words: Fiji, habitat differentiation, islands, Pacific, rain forest, Sovi Basin, species diversity, topography

INTRODUCTION

The high species diversity of tropical rain forests has fascinated biologists for more than six decades (Black *et al.* 1950). For example, 473 tree species with a diameter at breast height (dbh) ≥ 5 cm were recorded in a 1-ha plot in Amazonian Ecuador (Valencia *et al.* 1994). Many different factors have been proposed to explain this extraordinary diversity (Chesson 2000, Connell 1978, Hubbell & Foster 1986, Wright 2002). One of the best supported (although not necessarily one of the most important) of these is niche differentiation associated with micro-topographic variation in drainage, moisture and nutrients (John *et al.* 2007, Svenning 1999, Yamada *et al.* 2006).

Ridges, slopes, flats and other topographic microhabitats in tropical rain forests have been shown to have distinct communities (Clark *et al.* 1998, Webb & Peart 2000). This phenomenon is caused by tree species being significantly associated with certain topographic positions (Clark *et al.* 1998, Harms *et al.* 2001, Hubbell

& Foster 1986). While obligate habitat restriction is rare, association with certain microhabitats appears common (Clark *et al.* 1998, Phillips *et al.* 2003). Webb & Peart (2000) also found that certain families seem to have affinities for certain microhabitats, while on the other hand niche partitioning has been detected among species in Bornean Sterculiaceae (Yamada *et al.* 2006) and Amazonian Myristicaceae (Queenborough *et al.* 2007).

Islands present an interesting case, as they generally have biotas that are disharmonic and have lower species diversities than comparable continental habitats (Keppel *et al.* 2009, MacArthur & Wilson 1967). Compared with mainland habitats, this could result in larger realized niche space and hence lower habitat specificity (Roughgarden 1974). This would imply that communities in different topographic microhabitats should be less distinct. However, an alternative scenario would be that island species have similar niche width and habitat specificity as mainland species and, as a result, well-differentiated communities in different habitats with lower species diversity than mainland communities. In the Samoan archipelago, distinct ridge

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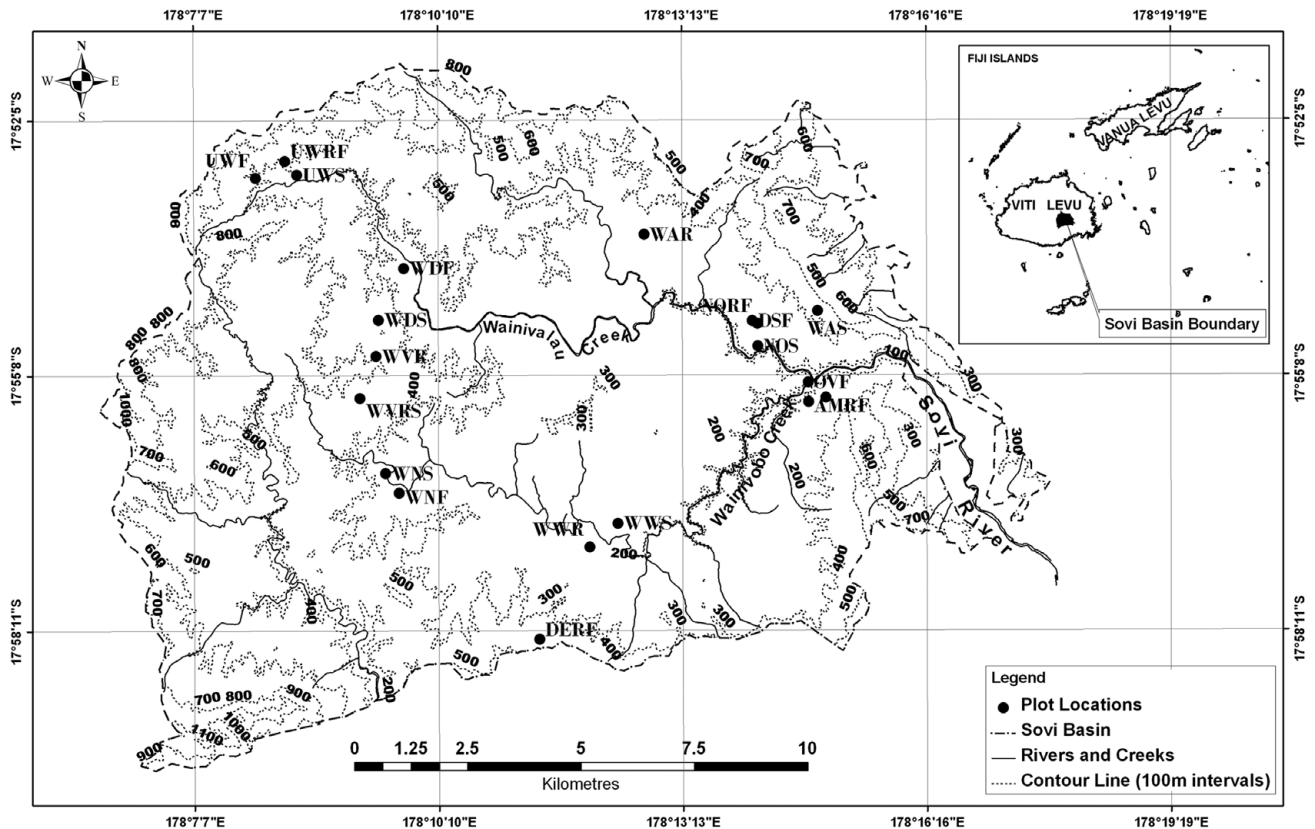


Figure 1. Location of study sites in the Sovi Basin in Fiji.

forest communities have been reported (Whistler 1980). Furthermore, forest structure and species composition have been found to vary considerably with respect to topography (Webb *et al.* 1999).

In this study we investigate whether tree species composition varies among different microhabitats in a remote lowland rain forest on Viti Levu, Fiji. We (1) test whether different topographic habitats (ridge, slope and flats) in this island rain forest have distinct species compositions, (2) determine which species and families have distinct habitat affinities, and (3) compare our results with the continental island of Borneo and the oceanic island of Tutuila in Samoa.

METHODS

Study site

The Sovi Basin, located on the island of Viti Levu (10 388 km²) in the Fiji Group, covers some 200 km², comprising lowland tropical rain forest (100–500 m asl) surrounded by mountain ranges (600–1300 m) in all directions (Figure 1). As a result, the basin has some of the most remote lowland rain forest in Fiji and has been protected in a partnership between local

landowners, Conservation International and Fiji Water. The basin is composed of a mosaic of volcanic rocks that originated 20–40 Mya and transected by the Wainavobo and Wainivalu rivers, which join and exit as the Sovi River through a gorge in the east of the basin (Hirst 1965). Four climate stations adjacent to the basin report high annual precipitation, ranging widely between 3000 and 5000 mm y⁻¹. This suggests that local topography greatly influences the amount of rainfall in the area. Although the Sovi Basin is currently (and has been for the last 100–200 y) uninhabited, it has a complex prehistoric settlement history, which is concentrated in the lower (eastern) and central parts of the basin. After European contact, the human population in Fiji and other Pacific Island countries decreased due to introduced diseases, and reduced warfare allowed the relocation of villages to more accessible locations (Bayliss-Smith 2006). There is no evidence that the uppermost (western) reaches of the Sovi Basin were ever settled.

Data collection

During two surveys, the first from 5–17 May 2003 and the second from 14–20 March 2004 (totalling 20 d), we surveyed 19 plots (10 × 60 m in size) in different

Table 1. Codes, characteristic features, plot sizes, tree species richness, percentage endemism (%E), basal area and density for all 19 study plots in the Sovi Basin. Topographic classes are defined in methods; average and standard deviation for species richness, basal area and density exclude DSF and WAS, which had a smaller plot size.

Code	Topography	Slope (°)	Plot size (m)	Altitude (m)	Richness	%E	Basal area (m ²)	Density (stems)
WWR	Ridge	0	10 × 60	180	29	48.3	2.14	73
WWS	Slope	35	10 × 60	160	26	53.8	2.45	53
NOS	Slope	45	10 × 60	140	21	61.9	1.50	34
NORF	Ridge flat	0	10 × 60	210	24	66.7	2.76	50
DSF	River flat	0	10 × 30	110	14	57.1	2.21	25
WAR	Ridge	0	10 × 60	220	23	69.6	2.70	62
WAS	Slope	50	10 × 30	140	21	57.1	2.25	29
OGRF	Ridge flat	0	10 × 60	210	26	46.2	2.86	33
AMRF	Ridge flat	10	10 × 60	140	24	54.2	4.79	44
UWF	Flat	0	10 × 60	500	26	61.5	3.39	56
UWS	Slope	40	10 × 60	420	25	64.0	4.50	62
UWRF	Ridge flat	0	10 × 60	500	31	58.1	2.98	71
WDF	Flat	0	10 × 60	260	24	58.3	4.67	40
WDS	Slope	20	10 × 60	500	33	63.6	3.17	63
WVR	Ridge	0	10 × 60	520	19	57.9	1.42	50
WVRS	Ridge slope	20	10 × 60	440	26	53.8	2.39	89
WNF	Flat	0	10 × 60	180	26	69.2	4.01	63
WNS	Slope	15	10 × 60	200	39	66.7	3.18	81
DERF	Ridge flat	0	10 × 60	450	34	64.7	6.09	95
Average					26.8	59.7	3.24	61.1
SD					5.0	6.4	1.23	16.7
Total					112	60.7	–	–

microhabitats (Table 1) throughout the Sovi Basin (Figure 1) on Viti Levu, Fiji's oldest (30–40 million y) and largest island. The four microhabitats differentiated in the field were flats (locations with a slope $\leq 10^\circ$), ridges (locations of higher elevation than the surrounding landscape and of a narrow (< 30 m), linear form), ridge flats (like ridges but wider (usually ≥ 50 m)) and slopes (locations with a slope $> 10^\circ$). Plots were set up parallel to elevational contour lines, except for slopes (where plots were set up perpendicular to contour lines). All plots are remote (more than 6-h walk from the nearest settlement) and were selected by choosing homogenous old-growth (Clark 1996) forest in the mature phase (Martínez-Ramos *et al.* 1988, Whitmore 1989). Two plots (site codes = DSF, WAS; see Table 1 for site codes) were only 10×30 m in size to ensure that they were located in homogenous forest and did not extend into different microhabitats.

Within each plot species identity and dbh (measured at 1.4 m height) were recorded for each tree with dbh ≥ 10 cm. We also recorded the topographic microhabitat (flat, slope, ridge flat or ridge), angle of the slope and elevation for each plot. All tree species encountered were identified in the field. If a plant could not be identified, herbarium samples were collected and then deposited and identified at the South Pacific Regional Herbarium (SUVA). Identifications were carried out using Smith (1979–1991) and Keppel & Ghazanfar (2006) and nomenclature follows these sources.

Data analysis

We calculated the total basal area of each tree (based on the measured dbh), which gives an indication of species dominance (Mueller-Dombois & Ellenberg 2002), of each species and used the software R 2.10.1 (R-Development-Core-Team; <http://cran.r-project.org/>) for all analyses. We conducted Kruskal's non-metric multidimensional scaling (NMDS) based on the Bray–Curtis dissimilarity coefficient (B ; if $B = 0$, sites have equal composition; if $B = 1$, sites have no species in common) of combined total absolute basal areas for each species in a plot using the *metaMDS* option to determine which sites shared similar species composition. Based on the NMDS plot, we excluded an outlying site (site code = DSF) from further analyses.

We then repeated the NMDS analysis without the excluded site and correlated the topographic microhabitat, slope and elevation of each site with the resulting NMDS plot using vector fitting (Dargie 1984, Kantvilas & Minchin 1990), which allows quantification of the strength of relationships between environmental variables and species composition through the correlation coefficient (r^2). The significance of r^2 was calculated by producing P-values based on 1000 permutations. To facilitate vector fitting, we coded the topographic microhabitats based on inferred increasing drainage as follows: flat (as 1), slope (2), ridge flat (2.5) and ridge (3).

Based on the NMDS plot, we divided sites into three groups, which had different species composition and

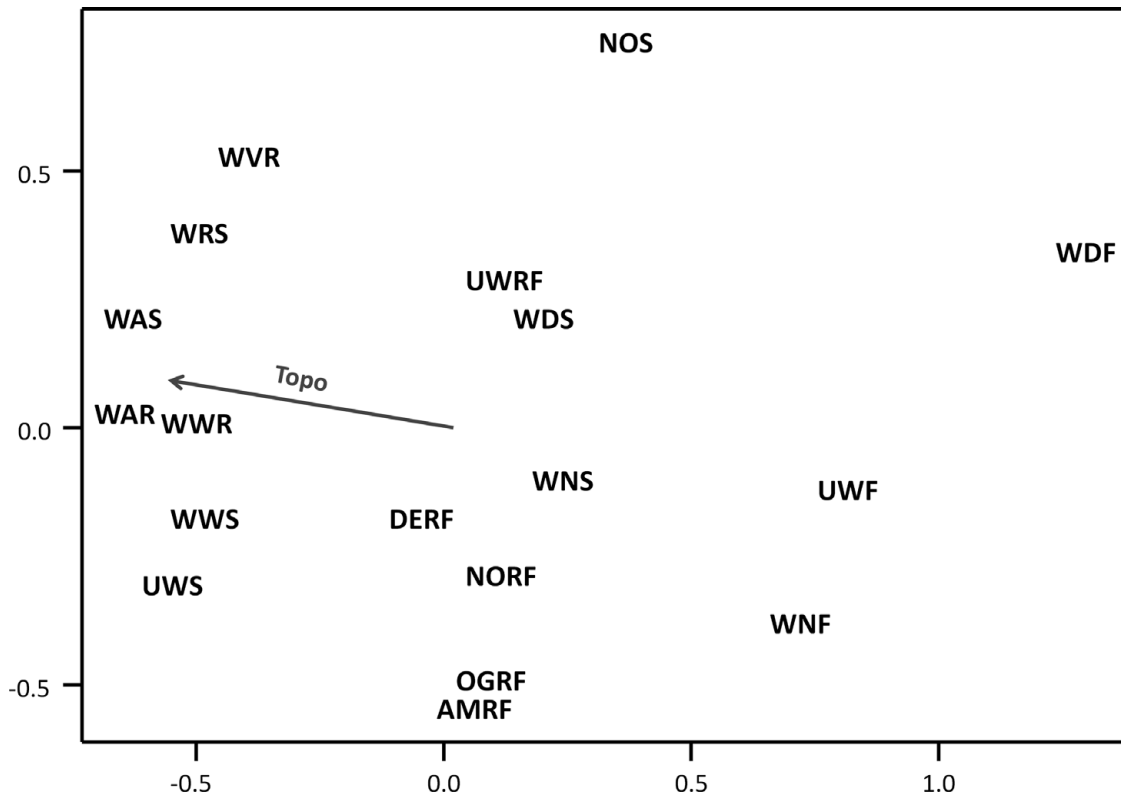


Figure 2. Non-metric multidimensional scaling (NMDS) for 18 study plots (DSF excluded) in the Sovi Basin, Fiji, based on basal areas of trees with dbh ≥ 10 cm. Last letter (s) of site codes indicate topographic location (R = ridge, RF = ridge flat, S = slope, F = flat). See Table 1 for site codes and details of plots. Stress = 18.5, two convergent solutions found after three attempts. Fitted onto this is the only significant explanatory variable topographic microhabitat (Topo; $r^2 = 0.532$, $P = 0.005$).

appeared to correspond to different drainage regimes: (1) ridges and steep ($> 30^\circ$) slopes (site codes = UWS, WAR, WAS, WVR, WRS, WWR, WWS), (2) moderate ($\leq 10\text{--}25^\circ$) slopes and ridge flats (site codes = AMRF, DERF, NORF, NOS, OGRF, UWRF, WDS, WNS), and (3) flats (site codes = UWF, WDF, WNF). We tested whether these three groups differed significantly in species composition using the multi-response permutation procedure (MRPP; Mielke *et al.* 1976). To minimize the effect of chance occurrences of species in plots, we focused on species (genera and families) that occurred at least in half of the plots within at least one of the three groups to test which species were strongly associated with particular microhabitats. For these selected taxa we conducted an indicator species analysis (Dufrêne & Legendre 1997) to test the significance of association with a particular habitat.

RESULTS

Species composition

In the 19 plots, which totalled 1.08 ha in area, we recorded 1003 trees of 112 species in 76 genera and 46 families (Appendix 1). *Syzygium* (Myrtaceae) was the most

diverse genus with seven species, followed by *Calophyllum* (Clusiaceae) and *Palaquium* (Sapotaceae) with five, and *Myristica* (Myristicaceae) with four species. The most species-rich families were the Clusiaceae, Euphorbiaceae and Sapotaceae with eight species each, followed by the Myrtaceae with seven species. Forty-six to 70% (mean = 60%) of species per plot were endemic to Fiji (Table 1). Basal area in the $10 \times 60\text{-m}$ plots (Table 1) ranged between 1.42 and 6.09 m^2 (mean = 3.24 m^2) and density between 33 and 95 trees (mean = 61 trees). Although the site with the highest density also had the highest basal area (Table 1), there was no significant correlation ($r^2 = 0.063$, $P = 0.250$) between the two variables.

NMDS including all sites produced three clusters, differentiated based on species composition. One of the flats studied (DSF) was an extreme outlier and formed a unique vegetation type, dominated by two species, *Retrophyllum vitiense* (Podocarpaceae) and *Calophyllum vitiense* (Clusiaceae). Because the species composition of this site was very different from any of the other plots analysed, it was excluded from other analyses.

The NMDS plot of the reduced data set was very similar to that of the complete one (Figure 2) and

Table 2. The 10 species with the greatest combined basal areas (m², stated after species name) in the three topographic microhabitats for 18 study plots (DSF excluded) in the Sovi Basin, Fiji, including trees with dbh \geq 10 cm. See Table 1 for site codes and details of plots and Appendix 1 for status (endemic/indigenous). RS (7 plots) = ridges and steep ($>30^\circ$) slopes, MS (8 plots) = moderate ($\leq 20^\circ$) slopes and ridge flats, FL (3 plots) = flats.

RS (7 plots, total area = 0.39 ha)	MS (8 plots, total area = 0.48 ha)	FL (3 plots, total area = 0.18 ha)
<i>Palaquium hornei</i> 2.85	<i>Gonystylus punctatus</i> 2.86	<i>Viticipremna vitilevuensis</i> 3.01
<i>Agathis macrophylla</i> 1.60	<i>Endospermum macrophyllum</i> 2.83	<i>Premna protusa</i> 0.85
<i>Dacrydium nidulum</i> 1.21	<i>Myristica gillespieana</i> 2.40	<i>Dillenia biflora</i> 0.83
<i>Haplolobus floribundus</i> 1.21	<i>Parinari insularum</i> 1.67	<i>Dysoxylum richii</i> 0.63
<i>Myristica gillespieana</i> 1.07	<i>Syzygium fijiense</i> 1.52	<i>Pisonia umbellifera</i> 0.50
<i>Endospermum macrophyllum</i> 0.89	<i>Calophyllum vitiense</i> 0.92	<i>Gmelina vitiensis</i> 0.47
<i>Gnetum gnemon</i> 0.67	<i>Calophyllum amblyphyllum</i> 0.85	<i>Gironniera celtidifolia</i> 0.47
<i>Calophyllum vitiense</i> 0.56	<i>Palaquium hornei</i> 0.81	<i>Bischofia javanica</i> 0.43
<i>Parinari insularum</i> 0.56	<i>Garcinia myrtifolia</i> 0.71	<i>Gonystylus punctatus</i> 0.41
<i>Heritiera ornithocephala</i> 0.56	<i>Dacrycarpus imbricatus</i> 0.68	<i>Palaquium porphyreum</i> 0.35

produced the same three clusters of plots: ridges and steep ($>30^\circ$) slopes (seven well-drained sites; left-hand side of Figure 2), moderate ($\leq 20^\circ$) slopes and ridge flats (eight plots with moderate drainage; centre) and flats (three plots with poor drainage; right-hand side). MRPP confirmed these groups to be distinct communities ($A = 0.1127$, $P < 0.001$). Topographic position ($r^2 = 0.532$, $P = 0.005$) was the only significant explanatory vector for species composition (as represented by the NMDS plot). The slope ($r^2 = 0.205$, $P = 0.172$) and elevation ($r^2 = 0.045$, $P = 0.590$) of a plot were not significant.

Well-drained plots (ridges and steep slopes) were dominated by *Palaquium hornei* (Sapotaceae), *Agathis macrophylla* (Araucariaceae), *Dacrydium nidulum* (Podocarpaceae) and *Haplolobus floribundus* (Burseraceae). Moderate slopes were dominated by *Gonystylus punctatus* (Thymelaeaceae), *Endospermum macrophyllum* (Euphorbiaceae), *Myristica gillespieana* (Myristicaceae), *Parinari insularum* (Chrysobalanaceae) and *Syzygium fijiense* (Myrtaceae). Members of the Verbenaceae (*Viticipremna vitilevuensis*, *Premna protusa*, *Gmelina vitiense*) dominated the flats, with *Dillenia biflora* (Dilleniaceae) and *Dysoxylum richii* (Meliaceae) being other important components of this community (Table 2).

Habitat associations

Forty-one species occurred in at least half the plots of at least one particular microhabitat (Table 3). Of these species 23 (56%) showed significant habitat association at $P \leq 0.05$. The remainder did not return significant P-values in the indicator species analysis. Of the 23 species that showed habitat association, 14 were associated with poorly drained habitats (categories FL and FL/MS in Table 3), five with well-drained habitats (categories RS and RS/MS in Table 3), and

four with sites of intermediate drainage (category MS in Table 3).

A few genera and families also showed association with certain habitats (Table 3). The families Burseraceae, Podocarpaceae and Sapotaceae, and the genera *Calophyllum* and *Palaquium* were significantly associated with well-drained habitats (categories RS and RS/MS in Table 3), while the families Lauraceae and Verbenaceae and the genera *Dysoxylum* and *Macaranga* (Euphorbiaceae) were associated with poorly drained habitats (categories FL and FL/MS in Table 3). The genus *Myristica* was associated with sites of intermediate drainage (category MS in Table 3).

DISCUSSION

Species richness and endemism of trees with dbh \geq 10 cm in the lowland rain forest of the Sovi Basin are high. Values are similar to the total value reported for four 50 \times 50-m plots (total = 1 ha) in Savura (124 species, 54.1% endemism), located about 25 km south-east of the Sovi Basin on the same island (Keppel *et al.* 2010). This suggests that Fiji's lowland tropical rain forests have high diversity (about 100 tree species ha⁻¹) and endemism (50–60%), compared with other Western Polynesian archipelagos (Keppel *et al.* 2010, Webb & Fa'auumu 1999, Webb *et al.* 1999, 2006). Although some of these studies in the Samoan archipelago used somewhat different plot sizes, the total sample sizes are comparable and indicate a diversity of about 30–40 tree species ha⁻¹.

Species composition appears to be very similar to the Savura site, with species of *Myristica*, *Calophyllum*, *Garcinia*, *Syzygium*, *Palaquium* and *Gonystylus punctatus* dominating in both locations (Keppel *et al.* 2005). It therefore appears that a group of the same species (an oligarchy) dominates large stretches of lowland tropical rain forest on Viti Levu island. This phenomenon has also been found in Amazonian rain forests (Duivenvoorden

Table 3. Proportion of sample plots occupied and habitat associations of species, genera and families for 18 study plots (DSF excluded) in the Sovi Basin, Fiji, including trees with dbh ≥ 10 cm. See Table 1 for site codes and details of plots. The column for habitat association states the habitat for a taxon and the associated probability (P-value) obtained from the indicator species analysis. If values for one taxon also apply to higher taxonomic levels, taxa are listed with a slash (/). Taxa higher than species level are indented in the first column. RS (7 plots) = ridges and steep ($> 30^\circ$) slopes, MS (8 plots) = moderate ($\leq 20^\circ$) slopes and ridge flats, FL (3 plots) = flats. NS = not significant in the indicator species analysis.

Taxon	Proportion of plots occupied			Habitat association
	RS	MS	FL	
<i>Agathis macrophylla</i> / <i>Agathis</i> / <i>Araucariaceae</i>	0.71	0.38	0	ns
<i>Aglaiia</i> sp.	0.14	0.63	0.67	FL/MS – 0.023
<i>Aglaiia</i> (<i>Meliaceae</i>)	0.43	0.63	0.67	ns
<i>Anacolosia lutea</i> / <i>Anacolosia</i> / <i>Olacaceae</i>	0	0.13	0.67	FL – 0.015
<i>Annonaceae</i>	0.71	0.63	0.33	ns
<i>Apocynaceae</i>	0.43	1.00	0.67	ns
<i>Baccaurea stylaris</i> / <i>Baccaurea</i>	0.14	0.63	0	MS – 0.049
<i>Burseraceae</i>	1.00	0.63	0.67	RS – 0.018
<i>Calophyllum amblyphyllum</i>	0.86	0.75	0.33	ns
<i>Calophyllum vitiense</i>	0.57	0.38	0	ns
<i>Calophyllum</i>	1.00	0.88	0.33	RS/MS – 0.018
<i>Canarium</i> sp./ <i>Canarium</i>	0.57	0.50	0	ns
<i>Cerbera manghas</i> / <i>Cerbera</i>	0.29	0.63	0	ns
<i>Clusiaceae</i>	1.00	1.00	0.33	ns
<i>Crossostylis seemanii</i> / <i>Crossostylis</i> / <i>Rhizophoraceae</i>	0.14	0	0.67	FL – 0.020
<i>Cryptocarya constricta</i> / <i>Cryptocarya</i>	0	0.38	0.67	FL – 0.024
<i>Dacrydium nidulum</i> / <i>Dacrydium</i>	0.57	0	0	RS – 0.013
<i>Dillenia biflora</i> / <i>Dillenia</i> / <i>Dilleniaceae</i>	0.14	0.38	1.00	FL – 0.006
<i>Dysoxylum richii</i>	0	0.25	0.67	FL – 0.013
<i>Dysoxylum</i>	0	0.50	0.67	FL – 0.047
<i>Endiandra</i> sp./ <i>Endiandra</i>	0.14	0.50	0.67	ns
<i>Endospermum macrophyllum</i> / <i>Endospermum</i>	0.57	0.63	0.33	ns
<i>Euphorbiaceae</i>	0.71	1.00	1.00	ns
<i>Garcinia myrtifolia</i> / <i>Garcinia</i>	0.86	0.88	0.33	ns
<i>Gironniera celtidifolia</i> / <i>Gironniera</i> / <i>Ulmaceae</i>	0	0.50	1.00	FL – 0.004
<i>Gmelina vitiensis</i> / <i>Gmelina</i>	0	0.13	0.67	FL – 0.039
<i>Gnetum gnemon</i> / <i>Gnetum</i> / <i>Gnetaceae</i>	0.86	0.63	0	RS – 0.011
<i>Gonystylus punctatus</i> / <i>Gonystylus</i> / <i>Thymelaeaceae</i>	0.43	1.00	0.67	MS – 0.025
<i>Haplolobus floribundus</i> / <i>Haplolobus</i>	1.00	0.50	0.67	RS – 0.004
<i>Heritiera ornithocephala</i> / <i>Heritiera</i>	0.57	0.25	0.33	ns
<i>Kingiodendron platycarpum</i> / <i>Kingiodendron</i>	0.14	0.38	0.67	ns
<i>Lauraceae</i>	0.14	0.75	1.00	FL/MS – 0.006
<i>Leguminosae</i>	0.14	0.50	0.67	ns
<i>Macaranga</i> sp.	0	0.25	0.67	FL – 0.024
<i>Macaranga</i>	0.14	0.25	1.00	FL – 0.007
<i>Meliaceae</i>	0.43	1.00	1.00	ns
<i>Myristica chartacea</i>	0.57	0.75	0.33	ns
<i>Myristica gillespieana</i>	1.00	1.00	1.00	RS/MS – 0.007
<i>Myristica grandifolia</i>	0.14	0.13	0.67	ns
<i>Myristica</i> / <i>Myristicaceae</i>	1.00	1.00	1.00	MS – 0.037
<i>Pagiantha thurstonii</i> / <i>Pagiantha</i>	0.29	0.75	0.67	FL/MS – 0.038
<i>Palaquium fidjense</i>	0.29	0.50	0.67	ns
<i>Palaquium hornei</i>	1.00	0.38	0	RS – 0.002
<i>Palaquium porphyreum</i>	0.71	0.13	0.33	ns
<i>Palaquium</i>	1.00	0.75	0.67	RS – 0.050
<i>Parinari insularum</i> / <i>Parinari</i> / <i>Chrysobalanaceae</i>	0.86	0.63	0.33	ns
<i>Pisonia umbellifera</i> / <i>Pisonia</i> / <i>Nyctaginaceae</i>	0.29	0	1.00	FL – 0.001
<i>Podocarpaceae</i>	0.71	0.25	0	RS – 0.050
<i>Premna protusa</i> / <i>Premna</i>	0	0.25	0.67	FL – 0.011
<i>Sapotaceae</i>	1.00	0.88	0.67	RS – 0.032
<i>Saurauia rubicunda</i> / <i>Saurauia</i> / <i>Actinidiaceae</i>	0	0	1.00	FL – 0.001
<i>Sterculiaceae</i>	0.57	0.63	0.67	ns
<i>Syzygium seemanii</i>	0.29	0.63	0.33	ns
<i>Syzygium effusum</i>	0.43	0.63	0	ns
<i>Syzygium fijiense</i>	0.71	1.00	0.67	MS – 0.023
<i>Syzygium</i> / <i>Myrtaceae</i>	1.00	1.00	1.00	ns

Table 3. Continued.

Taxon	Proportion of plots occupied			Habitat association
	RS	MS	FL	
<i>Vavaea amicorum/Vavaea</i>	0.29	0.88	0	MS – 0.004
Verbenaceae	0.14	0.38	1.00	FL – 0.001
<i>Viticipremna vitilevuensis/Viticipremna</i>	0.14	0.25	1.00	FL – 0.001
<i>Xylopia pacifica/Xylopia</i>	0.71	0.63	0.33	NS

1995, Pitman *et al.* 2001, Svenning *et al.* 2004) and has been attributed to low environmental heterogeneity (Pitman *et al.* 2001). The topography and soils of lowland rain forests in south-west Viti Levu are indeed mostly similar, being composed of a (sometimes steeply) undulating landscape on red-brown clay soils of volcanic origin.

Our results show that more than 50% of all common species have clear habitat associations. This value is higher than the 35% (17 of 49 species using Monte Carlo randomizations) that showed significant association with topographic habitat in Borneo (Webb & Peart 2000) but similar to that for Samoa's 53% (9 of 17 species with 10 individuals or more using chi-squared tests). Similar to other studies in mainland rain forests (Clark *et al.* 1998, Phillips *et al.* 2003) and in Samoa (Webb *et al.* 1999), we found that obligate habitat association is rare but that many species show a significant tendency towards habitat association. *Saurauia rubicunda* (Actinidiaceae) and *Dacrydium nidulum* were the only common species restricted to a particular physiographic habitat in this study. While the former may indeed be mostly restricted to creek banks, the latter commonly occurs in habitats other than ridges and slopes outside the lowland tropical rain forest (Keppel *et al.* 2006, Keppel & Tuiwawa 2007).

Considering that we only studied habitat associations in relation to topographic variation, which we assume to roughly correspond to soil drainage, and did not investigate other important factors such as soil nutrients (John *et al.* 2007, Palmiotto *et al.* 2004), our study provides conservative evidence for habitat partitioning of rain-forest trees and hence for ecological determinism playing an important role in facilitating co-existence (Svenning *et al.* 2004). Although our study does not permit direct comparisons because of different plot sizes and analyses, the realized niches of tree species in the island rain forest of this study and those in Samoa (Webb *et al.* 1999) do not appear to be broader than on continental Borneo (Webb & Peart 2000). In all three studies (Webb & Peart 2009, Webb *et al.* 1999, this study) a similar distinction of well-drained ridges/steep slopes, moderate slopes and flats was observed. The commonness of habitat specialization in Fijian and Samoan rain forest (Webb *et al.* 1999) also implies that competition amongst tree species may play an important

role in Pacific Island rain forest and cautions against generalizations about islands having lower levels of competition.

We detected some similarities at higher taxonomic levels (genus and family) between our results and those from Bornean (Webb & Peart 2000) and Samoan (Webb *et al.* 1999) rain forests. While comparisons are difficult because of different methods and analyses employed, *Calophyllum* and *Palaquium* were found to be primarily associated with well-drained habitats in all three studies. This may suggest that taxa retain their niches when colonizing islands, which are often assumed to have more vacant niche space, and hence that niche conservatism plays a role in the assembly of island communities.

While Fiji lowland rain-forest communities of ridges and slopes have been previously described (Keppel *et al.* 2005), the communities on stream flats have not. This community is dominated by distinct species, especially in the Verbenaceae, and forms a physiographic habitat type defined by having poorer drainage, experiencing brief, occasional floods after heavy downpours and as a result receiving regular deposits of alluvial materials. Because such stream flats are highly fertile and because human disturbance is often concentrated around watercourses, this community is likely endangered and good exemplars were restricted to the upper reaches of the Sovi Basin.

This study shows Fiji to be highly diverse compared with other Polynesian Pacific islands and provides some initial evidence for habitat partitioning among species in insular environments. While significant associations with topographic microhabitats are demonstrated for half of all common tree species, more detailed studies are required to quantify the strength of these associations. This would facilitate comparing the sizes of realized niches on islands and the mainland and an assessment, if lower species diversity does lead to broader realized niches.

ACKNOWLEDGEMENTS

The field surveys were part of the Pacific-Asia Biodiversity Transect (PABITRA) and the Sovi Basin biodiversity assessment. We would like to thank the *mataqalis* that

own land in the Sovi Basin for permitting us to enter and study on their land and for assisting us with numerous logistic aspects of our study. We are especially indebted to those landowners who accompanied us in the field and assisted with data collection. We would also like to thank Mosese Moceyawa, Nunia T. Thomas and Baravi Thaman for their assistance in the data collection. Figure 1 was produced by Sala Curuki of the National Trust for Fiji, incorporating data provided by the Department of Lands, Suva, Fiji. Janet Franklin of Arizona State University provided many useful comments on a draft of this paper.

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Appendix 1. Total basal area, family and status (e = endemic; i = indigenous) for all tree species with a dbh ≥ 10 cm in seven plots on ridges and steep ($> 30^\circ$) slopes RS, eight plots on moderate ($\leq 20^\circ$) slopes and ridge flats (MS), three plots on flats (FL) and one outlying plot on a flat (DSF), all located in the Sovi Basin. See Table 1 for site codes and details of plots.

Taxon	Family	Status	RS	MS	FL	DSF
<i>Agathis macrophylla</i>	Araucariaceae	i	1.601	0.542	0	0
<i>Aglaiia</i> sp.	Meliaceae	e	0.013	0.326	0.058	0
<i>Aglaiia vitiense</i>	Meliaceae	e	0.063	0	0	0
<i>Alangium vitiense</i>	Alangiaceae	e	0	0.133	0	0.015
<i>Alphitonia franguloides</i>	Rhamnaceae	i	0.014	0	0	0
<i>Alstonia costata</i>	Apocynaceae	i	0.025	0.246	0	0
<i>Alstonia vitiense</i>	Apocynaceae	i	0	0.010	0	0
<i>Anacolosia lutea</i>	Olacaceae	i	0	0.015	0.184	0
<i>Astromidium</i> sp.	Melastomataceae	e	0	0.011	0	0
<i>Atuna racemosa</i>	Chrysobalanaceae	i	0	0.170	0	0.116
<i>Barringtonia edulis</i>	Lecythidaceae	i	0	0.154	0.008	0.059
<i>Bischofia javanica</i>	Euphorbiaceae	i	0	0	0.427	0
<i>Burckella fijiensis</i>	Sapotaceae	e	0.017	0	0	0
<i>Burckella parviflora</i>	Sapotaceae	e	0.013	0.146	0	0
<i>Calophyllum amblyphyllum</i>	Clusiaceae	e	0.319	0.847	0.087	0
<i>Calophyllum cerasiferum</i>	Clusiaceae	e	0.330	0.045	0	0
<i>Calophyllum leptocladum</i>	Clusiaceae	e	0.162	0.038	0	0
<i>Calophyllum neo-ebudicum</i>	Clusiaceae	i	0	0.016	0	0
<i>Calophyllum vitiense</i>	Clusiaceae	e	0.564	0.920	0	0.318
<i>Canarium</i> sp.	Burseraceae	e	0.200	0.473	0	0.057
<i>Cerbera manghas</i>	Apocynaceae	i	0.083	0.252	0	0.018
<i>Citronella vitiensis</i>	Icacinaceae	e	0.043	0	0	0
<i>Crossostylis seemannii</i>	Rhizophoraceae	e	0.008	0	0.040	0
<i>Cryptocarya constricta</i>	Lauraceae	e	0	0.038	0.100	0
<i>Cyathea</i> sp.	Cyatheaceae	e	0	0	0.225	0
<i>Cyathocalyx insularis</i>	Annonaceae	e	0	0.030	0	0
<i>Dacrycarpus imbricatus</i>	Podocarpaceae	i	0.341	0.679	0	0
<i>Dacrydium nidulum</i>	Podocarpaceae	i	1.210	0	0	0
<i>Degeneria vitiensis</i>	Degeneriaceae	e	0	0.647	0.235	0.004
<i>Dendrocnide harveyi</i>	Urticaceae	i	0	0	0.014	0
<i>Dendrocnide vitiensis</i>	Urticaceae	e	0	0	0.027	0
<i>Dicksonia brackenridgei</i>	Cyatheaceae	e	0.010	0	0	0
<i>Dillenia biflora</i>	Dilleniaceae	i	0.009	0.366	0.825	0
<i>Diospyros</i> sp.	Ebenaceae	e	0.007	0	0	0
<i>Dolicholobium latifolium</i>	Rubiaceae	e	0	0.019	0	0
<i>Dolicholobium macgregorii</i>	Rubiaceae	e	0	0.016	0	0
<i>Dysoxylum lenticellare</i>	Meliaceae	e	0	0.127	0	0
<i>Dysoxylum richii</i>	Meliaceae	i	0	0.269	0.633	0
<i>Dysoxylum</i> sp.	Meliaceae	e	0	0.0745	0	0
<i>Elaeocarpus subcapitatus</i>	Elaeocarpaceae	e	0	0.154	0	0
<i>Emmenospermum micropetalum</i>	Rhamnaceae	e	0.030	0.014	0	0
<i>Endiandra elaeocarpa</i>	Lauraceae	i	0	0.024	0	0
<i>Endiandra</i> sp.	Lauraceae	e	0.010	0.650	0.213	0.008
<i>Endospermum macrophyllum</i>	Euphorbiaceae	e	0.886	2.826	0.305	0
<i>Excoecaria</i> sp.	Euphorbiaceae	e	0	0.010	0	0
<i>Fagraea berteriana</i>	Loganiaceae	e	0.108	0	0	0
<i>Fagraea gracilipes</i>	Loganiaceae	i	0.053	0	0	0
<i>Ficus fulvo-pilosa</i>	Moraceae	e	0	0.023	0	0
<i>Ficus smithii/pritchardii</i>	Moraceae	e	0	0.129	0.016	0
<i>Garcinia myrtifolia</i>	Clusiaceae	i	0.422	0.708	0.136	0
<i>Garcinia pseudoguttifera</i>	Clusiaceae	i	0.028	0.063	0	0
<i>Garcinia</i> sp.	Clusiaceae	e	0.106	0	0	0
<i>Gardenia</i> sp.	Rubiaceae	e	0	0.031	0	0
<i>Giromiera celtidifolia</i>	Ulmaceae	i	0	0.222	0.465	0
<i>Glochidion seemannii</i>	Euphorbiaceae	e	0	0.190	0	0
<i>Glochidion vitiense</i>	Euphorbiaceae	i	0.044	0.013	0	0
<i>Gmelina vitiensis</i>	Verbenaceae	e	0	0.166	0.471	0
<i>Gnetum gnemon</i>	Gnetaceae	i	0.666	0.109	0	0
<i>Gonystylus punctatus</i>	Thymelaeaceae	e	0.071	2.859	0.412	0
<i>Gymnostoma vitiense</i>	Casuarinaceae	e	0.025	0	0	0

Appendix 1. Continued.

Taxon	Family	Status	RS	MS	FL	DSF
<i>Haplolobus floribundus</i>	Burseraceae	i	1.209	0.338	0.028	0
<i>Heritiera ornithocephala</i>	Sterculiaceae	i	0.557	0.050	0.096	0
<i>Hernandia olivacea</i>	Hernandiaceae	e	0	0.133	0.009	0
<i>Kingiodendron platycarpum</i>	Fabaceae	e	0.010	0.128	0.058	0
<i>Macaranga harveyana</i>	Euphorbiaceae	i	0.040	0	0.032	0
<i>Macaranga</i> sp.	Euphorbiaceae	i	0	0.049	0.101	0.005
<i>Maniltoa grandiflora</i>	Fabaceae	i	0.111	0.269	0	0
<i>Maniltoa minor</i>	Fabaceae	e	0	0.063	0	0
<i>Melicope</i> sp.	Rutaceae	e	0.011	0.028	0	0
<i>Myristica castaneifolia</i>	Myristicaceae	e	0.068	0.113	0	0.015
<i>Myristica chartacea</i>	Myristicaceae	e	0.085	0.676	0.012	0
<i>Myristica gillespieana</i>	Myristicaceae	e	1.067	2.397	0.155	0
<i>Myristica grandifolia</i>	Myristicaceae	e	0.123	0.025	0.112	0
<i>Neuburgia corynocarpa</i>	Loganiaceae	e	0.020	0.037	0	0
<i>Neuburgia macrocarpa</i>	Loganiaceae	e	0.024	0.13	0	0
<i>Nothobaccaurea stylaris</i>	Euphorbiaceae	e	0.014	0.089	0	0
<i>Pagianta thurstonii</i>	Apocynaceae	e	0.025	0.319	0.310	0
<i>Palaquium fidjense</i>	Sapotaceae	e	0.043	0.195	0.097	0
<i>Palaquium hornei</i>	Sapotaceae	e	2.846	0.813	0	0
<i>Palaquium porphyreum</i>	Sapotaceae	e	0.276	0.018	0.352	0.010
<i>Palaquium</i> sp.	Sapotaceae	e	0.0234	0	0	0
<i>Palaquium vitilevuense</i>	Sapotaceae	e	0	0.107	0.0120	0.019
<i>Pandanus</i> sp.	Pandanaceae	e	0.153	0.052	0	0
<i>Parinari insularum</i>	Chrysobalanaceae	i	0.560	1.669	0.262	0
<i>Pisonia umbellifera</i>	Nyctaginaceae	i	0.035	0	0.495	0
<i>Pittosporum arborescens</i>	Pittosporaceae	i	0.056	0.008	0	0
<i>Planchonella</i> sp.	Sapotaceae	i	0	0.139	0	0
<i>Plerandra insolita</i>	Araliaceae	e	0	0.012	0	0
<i>Plerandra</i> sp. nova	Araliaceae	e	0.010	0	0	0
<i>Podocarpus affinis</i>	Podocarpaceae	e	0.040	0	0	0
<i>Podocarpus nerifolius</i>	Podocarpaceae	i	0.098	0.017	0	0
<i>Premna protusa</i>	Verbenaceae	e	0	0.084	0.848	0
<i>Retrophyllum vitiense</i>	Podocarpaceae	i	0	0	0	0.460
<i>Saurauia rubicunda</i>	Saurauriaceae	e	0	0	0.039	0
<i>Semecarpus vitiensis</i>	Anacardiaceae	i	0	0.106	0.073	0
<i>Storckiella vitiensis</i>	Fabaceae	e	0	0	0.246	0
<i>Syzygium decussatum</i>	Myrtaceae	e	0.290	0	0.193	0
<i>Syzygium diffusum</i>	Myrtaceae	e	0.023	0.345	0	0
<i>Syzygium effusum/rubescens</i>	Myrtaceae	i	0.108	0.167	0	0
<i>Syzygium eugenioides</i>	Myrtaceae	e	0.110	0.247	0	0
<i>Syzygium fijiens</i>	Myrtaceae	e	0.379	1.505	0.098	0
<i>Syzygium leucanthum</i>	Myrtaceae	e	0.016	0.124	0.124	0
<i>Syzygium</i> sp.	Myrtaceae		0.209	0.382	0.108	0
<i>Terminalia capitanea</i>	Myrtaceae	e	0	0.015	0	0
<i>Timonius affinis</i>	Rubiaceae	i	0.021	0.054	0	0
<i>Trichospermum calyculatum</i>	Tiliaceae	e	0	0.196	0.052	0
<i>Trichospermum richii</i>	Tiliaceae	i	0	0.234	0.192	0
<i>Turillia vitiensis</i>	Proteaceae	e	0.260	0.020	0.042	0
<i>Vavaea amicorum</i>	Meliaceae	i	0.041	0.243	0	0
<i>Veitchia</i> sp.	Arecaceae	e	0.009	0	0	0.004
<i>Viticipremna vitilevuensis</i>	Verbenaceae	e	0.020	0.323	3.007	0
<i>Xylopia pacifica</i>	Annonaceae	e	0.117	0.600	0.022	0
Total			16.585	27.330	12.068	1.107