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The Importance of Endemic Species to Forest Succession in Palau

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Abstract—Floristics of a chronosequence corresponding to forest succession were documented in the Ngermeduu Bay Drainage Area (NBDA), Babeldaob, Palau. Following the abandonment of Japanese agricultural communities in 1944, forest area in NBDA increased over 10%. However, species composition of these regenerated forests were previously unknown, and it remained unclear if or how past land use has influenced forest structure and composition. Therefore, I surveyed forests of different ages in NBDA to understand 1) how forest structure and composition changed in relation to forest age, and 2) the importance of endemic species to secondary succession following agricultural abandonment. Three stands in each of four vegetation categories were sampled (secondary vegetation, early succession forest, mid succession forest, mature forest), and species richness, diversity, composition and structure were determined. Results indicated that species richness and diversity were highest in early succession forests, while mature forest were dominated by a few characteristic species such as *Pinanga insignis* and *Manilkara udoido.* One introduced species, *Falcataria moluccana* (=*Albizia falcataria*), was present in both early and mid succession forest. While very few individuals were encountered, the large size of *F. moluccana* made this species an important component of successional forests. Despite past human impacts and introduced species, native species dominated forest structure and composition regardless of forest age. Moreover, endemic species in particular played a vital role in forest structure and composition, attesting to the uniqueness of these forests.

Introduction

In recent years, the ecology and conservation of island ecosystems have received considerable attention due to their importance to local and regional biodiversity. Despite the uniqueness of many forests throughout the Pacific Islands, forest communities on these islands have received little attention by ecologists

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beyond basic floristic studies (e.g., Fosberg et al. 1980, Otobed 1971, Stemmermann 1981) or vegetation descriptions (e.g., Cole et al. 1987, Ellison 1990, Mueller-Dubois & Fosberg 1998). Additional studies on forest dynamics are needed, not only to document baseline ecological interactions and processes, but also to provide valuable information that can be used to assess the integrity of forest communities in response to human impacts such as land clearing, agriculture, and the introduction of exotic species.

In response to the lack of quantitative studies of forest dynamics in the Pacific, several studies have recently documented not just forest composition, but also the relationship between species composition and environmental factors (e.g. Craig 1992, Franklin & Merlin 1992, Shimizu & Tabata 1991). Increased attention has also centered on forest recovery and succession following natural and human disturbances (Craig 1993, Franklin et al. 1999, Perry and Morton 1999, Webb & Fa'aumu 1999).

As part of a larger study of forest dynamics on the island of Babeldaob, Palau, I document changes in species composition and richness of forest communities following the abandonment of agricultural activities within the Ngermeduu Bay Drainage Area (NBDA). Currently, there are no published studies on forest succession in Palau, and studies on forest succession in Micronesia have been restricted to the Mariana Islands (Craig 1993, Morton et al. 2000, Perry & Morton 1999). Additional data are critical for understanding forest dynamics of the region, and are useful in evaluating the effect of past land use on forest structure and composition.

The NBDA is one of the most biologically significant areas in Micronesia. Located along the west-central coast of the island of Babeldaob the drainage area and adjacent marine communities have the most diverse set of habitats and species of all other areas studied in Micronesia (Figure 1, Maragos 1992). Offshore, the Ngermeduu region also represents one of Palau's most economically important areas, providing 25% of Palau's annual fish catch and 50% of the mangrove crab (*Scylla serrata*) harvest (Kitalong 1991).

Like most areas in Micronesia, the NBDA has been used extensively by people for hundreds of years. Prior to European contact (1596), Palauans cleared substantial areas of forests and created extensive terraces on mountain slopes and coastal hillsides. The purpose of these terraces remains unclear, though it has been suggested they were created for agricultural use in order to sustain a growing population (Luckling 1984, Parmentier 1987). The terracing system is evident still today, the majority of which supports grassland plant communities.

During the Japanese occupation of Palau, significant areas of forest in the NBDA were cleared for pineapple, sugar cane, and vegetable farming (Miles et al. 1994, Demei Otobed, pers. com.). Large-scale agricultural activities ceased following the take-over of Palau by the United States in 1944, and subsequent land use activities have been restricted to small-scale subsistence farming near villages. This abandonment led to a 10.9% (812 ha) increase in forest cover within the NBDA between 1947 and 1992 (Endress & Chinea, 2001). However, the

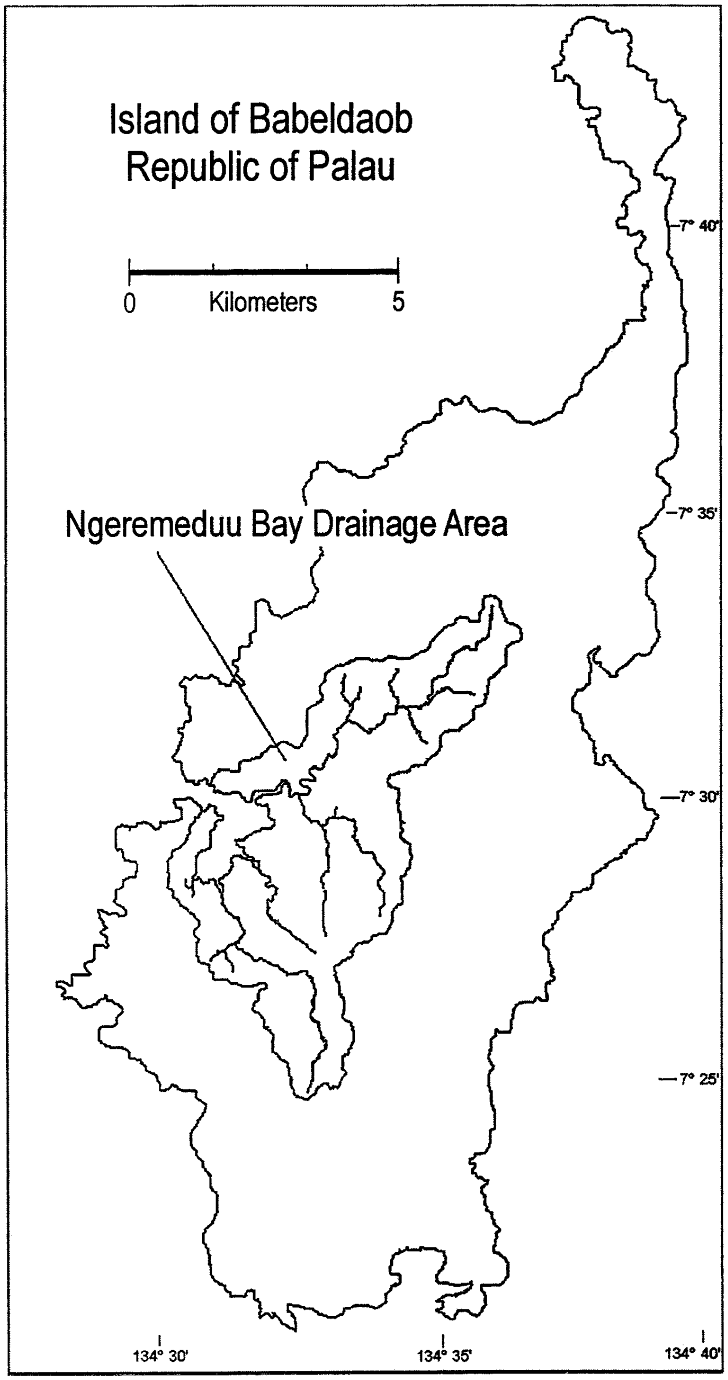

Figure 1. Ngermeduu Bay Drainage Area, Republic of Palau

Table 1. Characteristics of forest age categories.

Forest category	Age of forest (yrs.)
Secondary vegetation	0
Early succession	1-20
Mid succession	21-49
Mature	≥50

species composition of the regenerated forests is unknown, and it is unclear if or how past land use has influenced their structure and composition. Thus, I surveyed forests of different ages in NBDA to understand 1) how forest structure and composition changed in relation to forest age, and 2) the importance of endemic species to secondary succession following agricultural abandonment.

Materials and Methods

A Geographic Information Systems (GIS) database containing land cover maps of NBDA for three separate years (1947, 1976, and 1992) was used to differentiate forests of different ages and to select sites for floristic analysis. This GIS database was created as part of our larger study on forest dynamics of NBDA, and a detailed description of its construction is provided elsewhere (Endress and Chinea, 2001). Analysis was restricted to 'upland' forest. This term is used to be consistent with land cover classifications of Canfield et al. (1992) and Cole et al. (1987), and differentiates this forest type from swamp and mangrove forest communities.

The land cover maps for the three years were produced from two sets of aerial photographs (1947, black and white, 1:40,000 and 1992, color, 1:20,000), and a vegetation map from 1976 (based on black and white 1:10,000 photographs; Cole et al. 1987). Overlay analysis of the land cover maps produced a forest age map containing three forest categories (Table 1): mature forest (areas forested since 1947), mid-succession forest (areas converted to forest after 1947 and prior to 1976), and forest in the early stages of succession (areas converted to forest after 1976 and prior to 1992). In addition, areas of grassland with >50% cover of shrubs and small trees in the 1992 aerial photographs, and therefore appeared to be in the initial stages of forest succession, were classified as secondary vegetation and identified for floristic sampling.

Three stands in each of the four vegetation categories were sampled. Using the GIS database, sites were randomly selected (stratified random sample) throughout the NBDA. However, sites were restricted to be within 500 m of a road because much of NBDA is inaccessible due to lack of a road network.

Each sample plot consisted of three circular subplots, each with a radius of 5.15m, for a combined sample plot area of 250 m^2. Coordinates for the plots were obtained from the GIS database, and were used to mark the center of one of the subplots; the two other subplots were located 15 meters from either side of the center plot along the slope gradient.

Plots were visited in March and April 1997. At each plot, all species greater than 2.5 cm DBH (diameter at breast height) were identified, and their stem diameters measured. From these data, forest composition was described by calculating species richness and species diversity (inverted Simpson's and Shannon-Weiner indices), in addition to determining stem density and basal area. From this data, relative density (RD), relative basal area (RBA), and importance values (IV) were calculated for each species in each stand sampled. These parameters were calculated as follows:

$$RD = \frac{\text{No. of individuals of any one species}}{\text{No. of individuals of all species}} \times 100$$

$$RBA = \frac{\text{Basal area of any one species}}{\text{Basal area of all species}} \times 100$$

$$IV = \frac{RD + RBA}{2} \times 100$$

Results

Within the 12 sample plots, 48 taxa larger than 2.5 cm DBH were identified (see Appendix I for complete species list). While the majority of species were identified, species identification was incomplete, as several species were not flowering during field sampling. Therefore, a few species were identified only to the family or genera level.

Species Richness and Diversity

Data from the study plots indicated that species richness peaked in stands of early succession forest, with 32 species identified (average of 18 species per plot; Table 2). Secondary vegetation and mature forest had the fewest number of species encountered. Species diversity showed a similar trend where species diversity was highest in early successional forest, followed by mid succession forest. Secondary vegetation and mature forest had similar diversity values.

Forest Structure

Forest structure also varied along the chronosequence. The highest densities were recorded in early succession stands (mean = 4427 stems / ha), having almost twice as many stems as were found in secondary vegetation. A decrease in stem density was seen along the chronosequence from early succession to mature forest. As succession proceeded from secondary vegetation to mid succession forest, basal area increased, then decreased to 8433 m^2 per plot in mature forest stands.

Table 2. Summary of species richness, measures of species diversity, *D'* (inverted Simpson's index), *H'* (Shannon-Weiner index), and forest structure parameters along the forest chronosequence.

	Secondary Vegetation	Early Succession	Mid Succession	Mature Forest
Species richness	21	32	28	20
Mean richness / plot	11	18	16	12
Species richness SE	3.5	3.8	2.8	1.3
Species diversity				
Mean *D'* (inverted Simpson's)	5.80	9.95	7.40	4.32
Mean *H'* (Shannon-Weiner)	1.70	2.41	2.21	1.75
Mean Basal Area (m^2)	3685	10082	13724	8433
Basal Area SE	1742	3397	3089	1204
Mean Density (stems / ha)	2320	4427	3013	2480
Density st. SE	884	176	569	312

Species Composition

Secondary vegetation was comprised of a combination of grassland and forest species. The dominant canopy species as determined by importance values (Table 3), *Pandanus tectorius,* is found primarily in grasslands, while other dominant species such as *Alphitonia carolinensis, Macaranga carolinensis* var. *carolinensis*, and *Rhus taitensis,* are characteristic of early successional forest. Other species found this plant community include a number of grassland-associated species, such as *Melastoma malabathricum* var. *mariannum*, and *Eurya japonica* var. *nitida*, as well as forest species such as *Morinda* spp. and *Semecarpus venenosus.*

In the early successional forest stands sampled, the species with the highest importance value was the introduced species *Falcataria moluccana* (=*Albizia falcataria*). Only three individuals of *F. moluccana* were encountered (accounting for only 1% of the relative density); however, these stems were extremely large and therefore accounted for 30% of the total basal area sampled. The native species *A. carolinensis, Macaranga carolinensis* var. *carolinensis*, and *R. taitensis* were also quite common. Species associated with more mature forest such as Campnosperma brevipetiolata and *Garcinia* spp. were also present, though infrequent and often small, leading to their lower importance values.

Mid-successional forest contained a number of the same species as early successional forest including *F. moluccana*, but were dominated by different species. *Campnosperma brevipetiolata* was by far the most important component of the forest overstory followed by the endemic palm *Pinanga insignis* and *Garcinia* spp. Other common species included *Atuna racemosa* and *Symplocos racemosa* var *palauensis*.

Mature forest stands were dominated by *P. insignis* and the *Manilkara udoido,* while *Astronidium palauense* and *Cyathea lunulata* both had importance values above 5%. Less common species included, *Gmelina palawense, S. venenosus, Pandanus aimirikensis,* and *C. brevipetiolata.*

Table 3. Forest structure and composition along the forest succession chronosequence. Only species with IV ≥ 5% are presented (See Appendix 1 for complete species list).

Species	Basal Area (m^2)	Density	RBA	RD	IV
Secondary Vegetation 1992					
Pandanus tectorius	5766	23	52	13	33
Alphitonia carolinensis	692	53	6	30	18
Macaranga carolinensis var. *carolinensis*	1520	21	14	12	13
Rhus taitensis	554	9	5	5	5
Trichospermum ledermannii	459	9	4	5	5
Early-succession forest					
Falcataria moluccana	9016	3	30	1	15
Macaranga carolinensis	1502	63	5	19	12
Alphitonia carolinensis	3700	38	12	11	12
Rhus taitensis	3189	21	11	6	8
Campnosperma brevipetiolata	2286	10	8	3	5
Garcinia spp.	712	26	2	8	5
Cyathea lunulata	1307	17	4	5	5
Trichospermum ledermannii	1483	14	5	4	5
Eurya japonica var. *nitidia*	734	22	2	7	5
Mid-succession forest					
Campnosperma brevipetiolata	14991	15	36	7	22
Pinanga insignis	3207	31	8	14	11
Garcinia spp.	2958	26	7	12	9
Symplocos racemosa var. *palauensis*	55681	4	14	2	8
Atuna racemosa	404	21	1	9	5
Falcataria moluccana	4004	1	10	1	5
Mature Forest					
Pinanga insignis	7463	84	29	45	37
Manilkara udoido	7049	22	28	12	20
Astronidium palauense	2614	8	10	4	7
Cyathea lunulata	1110	12	4	6	5

Importance of Endemic and Introduced Species

Canopy species endemic to Palau were present throughout the chronosequence (Table 4). As forest succession proceeded, Palau endemics became increasingly important to forest structure and composition, from having importance values of 13% in secondary vegetation stands to 35% in mature forest.

In secondary vegetation, only one species endemic to Palau, *Trichospermum ledermannii,* was common (i.e., IV ≥ 5%), while five other endemics were present, but rare. As forests matured, the number of endemic species remained fairly stable, though their importance to forest structure and composition increased dramatically.

Two species found in the plots, *Alphitonia carolinensis* and *Semecarpus venenosus*, are endemic to the Western Caroline Islands. These species were present throughout the forest chronosequence, though their importance decreased as forest matured.

Table 4. Number of species and importance values of varies species groupings along the forest succession chronosequence.

	Number of species	Density	Basal Area (m^2)	RD	RBA	IV
Secondary Vegetation						
Palau endemics	6	24	1259	14	11	13
W. Caroline endemics	2	56	783	32	7	20
Other native species	13	94	9013	54	82	68
Introduced species	–	–	–	–	–	–
Forest since 1992						
Palau endemics	7	69	4715	21	16	18
W. Caroline endemics	2	50	4177	15	14	15
Other native species	22	210	12338	63	41	52
Introduced species	1	3	9016	1	30	15
Forest since 1976						
Palau endemics	6	69	10912	31	27	29
W. Caroline endemics	2	17	3153	7	8	8
Other native species	19	139	23103	62	56	59
Introduced species	1	1	4004	1	10	5
Forest since 1947						
Palau endemics	5	47	11350	25	45	35
W. Caroline endemics	2	10	1242	5	5	5
Other native species	13	129	12737	69	59	60
Introduced species	–	–	–	–	–	–

Only one exotic species, *F. moluccana*, was found in the study and was restricted to early and middle-aged forest stands. Only four individuals were present in the plots, but the large size of this species relative to native Palau species resulted in *F. moluccana* dominating early successional forest stands. These trees appear to be remnants of past land use, as no individuals were seen in areas of mature forest.

Discussion

Forest succession within NBDA was characterized by changes in species richness, diversity, forest structure and composition. Both species richness and diversity peaked in stands of young forest, and gradually decreased as forest matured. The decreases in species richness and diversity as forest age increased reflect the increased concentration of dominant species in mature forest. The two most important species in mature forest, *P. insignis* and *M. udoido*, had a combined importance of 57%, while the top two important species in early and mid succession forest were 27 and 33% respectively. Moreover, only four species in mature forest had importance values ≥ 5% while early successional forest had nine. This consolidation in mature forests is a typical pattern in forest succession, and is likely a result of canopy closure, which greatly decreas-

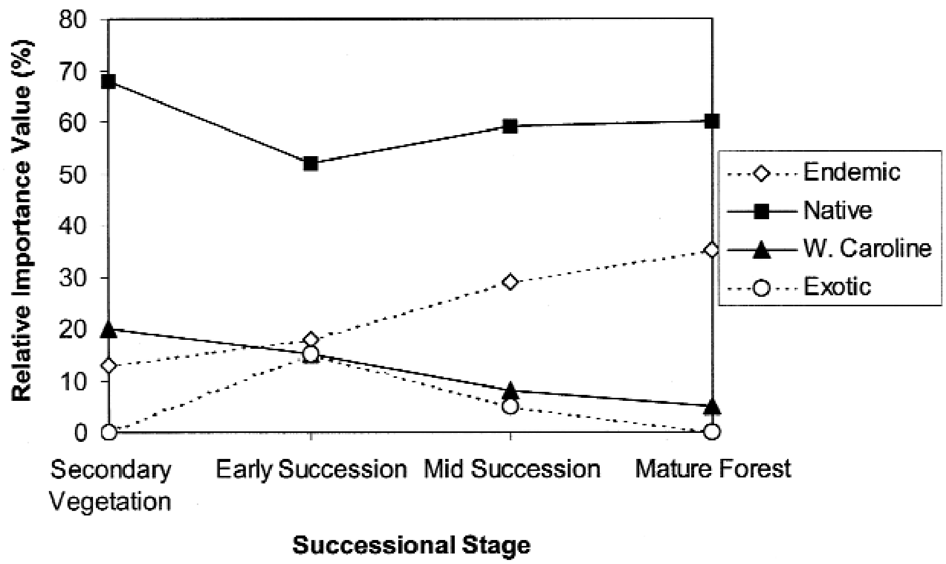

Figure 2. Changes in the importance values of species along the forest chronosequence, partitioned by species endemic to Palau, other species native to Palau, species endemic to the Western Caroline Islands, and non-native species.

es light availability in the forest understory. Thus, few species are able to tolerate this low light condition, resulting in a forest with lower species richness and diversity.

Falcataria moluccana was the only introduced species found in the study plots and appears to be confined to early and mid-successional forests. The presence of *F. moluccana* in successional forests indicates the influence of past land use on forest composition and structure. Within NBDA, *F. moluccana* was observed in areas of intense Japanese use, particularly along the Ngeremeskang River and near the village of Nekking. It is said that Japanese farmers planted *F. moluccana* for use as a shade tree for coffee and tea plantations (Marcelo Brel, pers. comm.).

During the Japanese occupation of Palau, over 230 species of fruits, vegetables, grasses, shrubs, and trees were introduced to Palau, most of which were evaluated at an Japanese agricultural experiment station located near the village of Nekking within the NBDA (Miles et al. 1994). Thus, it is surprising to some degree that only one introduced species was found in the forest plots. Increased sampling may identify additional non-native species in the forests of NBDA.

Given our reliance on three relatively small plots of each successional stage, and the inherent problems with substituting differently-aged stands for successional time, conclusions regarding succession in NBDA must be tentative. Numerous species found within NBDA, such as *Aglaia palauensis, Caesaria hirtella,* and *Finschia chloroxantha* were not found within the plots sampled. Moreover, variations in topography can affect forest structure and composition. In a rapid ecological assessment of NBDA, Canfield et al. (1992) found that slope and valley forests were dominated by *C. brevipetiolata* and *Pinanga insignis* while ridge communities were dominated by *Maranthes corymbosa.* In addition, ridge communities were more diverse and valley forest communities. Increased sampling to account not only for forest age but also topographic position would likely increase the number of species encountered as well as provide better estimates of the importance values of species within NBDA. Further study of the succession process is required.

Despite the limitations of this project, results from this study lead to several conclusions. First, species richness and diversity are highest in younger forests, while mature forest were dominated by a few characteristic species. Secondly, despite past human influences and numerous plant species introductions, native species dominated forest structure and composition regardless of forest age. Endemic species in particular, are important components Palau's native forests, attesting to their uniqueness. The importance of endemic species to forest structure and composition is impressive considering that endemic species account for only 9% of plants found in Palau (Canfield 1981).

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Appendix I. Taxa occurring in the plots representative of forest succession in NBDA, Palau, and their importance values; I = introduced species, N = species native to Palau, P = species endemic only to Palau, W = species endemic to the Western Caroline Islands (Yap and Palau). Taxa identified to the general level with both native and endemic species (i.e. *Morinda*) are classified as N/P.

Taxa	Palauan Name	Status	Secondary vegetation	Early succession	Mid succession	Mature forest
Alphitonia carolinensis	*elebiob*	W	18	12	4	1
Astronidium palauense	*mesekui*	P	–	< 0.5	–	7
Atuna racemosa	*charitem*	N	–	–	5	–
Calophyllum soulattri	*chesemoroch*	N	–	< 0.5	–	–
Campnosperma brevipetiolata	*kelela charm*	N	–	5	22	3
Cerebera floribunda	*chemeridech*	N	–	–	2	1
Commersonia bartramia	*eremallueang*	N	–	2	–	–
Cyathea lunulata	*chelu*	N	–	5	4	5
Dracaena multiflora	*orredakel*	N	< 0.5	< 0.5	< 0.5	–
Elaeocarpus joga	*degemerir*	N	–	1	< 0.5	2
Eurya japonica var. *nitida*	*eskiik*	N	3	5	< 0.5	–
Falcataria moluccana	*ukall ra ngebard*	I	–	15	5	–
Ficus sp. #1	–	N	< 0.5	1	1	2
Ficus sp. #2	–	N	–	1	< 0.5	–
Fragarea ksid	*ksid*	P	< 0.5	–	–	–
Garcinia spp.	*tilol*	P	–	5	9	–
Gmelina palawensis	*blacheos*	P	–	2	3	3
Horsfieldia palauensis	*chersachal*	P	–	< 0.5	4	1
Ixora casei kerdeu	*kerdeu*	N	–	< 0.5	1	–
Macaranga carolinensis var. *carolinensis*	*bedel*	N	13	12	4	< 0.5
Maranthes corymbosa	*bkau*	N	3	< 0.5	1	2
Manilkara udoido	*udeuid*	P	3	–	–	20
Melastoma malabathricum var. *mariannum*	*kui*	N	3	2	–	–
Morinda spp.	*ngel*	N/P	3	3	4	–
Neubergia celebica	*aralm*	N	–	–	< 0.5	–
Ophiorrhiza palauensis	*meldii*	P	1	–	–	–
Ormosia calavensis	*adapsung erket*	N	–	–	2	3
Pandanus aimiriikensis	*chertochot*	P	–	2	4	4
Pandanus sp. #1	*ongor*	N/P	–	< 0.5	–	–

Pandanus tectorius	*ongor*	N	33	–	–	–
Phaleria nisidai	*delalkar*	N	–	–	–	1
Phyllanthus palauensis	*ukellela chedib*	P	< 0.5	–	–	–
Pinanga insignis	*ebouch*	N	–	2	11	37
Pouteria obvata	*elangel*	N	–	2	< 0.5	–
Rhus taitensis	*chaues*	N	5	8	1	–
Semecarpus venenosus	*tonget*	W	1	3	3	4
Symplocos racemosa var. *palauensis*	*aptui*	P	4	4	8	–
Trichospermum ledermannii	*elsau*	P	5	5	–	–
unknown *Fabaceae*	–	–	1	< 0.5	–	–
unknown *Rubiaceae*	–	–	< 0.5	1	–	–
unknown sp. #1	–	–	–	–	–	1
unknown sp. #2	–	–	–	–	< 0.5	2
unknown sp. #3	–	–	–	–	–	< 0.5
unknown sp. #4	–	–	–	–	1	–
unknown sp. #5	–	–	–	< 0.5	–	–
unknown sp. #6	–	–	< 0.5	–	–	–
Wikstoemia elliptica	*rau*	N	2	1	–	–