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ECOLOGICAL CHARACTERISTICS OF A NATIVE LIMESTONE FOREST ON SAIPAN, MARIANA ISLANDS

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Abstract. I studied a remnant native limestone forest in the Marpi region, Saipan, to characterize the species composition, relative species importance, tree basal area, and tree density in that habitat. Using the point-quarter sampling technique on 400 canopy and understory trees each, I found that mean canopy and understory basal area were, respectively, 44.6 ± 25.1 and 1.4 ± 0.8 m^2/transect. Mean trees/ha in the canopy and understory were, respectively, 850.6 ± 193.2 and 2654.1 ± 844.5. *Pisonia grandis* overwhelmingly dominated in canopy basal area, whereas *Cynometra ramiflora, Pouteria obovata,* and *Guamia mariannae* dominated in the understory. *Cynometra ramiflora* occurred most densely in the canopy and *C. ramiflora* and *G. mariannae* had the highest densities in the understory. The relative measure of forest prevalence, the importance value, showed that *P. grandis* and *C. ramiflora* were the principal canopy species and *C. ramiflora* and *G. mariannae* were the major understory species. A model of forest dynamics is proposed in which *P. grandis* and other species largely absent from the understory are maintained in the forest through disturbance, which might facilitate vegetative propagation, flowering or survival of seedlings. Commonly fruiting, shade tolerant species like *C. ramiflora*, which were frequent in both the canopy and understory, may come to predominate under conditions of low forest disturbance. Despite centuries of human-related disruption, forest composition remains overwhelmingly native, suggesting that native forest is resistant to invasion by alien species.

With the exception of the Hawaiian Islands (summaries in Mueller-Dombois 1985, Gerrish 1990), the quantitative ecology of tropical Pacific island forests remains largely unstudied. Plant ecological investigations often have been descriptive accounts of distributions and plant associations (e.g. Maxwell 1982, Woodroffe 1985, 1987), although Ash (1987), Merlin (1991), and Franklin and Steadman (1991) provided quantitative data on Pacific islands south of the equator. Most botanical studies that include the Mariana Islands, Micronesia, have concerned plant systematics and floristics (e.g. Stone 1970, Fosberg et al. 1975, 1980). In addition, Fosberg (1960) gave descriptions of the principal plant associations of Micronesia and Moore (1973) and Muniappan (1976) each characterized native forest found along single transects on Guam.

To begin providing comprehensive quantitative data on Mariana Island forests, I studied the native limestone forests of Saipan. I characterized the species composition, relative species importance, tree basal area, and tree density in this habitat. From comparative data on the canopy and understory components of the forest, I made inferences concerning future trends in forest composition. Furthermore, I made qualitative comparisons of this study area with other tracts of limestone forest to assess the generality of my findings.

Native forest on Saipan is estimated to cover five (Engbring et al. 1986) to 19% (Young 1989) of the island. Most surviving native forest occurs on steep limestone escarpments and may be classified as limestone forest (forest that grows on limestone-derived soil), although examples of ravine forest growing on volcanic soil, *Casuarina-Pandanus* savannah, mangrove swamp, freshwater swamp and strand forest are also present (Fosberg 1960).

Because the native forests of Saipan have been subjected to centuries of human-related alteration, including cutting, burning, browsing by feral ungulates, war-related damage and the virtual extirpation

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FIG. 1. The Marpi limestone forest, with *Pisonia grandis* in the foreground and *Pandanus dubius* in the background.

of seed-dispersing Marianas Fruit Bats (*Pteropus mariannus;* Fosberg 1960, Wiles et al. 1989), the present appearance of Saipan's limestone forest likely reflects the combined effects of these factors. Hence, the following analysis must be considered in light of anthropogenic alterations. In this study, the taxonomic nomenclature of Raulerson and Rinehart (1991) has been followed.

METHODS

The Marpi region of Saipan has the most extensive and among the best developed native forest remaining on Saipan (Fig. 1). However, before World War II, level areas were cultivated for sugarcane (*Saccharum officinarum,* Fosberg 1960), which largely isolated the Marpi forest from other tracts of native forest. There are are no feral ungulates in this area, including no Sambar Deer (*Cervus unicolor*), but local residents report that pigs (*Sus scrofa*) were present ca. 1960.

To obtain data on the structure and species composition of the Marpi forest, I established 10 transects with starting points about 250 m apart. The first transect was located near the northern corner of the steep limestone escarpment known as Suicide Cliff. I placed others south along the escarpment's west slope and the last near its southern end. Transects were parallel to the slope contours at mid- to lower elevations, where forest was usually best developed. High elevation forest on steep slopes was often characterized by stunted, exposed growth. On each transect, I placed 10 sample points paced about 12 m apart (108 m total), which was sufficient to make each point independent (i.e. no overlap in trees between points). For comparison, l studied limestone forests qualitatively elsewhere on Saipan, particularly at Tapotchau, Gualo Rai, Naftan, Dandan, Talufofo, and Kagman, as well as on Guam, Rota and Tinian.

I used the plotless point-quarter sampling technique (Cottam and Curtis 1956) to measure four canopy and four understory trees/point. This method assumes that trees are randomly dispersed in the forest—an assumption that appeared to be met reasonably. Canopy trees were those first intercepting sunlight and understory trees were those growing below the canopy but taller than two m. For each tree, I measured the distance from the sample point to the center of the tree and the diameter at breast height (dbh). For the variety of tree growth forms encountered in the limestone forest, dbh proved the most equitable measure of diameter.

Point-quarter analysis yields data on the horizontal area covered by tree stems (basal area), number of stems/unit area (density) and dispersion of trees in the forest (frequency). From these three measures, I computed a relative importance index for each species known as the importance value (reviewed by Mueller-Dombois and Ellenberg 1974). For broad-leaved forests, the importance value is related to proportionate contribution of a species to forest foliage volume (Holmes and Robinson 1981). I also examined tree density and basal area separately, because they are distinct, absolute measures of overall tree occurrence.

For each species, I computed a ratio of importance values in the canopy versus the understory by dividing the smaller value by the larger and subtracting the quotient from one. For graphical clarity, I assigned positive values to species predominating in the canopy and negative values to those predominating in the understory. The more strongly a species was represented in the canopy, the closer its ratio was to 1 and, similarly, the more strongly it was represented in the understory, the closer its value was to −1. The importance value ratio highlights those species that predominate in either the

canopy or understory, thereby providing insights into potential temporal shifts in forest species composition.

RESULTS AND DISCUSSION

The two absolute measures of overall tree occurrence in the Marpi limestone forest, basal area (Fig. 2) and density (Fig. 3), varied substantially among transects, with the relative variance (as measured by the coefficient of variation, CV) similar in the canopy and understory. Canopy trees dominated in basal area, but understory trees had the greatest density (canopy basal area (m^2/transect): mean $\pm$ SD = 44.6 $\pm$ 25.1, CV = 56, understory: 1.4 $\pm$ 0.8, CV = 54; canopy trees/ha: mean = 850.6 $\pm$ 193.2, CV = 23, understory: 2654.1 $\pm$ 844.5, CV = 32).

The sum of basal areas (total basal area) for *Pisonia grandis* showed its overwhelming canopy dominance among trees (Table 1). It was the

largest species in the forest, with massive individuals to 242 cm dbh present. In contrast, the abundant but slender-trunked *Cynometra ramiflora* had comparatively low basal area. The irregularly distributed *Dendrocnide latifolia* dominated at only one transect. In the understory, *C. ramiflora* and the Marianas endemic *Guamia mariannae* predominated, although the irregularly distributed *Pouteria obovata* also had a comparatively high basal area (Table 2).

Canopy tree densities exhibited a divergent pattern from basal areas (Table 1). *Cynometra ramiflora* had the highest density, whereas *P. grandis* was less common. *Intsia bijuga* occurred commonly at the southernmost five transects but was virtually absent in the northern portion of the study area. Stumps of logged *I. bijuga* trees suggested that its distribution was at least in part an artifact of logging. It was the only native species in the Marpi forest that appeared to have been logged. In the understory,

TABLE 1. Occurrence of canopy trees in the Marpi forest, computed from all trees sampled and arranged in descending order by importance values.

| Species	Total basal area (m^2)	Trees/ha	Importance value
Pisonia grandis	302.89	70.0	85.7
Cynometra ramiflora	23.40	230.6	53.7
Intsia bijuga	16.43	70.0	20.4
Dendrocnide latifolia	27.31	35.0	14.8
Ficus tinctoria	7.68	43.2	13.5
Premna obtusifolia	8.56	47.4	13.1
Melanolepis multiglandulosa	4.60	39.1	11.2
Erythrina variegata	14.77	24.7	9.4
Guamia mariannae	1.02	30.9	9.1
Pouteria obovata	4.59	28.8	8.3
Ficus prolixa	7.50	22.6	8.2
Carica papaya	2.03	28.8	8.1
Ochrosia mariannensis	2.22	26.8	7.5
Aglaia mariannensis	2.46	26.8	7.2
Neisosperma oppositifolia	3.15	18.5	5.3
Albizia lebbeck	4.37	18.5	5.3
Leucaena leucocephala	1.00	18.5	4.9
Psychotria mariana	0.19	8.2	2.4
Pandanus dubius	0.66	8.2	2.2
Acacia confusa	3.60	4.1	2.0
Morinda citrifolia	0.50	6.2	1.9
Pandanus tectorius	0.49	6.2	1.5
Artocarpus altilis	3.84	2.1	1.5
Artocarpus mariannensis	2.11	2.1	1.1
Drypetes dolichocarpa	0.15	2.1	0.6
Cordia subcordata	0.09	2.1	0.6
Aidia cochinchinensis	0.03	2.1	0.6
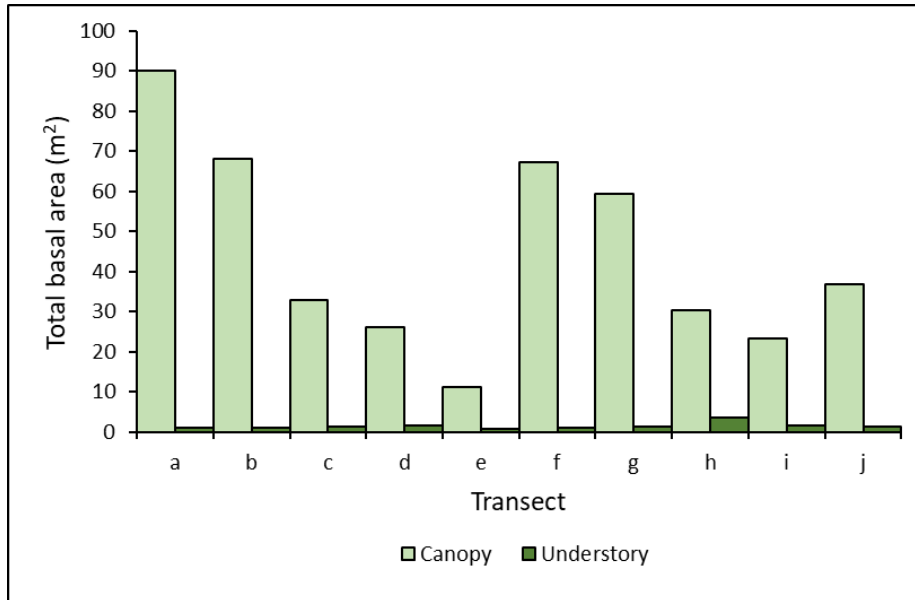
FIG. 2. The sum of basal areas of canopy and understory trees at each of 10 transects arranged from north (a) to south (j).

C. ramiflora and *G. mariannae* even more strongly predominated in density than they had in basal area (Table 2).

The relative measure of forest prevalence, the importance value, showed that *P. grandis* and *C. ramiflora* were the principal canopy species (Table 1), and *C. ramiflora* and *G. mariannae* were the major understory species (Table 2). Because *P. grandis* was not abundant, its importance value was largely a reflection of its basal area (Fig. 4). Canopy heterogeneity in basal area (Fig. 2) largely mirrored its uneven basal area distribution. In contrast to its canopy dominance, I encountered no understory *P. grandis* on transect points. I observed saplings and seedlings in the study area, sometimes appearing to be broken branches that had rooted, but only infrequently. A minimum age for some of the larger *P. grandis* specimens was provided by World War II shrapnel imbedded in their trunks, indicating an age >47 yr and possibly >100 yr.

In both the canopy and understory, *C. ramiflora* showed some tendency to increase in basal area from north to south, but its basal area declined sharply near the southern end of the study area (Fig. 5). However, the basal areas of the canopy and understory trees showed little relationship to each other ($r^2 = 0.30$, df = 8, $P = 0.12$). *C. ramiflora* averaged highest in canopy compared with understory basal area (canopy: mean = 2.34 ± 2.89 m^2; understory: 0.03 ± 0.02 m^2; $t = 2.46$, df = 8, P < 0.04).

G. mariannae also had its highest basal area in the canopy (although not significantly so; canopy: mean = 0.10 ± 0.11 m^2; understory: 0.03 ± 0.01 m^2; $t = 1.61$, df = 8, P = 0.15). Again, little relationship existed between the basal area of canopy and understory *G. mariannae* ($r^2 = 0.06$, df = 8, $P = 0.54$) and the distribution of basal areas in the study area showed no consistent pattern (Fig. 6).

The ratio of importance values for canopy and understory trees (Fig. 7) showed that I detected two common species, *P. grandis* and *I. bijuga*, only in the canopy. *P. grandis* flowers only rarely (although it flowered heavily in Feb.−Mar. 1991), and propagates vegetatively from broken branches (Stone 1970). Furthermore, *I. bijuga* also appears to flower infrequently on Saipan, although I found some fruits and seedlings during the study. The rarity of these species in the understory may indicate that reproduction occurs primarily after disturbance, such as after typhoons, or after some other unusual circumstance. The rarity of *D. latifolia* in the understory, even though it appears to flower and fruit regularly, suggests that this and other regularly fruiting canopy species with importance value ratios approaching one may have seeds that germinate poorly in shade and so may also profit from disturbance or other unusual circumstances.

I obtained support for the notion of disturbance-related reproduction by certain tree species after a September, 1991 typhoon, when the forest floor at Marpi was littered with numerous branches of *P. grandis and D. latifolia.* Many branches from both species rooted, sprouted leaves and flowered

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TABLE 2. Occurrence of understory trees in the Marpi forest, computed from all trees sampled and arranged in descending order by importance values.

Species	Total basal area (m^2)	Trees/ha	Importance value
Cynometra ramiflora	4.08	785.6	83.3
Guamia mariannae	3.02	686.6	74.2
Pouteria obovata	2.16	117.5	39.0
Aidia cochinchinensis	0.50	160.8	19.8
Eugenia palumbis	0.18	167.0	16.6
Aglaia mariannensis	0.49	92.8	9.3
Ochrosia mariannensis	0.70	61.9	9.2
Ficus tinctoria	0.44	68.0	9.1
Pandanus dubius	1.03	80.4	8.7
Morinda citrifolia	0.57	37.1	5.3
Carica papaya	0.21	37.1	4.9
Psychotria mariana	0.17	43.3	5.5
Premna obtusifolia	0.16	30.9	3.6
Maytenus thompsonii	0.13	30.9	3.1
Albizia lebbeck	0.11	12.4	1.4
Neisosperma oppositifolia	0.08	12.4	1.4
Erythrina variegata	0.08	12.4	1.4
Melanolepsis multiglandulosa	0.05	12.4	1.4
Ficus prolixia	0.16	6.2	0.8
Pandanus tectorius	0.03	6.2	0.7
Dendrocnide latifolia	0.03	6.2	0.7
Leucaena leucocephala	0.01	6.2	0.7

during Oct.−Nov. I did not observe other native tree species, including *I. bijuga*, to propogate vegetatively, however. *I. bijuga* may maintain itself in the forest by some other mechanism, such as fruiting after a period of unusual weather.

In contrast to these species, heavily fruiting, common canopy species like *Ficus tinctoria v. neoebudarum* and *C. ramiflora* reproduced readily in shade as demonstrated by their importance value ratios approaching or <0. In fact, seedling *C. ramiflora* were one of the most abundant components of the forest herbaceous layer in the wet season (June−Nov.). Although these suffer high mortality in the dry season, clearly enough survive to produce recruitment into the understory. Such species likely increase in abundance during periods of low forest disturbance.

Of those species predominating in the understory (Fig. 7), *G. mariannae, Aidia cochinchinesis, Eugenia palumbis* and *Maytenus thompsonii* are small trees that rarely grow large enough to invade the canopy (Stone 1970, Raulerson and Rinehart 1991). Other more robust, commonly fruiting species, such as *P. obovata, Ochrosia mariannensis* and *Aglaia mariannensis* may, based on their negative importance value ratio, increase in the forest canopy under conditions of low disturbance.

These are only preliminary data on recruitment dynamics in limestone forest; for a thorough assessment, data on such parameters as seed viability, dispersal, survivorship, and importance of vegetative propogation are needed. However, the data provide initial insights into the mechanisms of forest maintenance in this system. I propose a model for limestone forest dynamics: forest species composition is regulated by the frequency and intensity of external (i.e. typhoon) disturbance. A suite of vegetatively reproducing species that also flower after mechanical injury are maintained in the system by disturbance, and a suite of mostly sexually reproducing, shade tolerant species are maintained during times and in areas of limited disturbance.

The introduced *Leucaena leucocephala* and *Acacia confusa* occurred predominantly in the canopy (Fig. 7), and, therefore, appeared to have little reproductive success in this forest. However, the introduced *Carica papaya* was regular in the understory. Notably, of these introduced species, only the fleshy-fruited *C. papaya* is fed upon and probably dispersed by birds. *Albizia lebbeck* (introduced)
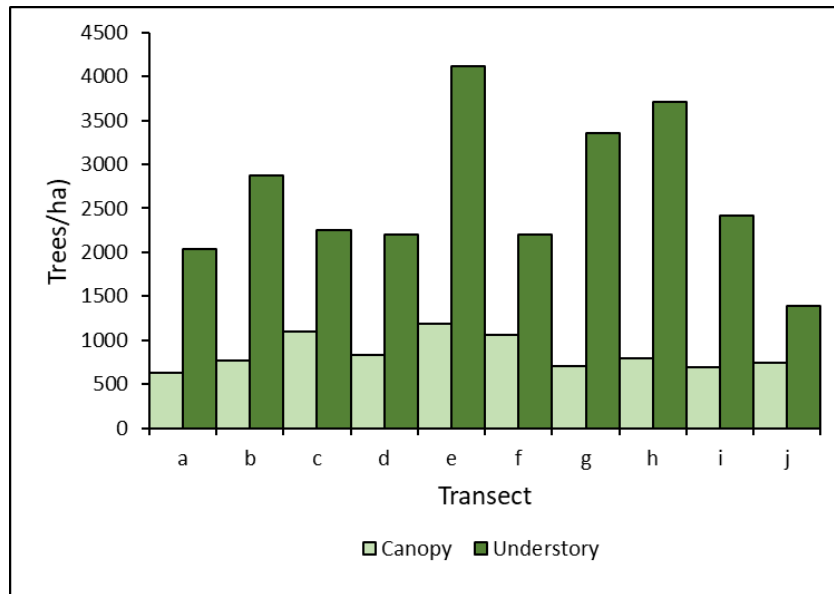
FIG. 3. Density of canopy and understory trees arranged at 10 transects arranged from north (a) to south (j)..

was limited to one transect, and was, therefore, too uncommon for any definitive statement to be made concerning its reproduction.

Recently introduced species (not including prehistorically introduced species like *Artocarpus altilis*, although now of limited significance in the limestone forest based on their importance values (Table 1, 2), require further study to determine their potential role in future forest composition. Based on importance values, they presently comprise 6.7% of the canopy and 2.3% of the understory. Like the similarly high percent native cover found by Merlin (1991) for the native woody vegetation of Mangaia, Cook Islands, this finding suggests that native forest is resistant to invasion by alien species. Only the transect at the northern end of the study area had relatively high cover by introduced species (26.3% of the canopy importance values). The vicinity of this transect, near the Japanese Last Command Post of World War II, was heavily bombed during the American invasion of Saipan. A circular patch of *L. leucocephala* on the cliffs above the Last Command Post, an area never cultivated, is a likely consequence of a very large explosion.

In addition to those located during sampling, I found the following tree species in the Marpi study area: *Annona reticulata* (introduced; scattered individuals), *Cerbera dilatata* (native; scattered individuals), *Casuarina equisetifolia* (native; scattered individuals), *Excoecaria agallocha* v. *orthostichalis* (native; scattered individuals), *Hernandia sonora* (native; several at slope base), *Barringtonia asiatica* (native; in intermittant stream valleys), *Hibiscus tiliaceus* (native; in intermittant stream valley),

Guettarda speciosa (native; scattered individuals), *Polyscias grandiflora* (native; scattered individuals), *Muntingia calabura* (introduced; forest edge), *Delonix regia* (introduced; single tree at high elevation), *Trema orientalis* v. *argentea* (native; forest edge), *Callicarpa candicans* (native; forest edge), *Streblus pendulinus* (native; southern end of study area only), *Allophylus timorensis* (native; scattered individuals), *Bauhinia monandra* (introduced; single clump of individuals), and *Pipturus argenteus* (native; forest edge and openings).

Besides these species, I encountered vegetative specimens identified tentatively as *Psychotria hombroniana* (native; scattered individuals). On the study transects, I combined two possible *P. hombroniana* understory specimens with *P. mariana* in analyses. Furthermore, because I observed no flowering or fruiting during the sampling period, I did not distinguish between *Eugenia reinwardtiana* and *E. palumbis*. Most individuals, as verified during their July flowering, appeared to be *E. palumbis* and are reported as such in tables and text.

Qualitative comparison of the Marpi forest with other limestone forests indicated a general similarity in appearance with low to mid-elevation forest elsewhere on Saipan and Tinian. Species proportions varied between sites, but a similar species assemblage was found throughout. The existing forest characteristics are likely in part a byproduct of human and feral animal activity, particularly in terms of species distributions and relative abundance, but the uniformity of its appearance even between islands suggests that the present limestone forest system retains some of its original features.
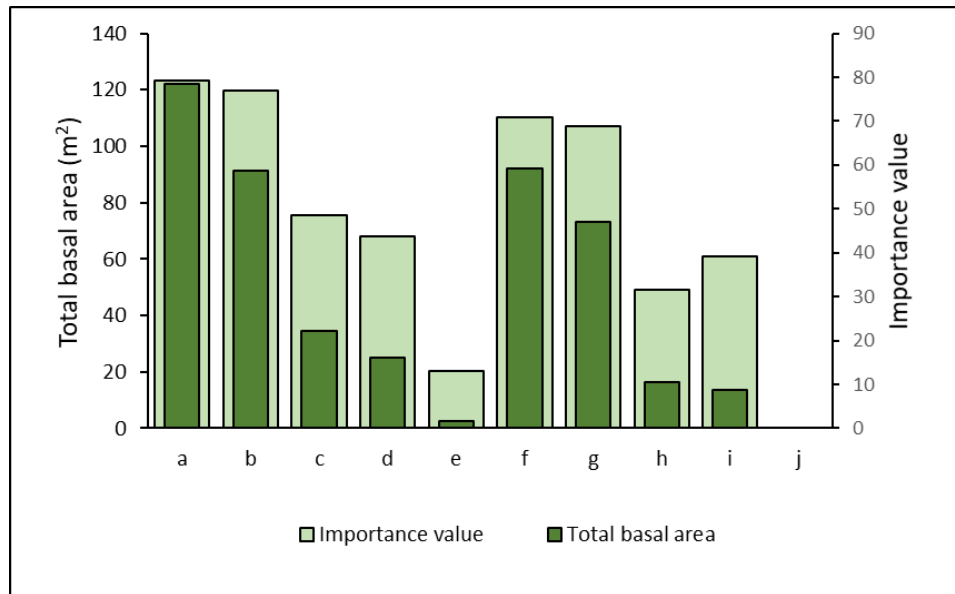
FIG. 4. Basal areas and importance values of *Pisonia grandis* at 10 transects arranged from north (a) to south (j).

In contrast to these forests, remnant limestone forest at the highest elevations of Mt. Tapotchau, Saipan and the high elevation plateau forest of Rota exhibited strong differences in appearance. These fog prone areas were cooler and wetter (Fosberg 1960, Young 1989) than the lower elevation forests and had high densities of epiphytic lichens, mosses, ferns and orchids. The forest floor was also typically moss-covered and tree species such as *Pandanus* spp., *Pisonia umbellifera* and *Claoxylon marianum* were characteristic. Moreover, a species of *Meryta* as yet undescribed in 1992 but since classified as *M. senfftiana* (Govaerts 2011), was present locally on the upper eastern slopes of Mt. Tapotchau (Fig. 8). On Rota, *Guettarda speciosa, Hernandia labrynthica, Fagraea galilai, Macaranga thompsonii, Cycas circinalis* and *Elaeocarpus joga* joined these as common tree species. The latter three are rare on Saipan and I have not found *F. galilai* on Saipan. Another notable species found only, albeit locally commonly, in the native forests of the Naftan peninsula was the Marianas endemic *Heritiera longipetiolala*, which also occurs regularly in the native forests of adjacent Tinian.

In contrast to this study, Moore (1973) found that limestone forest dominants at Pagat Point, Guam were *Mammea odorata* and *Eugenia reinwardtiana*. Similar *M. odorata*-dominated forests also may be in strand communities on Saipan. At Hilaan Beach, Guam Muniappan (1976) found *Aglaia marianennsis* and *Guamia mariannae* to be the dominant limestone forest species. In general, the more southerly, apparently less xerophytic lime-stone forests of Rota and Guam seem more diverse than those of Saipan, but whether this represents the original condition of the forests is uncertain.

The native limestone forest of the Marpi region may be characterized as having a canopy dominated by two widespread (Stone 1970) Indo-Pacific species, and an understory dominated by an endemic (Stone 1970) Marianas genus. Some species may be maintained in the system by disturbance, whereas others appear to recruit successfully into a closed forest canopy. In the absence of human and feral ungulate disturbance, the relative proportions of these species may be affected by the frequency and severity of typhoons and other natural disturbance. Despite centuries of human-related disruption, forest composition remains overwhelmingly native, suggesting that native forest is resistant to invasion by alien species.
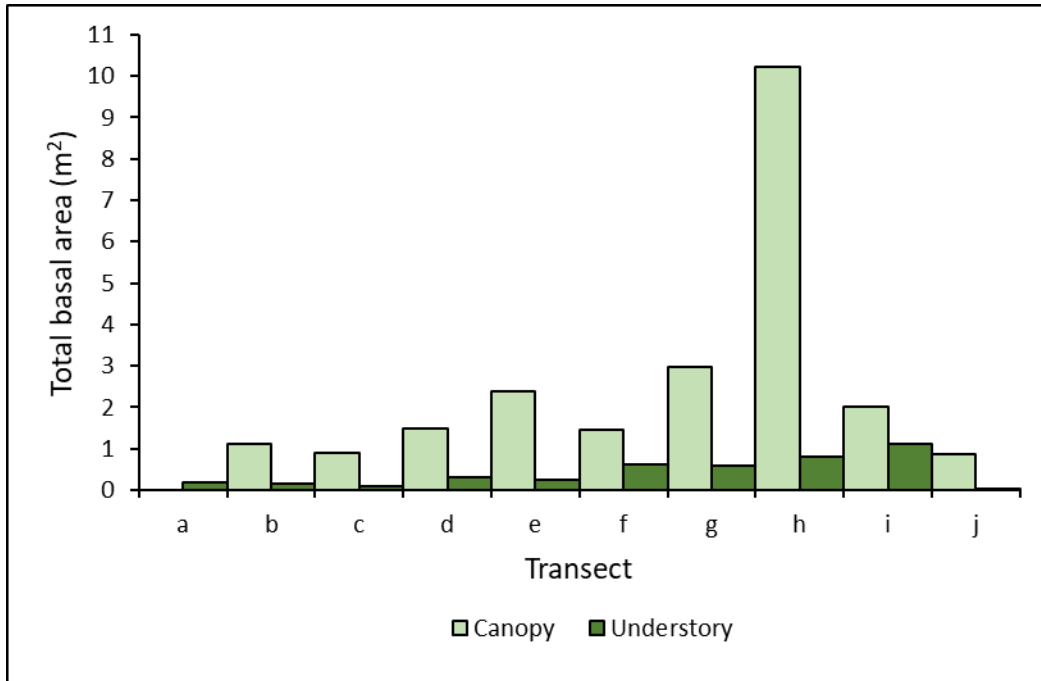
FIG. 5. Basal areas of canopy and understory *Cynometra ramiflora* at 10 transects arranged from north (a) to south (j).
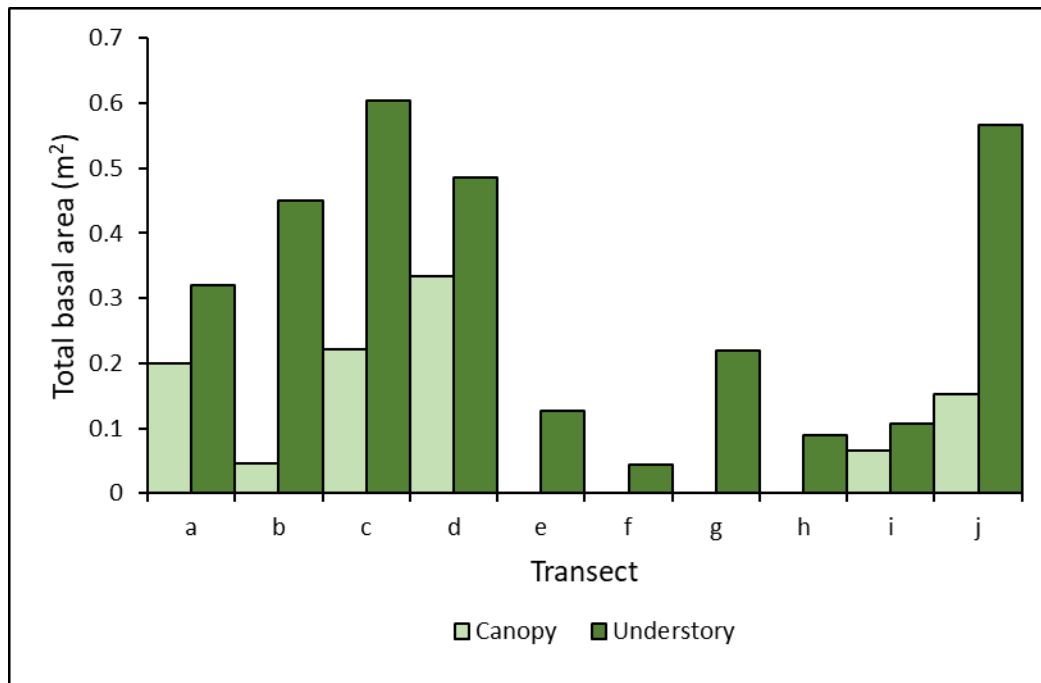

FIG. 6. Basal areas of canopy and understory *Guamia mariannae* at 10 transects arranged from north (a) to south (j).
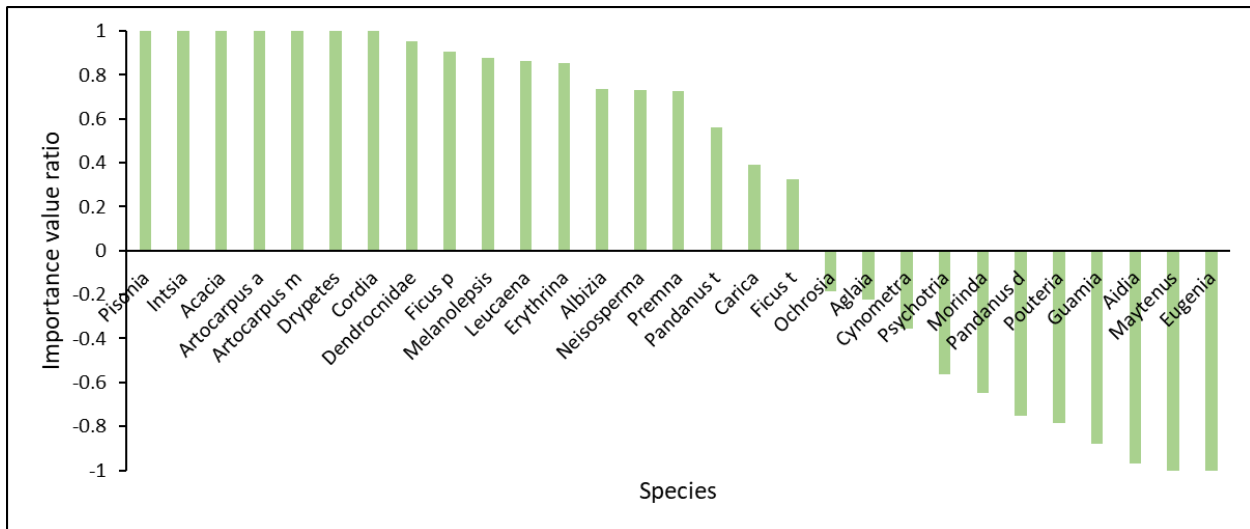
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FIG. 7. Ratio of canopy and understory importance values for tree species in the Marpi limestone forest.

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FIG. 8. Flowering *Meryta,* an undescribed species in 1992, photographed on the east slope of Mt. Tapotchau in 1993.

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