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Structure of a Limestone Forest on Northern Guam

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Abstract—Area 50 is a unique 24-ha patch of limestone forest on Andersen Air Force Base in northern Guam. In advance of feral deer and pig removal, we sampled the woody and herbaceous plant communities on 50 random plots, 30 inside Area 50 (experimental) and 20 outside Area 50 (control) to establish baseline conditions. The limestone forest in Area 50 included 41 genera from 27 families; 29 (71%) of these genera were indigenous. Plots within Area 50 had significantly more woody taxa, higher stem densities, and higher basal areas than control plots. However, mean species richness and stem density within the ground flora were similar between experimental and control plots. We identify three mechanisms by which alien taxa appear to be invading the native limestone forest: failure of many native overstory species to successfully regenerate, recruitment of mostly herbaceous alien species into the ground layer, and recruitment of mostly woody alien species along the forest edge. We also discuss sampling design and analytical considerations for quantifying vegetative changes after ungulate removal.

Introduction

Sambar deer (*Cervus mariannus*) and feral pigs (*Sus scofa*) were introduced to Guam in the 1770s and late 1600s, respectively (Conry 1988). By the mid 1980s, feral ungulate populations in the northern limestone forest were estimated to be as high as 110 pigs/km^2 and 212 deer/10 km of road transect (Conry 1988). These introduced ungulates are suspected of significantly impacting native floral communities in northern Guam by consuming seeds, fruits, and foliage, and ingesting or trampling plants that may germinate (Wiles et al. 1996). Wallowing and rooting by feral pig can be particularly damaging locally. Conry (1988), for

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example, reported a complex of wallows and feeding sites in one basin on northern Guam that extended over 2.3 ha. Several tree species of concern on Guam including *Serianthes nelsonii* (Wiles et al. 1996) and *Eleaocarpus joga* (Ritter & Naugle 1998), may be declining, in part, due to damage by feral ungulates.

Area 50 is a 600m x 400m rectangular patch of limestone forest in the Northwest Field of Andersen Air Force Base (AFB). In addition to tarmac on all four sides, this 24-ha area is surrounded by a 2.4-m high chainlink fence that was erected by 36 CEV/CES Environmental Flight to experimentally exclose sambar deer and feral pig. Area 50 is currently used as a site for outplanting of the endangered tree *Serianthes nelsonii* and as a release site for the endangered Guam rail (*Gallinallus owstoni*), an endemic species which previously persisted only in captivity. Management of this area is specifically addressed in the 1994 Integrated Natural Resources Management Plan for Andersen AFB.

Since exclosure of this area in 1991, some resident ungulates have been removed with the assistance of personnel from the Guam Division of Aquatic and Wildlife Resources, Guam National Wildlife Refuge, Wildlife Services (U.S. Department of Agriculture), and the Biological Resources Division (U.S. Geological Survey). As removal of feral ungulates nears completion, it is critical that the existing floral community be surveyed so that the baseline condition can be established. The efficacy of pig and deer removal to positively affect recovery of the native forest will ultimately be assessed by comparing subsequent changes in the floral community with these baseline data.

In this paper, we report the results of a study designed to quantify the woody, herbaceous, and germinating plant communities within Area 50 before feral ungulate removal, and to establish control plots in adjacent forest outside of Area 50. We also discuss a statistical design for assessing the relative magnitude of long-term changes in the floral community that may be attributable to feral ungulate removal versus the confounding effects of successional dynamics.

Methods

Woody vegetation with stems > 24 mm diameter-at-breast height (DBH) were sampled within fifty 300-m^2 circular plots. Ground flora was subsampled within 50 1-m^2 quadrats, each nested within the larger circular plot. Thirty experimental plots were located in Area 50 and twenty control plots were divided equally between Areas 35 and 44. Area 50 was bisected longitudinally and 15 circular plots were randomly allocated within each stratum. All plots on Areas 35 and 44 were randomly chosen within 200 m of the forest edge. All sampling was completed between Sep 1996 and Feb 1997.

Each plot was located using a compass and 100-m tape. Rebar was pounded into the ground at the center of each plot, identified with an aluminum tag, and marked with an orange-painted aluminum can to facilitate relocation. Tree calipers were used to measure all woody stems > 24 mm DBH by species within 9.77-m of the rebar (300 m^2). The presence of woody species < 25 mm DBH and any deer and pig sign were noted. The 1-m^2 quadrat was located 3 m north of the rebar and each quadrat was divided into four quarters. Herbaceous plants and woody seedlings with stems < 25 mm DBH were counted within each quarter by species. Both *Eugenia* (except *E. thompsonii*) and *Pandanus* were not distinguished by species due to difficulty in identification of some specimens, particularly younger individuals. However, *Pandanas tectorius* and *Eugenia reinwardtiana* were the predominately sampled species in these genera. Similarly, distinguishing *Ficus prolixa* from *F. microcarpa* var. *saffordii* proved to be problematic and data were pooled for these species. Raw data and coordinates for plot centers were reported in Morton et al. (1998).

Frequency, density, and dominance of all recorded woody and ground flora were calculated (Barbour et al. 1987). For the ground layer, dominance was the number of quarters (0 - 4) within a 1-m^2 quadrat on which a species occurred. The Importance Value (IV), a measure of the relative contribution of a given species to the floral community, was subsequently calculated for each species by averaging relative frequency, density, and dominance (Curtis & McIntosh 1951). Mean species richness, stem density, and basal area were also calculated for comparison of the woody flora in the experimental and control areas. Mean species richness and stem density were calculated for the ground layer component.

Plots within Area 50 were also separated into edge and interior classes to assess the effects of fragmentation on the forest community. All plots within 75m of the perimeter fence were considered edge plots and all others were considered interior plots. Species richness, stem density, and basal area were calculated for each class and compared using the Wilcoxon 2-sample tests.

We used SAS 6.12 for all data analyses. Nomenclature follows Stone (1970), unless superseded by Raulerson & Rinehart (1991, 1992).

Results

All control plots (100%) and 21 of 30 (70%) experimental plots had some sort of ungulate sign recorded on them. Most sign indicated feral pig activity including recent rooting, but some Sambar deer droppings and antler rubs were recorded. Six pigs were seen near one experimental plot and several were heard at different plots inside and outside Area 50. No deer were seen or heard in either the experimental or control areas.

Mean characteristics of the woody floral community differed between experimental and control plots (Table 1). On average, plots within Area 50 contained more woody taxa (Wilcoxon $Z = -3.06$, $P = 0.002$), higher stem densities (Wilcoxon $Z = -2.70$, $P = 0.007$), and higher basal areas (Wilcoxon $Z = -2.41$, $P = 0.016$) than plots within Areas 35 and 44. However, mean species richness and stem density within the ground flora did not differ between experimental and control plots (Table 1; $P < 0.85$).

Table 1. Mean characteristics of woody vegetation per 300-m^2 circular plot and ground vegetation per 1-m^2 quadrat inside (experimental) and outside (control) Area 50.

	Experimental (*n* = 30)			Control (*n* = 20)		
	mean	SE	CV[a]	mean	SE	CV
Woody flora (> 24 mm DBH)						
Species richness	9.23	0.47	27.82	7.00	0.54	34.37
Stem density	97.93	5.31	29.70	74.00	6.16	37.23
Basal area (m^2)	0.46	0.03	40.90	0.37	0.06	77.72
Ground flora (< 25 mm DBH)						
Species richness	5.27	0.32	33.05	5.55	0.56	45.46
Stem density	79.10	10.31	71.37	89.45	17.49	87.44

[a]Coefficient of variation.

EXPERIMENTAL (AREA 50)

We recorded 27 woody genera with stems > 24 mm DBH in Area 50 (Table 2). Only three of these genera, *Carica*, *Leucaena*, and *Triphasia* are considered introduced to Guam. Importance values suggest that *Premna obtusifolia*, *Leucaena leucocephala*, *Aglaia mariannensis*, and *Guamia mariannae* contributed significantly to the existing forest structure. *Premna* represented the most basal area of any species, *Leucaena* occurred in the highest stem densities, and *Aglaia* was the most widely distributed species over Area 50. Several genera that are considered components of more advanced seral stages, such as *Elaeocarpus*, *Ficus*, *Intsia* and *Tristiropsis*, were present but poorly represented by a few large individuals (Table 2). *Artocarpus*, *Drypetes*, *Elaeocarpus*, *Glochidion*, and *Macaranga* were rare within Area 50, each found on only 1 of 30 sampled plots (Table 2). *Allophylus* sp. and *Maytenus thompsonii* occurred on the sample plots but were not recorded due to DBHs < 25 mm.

Very few regenerating or germinating tree genera were detected within the 1-m^2 nested quadrats. *Aglaia*, *Casuarina*, *Eugenia*, *Glochidion*, *Guamia*, *Morinda*, *Neisosperma*, *Pandanus*, and *Premna*, all indigenous Micronesian genera and all represented in larger size classes (> 24 mm DBH), were poorly represented within the ground layer (Table 3). Several other native genera, *Tristiropsis*, *Elaeocarpus*, *Macaranga*, *Pouteria*, *Drypetes*, *Artocarpus*, *Intsia*, and *Cycas* were absent in the ground layer. Tangantangan (*Leucaena leucocephala*), an introduced species, was the only tree species that appeared to have good recruitment within Area 50 (Table 3).

Flagellaria indica, a native woody vine, grew in high densities over much of the ground within Area 50 (Table 3); it frequently impeded walking. *Passiflora suberosa*, an introduced herbaceous vine, occurred frequently and abundantly on plots, particularly where gaps in the canopy occurred. Other woody and herbaceous creepers included *Jasminum*, *Mikania*, *Momordica*, and *Operculina*, only the first of which is native. Ferns were represented by two species of *Polypodium*,

Table 2. Composition of woody flora (> 24 mm DBH) within thirty 300-m^2 circular plots sampled inside (experimental) Area 50.

SPECIES	Frequency		Density		Dominance		IV[b]
Aglaia mariannensis	26	(9.4)[a]	385	(13.1)	1.27	(9.2)	10.6
Artocarpus mariannensis	1	(0.4)	3	(0.1)	0.12	(0.9)	0.5
Carica papaya[c]	12	(4.4)	31	(1.1)	0.38	(2.7)	2.7
Casuarina equisetifolia	1	(0.4)	124	(4.2)	0.37	(2.7)	2.4
Cycas circinalis	6	(2.2)	15	(0.5)	0.26	(1.9)	1.5
Drypetes dolichocarpa	1	(0.4)	1	(0.0)	0.01	(0.1)	0.2
Elaeocarpus joga	1	(0.4)	2	(0.1)	0.17	(1.3)	0.6
Eugenia spp.	12	(4.4)	23	(0.8)	0.02	(0.2)	1.8
Ficus spp.	2	(0.7)	2	(0.1)	0.01	(0.1)	0.3
Ficus tinctoria	3	(1.1)	4	(0.1)	0.05	(0.4)	0.5
Glochidion marianum	1	(0.4)	2	(0.1)	0.01	(0.0)	0.2
Guamia mariannae	26	(9.4)	398	(13.6)	0.98	(7.1)	10.0
Guettarda speciosa	4	(1.5)	11	(0.4)	0.10	(0.7)	0.8
Hibiscus tiliaceus	16	(5.8)	379	(12.9)	0.95	(6.9)	8.5
Intsia bijuga	3	(1.1)	8	(0.3)	0.22	(1.6)	1.0
Ixora triantha	3	(1.1)	8	(0.3)	0.01	(0.1)	0.5
Leucaena leucocephala[c]	23	(8.3)	491	(16.7)	1.30	(9.4)	11.5
Macaranga thompsonii	1	(0.4)	1	(0.0)	0.06	(0.5)	0.3
Melanolepis multiglandulosa	16	(5.8)	38	(1.3)	0.11	(0.8)	2.6
Morinda citrifolia	15	(5.4)	174	(5.9)	0.22	(1.6)	4.3
Neisosperma oppositifolia	11	(4.0)	67	(2.3)	0.36	(2.6)	3.0
Pandanus spp.	19	(6.9)	71	(2.4)	0.83	(6.0)	5.1
Pouteria obovata	8	(2.9)	15	(0.5)	0.05	(0.4)	1.3
Premna obtusifolia	25	(9.1)	438	(14.9)	4.60	(33.4)	19.1
Scaevola sericea	3	(1.1)	13	(0.4)	0.01	(0.1)	0.5
Triphasia trifolia[c]	15	(5.4)	85	(2.9)	0.10	(0.7)	3.0
Tristiropsis obtusangula	9	(3.3)	25	(0.9)	0.70	(5.1)	3.1
Vitex parviflora[c]	14	(5.1)	124	(4.2)	0.63	(4.6)	4.6
Sum	277	(101)	2938	(100)	13.90	(101)	100.5

[a]Values inside parentheses are relative frequency, relative density, and relative dominance, respectively; see text for details.

[b]IV = Importance Value = the average of relative frequency, density, and dominance for a given species.

[c]Introduced species.

Table 3. Composition of ground flora (25 mm DBH) within thirty 1-m^2 quadrats sampled inside (experimental) Area 50.

SPECIES	Frequency		Density		Dominance		IV[b]
Aglaia mariannensis	3	(1.9)[a]	9	(0.4)	5	(1.3)	1.2
Bidens alba[c]	8	(5.1)	414	(17.5)	31	(8.1)	10.2
Caesalpinia major	1	(0.6)	1	(0.0)	1	(0.3)	0.3
Casuarina equisetifolia	1	(0.6)	2	(0.1)	2	(0.5)	0.4
Chromolaena odorata[c]	2	(1.3)	4	(0.2)	2	(0.5)	0.7
Eugenia palumbis	1	(0.6)	6	(0.3)	3	(0.8)	0.6
Eugenia reinwardtiana	1	(0.6)	1	(0.0)	1	(0.3)	0.3
Flagellaria indica	22	(13.9)	637	(26.8)	73	(19.2)	20.0
Glochidion marianum	1	(0.6)	8	(0.3)	2	(0.5)	0.5
Guamia mariannae	4	(2.5)	11	(0.5)	6	(1.6)	1.5
Jasminum marianum	2	(1.3)	17	(0.7)	8	(2.1)	1.4
Leucaena leucocephala[c]	17	(10.8)	261	(11.0)	51	(13.4)	11.7
Melanolepis multiglandulosa	4	(2.5)	32	(1.4)	9	(2.4)	2.1
Mikania scandens[c]	13	(8.2)	83	(3.5)	25	(6.6)	6.1
Momordica charantia[c]	7	(4.4)	30	(1.3)	11	(2.9)	2.9
Morinda citrifolia	2	(1.3)	9	(0.4)	3	(0.8)	0.8
Neisosperma oppositifolia	1	(0.6)	1	(0.0)	1	(0.3)	0.3
Nephrolepis biserrata	6	(3.8)	117	(4.9)	15	(3.9)	4.2
Nephrolepis hirsutula	9	(5.7)	152	(6.4)	20	(5.3)	5.8
Operculina ventricosa[c]	1	(0.6)	14	(0.6)	3	(0.8)	0.7
Pandanus tectorius	5	(3.2)	29	(1.2)	9	(2.4)	2.3
Paspalum spp.[c]	2	(1.3)	4	(0.2)	2	(0.5)	0.7
Passiflora suberosa[c]	15	(9.5)	177	(7.5)	41	(10.8)	9.2
Piper guahamense	3	(1.9)	41	(1.7)	7	(1.8)	1.8
Polypodium punctatum	5	(3.2)	126	(5.3)	7	(1.8)	3.4
Polypodium scolopendria	7	(4.4)	107	(4.5)	12	(3.2)	4.0
Premna obtusifolia	2	(1.3)	8	(0.3)	3	(0.8)	0.8
Pyrrosia lanceolata	1	(0.6)	26	(1.1)	3	(0.8)	0.8
Scaevola sericea	1	(0.6)	2	(0.1)	2	(0.5)	0.4
Triphasia trifolia[c]	10	(6.3)	40	(1.7)	21	(5.5)	4.5
Zeuxine fritzii	1	(0.6)	4	(0.2)	2	(0.5)	0.4
Sum	158	(99.8)	2373	(100.1)	381	(100.2)	100.0

[a]Values inside parentheses are relative frequency, relative density, and relative dominance, respectively; see text for details.

[b]IV = Importance Value = the average of relative frequency, density, and dominance for a given species.

[c]Introduced species.

two species of *Nephrolepis*, and *Pyrrosia lanceolata*. *Paspalum* was the only grass genus (introduced) found on quadrats sampled inside Area 50. Although *Bidens alba* occurred on only eight plots, it often covered almost 100% of quadrats on which it occurred. *Zeuxine fritzii*, a terrestrial orchid, was found on one quadrat.

Interior Versus Edge

Species richness of woody flora was significantly higher in the interior of Area 50 than within 75 m of the surrounding fence (Wilcoxon $Z = -2.234$, $P = 0.026$). Mean number of species for the 18 interior plots was 10.1 per 300 m^2 (SE = 0.56), but only 7.9 per 300 m^2 (SE = 0.68) for the 12 edge plots. Several woody species were not equitably distributed within Area 50. *Artocarpus mariannensis, Cycas circinalis, Drypetes dolichocarpa, Elaeocarpus joga, Ficus tinctoria,* and *Intsia bijuga* were only found in the interior of Area 50, mostly along a low ridge. However, *Casuarina equisetifolia, Glochidion marianum, Macaranga thompsonii,* and *Scaevola sericea* were found only in edge plots. Importance values suggest that *Premna, Aglaia,* and *Guamia,* all native, were dominant genera in the forest structure within the interior of Area 50. *Leucaena, Premna, Hibiscus,* and *Vitex,* two of which are introduced, were dominant genera along the forest edge. Mean stem density and basal area of woody flora did not differ between edge and interior plots ($P > 0.17$).

Mean species richness and stem density of ground cover did not differ between interior and edge quadrats ($P > 0.27$). Importance values suggest that *Flagellaria, Leucaena,* and *Bidens* were dominant ground cover components in both edge and interior plots; however, *Passiflora* was more prevalent in edge plots and *Mikania* was important on interior plots. Several other species were not equitably distributed within Area 50. *Casuarina, Morinda, Neisosperma,* and *Scaevola* with stems 25mm DBH were found only on quadrats within 75 m of the perimeter fence. In contrast, regenerating *Aglaia, Eugenia,* and *Premna* were found only on interior quadrats.

Control (Areas 35 and 44)

In contrast to Area 50, the interiors of Areas 44 and 35 were composed of secondary growth with some large gaps in the canopy created by fallen trees. The edge surrounding Area 44 was primarily *Casuarina equisetifolia* whereas *Hibiscus tiliaceus* was the major component of the edge in Area 35.

We recorded 24 woody genera with stems > 24 mm DBH, only three of which are nonnative, in control plots outside of Area 50 (Table 4). Importance values suggest that *Premna, Hibiscus,* and *Guamia* were significant components in the forest structure (Table 4). *Cestrum diurnum, Discocalyx megacarpa, Maytenus thompsonii,* and *Psychotria mariana* occurred on control plots but not on plots sampled within Area 50. *Artocarpus mariannensis, Carica papaya, Drypetes dolichocarpa,* and *Ficus prolixa,* although present on plots within Area 50, were not recorded on control plots; however, *C. papaya* and *F. prolixa* were observed

Table 4. Composition of woody flora (> 24 mm DBH) within twenty 300-m² circular plots sampled outside (control) Area 50.

SPECIES	Frequency		Density		Dominance		IV[b]
Aglaia mariannensis	16	(11.6)[a]	99	(6.7)	0.27	(3.6)	7.3
Casuarina equisetifolia	1	(0.7)	75	(5.1)	0.37	(4.9)	3.6
Cestrum diurnum[c]	5	(3.6)	10	(0.7)	0.01	(0.1)	1.5
Cycas circinalis	5	(3.6)	31	(2.1)	0.81	(10.9)	5.5
Discocalyx megacarpa	1	(0.7)	1	(0.1)	TR[d]		0.3
Elaeocarpus joga	1	(0.7)	1	(0.1)	0.57	(7.6)	2.8
Eugenia spp.	2	(1.5)	4	(0.3)	0.01	(0.1)	0.6
Ficus tinctoria	1	(0.7)	2	(0.1)	0.01	(0.1)	0.3
Glochidion marianum	1	(0.7)	1	(0.1)	0.01	(0.1)	0.3
Guamia mariannae	11	(8.0)	234	(15.9)	0.51	(6.9)	10.2
Hibiscus tiliaceus	16	(11.6)	366	(24.8)	0.88	(11.8)	16.1
Intsia bijuga	1	(0.7)	1	(0.1)	0.07	(1.0)	0.6
Leucaena leucocephala[c]	8	(5.8)	50	(3.4)	0.11	(1.5)	3.5
Maytenus thompsonii	2	(1.5)	5	(0.3)	0.01	(0.2)	0.7
Melanolepis multiglandulosa	6	(4.4)	15	(1.0)	0.06	(0.8)	2.0
Morinda citrifolia	12	(8.7)	163	(11.1)	0.26	(3.5)	7.7
Neisosperma oppositifolia	11	(8.0)	139	(9.4)	0.70	(9.4)	8.9
Pandanus spp.	9	(6.5)	43	(2.9)	0.65	(8.8)	6.1
Premna obtusifolia	15	(10.9)	196	(13.3)	2.00	(26.9)	17.0
Psychotria mariana	1	(0.7)	2	(0.1)	TR		0.3
Scaevola sericea	2	(1.5)	8	(0.5)	0.01	(0.1)	0.7
Triphasia trifolia[c]	10	(7.3)	28	(1.9)	0.03	(0.4)	3.2
Tristiropsis obtusangula	1	(0.7)	2	(0.1)	0.08	(1.1)	0.6
Vitex parviflora	2	(1.5)	4	(0.3)	0.05	(0.6)	0.8
Sum	140	(101.5)	1480	(100.3)	7.48	(100.2)	(100.6)

[a]Values inside parentheses are relative frequency, relative density, and relative dominance, respectively; see text for details.

[b]IV = Importance Value = the average of relative frequency, relative density, and relative dominance for a given species.

[c]Introduced species.

[d]TR = trace, where absolute values are < 0.005 and relative values are < 0.05.

TABLE 5. Composition of ground flora (< 25 mm DBH) within twenty 1 m^2 quadrats sampled outside (control) Area 50.

SPECIES	Frequency		Density		Dominance		IV[b]
Aglaia mariannensis	1	(0.9)[a]	2	(0.1)	1	(0.4)	0.5
Bidens alba[c]	8	(7.2)	228	(12.7)	27	(10.4)	10.1
Capsicum frutescens[c]	1	(0.9)	1	(0.1)	1	(0.4)	0.5
Cestrum diurnum[c]	1	(0.9)	3	(0.2)	1	(0.4)	0.5
Chromolaena odorata[c]	2	(1.8)	7	(0.4)	4	(1.5)	1.2
Euphorbia chamissonis	1	(0.9)	3	(0.2)	2	(0.8)	0.6
Euphorbia cyathophora[c]	1	(0.9)	9	(0.5)	3	(1.2)	0.8
Euphorbia spp.[c]	1	(0.9)	6	(0.3)	4	(1.5)	0.9
Eugenia reinwardtiana	1	(0.9)	1	(0.1)	1	(0.4)	0.5
Eustachys petraea[c]	1	(0.9)	7	(0.4)	3	(1.2)	0.8
Flagellaria indica	11	(9.9)	175	(9.8)	27	(10.4)	10.0
Guamia mariannae	3	(2.7)	5	(0.3)	5	(1.9)	1.6
Hibiscus tiliaceus	1	(0.9)	10	(0.6)	3	(1.2)	0.9
Humata heterophylla	1	(0.9)	2	(0.1)	1	(0.4)	0.5
Jasminum marianum	1	(0.9)	1	(0.1)	1	(0.4)	0.5
Leucaena leucocephala[c]	6	(5.4)	43	(2.4)	12	(4.6)	4.1
Malvastrum coromandelianum[c]	1	(0.9)	1	(0.1)	1	(0.4)	0.5
Melanolepis multiglandulosa	4	(3.6)	30	(1.7)	11	(4.2)	3.2
Mikania scandens[c]	7	(6.3)	19	(1.1)	16	(6.2)	4.5
Momordica charantia[c]	3	(2.7)	10	(0.6)	7	(2.7)	2.0
Morinda citrifolia	3	(2.7)	4	(0.2)	4	(1.5)	1.5
Neisosperma oppositifolia	2	(1.8)	8	(0.5)	3	(1.2)	1.1
Nephrolepis biserrata	5	(4.5)	324	(18.1)	17	(6.5)	9.7
Nephrolepis hirsutula	3	(2.7)	76	(4.3)	9	(3.5)	3.5
Operculina ventricosa[c]	1	(0.9)	2	(0.1)	1	(0.4)	0.5
Pandanus tectorius	1	(0.9)	23	(1.3)	4	(1.5)	1.2
Paspalum spp.[c]	2	(1.8)	78	(4.4)	8	(3.1)	3.1
Passiflora suberosa[c]	14	(12.6)	157	(8.8)	37	(14.2)	11.9
Pennisetum polystachyon[c]	2	(1.8)	13	(0.7)	4	(1.5)	1.4
Pilea microphylla[c]	4	(3.6)	158	(8.8)	13	(5.0)	5.8
Polypodium punctatum	3	(2.7)	298	(16.7)	6	(2.3)	7.2
Polypodium scolopendria	4	(3.6)	64	(3.6)	7	(2.7)	3.3
Spermacoce assurgens[c]	2	(1.8)	4	(0.2)	2	(0.8)	0.9
Stachytarpheta jamaicensis[c]	2	(1.8)	3	(0.2)	3	(1.2)	1.0
Triphasia trifolia[c]	5	(4.5)	10	(0.6)	8	(3.1)	2.7
Wikstroemia elliptica	1	(0.9)	1	(0.1)	1	(0.4)	0.5
Unknown	1	(0.9)	3	(0.2)	2	(0.8)	0.6
Sum	111	(99.9)	1789	(100.6)	260	(100.3)	(100.1)

[a]Values inside parentheses are relative frequency, relative density, and relative dominance, respectively; see text for details.

[b]IV = Importance Value = the average of relative frequency, relative density, and relative dominance for a given species.

[c]Introduced species; however, *Euphorbia* and *Leucaena* have both native and introduced species represented on Guam.

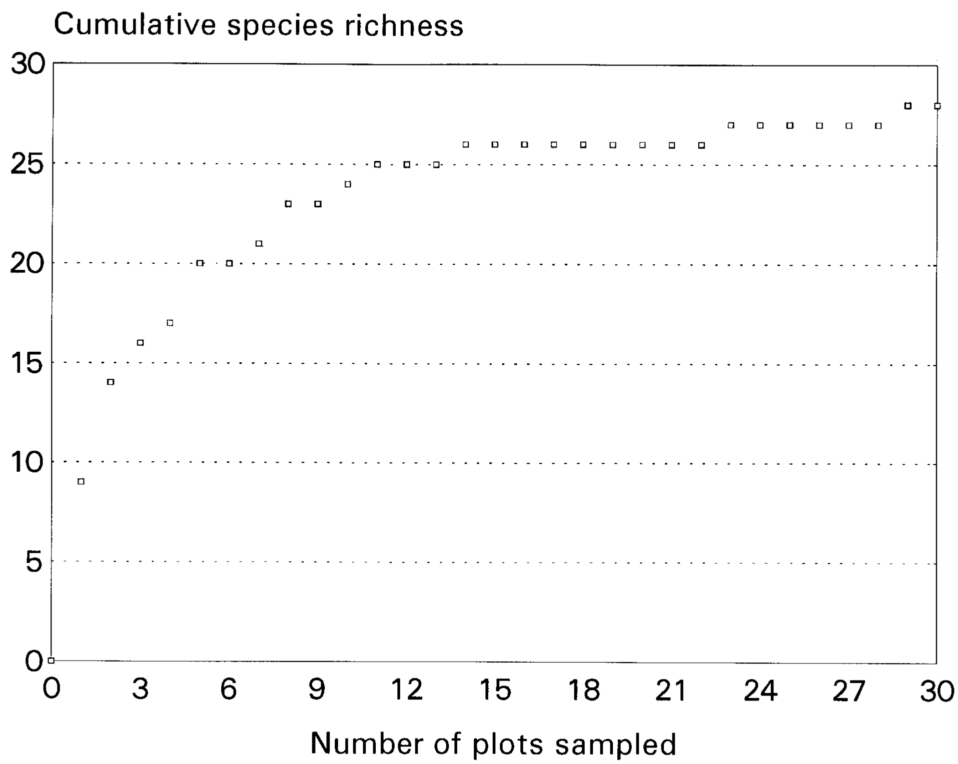

Figure 1. Number of new woody species (>24 mm DBH) identified within Area 50 relative to the number of 300-m[2] plots sampled.

on Areas 35 and 44 but were not recorded on sample plots. *Aglaia, Guamia, Hibiscus, Melanolepis, Morinda, Neisosperma,* and *Pandanus* were found in the ground layer and are apparently regenerating, albeit poorly (Table 5). Similar to Area 50, regenerating *Tristiropis, Psychotria, Premna, Maytenus, Intsia, Ficus, Elaeocarpus,* and *Cycas* were not represented in the ground layer (Table 5).

Thirty-seven species were recorded in the ground flora of the control plots (Table 5). Similar to Area 50, IVs suggest that *Passiflora, Flagellaria* and *Bidens* were dominant components in the ground cover on control plots in Areas 35 and 44. However, high densities of *Nephrolepis biserrata* and *Polypodium punctatum* (Polypodiaceae) were patchily distributed throughout these areas. Ground layer species that were recorded in Area 50 but not on control plots included *Caesalpinia major, Casuarina equisetifolia, Eugenia palumbis, Glochidion marianum, Piper guahamense, Premna obtusifolia, Pyrrosia lanceolata,* and *Zeuxine fritzii* (Tables 3, 5). Species recorded only in the control plots included *Capsicum frutescens, Cestrum diurnum,* three *Euphorbia* sp., *Eustachys petraea, Hibiscus tiliaceus, Humata heterophylla, Malvastrum coromandelianum, Pennisetum polystachyon, Pilea microphylla, Spermacoce assurgens, Stachytarpheta jamaicensis,* and *Wikstroemia elliptica* (Tables 3, 5).

We were concerned that detected differences in mean species richness between control (n = 20) and experimental (n = 30) plots may be due to unequal sample sizes. The cumulative number of woody species detected was plotted against the number of plots sampled within Area 50 (Figure 1). After 12 random plots were sampled, the point at which the curve clearly asymptotes, 89% of the 28 species identified were detected. Sampling an additional 10 plots inside of Area 50, a 50% increase in sample size, resulted in only two more detected species or a 7.7% increase in the estimate of species richness at n = 20.

Discussion

The vegetation within Area 50 is generally representative of the mixed mesophytic evergreen dicotyledonous forest that Fosberg (1960) described for the elevated hard limestone plateau on northern Guam. Despite its proximity to the old airstrip in Northwest Field with its history of human disturbance (Perry & Morton 1999), Area 50 sustains a fairly diverse, native floral community that is favorably comparable in composition to other areas of Guam. Previous estimates of species richness in limestone communities along elevational transects on Guam have ranged from 38 (Moore 1973) to 55 species (Muniappan 1976). In our study, 41 genera representing 27 families were found within Area 50 (Tables 2, 3). Twenty-nine of these genera (71%) were indigenous in origin and several are considered somewhat rare on northern Guam (e.g., *Drypetes* and *Tristiropsis*). After the field portion of this study was completed, several speciments of *Tabernaemontana rotensis* (Apocynaceae) were found in two clusters within Area 50 (G. Wiles, pers. com.). This endemic species is very rare and has been reported previously from only four sites outside of Andersen AFB: Asanite Point (Stone 1970), Iates Point, Mt. Alifan (University of Guam herbarium specimens), and Anao Point (G. Hughes, pers. com.).

We had expected mostly native flora within Area 50. Lee (1974) found that 36% of 41 species in the hard limestone plateau were endemic, the most endemism of any habitat on Guam; conversely, nonnative species were more common in habitats other than that which occurred on hard limestone plateau. Craig (1993) similarly concluded that despite centuries of human disruption, the composition of the limestone forest in the Marpi region on Saipan remained overwhelmingly native, suggesting resistance to invasion by alien species. Although the existing forest structure within Area 50 is predominantly native in composition, our data suggest that nonnative species are successfully and pervasively invading this 24-ha forest patch via three mechanisms: (1) failure of many native overstory species to successfully regenerate, (2) recruitment of alien species, primarily herbaceous, into the ground layer, and (3) recruitment of alien species, primarily woody, along the forest perimeter.

The failure of many native trees to successfully regenerate in the existing environment on Guam has been documented previously by Wiles et al. (1996), Schreiner (1997), and Ritter & Naugle (1999). Despite a few mature individuals of *Tristiropsis obtusangula, Intsia bijuga, Elaeocarpus joga*, and *Artocarpus mariannensis,* we found no evidence that upper canopy components were regenerating in the ground flora. Most of the forest structure within Area 50 is composed of *Premna*, *Leucaena*, *Guamia*, and *Aglaia* (Table 2). *Premna*, *Guamia*, and *Aglaia*, all native midcanopy and lower canopy species, were found in a few plots at very low densities within the ground layer, suggesting that some successful germination was occurring. Their relative success in Area 50, however, is more likely due to their ability to asexually reproduce; i.e., stump-sprout. In contrast, tangantangan (*Leucaena leucocephala*), an introduced leguminous tree, was abundantly distributed over half of the plots and appeared to be regenerating well by both sexual and asexual means (Tables 2, 3).

Although pollinators and dispersers of many of the native flora are unknown, it is apparent that the local extirpation of most of the native avifauna (Savidge 1987) and the dramatic decline in the Guam population of Mariana fruitbats (*Pteropus mariannus;* Wiles et al. 1989) must have severely depressed pollination and dispersal rates of indigenous species. Craig (1993) observed that native flora which recolonized a tangantangan thicket on Saipan tended to be species with fleshy or semi-fleshy fruits; i.e., those that are typically dispersed by indigenous forest birds and rats (*Rattus* sp.). Both of these dispersal vectors are in very low numbers on Guam due to predation by brown tree snakes (*Boiga irregularis;* Rodda et al. 1997).

Even when fruits successfully germinate, herbivory and trampling by feral ungulates may be problematic (Conry 1988). Wheeler (1979) reported that Sambar deer are known to consume the seeds and fruits of at least 23 species, including *Cycas circinalis*, *Eugenia* sp., *Discocalyx megacarpa*, *Artocarpus altilis (incisus* [sic]) and *Premna obtusifolia (interifolia* [sic]). Conry (1989) reported that feral pigs ingest the fruits of *Morinda citrifolia, Pandanus tectonius, Cycas circinalis*, *Artocarpus mariannensis*, *Premna obtusifolia*, and *Ficus* sp. Schreiner (1997) reported browsing by deer on the seedlings of *Macaranga thompsonii, Intsia bijuga,* and *Elaeocarpus joga.*

The invasion of nonnative species into the ground layer was expected in disturbed, open sites (Lee 1974). *Paspalum, Chromolaena*, and *Bidens,* all herbaceous taxa, tended to occur in these areas. However, *Mikania, Operculina, Momordica*, and *Passiflora* are herbaceous vines that occurred frequently and abundantly both in open areas and elsewhere within Area 50, often heavily overgrowing the forest canopy. Whereas only 11% of taxa in the forest structure were introduced (Table 2), 29% of the species recorded in the ground layer were introduced and 78% of these were herbaceous (Table 3). Similarly, MacDonald et al. (1988) reported that most invading species in Mediterranean-type climates worldwide are herbaceous.

Invasion along the forest edge, particularly by woody species, also compromised the integrity of the native forest in Area 50; i.e., an "edge effect". Two of four woody species that dominated the forest structure within 75 m of the perimeter fence (≈50 m of the forest edge) were introduced. *Leucaena leucocephala* and

Vitex parviflora were particularly prevalent within the canopy of the forest edge, although both occurred at low densities within the forest interior. In contrast, the four woody species with the highest IVs within the interior were native. A salient point is that regenerating *Aglaia*, *Eugenia*, and *Premna*, dominant understory components in a maturing limestone forest, were found only in interior quadrats and not along the edge. Concommitantly, several native genera including *Casuarina*, *Morinda*, *Neisosperma*, and *Scaevola*, that are generally considered pioneer or early successional flora in the Marianas, were found only along the edge. This skewed distribution of vegetation within Area 50 resulted in a woody species richness that averaged significantly lower along the edge than within the interior of Area 50. However, there was no evidence that mean species richness of the ground layer differed between interior and edge quadrats.

Whether the three mechanisms identified here are operable in other limestone forest fragments is unknown. Area 50 was partially bulldozed along its perimeter during and after World War II, which may have affected the residual seed bank in those areas (Perry & Morton 1999). Additionally, the asphalt that surrounds Area 50 serves as a heat sink and likely increases the soil and ambient air temperature along the perimeter edge. Both of these factors may contribute uniquely to the successional dynamics in Area 50.

It is apparent that there are significant differences in the vegetation composition between the experimental (Area 50) and control plots (Areas 35, 44). This is an intrinsic problem with designing and analyzing exclosure experiments in the wild; it is essentially impossible to ensure that both the control and experimental plots are identical initially, at time t_1. At some subsequent time, t_2, after the enclosure has been erected and feral ungulates have been removed, the floral community in the controls and experimental plots are again measured and compared. Typically, these data would be compared in an analysis of variance, with treatment and time as main effects. However, the changes in community structure as a result of the exclosure (i.e., the treat X time interaction) cannot necessarily be attributed to the effects of ungulate grazing or browsing because successional dynamics may have been different due to intrinsic differences in community structure at t_1. In other words, the treatments would have differentially changed regardless of the presence or absence of the exclosure. This confounding of data is a result of one type of what Hurlbert (1984) termed “pseudoreplication”; i.e., the failure to truly replicate treatments.

In our study, we randomly allocated sample plots both within and without Area 50, knowing a priori that the vegetation in the latter had been more recently disturbed than in the former. To compensate somewhat for this initial difference between experimental and control, we propose that the plots sampled at t_1 be resampled at t_2. This type of paired sampling will allow calculation of d, the difference in a given parameter value between t_1 and t_2. Mean d and its associated variance are then compared between treatments using a t-test or Mann-Whitney u-test. This statistical approach steps around the inherent problem of having initial differences in samples because it evaluates the *magnitude* of the differences at t_1 and t_2. This approach has been used to a limited extent in vegetation analyses, at least with point-frame data. Loope & Scowcroft (1985) noted that some statisticians hold that point-frame data can be analyzed with *t*-tests to indicate the degree of difference between fenced and unfenced areas and before and after fencing.

It is not critical that subsequent sampling of the flora occur at the original sites. If plots are randomly distributed (albeit independently of one another) at both t_1 and t_2, then collective samples should be representative of the floral community at each of those times (cf. Marcum & Loftsgaarden 1980). However, the power to distinguish differences that may occur is greatly diminished because of the lack of pairing; i.e., the inability to calculate *d*. We strongly recommend that the individuals who conduct a follow-up survey elect to resample the sites that were evaluated in this study.

In a review of 51 exclosure studies in Hawaii, Loope & Scowcroft (1985) reported that grazing and trampling by feral and domesticated ungulates had varying impacts on native vegetation including suppressed reproduction, reduced seedling survivorship, increased asexual sprouting, reduced growth, and local extirpation of endemic species. Our baseline study was not intended to address all of these mechanisms. In retrospect, we should have tagged and measured a subsample of trees on each plot to evaluate growth rates and recorded the number of stems of each species that were stump-sprouting to estimate the proportion of the population that was asexually reproducing. We recommend that both of these parameters be measured in subsequent exclosure studies.

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