Micronesica 31(2):125–142. 1999

Regeneration rates of the woody vegetation of Guam's Northwest Field following major disturbance: land use patterns, feral ungulates, and cascading effects of the brown treesnake

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Abstract—Little is known about the rates at which native forest in the Marianas regenerates following major anthropogenic disturbance, especially ones including the removal of seed banks. Moreover, though some tree species are considered typical of primary or secondary forest, this is generally based on current forest phenology, not on a detailed time-series analysis of frequency following perturbation. This paper presents a study designed to address these issues.

The Northwest Field area in northern Guam provides an ideal venue for such a study. Various plots were affected by anthropogenic (military) factors. We obtained records of all major disturbances since World War II. We identified four plots. One had not suffered major disturbance in the last 100 years, one suffered some effects in 1945, one was totally bulldozed in 1945, and two were bulldozed in 1945, then again in 1965. We surveyed the vegetation at these five adjacent plots.

We found that undisturbed forest was more diverse, and contained more species considered typical of primary forest, than plots razed in 1965 or 1945. Some tree species, such as *Casuarina*, showed a clear "decreaser" pattern, being more common following the disturbance than later on. Others, such as *Aglaia*, showed an "increaser" pattern, becoming more common as time from disturbance increased. Some, such as *Pandanus*, showed no clear pattern with time. We discuss these patterns, and three proposed mechanisms that might be responsible for the slow regeneration of forest at this site. Our data provide direct support for the importance of anthropogenic land-use patterns. They are also consistent with negative impacts due to feral ungulate grazing and absence of seed dispersers due to brown treesnake predation.

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Introduction

The vegetation of the Mariana Islands has been fairly well described on a large scale (Safford 1905, Fosberg 1960, Stone 1970, Falanruw et al. 1989, Raulerson & Rinehart 1991, 1992). However, detailed information on the vegetation composition at specific sites is uncommon (for exceptions see Craig 1992, Morton et al. 1999). Winds are a major natural structuring force in the local vegetation. Especially catastrophic are typhoons, some producing gusts measuring over 300 km/hr and bearing torrential rains (e.g., Stone 1970, Lawrence & Dougherty 1993). Surprisingly, information on the response of the local vegetation to, and its recovery following, perturbation is scant.

Humans have been in the Marianas for at least 3500 years (Craib 1983, Steadman 1995), and their influences have been both chronic and acute (Pregill 1998, Steadman 1995). European reports from the 1500s, immediately after first contact by Magellan, are vague on the topic of Guam's flora. They generally indicate extensive clearings and agriculture, including rice and cultivation of coconuts (e.g., Legazpi 1565, in Blair & Robertson 1903). Later descriptions suggest extensive damage to the forest. For example, Arago (1823) reported: "The imagination, spoilt, as it were, by the picture of the splendid fields of the Molucca islands, could not conceive a sky less pure, a vegetation less luxuriant, in a climate almost the same. …Trees are rare on the mountains. Vast masses of bare rock form a painful contrast to patches of a yellowish green, from the midst of which, however, rise at intervals slender trees, crowned with a few pale leaves. The skirts of the shore alone exhibit rich clumps of smiling verdure. …Hills shadowed by vigorous and useless trees surround smiling vales, where weeds grow by the thousands among a few blades of rice and Indian corn." Archeological reports confirm the region's fauna has also been seriously altered by these early settlers (Steadman 1995). The rate of disturbance has not slowed since then. All the major islands in the Mariana chain endured considerable destruction during World War II (WWII), a result of both war-time construction and extensive bombing during various campaigns (Baker 1946, Morison 1953). Today, undisturbed habitats are uncommon on all major Mariana islands (North to south: Tinian, Saipan, Rota and Guam; Engbring et al. 1986).

Introduced plants and animals, some of them extremely invasive, form another type of man-made problem facing the flora of Guam. Large areas on Guam are covered with tangantangan (*Leucaena leucocephala).* This invasive legume was initially used on Guam for hedges and quickly escaped (Safford 1905). It was further intentionally spread over much of the southern Marianas after WWII to prevent erosion (Engbring et al. 1986). Stone (1970) reported that about 63 percent of all plant species on Guam were introduced. This is a very high percentage, even in comparison to values recorded in other highly impacted island ecosystems (reviewed in Brockie et al. 1988). Current values are unknown, but are likely to have increased even further as commerce to Guam has grown in the past three decades. Philippine deer (*Cervus mariannus)* and feral pigs *(Sus scrofa)* are also common on the island, having been introduced before 1800 (Safford

1905, Intoh 1986, Wiles et al. 1999). Like other ungulates (e.g., Brockie et al. 1988), these feed on and damage plants, spread the seeds of invasives, and their trails and rooting create habitat conducive to invasives (e.g., Cuddihy & Stone 1990). However, the potentially beneficial effects ungulates have in some habitats, including spread of native seeds (recently summarized by Olff & Ritchie 1998), remain untested on Guam. Another factor is the arrival of the brown treesnake *(Boiga irregularis)* on Guam around 1950. The ensuing near-complete extirpation of native birds and fruit bats (Rodda et al. 1997, Fritts & Rodda 1998) has considerably reduced the availability of pollinators and seed dispersers. Birds and bats are crucial elements in the regeneration of similar forest on nearby Saipan (Craig 1993) and were probably essential elements on Guam (Lawrence & Dougherty 1993). Their absence could seriously change forest regeneration dynamics (Lawrence & Dougherty 1993, Schreiner 1997, Ritter & Naugle 1999).

Next to nothing is known about natural vegetation regeneration in the Marianas (Craig 1993). Similarly, little information exists on the process of forest regeneration in the absence of a seed bank. It is common to see large areas covered with vines shortly after a typhoon has created openings in the forest. Such events can have serious ecosystem impacts (Horvitz 1997, Schmitz et al. 1997), including inhibition of native tree regeneration (Horvitz et al. 1998). However, the details of this establishment and the replacement of vines by woodier vegetation have not been documented in Guam. The uniqueness of the impact of the brown treesnake makes studying the process on Guam even more desirable. The main goal of this study was therefore to study the process of natural reestablishment of trees following major devastation including likely loss of entire seed banks. We used historical information on land use to infer the causes for the present patterns, gauge the rate of the regeneration process, and identify species that increase and decrease in the habitat as time from disturbance increases. We studied plots that suffered major disturbance at known historical times, identified casual hypotheses that might explain slow regeneration and reduced forest diversity, and preliminarily evaluated them.

Materials and Methods

Study Locations and Vegetation Information

Northwest Field (marked on older maps as North West Field, and here abbreviated as NWF) is located in northern Guam (13º37'N, 144º51'E) and encompasses approximately 470 ha. The part of Guam’s northern plateau containing NWF and adjacent portions of Andersen Air Force Base includes some of the best preserved and most pristine forests left on Guam (Quinata 1994). Two recent surveys (Perry et al. 1997, Morton et al. 1998, 1999) provide detailed descriptions of the vegetation in this area, though the authors used slightly different sampling methods. Perry et al. (1997) employed a line transect survey method at two plots having a total area of approximately 70 ha. Plot I was 40.5 ha in size and plot II was about 29.5 ha. Morton et al. (1998) used a circular plot approach to study

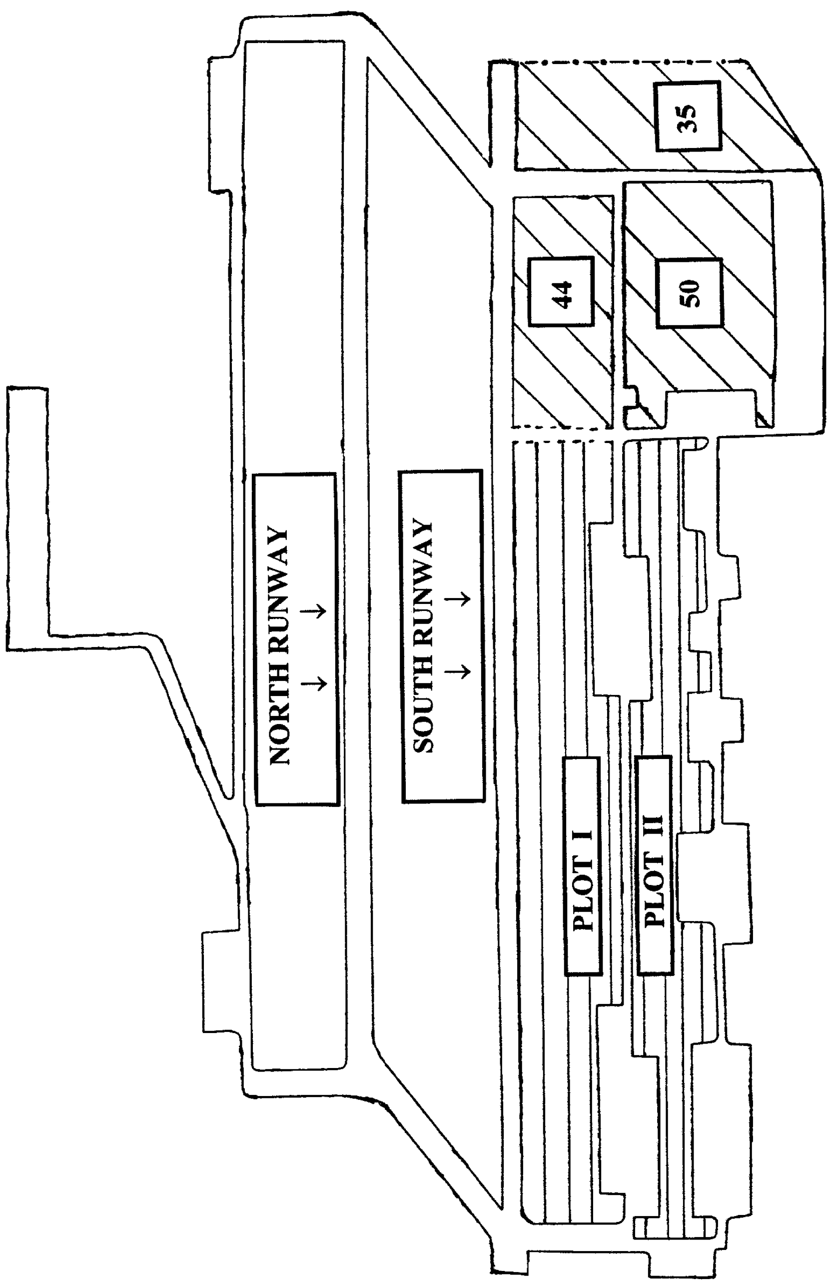

Figure 1. Map of the study site, showing the relative locations of the five study plots on Northwest Field, Ansersen Air Force Base, Guam. Sites surveyed by Perry et al. (1997) are denoted by horizontal lines, those surveyed by Morton et al. (1998) by diagonal lines. Broken lines denote very badly degraded asphalt, and dot-dashed line marks the far edge of the part of Area 35 surveyed.

three smaller plots. These are identified as Area 35 (sampled area was about 20 ha), Area 44 (17 ha), and Area 50 (24 ha). The five plots are located immediately next to one another (Figure 1), sharing climatic conditions, soil type, and large-scale anthropogenic effects. Thus, any differences between them should be traceable to specific historical events associated with the construction of the airfield (see historical information, below). The area contains stretches of native limestone forest (Fosberg 1960), as well as grass, weeds, and secondary growth such as *Casuarina* stands. Parts are mainly covered with primary forest, whereas others chiefly contain secondary growth (Quinata 1994, Perry et al. 1997, Morton et al. 1998). Like other forest on Guam, emergent trees are rare and most or all the canopy is under 15 m tall.

Data were taken from Perry et al. (1997) and Morton et al. (1998) and complemented by unpublished information from original survey notes. Since they are not easily available, data taken from these sources are presented below. We chose fourteen woody genera for our main analyses since these were commonly sampled by both survey teams. Relative abundance, a diversity metric reported by both teams, was used in all comparisons. Trees were identified as native (primary or secondary forest) or introduced based on Stone (1970), Raulerson & Rinehart (1991), and references therein. Statistical analyses were performed using SAS and SPSS.

Historical Information

Limited published information is available about pre-WWII Guam, and forms the basis for the information provided below. Early sources include descriptions given by the first Europeans to contact the residents of the island; recent ones were published shortly after the war. These sources provide a broad description of the area prior to 1940, but few precise details.

The U.S. military kept fairly detailed historical records of their activities in Guam, including the NWF area, during and after the war. Much information about the fighting has been published by the U.S. government and by independent sources (e.g., Anon. 1947, Lodge 1954, Morison 1953), but most relevent information about the history of NWF itself remains unpublished. Many of those are kept by the Base Historian of Andersen Air Force Base, of which NWF is a part. The 36 Air Base Wing supplied us with unpublished written and photographic records of the construction of the airfield and its major upgrades since. These are the source for all unattributed information provided below. Combined, these sources document all the major impacts on the five study plots within the past half century.

Results

Vegetation Comparison

Fourteen woody genera were relatively common in at least one plot (Table 1). Areas 35 and 50 held considerably more woody species (21 and 26, respectively) than did the other three plots (14 species in Area 44 and Plot II, 15 in Plot I). Many of the typically primary native limestone forest species identified on NWF (e.g., *Aglaia*, *Cycas*, *Guamia*, *Intsia)* were found only or mostly in Areas 35 and 50. Other species (e.g., *Pandanus*, *Morinda)* were also found in native forest, but are especially typical in secondary limestone forest. These were found in most or all plots, but especially in the three more impacted sites (Area 44, Plots I, II). A similar pattern was found for *Casuarina*, a species typical of secondary limestone forest, and *Triphasia*, an introduced invasive. In many cases (e.g., *Guamia*, *Morinda)* relative frequencies differed markedly between plots, although some genera (e.g., *Premna)* were relatively equally well represented in all five. Overall, the differences between the five plots in tree species compositions were highly significant (x^2 test, x^2=235.3, df=56, p<0.0001).

Area 50 and Area 35 were composed of a greater proportion of native primary forest trees. These plots had a much lower frequency of common native sec-

Table 1. Comparison of common trees found at the five plots surveyed at Northwest Field, Andersen Air Force Base, Guam. Data are from Perry et al. (1997), Morton et al. (1998) and from unpublished data collected by the authors. Numbers are percentage of all trees encountered at each plot.

Plant genus	PLOT I	PLOT II	PLOT 35	PLOT 44	PLOT 50
Native, primary forest:					
Aglaia	1.4	5.7	8.3	5.9	9.2
Cycas	0.0	0.0	3.9	0.0	2.1
Ficus	0.0	1.7	0.1	0.0	1.8
Guamia	0.5	0.0	26.6	0.5	9.2
Neisosperma	7.4	0.0	10.1	6.4	3.9
Native, secondary forest:					
Casuarina	2.8	1.1	0.0	8.2	0.4
Hibiscus	18.1	11.4	15.0	33.6	5.7
Melanolepis	0.9	5.7	1.4	0.9	5.7
Morinda	28.4	21.1	10.6	16.1	5.3
Pandanus	8.8	9.1	3.7	1.3	6.7
Premna	5.6	12.6	11.2	16.9	8.8
Other species (native)	13.9	13.9	4.9	2.4	22.8
Introduced:					
Leucaena	5.6	5.7	0.9	6.7	8.1
Triphasia	1.9	4.0	3.3	0.5	5.3
Vitex	4.7	8.0	0.0	0.6	5.0

Table 2. Percentage of common trees found at the five plots surveyed at Northwest Field that are native (typical of primary forest or secondary forest) or introduced. Genera included are those listed in Table 1, and assignation to category follows the authorities cited in the text

Plant category	Plot I	Plot II	Area 35	Area 44	Area 50
Native, primary forest	10.8	8.5	49.0	11.8	36.5
Native, secondary forest	75.2	71.0	46.4	80.1	40.5
Introduced	14.0	20.5	4.6	8.1	23.0

ondary forest species, and a much higher frequency of native primary forest species, than did the three other plots (Table 2). The difference among the five plots in the percentage of vegetation that were introduced, native primary or native secondary was statistically significant (x^2 test, x^2=95.6, df=8, p<0.0001).

For the eight most common species in our sample we also tested the heterogeneity within plots by comparing within and between-plot variability (Table 3). Areas 35 and 44 were less extensively sampled. To account for this we conducted the analysis in two ways. First we used only data from plots I and II and Area 50, then we repeated the analysis with data for Areas 35 and 44 added. Percentage coverage by *Pandanus* was not significantly different by either analysis (ANOVA, p>0.3 in both cases), suggesting all plots had similar proportions of this species. Results for *Hibiscus*, *Leucaena*, *Neisosperma*, and *Premna* were ambiguous, significant in one analysis but not the other. This suggests there may be some differences between the plots in their prevalences, but these are not overwhelming. Finally, significant differences were indicated by both analyses for *Aglaia*, *Guamia*, and *Morinda*. Of these, *Aglaia* and *Guamia*–both primary forest species–were more common in Areas 35 and 50 than at other sites. *Morinda*, a species typical of secondary forest, was less common at these two plots.

Table 3. Inter-plot variability in abundance of the eight most common trees found at Northwest Field, Andersen Air Force Base, Guam. Data are mean and standard deviation (SD, in parentheses) of percentage coverage, derived from unpublished data collected by the authors.

Plant	P L O T				
genus	I	II	35	44	50
Aglaia	1.0 (2.2)	6.0 (7.7)	8.3 (7.3)	5.8 (9.3)	13.2 (12.9)
Guamia	0.4 (1.4)	0.0 (—)	26.6 (14.8)	0.5 (1.1)	13.7 (10.4)
Hibiscus	18.9 (17.5)	13.2 (14.1)	15.0 (15.7)	33.6 (33.3)	11.6 (16.1)
Leucaena	5.9 (8.3)	6.5 (6.9)	0.9 (3.0)	6.7 (8.9)	16.4 (20.1)
Morinda	12.7 (6.4)	12.7 (12.6)	10.6 (22.2)	16.1 (17.7)	6.3 (14.1)
Neisosperma	5.9 (10.6)	0.0 (—)	10.1 (11.0)	6.4 (10.6)	2.1 (4.8)
Pandanus	6.4 (8.8)	6.6 (7.2)	5.3 (11.8)	2.0 (4.1)	2.4 (3.1)
Premna	6.6 (7.7)	11.0 (15.1)	11.2 (9.9)	16.9 (22.7)	16.2 (14.8)

Historical Information

Few data specific to our plots exist. The review below sometimes covers relevent events that impacted the entire island, but mostly centers on events in northern Guam or the NWF area. As reviewed above, Chamorros have been on Guam for a long period and have seriously impacted its forests. However, by the early 1900s, population on Guam was concentrated around the center of the island. Pictures taken during the island's recapture show large areas in the more heavily populated center of the island were bare of trees (Crowl 1993, Lodge 1954). In contrast, no villages were located on the part of the northern plateau containing NWF (Thompson 1947). A 1939 census shows Yigo and Machanao as the only two municipalities in the northern part of the island. Together they held about three percent of Guam's total population. With 330 and 377 residents, respectively, the population density in the region was the lowest anywhere in Guam at the time (Thompson 1947). The period before WWII, and especially the decade just before it, thus appears characterized by relatively little disturbance to northern natural habitats (Baker 1946).

Guam was heavily bombarded prior to the American re-invasion in 1944, resulting in the destruction of over 80 percent of the structures on the island (Morison 1953). However, the Japanese had considered the northern part of the island relatively secure from invasion, and had consequently placed relatively few forces there. Bombing was concentrated primarily on strategic sites, and recapture of northern Guam was primarily achieved through ground assault (Baker 1946, Crowl 1993, Lodge 1954). Consequently, Guam's recapture resulted in relatively little additional devastation of northern native forest. American soldiers involved in the recapture of the area reported dense forest through which they had to use machetes to advance, in which they often became lost, and which greatly impeded vision and operations. A few clearings already existed, and were being used by the Japanese. For the most part, however, fighting in the northwest part of the island was light and the area remained relatively undisturbed (Anon. 1947, Crowl 1993, Gailey 1988, Lodge 1954).

At the end of the war, the residents of Machanao were displaced to make room for military installations (Thompson 1947). Early in 1945 construction of two airfields, North Field (now the active runway system of Andersen Air Force Base) and NWF, was begun in the area by the American military. Both were intended to serve heavy B-29 bombers, and were consequently rather large. Construction of the two 2.8 km runways at NWF, as well as their associated taxiways and structures, resulted in major forest disturbance. The project required major habitat modification. Heavy bulldozers were used to scrape the ground to bedrock, cut through the limestone bedrock, and fill large potholes (Anonymous 1947). Some rock piles still remain from that work. The south runway was completed on 1 June 1945, and the north runway became operational a month later. Some construction was conducted in the following months to complete their barracks and offices. Aerial photographs from the period show that three of our plots

(I, II and 44) were almost totally cleared, Area 50 was mostly (about 75 percent) left intact, and Area 35 remained untouched.

The war ended two months after construction of the runways was completed. Various units were based at NWF until 1949, when it was deactivated. By 1955, only one building was still intact at the airfield itself. In 1960 the nearby temporary housing units were vacated, and typhoon Karen destroyed most of the structures in 1962. The Vietnam War again increased the traffic of heavy bombers in the mid 1960s. In 1965, the south runway and nearby taxiways were repaired, and it appears Plot I and Area 44 were again cleared. The field primarily served for emergency operations, and was again inactivated once the war ended. Aerial photographs taken during the past fifteen years show all study plots covered with vegetation. However, plant cover in Plot I appears sparser than in other areas, with many bare patches being evident. No clear signs of the housing area, or any other of the field's original structures, can be seen. Apart from a small installation, built in 1965 and located on a small section of the taxiways, NWF has not seen regular use since. However, the Air Force has maintained the south runway operational for emergency and training uses by regularly clearing the vegetation that encroaches on it.

Public hunting was initiated at NWF in the 1960s and has been almost continuous since then. Hunting was suspended during part of the Vietnam War, and again in the late 1980s, but NWF has been continuously open for hunting since 1990 (U.S. Fish and Wildlife Service 1995, R.D. Anderson pers. com.). Of all legal hunting sites on Guam NWF has consistently been the most heavily hunted for both deer and pig (Wheeler 1979a,b, Conry 1986, Aguon 1990a,b). Currently both Plot I and Plot II are off-limits to hunting, whereas Areas 35, 44, and 50 are regularly hunted. A tall (about 2 m) chain-link fence erected around Area 50 in January 1992, with the intention of creating an ungulate exclosure on the plot. Pig and deer removal efforts have been continuous but inconsistent in their intensity. At one point, the estimated combined number of pigs and deer inside was reduced to less than ten. However, these quickly reproduced and increased in numbers (U.S. Fish and Wildlife Service 1995). An intensive ungulate removal program began in 1997, but some deer and pigs still remained on the plot in 1998 (H.C. Hirsh pers. com.).

Discussion

The NWF area currently contains vegetation typical of both primary and secondary limestone forest, as well as invasive weeds (Perry et al. 1997, Morton et al. 1998, 1999). In all, Perry et al. (1997) identified fifteen common tree species covering 86 percent of the sampled area in Plot I and II. Four common shrubs covered about 24 percent of the area, vines and epiphytes covered fifteen percent, and tall weeds, ferns and monocots together covered sixteen percent. Bare ground covered fifteen percent of the area they surveyed (numbers add up to more than 100 because of overlapping forest layers). Morton et al. (1998) identified 27

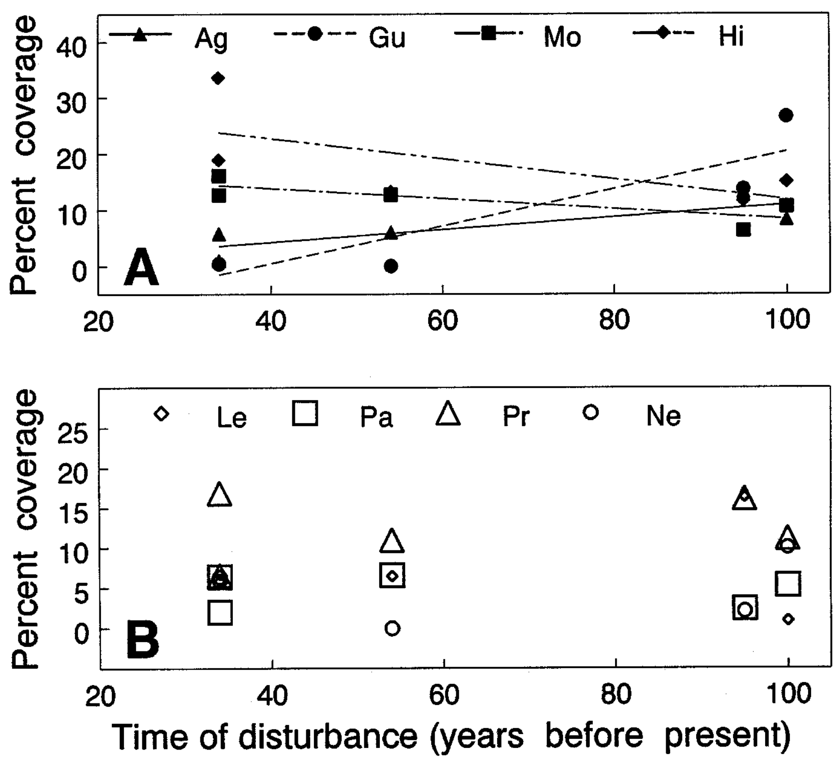

Figure 2. Relative frequency of eight common tree species at five Northwest Field plots as a function of time from last major disturbance. We arbitrarily set 100 years as the value for Area 35, for which no record exists of recent impact, and 95 years for slightly impacted Area 50. A: four species showing high correlation coefficients (rho>0.65) in Spearman non-parametric correlations: Ag–*Aglaia,* Gu–*Guamia,* Hi–*Hibiscus,* Mo–*Morinda.* B: four species showing low correlation coefficients (rho<0.25): Le–*Leucaena,* Ne–*Neisosperma,* Pa–*Pandanus,* Pr–*Premna.* The number of plots is too small for meaningful statistical analyses of these trends.

main woody species in Area 50 and 24 in Areas 35 and 44. Area 50 had 31 species of ground plants, and Areas 35 and 44 had 37. Unfortunately, Morton et al. (1998) did not record the prevalence of bare ground in these areas.

Limestone substrate of the type found in the entire Northwest Field area supports most of Guam's endemic plants, possibly because it provides a greater diversity of niches than other available substrates (Stone 1970). The five plots evaluated share soil type, rainfall, and other climatic and environmental factors. Thus, in the absence of external influences we would have expected the woody flora to be similar and diverse at all five. This was not the case. Areas 35 and 50 were relatively similar in their woody vegetation, and the slightly smaller number of species in the former can be attributed to the lower sampling effort there. The species-area curve provided by Morton et al. (1998) for Area 50 suggests the true number of woody species in Area 35 is virtually the same as in Area 50. In contrast, the other three plots were much less diverse, especially where old-growth natives were concerned.

Our findings thus raised the question why Areas 35 and 50 differ from the other three plots to such a great extent. We identified three main hypotheses for explaining this situation: prior land use history (Perry et al. 1997); ungulate damage (Conry 1988, Perry et al. 1997, Schreiner 1997, Morton et al. 1998, 1999, Ritter & Naugle 1999, Wiles et al. 1999, and references therein); and loss of pollinators and seed dispersers due to predation by the introduced brown treesnake *(Boiga irregularis)* and its cascading effects (Lawrence & Dougherty 1993, Schreiner 1997, Ritter & Naugle 1999).

Land Use History

Perry et al. (1997) suggested prior land use patterns might have been important in producing differences in the vegetation of adjacent plots. Our analysis is most appropriate for testing this hypothesis and provides considerable support for it. The entire NWF area was apparently mostly undisturbed at the end of the fighting in 1944, before airfield construction (Anonymous 1947, Crowl 1993, Gailey 1988). Area 35 was left untouched and Area 50 remained mostly intact during the construction of the airfield in 1945. They currently possess the most diverse forest seen in our study. The other three plots were totally razed at the time. They currently contain many native plant species and appear to be regenerating naturally, albeit slowly. As predicted from this hypothesis, Plot I and Area 44, the most recently impacted due to work carried out during the Vietnam War, were the poorest in tall, slow-growing primary native forest trees such as *Ficus.*

Many sources list certain species as “increasers” or “decreasers.” Increasers are ones that increase in frequency as time from disturbance increases, while decreasers become more common soon after a disturbance (e.g., Rogers & Stride 1997). Despite this, we were unable to find quantitative measures associated with these categories for local species. To begin describing these types more numerically we plotted relative frequency against time of most recent major disturbance (Fig. 2). Viewed this way it becomes clear that *Aglaia* and *Guamia* both gradually increase in frequency as time from latest disturbance increases, as would be expected of primary forest species (Fig. 2A). Secondary species such as *Hibiscus* and *Morinda,* on the other hand, become less common as time from disturbance grows. Some species, however, show no clear pattern with time (Fig. 2B). Of the less common trees, *Cycas* showed a definite increaser pattern, *Casuarina* showed a definite decreaser pattern, and the rest showed no clear pattern.

One possible cause for the difference between the two undisturbed and three heavily impacted plots could be bulldozing, which has likely affected soil or hydrological characteristics. If so, we would have expected to see a similar pattern emerge in other sites experiencing similar fates. The work of Craig (1993) offers a suitable comparison to our Plot II, as both were bulldozed at about the same time and remained mostly untouched since. Contrary to this prediction, limestone forest on Saipan has regrown more rapidly and resembles primary forest to a greater extent (Craig 1993).

Another effect of the bulldozing carried out at NWF was fragmentation of the habitat and creation of extensive edge effects (Morton & Amidon 1999). Presence of roads allows species such as *Casuarina* to prosper and affects the woody vegetation composition and reduce its species richness for tens of meters. In Area 50, for example, introduced woody species dominated a 50 m wide strip along the forest edge (Morton & Amidon 1999). Especially narrow plots or other forested fragments may thus be impacted almost throughout.

We found a relatively small difference between plots last devastated in 1945 (Plot II) and 1965 (plot I, Area 44). This suggests we should not expect the forest in these plots to resemble their more intact neighbors in the next few decades either. Guam's present human population density is similar to India's (Rodda et al. 1998), leaving the small amount of native vegetation highly fragmented. Our findings thus justify the protection currently given to Area 50 in both military and civilian conservation efforts. It further suggests protecting Area 35 might well also be warranted.

Ungulate Damage

The positive effects ungulates can have on diversity and regeneration rate in at least some habitats (Olff & Ritchie 1998) remain untested on Guam. On the other hand, many sources indicate deer and pigs negatively impact forest regeneration on Guam (Conry 1988, Perry et al. 1997, Schreiner 1997, Morton et al. 1998, Ritter & Naugle 1999, Wiles et al. 1999, and references therein). Our data are not directly applicable to testing this claim, but are consistent with it. Hunting has been used for recreation, as well as a management tool for controlling ungulate populations in the NWF area. Reports of the Guam Division of Aquatic and Wildlife Resources (Aguon 1990a,b, Conry 1986, Wheeler 1979a,b) indicate the area has been more heavily hunted than any other part of the island. Although Plots I and II were closed to hunting, ungulates freely move between them and the hunted areas (G. Perry unpublished). Thus, the great similarity between Plot I and Area 44 was expected. The extensive ungulate spoor and damage recorded in all five plots (Perry et al. 1997, Morton et al. 1998) suggest the management effects of hunting were quite small. Thus, either more extensive hunting is required, or additional tools should be brought to bear.

An increase in ungulate populations at NWF since the mid 1940s could explain the slow recruitment we found at Plot I and Area 44. No precise data are available on ungulate numbers in the area. In the 1960s, Guam's Division of Aquatic and Wildlife Resources began conducting rough estimates of ungulate population trends at a nearby un-hunted site. These surveys suggest a population decrease in the late 1970s (Wheeler 1979a,b), an increase during the 1980s (Conry 1986, Aguon 1990a), and a decrease in the 1990s (G.J. Wiles pers. com.). However, they are self-admittedly unreliable (e.g., Conry 1986) and not completely comparable.

Both ungulate species were introduced to the Marianas before 1800 (Safford 1905, Intoh 1986). This should be more than long enough to have prevented recruitment at the two plots that were not cut down in 1945 if these were responsible. In light of the existence of seedlings in Area 50 (Morton et al. 1998), the lack of better regeneration, especially in Plot II, is puzzling. However, both *Aglaia* and *Guamia* appear especially resistant to pig and deer damage (Wiles et al. submitted). Seedlings of both were found in Area 50, though at least some of the *Guamia* seedlings reported by Morton et al. (1998) may have resulted from asexual "stump sprouting," rather than from sexual reproduction. Thus, although pig and deer damage appears a likely factor in the slow regeneration observed in this study, we believe it is insufficient to explain all the observed patterns.

Indirect Bown Treesnake Effects

Several studies have documented the massive direct effects resulting from the introduction of the brown treesnake to Guam (see Fritts & Rodda 1998, for the most recent review). Less is known about the precise impacts resulting from the subsequent loss of avian and mammalian seed dispersers and insect predators. The third casual hypothesis for slow regeneration at NWF identifies the brown treesnake as a likely culprit (Lawrence & Dougherty 1993, Schreiner 1997, Ritter & Naugle 1999).

Having virtually exterminated all native seed dispersers, the snake has instigated a series of cascading effects that are very poorly understood (Rodda et al. 1997, Fritts & Rodda 1998). Thus, an impact at one trophic level has had strong indirect effects at others. For example, *Lantana* is an introduced plant pest that was once common on Guam and remains so in parts of the Northern Marianas. It has largely disappeared from Guam, possibly as a result of the snake-caused loss of its avian seed dispersers (Denton et al. 1991). At NWF, Perry et al. (1997) found new *Lantana* in a single clearing, and Morton et al. (1998) recorded none. Ritter & Naugle (1999) recently suggested the absence of appropriate seed dispersers may be contributing to the lack of recruitment in *Elaeocarpus joga*, a regionally endemic climax forest tree. *Elaeocarpus joga* was probably dispersed by pigeon-sized birds (Raulerson & Rinehart 1991). Unfortunately, little is known about the ecology of pre-snake Guam, and the natural dispersers of most native trees remain poorly known. In Florida, Horvitz (1997) and colleagues have shown that storm damage resulted in openings which attracted frugivorous birds. These, in turn, helped increase seedset and speed vegetation regeneration. Likely, such effects also occurred in Guam before the snake arrived, and the long-term effect also includes a slowing down of post-storm damage regeneration.

Conclusions

While our findings are consistent with the scenerio above, we have no data that can be directly applied to testing it. Even the most recently regenerated forest we studied at NWF began growing in the 1960s or 1970s, long before the brown treesnake irrupted there in the early 1980s (Rodda et al. 1992). Perhaps, as Craig

(1993) suggested, primary forest species require a microhabitat that is not available in newly regrown forest. For example, the vine tangles that are so common in newly regenerated forest in Guam may either directly compete with the slow-growing seedlings or reduce the amount of sun reaching them too much (e.g., Horvitz 1997). If this is the case then seed dispersers would have already been gone by the time conditions were right for these species to start growing again. In less-disturbed areas, however, the snake was still absent when the old-growth trees currently seen started growing, explaining their presence in the two older plots. Since reduction in species diversity has been empirically shown to alter ecosystem function (Naeem et al. 1995), such effects are of major concern. What started with the accidental introduction of the brown treesnake may be continuing with changes in tree diversity. Worse, through altering basic ecological processes it could ultimately lead to wide-ranging changes in the biogeochemical processes that underlie all of Guam's ecosystems (Naeem et al. 1995, and references therein).

As human impacts increase and large areas are denuded of vegetation, the importance of understanding recovery from catastrophic removal, as oppossed to partial impacts, increases. Our study suggests regeneration of limestone forest in Guam following such catastrophic removal is slower than on nearby islands. Three hypotheses have been offered to explain this: past use patterns, ungulate damage, and cascading ecological effects due to extermination of pollinators and seed dispersers by the brown treesnake. Our results support the first and are consistent with the other two. Most likely, in our opinion, all three played a role. However, both ungulate damage and indirect effects due to the snake require a more direct test before firm conclusions can be drawn. Moreover, only one set of data for the region is presently available for comparison with ours (Craig 1992, 1993). We hope this study will stimulate additional work which will allow these hypotheses to be further tested. A better understanding of the rate and trajectory of post-disturbance recovery at NWF would improve our ability to successfully manage Guam's forest habitats and begin restoring them. Inasmuch as such conclusions can be generalized, they should greatly enhance conservation efforts at other locations as well.

Acknowledgements

We thank Andersen Air Force Base, and especially H.C. Hirsh and A. Miller, for access to the site and to the historic information on it. H.C. Hirsh, S.J. Kot, L. Raulerson, G.H. Rodda, R.J. Rondéau, and G.J. Wiles provided helpful comments on the manuscript. We also thank G.J. Wiles for access to unpublished hunting records for NWF. Vegetation sampling was funded by Ohio State University through a grant from the Department of Interior's U.S. Geological Survey, Biological Resources Division, and by the 36 CEV/CES Environmental Flight at Andersen Air Force Base.

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Received 12 July 1998, revised 22 Jan. 1999