

Conservation Value of Remnant Forest Patches: Tree Composition, Spatial Patterns, and Recruitment in the Ottoville Lowland Forest, American Samoa¹

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Abstract: Native forests increasingly have been reduced to remnant fragments on many Pacific islands. Island and continental ecosystems differ in a number of ways that may increase conservation value of such forest fragments on islands. However, few studies have examined performance of tree populations in Polynesian forest fragments. We tested potential conservation value of the largest contiguous patch of lowland lava flow forest on Tutuila, American Samoa, by determining uniqueness, potential vulnerability, and possible viability of the tree community therein. We recorded 1,186 trees ≥ 10 cm dbh (diameter at breast height) from 37 species in 12 transects (each 10 m wide) running from edge to edge across the forest, as well as 1,332 seedlings and 991 saplings within 62 miniplots (each 25 m²). Locations within the forest of all 462 trees ≥ 30 cm dbh, of the 10 most dominant species, were then plotted. The most dominant tree species was *Pometia pinnata*. Similarity indices between the study site and other protected forests on Tutuila were very low. Spatial distributions and abundances of adult trees, as well as the dispersed distribution of seedlings and saplings, suggested low vulnerability to spatially discrete disturbances. We found evidence of potential edge effects in seedling distributions of two species. Abundances of seedlings and saplings indicated a high potential for continued recruitment of characteristic tree species. Species composition of these recruits is largely composed of characteristic primary forest species rather than secondary forest or invasive species. These results show that even very small forest fragments may have substantial value for conservation, because they can combine high within-island uniqueness with a relatively high likelihood of persistence if left undisturbed.

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HUMAN ACTIVITIES and attendant habitat fragmentation may have substantial negative effects on forested habitats (e.g., Lovejoy et al. 1983, Burkey 1995, Benítez-Malvido and Martínez-Ramos 2003). Especially in the smaller land masses of the Pacific, forest fragments are often tiny remnants of habitat. In theory, such small fragments may have substantial conservation value (e.g., Turner and Corlett 1996, Rudd et al. 2002, Teo et al. 2003). This value, however, depends on the long-term stability of the remnant forest patches. Herein we examine the justifications for conservation, and potential viability, of one such remnant forest.

The Ottoville Lowland Forest (OLF) is a fragment (ca. 12 ha) of the “Tava-Mamala Forest” (Whistler 1980) that once covered the Tafuna Plain of Tutuila Island, American Samoa. The OLF has long been thought of as unique, both because it occupies areas of largely uneroded volcanic rubble (Amerson et al. 1982*b*) and because of the presence of very rare tree species such as *Dendrocnide barveyi* (Seem.) Chew (Amerson et al. 1982*a*). For that reason, efforts to survey and preserve the area were initiated more than a decade ago, based on botanical, cultural, and zoological grounds (Trail 1993, Whistler 1993).

One prerequisite of a conservation effort is an assessment of the tree species composition in the forest. Whistler (1993) documented the plant species composition of the OLF and recommended its preservation. That survey was conducted in the aftermath of substantial disturbance caused by hurricanes Ofa (in 1990) and Val (in 1991); because of the short time interval between that survey and ours, it is likely that the tree species inventory remains valid today. For this reason, we saw no need to document the species composition of the area.

A second prerequisite is a demonstration that the area actually represents a unique habitat type. This is especially true in a country with limited land area, such as American Samoa, where about 16% of the land is already protected in the National Park of American Samoa. However, the terrestrial portion of the Tutuila unit of the national park is primarily lowland forest that occurs on hills

(Webb et al. 1999) rather than the generally flat substrate that characterizes the OLF. To compare the OLF with other forests on Tutuila, we used species occurrence and size data to determine the structure and species composition of trees within the OLF. We then compared these data between the OLF and four Long-Term Monitoring Plots (Webb and Fa'aumu 1999).

A third prerequisite is determining whether protecting a habitat patch is sufficient to preserve the existing assemblage of plant species and to ensure the survival of characteristic tree species. This is a particular concern with a single small patch, in which species may be vulnerable to many factors (e.g., Lovejoy et al. 1986, Leigh et al. 1993, Mangel and Tier 1994). Because it was impractical to address all possible threats in a single study, we focused on two that seemed the most probable:

(1) First-order (direct) threats: hurricanes and diseases. The forests of American Samoa are subject to frequent natural disturbances, both from hurricanes and tropical storms (Mueller-Dombois and Fosberg 1998) and from virulent fungal pathogens (Brooks 2002). The spatial distribution of a tree species affects its vulnerability to such threats, because hurricane damage is not uniformly distributed across space (Elmqvist et al. 1994) and fungal infection occurs from root-to-root contact (Brooks 2002). A tree species with a spatially restricted or clumped distribution may be catastrophically affected by a swath of hurricane damage or a local fungal outbreak. To assess the potential vulnerability of the OLF to these threats, we determined the spatial distribution of all large trees in the OLF.

(2) Second-order (indirect) threats: isolation and small size. The OLF is a relatively isolated patch of forest, and its small size increases the proportion of the forest that is subject to edge effects and disturbance. Such processes can have many important effects on forest fragments (Laurance and Bierregaard 1997). Direct or indirect reductions in seedling recruitment could leave a relict population of adult trees with no replacements if the patch becomes dominated by

secondary forest species (Benítez-Malvido and Martínez-Ramos 2003). We determined abundances of seedlings and saplings in the OLF to assess the potential recruits available to sustain the existing composition of the forest. We also plotted the distribution of these recruits in the forest, to assess the possibility of edge effects or very localized seedling establishment.

Therefore, the objectives of this study were threefold: (1) to test the uniqueness of the OLF by comparing its species composition with that of four other lowland forest sites on Tutuila; (2) to predict the vulnerability of the dominant tree species in the OLF to possible disturbance at three scales by determining the spatial pattern of canopy trees; (3) to predict the viability of the dominant tree species in the OLF by determining the abundances and spatial pattern of seedlings and saplings.

MATERIALS AND METHODS

This study was conducted on the island of Tutuila, American Samoa, located at approximately 170° 44' W and 14° 20' S. We felt it was important to collect spatially explicit data that sampled a substantial fraction of the largest contiguous area of the OLF (Figure 1). We created 12 transects 10 m wide (with 25 m between transect centers) along the south edge of the OLF, for a transect sampling area of 3.1 ha (~20% of the largest contiguous habitat patch). Each transect ran from the south to the north edge of the forest. Within each transect, the diameter at breast height (dbh), species, and spatial coordinates of all trees ≥ 10 cm dbh were determined. The multiple, netlike trunks of *Ficus prolixa* can produce large but possibly inaccurate values for dbh and basal area, and separate trunks from an individual tree often fell both inside and outside the transect area. We calculated the dbh in these cases around each separate trunk that fell within the transects and then summed the values for the individual trunks to create a total value per banyan. This species was omitted from most analyses, due to the high variance in these estimates, its absence from the Long-Term Monitoring

Plots (although it is widespread in ridge forests on Tutuila), and its exclusion from the calculations in Whistler (1993). We also collected dbh, species, and location data for all trees of ≥ 30 cm dbh that occurred within the OLF but outside the area covered by the transects.

One circular (2.82-m radius; 25 m²) miniplot centered on the midline of the transect was located randomly within each 50-m interval along each transect. All saplings and seedlings were counted and identified within each miniplot. Because of the irregular edges of the forest, we surveyed a total of 62 miniplots. Due to the difficulty of distinguishing *Dysoxylum maota* Reinecke and *D. samoense* A. Gray at the seedling stage, data from these two species were combined for some subsequent analyses.

All data were collected in April 2001 by a consistent set of personnel from the American Samoa Government, Department of Marine and Wildlife Resources (DMWR) and the American Samoa Community College, Land Grant. Comparisons with other lowland forests on Tutuila were based on data compiled from four 1.2-ha DMWR Long-Term Monitoring Plots. Some of those Long-Term Monitoring Plot data have been previously published (e.g., Webb and Fa'aumu 1999). Relative dominance, *t* tests, correlations, summary data analyses, similarity indices (Krebs 1999), and other manipulations of the data sets were conducted using SAS (vers. 8.1, SAS Institute, Cary, North Carolina).

Spatial patterns within each species of large canopy trees (≥ 30 cm dbh) were analyzed using SPPA (vers. 1.1.1 [Haase 1995]) software. Statistically significant deviations from a spatially random distribution were determined by comparison of the Ripley's Supremum (K) of the data to the distribution obtained from 999 randomizations of the same location data. This method is less prone to edge effects than other methods (Haase 1995), an important consideration in a study area of this size. We tested for randomness in spatial distributions at several spatial scales, because spatial point patterns are often scale dependent (Dale 1999). First, we

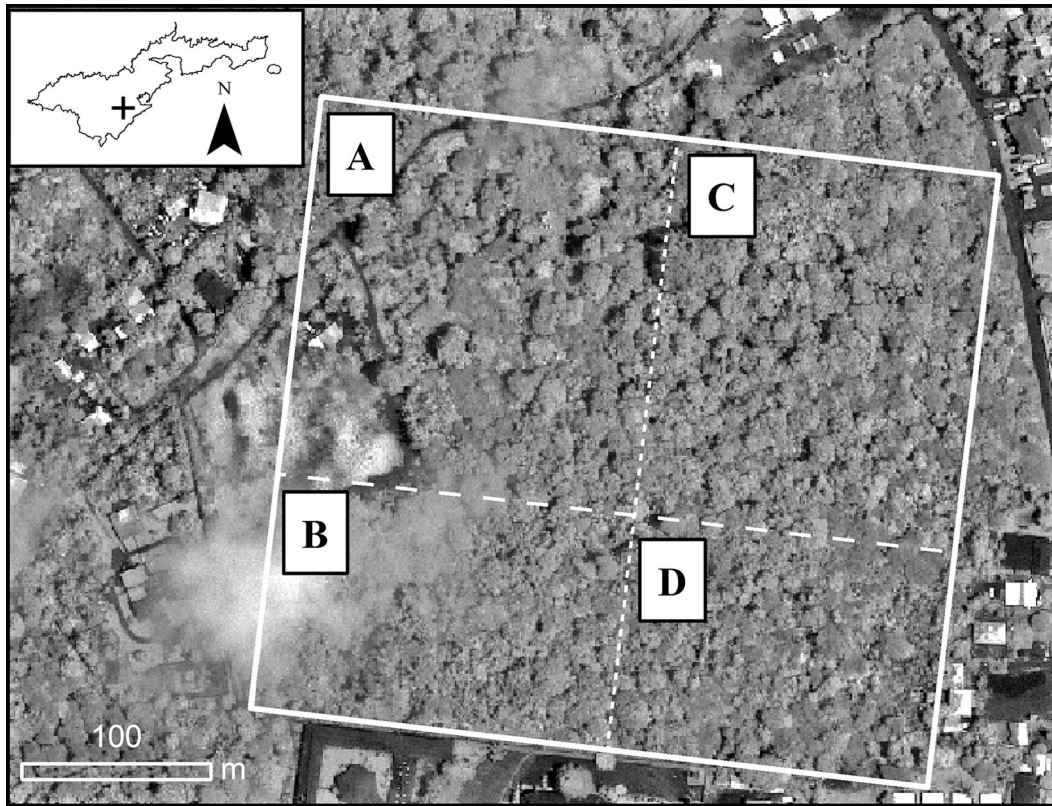


FIGURE 1. Satellite image (IKONOS, Space Imaging Systems, 2001) of the Ottoville Lowland Forest and surrounding area, with an inset showing the location of the image on Tutuila Island, American Samoa. The white rectangles are the areas used in the analyses of spatial pattern in adult trees (Table 4). A (the area enclosed within the largest rectangle, including areas B, C, and D) represents the approximate location of the spatial plots shown in Figure 2. B is the fraction of area A south of the dashed line, C the fraction east of the dotted line, and D is the intersection of areas B and C.

tested for spatial randomness in a rectangular area of the forested area we surveyed (rectangle A in Figure 1; ~12.3 ha total). Then we tested distributions within three smaller subsets of the study area, in an attempt to detect spatial heterogeneity at various spatial scales. One of these subsets removed approximately the northern half of the area from the analysis (Figure 1, B; ~4.6 ha), and another removed the western half (Figure 1, C; ~7.0 ha). The last was an area of what appeared to be some of the most intact primary forest and included only the intersection of subsets B and C (Figure 1, D; ~2.1 ha).

We calculated a simple correlation be-

tween abundances of seedlings, saplings, and adults with each species as a single datum. We used Spearman's rank correlations because of the potentially large variance in numbers of individuals among different species and excluded species for which no canopy-sized individuals could occur. We also graphically examined the size structure of the population, by plotting the number of individuals per hectare in each size class for each species. Because seedlings and saplings were only sampled in the transects, we did not use spatially explicit SPPA to test their spatial pattern. Instead, we plotted the frequency distributions of seedlings and saplings

among the miniplots, as well as the proximity of these miniplots to the edges of the OLF. We created six seedling and sapling abundance categories, representing miniplots in which we counted 1–5, 6–10, 11–15, 16–20, 21–25, and >25 individuals. We also created seven categories reflecting the distance in meters from the forest edge for a given miniplot: ≤10, 11–20, 21–30, 31–40, 41–50, 51–100, and >100.

RESULTS

We encountered a total of 1,186 individual trees from 37 species in the transects. *Ficus prolixa* Forst. ($n = 3$) was the most dominant species, in spite of their low numbers, with an estimated relative basal area of 49%. Ignoring *F. prolixa*, the three species with greatest total basal area were *Pometia pinnata* Forst., *Dysoxylum maota*, and *D. samoense* (Table 1). Our rankings differ from those of Whistler (1993) mainly in the increased prevalence of edge species (*Macaranga harveyana* Muell. Arg. and *Pipturus argenteus* [Forst. f.] Wedd.) and agroforest species (*Mangifera indica* L. and *Cocos nucifera* L.) in our samples. This difference is attributable to differences in sampling protocols (cf. Whistler [1993], who sampled a roughly circular area parallel to the perimeter of the forest), rather than a short-term shift in forest structure. The dbh of trees in the OLF is slightly but significantly greater than in other forests: $t = 2.80$, $P < .006$ (ln-transformed with Cochran's correction for unequal variances, $\mu_{OLF} = 22.5$ cm [$n = 1,186$], $\mu_{LTM} = 21.4$ cm [$n = 2,799$]).

We compared the species composition between the OLF and the four Long-Term Monitoring Plots from other locations on Tutuila (Webb and Fa'aumu 1999). We calculated the relative dominance at all five sites (Table 2). Two of the 10 most dominant species in the OLF (*Pometia pinnata* and *Pisonia umbellifera* [Forst.] Seem.) were not found in the Long-Term Monitoring Plots, and two other large forest species (*Dysoxylum maota* and *Elaeocarpus ulianus* Christoph.) were not ranked in the top 10 of any Long-Term Monitoring Plot. To test the significance of

TABLE 1

Tree Species Recorded from 12 Transects Covering ~3.1 ha of Ottoville Lowland Forest, Ranked by Basal Area (16 Other Species with Relative Dominance <1% Are Omitted)

Species	n	Relative Basal Area (%)	2001 Rank	1993 Rank ^a
<i>Ficus prolixa</i> ^b	3	49	—	—
<i>Pometia pinnata</i>	100	22	1	2
<i>Dysoxylum maota</i> ^c	181	13	2	1
<i>Dysoxylum samoense</i> ^c	74	11	3	3
<i>Cananga odorata</i>	119	9	4	7
<i>Macaranga harveyana</i>	218	8	5	12
<i>Planchonella samoensis</i>	45	7	6	4
<i>Pisonia umbellifera</i>	88	5	7	5
<i>Elaeocarpus ulianus</i>	30	4	8	11
<i>Pipturus argenteus</i>	115	4	9	27
<i>Myristica inutulis</i>	32	2	10	10
<i>Syzygium samarangense</i>	11	2	11	9
<i>Macaranga stipulosa</i>	6	1	12	6
<i>Mangifera indica</i>	6	1	13	—
<i>Cocos nucifera</i>	16	1	14	—
<i>Dendrocnide harveyi</i>	6	1	15	12
<i>Ficus godeffroyi</i> ^d	40	1	16	—
<i>Alphitonia zizyphoides</i>	5	1	17	31
<i>Artocarpus altilis</i>	11	1	18	24
<i>Rhus taitensis</i>	10	1	19	28
<i>Adenanthera pavonina</i>	13	1	20	25

^a Based on basal area reported in Whistler (1993).

^b Excluded from calculation of relative basal area for the other species (see Materials and Methods).

^c Identification was not certain for 11 individual *Dysoxylum*. Those individuals are omitted from this table, but their exclusion might alter these rankings slightly.

^d We assigned trees to this species that may have been assigned to *F. scabra* or *F. tinctoria* by Whistler (1993), although we also recorded *F. scabra* ($n = 3$) and *F. tinctoria* ($n = 10$).

this apparent difference, we calculated similarity indices (Krebs 1999) for each possible pairwise comparison between the different areas (Table 3). Sorenson's indices did not show clear differences between the species present in the Long-Term Monitoring Plots and the OLF. The single lowest similarity ($S_s = 0.35$) was between the OLF and the Vatia Long-Term Monitoring Plot, but two of the next three lowest S_s were between Long-Term Monitoring Plots, not a Long-Term Monitoring Plot and the OLF. Thus, based strictly on species occurrences (i.e., S_s), there were as many differences between the Long-Term Monitoring Plots as between

TABLE 2

The Top 10 Tree Species, Ranked by Basal Area, in Five Forested Areas on Tutuila, American Samoa

OLF	Alava LTMP ^a	Amalau LTMP ^a	Maloata LTMP	Vatia LTMP ^a
<i>Pometia pinnata</i> ^b	<i>Rhus taitensis</i>	<i>Inocarpus fagifer</i>	<i>Canarium vitiense</i>	<i>Canarium vitiense</i>
<i>Dysoxylum maota</i>	<i>Adenanthera pavonina</i>	<i>Bischofia javanica</i>	<i>Syzygium inophylloides</i>	<i>Syzygium inophylloides</i>
<i>Dysoxylum samoense</i>	<i>Myristica inutulis</i>	<i>Dysoxylum samoense</i>	<i>Calophyllum neo-ebudicum</i>	<i>Myristica inutulis</i>
<i>Cananga odorata</i>	<i>Hibiscus tiliaceus</i>	<i>Canarium vitiense</i>	<i>Myristica inutulis</i>	<i>Buchanania merrillii</i>
<i>Macaranga harveyana</i>	<i>Neonauclea forsteri</i>	<i>Garuga floribunda</i>	<i>Diospyros samoensis</i>	<i>Calophyllum neo-ebudicum</i>
<i>Planchonella samoensis</i>	<i>Canarium vitiense</i>	<i>Neonauclea forsteri</i>	<i>Inocarpus fagifer</i>	<i>Myristica hypargyrea</i>
<i>Pisonia umbellifera</i> ^b	<i>Buchanania merrillii</i>	<i>Canarium harveyi</i>	<i>Rhus taitensis</i>	<i>Canarium harveyi</i>
<i>Elaeocarpus ulianus</i>	<i>Canarium harveyi</i>	<i>Myristica inutulis</i>	<i>Hibiscus tiliaceus</i>	<i>Diospyros samoensis</i>
<i>Pipturus argenteus</i>	<i>Bischofia javanica</i>	<i>Barringtonia asiatica</i>	<i>Neonauclea forsteri</i>	<i>Planchonella samoensis</i>
<i>Myristica inutulis</i>	<i>Cananga odorata</i>	<i>Hibiscus tiliaceus</i>	<i>Alphitonia zizyphoides</i>	<i>Neonauclea forsteri</i>

Note: All the Long-Term Monitoring Plots (LTMPs) are composed of lowland ridge forest, although the Alava plot is considered a young, relatively recently disturbed area (Webb and Fa'auu 1999).

^a Located in the National Park of American Samoa.

^b No individuals of these species were recorded in the LTMPs.

TABLE 3

Similarity Indices among Pairs of Sites Listed in Table 2 (but Including All Tree Species Present in Each Community)

	OLF	Alava	Amalau	Maloata	Vatia
OLF		0.53	0.65	0.55	0.35
Alava	0.13		0.62	0.69	0.68
Amalau	0.19	0.73		0.65	0.53
Maloata	0.12	0.77	0.77		0.49
Vatia	0.13	0.66	0.72	0.90	

Note: Sorenson's Index (S_s , above the diagonal) reflects simple presence/absence of species, whereas Morisita's Index (C_i , below the diagonal) incorporates the relative abundances of the constituent species in each community. A higher number indicates increasing similarity.

the Long-Term Monitoring Plots and the OLF. Morisita's C_i , which incorporates relative abundance, showed significant differences between the OLF and the Long-Term Monitoring Plots: all four of the least-similar pairwise comparisons involve the OLF, and all were much lower than the similarity indices between pairs of Long-Term Monitoring Plots (Table 3).

Spatial patterns in eight of the 10 most common tree species of the OLF were significantly clumped at the largest scale we tested (area A in Figure 1; column A in Table 4; the entire area within an individual plot in Figure

2). This may be attributable to a disturbed area in the northwest corner of the forest, visible in Figure 1 and reflected in the open space above and to the west of a northwest diagonal in most of the panels in Figure 2, which perforce causes clumping of the tree distributions at this scale of analysis. Only *Myristica inutulis* (Rich ex A. Gray) Sinclair and *Syzygium samarangense* ([Bl.] Merr. & Perry) were randomly distributed at this scale.

The three most dominant tree species (*Pometia pinnata*, *Dysoxylum maota*, and *D. samoense*) were significantly clumped at intermediate spatial scales (Table 4), although all were widespread within the boundaries of the forest (Figure 2). Conversely, less abundant species such as *Pisonia umbellifera* and *Macaranga harveyana* were randomly distributed (Table 4). Both *Cananga odorata* (Lam.) Hook f. & Thoms. and *Elaeocarpus ulianus* were randomly distributed in some areas of the forest (e.g., subset B) but not in others (e.g., subset C) (Table 4, Figure 1).

At the smallest scale we tested (area D in Figure 1) the sample sizes of some species were quite small, but five species had more than 10 individuals. Four of these five species were randomly distributed (Table 4). The exception is *Pometia pinnata*, which is not randomly distributed at any scale we analyzed (Table 4).

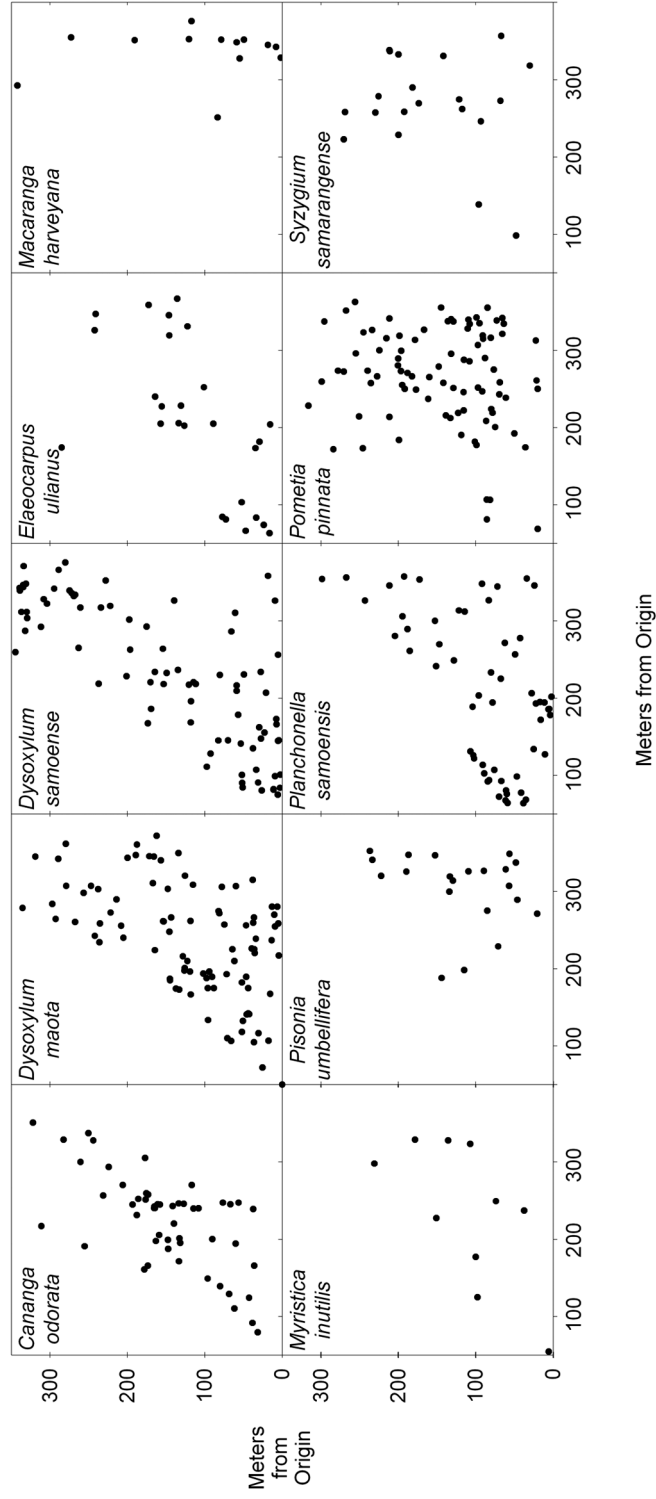


FIGURE 2. Locations in the Ottoville Lowland Forest of individual trees of ≥ 30 cm dbh from 10 species. Each panel corresponds to area A of Figure 1.

TABLE 4

Tests for Spatial Randomness of the Dominant Tree Species in the Ottonville Lowland Forest Based on Trees ≥ 30 cm dbh

Species	A (~12 ha)	B (~5 ha)	C (~7 ha)	D (~2 ha)
<i>Pometia pinnata</i>	(87)**	(44)**	(75)**	(35)**
<i>Dysoxylum maota</i>	(92)**	(55)**	(61)**	(28)ns
<i>Dysoxylum samoense</i>	(83)**	(42)**	(53)**	(14)ns
<i>Cananga odorata</i>	(52)**	(18)ns	(34)**	(8)ns
<i>Macaranga harveyana</i>	(13)**	(10)ns	(13)ns	(9)ns
<i>Planchonella samoensis</i>	(58)**	(45)**	(29)ns	(16)ns
<i>Pisonia umbellifera</i>	(21)**	(12)ns	(19)ns	(11)ns
<i>Elaeocarpus ulianus</i>	(26)**	(14)ns	(16)**	(5)ns
<i>Myristica inutilis</i>	(10)ns	(6)ns	(7)ns	(3)ns
<i>Syzygium samarangense</i>	(20)ns	(8)ns	(18)ns	(6)ns
Ten dominant species combined	(462)**	(254)**	(325)**	(135)++

Note: *Pipturus argenteus* is omitted because it has very few individuals in this size class. It is replaced by *Syzygium samarangense*. Each column represents tests only of those trees occurring within the corresponding subset (area A, B, C, or D from Figure 1) of the study area. The number of individuals is given in parentheses in each case.

** Significantly clumped spatial distribution based on Ripley's Supremum; ns, random distribution; ++, significantly overdispersed (regular) spatial distribution.

We also combined the dominant tree species for spatial analysis. At the three largest scales we found significant clumping of stems (Table 4). Conversely, trees at the most local scale were significantly overdispersed (i.e., more evenly distributed than expected by chance). Thus, when all species are considered together there is significant spatial heterogeneity within large sections of the OLF. These patterns disappear only at the smallest scales and within the most intact parts of the forest.

We counted a total of 1,322 seedlings from 34 species and 991 saplings from 30 species was counted in the miniplots, in addition

to approximately 35 non-tree and ground cover species. Abundances per hectare were significantly correlated (based on Spearman's rank correlations) between the size classes ($n = 37$ species; seedlings versus saplings: $r = 0.85$, $P < .0001$; seedlings versus canopy trees: $r = 0.53$, $P < .0009$; saplings versus canopy trees: $r = 0.60$, $P < .0001$). However, when we excluded very rare species (i.e., those for which 10 or fewer individuals, regardless of size class, were detected), only the correlation between seedlings and saplings was significant ($n = 22$, $r = 0.87$, $P < .0001$).

The overall size structure in the OLF provides evidence of a substantial potential for recruitment (Figure 3). Dominant canopy species (*Pometia pinnata*, the two *Dysoxylum* species, and *Cananga odorata*) all exhibited high abundances of both seedlings and saplings, as well as approximately continuous distributions of adult sizes. *Pisonia umbellifera*, in contrast, had a peak in abundance in the sapling and intermediate size categories. *Macaranga harveyana* and *Pipturus argenteus* had substantially fewer (or none, in the case of *P. argenteus*) seedlings than adults (Figure 3).

The majority of recruits occurred in low abundances within any particular miniplot (Figure 4). *Pometia pinnata* and *Dysoxylum* spp. were characterized by many aggregations of recruits, including some of 25 or more seedlings per miniplot, but this occurred in addition to widespread recruitment in low numbers. *Planchonella samoensis* H. J. Lam ex Christoph. and *Syzygium samarangense* occasionally occurred in clusters of 15 or more recruits per miniplot. Both *Elaeocarpus ulianus* and *Pisonia umbellifera* had low numbers of seedlings.

There was no clear-cut relationship between sapling recruitment and edges (Figure 4). All species had at least some saplings within 10 m of the forest edge. Even nominally edge species such as *Pipturus argenteus* and *Macaranga harveyana* showed some recruitment of sapling-sized individuals well away from the edges of the OLF, presumably into gaps. The distribution of seedlings was much more heterogeneous. In four species we observed no seedlings fewer than 10 m from an edge: *Elaeocarpus ulianus*, *P. argenteus*, *Piso-*

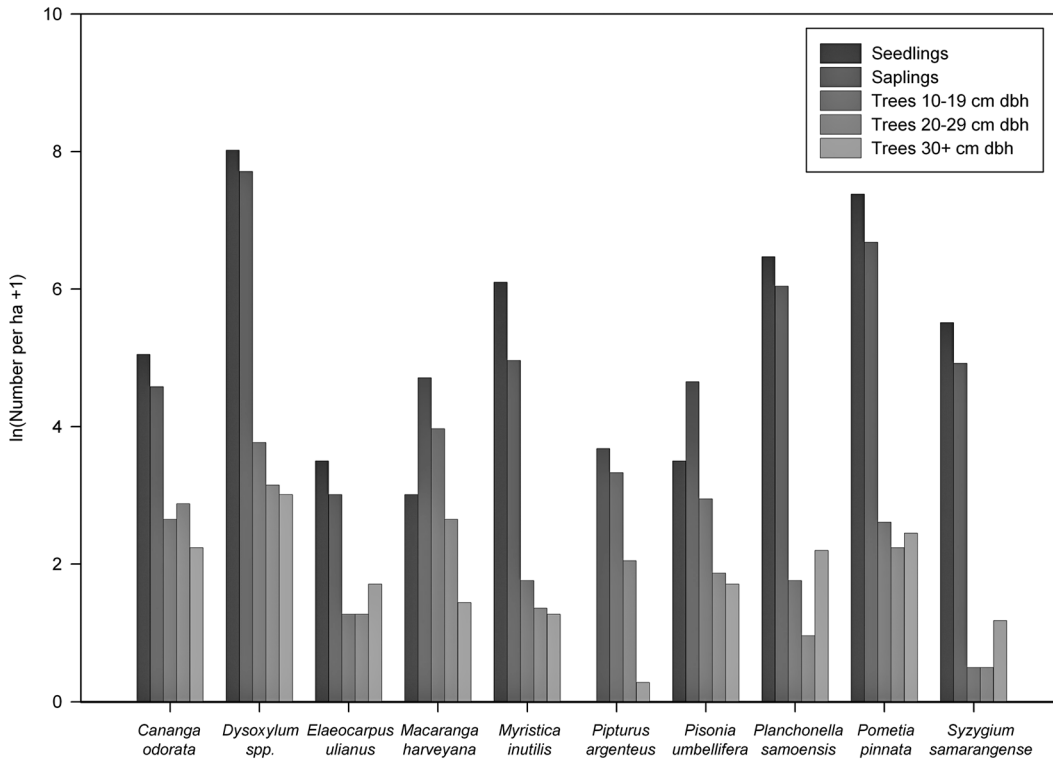


FIGURE 3. The size-class structure of 10 tree species in the Ottoville Lowland Forest. *Dysoxylum* spp. includes both *D. maota* and *D. samoense* because the seedlings of each species are difficult to distinguish.

nia umbellifera, and *Syzygium samarangense*. Conversely, both *Dysoxylum* species and *Planchonella samoensis* showed no obvious relationship between abundances of seedlings and forest edges. The most dominant species, *Pometia pinnata*, had spatially widespread recruitment, albeit with the greatest abundances farthest from the forest edge.

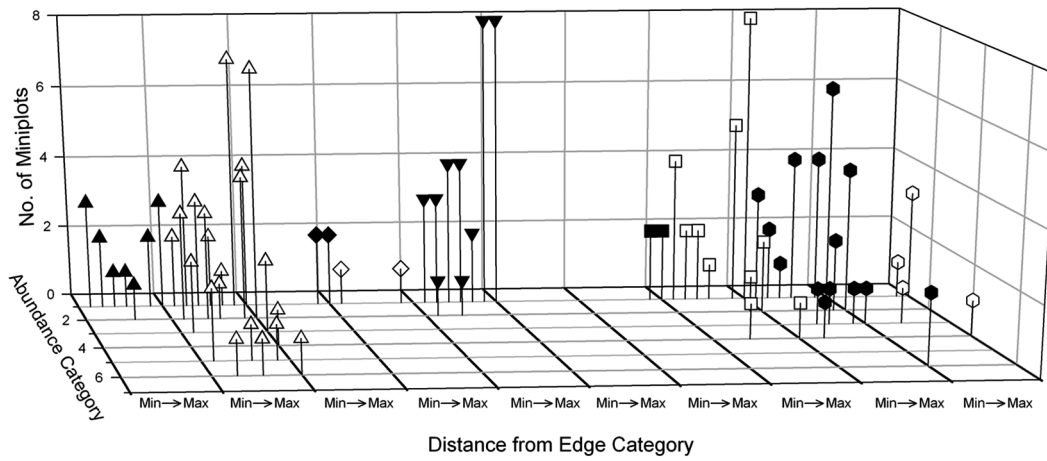
There was no consistent relationship between the spatial distributions of adults, seedlings, and saplings. For example, *Pometia pinnata* adults exhibited a clumped distribution at all scales (Table 4, Figure 2) and yet most miniplots in which it occurred had only one or a few recruits (Figure 4). Conversely, recruits were abundant and occasionally clumped in both *Planchonella samoensis* (in which large trees were common and randomly distributed at one of three scales) and

Myristica inutilis (in which large trees were rare and randomly distributed at all scales [Figures 2, 3 and Table 4]).

DISCUSSION

Our results show that the OLF represents a unique component of the vegetation of American Samoa. The composition and structure of the forest are significantly different from those found in other lowland forest sites on Tutuila. It is conceivable, of course, that patches similar to the OLF might occur elsewhere on Tutuila. However, lava flow forests (Whistler 2002) like the OLF typically occur on flat or gently sloping terrain that has a volcanic rubble substrate. Tafuna is essentially the only area of Tutuila with such a substrate that is not characterized by steep

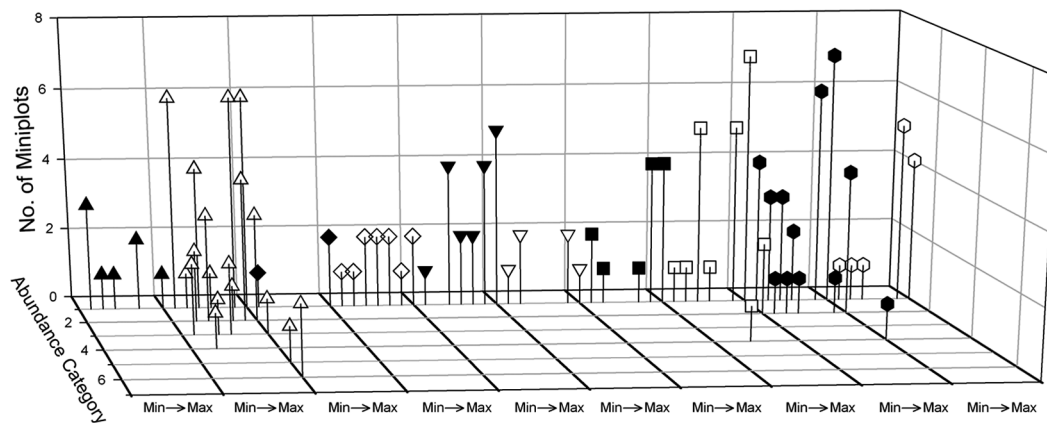
A. SEEDLINGS



Distance from Edge Category

- ▲ *Cananga odorata*
- △ *Dysoxylum* spp.
- ◆ *Elaeocarpus ulianus*
- ◇ *Macaranga harveyana*
- ▼ *Myristica inutilis*
- ▽ *Pipturus argenteus*
- *Pisonia umbellifera*
- *Planchonella samoensis*
- *Pometia pinnata*
- *Syzygium samarangense*

B. SAPLINGS



Distance from Edge Category

FIGURE 4. Spatial grouping and distance from edge of seedlings (A) and saplings (B) from 10 tree species in the Ottoville Lowland Forest, and the number of 25-m² miniplots in which they occurred. "Abundance Category" indicates spatial clumping in six categories from 1 (one to five individuals per miniplot) to 6 (>25 individuals per miniplot). "Distance from Edge Category" indicates distance from the forest edge in seven categories from Min (≤10 m) to Max (>100 m).

slopes. Indeed, of 41 plots analyzed by Amer-son et al. (1982b), *Pometia pinnata* occurred in only three: one on Ta'u Island, one in a heavily disturbed forest that has since been denuded, and one within 1 km of the OLF. Finally, Tafuna is highly disturbed, with substantial loss of forest cover since the 1960s (American Samoa Government, unpubl. aerial and satellite images). There are no other patches of native lava flow forest in Tafuna that even approach the size of the OLF (pers. obs.), in spite of the small size of the OLF itself. For these reasons, we are confident that this patch represents a true remnant and that similar areas of its size are not present elsewhere on Tutuila. Thus, the low replaceability of the OLF argues that it warrants a high conservation priority.

Our analyses also suggest that the OLF can persist as a functional and unique forest if it is protected from human disturbance. Although a large number of natural factors can affect persistence of plant populations in habitat fragments (Laurance and Bierregaard 1997), we were most concerned that direct threats to adult survival (e.g., hurricanes and diseases) and indirect threats to recruitment (e.g., edge effects) would reduce the conservation value of the OLF even if protective measures were instituted.

To predict the vulnerability of the OLF to hurricanes and diseases we tested the spatial patterns of trees and recruits. Our main assumption was that aggregations (i.e., clumping within a species) increase vulnerability of a species to spatially discrete disturbances such as hurricanes. However, spatial aggregation may be beneficial if it reduces between-group transmission of pathogens such as *Phellinus noxius* (Swinton and Anderson 1995). We found significant clumping among adult trees at several spatial scales, both within several characteristic species (including *Dysoxylum maota*, *Dysoxylum samoense*, *Elaeocarpus ulianus*, and *Pometia pinnata*) and when we tested all species together. At the smallest spatial scale, however, neither the tree community as a whole nor any species except *P. pinnata* exhibited significant clustering.

These statistics seem to warrant concern,

but we feel that the overall structure of the OLF is likely to be robust to spatially discrete threats. First, the majority of dominant tree adults either are randomly distributed (22 of 40 cases we tested) or are widespread and occur in high abundances (10 of 18 of the significantly clumped cases). High abundances presumably provide a buffer against mortality caused by hurricanes, which are unlikely to cause greater than 60% mortality (Elmqvist et al. 1994). Second, the persistence of adult trees in the OLF after hurricanes Ofa (1990) and Val (1991) suggests that these species have substantial hurricane resistance (Whittler 1993). Third, at the most local scale the entire tree community was significantly overdispersed (regularly distributed). This could ameliorate the impact of generalist pathogens such as *Phellinus noxius* (Brooks 2002) on any one tree species.

Nevertheless, there remains cause for concern in three cases. First, the local clustering of *Pometia pinnata* may increase the risk to this species from specialist pathogens or herbivores (but cf. Lieberman and Lieberman 1994). Second, the randomly distributed but relatively uncommon *Syzygium samarangense* may be at generally increased risk of local extinction (Boughton and Malvadkar 2002). Third, *Elaeocarpus ulianus* has high vulnerability within the OLF, because adults are significantly clumped at two spatial scales and occur in relatively low abundances. Any plan to preserve the OLF should perforce include a focused risk assessment of these three species.

Indirect threats such as isolation and edge effects may also affect the viability of tree populations in forest fragments. To test this possibility we examined the abundances and spatial distributions of seedlings and saplings (i.e., recruits). We assumed that overall recruit abundances were indicators of two factors important to population viability: (1) the productivity of the mature trees in the OLF and (2) the suitability of the substrate for seed set.

It is possible that seeds could have been transported to the OLF from other sites. All tree species occur elsewhere on Tutuila, and

all have fruits that can be dispersed by volant vertebrates. However, transfer from outside the OLF is unlikely to be the case for the majority of recruits, especially for those species with abundant seedlings. First, long-distance dispersal is expected to be a relatively rare phenomenon (Willson and Traveset 2000). Second, recruit abundances will not necessarily correspond with abundances of adults (Harrington et al. 1997), especially if recruitment is occurring from outside the forest. We found, however, a strong positive correlation between abundances of seedlings, saplings, and adults across all tree species.

The life-stage structure of the dominant species in the OLF suggests healthy populations of most species. There is an approximately linear decline in the frequencies between seedling, sapling, and adult stages, except in two gap-colonizing species (*Macaranga harveyana* and *Pipturus argenteus*) and in *Pisonia umbellifera*, which occurs widely but in low numbers in undisturbed forests (Amerson et al. 1982*b*). In *P. umbellifera* recent recruitment may have been, or may be becoming, limited, a situation that warrants further study.

The spatial distributions of seedlings and saplings show potential edge effects in two of the dominant tree species: *Elaeocarpus ulianus* and *Pisonia umbellifera*. In those two species we found no seedlings within 50 m of an edge of the OLF. However, both species occur in relatively low abundances and both have saplings in close proximity to edges. Because our data are from random samples, systematic or focal sampling of these species would be prudent when considering conservation measures for the OLF. Nevertheless, our results suggest potential edge effects in 20% of the dominant species, in spite of the apparent overall health of the OLF. These data argue against any incursions that might increase the proportion of edge.

Spatial clustering of recruits is primarily a concern in species with relatively few individuals or if recruits are exclusively found in groups. Because this was not the case in the OLF, there appears to be little risk that a spatially discrete disturbance such as a hurricane would dramatically alter recruitment patterns

in the forest. However, such disturbances might potentially have substantial impacts on species that have very low abundances of recruits (i.e., *E. ulianus* and *P. umbellifera*) regardless of their dispersion in space.

CONCLUSIONS

Our results show that in spite of its small size and relative isolation, the OLF has a considerable value for conservation. It contains a substantially unique flora. The dominant tree species generally appear capable of long-term viability. However, the data also suggest an inherent fragility, with low recruit abundances and possible edge effects in at least two of the dominant species.

Tree species may also exhibit deleterious effects of fragmentation over long time scales (Ledig 1986, Brook et al. 2002). Our analyses are based on the forest as it is currently constituted. We cannot predict with certainty the performance of the tree species therein over the long term or if the fragmentation of the forest were to increase. However, our findings argue that small remnant patches of habitat may indeed be worth conserving, especially in tropical island ecosystems such as American Samoa that have generalist, volant dispersers and pollinators.

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