

# GARDENS GONE WILD: HUMAN IMPACTS ON FOREST STRUCTURE AND REGENERATION ON MO'OREA, FRENCH POLYNESIA

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*Abstract.* The islands of the South Pacific are filled with examples of early human populations manipulating natural resources in order to improve their lives. On islands like Tahiti and Mo'orea in French Polynesia, the evidence of pre-historic human activity can still be seen in the form of archaeological sites and forest composition. This study examined the relationship between humans and the forest by surveying seedlings and mature trees on three treatment types: disturbed archaeological sites (cleared to bare mineral soil in 2008), non-disturbed pre-historic settlement structures, and control sites with no pre-historic structures. Based on the distribution of seedlings across the three sites, species were separated into three categories: disturbance tolerant, disturbance intolerant, and no preference. Combining mature plant and seedling data showed that species composition did not vary with any statistical significance across the three treatment types by introduction method, propagation method, status, or canopy cover. Diversity indices for each treatment type showed little variation in diversity between the treatments. Future research on a larger geographical scale may reveal more significant variation in forest composition associated with pre-historic human activity.

*Key words:* Mo'orea, French Polynesia, vegetation, forestry, forest composition, forest dynamics

## INTRODUCTION

In contemporary thinking, the term "forest" suggests something natural and wild; a forest is a place where human influence has not yet reached. This view, while romantic and pleasant, is hardly true of all (or even most) forests. In reality, forests have been heavily influenced by indigenous human populations for thousands of years all around the world (Anderson 2005, Fairhead and Leach 2002, Huntsinger and McCaffrey 1994), especially those on the islands of the South Pacific (Kirch 2009a). As islands, they lacked room for population expansion, yet the relatively little effort it took to find and grow food meant pre-European populations were often very dense. This resulted in an ongoing need for resource development, exploitation, and use, which was responsible for drastic

changes in these island ecosystems (Kirch 2009a).

When human populations first arrived in French Polynesia c. 1350 years BP (Kirch 2009b), forests on the high islands of Tahiti and Mo'orea looked quite unlike the forests of today (Lepofsky 2003). Indigenous tree species such as *Hibiscus tiliaceus*, *Ficus prolixa*, *Ficus tinctoria*, *Barringtonia asiatica*, and *Neonauclea forsteri* dominated (Lepofsky et al. 1996). These species today (with the exception of *Hibiscus tiliaceus*) are found only occasionally in a forest dominated by *Inocarpus fagifer*, *Syzygium malaccense*, *Aleurites moluccana*, and *Hibiscus tiliaceus* (Lepofsky et al. 1996). This change in forest composition is directly attributable to anthropogenic activities.

The indigenous tree species of Polynesia provided little in the way of subsistence for the early colonizers of the islands (Barrau

1961, Rolett 2008). When the early inhabitants of the Pacific moved east from Tonga and Samoa in double-hulled canoes, they brought the crops they had been cultivating on other islands with them (Barrau 1961, Kirch 2009b). These assorted food crops, referred to as “canoe plants,” were the basis for the vast majority of agricultural systems on Polynesia’s high islands (Barrau 1961), and became an essential source of food for growing populations (Kirch 2009a).

By A.D. 1200-1300, many of these canoe plants were already “well established” (Lepofsky et al. 1996) on the island of Mo’orea. Notable introductions included *Inocarpus fagifer*, *Syzygium malaccense*, *Artocarpus altilis*, and *Aleurites moluccana* (Lepofsky et al. 1996). Large population sizes (Kirch 2009a) and the increasing need for subsistence led to the development of the upper ‘Opunohu Valley for agricultural purposes, sometime after A.D. 600 (Lepofsky et al. 1996). Extensive human activity in this part of the valley is evidenced by the great density of *marae*, housing structures, and terracing researched extensively by archaeologists in recent decades.

When Europeans arrived in the Society Islands approximately 400 years after the development of the ‘Opunohu Valley, (Barrau 1961) they introduced new cultigens and agricultural techniques. The difficult work of terracing and irrigation in the upper valley became obsolete (Barrau 1961, Lepofsky 2003). Although much of what present-day populations (referred to as Maohi) subsist on is imported, most households on Tahiti and Mo’orea still cultivate house gardens (Barrau 1961, Lepofsky 2003), and have moved from the upper valley back down to the coastal areas (Barrau 1961).

The forest in the mid-elevations of the ‘Opunohu Valley is now nearly entirely secondary forest characterized by a mix of native species, with “assorted cultigens” (Lepofsky et al. 1996, Lepofsky 2003) that were planted by pre-European peoples that have now become naturalized, and non-canoe-

plants that have been introduced more recently. The naturalization of the species from these abandoned agricultural fields has created a rather singular forest on Mo’orea, where the dominant forest species can be directly linked to human activity on the island, yet there is a thriving ecosystem that manages to exist without continued human influence.

As a result, the forest structure on Mo’orea includes three distinct groups that include nearly every species: (1) indigenous species, (2) Polynesian introductions, and (3) European introductions. Present-day forest composition in the upper ‘Opunohu valley is essentially a mix of all three, with Polynesian introductions dominant (Lepofsky et al. 1996), and indigenous and European introductions interspersed throughout. This study examines the influence of humans on the forest from two approaches: a forest dynamics study and a forest composition study.

#### *Research Approach* *Forest Dynamics Study*

To understand forest dynamics on Mo’orea, three aspects were studied. The first examined recently disturbed areas to determine the species composition of forest regeneration in order to understand how the dominance of Polynesian introduced species is likely to change with the addition of more recent European introductions. This was done by comparing vegetation on three different areas: (1) the “natural” forest, (2) pre-historic structures that have not been recently disturbed, and (3) pre-historic structures that were recently cleared to bare mineral soil and then allowed to regenerate.

One major factor expected to contribute to the species composition of regeneration and the influence of humans in all three areas is propagation method. Many of the canoe plants now naturalized in the secondary forest have large seeds/fruits (logically so as they were used for sustenance by pre-European

populations). These have a harder time dispersing over long distances, compared to many of the recent introductions, which are frequently wind dispersed (*Falacartaria moluccana*, *Spathodea campanulata*, *Leucaena leucocephala*) and have seeds that can travel far with little effort. After surveying the vegetation on and around these sites, we used the rate of propagation and germination of indigenous, Polynesian introduced, and European introduced species to determine the “stability” of the current forest structure on Mo’orea.

### *Forest Composition Study*

The second focus of this study was to discover the extent to which this past human influence was still a factor in present day forest structure. As noted by Kirch in 2009, many of the impacts pre-European populations had on the islands of the South Pacific were irreversible (Kirch 2009a), which implies that they can still be seen today. While this is certainly true of forest structure on Mo’orea at a larger scale, this study sought to use the life histories of certain Polynesian introduced species and pre-historic Polynesian settlement structures to find more subtle variations in species composition linked to prehistoric Polynesian activity.

To test this, the rate of occurrence of species of significance to Polynesian culture was compared on structures (non-treated sites) and non-structured areas (control sites). Although some species are now ubiquitous in the ‘Opunohu Valley, others are not, due to variations in reproduction, for example ti (*Cordyline fruticosa*) and breadfruit (*Artocarpus altilis*), which are sterile in Eastern Polynesia (Hinkle 2007). Vegetation differences were analyzed using what is known about Polynesian plant preferences and the ability of those plants to disperse to see if differences could be attributed to Polynesian management. Additional analyses including edge effect and canopy cover were also done

to test alternative variables that may have influenced forest composition.

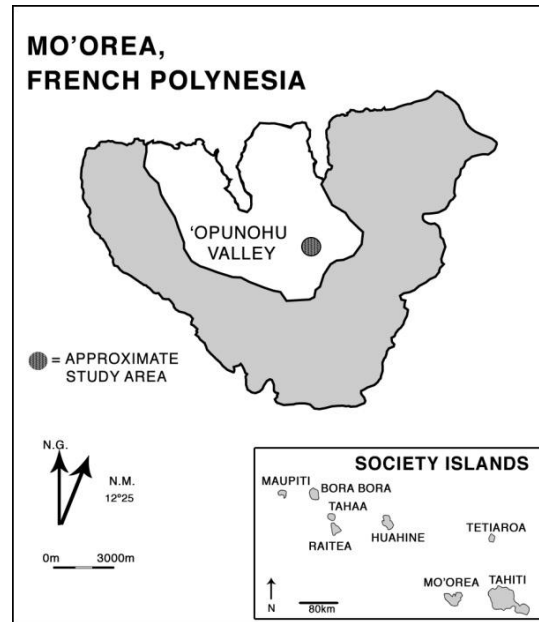


FIG. 1. Map of Mo’orea and the Society Islands indicating study area.

## METHODS

### *Site description*

All eighteen sites were located in the ‘Opunohu Valley on the island of Mo’orea, French Polynesia (17°30’S, 149°50’W) (Figure 1). Sampling was done between September and November 2010. The ‘Opunohu Valley is located in the center of the island (Fig. 1). Sites were chosen based on previous archaeological research done in 2008 by Dr. Jennifer G. Kahn and Dr. Patrick V. Kirch. This complex of pre-historic structures, referred to as ScMo-124, includes *marae* (temples), housing structures, and terraces built by pre-European peoples for worship, agriculture, and dwelling. As part of Kahn and Kirch’s research, many structures within the 124-complex (Fig. 2) were cleared to bare mineral soil in 2008 (with the exception of large woody plants that would require a chainsaw to remove). Six of these sites were chosen as “disturbed” sites for this study

(*cleared*). For comparison, six more sites that contained pre-historic structures were chosen that had no clearing on them (*non-treated*). As controls, six nearby sites were chosen that had no structures (*control*). All sites were on varying structure types (Fig. 2). Cleared sites were chosen based on their size and structure type. Non-treated and control sites were picked based on their proximity to cleared sites to help control for externalities.

#### *Data Collection*

Data collection was separated into two types: “seedling” and “mature.” Seedlings (non-reproductive plants) were only sampled on structures. Each structure was separated into multiple strata, which were two-meter wide “bands” starting from the edge and moving inward. Within each band, two two-meter by two-meter plots were randomly placed. Placement of plots was randomized using a compass from the center of each site to find a random azimuth. All plants inside each plot were tallied by species. Outside, all mature (of reproductive age) plants within a ten-meter perimeter of the inside area were tallied. Additionally, all mature trees within the inside area were recorded.

#### *Forest Dynamics Study*

Seedling and mature plant data collected was converted to plants per square meter. The average number of individuals per square meter by species by treatment type (cleared, control, no treatment) was used to analyze differences in the distribution of plants in each treatment type.

#### *Forest Composition Study*

Data on the life history of each species was gathered to establish the expected distribution of each species. These life history characteristics include: (1) introduction method, (2) status, and (3) propagation method. The average density of both seedlings and mature plants on non-treated (structure) and control (non-structured) treatments was compared in order to determine if anthropogenic activity or other plant characteristics can explain species composition. The significance of each variable was tested using an ANOVA in JMP 9.

Other factors that could potentially influence forest composition, including canopy cover and edge effects, were also measured. Canopy cover was recorded at all sites using a spherical densiometer. Measurements were taken at the center of each site tree times and averaged. The average canopy cover at each site was used to determine the average canopy cover that each species was found most frequently in.

Additionally, seedling and mature plant data from each site was analyzed to determine if there was a significant difference in plant diversity for each treatment type. The level of diversity was calculated using Simpson’s Diversity Index, which uses the equation:

$$D = 1 - \frac{\sum_{i=1}^s (n_i(n_i - 1))}{N(N - 1)}$$

where D is the diversity index (a value between zero and one, where one represents infinite diversity and zero represents none), n is the number of individuals of each species, N is the total number of individuals found, and S is the number of species.

## RESULTS

#### *Forest Dynamics Study*

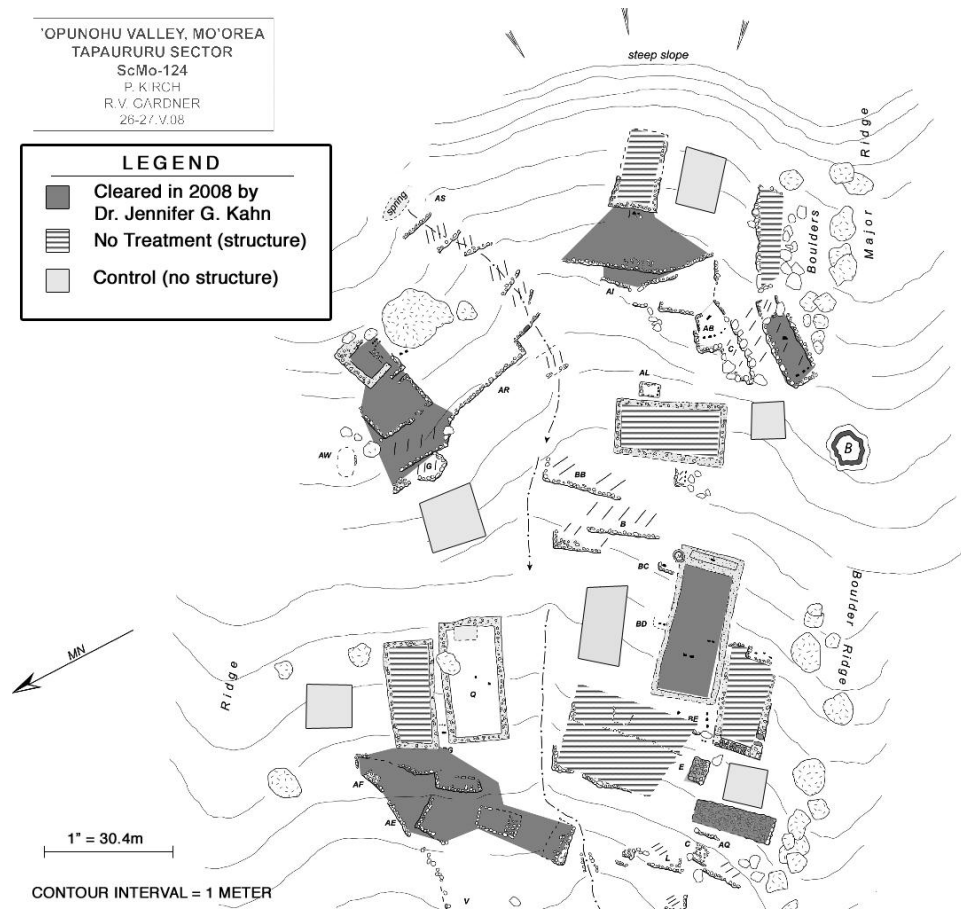


FIG. 2. Map of study sites by treatment type. Base map provided courtesy of Dr. Patrick V. Kirch.

Using variation in seedling distribution, plants were separated into three categories: disturbance tolerant (1), disturbance intolerant (2), and no preference (3). Species placed in the disturbance tolerant category had a higher rate of occurrence at cleared sites than at both control and non-treated sites. Disturbance intolerant species were those that had a lower

rate of occurrence at cleared sites than control or non-treated. Species that had no preference did not have a statistically significant difference in distribution between the three sites.

### 1.1 Disturbance Tolerant Species

TABLE 1. Average seedling densities of disturbance tolerant species. Values for cleared sites were higher than values for control and non-treated sites.

Species	Cleared (seedlings/m <sup>2</sup> )	Control (seedlings/m <sup>2</sup> )	No Treatment (seedlings/m <sup>2</sup> )	Species Description*
<i>Aleurites moluccana</i>	0.146	0.021	0.083	N, P, A/S
<i>Alpinia purpurata</i>	2.479	0.292	0.271	C, P, V
<i>Cananga odorata</i>	0.042	0.000	0.021	N, E, A
<i>Neonauclea forsteri</i>	0.375	0.000	0.063	I, W
<i>Rubus rosifolius</i>	0.354	0.000	0.000	IV, E, A
<i>Spathodea campanulata</i>	0.646	0.000	0.146	IV, E, W

\*Key:

I = Indigenous, N = Naturalized, IV = Invasive, C = Cultivated, P = Polynesian Introduction, E = European Introduction, A = Animal dispersal, S = Seedfall, V = Vegetative, W = Wind

Species that fit this category have a higher average density of seedlings (immature plants) per square meter in the cleared treatment sites than either of the other treatments. This category includes *Aleurites moluccana*, *Alpina pupurata*, *Cananga odorata*, *Neonauclea forsteri*, *Rubus rosifolius*, and *Spathodea campanulata* (Table 1). For some species, the distribution difference is very large. *Alpina pupurata* has an average density of 2.479 saplings/m<sup>2</sup> among cleared sites, but only an average density of 0.292 saplings/m<sup>2</sup> and 0.271 saplings/m<sup>2</sup> at control and non-treated sites respectively. Others have a relatively small difference in distribution, such as *Aleurites moluccana*, which have average densities of 0.125 saplings/m<sup>2</sup>, 0.021, and 0.083 saplings/m<sup>2</sup> at cleared, control, and non-treated sites. This category includes indigenous, naturalized, and invasive species.

### 1.2 Disturbance Intolerant

Disturbance intolerant species were found to have lower average density at cleared sites than at both control and non-treated sites. The four species that fit this requirement are *Castilla elastica*, *Inocarpus fagifer*, and *Syzygium malaccense*, three naturalized/invasive species (Table 2).

### 1.3 No preference

Of the remaining species found, three were found to have no preference for disturbed or non-disturbed areas. These species have an average density greater than zero for all three treatments, but do not fit either of the other two categories. One species of note, *Miconia calvescens*, a highly invasive recent introduction, has an identical

TABLE 2. Average seedling densities of disturbance intolerant species. Values for cleared sites are lower than values for control and non-treated sites.

Species	Cleared (seedlings/m <sup>2</sup> )	Control (seedlings/m <sup>2</sup> )	No Treatment (seedlings/m <sup>2</sup> )	Species Description*
<i>Castilla elastica</i>	0.021	0.042	0.050	N, E, A
<i>Inocarpus fagifer</i>	1.729	5.000	3.708	N, P, S
<i>Syzygium malaccense</i>	0.571	3.708	1.500	N, P, S

\*Key:

I = Indigenous, N = Naturalized, IV = Invasive, C = Cultivated, P = Polynesian Introduction, E = European Introduction, A = Animal dispersal, S = Seedfall, V = Vegetative, W = Wind

TABLE 3. Average seedling densities of species with no preference for disturbed or non-disturbed areas. Values for all three site types are greater than zero, but do not fit into the disturbance tolerant or intolerant categories.

Species	Cleared (seedlings/m <sup>2</sup> )	Control (seedlings/m <sup>2</sup> )	No Treatment (seedlings/m <sup>2</sup> )	Species Description*
<i>Angiopteris evecta</i>	0.042	0.042	0.063	I, V/W
<i>Hibiscus tiliaceus sub. tiliaceus</i>	0.125	0.125	0.313	N, P, V/S
<i>Miconia calvescens</i>	0.104	0.104	0.104	IV, E, A/S

\*Key:

I = Indigenous, N = Naturalized, IV = Invasive, C = Cultivated, P = Polynesian Introduction, E = European Introduction, A = Animal dispersal, S = Seedfall, V = Vegetative, W = Wind

distribution across all three treatments. The other two, *Hibiscus tillaceus sub. tiliaceus* and *Angiopteris evecta*, both native, have an identical average density for the cleared and control treatments, and a slightly higher density for non-treated sites (Table 3).

*Forest Composition Study*  
2.1 Introduction method

Average plant density (both seedlings and adults) varied by treatment type for all three introduction methods (Table 4). For European introduced species, the average density on cleared sites was nearly seven times higher than the average density on control sites (0.152 plants/m<sup>2</sup> to 0.023 plants/m<sup>2</sup>), and was also very high when compared to the density on non-treated sites. Indigenous species had about the same average density on cleared and non-treated sites, which was about double the average density on control sites.

Polynesian introduced species had a distribution completely opposite that of indigenous species—densities were very similar on cleared and non-treated sites, and the control site had about double the average density. An ANOVA of treatment and introduction yielded a p-value of 0.539 (Table 7), indicating this variation was not statistically significant.

2.2 Propagation Method

Animal, vegetative, and wind propagated species appeared to have the most successful colonization at cleared sites, while seedfall propagated species had the lowest average density on cleared sites (Table 5). Wind and animal propagated species had the lowest densities on control sites, while vegetative species had about the same average density on control and non-treated sites. ANOVA

TABLE 4. Average plant densities by treatment by introduction method.

Introduction Method	Cleared (plants/m <sup>2</sup> )	Control (plants/m <sup>2</sup> )	No Treatment (plants/m <sup>2</sup> )
European Introduction	0.152	0.023	0.043
Indigenous	0.110	0.047	0.103
Polynesian Introduction	0.756	1.366	0.856

TABLE 5. Average plant densities by treatment by propagation method.

Propagation Method	Cleared (plants/m <sup>2</sup> )	Control (plants/m <sup>2</sup> )	No Treatment (plants/m <sup>2</sup> )
Animal	0.122	0.032	0.054
Seedfall	0.500	1.800	1.068
Vegetative	0.362	0.103	0.134
Wind	0.518	0.006	0.108

TABLE 6. Average plant densities by treatment by status.

Status	Cleared (plants/m <sup>2</sup> )	Control (plants/m <sup>2</sup> )	No Treatment (plants/m <sup>2</sup> )
Cultivated	2.628	0.546	0.433
Indigenous	0.110	0.047	0.103
Naturalized	0.203	0.520	0.407
Invasive	0.463	1.000	0.458

analysis for treatment and propagation method yielded a p-value of 0.089 (Table 7).

### 2.3 Status

The cultivated species, *Alpinia purpurata*, had the highest density on cleared sites, with a much lower density on control and non-treated sites. Indigenous species had a similar average density on cleared and non-treated sites (about 0.1 plants/m<sup>2</sup>), with an average density on control sites of about half (0.047 plants/m<sup>2</sup>). Naturalized species had a higher average density on control and non-treated sites than cleared. Invasive species had the highest average density on control sites, which was nearly double the average density on cleared and non-treated sites. The ANOVA for treatment type and status yielded a p-value of 0.307 (Table 7), which makes this interaction not statistically significant.

### 2.4 Canopy Cover

Canopy cover values for saplings found at cleared sites indicate that some species, such as *Rubus rosifolius*, with an average of 45%, have very little shade tolerance, while others such as *Castilla elastica*, with an average of 84% are found frequently in denser forests. (Table 8).

TABLE 8. Average percent canopy cover weighted by species

Species ID	Average % Canopy Cover/Species (weighted)
<i>Aleurites moluccana</i>	71
<i>Alocasia macrorrhizos</i>	80
<i>Alpinia purpurata</i>	59
<i>Angiopteris evecta</i>	72
<i>Cananga odorata</i>	75
<i>Castilla elastica</i>	84
<i>Hibiscus tiliaceus sub.</i> <i>Tiliaceus</i>	49
<i>Inocarpus fagifer</i>	72
<i>Jossinia reinwardtiana</i>	71
<i>Miconia calvescens</i>	64
<i>Neonauclea forsteri</i>	70
<i>Rubus rosifolius</i>	45
<i>Spathodea campanulata</i>	67
<i>Syzygium malaccense</i>	68

TABLE 7. ANOVA values for each variable. Statistical tests were done in JMP 9.

Source	Number of Parameters	Degrees of Freedom	Sum of Squares	F Ratio	Prob > F
Treatment	2	2	4.752807	0.907	0.4046
Propagation	3	3	65.790693	8.8048	<.0001
Introduction	2	2	70.144396	13.9597	<.0001
Status	4	4	29.141696	2.7807	0.0267
Treatment*Introduction	4	4	7.83267	0.7794	0.5391
Treatment*Propagation	6	6	27.652561	1.8504	0.0885
Treatment*Status	8	8	24.836285	1.1849	0.307



## 2.5 Diversity Indices

The Simpson's Diversity Index values averaged for each treatment type indicate that the cleared and non-treated treatments have a slightly higher diversity index than the control treatment (Table 9).

TABLE 9. Simpson's Diversity Index values by treatment.

Type	Average Diversity Index	Standard Deviation
Cleared	0.655	0.133
Control	0.553	0.227
No treatment	0.690	0.098

## DISCUSSION

### *Forest Dynamics Study*

#### *1.1 Disturbance tolerant species*

Disturbance is defined as "any relatively discrete even in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (Pickett & White 1985). A disturbance tolerant species is thus a species that has the ability to either persist throughout a disturbance, or a species that can quickly re-establish in the post-disturbance ecosystem. In the context of this study, the disturbance was the clearing of vegetation on the archaeological sites in 2008, and a disturbance tolerant species is one that is able to easily re-colonize these areas.

Disturbance, especially types not integral to normal ecosystem function (fire as a normal disturbance in the California chaparral, for example), is also closely linked to the success of invasive species (Hobbs and Huenneke 1992). Frequently these areas are difficult for indigenous plants to colonize, as they have not evolved to respond to atypical disturbances. Invasive species on the other hand may have

traits that allow them to thrive under post-disturbance conditions, allowing them to overtake indigenous species and successfully establish in a new area (Bellingham et al. 2009). It has even been stated that it may be impossible for exotic species to invade new ecosystems without some kind of disturbance to get them started (Lake and Leishman 2004).

The six species categorized as disturbance tolerant appear to fit this description, for the most part. Five of the six are introduced, and all have propagation methods typically associated with plants with high propagation pressure. However, the presence of *Neonauclea forsteri*, a wind dispersed, indigenous species initially seems somewhat out of place. Yet examining the life history of *Neonauclea forsteri* may explain why.

The term "indigenous," while used for both mainland and island species, does not necessarily have the same implications for both areas. The reality is that each and every plant species colonized that island at some point in time. The only real difference between indigenous species and introduced is that the indigenous species colonized and established on the islands independently, where naturalized and invasive species had human assistance. This phenomenon suggests that in order for the first indigenous species to colonize successfully, they may have had traits similar to those generally attributed to invasive species on continents.

*Neonauclea forsteri* is one of the few indigenous tree species that is wind dispersed. When the agricultural systems of the 'Opunohu Valley were abandoned post-European arrival approximately 250 years ago (Kirch 2009), indigenous species would have had to compete in these disturbed areas with Polynesian introduced species (that had been aided by humans) to colonize the freshly abandoned land. As most Polynesian introductions were used for food crops, they tend to propagate vegetatively or by seedfall. *Neonauclea forsteri's* ability to disperse by wind, allowing it to spread further than the Polynesian introductions and more quickly,

may be why it is able to maintain a strong presence with these species despite their dominance in the area.

In addition to having a relatively uncommon method of dispersal compared to Polynesian introduced species, *Neonauclea forsteri* has an entirely unique life history. As a seedling, it is epiphytic on rocks (Butaud et al. 2008). In the field, all *Neonauclea forsteri* seedlings observed were growing on a rock, and most adult trees appeared to have a large rock entangled in their roots. This unique ability allows *Neonauclea forsteri* circumvent competition with most other tree species, including other wind dispersed species. This suggests that while *Neonauclea forsteri* may never become a dominant species in the forest of the 'Opunohu Valley, it is not likely to be completely eradicated by competition either.

The other species in this category, *Aleurites moluccana*, *Alpina purpurata*, *Cananga odorata*, *Rubus rosifolius*, and *Spathodea campanulata*, are a mix of naturalized and invasive, Polynesian introduction and European introduction. *Aleurites moluccana* and *Alpina purpurata*, the Polynesian introduced species, both have propagation methods aside from seedfall, which may explain their ability to colonize disturbed areas with relative ease. These two species are also described as naturalized. The relatively low densities at which these species were found compared to *Rubus rosifolius* and *Spathodea campanulata* may illustrate the difference between what is considered naturalized and invasive by Butaud et al.—unlike the naturalized species, *Rubus rosifolius* and *Spathodea campanulata* were found at high enough densities at some sites to inhibit the growth of most other species.

### 1.2 Disturbance Intolerant Species

Unlike the disturbance tolerant species, disturbance intolerant species were relatively similar in terms of life history. All three were introduced, one by Europeans and the other

two by Polynesians. The two Polynesian species in this category, *Inocarpus fagifer* and *Syzygium malaccense*, both propagate by seedfall, and are considered dominant species in the 'Opunohu Valley (Lepofsky et al. 1996). Returning to previously mentioned disturbance theory, the species that typically fit into this category are native species that have not adapted to disturbance. While the clearing of vegetation for archaeological sites is not a typical disturbance for any ecosystem, it is interesting to note that even indigenous species appeared to deal with this disturbance better than these two common Polynesian introductions.

### 1.3 No preference

Two of the species in this category, *Angiopteris evecta* and *Hibiscus tiliaceus sub. tiliaceus* are indigenous. *Hibiscus tiliaceus sub. tiliaceus* is still considered a dominant species in the 'Opunohu Valley (Lepofsky et al. 1996). Like *Neonauclea forsteri*, *Hibiscus tiliaceus sub. tiliaceus* has a relatively unique life history. According to Butaud et al., *Hibiscus tiliaceus sub. Tiliaceus* is likely dominant due to its superior “capacity of recolonization” (Butaud et al. 2008)—*Hibiscus tiliaceus sub. tiliaceus* has branches that can double as roots, and will create new shoots nearly anywhere. It will often grow so densely that other species cannot compete. This may also explain why it did not fit into the disturbance tolerant category as perhaps would be expected, as it is nearly impossible to define what one “seedling” or even tree of *Hibiscus tiliaceus sub. tiliaceus* is.

*Angiopteris evecta* is one of the few non-tree species included in this study. As it is essentially a giant fern, it is not likely that this species would be subject to the same level of competitive interaction that tree species deal with. This explains its relatively even distribution across all treatments.

The third species in this category, *Miconia calvoescens*, has recently been the subject of

much scientific interest. Often referred to as "The Purple Botanical Plague," it holds the dubious honor of being the most prevalent and disruptive invasive species in the Society Islands. It was introduced in 1937 from a botanical garden, but was not much of a concern until around 1970 (Meyer and Florence 1996). It is known for its ability to grow with great virility virtually everywhere on the islands of Tahiti and Mo'orea, and forms monotypic stands, displacing all other species. In this study, *Miconia calvescens* was found at exactly the same densities across all three treatments. While this is quite dissimilar to the other two invasive species of potential concern mentioned earlier (*Rubus rosifolius* and *Spathodea campanulata*), the ubiquitous presence of this species explains why it is of even greater concern. While the other two appear to require disturbance to successfully establish, *Miconia calvescens* can flourish in all areas, unaided by disturbance. Although not found in especially high densities in this study area at this point in time, there is a good chance that within the next few years it may be a significant problem.

### *Forest Composition Study*

#### *2.1 Introduction method*

Although introduction method is not typically a factor that would contribute to forest composition, the unique aspects of forest history in the 'Opunohu Valley suggest that introduction method may have some impact. As mentioned earlier, when the agricultural systems in the upper valley were abandoned, the species that remained were Polynesian introduced arboricultural and horticultural crops (Barrau 1961, Lepofsky et al. 1996, Lepofsky 2003). In addition to having received human assistance in colonizing these areas, many of these species quickly naturalized and spread throughout the entire valley (Lepofsky et al. 1996).

The hypothesis that Polynesian introduced species would be found at higher

densities near pre-historic structures ultimately wound up being statistically insignificant, however it is interesting to note that the highest average density by far of Polynesian introduced species was found on the control treatment (Table 4). Conversely, both European introduced and indigenous species had the lowest average density at control sites. This may be due to the fact that Polynesian introductions are clearly dominant in this area (Lepofsky et al. 1996). At all three treatments the density of Polynesian introduced species was much higher than that of European or indigenous species. The fact that these species have had such success in this area may explain why there was no statistically significant variation between introduction method and treatment type.

The density of pre-historic structures in this area (Fig. 2) may also have contributed to the ubiquitous nature of these Polynesian introductions, and further explain the lack of detectable difference in their distribution. Despite this, future research encompassing a larger study area may reveal differences in the density of Polynesian introductions based on human influence. While rotation ages of forests in continental North America are regularly upwards of 80 years, this length of time in tropical ecosystems can have significantly more change. It is entirely possible that in the 250 years since Polynesian populations moved to the coast, this region of the 'Opunohu Valley has become saturated by Polynesian introductions. Comparison of forest composition across multiple valleys where human populations were not as dense may tell a different story.

#### *2.2 Propagation method*

Propagation has been a frequent topic of research in the last few decades. Most of this research has come from attempting to generalize the characteristics of invasive species (Rejmánek and Richardson 1996, Lonsdale 1999). Research has shown

repeatedly that the most accurate predictor of invasive success is propagule pressure, which relates to both propagule size and the number of propagule events (Lockwood et al. 2005). Although little is known about propagule pressure for these species, the propagation method itself can be important in determining the ability of species to spread to new areas.

It can be assumed that species that propagate via animal or wind can disperse further distances more easily than those that disperse by seedfall or vegetatively, which require mature trees to be in relatively close proximity. Average plant density by treatment by propagation method showed that seedfall propagated species had the highest rate of occurrence of all propagation methods on control and non-treated sites, yet was just below wind propagated species on cleared sites (Table 5). This indicates that they may not have as high a success rate when faced with competition from wind propagated species, which had the highest density by far on cleared sites (Table 5).

This difference could possibly be explained by the amount of time since disturbance—two years may simply not be enough time for seedfall propagated species to have spread to the cleared sites. However, it may be of concern for future species diversity. The majority of wind propagated species are of European introduction, making them relatively recent. This suggests that should a relatively large-scale atypical disturbance occur in this area, significant changes in species composition could occur as wind, animal, and even vegetatively propagated species seem to have the advantage in terms of successful germination of disturbed sites.

### 2.3 Status

As mentioned earlier, it is generally assumed in disturbance ecology that invasive species tend to benefit from disturbance, and indigenous species as a result tend to suffer

(Hobbs et al. 1992, Lake et al. 2004). The average density by status at each treatment (Table 6) in this study appear to completely contradict this theory. The indigenous species were found in the highest density on cleared and non-treated sites, while naturalized and invasive species were both highest on control sites. This may be further evidence supporting the idea that indigenous island species on Mo'orea such as *Neonauclea forsteri* and *Hibiscus tiliaceus sub. tiliaceus* behave more like invasive continental species because of the traits necessary for island colonization and requiring a unique enough niche to avoid competition from Polynesian introductions.

Ultimately, this difference can most likely be attributed to the methods by which each species' status was described. The only species in this study described as cultivated by the Herbarium of French Polynesia, *Alpinia purpurata*, can be seen to clearly favor disturbed sites, yet it is unclear why the species is differentiated from the others when it is growing independently of human aide. This is especially puzzling when considering the fact that *Cordyline fruticosa* and *Artocarpus altilis*, two Polynesian introduced species that are sterile in French Polynesia, are described as naturalized.

Additionally, the differentiation between naturalized and invasive species is unclear. *Inocarpus fagifer*, a Polynesian introduced species that is now dominant, is described as naturalized, while *Syzygium malaccense*, another Polynesian introduced dominant species, is described as invasive. This is of even greater concern when considering the sheer abundance of *Syzygium malaccense*—it accounts for a majority of the invasive species density.

Based on these details and the lack of a statistically significant p-value to support the hypothesis, it is difficult to make any definitive statements about the distribution of plants by status across the different treatments. In reality, defining these species as anything more complicated than "indigenous"

and “introduced” may be impossible with any certainty.

#### 2.4 Canopy cover

Canopy cover is frequently used as a proxy for the amount of light that reaches the understory of a forest ecosystem. Forest species tend to be defined as either “shade-tolerant” or “shade-intolerant,” indicating their ability to survive in areas of varying amount of canopy cover. Although the forests of Mo’orea are not as dense as many tropical forests, the amount of light accessible to plants in the understory can still be an important factor in the distribution of some species. Canopy cover among these sites ranged from 45% to as high as 86%, indicating the high amount of variation in this study area alone. Although there was some difference in the average canopy cover by species, it is impossible to state any statistically definitive difference in the distribution of species based solely on canopy cover. While this can likely mostly be attributed to the small sample size, more refined methods such as measuring canopy cover above each seedling may give more insight into the impact of canopy cover on species distribution.

#### 2.5 Diversity Indices

The lack of variation in diversity indices between the treatment types may be the most revealing result of this study. Despite the fact that some of the disturbed sites appeared incredibly different from control and non-treated sites by observation, overall the diversity at each treatment was fairly similar. Considering the relatively small sample area, this is not entirely unexpected, and implies there is a possibility that increasing the range of study may reveal more significant results.

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