

THE EFFECT OF LOCAL PROPAGULES ON PLANT RECOLONIZATION IN TROPICAL FOREST ECOSYSTEMS IN MO'OREA, FRENCH POLYNESIA

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Abstract. The process of plant recolonization takes place over a broad range of magnitudes and timescales. Studies of recolonization in tropical forest ecosystems are few in number making it an important addition to the ecological literature. To determine the effect of propagules and biotic factors such as sunlight, substrate and clearing level on the recolonization of plants, previously-cleared plots were paired with adjacent, untouched plots in the forest. Species were identified in the plots and their abundance and presence or absence was compared across the system to determine if one factor was more significant than another. The effect of propagules from the adjacent plot, sunlight availability and level of clearing were important determinants in what species were able to recolonize. Substrate did not show variation. Various biotic and abiotic factors are identifiable as determinants in recolonization but the complexity of interactions in tropical forest ecosystems makes predictions challenging.

Key words: recolonization; propagules; restoration; regeneration; Mo'orea, French Polynesia

INTRODUCTION

Ecological disturbances are a common feature of everyday life. The media covers a wide range of of natural disasters, human expansion and disease that are capable of clearing, and often do clear, large expanses of land. Many of these disturbances can be predicted, controlled or contained but what is less understood is the process following a disturbance (Summerville, 2008).

Where there is disturbance, there will be regeneration. The recent rise of conservation biology has renewed interests in the effects of community dynamics (Ouborg, 1993). After a disturbance, species will begin to recolonize, or return to a place that was previously-cleared. But the method by which this is accomplished and the abundance of each species that returns is often difficult to predict (Seabloom et al, 2003, Bazzaz, 1979, Freckleton, 2002). Due to the abundance and biotic and abiotic factors, there are compounding variables that often make conclusions hard to draw (Bazzaz, 1979, Seabloom et al, 2003).

Observing and recording the biotic and abiotic influences on the individuals within allows us to learn about the internal dynamics of an ecological community (Roughgarden, 1986, Seabloom et al, 2003). Interactions among plants add to our knowledge of spatial dynamics (Freckleton,

2002), competition (Franco, 1988), conservation of native species (Seabloom et al, 2003), and even bigger concepts as encompassing as evolutionary theory (Thorpe, 2011).

Many scientists have conducted research looking into the factors that affect recolonization, especially in recent years. Of the studies conducted, several have concluded that the most important factor in recolonization is the biotic effect of the surrounding plant community and seed bank (Elton, 1958; Thorpe, 2011; Ouborg, 1993, Mack and Harper, 1977, Kotanen, 1997). Others hypothesize that although biotic factors do play a role in recolonization, environmental, or abiotic conditions are much more important (Svenning et al, 2008). Factors such as sunlight are hypothesized to have the greatest effect increase variability and energy exchange (Bazzaz, 1979). Other factors like the intensity of disturbance (Fahrig et al, 1994, Kirmer et al, 2008, Urbanska et al, 1997) affect how soon a plot can recover. Substrate was also found to be important in determining genetic similarity of species (Alvarez et al, 2009). Soil and litter characteristics directly affected the health of the ecosystem therefore the plants that grew there (Kirmer et al, 2008, Urbanska et al, 1997, Svenning et al, 2008). Finally, in some systems, it is a combination of abiotic and biotic factors that influence plant regeneration (Seabloom et al, 2003).

Despite the advances that restoration ecology has made over the years, little in the way of recolonization has been studied in tropical forest ecosystems. Yet, this is becoming more important with the rate in which humans are developing the land, especially in tourist-economy locations. I sought to add to the current literature a snapshot of what tropical forest ecosystems consist of after a disturbance with the hopes that it would serve the growing need to protect these diminishing ecosystems.

This goal of this study is to identify the various biotic and abiotic factors that influence the regeneration of plant species in tropical forest ecosystems in Mo'orea, French Polynesia.

Specifically, I asked the following questions.

1. Is propagule pressure, or the effect of the outside community seedbank, the most important factor in describing the regenerating plant community?

2. How do abiotic factors such as sunlight, intensity of clearing, substrate type, soil and litter affect the regenerating plant community?

3. Can this information be used to understand and predict community composition and the success of individual species in a tropical forest?

I hypothesized that propagule pressure would be the most important factor determining recolonization because I did not believe these abiotic factors would vary too much across a forest ecosystem. Secondly, I predicted that sunlight would increase the individuals in a plot because more energy is captured for photosynthesis. I hypothesized soil moisture, soil chemistry and litter would not be important factors but the level of clearing and substrate type would be important.

To conduct this research, I sampled previously-cleared and untouched plots in the forest. I identified the species present, took measurements for each individual and noted the various abiotic factors present in the plot.

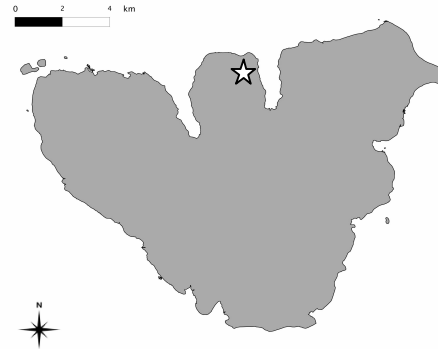
METHODS

Study site

This study was conducted from October to November, 2011 on the island of Mo'orea, French Polynesia in the South Pacific (Figure 1). Mo'orea is located approximately 17 km northwest of Tahiti in the Society Island Archipelago. The island is 134² km in area

with a maximum elevation of 1207m (ORSTOM, 1993) and an annual average rainfall of between 3-4 m per year (Pasturel, 1993).

FIGURE. 1. A map of Mo'orea, French Polynesia showing a star mapping the study site in Opunohu Valley.



The study study sites are located in the Opunohu Valley at the Three Pines trail (17°32'23.55"S, 149°49'33.08"W) in an ancient religious ceremonial site called a marae complex (Figure A1). The site is 238 m in elevation and amidst trailheads for the Belvedere overlook point, Three Coconuts trail and Three Pines trail.

In 2008, this site was used by archeologists conducting research on Polynesian culture and religious practices. Individual marae structures were cleared using a classification of three categories: (1) lightly cleared with machetes, (2) heavily cleared using rakes and (3) excavated. Each marae structure was of varying size, shape, and location in the forest.

The site was chosen for my research because it presented a fixed time period of human disturbance in one location. I selected 21 previously cleared marae to study; 7 from each clearing level. I was limited in my sample size by what had been cleared by the same researchers in the same method during that year.

SITE SAMPLING

My research was conducted using a transect to measure 5x5 m square plots in both the 21 previously-cleared plots (Figure 2) and 21 untouched sites adjacent to my plots. When selecting an adjacent plot I picked a site that had not been cleared by archeologists in 2008, at least 5 m from any hiking trail to reduce human trampling and in between 5 and 7 m distance from the edge of the paired

previously-cleared plot. The adjacent plot could not be located in between two previously-cleared plots or anywhere with significantly different topography (different elevation and steep slopes were the only excluding factors I came across). The grid was centered inside each plot to minimize edge effects.

VEGETATION SAMPLING

I systematically walked through each plot I sampled, identifying the species present. For each individual I measured the height, canopy width, stem diameter or diameter at breast height (DBH) for adult trees, and counted the leaves for seedlings. I followed this same process for the adjacent plots. Every site was marked with flagging tape and its GPS coordinates were noted for reference.

In plots where the ground cover was dominated by grasses, counting individual species was not feasible. In these instances, I set up a one meter transect and recorded what species were present at every centimeter along that line.

MEASUREMENT OF ASSOCIATED ABIOTIC FACTORS

The amount of sunlight present in the plots was measured by percent canopy cover. Using Lemmon's Model-C spherical densiometer I calculated the density of the forest overstory thus the amount of sunlight unable to penetrate through to the ground.

The level of clearing was noted for each plot using the gradient established by archeologists in 2008. Plots that were lightly cleared were done so with machetes bushwacking canopy cover. Heavily cleared sites were raked so the groundcover was removed including litter and the seedbank. Excavated sites had soil removed from them.

Substrate was noted for each plot. Most of the focus was between pure rock platform substrate or soil substrate. I also estimated the percent cover of loose rock in each soil substrate plot.

Soil samples were collected in plastic 40 mL vials and taken back to the lab for analysis. Soil chemistry was analyzed for nitrogen, phosphorus and potassium using LaMotte's Soil N-P-K kit from GLOBE.

Litter samples were also taken from from each site. Groundcover, including seeds and dead matter was collected from a 0.5x0.5

m quadrat. In the lab, samples were dried in a drying oven for at least a week and the biomass was weighed and recorded.

STATISTICAL ANALYSIS

The data collected from the field was then analyzed using JMP 9 (SAS Institute, 2011).

I used Principal Component Analysis (PCA) to visually describe associations among plots, based on plant species found there.

To answer the question of how propagule pressure influences the recolonization of previously-cleared plots, I compared the paired plots (regenerating plot and its adjacent plot) to plots with no association. I reformatted my data from abundance measurements to presence absence data. To determine the dissimilarities among the plots, I created a Euclidean distance matrix on JMP that compared all possible plot combinations. I calculated the mean value of all paired sites (21 pairs) and the mean of every other combination. I ran a t-test to determine if the differences between the means of paired plots was smaller than that of unrelated plots meaning propagule pressure was a factor in recolonization.

To calculate the effect of sunlight on the three different clearing types, I ran a oneway analysis of variance (ANOVA) test with the three clearing levels as the independent variable and sunlight as the dependent variable. I used linear regressions to compare individual species' response to an increase in sunlight in plots. Lastly, to compare species' responses to sunlight, I ran a Chi-Square test to compare two species of trees, *Inocarpus fagifer* to *Spathodea campanulata* as the percent sunlight increased in plots.

I used a one-way ANOVA to determine the effect of clearing level on the distances between paired plots. I then used a Tukey-Kramer HSD test to compare the three difference categories of clearing to each other to determine which levels of clearing showed significant differences.

RESULTS

SITE SAMPLING

In the 42 plots I sampled, there were 51 different species, 1706 individuals and a myriad of intertwined community dynamics. Species' abundance varied from 1 to 674 individuals. Tahitian Chestnut, *Inocarpus fagifer* (Fabaceae) was the most abundant

species found in my plots (Figure 3). There were plots sampled where *I. fagifer* was almost alone save a few fern species found in the buttress roots: *Devalia solida* and *Teratophyllum wilkesianum*.

Shampoo Ginger, *Zingiber zerumbet* (Zingiberaceae) was the next most common species with 322 individuals. It was mostly found as small seedlings around 20-50 cm tall clumped together on soil with protruding sunlight in the canopy.

Malay Apple, *Syzygium malaccense* (Myrtaceae) was able to occupy plots with *I. fagifer* while the African Tulip Tree, *Spathodea campanulata* (Bignoniaceae) was in direct competition with *I. fagifer*.

The community dynamics of the plots are organized in a Principal Component Analysis (PCA) (Figure 4). This is used as a reference to how species were distributed in plots. *I. fagifer* appears alone on the diagram. In the bottom right corner directly across are the species that were found in opposite

Sunlight was one of the best ways to distinguish species from one another (Figure 4). The individual dots represent the plots in the study. Their color corresponds to sunlight. Darker dots are heavier canopy covered plots. Lighter dots represent more sunlight availability. Darker dots are clumped together more in the left central part of the figure corresponding to *I. fagifer* (Figure 3). Directly opposite of that are lighter colored dots that show plots where *Z. zerumbet*, *A. evecta*, *H. tiliaceus* and *S. campanulata* are found. Component 1 describes 28.2% of the data while Component 2 describes 20.6% of the data for a combined 48.6% of the data explained (JMP, 2011).

VEGETATION SURVEY

The effect of local propagules is most significant in lightly cleared plots with heavy canopy cover. The means of the paired plots (regenerating plot and its adjacent plot) are

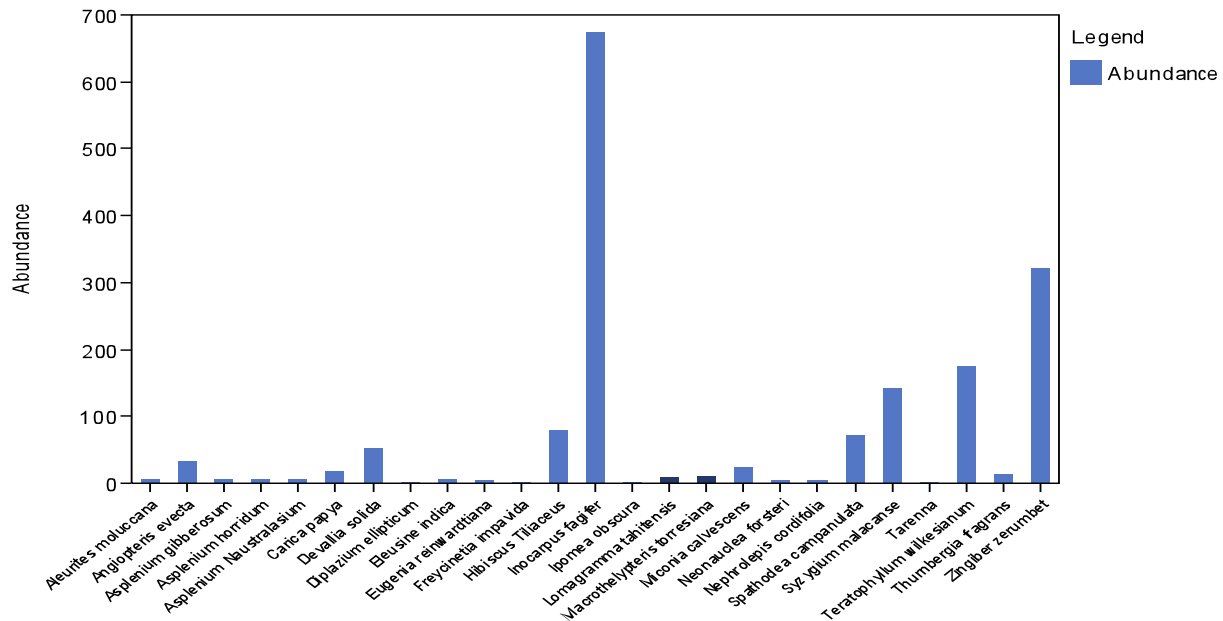


FIGURE 2. The abundance of species found in the 42 plots in this experiment. *I. fagifer* was by far the most dominant species with *Z. zerumbet*, the next most abundant species with less than half. There were a total of 51 species sampled in this experiment but only the most common are shown here.

conditions to that of *I. fagifer*. The third distinguishable group falls in between *I. fagifer* and the heliotropic group in the upper right corner showing there are shared similarities with both regions.

significantly smaller than that average of other unrelated plots (Figure 5). This shows that plots in close proximity to each other spatially were also closer in plant composition. This supports the hypothesis that propagule

pressure affects regeneration (JMP, 2011, t-Test, $t^2 = -2.54$, $df=203$, $P = 0.011^*$).

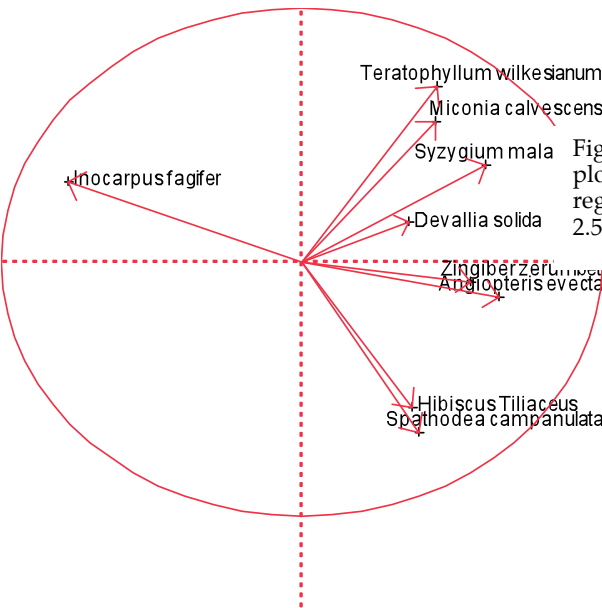


FIGURE 3. Results of a PCA describing the relatedness of species in their plots. Species that are found close together represent plants that are found together in my study.

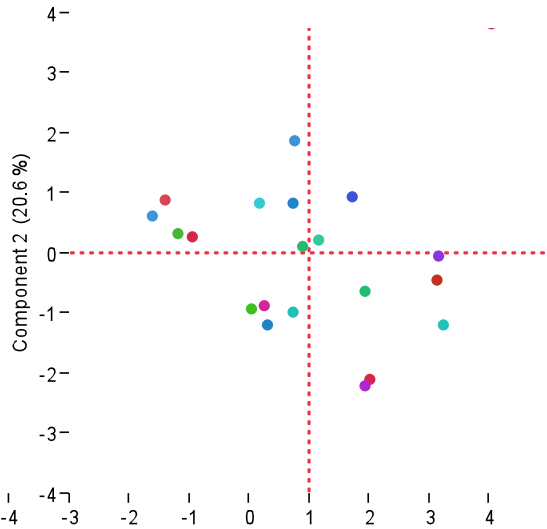


Figure 4 Similarities of plots according to sunlight availability. Darker dots represent heavy canopies and lighter plots represent sunlight availability. Component 1 and 2 describe 48.6% of the data.

MEASUREMENT OF ASSOCIATED ABIOTIC FACTORS

CANOPY OPENNESS

On the ecosystem level, the amount of sunlight available to plants affected how similar plots were to each other (Figure 6). Using the same Euclidean distance matrix based on presence absence data, plots with more sunlight were significantly more variable than plots with dense canopy cover (one-way ANOVA, $F_{1,19}=7.36$, $P=0.013^*$).

Figure 5 average distances between paired and other plots show the effect of propagule pressure on the regenerating plant community (JMP, 2011, t-Test, $t^2 = -2.54$, $df=203$, $P = 0.011^*$).

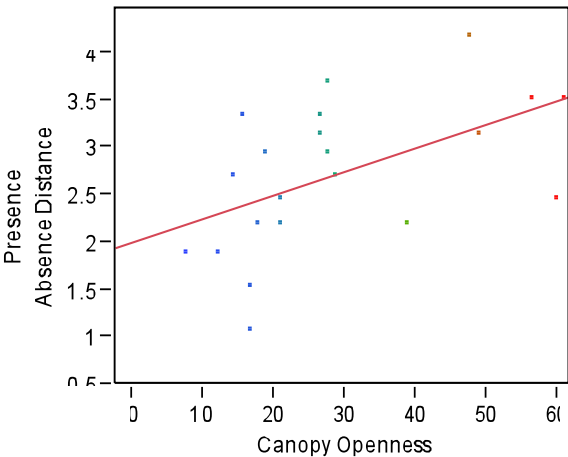
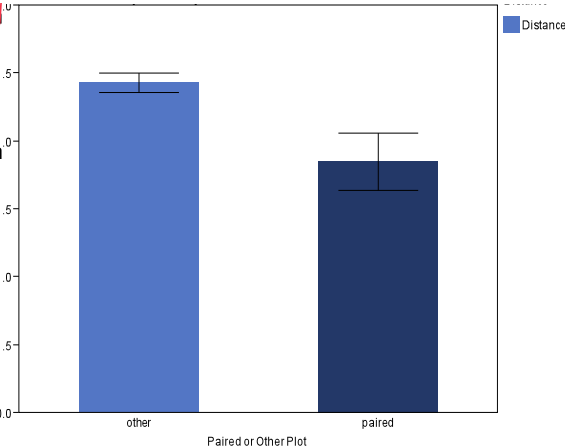


Figure 7 The relationship between percent open canopy and presence/absence of species on the ecosystem scale. More sunlight caused greater variation in the plant composition (one-way ANOVA, $F_{1,19}=7.36$, $P=0.013^*$).

Sunlight was not an important factor for most individual species. However for *I.*

fagifer, the increase in sunlight negatively correlated to the species abundance (JMP, 2011, one-way ANOVA, $F_{1,19}=10.18$, $P=0.0048^*$).

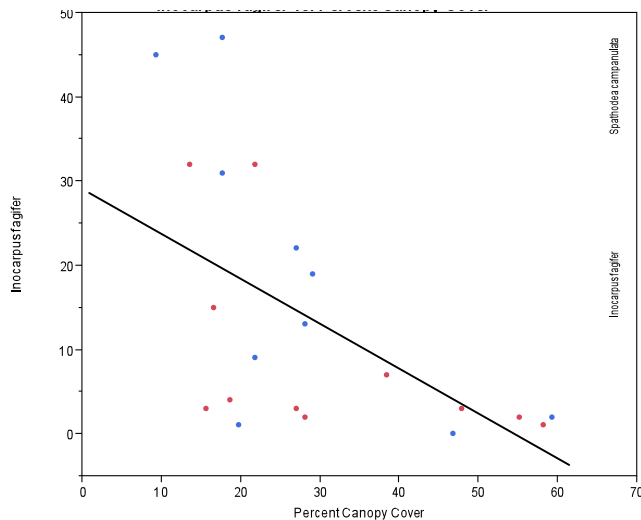
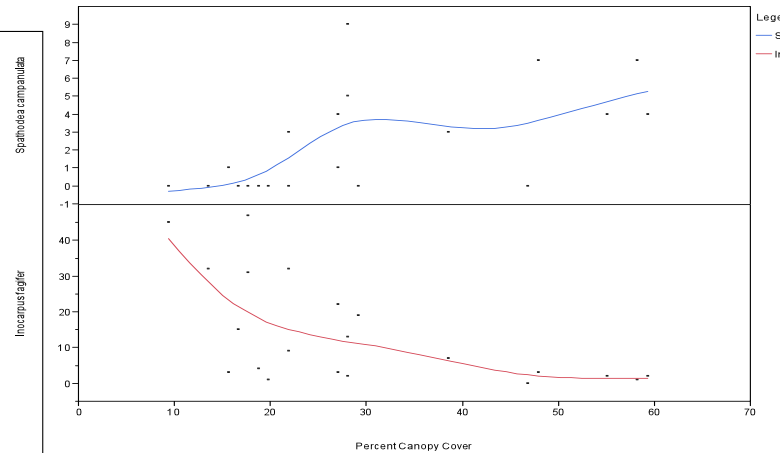


Figure 8 shows the negative correlation between sunlight and the abundance of *I. fagifer* (one-way ANOVA, $F_{1,19}=10.18$, $P=0.0048^*$).

The relationship between two competing species: *I. fagifer* and *S. campanulata* is sunlight-dependent (Figure 8). *S. campanulata* was relatively unseen in *I. fagifer* plots but as the sunlight increased, the abundance of *S. campanulata* linearly increased also (JMP, 2011, one-way ANOVA, $F_{1,19}=9.92$, $P=0.0053$). But the species did not coexist together in plots with open canopies (Figure 9). As sunlight increased, *I. fagifer* decreased (Figure 7) and was replaced by *S. campanulata* (JMP, 2011, Chi-square, $\chi^2=39.68$, $df=23$, $P=0.016$).

A third tree species, *S. malaccense*, was not affected by sunlight or the competition between *I. fagifer* or *S. campanulata* (JMP, 2011, one-way ANOVA, $F_{1,19}=0.9604$, $P=0.3394$).

Figure 8. The relationship between sunlight and *S. campanulata* is linear. The relationship between sunlight and *S. campanulata* compared to *I. fagifer* (JMP, 2011, Chi-square, $\chi^2=39.68$, $df=23$, $P=0.016$).



LEVEL OF CLEARING

The level of clearing, analyzed using abundance data for species, did not show variation among clearing types (JMP, 2011, one-way ANOVA, $F_{2,18}=1.29$, $P=0.29$). However, when I changed the format of my data from abundance to presence absence, the level of clearing was an important factor in determining what species were able to recolonize the land (Figure 9). The average distances between regenerating plots (untouched plots were excluded because they were not cleared) of the three clearing types were compared. Lightly cleared plots had the least differences in plant community while heavily cleared plots showed the greatest variation (JMP, 2011, one-way ANOVA, $F_{2,18}=3.96$, $P=0.037^*$).

Comparing the three types of clearing to themselves showed that the most important difference in clearing is the step between lightly clearing a plot and heavily clearing the plot (JMP, 2011, Tukey-Kramer HSD, 0.063). Excavation was not an important factor for regenerating species.

Comparing the level of disturbance by clearing on the species level was an important consideration for *I. fagifer* (Figure 11). The likelihood of regeneration was much higher for *I. fagifer* of the level of clearing was minimal (JMP, 2011, one-way ANOVA, $F_{2,18}=5.1902$, $P=0.016^*$). The differences between excavation and the other two clearing types had little influence on *I. fagifer*. Similarly to the clearing level on the ecosystem level, the most important difference is between light and heavy clearing (JMP, 2011, Tukey-Kramer HSD, 3.097*).

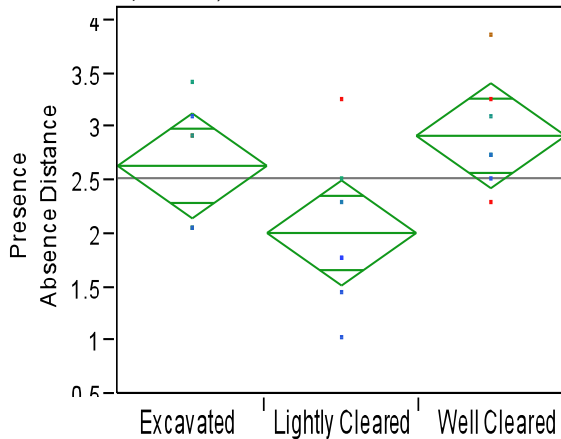


Figure 9 The effect of human clearing on the presence or absence of species in regenerating plots. Lightly cleared plots had the least differences in plant community while heavily cleared plots showed the greatest variation (JMP, 2011, one-way ANOVA, $F_{2,18}=3.96$, $P=0.037^*$).

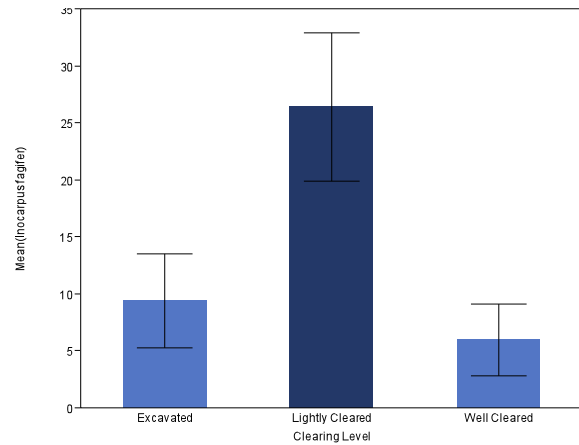


Figure 10 reaction of *I. fagifer* to different levels of clearing. The success is negatively correlated as disturbance increases (JMP, 2011, one-way ANOVA, $F_{2,18}=5.1902$, $P=0.016^*$). The most important difference is between light and heavy clearing (JMP, 2011, Tukey-Kramer HSD, 3.097*).

Substrate was not an important factor in recolonization like hypothesized (Figure 11). The regenerating plot showed no differences in plant composition depending on the rock platform substrate or soil substrate (JMP, 2011, one-way ANOVA, $P=0.84$).

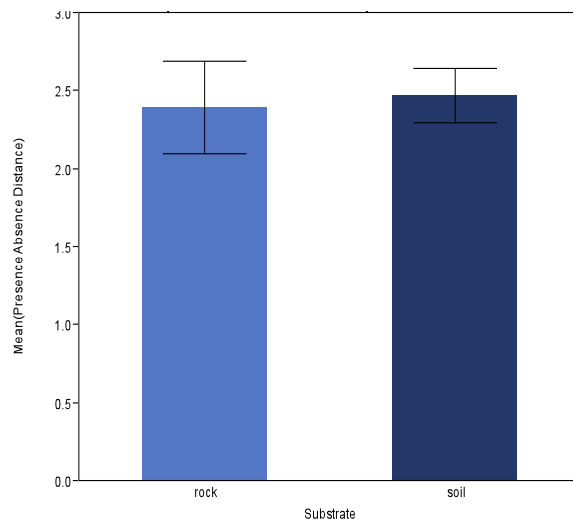


Figure 11 shows no statistical significance between plots with rock platform substrate and soil substrate (JMP, 2011, one-way ANOVA, $P=0.84$).

DISCUSSION

The results of my research show that the recolonization of plants in tropical forest ecosystems is at least in part a result of propagule pressure from adjacent forest composition. Plots that are located close to each other spatially are more similar than a random plot in the forest (Figure 4). Sunlight was one of the most important factors in facilitating competition between native species like *I. fagifer* and its invasive competitor, *S. campanulata* (Figure 8). Increased sunlight also caused the regenerating plot to be significantly different than its paired untouched plot (Figure 6). Furthermore, the level at which disturbances occur affects how plants are able to recover. Substrate was not an interesting explanation for species abundance (Figure 11).

The overall site dynamics show that species in these plots are highly segregated due to several factors, the most important of which seem to be sunlight availability. The PCA (Figure 2) shows plants that are found together and also how this correlates to sunlight availability (Figure 3). These clusters were consistently maintained across other factors as species reacted similarly. One example of such was the level of clearing. *I. fagifer* showed significant preferences for uncleared plots (Figure 10) while heliotropic plants that were often invasive or non native preferred disturbed places that allowed openings for invasion.

Considering that species are grouped together in the PCA by sunlight, it was surprising that sunlight was not a bigger factor for individuals. On the ecosystem level, there was more variation in plots with more sunlight but species did not show a trend. Some of this could be due to the surprising lack of diversity I encountered in the forests. The overwhelming abundance of *I. fagifer* proved difficult in analyzing results because it tended to overshadow any minor changes in an ecosystem. That is why I had better results analyzing my data based on presence absence. Many of the significant results I found were not important when analyzed by abundance and much of this could be because of the frequency of *I. fagifer*.

Plots that did show variation did not completely limit those species from encroaching on other areas even if conditions were not ideal. This blurred the boundaries of a trend that seemed rather clear during preliminary observations. Species like *D. solida*, *T. wilkesianum* and *S. malaccense* display the traits of a generalist that allows it the flexibility and adaptation to exist in conditions

that other plants cannot (Figure 1). In plots completely dominated by *I. fagifer*, these two ferns, *D. solida* and *T. wilkesianum* could be found climbing along the trunk of the tree or wedged in the large buttress roots. In plots without *I. fagifer*, they were generally much larger and found rooted in the soil in groups together. Although they were frequent in sunlit plots, their density tended to decrease as grass species colonized, creating a thick groundcover.

The results from the experiments with the levels of clearing was different from my original hypothesis. I expected excavated sites to suffer the most when it came to regeneration because of the manipulated soil, root system and seedbank. The results show that the lightly-cleared plot is the best choice if the end result is for that plot to return to its previous state. Heavy clearing caused the greatest change in the ecosystem and excavation fell in between the two levels (Figure 9).

I believe the major influence that made heavily-cleared plots so different from lightly cleared plots is the loss of litter and seedbank. Heavily-cleared sites were raked by archeologists and the groundcover was removed. This effectively eliminated the next generation of seedlings, allowing whatever species has effective long-distance seed dispersal recolonize. And it seems as if this was the case because heavily-cleared plots showed a greater variety of species present.

A personal communication with one of the archeologists doing research at the marae complex in 2008 explained why excavation was not as big of a factor as I hypothesized. Although soil was dug out and removed along with litter and the seedbank, at the end of the research, the soil was returned to its place. This could have in fact been beneficial for aerating and turning over the soil to assist with germination (Kirch, personal communication). This research suggests that the effect of the level of clearing is important in plant recolonization when the seedbank, soil and litter are manipulated.

In the beginning of the experiment, I hypothesized that substrate would show a different plant community because it would exclude big, rooting species like trees. But the results suggest that either substrate is not important or it was simply not as important as other factors (Figure 11). Also, because the only sites I could sample were the ones previously cleared in 2008, I was limited in site selection. Only four of my 42 plots were on a rock platform substrate. Upon closer

investigation, substrate may in fact prove to be a factor.

One of the most interesting facets of this data is the competition between species in the plots. While some species like *I. fagifer* have created conditions that allow it to dominate most of the ecosystem, heliotropic plants have a different method for survival. These species were all able to colonize an area quickly to rapidly outcompete and replace surrounding species.

When looking at the distribution of *I. fagifer* in the forest, it seems fairly clear that the species prefers dense canopy cover (Figure 7). However, the literature cites *I. fagifer* as a species that prefers sunlight and open canopy (Pauku, 2006). This suggests that *I. fagifer* has not always filled the niche in the forest that it currently fills. Instead, this tree could have evolved over time from a habitat with optimal sunlight but more competition to a niche with sub-optimal conditions but no competition.

It is also feasible that non native species encouraged this change. *S. campanulata* is cited as one of the worst world invaders of any species (Lowe, 2004). It has already been shown that when competing for sunlight, *S. campanulata* dominates (Figure 8). Upon its introduction, *I. fagifer* would have to adapt its methods for survival. Pauku also claims that seedlings are only really able to generate below the canopy of the parents tree (Pauku, 2006). My observations in the field support this idea.

The dynamics between two competing tree species like *I. fagifer* and *S. campanulata* describe the effect of disturbances on an ecosystem. One of the most important aspects for survival for these naturalized species, especially trees like *Neonauclea forsterii*, *S. malaccense* and *I. fagifer* is the importance of fully-grown, seed-producing trees. Any disturbance caused by humans or nature opens up an area in the forest for a completely new species to take root. There are habitat and environmental conditions that species prefer but this is not always reflected in the niche that the species, like *I. fagifer*, fills. Because of this, predicting what species will be able to recolonize a previously-cleared plot cannot be answered by studying a few abiotic and biotic factors.

Interactions among plants and various species of consumers, dispersers and pollinators has been widely studied, but equally interesting and unknown is the relationship between plants themselves (Thorpe, 2011).

Island plant communities are continually changing with time, adapting to new invasions, disturbances and change (Cody, 2006). Plants interfere and interact with each other to modify the environment (Mack & Harper, 1977). Franco and Harper talk about a "competition-effect wave" where you cannot quantify the amount of pressure one neighbor exerts on another because it doesn't take into account the pressure the first neighbor experienced (Franco & Harper, 1988). These modifications that occur in plants result from pressure and opportunity of habitat disturbances. As the scientific community and the general public become more concerned with the few remaining native species in tropical islands, conservation biology will become increasingly more important (Ouborg, 1993).

There is much room for advancements and further research in regeneration in tropical forests. Specially looking into the habitat niche of *I. fagifer* and possible explanations for this. If the species was able to compete in sunlight areas, would it? Or is it so adapted to its current niche that it is now more profitable for the species to live in dense canopy covered plots if that means being surrounded by only itself?

S. campanulata may have a negative effect on *I. fagifer* through competition, but does the increase in biodiversity that it stimulates by removing *I. fagifer* from plots have an overall positive effect on the ecosystem, despite its highly invasive status?

If archeologists did not replace the soil in a plot, replaced it with sterile soil or moved the soil to another plot, how would the community dynamics be changed?

There is so much more waiting to be discovered and explained in this ecosystem that directly affects other tropical forests and any ecosystem faced with similar competition by invasive species or disturbance. It is important for this work to be done in places like Mo'orea, French Polynesia where tourism is so important. Livelihoods rely on commercial expansion, agriculture and development. As they turn to forests as the new source of land for these plans, conservation biologists must be prepared to adapt and remedy these situations in the best possible manner to conserve the last of biologically important ecosystems.

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APPENDIX



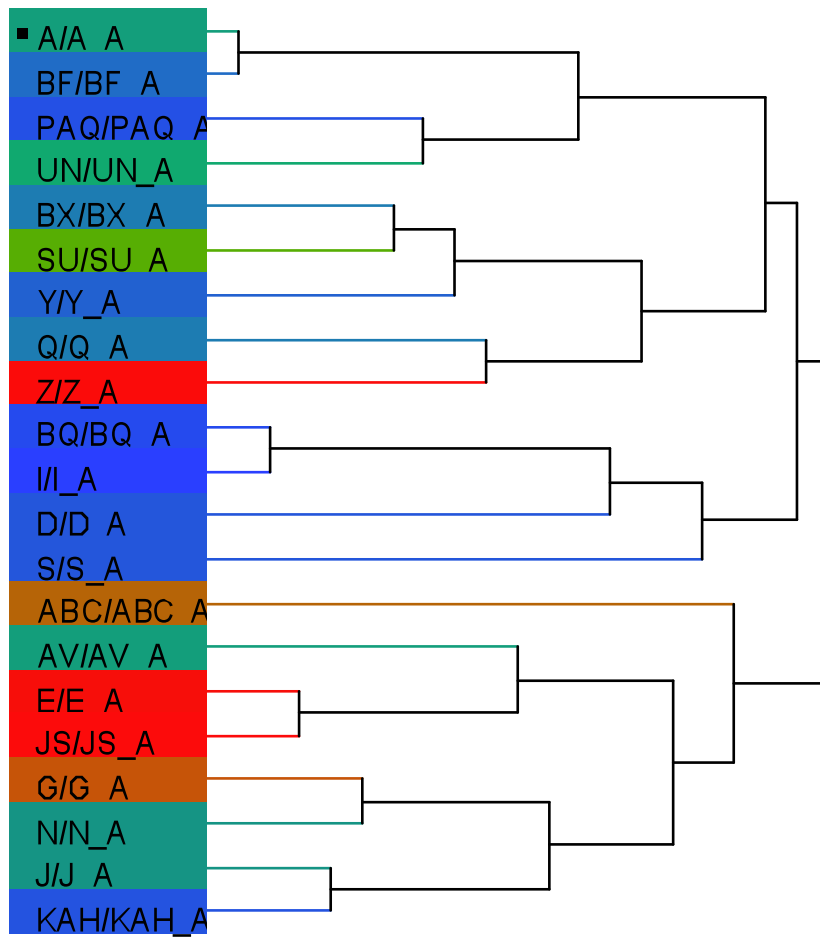


Figure A1 Map of the marae complex where sites are located. Rectangles identify site locations. Colors indicate the level of clearing described by archeologists. (Kirch, personal communication)