

PROPAGULE HERBIVORY ON THE COASTAL STRAND OF MOOREA, FRENCH POLYNESIA

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Abstract. Herbivory within plant communities is the result of many interacting factors. While, there have been numerous studies examining the patterns and factors that affect herbivory on continental systems, few studies have been done on oceanic islands. This study aims to determine what factors affect herbivory on oceanic islands and will focus on coastal strand communities. Coastal strand systems on Moorea, French Polynesia are unique in that they often contain remnant patches of native vegetation intermixed with introduced species. To determine the role of interacting factors, manipulations of propagules were conducted for 9 coastal species. Along with that, relative herbivore densities were estimated to determine if they had any correlation with herbivory. Results suggested that proportion of herbivory was not due predominantly to any one of the factors tested; instead, responses were for the most part, species specific. These species specific responses may be explained by interspecific variation among propagule characteristics. By studying the patterns and factors affecting herbivory on the coastal strand, this study could potentially help in the conservation efforts of restoring plant communities.

Key words: dispersal agents; community structure; Moorea, French Polynesia; herbivory, coastal strand

INTRODUCTION

Plant communities are shaped by a variety of factors, and there are many models that try to explain the co-existence of numerous species in certain communities (Grubb 1977). Of particular importance to these models is the fact that when any one plant individual dies, a gap is created for new individuals to take its place. Whether or not the individuals filling in this gap are of the same species depends on both biological interactions as well as the physical limitations of the environment (Crawley 2009). One major interaction affecting the distribution and abundance of plants within communities is the fate of their dispersal agents (Nathan & Muller-Landau 2000). Therefore, if dispersal agents, inherently seeds, are limited then changes in community structure can occur.

There are two mechanisms by which seed limitation can occur: either propagules never arrive at a suitable microsite (Turnbull et al. 2000) or the propagules are destroyed by predators or pathogens before they can

establish (Crawley 2000). Although plants generally produce copious amounts of propagules (Harper 1977), much of them are damaged or consumed before, during, and after dispersal. In fact, research by Orrock et.al (2006) suggests that reduced occupancy and persistence of plant species may be generated by seed limitation due more to damage and consumption than by the inability to reach a suitable site. Therefore, damage/consumption of dispersal agents may have major effects on the reproductive success of individuals, the spatial patterns of populations, and the diversity of tree communities (e.g., Janzen 1970, Connell 1971, Howe and Smallwood 1982). The fact that propagule damage often differs among plant species in the same community (Willson & Whelan 1990), coupled with Orrock et. al's findings, suggests that herbivory of propagules may play an important, and yet largely unknown role in determining the landscape-level distribution of plants.

There are many predictions for the ways in which herbivory affects plant communities.

For example in most tropical forests, herbivory is suggested to be density-responsive with most damage concentrated near adults where propagules are most abundant (Janzen 1970; Connell 1971). As a consequence, population levels within these systems are expected to remain relatively low, with regularly spaced adults, and a high diversity of tree species (Janzen 1970; Connell 1971). While this model has been the basis of many studies in tropical forests on continental systems (Hyatt et. al 2003) it is unclear whether oceanic tropical islands follow similar patterns.

Islands are often simpler than mainland ecosystems (Hansen et. al 2008) and island communities often lack floral and faunal diversity due to distance from the mainland and difficulty in successful establishment. Usually these communities are composed largely of hyperabundant species that lack predators (Terborgh 2001). In fact, many functional groups are often missing or underrepresented while other groups are overrepresented, including rodents and generalist herbivores (Terborgh et al. 2001). In the presence of these faunal assemblages, the communities of small and medium islands often experience recruitment failure or changes in species distribution (Terborgh et al. 2001, 2006). Therefore, it is possible that in these types of systems, recruitment could be suppressed by excess damage to dispersal agents in the presence of hyperabundant herbivores (Terborgh 2001).

It is because of this, that the factors affecting herbivory within communities may be especially important on islands. Usually because of strong geographic isolation and small size there is a lower presence of native flora (Meyer 2004). Moreover, native flora and fauna are often crammed into small remnant patches of native habitat (Hansen et. al 2008). One such example is that of island coastal strands, which consist mainly of littoral species. The dispersal methods and characteristics of these plants limit their establishment to narrow zones of vegetation on the shore (Whistler 1992). In these coastal systems, zonation patterns are thought to be the result of physiological adaptation to different gradients in salinity and tidal

inundation (Smith 1987) as well as a response to varying levels of herbivore damage (Janzen 1971). As a result, observed composition of plant communities might result from differential distributions of herbivores.

Being an oceanic island consisting of a fair number of both native and introduced species, the island of Moorea in French Polynesia provides an excellent opportunity to evaluate the damage of dispersal agents within the coastal strand community. The island's small size and relatively predator-free state has created conditions of hyperabundant generalists, which include rodents and land crabs. Therefore, I chose to address the following questions in order to evaluate the impacts of herbivory on plant species on the coastal strand: (1) Do coastal strand communities differ? (2) Is damage to dispersal agents density-dependent? (3) Is the amount of damage on a particular species related to its propagule characteristics? (4) What is the intensity of herbivory on certain plant species and does it vary across sites? (5) Is herbivory of plant species correlated with differential predator distributions?

It was hypothesized that different coastal strand communities would have different compositions of plant species and therefore herbivory would vary across sites. Furthermore, it was also predicted that different species would have different levels of herbivory. In accordance with past research (Janzen 1970) it was predicted that damage to propagules would be density-dependent and that woody plants exhibiting dominance would have higher amounts of propagule damage. Along with that, it was hypothesized that propagules with certain characteristics such as fleshier husks would be preferred over others, and that overall intensity of herbivory would differ in accordance to the type and density of large herbivores. Overall by addressing these questions, this study hoped to understand the role that herbivory might play in affecting the distribution of plant species on the coast.

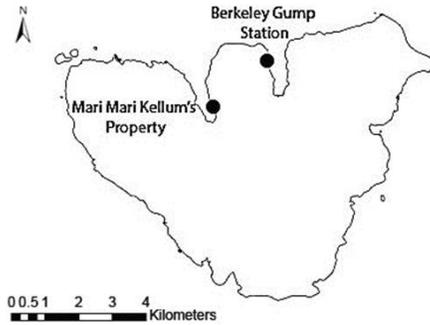


FIG.1. Study sites used during research project. Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley.

METHODS

Study sites and focal species

This project took place on two main areas within the island of Moorea (FIG.1). The first study area was the coastal strand surrounding the UC Berkeley Gump station (17°29'28.12" S 149°49'34.32") and the second was the coastal strand encompassing Mari Mari Kellam's property (17°30'51.34"S, 149°50'53.42"W). Sampling was concentrated at these locations and consisted of finding the appropriate plant species for experimental treatments. The focal species for this study were: *Cocos nucifera*, *Barringtonia asiatica*, *Scaevola taccada*, *Thespesia populnea*, *Calophyllum inophyllum*, *Morinda citrifolia*, *Terminalia catappa*, *Cordia subcordata*, and *Fagraea berteriana*.

Field surveys

Surveys of species abundance and distribution were done to characterize the coastal strands at each site. This consisted of walking along each site and tallying the number of representatives present from each focal species. Ultimately, the survey was used to test for differences between the two coastal strand communities.

Density dependence

To determine the effects of propagule density on herbivory, arrays of different

densities for each species were placed at each study area. Propagules were placed two meters from the base of a tree of the same species and arranged in either a high or low density treatments. The high density treatment consisted of propagules that were clumped together while the low density treatment consisted of propagules that were spaced 1m apart to form a grid pattern (see FIGs. 2a and 2b). In order to reduce the effects

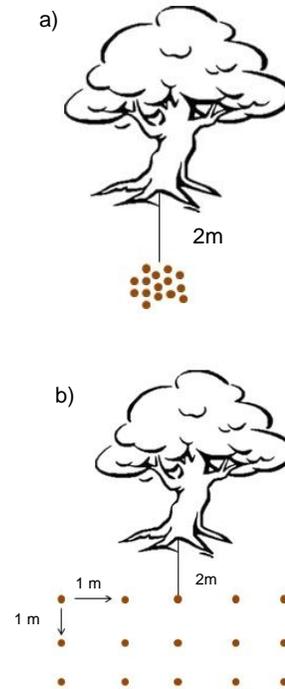


FIG. 2. Experimental set-up for high density (a) and low density (b) treatments.

of confounding factors that could come from propagules already present on the ground, the locations where the experimental manipulations were conducted were first cleared of fallen propagules. Proportion herbivory was recorded for each treatment.

Effects of age

To assess whether the physical state of the propagule had any correlation with herbivory, I set up manipulations that compared young propagules (still attached to fruiting adult tress) to older propagules (resembling those

naturally found on the ground). Set up was similar to that of the density manipulations but instead of differences in spacing, propagules were arranged in clumps of similar age at the base of representative adults.

Shelled propagules

Following similar protocol to the previous sections, this study also looked at herbivory on shelled propagules. The species *Thespesia populnea*, *Calophyllum inophyllum*, and *Terminalia catappa* produced hard shelled fruits with either a large seed or multiple seeds inside. Manipulations for this factor consisted of an unshelled treatment (propagule in its natural state) and a shelled treatment with the hard exterior removed from the propagule to expose just the seed.

Preference tests

To look at preference by large herbivores for certain species, propagule arrays consisting of all focal species were placed at each site. These preference tests were replicated six times and consisted of a member of all focal species placed side by side on the coastal strand. These trials were used to test for differences in selecting any one species over another.

To try and distinguish damage between herbivores, seven randomly caught crabs were brought into the lab and preference trials for all propagule species were conducted. Each crab was subjected to a six day trial during which all propagules of the focal species were placed in its terrarium. The order at which the individual crabs ate or damaged propagules was noted.

Native vs introduced

To determine if the categories of native or introduced had effects on prop herbivory, data from all experimental treatments was averaged and consolidated into two categories. Per Whistler 1992, *C. inophyllum*, *S. taccada*, *C. subcordata*, *B. asiatica*, and *F. berteriana* were classified as native (pre human introduction) while *C. nuciferas*, *T. catappa*, and

M. citrifolia, and *T. populnea* were classified as introduced (polynesian or european).

Intensity of herbivory

To characterize the overall intensity of herbivory on different propagules, proportion herbivory was averaged across all experimental manipulations and differentiated across sites.

Herbivore distributions

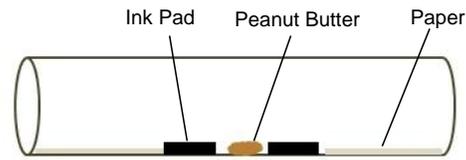


FIG. 3. Track pad design

In order to correlate herbivory with relative abundance of large herbivores at each study area, track pads (FIG. 3) were placed at each focal tree species where an experimental manipulation had been conducted. Track pads were assembled using PVC pipes that were approximately 20 inches long, black paint, white copy paper, and sponges. A very small amount of peanut butter was used as bait in the center of the pvc pipe and paper lined both entrances to ensure that tracks would be attained no matter which entrance the herbivore used. In addition, crab burrows within a 3 m radius of experimental manipulations were counted as a way of quantifying crab densities.

Statistical Analysis

Analysis of data were done using R statistical software package (R Development Core Team 2013). Statistical testing primarily used anovas (aov) and general linear models (GLMs) to test experimental manipulations as well as preference tests.

All models initially included all predictor variables and two-way interactions; p-values were obtained by stepwise model simplification (for GLMs). GLMs were mainly used for presence/absence data (for analysis

of shelled propagules and rat densities) using binomial family distributions.

Tests done using anovas (for density dependence, effects of age, laboratory preference trials, and crab densities) included models that were reduced using backwards simplification. When appropriate, post-hoc Tukey tests were run to make pairwise comparisons.

T-tests were run to compare the relationship between two variables (Native v. Introduced). For non-parametric data (field preference tests) Kruskal Wallis tests were run to test for significance between predictor variables. Pairwise comparisons were made using post-kruskal tests (glht).

Correlation tests using the Pearson method were used to analyze the relationships between rat presence and proportion herbivory as well as between crab presence and proportion herbivory.

Chi-square tests were run to compare species distributions and herbivory intensity across sites as well as herbivore densities across sites.

RESULTS

Field Surveys

The composition of the coastal strands at both study sites were significantly different (χ^2 , $df=9$, $p < 0.001$). Surveys (Appendix A: Tables A1 and A2) showed that the coastal strand of the Gump station was highly dominated by the halophytic species *Scaevola taccada* and *Cocos nucifera* along with other proper strand species including *Terminalia catappa* and *Thespesia populnea*. On the other hand the coastal strand of Mari Mari Kellam's property was comprised largely of *Cocos nucifera* and contained species not present at the UCB Gump station (including *Calophyllum inophyllum*, *Fagraea berteriana*, and *Morinda citrifolia*).

Density dependence

Proportion herbivory on propagules of the focal species was significantly affected by density manipulations and interactions at the species level (FIG.4). Density treatments

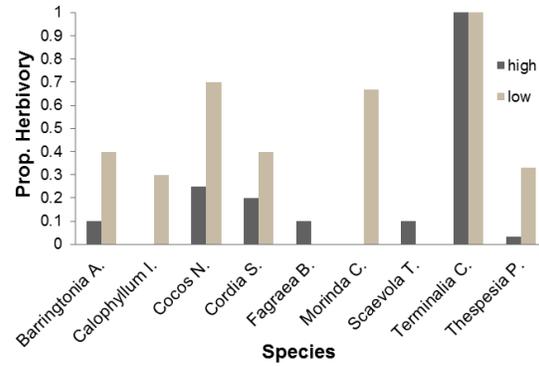


FIG.4. Prop. Herbivory is plotted against propagule species and separated by density treatments (high, low). Species are in alphabetical order.

significantly affected species-level response, with each species reacting differently to the manipulations (Anova: $F_{8,26} = 6.67$, $p < 0.001$). In addition, there was a significant interaction between density treatments, tending towards a negative interaction with high density treatments (Anova: $F = 1.26$, $p = 0.006$). Pairwise comparisons revealed that the species *Terminalia catappa* exhibited the most drastic difference in herbivory when compared to all other focal species (TukeyHSD: $p_{BT}=0.02$, $p_{CT}=0.0004$, $p_{MT}=0.004$, $p_{FT} < .001$, $p_{ST} = 0.007$, $p_{TC} < .001$, $p_{TT} < 0.001$)

Effects of age

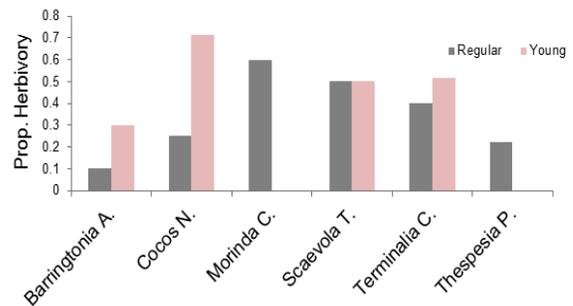


FIG.5. Proportion Herbivory is plotted against species (in alphabetical order) and separated by treatment.

Herbivory did not significantly vary under age manipulations (FIG.5) The interaction factors of age, species, and site had no significant effect on the proportion of herbivory which suggests that there is no correlation between herbivory and the physical state of a dispersal agent. (Anova: $F_{1,16} = 0.002$, $p = 0.964$; $F_{5,16} = 0.800$, $p = 0.569$; $F_{1,16} = 0.004$, $p = 0.952$)

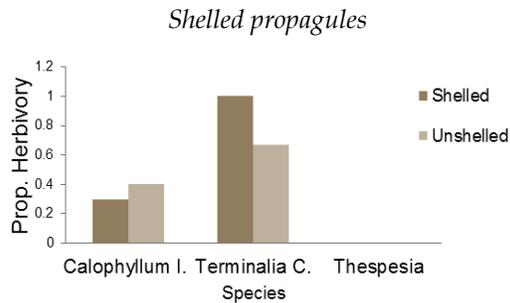


FIG. 6. Proportion herbivory is plotted against the three species that produced shelled propagules. Data is separated by treatment.

Model comparisons determined that the best fit model for these manipulations was one that included site and species as well as the interaction term between treatment and species (GLM (binomial), $df = 1$, $p = 0.014$). Success, defined as whether or not the propagule was damaged/ eaten under shelled and unshelled treatments, was found to significantly depend on the study site (χ^2 value = 12.6, $p < 0.001$). There was also a significant difference in success at the species level (χ^2 value = 46.9, $p < 0.001$). While the treatment itself did not produce significant differences in success (see FIG.6 ; χ^2 value = 1.51, $p = 0.21$), it was found that treatments interacted differently with each focal species and produced significantly different effects on success (χ^2 value = 6.03, $p = 0.01$).

Preference tests

Herbivores on the coastal strand that naturally cause damage to propagules on the ground were found to significantly prefer certain species over others (Kruskal-Wallis, $df = 8$, $p < 0.001$). Pairwise comparisons revealed that the species *F. berteriana*, *M. Citrifolia*, and *S. taccada* were preferred over *B.*

asiatica (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$), *C. inophyllum* (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$), *C. nuciferas* (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$), *C. subcordata* (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$), *T. catappa* (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$), and *T. populnea* (glht: $p = 0.03$, $p < 0.001$, $p = 0.03$). Furthermore, *M. Citrifolia* was preferred over *F. berteriana* (glht: $p = 0.3$) but not over *S. taccada* (glht: $p = 0.3$).

Captive members of the species *C. carnifex*, significantly preferred to damage/consume certain propagules over others (Appendix A: FIG. A3; Anova, $F_{8,54} = 12.3$, $p < 0.001$). Pairwise comparisons revealed that *Scaevola taccada* was preferred over all other propagules. (TukeyHSD: for all comparisons $p < 0.001$)

Native vs. introduced

Proportion herbivory was not significantly different between the categories native and introduced (Appendix A: FIG A1; T-test, $t = 0.41$, $p = 0.69$)

Intensity of herbivory

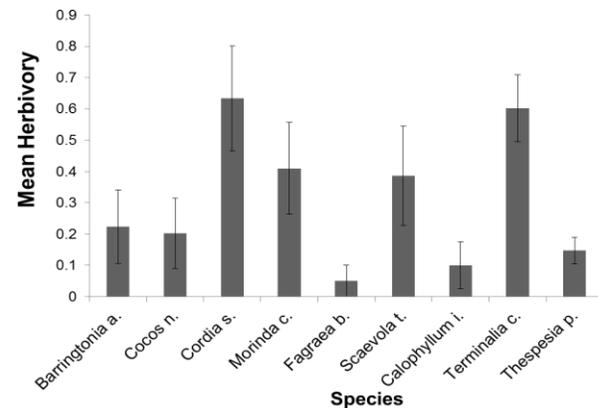


FIG. 7. Proportion Herbivory was averaged over all experimental treatments and plotted against species (± 1 SE)

Intensity of herbivory on the propagules of the focal species did not differ across site (χ^2 , $df = 8$, $p = 0.992$) nor was it significantly different among species (FIG. 7; Anova, $F_{9,8} = 2.52$, $p = 0.103$).

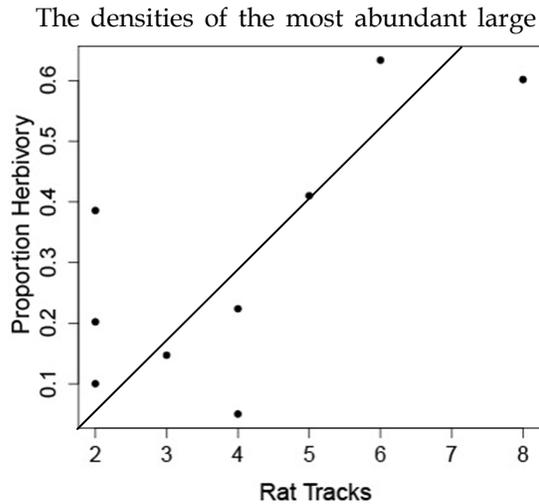


FIG.8. Proportion herbivory is plotted against the average number of rat tracks found at each study species. Each point corresponds to one of the focal species

herbivores did not differ across sites (Appendix A: FIG. A2). While there was no significant difference in the presence of rats at either site (χ^2 , $df = 1$, $p = 0.28$), there was a relationship between the densities of rats present among the focal plant species as well as a significant difference between rat presence and distance from the base of a tree (GLM (binomial), $\chi^2 = 18.9$, $p = .02$; $\chi^2 = 19.6$, $p = .008$)

Number of crab burrows did not vary among site (χ^2 , $df = 1$, $p = 0.35$) but did significantly differ between plant species (Anova, $F_{8,32} = 2.68$, $p = 0.02$). A Post-hoc test revealed no significant pairwise differences, suggesting a model wide difference between the number of crab burrows and the study species.

There was no significant correlation between proportion herbivory and the number of crab burrows. (Pearson's correlation test, $t = 1.25$, $p = 0.21$). There was however, a positive correlation between prop. herbivory and rat tracks (FIG. 8; Pearson's correlation test, $t = 2.82$, $p = 0.02$).

The coastal strand communities sampled were found to differ in community composition but not in intensity of herbivory. Moreover, responses to possible interacting factors affecting herbivory were found to be highly variable.

Coastal strand communities

In congruence with my initial hypothesis, it was found that the distribution of plant species on different coastal strands varied. The variation of vegetation could possibly be explained by the patterns of succession that take place on Oceanic islands. Moorea is a true oceanic island, never having been connected to any continental land mass; therefore, indigenous flora have been completely derived from propagules that were sea, wind, or bird dispersed (Fosberg 1992). Complexity in vegetation is thought to have increased with new arrivals that came with the introduction of humans (Whistler 1992). It therefore makes sense that strand communities would vary as a response to the interplay of vegetative introductions over time. A very large factor that could also play a role in structuring coastal communities is human settlement and modification. The coastal flats of Moorea have been areas of high human presence since Polynesian times and have been subjected to cultivation, clearings, and landscaping with ornamentals; all of which alter plant communities (Fosberg 1992). Apart from anthropogenic induced differences, variation in the coastal strand may also be due to differences in amounts of tidal inundation as well as salinity (Smith 1987).

Density dependence

Results did not support the initial prediction that proportion herbivory was positively correlated with high density treatments. Although studies on continental land masses have experimentally demonstrated that scattered seeds have a lower risk of consumption than aggregated seeds (Mendosinos et. al 2005), I did not find this relationship. Instead, experimental

manipulations suggested that differences at the species level produced varying effects on proportion herbivory, with a trend that indicated the possibility of a negative correlation with high density treatments. This could indicate that oceanic islands follow different patterns of herbivory than continental systems.

For instance, coastal strand communities might exhibit higher instances of herbivore satiation. In general, those plants that escape by predator satiation produce larger amounts of dispersal agents than those that escape through other direct defenses (Janzen 1971). This larger dispersal output could be enough to swamp local herbivores and cause differences in the way each species responded to density. It is also known that dispersal output varies considerably among plants due to differential fecundity and plant size (Nathan and Mueller-Landau 2000). Both these factors could affect herbivore visitation rates to certain tree species and therefore indirectly affect proportion herbivory.

Overall, results suggest that on the coastal strand, herbivory may not be as closely tied to density and that herbivores do not search selectively for clumped aggregations of dispersal units. Further investigation of consumption/damage of propagules, perhaps with a higher number of replicates that also looks at microsite and relative seed output, may determine that habitat characteristics and seed output play more of a role than the densities of the propagules themselves.

Propagule characteristics

Analysis of data supported the notion that certain propagules and characteristics are preferred by coastal seed herbivores over others; this was shown both by herbivory experiments as well as lab and field preference trials.

When analyzing the effects of a dispersal agent's physical state, age did not significantly affect proportion of herbivory on propagules. This might suggest that herbivores ingesting propagules of the focal species might be less concerned with the outer covering and instead interested in the seeds found within dispersal agents. Studies have shown that seeds can be

valuable resources when compared to ripe fruit pulp (Norconk et. al 1998). Norconk's study (1998) suggests that nutrient composition of seeds might be of higher value to herbivores as they are often found to be rich in lipids, sugars, and protein while being relatively low in tannins. It would be interesting to collect observational data on herbivores of the coastal strand and note what part of a propagule they ingest.

Within the propagules that had a shelled exterior, proportion herbivory varied among species and was also partly affected by whether or not the propagule had its shell intact. Variations in herbivory under this manipulation could very well be affected by the foraging behavior of herbivores. As dictated by optimal foraging theory, animals that forage for food should select, from the potential food items encountered, the ones which maximize value relative to cost (Kaufman 1981). Therefore it would depend on the organism acting as the herbivore to choose a food source with the highest value. Whether or not the hull of a particular propagule is edible or an added cost associated with getting at the seed could possibly cause differences in herbivory at the species level.

Both lab and field preference tests indicated that herbivores of the coastal strand had a preference for certain species over others. Field and lab results showed that herbivores exhibited similar preferences, choosing to mainly consume/damage the species *M. citrifolia*, *S. taccada*, and *F. berteriana*. These three species shared the characteristic of having fleshy propagules but varied in size. Of these three species the smaller sized *S. taccada* was the most preferred in both the lab and field. These results were in congruence with my prediction that propagule morphology would play a role in the amount of herbivory received. It makes sense that species with harder fruits such as *C. nucifera* would be less preferred because physical defenses such as hard outer coverings are predicted to reduce propagule damage (Alcantara 2000). Many studies that have looked at morphological traits of dispersal agents have shown that size-related traits, more than size itself, may be responsible for

selection criteria used by herbivores (Alcantara 2000; Kollmann et al. 1998; Janzen 1969). For example, thickness usually correlates with size, and a thicker cover increases the handling time for successfully processing a propagule (Alcantara 2000). This suggests that perhaps *S. taccada* provides the highest value for cost of handling when compared to the other propagules. To come to more conclusive results as to why certain species were preferred over others, future studies could look at palatability by examining tannin concentrations of propagules as well as collect data on handling times for each species.

Results determined that there was no difference in herbivory when the focal species were categorized into either native or introduced. This result contrasted against the notion that introduced species on the island of Moorea would have experienced higher herbivory due to their origin as cultivated crops. Since many introduced species are used for food (Whistler 1992) it would make sense that their fruits would have been selected for size and palatability and as a result might have been subjected to higher levels of herbivory. This relationship was not found.

On the other hand, it could have also made sense that introduced species would have undergone less herbivory. Introduced species often are successful in their establishment because of escape from the effects of their own natural enemies (Torchin et. al 2003). Studies across taxa have shown that introduced populations are often less heavily parasitized than native populations (Torchin et. al 2003). Although for plant species, the release from predators and pathogens depends on the time of introduction (Torchin and Mitchell 2004), it is expected that they would be less affected than natives.

Either way, a difference in herbivory was expected between these two categories. Again, factors such as the time of introduction could have played a role as well as the morphological groupings existing only within one of the categories. Perhaps increasing the number of species under study and having more accurate methods of quantifying

herbivory and damage to dispersal agents would have yielded different results.

Intensity of herbivory

The lack of difference in herbivory across site and species was surprising. It was expected that because of differences in fecundity, size, percent cover, and other biotic factors that the plant species studied would vary. For example *B. asiatica* produces a propagule with a large tough husk that envelops a large nut; the husk has been traditionally used to stun fish by local fishermen (Whistler 1992). Its potentially poisonous properties could have been a factor that affected the intensity of herbivory. Along with that, host-specificity was a factor that was predicted to produce differences in herbivory. During initial observations it seemed that rats on the island of Moorea exhibited specificity to coconuts on the coast, further observations suggested this was not the case.

Herbivore distributions

Preliminary observations revealed that the most common large herbivores that could potentially damage and consume propagules were rats and the land crab, *C. carnifex*. As abundant generalists, a differential distribution of these two groups across sites could have potentially caused large effects on the species composition and intensity of herbivory of plants. Yet analysis showed that densities of these herbivores did not differ by site. This result could perhaps be linked to the fact that there was also no difference in the intensity of herbivory between sites.

Although densities of these herbivores did not differ by site, at the species level, the number of crab burrows and rat tracks (proxies for density) significantly differed by species. This suggests that presences of these herbivores at certain species could have correlations that may affect amount of herbivory. Correlation tests showed that only rat species significantly correlated (positive) with herbivory. This may suggest that rats are responsible for most of the damage to propagules on the coastal strand. It could be that rats are more generalist than land crabs

which are, at least on the island of Moorea, primary consumers of leaf litter and occasionally propagules of *C. inophyllum* and mangrove species (Zerbib 2007). Still, more data is needed in order to be able to differentiate between damage actually done by rats vs. land crabs.

Conclusion

Although this study showed some conclusive results that determined herbivory was affected by differences at the species level, differences in density, and by the interaction between species with shelled/unshelled propagules, there were several factors that could have affected the results.

One major limitation of this study was the inability to differentiate between damage and consumption of a propagule. Because of the inability to physically see the fates of propagules under manipulation (whether they were removed by humans, eaten by herbivores, stepped on, etc.) I had to refer to any damage including removal of the propagule as herbivory. This could have resulted in inaccurate portrayals of the way certain factors affected my study system.

Along with that, the locations of experimental manipulations were a confounding factor that was not addressed. Generalist organisms often base their foraging strategies on amount of cover present (Campbell and Atkinson 2001). Placing manipulations of propagules in open vs. covered areas could have affected the results.

When it came to addressing the densities of herbivores, the proxies used may have not been that accurate. Track pads may not have accurately depicted rat presence (trapping would have provided a better estimate). As for the crabs, relying on crab burrows to estimate density could have also provided an inaccurate estimate as burrows could have been empty.

The findings of this study pose even more questions about the fate of propagules on the coastal strand. For example, how much damage can propagules endure before their germination is affected? This question could be addressed through germination studies that include propagules with varying

intensities of damage. Along with that, future research can focus on dispersal patterns of plant species to see if herbivory correlates with sapling survival.

This study provides a snapshot of herbivory on the coastal strand and its results prompt the question of whether this study could aid in the conservation of coastal habitat. By characterizing differences in the factors that affect herbivory, it might be easier to determine what plan of action to take when employing conservation efforts therefore creating serious implications for the conservation and management of plant species on oceanic islands.

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APPENDIX A

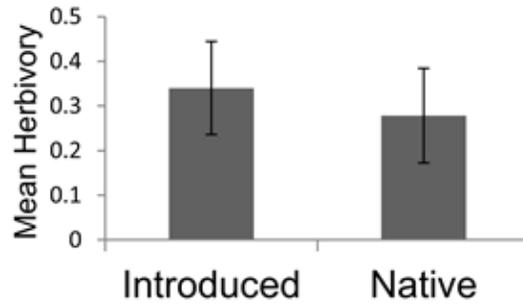


Figure A1: Prop. Herbivory has been averaged over experimental treatments as well as species (± 1 SE) and plotted against the categories of native and introduced

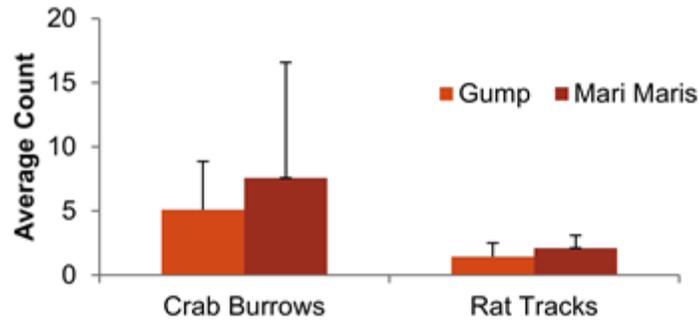


Figure A2: Average counts of herbivore densities plotted by site (± 1 SE)

Tables A1 and A2: Show species count for both study sites

| Table A1: Mari Mari Kellam's | | Table A2: UCB Gump Station | |
|-------------------------------|-------|-------------------------------|-------|
| Species | Count | Species | Count |
| <i>Barringtonia asiatica</i> | 9 | <i>Barringtonia asiatica</i> | 1 |
| <i>Calophyllum inophyllum</i> | 2 | <i>Calophyllum inophyllum</i> | 0 |
| <i>Cocos nucifera</i> | 46 | <i>Cocos nucifera</i> | 13 |
| <i>Cordia subcordata</i> | 5 | <i>Cordia subcordata</i> | 2 |
| <i>Fagraea berteriana</i> | 4 | <i>Fagraea berteriana</i> | 0 |
| <i>Morinda citrifolia</i> | 2 | <i>Morinda citrifolia</i> | 0 |
| <i>Scaevola taccada</i> | 1 | <i>Scaevola taccada</i> | 16 |
| <i>Terminalia catappa</i> | 7 | <i>Terminalia catappa</i> | 4 |
| <i>Thespesia populnea</i> | 1 | <i>Thespesia populnea</i> | 4 |