

A STUDY ON THE HERBIVORY, BIOACTIVITY, AND PHYLOGENETICS OF THE COASTAL PLANT COMMUNITIES ON MOOREA, FRENCH POLYNESIA

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Abstract. Community composition is greatly influenced by many biological interactions, such as competition, mutualism, and herbivory. Oppositely, species assemblage can also incite changes within the community; the emergence of bioactivity in plants to combat herbivory is an example of one such interaction. These components can also be studied from an evolutionary perspective, which can provide insight into trait evolution. This study aimed to investigate the correlations between herbivory, bioactivity, and genetic relationships between the coastal plant species on Moorea, French Polynesia. A survey of 13 plant community transects was completed and percent herbivory and the number of each type of hole was calculated for several leaves of each species at each transect. A phylogeny was also created for the nine plant species included, and herbivory and bioactivity were mapped onto the tree. Herbivory was statistically significant among both transects and species, and hole type varied by species, all suggesting that each community attracts a different set of insect herbivores. Herbivory and bioactivity were significantly correlated, but neither showed correlation with the phylogeny. This suggests that community composition plays a larger role on these interactions than phylogenetics, although outside evidence still advocates for the evolutionary approach to community ecology research.

Key words: coastal plants; angiosperm; community structure; herbivory; bioactivity; phylogenetics; *Barringtonia asiatica*; *Calophyllum inophyllum*; *Cordia subcordata*; *Hernandia nymphaeifolia*; *Hibiscus tiliaceus*; *Inocarpus fagifer*; *Morinda citrifolia*; *Terminalia catappa*; *Thespesia populnea*

INTRODUCTION

Ecological communities are rarely formed by chance; the evolutionary processes by which they develop often lead to a very specific, organized set of organisms with specialized interactions (Crawley 2009, Kraft et al. 2007, Stanton 1983). With natural selection as the driving method, interactions such as competition, mutualism, herbivory, dispersability, and more have a considerable influence on community assemblage (Cavendar-Bares et al. 2009, Gillespie 2004, Raven et al. 2011, Ricklefs 1987, Weiher & Keddy 1999).

A crucial interaction within many terrestrial communities is between insect herbivores and the plant species that they affect. Studies show that this relationship is reciprocal; the species within a plant community determine the insects present, acting as a food source, and those insects in turn determine plant species abundance as they are eaten by the insects (Agrawal et al. 2012, Cavendar-Bares et al. 2009, Gillespie 2004, Raven et al. 2011, Weiher & Keddy

1999). To avoid herbivory, many plants select for resistance traits, such as accumulating bioactive chemicals in their leaves or stems that are toxic to insects (Delphia et al. 2007, Pare & Tumlinson 1999, Walling 2000). If insects can be deferred to other plant individuals by such resistance, then a plant can grow freely and fully compete for niche space; one example of this is some plants are able to flower earlier in the absence of herbivory and accelerate reproduction (Agrawal et al. 2012). Although most plants would benefit, the development of chemical defenses does not occur in every situation and requires selection due to an herbivore threat in the community (Hare 2012). This emphasizes the importance of ecological context in the evolution of defensive traits, particularly community composition at a specific time (Hare 2012, Ricklefs 1987).

The relationships among members of a community can also be expressed in the form of a phylogeny, or evolutionary tree (Webb 2002). Such trees display relationships that can be used to study many different aspects of the community, such as trait evolution,

competition, reproductive success, and niche differentiation (Cavendar-Bares et al. 2009, Emerson & Gillespie 2008, Webb 2002). Phylogenetic analysis can also reveal modes of evolution, such as whether a trait emerged via punctuated equilibrium or gradualism (Kraft et al. 2007, Pagel 1999). This approach is particularly important on islands because of their extreme isolation and low species richness, which makes them model systems for community phylogenetic studies (Keppel 2014, Roderick & Percy 2008).

My research explored the relationship between insect herbivory and bioactivity from the perspective of community composition and phylogenetics. I asked the following questions within the scope of the coastal plant species on Moorea, French Polynesia. How does the bioactivity of these plant species relate to their rates of insect herbivory? Does close phylogenetic relationship correlate with similar rates of insect herbivory or avoidance, or with bioactivity? Do the types of herbivorous insects in a community depend on the specific set of plants present? I hypothesized that community composition has a significant effect on herbivory levels and present insect communities. I hypothesized that bioactivity is negatively correlated with herbivory rates based on previous data and evolutionary plant defense strategies (Chan 2009, Delphia et al. 2007, Pare & Tumlinson 1999, Walling 2000). I also hypothesized that, due to phylogenetic conservatism, plant species that are closely related to one another will display similar levels of herbivory and bioactivity.

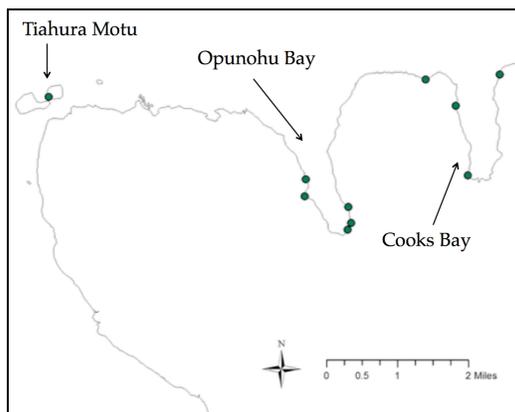


FIG. 1. Sites sampled in this study, indicated by the dots. Each site contained one 50 meter transect, except for the Gump station site which contained four transects.

METHODS

This study was conducted on the island of Moorea, French Polynesia between October 8th, 2014 and December 11th, 2014.

Study site

For logistical reasons, the field sites were limited to coastal strands within Cooks Bay and Opunohu Bay on Moorea (Fig. 1). In addition, the Tiahura motu was also included as a comparison between coral sediment and volcanic island coastal strands. Each site consisted of relatively undisturbed coastal strands where vegetation had grown without obvious human influence (e.g., lack of sea walls obstructing colonization). A total of 10 sites and 13 transects were identified and measured in this study (Appendix A).

Study organisms

From an initial survey of the coastal region in the two bays, several plant species were identified and used for herbivory sampling. These species were narrowed down to only include tree species to make the taxa size more manageable. These tree species included *Barringtonia asiatica*, *Calophyllum inophyllum*, *Cordia subcordata*, *Hernandia nymphaeifolia*, *Hibiscus tiliaceus*, *Inocarpus fagifer*, *Morinda citrifolia*, *Terminalia catappa*, and *Thespesia populnea*. The species were identified based on information found in Whistler's "Coastal flowers of the tropical Pacific" (1980).

Field Survey

A survey of the main coastal plant species was completed via 50 × 4 meter transects at each site within each of the two bays, except for the Tiahura motu site which contained a 50 × 12 meter transect due to the distance of the plants from the shore. Each site contained one 50 meter transect, except for the Gump station site which contained 4 transects. A total of 13 transects were identified and measured in this study. A 50-meter transect tape was laid out along the coast and the location of each individual tree was recorded by species and general size. General habitat description was recorded for each site, including shoreline characteristics, density of plant life, and coral/rock/sand observations.

Leaf collection

To measure percent herbivory, individual leaves were collected for analysis. For each transect, one individual tree of each species present was chosen for leaf collection. Per individual, four branches and five leaves from each branch were collected and photographed (20 leaves total per tree). Each branch faced water-side, left, right, or mountain-side (directions based on the perspective of facing the island from the water). The leaves were selected based on an even spacing from one end of the branch to the other, only choosing fully developed leaves. Each leaf was photographed against graph paper with a label indicating tree number and location on the tree. Using ImageJ, herbivory area and total leaf area was measured and divided in Excel to calculate percent herbivory. In addition, the type of herbivory on each leaf was recorded; the categories included smooth damage on leaf margin (Generalist Orthopterans; grasshoppers, crickets, etc), rough damage on leaf margin (Generalist Lepidopterans; moths and butterflies), smooth holes (Chrysomelidae; leaf beetles, & Curculionidae; weevils), and rough holes (Geometridae; geometer moths, inchworms) (Dyer *et al.* 2010). Appendix B shows the hole type key.

Bioactivity research

The bioactivity of each species was categorized by type, including bioactive and not bioactive. The information on each plant was obtained from a survey of medicinal plants in the South Pacific completed by the World Health Organization (WHO 1998).

Phylogenetic analysis

A tree was created that related all the plant species in this study using Mesquite (mesquiteproject.org) and MRBAYES Bayesian inference of phylogeny (Huelsenbeck & Ronquist 2001). DNA sequences for the *rbcL* gene of each species, which is a commonly used gene in plant phylogeny studies, were collected from GenBank (www.ncbi.nlm.nih.gov/genbank) and aligned by eye (see Appendix C for sequence alignment details) (Gielly and Taberlet 1994). The aligned DNA sequence data was imported into CIPRES (www.phylo.org) and MRBAYES was applied to create a phylogeny (with 2 runs and 4 chains). Mesquite was then

used to map characters onto the tree, including bioactivity and herbivory rates, by square-changed parsimony reconstruction.

Statistical analysis

A Chi-square test was performed on Excel to test the differences in species composition between transects. All other statistical tests were performed in RStudio. Kruskal-Wallis rank sum tests were performed to compare a variety of paired variables. Percent herbivory was the dependent variable and separate tests were run with transect number and species as independent variables. Rank sum tests were performed for each species, with transect as the independent variable and percent herbivory as the dependent variable. Dunn post-hoc tests were performed for each rank sum test to identify specific significance. Rank sum tests were also performed on hole type data for each species, with hole type as the independent variable and number of holes as the dependent variable. An alpha value of 0.05 was used to identify significance for all tests.

RESULTS

Of the 9 tree species, *Hibiscus tiliaceus* (51 individuals), *Inocarpus fagifer* (24) and *Terminalia catappa* (37) were the most abundant species across all transects, but *H. tiliaceus* and *T. catappa* were more spread out among all the sites (found at all but 2 transects), unlike *I. fagifer* which was only found at 3 transects. A wide variety of community compositions were found at the 13 transects (Fig. 2). For example, several transects are mostly dominated by *H. tiliaceus*, such as 1, 2, 3, 6, 7, and 10, while others have a more even array of species composition, such as 4, 9, and 12. The Chi square test also showed significant differences between the transects ($p=7.63e-20$).

Using the percent herbivory measured as described, average percent herbivory for individual transects and species were calculated (Fig. 3A, 3B). Both percent herbivory among transects ($p=2.86e-15$) and percent herbivory among species ($p=8.71e-12$) were statistically significant (Appendix D). Transect 4 was the only one that was significantly different from every other transect, and *T. catappa* was the only species that significantly differed from all other species. In addition, there were significant herbivory differences with all species at

different transects; a graphical representation of herbivory data for *Thespesia populnea* ($p=0.0091$) as an example is shown in Fig. 4, and the p values for all species are shown in Appendix D.

Hole type showed statistical significance for all species except *Calophyllum inophyllum*, *Hernandia nymphaeifolia*, and *Morinda citrifolia*. The average number of each hole type for each plant species is shown in Table 1, and the p

values associated with the Kruskal-Wallis rank sum tests are shown in Table 2.

Five of the nine tree species were bioactive (Table 3), and bioactivity showed significant correlation with average percent herbivory of each species ($p=0.004$).

MRBAYES and Mesquite produced a phylogeny containing the species that was corroborated with a published phylogeny of angiosperms. (Soltis, *et al.* 2000) (Fig. 5A, 5B).

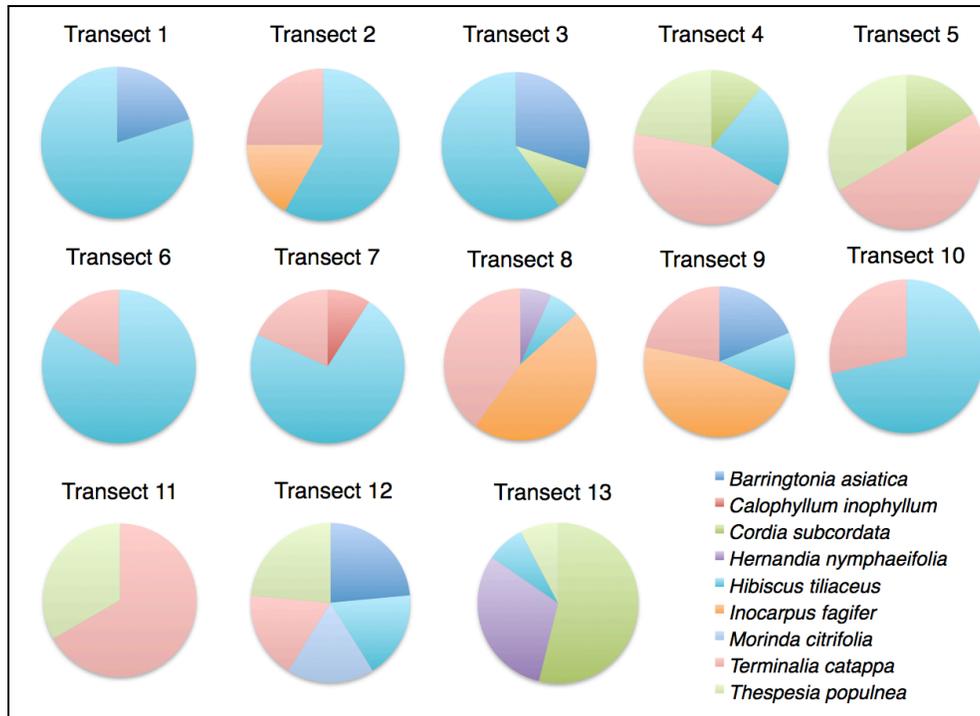


FIG. 2. Charts indicating the percentage of each species present at each transect.

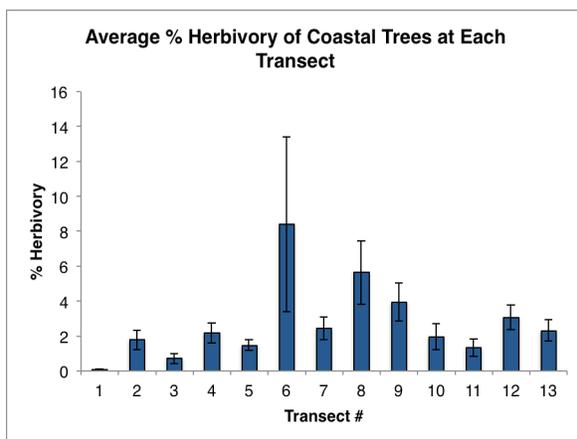


FIG. 3A. Bar chart comparing average percent herbivory with transect number. Error bars represent standard error of data.

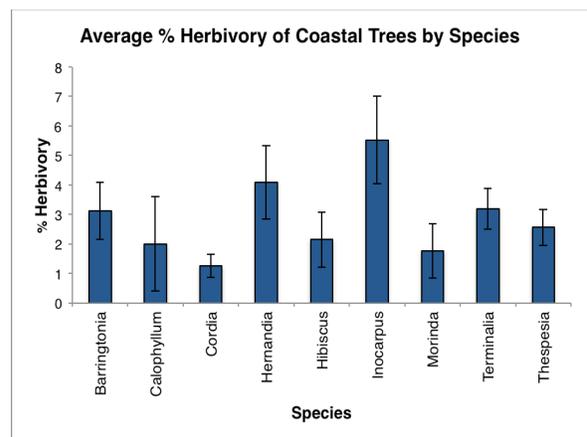


FIG. 3B. Bar chart comparing average percent herbivory levels with species. Error bars represent standard error of data.

TABLE 1. Average number of each hole type for each species. Bold numbers indicate the most abundant hole type for that species.

Species	Smooth margin	Rough margin	Smooth hole	Rough hole
<i>B. asiatica</i>	0.04	0.66	0.05	1.90
<i>C. inophyllum</i>	0.15	0.30	0.00	0.15
<i>C. subcordata</i>	0.03	0.45	0.14	1.09
<i>H. nymphaeifolia</i>	0.00	0.70	0.05	3.00
<i>H. tiliaceus</i>	0.01	0.55	0.02	5.56
<i>I. fagifer</i>	0.02	2.12	0.02	0.87
<i>M. citrifolia</i>	0.20	0.65	0.55	0.45
<i>T. catappa</i>	0.06	2.05	0.14	7.00
<i>T. populnea</i>	0.91	0.31	0.11	0.08

TABLE 2. P values for each hole type for each species. Bold numbers indicate significant differences in hole type for that species.

Species	Smooth margin	Rough margin	Smooth hole	Rough hole
<i>B. asiatica</i>	0.03	2.75e-06	0.03	0.001
<i>C. inophyllum</i>	---	---	---	---
<i>C. subcordata</i>	0.57	4.26e-05	0.001	0.06
<i>H. nymphaeifolia</i>	---	0.11	1	0.29
<i>H. tiliaceus</i>	0.03	1.22e-06	0.62	1.65e-07
<i>I. fagifer</i>	0.37	0.002	0.37	0.002
<i>M. citrifolia</i>	---	---	---	---
<i>T. catappa</i>	0.09	1.86e-09	0.61	2.09e-08
<i>T. populnea</i>	0.002	0.007	0.02	0.4

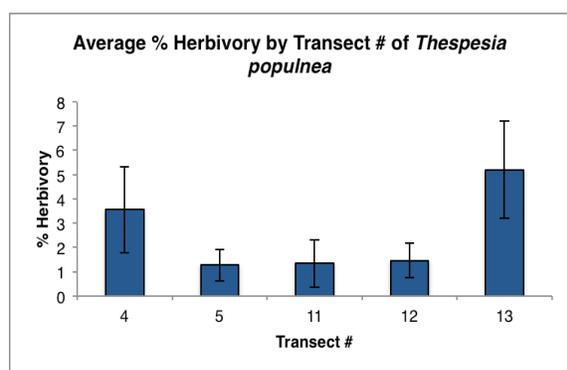


FIG. 4. Bar chart indicating the average % herbivory of *Thespesia populnea* at each transect. Error bars represent standard error of data.

TABLE 3. Average percent herbivory and bioactive status of each species. "+" indicates that the species is bioactive, and "-" indicates that the species is not bioactive.

Species	Average % Herbivory	Bioactive Status
<i>B. asiatica</i>	3.11	+
<i>C. inophyllum</i>	2.00	+
<i>C. subcordata</i>	1.25	-
<i>H. nymphaeifolia</i>	4.09	-
<i>H. tiliaceus</i>	2.14	-
<i>I. fagifer</i>	5.52	-
<i>M. citrifolia</i>	1.76	+
<i>T. catappa</i>	3.19	+
<i>T. populnea</i>	2.56	+

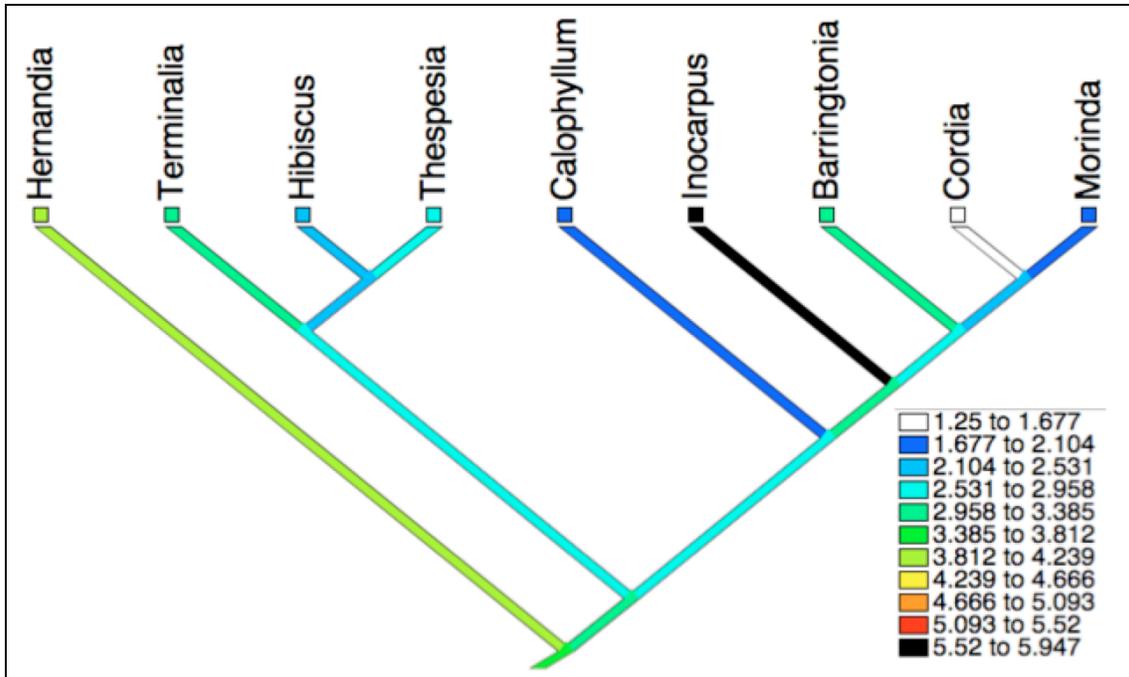


FIG. 5A. Phylogeny with % herbivory mapped onto the tree. Each color represents a range of percent herbivory, which associates with the branch colors on the tree.

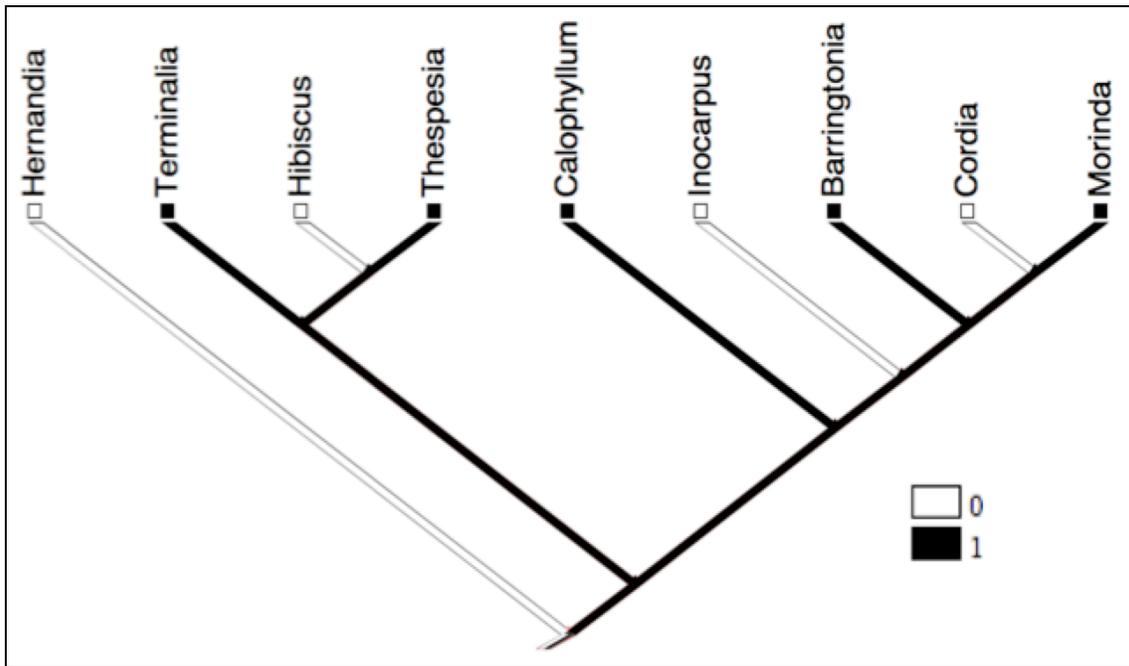


FIG. 5B. Phylogeny with bioactivity mapped onto tree. Bioactive species are represented on the tree by the color black, and not bioactive species are represented by white, according to the legend.

DISCUSSION

The significance of species composition between transects supports my hypotheses; transect differences would be necessary to detect herbivory differences caused by community variation. The high incidence of varying community composition hints at the prospect of other major differences between transects, such as herbivore populations (Stanton 1983). A limitation of the survey study was the imbalanced number of individuals per species. With more locations and altered methods, the survey could have yielded a balanced design, which would have allowed additional analysis to be possible.

Average percent herbivory showed quite a significant difference among both transects and species (Fig. 3A, 3B). The significance among transects directly suggests that there are differences between them, although this could be referring to previously shown community variation. The additional significance of herbivory among species supports the hypothesis that there are different insect communities present at each transect, likely due to the species present at the site. This is corroborated by varying herbivory levels among several species at different transects (Fig. 4, Appendix D). Assuming that the chemical and structural components of the species remain the same regardless of location, different insect populations are likely present at each site, either in amount or type of insect. This suggests a constant push and pull between the effects that community and species have on herbivory in which the insect herbivores are influenced by community composition as well as the properties of individual species.

Since the community composition of Transect 13 (Tiahura Motu site) had significantly different community composition, I expected that it might also yield different herbivory results. Transect 13 was only different from five of the twelve other transects (Appendix D), suggesting that the coral sediment (instead of volcanic rock) does not highly affect insect herbivory at this site.

To support these conclusions further, hole type data showed significant differences for several species and hole types. Both bioactive (*Barringtonia asiatica*, *Terminalia catappa*, and *Thespesia populnea*) and not bioactive (*Cordia subcordata*, *Hibiscus tiliaceus*, and *Inocarpus fagifer*) species showed significantly different hole types, providing further evidence that

insect populations differ in composition between sites. The rough holes (Geometer moths, inchworms) yielded the highest number of holes on average for five of the nine species (Table 1), suggesting that Geometridae herbivores were dominant for those species. The rough margin holes yielded the highest number of significant p values across species (Table 2), indicating that Generalist Lepidopterans (moths and butterflies) demonstrate the most varied herbivory levels of the four insect types studied. This could be because some Lepidopterans have adapted to withstand certain bioactivity in plants, allowing them to eat both bioactive and not bioactive plants as shown by these results (Table 3). Another study described the ability of some Lepidopteran herbivores to detoxify benzoxazinoids in plants (Wouters *et al.* 2014), and it is possible that a similar effect occurred in this case. A future study could expand on the insect species that are found to eat these plants, possibly by conducting experimental trials to compare which plants that insects from different sites choose to eat (Prado 2006). One could also expand on the insect types found between sites to determine exactly which insects are found at specific locations.

One limitation of the herbivory study was the selection of leaves that could be picked for analysis. Many of the trees were quite tall with most leaves out of reach, which greatly limited which leaves would be analyzed, as well as which trees were sampled. The insect herbivory key was also not ideal for this study as it was created for a different location; a key for the specific insect herbivores of Moorea would have been preferable. Third, the statistical analysis could have been affected by the large number of leaves with no herbivory, possibly skewing the results with too many zeros; altering the analysis could help prevent this.

As shown in many other previous studies (Delphia *et al.* 2007, Pare & Tumlinson 1999, Walling 2000), bioactivity and herbivory levels are significantly correlated (Table 3). Despite the herbivory differences found within species, there is still significant correlation between species and bioactivity regardless of location. The presence of bioactivity in some plants could even be the reason for any correlation between herbivory and species, especially when herbivory already varies by transect. The only stark outlier is *Cordia subcordata*, which had the lowest average percent herbivory, despite not showing any bioactivity (Fig 3B). This discrepancy could be

due to a structural aspect of the *C. subcordata* leaves that turns insects away.

The herbivory and bioactivity characters mapped on the phylogeny in Fig. 5A and 5B imply that they are not correlated. No cluster of herbivory level is perceived on the phylogeny, and bioactivity seems as uncorrelated as possible. These characters are examples of homoplasy, and bioactivity could even be considered maximally homoplastic, meaning that the trait evolved independently in each species. The evidence in this study suggests that genetic relationships do not play an active role in the herbivory or bioactivity of these plant species. This lack of correlation further supports the great effect of community composition and bioactivity on herbivory levels.

Overall, this study showed a large significance between herbivory, site, species, and bioactivity, indicating that the transect communities are different in both plant and insect populations. The differences in hole type among the leaves also supports this conclusion. Despite the lack of correlation of phylogeny with bioactivity and herbivory, there is still much evidence supporting this aspect of community ecology research (Cavendar-Bares *et al.* 2009, Kraft *et al.* 2007, Jablonski 2008, Roderick & Percy 2008). With a larger group of taxa and more varying bioactivity levels, a pattern between these characteristics may emerge in a future study. One could also make a comparison between the plant species on both mainland and island, for example between Australia and Moorea, to see if the insect population differ or interact differently with the plants. This study emphasizes the importance of how species composition influences biological interactions within a group of species, and demonstrates how these interactions can determine the fate of an entire community.

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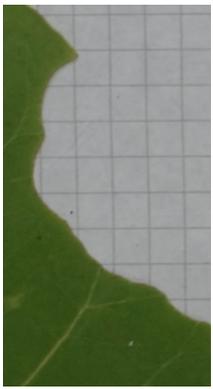
APPENDIX A

GPS data indicating all 10 sites found in this study and corresponding transects.

Site Name	GPS	Transect #
Medical lab	S 17° 29.127' W 149° 49.020'	1
Are's Market	S 17° 30.359' W 149° 49.448'	2
Gump Station	S 17° 29.489' W 149° 49.587'	3, 4, 5, 6
B/w Bays	S 17° 29.175' W 149° 49.969	7
Mari Mari Kellum's	S 17° 30.456' W 149° 50.588'	8
White Bridge	S 17° 30.923' W 149° 50.950'	9
Black Sand Beach	S 17° 31.005' W 149° 50.996'	10
Magasin Urufara	S 17° 30.586' W 149° 51.539'	11
Storage Containers	S 17° 30.376' W 149° 51.522'	12
Tiahura Motu	S 17° 29.201' W 149° 54.456'	13

APPENDIX B

Examples of the different hole types observed in this study and the insects associated with them. Hole types include smooth edge, rough edge, smooth hole, and rough hole. This key originates from Lee Dyer's herbivory key for *Piper* plants in Costa Rica (2010).

	Smooth Margin	Rough Margin	Smooth Hole	Rough Hole
Example Leaf				
Insect Type	Generalist Orthopterans (grasshoppers, crickets, etc)	Generalist Lepidopterans (moths and butterflies)	Chrysomelidae (leaf beetles) & Curculionidae (weevils)	Geometridae (geometer moths, inchworms)

APPENDIX C

GenBank accession numbers, taxonomic names, and location of sample collection for the *rbcL* DNA alignment sequences used to create the phylogeny presented in this study. Sequences were aligned by eye using Mesquite.

Accession numbers	Taxonomic names	Location of sample collection
EU980812.1	Barringtonia asiatica	New Caledonia
HQ332016.1	Calophyllum inophyllum	n/a*
JQ626086.1	Cordia sp.	n/a
KF496470.1	Hernandia nymphaeifolia	n/a
AY289678.1	Hibiscus tiliaceus	n/a
JN083773.1	Inocarpus fagifer	n/a
AJ318448.1	Morinda citrifolia	New Guinea
FJ381811.1	Terminalia catappa	n/a
GU981732.1	Thespesia populnea	n/a

*Most sample locations not found on GenBank or associated papers.

APPENDIX D

P values from the Dunn tests comparing herbivory across transect and species pairs. Column and row headings of each cell indicate the two variables that were included in the test. Bolded numbers indicate significant value. Overall p values from the Kruskal-Wallis tests are above each corresponding table.

Site Comparison ($p=2.86e-15$)

Transect	9	3	12	1	10	4	8	7	6	2	13	5
3	0.0007											
12	0.0048	0.254										
1	0.0000	0.051	0.0096									
10	0.0000	0.0504	0.0106	0.4523								
4	0.0000	0.0000	0.0000	0.0000	0.0000							
8	0.0000	0.0051	0.0006	0.1324	0.176	0.0004						
7	0.0000	0.0077	0.0009	0.1967	0.2513	0.0001	0.3727					
6	0.0000	0.0016	0.0001	0.0792	0.1178	0.0003	0.4242	0.2887				
2	0.0000	0.0029	0.0004	0.0709	0.0979	0.0038	0.3224	0.22	0.3755			
13	0.0001	0.2067	0.0793	0.2811	0.2578	0.0000	0.0691	0.1009	0.0417	0.038		
5	0.0000	0.0006	0.0000	0.0472	0.0791	0.0004	0.3556	0.2198	0.4265	0.4286	0.0261	
11	0.0000	0.0182	0.0026	0.3104	0.3676	0.0000	0.2556	0.3599	0.1798	0.1434	0.1627	0.1249

Species Comparison ($p=8.71e-12$)

Species	<i>Barringtonia</i>	<i>Calophyllum</i>	<i>Cordia</i>	<i>Hernandia</i>	<i>Hibiscus</i>	<i>Inocarpus</i>	<i>Morinda</i>	<i>Terminalia</i>
<i>Calophyllum</i>	0.1823							
<i>Cordia</i>	0.3308	0.2644						
<i>Hernandia</i>	0.0604	0.0271	0.0282					
<i>Hibiscus</i>	0.4002	0.2034	0.3907	0.0262				
<i>Inocarpus</i>	0.0208	0.013	0.0073	0.408	0.0045			
<i>Morinda</i>	0.3945	0.1766	0.2931	0.1969	0.3345	0.1382		
<i>Terminalia</i>	0.0000	0.0002	0.0000	0.0375	0.0000	0.0381	0.0104	
<i>Thespesia</i>	0.2075	0.3349	0.3618	0.0119	0.2296	0.002	0.22	0.0000

Species comparison by transect

Barringtonia asiatica ($p=4.024e-07$)

Transect	9	3	12
3	0.0461		
12	0.0002	0.0327	
1	0.0000	0.0002	0.0307

Cordia subcordata ($p=0.353$)

Transect	3	5	4
5	0.3473		
4	0.2803	0.4249	
13	0.0429	0.0926	0.128

Hernandia nymphaeifolia ($p=0.403$)

Transect	8
13	0.2015

Hibiscus tiliaceus (**p=2.836e-08**)

Transect	9	10	3	4	8	12	7	6	1	2
10	0.349									
3	0.058	0.025								
4	0.0071	0.0023	0.1894							
8	0.0000	0.0000	0.0007	0.0107						
12	0.0002	0.0000	0.0255	0.1418	0.1099					
7	0.0005	0.0001	0.0438	0.2036	0.0707	0.4039				
6	0.0057	0.0018	0.1687	0.4684	0.0132	0.1604	0.2268			
1	0.0000	0.0000	0.0068	0.0561	0.2386	0.3029	0.2238	0.0657		
2	0.0000	0.0000	0.004	0.0382	0.2989	0.2422	0.1729	0.0453	0.4273	
13	0.0168	0.006	0.29	0.372	0.0043	0.081	0.124	0.3424	0.0278	0.018

Inocarpus fagifer (**p=0.02**)

Transect	9	8
8	0.1488	
2	0.0034	0.0483

Terminalia catappa (**p=0.0004**)

Transect	9	10	4	8	12	7	5	6	11
10	0.4086								
4	0.2106	0.2833							
8	0.0004	0.0008	0.0049						
12	0.0859	0.1281	0.287	0.0218					
7	0.1051	0.0689	0.0198	0.0000	0.0044				
5	0.3575	0.2755	0.1211	0.0001	0.0417	0.1874			
6	0.2126	0.1518	0.0546	0.0000	0.0152	0.3244	0.3328		
11	0.4771	0.3864	0.1944	0.0003	0.0772	0.116	0.3791	0.2297	
2	0.4853	0.423	0.2214	0.0004	0.0918	0.0986	0.3438	0.202	0.4624

Thespesia populnea (**p=0.0091**)

Transect	12	4	5	11
4	0.1967			
5	0.0568	0.2332		
11	0.4714	0.1774	0.0491	
13	0.0296	0.0031	0.0003	0.0348