

UNTANGLING INVASION DYNAMICS: EVALUATING THE ENEMY RELEASE HYPOTHESIS WITHIN PLANT COMMUNITIES ON MOOREA

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Abstract. The enemy release hypothesis is a widely studied hypothesis that explains the success of invasive species through their release of natural predators, resulting in less predation of invasive species when compared to native counterparts. Studies of the enemy release hypothesis largely focus on the dichotomy between native and invasive plants with a strong focus on continental systems. This study aims to take a novel approach by studying the enemy release hypothesis amongst native, resident, and invasive plants on the small isolated oceanic island system of Moorea. To evaluate this hypothesis, 12 plants were selected, 4 within each group (native, resident, and invasive) and were then analyzed for the percent, diversity, and specialization of herbivory. Plants were selected based off abundance within the Opunohu Valley comparisons between species. 50 leaves were collected from the forest floor within a 3-meter radius of the study plant, and herbivory damage was analyzed according to damage type, percent damage, diversity of damage, host specificity, and functional feeding group of damage. This was repeated for 5 different individuals for each of the 12 study species, making a total of 60 sites where leaves were collected. Native and Resident plants were found to have significantly more damage, diversity of damage and more specialized damage when compared to their invasive counterparts, suggesting strong support for the enemy release hypothesis. While significant differences were found amongst native and invasive plants, very few significant differences were found between native and resident plants, suggesting the naturalization of those species on the island. The enemy release hypothesis in part explains the success of invasive species on Moorea as their escape from natural specialist predators is a major factor in their invasion. It also begins to explain plant insect evolutionary relationships by illustrating that more time spent in this system results in increased predation. Thus, allowing for insect adaptation alongside plants creating uniquely specialized relationships.

Key words: *enemy release hypothesis; plant-insect interactions; leaf litter; French Polynesia; insect herbivory; biotic resistance; invasion*

INTRODUCTION

Native ecosystems and their biodiversity are increasingly threatened by the introduction of invasive exotic species, which can quickly proliferate, cause habitat degradation, outcompete native species, and drive changes in species distributions, declines, and extinction (Mainka and Howard 2010). The enemy release hypothesis (ERH) suggests that part of an invasive species' success comes from the fact that when introduced to a new ecosystem, they are freed from their natural predators and receive less predation than they would in their native environment (Wolfe 2002). This hypothesis is rooted in the prediction that native species coevolved with their predators and therefore are more susceptible to predation than non-native exotic species (Wolfe 2002). Evidence in support of the ERH comes from a variety of systems, combining theories of biological invasion (Lonsdale

1999, Kolar and Lodge 2001, Ludsin and Wolfe 2001) with our understanding of evolutionary relationships and coevolution, (Thompson 1989, Berenbaum 1990, Hougen-Eitzman and Rausher 1994) with a myriad of studies confirming these theories and finding support for the ERH (Liu and Stiling 2006, Morrison and Hay 2011, Harvey et al. 2015).

However, another body of research led to the development of the biotic resistance hypothesis; which suggests that rather due to the coevolution of predators and prey, native species will have evolved specific adaptations to defend against their native predators while invasive species will not, and therefore be more susceptible to predation (Maron and Vilà 2001). The study conduction by Maron and Vilà was one of the first to reevaluate the ERH, utilizing empirical studies to conclude that the ERH does not always prevail. They suggest that differences in life history traits and demographics of

herbivore populations dictate which of the two hypotheses are the most likely explanation (Maron and Vilà 2001). The reevaluation bolstered support for the biotic resistance, and studies that failed to find support for the ERH have turned to theories like biotic resistance for the alternative results (Morrison and Hay 2011, Beaury et al. 2020, Dias et al. 2020).

More recent research has emphasized that both the enemy release and biotic resistance hypothesis can both be at play in a given ecosystem. In particular, the biotic resistance hypothesis emphasizes the effect of native diversity and generalist predator populations, while the ERH puts emphasis on the effects of specialist predators (Tallamy et al. 2010). Consequently, while invasive species may escape their native specialists and experience reduced predation in accordance with the ERH, they can also encounter large generalist predator populations that native species are adapted to defend against, which aligns with the biotic resistance hypothesis (Morrison and Hay 2011). Understanding whether the ERH or biotic resistance, or both, are at play in a given ecosystem almost always requires specific studies of these contrasting effects.

The ERH is rooted in predictions on evolutionary relationships between specialist predators and prey, therefore selecting systems that have large native specialist predator populations is important. Phytophagous insect predators are largely specialists, having extreme host specificity, with many evolving adaptive traits to tolerate or sequester plant toxins (Stotz et al. 1999). Insects are highly diverse in their methods of herbivory and cause a variety of unique damage types which can be grouped into functional feeding categories such as leaf mining, surface feeding, hole feeding, margin feeding, skeletonization, etc. (Labandeira et al. 2007). Damage types are a trait-based, functional, representation of insect taxa, measured by herbivory damage, and serve as indicators of how insects access the foliage of a plant (Swain et al. 2022). While it is often hard to discern the exact insect creating the damage type, damage types as a whole can allow us to understand the diversity of insects feeding on certain plants. Hence, higher damage type diversity suggests higher diversity of insect predators.

To understand the ERH in relation to plant-insect interactions, it is important to consider the principal interactions at play in almost all plant-insect communities. Each plant is affected by its own specialist herbivores that selectively feed on that plant as well as generalist herbivores that effect the majority of plants. The ERH then relies on the assumption that introduced plants are no longer

affected by their specialist herbivores due to the absence of those specialists in the new (introduced) region (Keane and Crawley 2002). However, that simple assumption is not always the case as host plant preference can be plastic and introductions of plants can cause shifts in insect herbivory preferences (Bernays 2001). In fact, prior studies have revealed varying outcomes in insect response to non-native introductions; some studies have shown invasive plants being suitable or even preferred by insect populations (Parker and Hay 2005, Reddy et al. 2011, Schultheis et al. 2015), while other studies have found invasive plants being toxic or resistant, with insect populations strongly favoring native plants (Keeler and Chew 2008, Cincotta et al. 2009, Ding and Blossey 2009, Tallamy et al. 2010). Factors such as invasive species chemistry, evolutionary relationships to native species, and native plant diversity all play a role in the ability of introduced species to escape predation (Bezemer et al. 2014).

Many studies have explored the relative importance of ERH and biotic resistance, but most have focused their efforts on mainland communities or more diverse communities with large generalist populations (Morrison and Hay 2011, Harvey et al. 2015). A smaller number of studies have focused on small, isolated islands with lower diversity (but see Norghauer et al. 2011). Smaller more remote oceanic islands often lack the diversity and complexity of mainland systems, providing a unique opportunity to study evolution as isolation allows for rapid population change and adaptation (Schofield and George 1997). For this same reason, remote islands communities are specifically vulnerable to invasion, stressing the importance of studying hypothesis like the ERH in systems like these (Mueller-Dombois and Loope 1989, Paulay 1994, Kueffer et al. 2010).

The overall goal of this study is to test the enemy release hypothesis by characterizing how different types of insect damage are distributed across a suite of native, invasive, and resident plants on the island of Moorea in French Polynesia. Moorea provides an excellent opportunity to test the ERH because it is a small, isolated island which is not only vulnerable to invasion but also provides a unique opportunity to study evolution, as mentioned previously. (Vitousek 2002, Warren et al. 2015), DiNapoli and Leppard 2018). Therefore looking at the ERH on Mo'orea within plant communities will provide unique insight into methods of invasion and help us understand evolutionary dynamics on isolated islands, untangling relationships between native plants and their natural predators. In addition, adding the intermediate resident category will

introduce a unique facet that is often ignored within studies of the ERH. In particular, I will test these ideas by analyzing herbivory and diversity of herbivory among native, resident, and invasive plants as well as between confamilial species pairs. Based on the enemy release hypothesis, I predict that (i) leaf damage will be greatest on native species due to the coevolution of insects and native host plants and that damage will be least prevalent on invasive species due to their evasion of predators in this new ecosystem. (ii) I further predict that damage type diversity will be greatest among native plants due to greater diversity of herbivores feeding on native plants, as they affected by a larger suite of both generalist and specialist predators. (iii) Finally, within confamilial pairs, damage differences will be amplified, and native plants will exhibit more damage than their resident or invasive counterparts.

METHODS

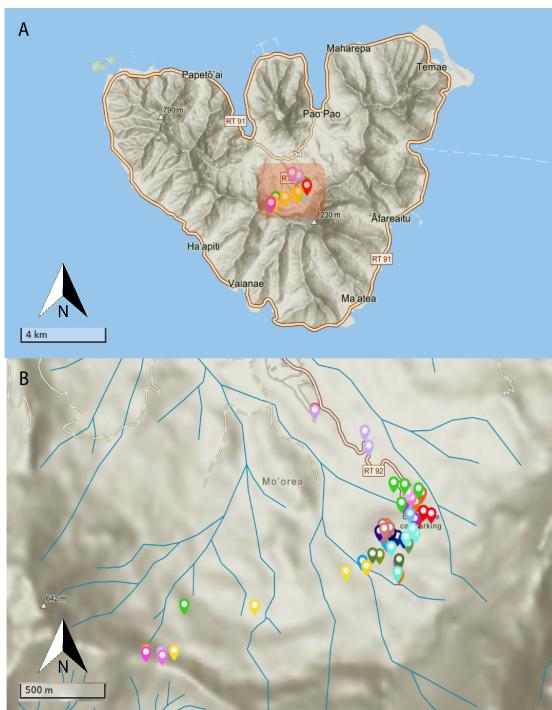


Fig 1. Maps of Mo'orea, French Polynesia displaying collection sites. Map A shows location of collection within the island at large with region shown in map B highlighted in red. Map B shows a zoomed in view of collection sites and has plots of localities of all plants sampled color coded by species.

Study sites

This study took place on Mo'orea, a small, isolated, volcanic island that forms part of the Society Islands in French Polynesia. Data collection took place from 4 October to 5 November 2023; from the end of the dry season moving into the wet season. Data was collected in a mid-elevation tropical forest in the Opunohu Valley between elevations of 200-400 meters in the Belvedere Lookout area, primarily along the Three Coconuts Trail (-17.540473, -149.826608). Moorea's forests have relatively low species diversity and a high number of invasive plants with native plants being concentrated in higher elevation habitats (Meyer and Florence 1996, Pouteau et al. 2012). The forest in the Opunohu Valley is characterized by high canopy cover and heavy leaf litter with a high density of low-lying shrubs and ferns along the forest floor.

Study species

This study investigated 12 abundant plant species in the Opunohu Valley on Moorea. These 12 species were grouped into the following categories: Native, Resident, and Invasive, with 4 species in each of those respective groups. The species were selected due to their relative abundance, presence within the same region, and to control for phylogeny, multiple species within the same genus or family were selected to act as points of more direct comparison (See Appendix A, Table B).

Leaf litter collection

Plots were selected by finding a study species within the forest of the Opunohu Valley between 200 and 400 meters in elevation. For each site, I walked 5-10 meters off the trail into the forest and randomly collected 50 leaves of the study species from the forest floor, within a 3-meter radius of the study species. Leaf litter was collected as an indirect method that allowed for a fuller survey on the entire plant including the upper canopy regions. The GPS coordinates of each site, canopy cover, weather conditions, and major surrounding vegetation were recorded. Collected leaves were pressed and numbered in accordance with the site collected and given a unique numerical ID. This process was repeated at 5 different sites for each of the 12 representative species, making a total of 60 sites and 3,000 individual leaves.

Herbivory analysis

Leaves were analyzed to determine the functional feeding group of the damage, specific damage type (DT), host specificity, percent damage (herbivory index), and specificity of damage. Each

data point represents a specific damage type on a leaf, if multiple damage types were present on a leaf, it received multiple data entries; leaves that did not have damage were recorded as NA and marked as 0 in the percent damage category. Leaf damage was sorted into categories based on how the insect accessed the leaf tissue. The functional feeding categories were as follows: hole feeding, margin feeding, surface feeding, mining, galling, skeletonization, oviposition, piercing and sucking, and fungal damage (Labandeira et al. 2007). Damage was then categorized more specifically into one of the 150 specific damage types described in the “Guide to Insect Damage Types on Compressed Fossils” (Labandeira et al. 2007). Damage specificity was further categorized using a host specificity score from 1 to 3, with 1 being most generalized and 3 being most specialized (Labandeira et al. 2007). Certain damage types could not be categorized using the “Guide to Insect Damage Types on Compressed Fossils” and in such instances, I categorized these leaves by providing my own damage type numbers, labeled as MDT (see appendix A, Fig. A). Finally, an herbivory index was estimated by determining the percent of the leaf affected by damage. A grid was used to maintain consistent estimation of percent damage, and randomly selected leaves from each site were re-evaluated to ensure consistency of estimation.

Statistical analyses

To test for differences in overall herbivory within my study species I ran a nested ANOVA comparing the percentage of leaves with herbivory within each species nested by group (Native, Resident, Invasive). I calculated the percent of leaves affected by herbivory for each of the 5 sites for each species and utilized those data points for my ANOVA. Leaves with more than 1.5% total herbivory were considered damaged by herbivory, while any leaf with 1.5% or less herbivory was considered undamaged.

To analyze the diversity of herbivores, I first calculated the Shannon Diversity Index for each site. I then utilized those values to run a two-way ANOVA to investigate the drivers of leaf damage due to herbivory on each of the 12 species and 3 groups. I performed a rarefaction analysis looking at the number of leaves collected versus the number of different damage types observed for each of my major groups (native, resident, and invasive). I then ran an ANOVA to test for differences among total damage diversity collected for the three groups. This allowed me to understand if I collected a sufficient sample of leaves to represent the diversity of damage types within the population and compare the

total captured diversity between the three groups. I further ran a nested ANOVA to look for differences in the distributions of damage between native, invasive, and resident plant damage across functional feeding categories. Finally, I utilized the host specificity values defined by the “Guide to Insect Damage Types on Compressed Fossils” to run a one-way nested ANOVA to determine differences in the specificity of damage types between my different groupings.

I repeated my herbivory diversity tests and percent herbivory tests between my selected confamilial pairs. I utilized t-tests and chi-square tests to analyze the differences in percent damage and damage diversity between *Lantana camara* and *Duranta erecta*, *Hibiscus tiliaceus* and *Hibiscus rosa-sinensis*, and *Neonauclea forsteri* and *Morinda citrifolia*. For my confamilial trio, I utilized an ANOVA to look at the percent damage and damage diversity between *Metrosideros collina*, *Syzygium cumini*, and *Syzygium malaccense*.

RESULTS

(i) Percent Herbivory Across Native, Resident, and Invasive Species

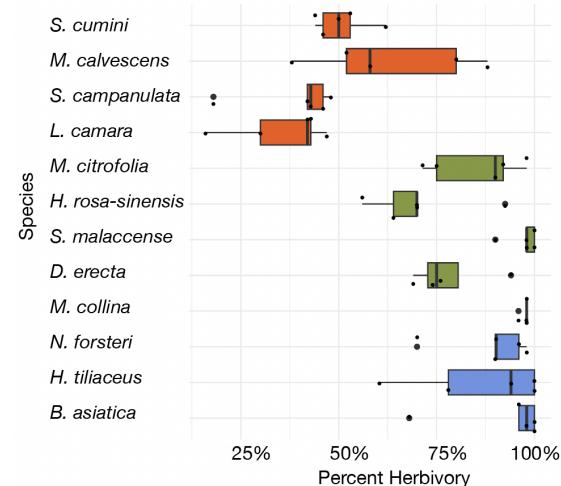


Fig. 2 Boxplot of the percentage of leaves affected by herbivory for each site compared across species, grouped into Native(blue), Resident(green), and Invasive(orange) categories . (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site)

Differences in the percent of leaf damage found at each site were significant between the plant groups (native(blue), resident(green),

invasive(orange)) (ANOVA, $p < 0.001$, $F = 51.71$). Significant differences were observed between native and invasive ($p_{adj} < 0.001$) as well as resident and invasive plants ($p_{adj} < 0.001$) however no significant differences were found between native and resident groups. The results show native and resident plants receive significantly more damage than invasive plants (Fig. 2).

(ii) Herbivory Diversity Across Native, Resident, and Invasive Species

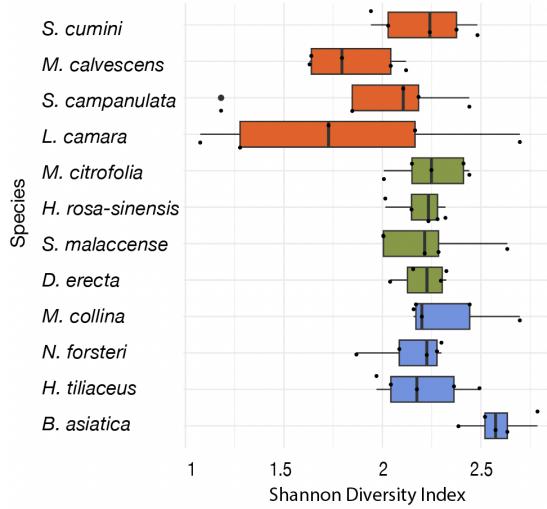


Fig. 3 Boxplot of Shannon diversity index distributions of damage type across each species further group by color into the categories, Native(blue), Resident(green) and Invasive(orange). (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site)

Shannon diversity was calculated for the damage types found within each site and compared across groups with significant differences found between the groups (ANOVA, $p < 0.001$, $F = 7.698$). There was significantly more diversity found in native sites when compared to invasive sites ($p_{adj} = 0.0005944$) and more diversity found in resident sites when compared to invasive sites ($p_{adj} = 0.028116$). Shannon diversity was highest in native plants and lowest in invasive plants with resident plants falling in the middle (Fig. 3). No significant differences were found between native and resident species.

The number of unique damage type occurrences was tabulated for each site and when compared, significant differences of the total diversity of

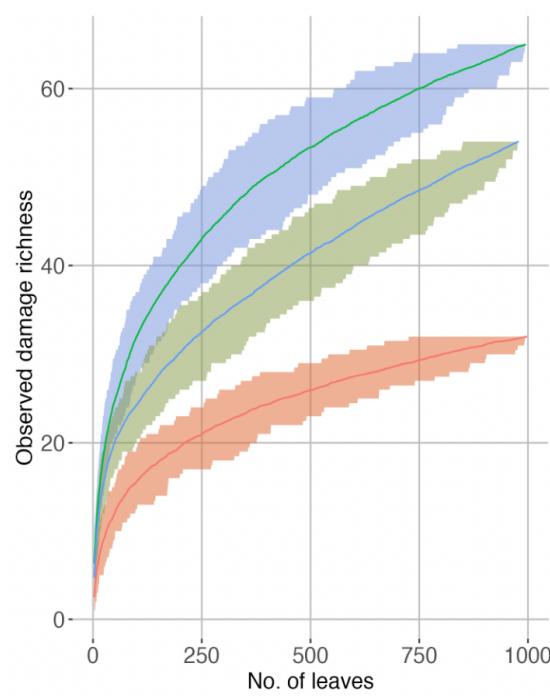


Fig. 4 Rarefaction Curve showing number of unique damage types accumulated as the sample size of leaves increases. Grouped into native(blue), resident(green) and invasive(orange) categories. Shaded region

TABLE 1. Unique damage types found within each species and their number of occurrences.

Species	Unique Damage Types for Species
B. asiatica	DT43(2), DT37(3), DT128(1), MDT06(20), DT17(1), DT68(1), DT59(1)
H. tiliaceus	DT79(2)
H. rosa-sinensis	DT125(1), DT184(1), DT122(1)
N. forsteri	MDT02(41)
S. malaccense	DT20(1), DT57(1), MDT01(216)
M. calvescens	DT07(1)
S. cumini	DT59(1)
M. collina	MDT03(8), DT127(1), DT146(1), DT102(9), DT104(2), DT48(2), DT131(1)
D. erecta	MDT04(6), MDT05(8), MDT07(2), DT100(1), DT106(1)
M. citrofolia	DT42(1), DT32(1)

Note: Number within parenthesis indicates number of occurrences of the damage type

damage collected at each site were found significant between all three groups (ANOVA, $p < 0.001$, $F = 23.96$). Native damage diversity collected being the highest, followed by resident damage diversity, and finally invasive damage diversity being the lowest. The differences are illustrated with a rarefaction analysis curve of accumulated diversity of damage types as sample size increases (Fig 4). The invasive rarefaction curve appears to begin to level off, suggesting an accurate capture of damage diversity. On the other hand, native and resident curves continue to increase, implying that if more leaves were collected damage diversity may also increase (Fig 4).

Additionally, when looking at the unique damage types within species, certain types of damage were isolated to one species. Damage types that were unique to an individual species were reported in a table in order to further assess the

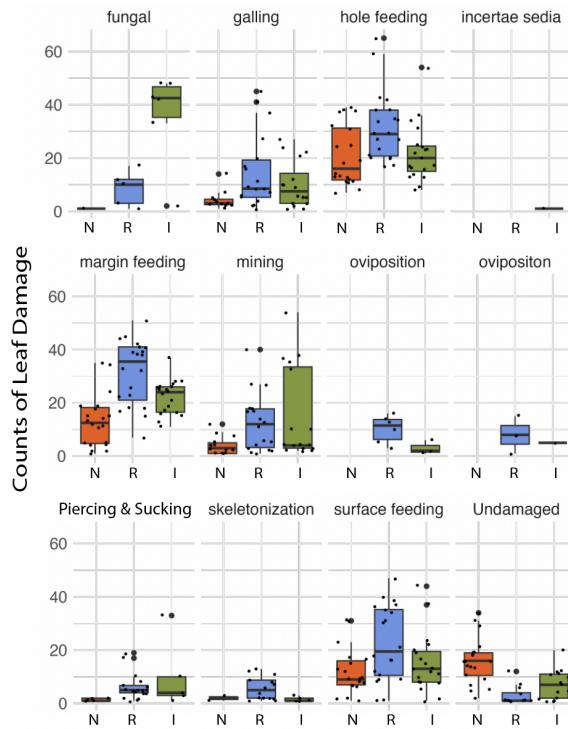


Fig. 5 Counts of the occurrences of damage types in the functional feeding categories by group. Each panel displays one of the 12 functional feeding groups and shows the counts of occurrences of that specific functional feeding damage for each site and is further divided into Native (blue), Resident (green) and Invasive (orange) within each panel. (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site)

specificity of damage within species groupings (Table 1). *B. asiatica*, *M. collina* and *D. erecta* had the most different types of damage unique to their species while *S. cumini* and *M. calvescens* had the least, with only one singular occurrence. *S. malaccense* and *N. forsteri* had the highest counts of occurrence for their unique damage types.

Significant differences were also found in distribution of damage between the functional feeding groups in native(blue), resident(green) and invasive(orange) groupings (ANOVA, all $p < 0.001$, $F = 3.843$). Within specific categories native plants had significantly more occurrences of galling, surface feeding, margin feeding, hole feeding, and mining when compared to invasive plants. When looking at the counts of occurrences of each damage type across groups, native plants had the highest occurrences of damage in almost all categories, though oviposition, skeletonization and piercing and sucking were not significant (Fig. 5). Resident plants also received significantly more fungal damage and mining damage when compared to invasive plants. The only category resident plants dominated was fungal damage. Invasive plants had the highest proportion of undamaged leaves (Fig. 5)

Damage types were given a specificity score, (1=generalized feeding, 2=moderate specialization 3 = most specialized feeding) given assumed host

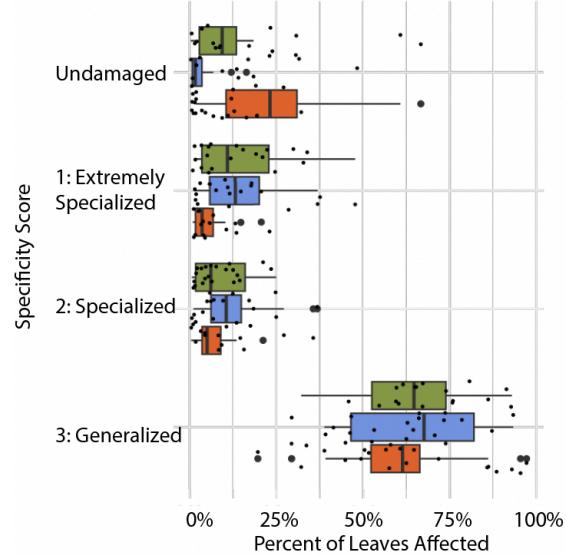


Fig. 6 Differences in damage diversity specialization across native(blue), resident(green) and invasive(orange) groups. Shows proportion of leaves in each overarching group that fall into categories 1, 2, 3 of damage specialization. (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site)

specificity and proportions of each specificity score were calculated for each site. The proportions of damage specificity were found significant between native and invasive as well as resident and invasive (ANOVA, $p<<0.001$, $F = 12.88$). Native and resident plants had no significant differences in any categories of damage. Native plants had the highest damage in all categories with significantly more damage in all specificity categories than invasive plants (Fig. 6). Residents had significantly higher damage than invasive plants in specificity categories 1 and 3 (Fig. 6). Invasive plants also had the highest proportion of undamaged leaves (Figs 6).

(iii) Differences and Diversity Between Confamilial Pairs

These same statistical tests and analyses performed on my native, resident and invasive species were performed between my confamilial pairs: Myrtaceae Family: *S. cumini*(invasive), *S. malaccense*(resident) and *S. collina*(native), Verbenaceae Family: *L. camara*(invasive) and *D. erecta*(resident), Rubiaceae Family: *M. citrofolia*(resident) and *N. forsteri*(invasive) and Malvaceae Family: *H. tiliaceus*(native) with *H. rosa-sinensis*(resident).

M. collina and *S. malaccense* were found to have significantly higher proportions of leaves affected by damage than *S. cumini* (Fig. 2) (ANOVA, $p<0.001$). Significant differences were found between *L. camara* and *D. erecta* in the proportion of leaves affected by herbivory (t-test, $p = 0.001006$). No significant differences were found in the percent of damaged leaves between both *M. citrofolia* and *N. forsteri* and *H. tiliaceus* and *H. rosa-sinensis*. (Fig. 2)

When comparing Shannon diversity between *S. cumini*, *S. malaccense* and *M. collina*, no significant differences were found, however, significant differences were found between the total counts of unique diversity at each site (ANOVA, $p = 0.0437$). *M. collina* has the highest number of unique damage types represented which was significantly more than *S. cumini* which had the least (Fig. 7).

Despite *D. erecta* having a higher Shannon index on average as well as a higher number of unique damage types when compared to *L. camara*,

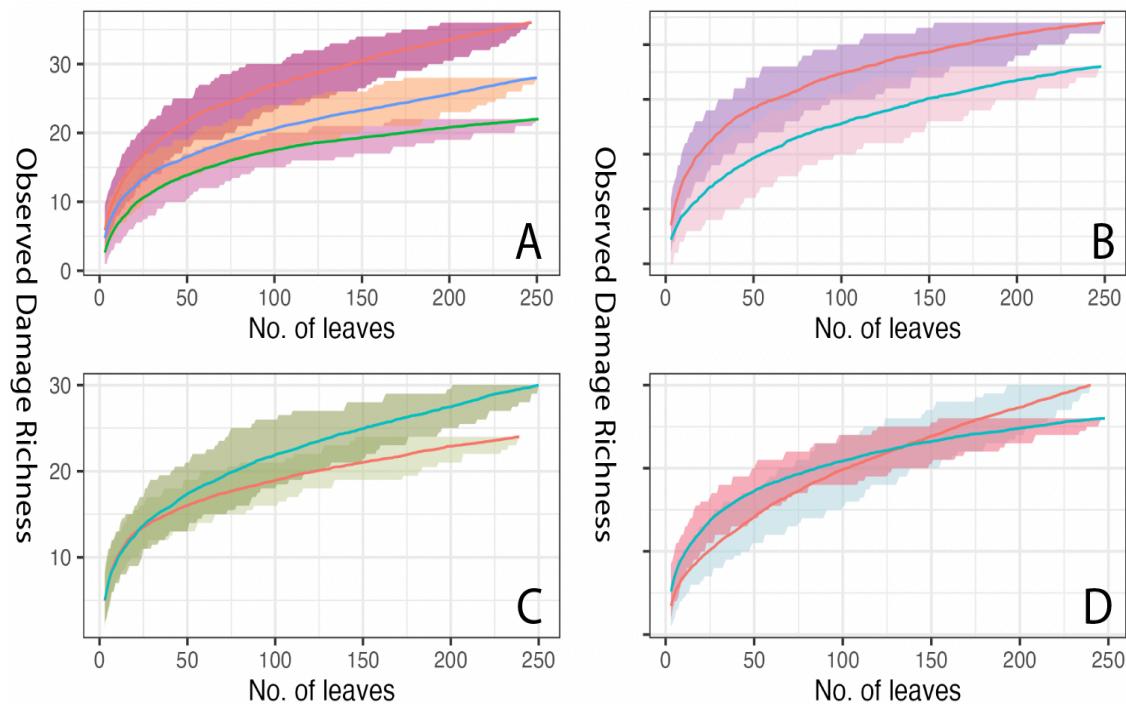


Fig 7. Rarefaction curves for the 4 sets of confamilial groupings showing accumulated diversity of damage types observed as increasing numbers of leaves were collected. Only *M. collina* and *S. cumini* had statistically significant differences. Plot A shows comparisons of observed damage richness in the Myrtaceae family, *M. collina* in dark purple (left), *S. cumini* in pink (middle), and *S. malaccense* in orange (right). Plot B shows comparisons of Verbenaceae family, *D. erecta* in purple and *L. camara* in pink. Plot C shows comparisons of the Rubiaceae, *M. citrofolia* in light green and *N. forsteri* in dark green. Plot D shows comparisons of the Malvaceae family *H. rosa-sinensis* in pink and *H. tiliaceus* in blue.

no significant differences were found in the Shannon diversity of the two species (t-test, $p = 0.2799$) nor the amount of unique damage types found within each species (t-test, $p = 0.05601$).

No significant differences were found in the Shannon diversity, or the number of unique damage types collected between both *M. citrofolia* and *N. forsteri* and *H. tiliaceus* and *H. rosa-sinensis*.

S. cumini, *S. malaccense* and *M. collina*, differed significantly in the distribution of the specificity of their damage types (ANOVA, $p < 0.001$). *M. collina*'s damage was more specialized than *S. cumini* having significantly more damage in categories 2 and 3 when compared to invasive plants ($P_{adj} = 0.0093103$, 0.0277797). When comparing *M. collina* to *S. malaccense* significant differences were found in damage specificity categories 1 and 2, *M. collina* having a higher proportion of specificity category 2 ($P_{adj} = 0.0000467$), and *S. malaccense* having higher proportions in category 1 ($P_{adj} = 0.000426$). *M. collina* had the highest proportions of leaves in categories 2 and 3 while *S. malaccense* dominated in category 1 and *S. cumini* had the highest proportion of undamaged leaves (Fig. 8).

Differences in damage specificity were also found to be significant between *L. camara* and *D. erecta*. *D. erecta* had significantly more specialized damage in category 3 while *L. camara* had significantly more undamaged leaves (Chi-square, $p < 0.001$). *D. erecta* also had more damage in categories 1 and 2 than *L. camara*, however, it was found to be insignificant (Fig 8).

M. citrofolia and *N. forsteri* differences in damage specificity were also found to be significant with *N. forsteri* having significantly more damage type 1 and 2 while *M. citrofolia* had significantly more of damage type 3 (Chi-square, $p < 0.001$).

Comparing *H. tiliaceus* with *H. rosa-sinensis* it was found that *H. tiliaceus* had higher proportions of leaves affected by damage scores 1 and 3 while *H. rosa-sinensis* had higher proportions of leaves affected by damage score 2 and unaffected leaves (t-test, $p < 0.001$).

Significant differences in the distribution of damage across functional feeding groups was found to be significant for all confamilial pairs. Within *S. cumini*, *S. malaccense* and *M. collina* significant differences were found between, *M. collina* and *S. cumini* (ANOVA, $P_{adj} = 0.0005111$) and *S. malaccense* and *S. cumini* (ANOVA, $p_{adj} =$

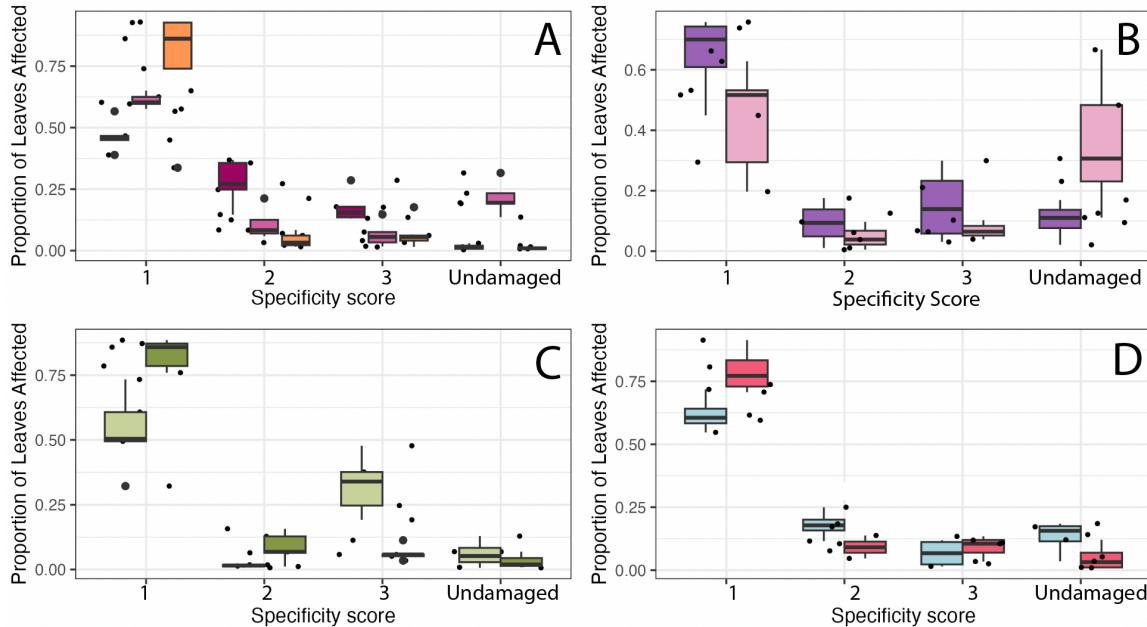


Fig. 8 Box plots comparing the distribution of specificity scores between confamilial groupings. (1= Generalized, 2= Specialized, 3= Extremely Specialized). Plot A shows comparisons of the damage specificity in the Myrtaceae family, *M. collina* in dark purple (left), *S. cumini* in pink (middle), and *S. malaccense* in orange (right). Plot B shows comparisons of Verbenaceae family, *D. erecta* in purple and *L. camara* in pink. Plot C shows comparisons of the Rubiaceae, *M. citrofolia* in light green and *N. forsteri* in dark green. Plot D shows comparisons of the Malvaceae family *H. rosa-sinensis* in pink and *H. tiliaceus* in blue. (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site).

0.0006730), however no significant differences were found between *S. malaccense* and *M. collina*. The undamaged category had higher counts of *S. cumini* when compared to the two other species. *M. collina* had the highest counts of galling, oviposition, margin feeding, piercing and sucking, and mining while *S. malaccense* had the highest counts of fungal damage and hole feeding (See Appendix A, Fig. C).

Significant differences were also found in the distribution of damage across functional feeding categories between *D. erect* and *L. camara* (Chi-square, $p<<0.001$). *D. erecta* had higher counts of damage in the categories galling, margin feeding, oviposition, fungal, interface sedia, piercing and sucking, skeletonization and surface feeding compared to *L. camara* (See Appendix A, Fig. C). *L. camara* only had higher counts of hole feeding and undamaged leaves (See Appendix A, Fig. C).

N. forsteri and *M. citrofolia* also had significantly different distributions across functional feeding groups (Chi-square, $p<<0.001$). *N. forsteri* had higher counts of fungal damage, galling, hole feeding, margin feeding, oviposition, piercing and sucking, skeletonization, and surface feeding while *M. citrofolia* had only higher counts of mining (See Appendix A, Fig. C).

Finally significant differences were found when comparing *H. tiliaceus* and *H. rosa-sinensis* (t-test, $p<0.001$). *H. tiliaceus* had higher counts of surface feeding, hole feeding, margin feeding, mining, piercing and sucking, and skeletonization while *H. rosa-sinensis* had higher counts of galling, oviposition, and unaffected leaves.

DISCUSSION

The enemy release hypothesis (ERH) has been tested time and time again in a variety of systems finding mixed results, some in support of the hypothesis (Keane and Crawley 2002, Wolfe 2002, Cincotta et al. 2009, Harvey et al. 2015) and others pointing support toward the biotic resistance hypothesis (Maron and Vilà 2001, Morrison and Hay 2011, Beaury et al. 2020, Dias et al. 2020). This study has produced interesting and novel results as the ERH is severely understudied in island systems with most studies focusing on larger continental systems (Cincotta et al. 2009, Harvey et al. 2015, Beaury et al. 2020) or testing the hypothesis through the study of insect selectivity (Liu et al. 2006, Morrison and Hay 2011, Mlynarek 2015). Additionally, many studies have forgone the intermediate category of resident plants focusing purely on native and invasive plants. However, because the ERH is a hypothesis rooted in assumptions about evolutionary relationships, the

study of resident plants has strengthened our findings. The findings of this study strongly suggest support for the enemy release hypothesis, as it was found that both native and resident plants received significantly more herbivory, more diverse, and specialized herbivory when compared to invasive plants. Invasive plants consistently received the least damage and were primarily affected by generalists with significantly lower counts of damage in specificity categories 2(moderate specialization) and 3(extreme specialization). Invasive plants also had significantly less diversity in both the Shannon diversity index, number of unique damage types and across functional feeding groups, pointing towards less variety and specificity of insect predators. These results were further confirmed by the study of confamilial groupings which remained in agreement with results of the overarching groupings.

While the ERH used to be a much more general theory, studies have continued to find as much evidence contradicting it, as there is evidence supporting it, suggesting different systems have different methods driving invasion (Heger and Jeschke 2014). Hence, the need to subdivide the hypothesis is essential in untangling the relationships, as many factors are at play(Heger and Jeschke 2014). This study has successfully subdivided the hypothesis by looking at specialization of feeding, diversity of feeding, feeding across functional feeding groups, as well as adding resident plants to the study to look at another point in evolutionary time. Invasive plants were found to have significantly trailed both resident and native species in percent, diversity, and specialization of damage in both overall groupings and within confamiliar groupings. This is exactly what the enemy release hypothesis predicts, and it appears invasive species are indeed escaping their natural predators, which in large can help explain their successful invasion. By looking at the subset of data not only do we see that invasive plants have lower percentages of leaves affected, but the lack of diversity and specialization show that less insects feed on invasive plants. This insinuates it is largely generalist insects, showing very little signs of coevolution or range expansion of insect herbivores with invasive plants. This study concludes that within Moorea's tropical forest communities' invasive plants are freed from their natural specialist predators and therefore are able to outcompete both native and resident plants because they are subjected to much less and much more generalized herbivory (Keane and Crawley 2002, Heger and Jeschke 2018).

The assumption that resident plants would receive an intermediate amount of damage was disproven because native and resident plants had very little significant differences between them. The only major differences being the total unique accumulated damage types in which native plants were found to have higher counts than resident plants and distributions across functional feeding groups which was significantly different between all groupings. The lack of difference in amount of damage between native and resident plants suggests naturalization of these plants as there has been sufficient evolutionary time for plant-insect adaptations to occur (Benson et al. 1975, Berenbaum 1990, Wheat et al. 2007). 3 out of the 4 resident plants in this study were introduced to Mo'orea around the time of Polynesian contact (~950 AD) providing ample evolutionary time for insects to adapt to feed off these new introductions (Kirch and Kahn 2007). Consequently, the invasive plants in this study were all introduced relatively recently to the island between 1850-1950, having characteristics that enable them to be successful invaders in addition to lacking the time to allow insects to significantly alter feeding habits (Meyer and Florence 1996). It is likely these resident plants may have been around long enough for predators to expand their feeding niches to now include resident plants and adapt alongside them, successfully naturalizing them into this system.

The differences between native and resident plants have continued to support this hypothesis as the main differences were across functional feeding categories and the total diversity of damage. The fact that native and resident plants had different types of damage affecting them, further suggests naturalization as it points to the fact that resident and native plants may both have their own unique specialized predators. Both native and resident plants had certain damage types that only appeared on one species, suggesting specialized feeding methods and unique insect predators adapted to specific species or a smaller range of species (Labanderia and Phillips 1996, Xu et al. 2018). Invasive plants only had two isolated instances of a unique damage type occurring suggesting little to no specialization of insect herbivores on invasive plants. This is consistent with the ERH, finding that invasive plants are escaping specialist predators.

D. erecta which is an ornamental shrub is the only resident species in this study that was not introduced at the time of Polynesian contact and was likely introduced to Moorea sometime post Polynesian contact, though the exact date is unknown (Powell 1977, Ragone et al. 2001, Moroni and O'Leary 2020). *D. erecta*, while currently

considered a resident plant as it does not threaten native ecosystems and proliferate at the rate of invasives, it is of interest because it received the least amount of herbivory within the resident category and has several closely related relatives on the island that are invasive (*L. Camara*, *S. urticifolia*, *L. montevidensis*). *D. erecta* therefore gives us a glimpse into another point in evolutionary time, however, not enough resident plants were studied post Polynesian introduction to make any clear predictions. Studying herbivory of resident plants on islands across different points in time would be an interesting future direction of the study. Naturalization is a key part of the process of invasion, studying resident plants across different points of introduction could decipher how plants invade regions as well as further investigate the idea that evolutionary time on the island is linked to the resident plant naturalization (Richardson and Pyšek 2012, Pyšek and Richardson 2006, Richardson and Pyšek 2012, Zenni et al. 2014).

Rates of invasion are hard to predict and oceanic islands are specifically vulnerable as they lack both saturation and diversity of species, providing ample room for the rapid proliferation of invasive species (Sax and Gaines 2008). Due to the fact that Moorea is a small island system with relatively low diversity, high amounts of disturbance, as well as high levels of endemism, it is primed to be susceptible to invasion (Rejmanek and Richardson 1996, Lonsdale 1999). Invasion has proven to be detrimental to native species on Mo'orea, plants like *Miconia calvescens* and *Spathodea campanulata* have proven to spread and affect native ranges. Invasive plants have had large impacts on coastal regions which have been impacted through high disturbance, in turn, isolating most native ranges to undisturbed habitat in higher elevations (Meyer and Florence 1996, Meyer et al. 2015). While it is clear that invasive species are evading their insect predators and affecting native plant communities, the rate at which it is happening is still unknown, and future trajectories of these invasive species and their effects on native communities requires further research (Roughgarden 1986).

Most papers that have studied the enemy release hypothesis have looked at more complex continental systems finding a variety of different outcomes. Most of which acknowledge the effects of the enemy release but ultimately refute it due to alternative factors such as biotic resistance, fluxes in species distributions, shifts in native niches, and human impacts which outweigh the effects of the ERH (Maron and Vilà 2001, Heger and Jeschke 2014, Zimmermann et al. 2014, Beaury et al. 2020,

Dias et al. 2020). Due to the fact that Mo’orea is an oceanic island, there is a reduction of external factors to the system and thus evolutionary systems are made much more clear (Vitousek 2002, Warren et al. 2015). This allows us to confidently link the success of plant invasion more directly to plant-insect evolutionary relationships.

Island systems as explained, are ideal places to study evolution and finding support of the ERH on islands provides very strong evidence linking species invasive tendency largely to escape from specialist predators. It also provides evidence, linking increased evolutionary time on an island to increased predation. However, even on island there are other factors at play (Vitousek 2002, Warren et al. 2015, DiNapoli and Leppard 2018). The lack of abundance of species in the same family has allowed familial differences between species to be in effect. Plants have both physical and chemical defenses to herbivores which are also at play, things such as nitrogen content, secondary metabolites, and physical barriers like thorns, trichomes, waxes all affect how plants are affected by herbivory (Mattson 1980, Arimura et al. 2005). Several plants used in this study have known insect defenses such as *B. asiatica*, a native plant, which had several chemical compounds that produce insecticidal properties. However, *B. asiatica* was one of the most highly damaged species, strongly suggesting support for the ERH and coevolution of insect predators as the chemical defenses seem to be evaded by insects (Umaru et al. 2018, Mangawang et al. 2020). *M. collina* is another native plant that was found to have high levels of herbivory despite having physical defenses such as thicker leaves and pubescence on the underside. Insects seemed to have evaded these defenses as *M. collina* had high amounts of damage and very high damage diversity (Lee 1981). The use of confamilial groupings attempted to reduce these effects. However, while the results remain consistent in light of the known defenses, further studies into the compositions and defenses of these species would be important in further untangling the root causes of the patterns observed. Additionally due to the lack of confamilial species on the island future studies should sample a much higher diversity of species, not only increasing sample sizes but by diversifying the species in each group. While there will be outliers, the increase in sheer diversity removes some confounding factors related to species differences.

Future studies could expand this study to looking at a broader range of species as well as more species across different points in time to better understand the evolutionary relationships at play. Repeating this study on nearby islands could

provide interesting insights into patterns of invasion and evolutionary history in the region. Finally, discerning which insects are preying on these plants and looking into invasive plants’ natural predators could further help us understand why the invasions are successful and the complexity of insect plant interactions.

The results of this study strongly show support for the enemy release hypothesis as a factor in the success of invasive species on Mo’orea. The results also suggest the naturalization of resident plants in the study as they have received comparable amounts of herbivory and herbivory diversity, with both native and resident plants showing evidence of unique specialized predators. This study is bolstered by the use of an oceanic island system as well as the use of the intermediate category of resident plants, which provide a novel look at this hypothesis in an understudied system.

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APPENDIX A

FIG. A.

Descriptions and pictures of damage types categorized and defined outside the damage types in the “Guide to Insect Damage Types on Compressed Fossils”

MDT01: Fungal Damage

Blotchy raised polyobate marks, waxy to the touch. Can range in size from larger patches to more dispersed spots across leaf. Seem to cluster around major veins avoiding 1 degree veins but following 1 degree and 2 degree veins in clusters.

Host specificity score: 1



MDT02: Fungal Damage

Patches of dark-colored leaf tissue, edges can be defined or diffused. Patches have slightly shallow indentation on leaf surface.

Host specificity score: 1



MDT03: Oviposition Damage

Circular raised marks that appear burst open when viewed under a microscope. Very small (~1mm) and has 3 to 4 triangular sections that open the white pocket circular pocket on leaf surface.

Host specificity score: 3

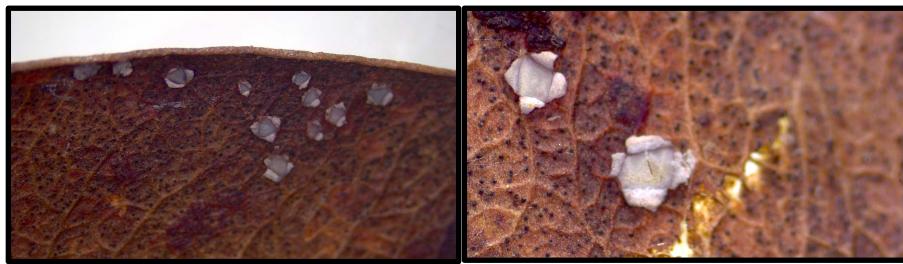


Fig. A Cont.

MDT04: Oviposition Damage

Raised pustule like spots, often clustered on leaves. Have a darkened defined center and may extend outward, very small, less than 1mm.

Host specificity score: 3



MDT05: Mining Damage

Black trails following venation of leaves, start thinner and slightly thick along vein. Have a defined terminal chamber.

Host specificity score: 3



MDT06: Oviposition damage

Patched of darkened leaf tissue with small, raised bumps clustered within them.

Host specificity score: 3



MDT07: Oviposition damage

Long segmented damage, raised from leaf surface tissue, ~1cm.

Host specificity score: 3

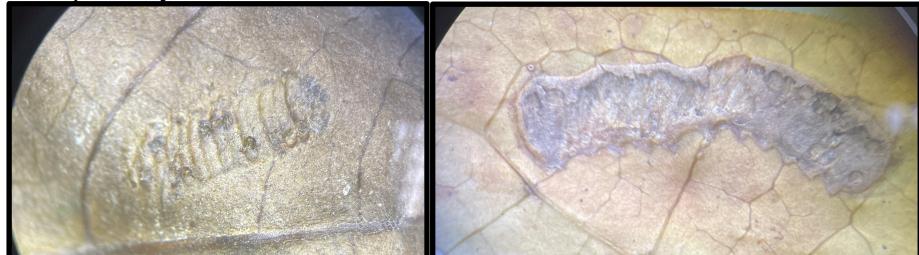


TABLE B. Table of information on study species taxonomy, origin and predominate characteristics.

Family	Species	Country of Origin	Group	Description
Malvaceae	<i>Hibiscus tiliaceus</i>	Australia, South East Asia and the South Pacific	Native	Leaves are heart-shaped and up to 30 cm long and flowers have 5 petals and fade from yellow to pinkish-red with age (Murdock 1999).
Malvaceae	<i>Hibiscus rosa-sinensis</i>	Vanuatu	Resident	Leaves are ovate to lanceolate, minorly stellate-hairy with margin dentate to serrate. Flowers have 5 petals and are solitary, usually bright red but often pink, orange, yellow, or white (Murdock 1999).
Myrtaceae	<i>Metrosideros collina</i>	French Polynesia, the Cook Islands, and the Pitcairn Islands	Native	Native shrub found from mid to high-elevation exposed regions. Leaves vary from elliptic to obovate to lanceolate and flowers have red stamens (Murdock 1999).
Myrtaceae	<i>Syzygium malaccense</i>	Tropical Asia and Australia	Resident	Flowering tree/shrub deliberately brought by Polynesians to remote Oceania as canoe plants (Whistler and Elevitch 2006). Leaves are oblong with acuminate apices and have pink flowers that produce a red or white apple-shaped fruit (Murdock 1999).
Myrtaceae	<i>Syzygium cumini</i>	Indian subcontinent and Southeast Asia	Invasive	Leaves are lanceolate and flowers contain 4 white petals in cymes with at least 3 flowers and produce a dark purple ovoid fruit (Murdock 1999).
Rubiaceae	<i>Neonauclea forsteri</i>	French Polynesia	Native	Tall flowering tree native to Mo'orea. Leaves are elliptic and brochidodromous with a percurrent tertiary vein. Flowers are an inflorescence with a globulose multiple fruit. Fruit-bearing tree introduced to Mo'orea and other areas in the Pacific by Polynesian sailors (Morton 1992). Has opposite, glabrous leaves that can reach up to 45 cm long, and flowers are borne in clusters directly on the conglomerate fruit (Murdock 1999).
Rubiaceae	<i>Morinda citrifolia</i>	Southeast Asia and Australasia	Resident	Has light green elliptic to ovate leaves and clusters of light blue, white, or lavender flowers, fruiting a small globose yellow berry (Aymard C. and Grande A. 2012). Fruits are toxic containing alkaloid isoquinoline in addition to the monoterpenes and leaves contain saponins (Hiradate et al. 1999, Donkor et al. 2019).
Verbenaceae	<i>Duranta erecta</i>	Mexico and South America	Resident	Leaves are broadly ovate, and opposite and have small tubular-shaped flowers arranged in clusters whose colors can range from red, yellow, white, pink to orange depending on maturity and location (Sharma et al. 1988). Contains hepatotoxins that cause cholestasis in grazing animals (Sharma et al. 2007).
Verbenaceae	<i>Lantana camara</i>	American Tropics	Invasive	Leaves and ovate, sessile and become striped with red/purple as they age. Fruit buoyant and dispersed by ocean currents and likely arrived in Mo'orea this way. All parts of the tree are poisonous containing saponins (Murdock 1999)
Lecythidaceae	<i>Barringtonia asiatica</i>	Asia and Islands of the western Pacific Ocean, including Mo'orea	Native	Leaves are predominately 3 veined with a maroon underside and green top. Flowers are white/pink and borne in cymes (Murdock 1999)
Melastomataceae	<i>Miconia calvescens</i>	Mexico and Central and South America	Invasive	Leaves are pinnately compound and ovate. Has showy red-orange flowers with a curved corolla and 5 petals (Murdock 1999).
Bignonias	<i>Spathodea campanulata</i>	Africa	Invasive	

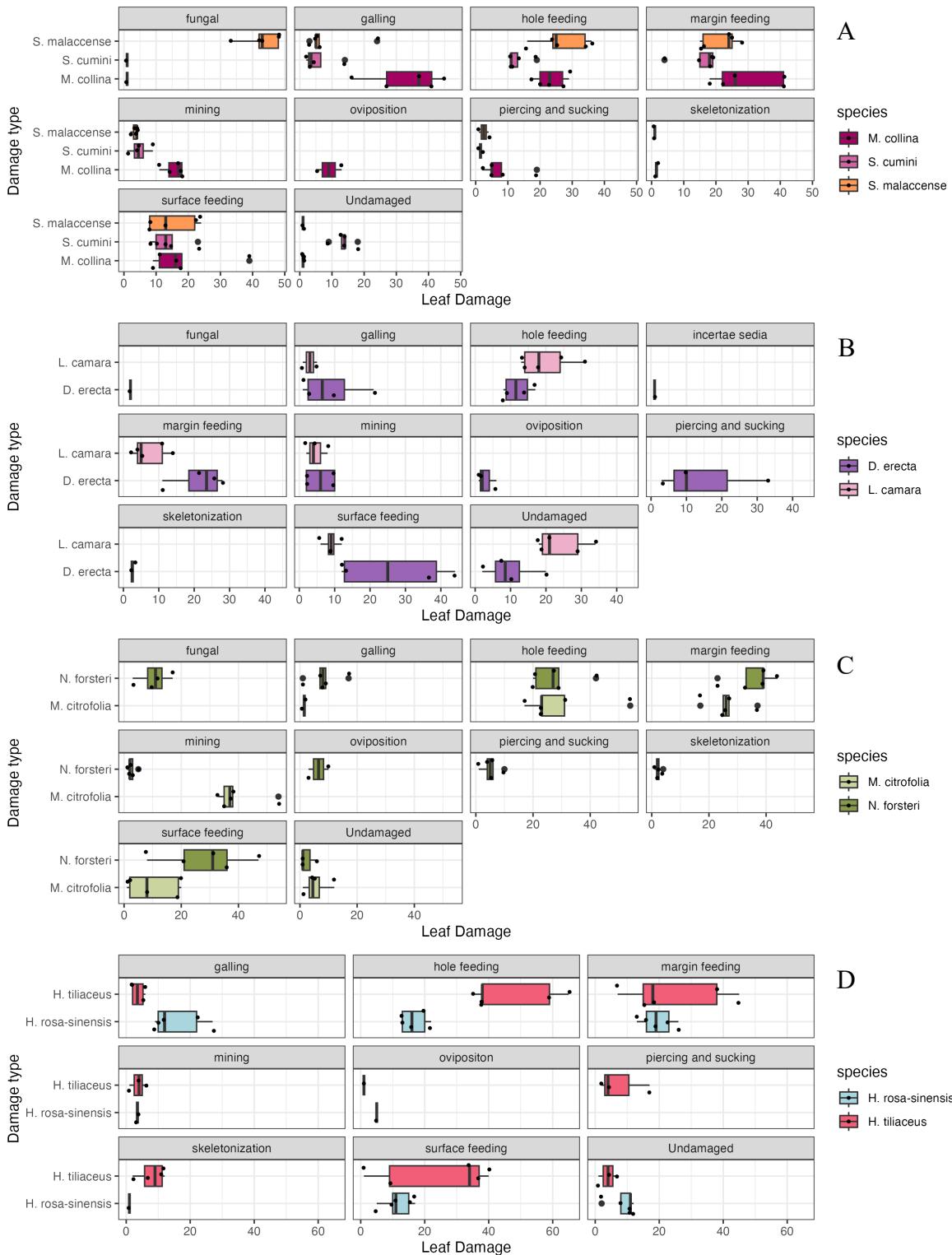


FIG C. Box plot showing the distributions of leaf damage across different functional feeding groups between confamilial groupings. Each panel within the plots represent the counts of damage within each functional feeding category. Plot A shows comparisons of the damage specificity in the Myrtaceae family, M. collina in dark purple (left), S. cumini in pink (middle), and S. malaccense in orange (right). Plot B shows comparisons of Verbenaceae family, D. erecta in purple and L. camara in pink. Plot C shows comparisons of the Rubiaceae, M. citrofolia in light green and N. forsteri in dark green. Plot D shows comparisons of the Malvaceae family H. rosa-sinensis in pink and H. tiliaceus in blue. (mid-bar = mean, box = upper and lower quartiles, whiskers = maximum and minimum, dots = value for each site).