PATTERNS OF INSECT HERBIVORY ON INDIGENOUS *HIBISCUS TILIACEUS* AND INTRODUCED *HIBISCUS ROSA-SINENSIS* ACROSS HUMAN IMPACTED AREAS IN MO'OREA, FRENCH POLYNESIA

ROXANNE S. ARDESHIRI

Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA

Abstract. It is widely recognized in the field of conservation biology that anthropogenic influences resulting in habitat loss and forest fragmentation pose as a major threat to the integrity of forest ecosystems. Herbivorous insects are known to facilitate the process of nutrient cycling in forests, thus it is important to understand how human disturbance may be affecting their activity. This study investigates how the prevalence of insect herbivory on and between indigenous *Hibiscus tiliaceus* and introduced *Hibiscus rosa-sinensis* changes across human impacted areas featuring coastal infrastructure, agriculture, as well as high elevation roads and hiking trails within Mo'orea, French Polynesia. The results have shown that there is significant variation in insect herbivory estimates across human impacted areas as well as between *H. tiliaceus* and *H. rosa-sinensis*, two related species that share different evolutionary histories.

Key words: herbivory; *insects;* Hibiscus tiliaceus; Hibiscus rosa-sinensis; *anthropogenic; fragmentation; Mo'orea, French Polynesia; agriculture; edge effect*

INTRODUCTION

An overarching theme in the field of conservation biology is that human land use resulting in habitat loss or fragmentation poses as a major threat to biodiversity and ecosystem functioning (Huston 2005, Valladeres *et al.* 2006). In order to better understand how anthropogenic influences affect forest ecosystems, it is pertinent to investigate the organisms responsible for facilitating ecosystem functioning. It is known that insects play major functional roles in forest ecosystems such as nutrient cycling, seed dispersal and pollination (Didham *et al.* 1996). Herbivorous insects in particular have been shown to increase rates of nutrient cycling, which ultimately increases plant productivity (Belovsky and Slade 2000). In a world where human activity is ubiquitous and constantly increasing, it is important to evaluate how anthropogenic disturbance is affecting herbivorous insect-plant interactions. This notion is the prime mover behind this study, which delineates patterns of insect herbivory in indigenous *Hibiscus tiliaceus* and introduced *Hibiscus rosa-sinensis* across human impacted areas in Mo'orea, French Polynesia.

The Edge effect principle is a well-studied concept in conservation biology, which states that within a fragmented landscape, changes in microclimate around forest edges can result in 'edge effects' (Wiens 1976, Harris 1988). A majority of studies on herbivore activity associated with forest edges show that there are higher levels of herbivore biodiversity, herbivore abundance, and herbivory rates (Wirth *et al.* 2008). It has also been shown that agricultural activity can increase the prevalence of herbivorous insects around agriculture-natural edges (Kogan and Turnipseed 1987, McKone *et al.* 2001). Pesticide contamination into forest edges adjacent to agricultural fields may also adversely affect insect biodiversity and abundance (Frampton 2002).

Human infrastructure that leads to fragmentation may pose as a dispersal challenge for herbivorous insects, thus patterns of coexistance between generalist and specialist herbivorous insects may show variation across a fragmented landscape (Kareiva and Wennergren 1995, Tscharntke *et al.* 2002). Mo'orea, French Polynesia, the study location for this research, provides a suitable landscape to study the prevalence of herbivory across human impacted areas featuring agriculture, forest fragmentation, and human infrastructure.

Both a native and introduced congeneric plant species were chosen for this study because patterns in herbivory are likely to differ for native versus introduced plant species, supported by several hypotheses referred to as the Enemy Release Hypothesis (ERH) and the Increased Susceptibility

Hypothesis (ISH) (Keane and Crawley 2002, Hokkanen and Pimentel 1989). The ERH rationalizes that the success of invasive plant species is because they are free from their co-evolved natural enemies. The ISH states that introduced species may be more susceptible to herbivory due to the lack of co-evolved defense mechanisms to deter native herbivores in the area of introduction. *H. rosa-sinensis* is an introduced non-invasive ornamental that better fits the ISH and other findings that suggest non-invasive exotic plants are more susceptible to herbivory (Cappuccino and Carpenter 2005).

The present study assesses patterns in herbivory for *H. tiliaceus* and *H. rosa-sinensis* across areas exhibiting different types of human influence in Mo'orea, French Polynesia. This research will investigate whether or not these patterns in herbivory support the edge effect principle and previous findings that show human-created edges around agriculture fields and forests are associated with a higher prevalence of insect herbivory. This study will also determine whether or not these two related *Hibiscus* species with different evolutionary histories will show similar or contrasting patterns of herbivory across different types of human impacted areas.

METHODS

Study Organisms & Herbivory

An indigenous and introduced *Hibiscus* species from the plant family Malvaceae were chosen for surveying patterns of herbivory in this study because of their ubiquity within human-impacted areas of Mo'orea, French Polynesia. The indigenous *Hibiscus tiliaceus* also known as Beach Hibiscus and purau (Tahitian) is a pan-tropical evergreen sprawling tree with large heart shaped leaves (Elevitch and Thomson 2006). The introduced *Hibiscus rosa-sinensis* also known as Rose of China and aute (Tahitian) is a popular cultivated ornamental shrub with small leaves and a variety of flower color morphs. *H. rosa-sinensis* was introduced to French Polynesia with the arrival of the Polynesians for medicinal purposes, but the native origins of this highly cultivated species is still debated (Florence 2004, Anderson 2007).

Two insect-herbivory types were observed and recorded in this study, yet there is a gap in knowledge pertaining to herbivorous insects associated with these *Hibiscus* species in French Polynesia. Leaf chewing was present on and recorded for both *H. tiliaceus* and *H. rosa-sinensis*, whereas gall forming was only present on and recorded for *H. rosa-sinensis*. Identification of the herbivorous insects associated with the recorded herbivory patterns was not heavily investigated in this study, but two unidentified green Lepidoptera caterpillars were found to feed on the leaves of *H. tiliaceus*, and some literature suggests that the gall formers on *H. rosa-sinensis* may be *Aceria hibisci* also known as the Hibiscus Erineum Mite (Hara *et al.* 2001, Welbourn *et al.* 2008).

Human Impacted Areas

Sampling of *H. tiliaceus* and *H. rosa-sinensis* took place in three localities with varying levels of anthropogenic influence in Mo'orea, French Polynesia (Fig. 1). The anthropogenic influences found within each site include coastal roadsides and residential development, agriculture fields, and high elevation roadsides and hiking trails. Sampling at the UCB Gump Research Station (17°29'26.43"S, 149°49'35.80"W) took place along coastal roadsides and buildings. Sampling at the agriculture school, Lycee Agricole d'Opunohu (17°31'58.67"S, 149°50'0.17"W), took place within and along the perimeter of the property. Sampling at the Belvedere lookout (17°32'25.37"S, 149°49'36.68"W) took place along roadsides and hiking trails within close proximity to the lookout.
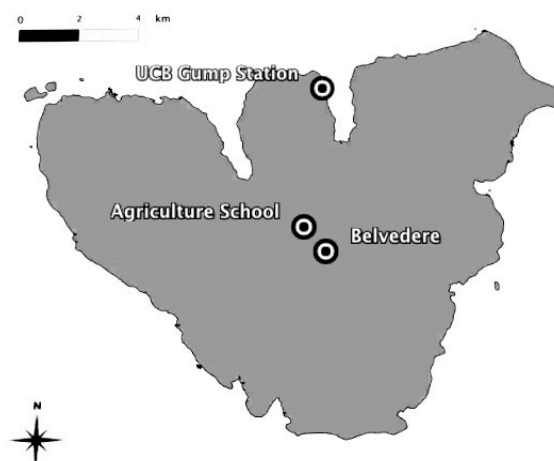

FIG. 1. Map of Mo'orea, French Polynesia featuring human impacted sampling locations.

Ten *H. tiliaceus* and *H. rosa-sinensis* individuals were randomly selected for sampling at each study site. For each individual, a 10m-diameter conspecific and heterospecific tree density was recorded, as well as diameter at breast height (DBH) for *H. tiliaceus* and tree height for *H. rosa-sinensis* as a proxy for age.

Three branches within reaching distance on different areas of the tree were then randomly selected for herbivory sampling. For each branch, the number of leaves, number of leaves with herbivory, and number of leaves with each herbivory type was recorded. The numbers corresponding to leaves with herbivory, leaves with leaf chewing, and leaves with galls were divided by the total number of leaves to calculate percentages referred to as Herbivory Intensity, Leaf Chewing Intensity, and Gall Intensity respectively. One-way ANOVA and Tukey-Kramer multiple comparisons tests (JMP) were carried out to determine the variation of these Intensities across sites and unpaired t-tests (JMP) were run to determine the interspecific differences when applicable.

Herbivorous insect leaf damage was estimated for gall formers in *H. rosa-sinensis* and for leaf chewers in both *H. tiliaceus* and *H. rosa-sinensis*. The magnitude of gall insect damage on leaves of *H. rosa-sinensis* was recorded by taking a gall count for up to 10 leaves per branch per individual. The magnitude of leaf chewing insect damage on leaves was recorded with use of a 5-degree Leaf Chewing Insect Damage Index (LCIDI) for up to 10 leaves per branch per individual of both *H. tiliaceus* and *H. rosa-sinensis* (Table 1). Leaves were visually examined to estimate the percent of leaf damage, then the LCIDI values were recorded in accordance with their leaf damage ranges. LCIDI values were then converted to the midpoints of their respective leaf damage ranges, and these values were averaged and used for statistical analysis. One-way ANOVA and Tukey-Kramer multiple comparisons tests (JMP) were carried out to determine the variation in Gall Insect Damage and Leaf Chewing Insect Damage across sites. Unpaired t-tests (JMP) were run to determine the interspecific differences when applicable.

Linear regressions (JMP) were also carried out to determine how the proportions of leaf herbivory type respond as a function of increasing Herbivory Intensity in *H. rosa-sinensis* individuals.

TABLE 1. Leaf Chewing Insect Damage Index (LCIDI) was used to estimate the magnitude of leaf chewing insect damage on leaves of *H. tiliaceus* and *H. rosa-sinensis.* LCIDI values were recorded in accordance with their leaf damage ranges. LCIDI values were replaced with their leaf damage midpoints for statistical analysis.

LCIDI	Leaf Damage Range (%)	Leaf Damage Midpoints
1	$0 < LD \leq 5$	2.5
2	$5 < LD \leq 25$	15.5
3	$25 < LD \leq 50$	38
4	$50 < LD \leq 75$	63
5	$75 < LD \leq 100$	88

RESULTS

There was significant variation in Herbivory Intensity for *H. tiliaceus* (One-way ANOVA, $F_{2, 27}=37.50$, P<0.0001) and *H. rosa-sinensis* (One-way ANOVA, $F_{2,27}=144.76$, P<0.0001) across sites (Fig. 2). For *H. tiliaceus*, Herbivory Intensity values were 35.2 ± 14.9, 52.6 ± 14.2 and 86.2 ± 10.6 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively, and they significantly increased across sites (G-B Tukey-Kramer, P=0.0194; G-A Tukey-Kramer, P<0.0001; B-A Tukey-Kramer, P<0.0001). For *H. rosa-sinensis*, Herbivory Intensity values were 20.1 ± 7.6, 78.7 ± 12.0 and 87.1 ± 8.6 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. Herbivory Intensity was significantly lowest at UCB Gump Station (G-B Tukey-Kramer, P<0.0001; G-A Tukey-Kramer, P<0.0001), but showed no significant difference between the Belvedere and the Agriculture School (B-A Tukey-Kramer, P=0.1410).

Interspecific comparisons of Herbivory Intensity showed significant differences at UCB Gump Station (t-test, $t_{14}=3.51$, P=0.0034) and Belvedere (t-test, $t_{18}= -3.56$, P=0.0022), but not at the Agriculture School (t-test, $t_{18}=0.84$, P=0.4099).
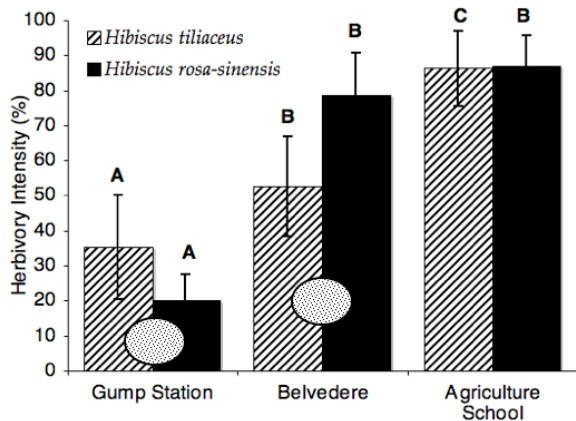
FIG. 2. Herbivory Intensity of *H. tiliaceus* (n=10) and *H. rosa-sinensis* (n=10) across sites. Herbivory Intensity represents the proportion of leaves affected by insect herbivory. Herbivory Intensity is significantly different in all site pairings for *H. tiliaceus* (G-B, P=0.0194; G-A, P<0.0001; B-A, P<0.0001), and in site pairings with UCB Gump Station for *H. rosa-sinensis* (G-B, P<0.0001; G-A, P<0.0001). Interspecific Herbivory Intensity showed significant differences at UCB Gump Station (P=0.0034) and Belvedere (P=0.0022). Different lettering between sites denotes significant differences in species specific Herbivory Intensity. White circles denote significant differences in Herbivory Intensity between species. Data are means with error bars denoting ± standard deviation.

There was significant variation in Leaf Chewing Intensity for *H. tiliaceus* (One-way ANOVA, $F_{2,\ 27}$=37.50, P<0.0001) and *H. rosa-sinensis* (One-way ANOVA, $F_{2,27}$=11.44, P=0.0003) across sites (Fig. 3). For *H. tiliaceus*, Leaf Chewing Intensity values were 35.2 ± 14.9, 52.6 ± 14.2 and 86.2 ± 10.6 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively, and they significantly increased across sites (G-B Tukey-Kramer, P=0.0194; G-A Tukey-Kramer, P<0.0001; B-A Tukey-Kramer, P<0.0001). For *H. rosa-sinensis*, Leaf Chewing Intensity values were 18.5 ± 8.1, 35.8 ± 15.1 and 46.9 ± 15.6 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. Leaf Chewing Intensity was significantly lowest at UCB Gump Station (G-B Tukey-Kramer, P=0.0200; G-A Tukey-Kramer, P=0.0002), but showed no significant difference between Belvedere and the Agriculture School (B-A Tukey-Kramer, P=0.1701).

Interspecific comparisons of Leaf Chewing Intensity showed significant differences at UCB Gump Station (t-test, t_{15}=3.78, P=0.0018), Belvedere (t-test, t_{18}=3.62, P=0.0020), and the Agriculture School (t-test, t_{15}=7.55, P<0.0001).
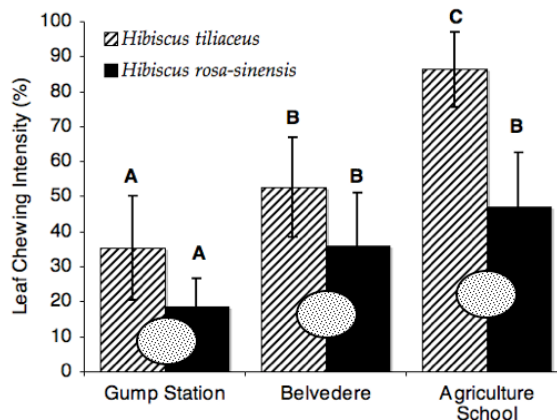

FIG. 3. Leaf Chewing Intensity of *H. tiliaceus* (n=10) and *H. rosa-sinensis* (n=10) across sites. Leaf Chewing Intensity represents the proportion of leaves affected by leaf chewing herbivory. Leaf Chewing Intensity is significantly different in all site pairings for *H. tiliaceus* (G-B, P=0.0194; G-A, P<0.0001; B-A, P<0.0001), and in site pairings with UCB Gump Station for *H. rosa-sinensis* (G-B, P=0.0200; G-A, P=0.0002). Interspecific Leaf Chewing Intensity showed significant differences between UCB Gump Station (P=0.0018), Belvedere (P=0.0020), and the Agricultural School (P<0.0001). Different lettering between sites denotes species specific significant differences in Leaf Chewing Intensity. White circles denote significant differences in Leaf Chewing Intensity between species. Data are means with error bars denoting ± standard deviation.

There was significant variation in Gall Intensity for *H. rosa-sinensis* (One-way ANOVA, $F_{2,27}$=48.98, P<0.0001) across sites (Fig. 4). Gall Intensity values were 2.0 ± 2.1, 63.8 ± 16.3 and 67.0 ± 23.5 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. Gall Intensity was significantly lowest at UCB Gump Station (G-B Tukey-Kramer, P<0.0001; G-A Tukey-Kramer, P<0.0001), but showed no significant difference between Belvedere and the Agriculture School (B-A Tukey-Kramer, P=0.8983).
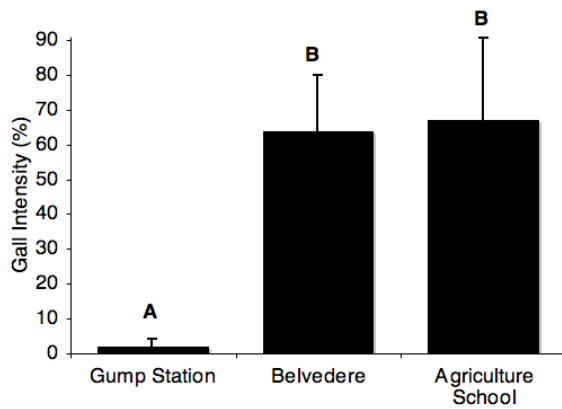
FIG. 4. Gall Intensity of *H. rosa-sinensis* across sites (n=10). Gall Intensity represents the proportion of leaves affected by gall herbivory. Gall Intensity is significantly different in site pairings with UCB Gump Station (G-B, P<0.0001; G-A, P<0.0001). Different lettering between sites denotes significant differences in Gall Intensity. Data are means with error bars denoting ± standard deviation.

There was significant variation in Leaf Chewing Insect Damage Indices (LCIDI, see Methods) for *H. tiliaceus* (One-way ANOVA, $F_{2, 27}=9.04$, P=0.0010) and *H. rosa-sinensis* (One-way ANOVA, $F_{2,27}=4.72$, P=0.0174) across sites (Fig. 5). For *H. tiliaceus*, LCIDI values were 9.8 ± 2.7, 19.6 ± 5.1 and 28.2 ± 15.8 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. LCIDI was significantly lower at UCB Gump Station than the Agriculture School (G-A Tukey-Kramer, P=0.0006) and showed no significant difference between Belvedere and the other sites (G-B Tukey-Kramer, P=0.0777; B-A Tukey-Kramer, P=0.1367). For *H. rosa-sinensis*, LCIDI values were 7.6 ± 2.8, 13.7 ± 5.0 and 16.2 ± 9.6 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. LCIDI was significantly lower at UCB Gump Station than the Agriculture School (G-A Tukey-Kramer, P=0.0158) and showed no significant difference between Belvedere and the other sites (G-B Tukey-Kramer, P=0.1055) (B-A Tukey-Kramer, P=0.6616).

Interspecific comparisons of LCIDI showed a significant difference at Belvedere (t-test, $t_{18}=2.65$, P=0.0162), but not at UCB Gump Station (t-test, $t_{18}=1.76$, P=0.0953) or the Agriculture School (t-test, $t_{15}=2.06$, P=0.0574). Although it is worth noting that the Agriculture School marginally showed a significant difference.
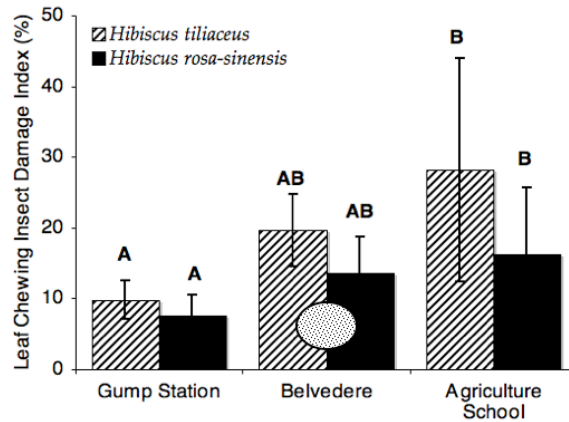

FIG. 5. Leaf Chewing Insect Damage Indices (LCIDI, see Methods) for *H. tiliaceus* (n=10) and *H. rosa-sinensis* (n=10) across sites. LCIDI was significantly different between UCB Gump Station and the Agriculture School for both *H. tiliaceus* (G-A, P=0.0006) and *H. rosa-sinensis* (G-A, P=0.0158). Interspecific LCIDI showed a significant difference at Belvedere (P=0.0162). Different lettering between sites denotes species specific significant differences in LCIDI. White circles denote significant differences in LCIDI between species. Data are means with error bars denoting ± standard deviation.

There was significant variation in Gall Insect Damage on *H. rosa-sinensis* (One-way ANOVA, $F_{2,27}=23.04$, P<0.0001) across sites (Fig. 6). Gall Insect Damage values were 1.6 ± 0.3, 6.0 ± 1.9 and 6.3 ± 2.3 (mean ± standard deviation) for UCB Gump Station, Belvedere and the Agriculture School respectively. Gall Insect Damage was significantly lowest at UCB Gump Station (G-B Tukey-Kramer, P<0.0001; G-A Tukey-Kramer, P<0.0001), but showed no significant difference between Belvedere and the Agriculture School (B-A Tukey-Kramer, P=0.9194).
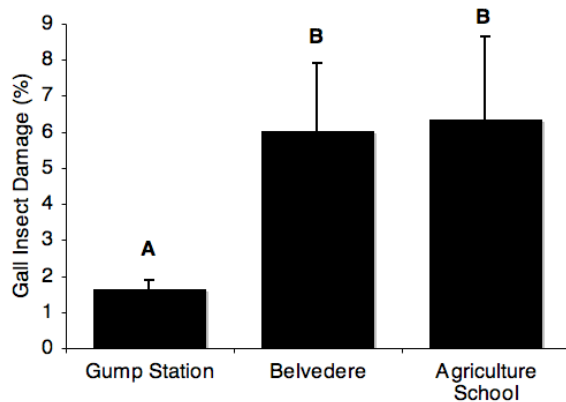
FIG. 6. Gall Insect Damage on *H. rosa-sinensis* across sites (n=10). Gall Insect Damage represents the average number of galls on gall-infected leaves. Gall Insect Damage was significantly different in site pairings with UCB Gump Station (G-B, $P<0.0001$; G-A, $P<0.0001$). Different lettering between sites denotes significant differences in Gall Insect Damage. Data are means with error bars denoting ± standard deviation.

There were significant correlations between the proportions of Leaf Herbivory Type and Herbivory Intensity for *H. rosa-sinensis* (Fig. 7). Leaves with leaf chewing only significantly decrease as a function of increasing Herbivory Intensity (6a linear regression, $R^2=0.76$, $P<0.0001$), while leaves with galls only and those with both herbivory types significantly increase (6b linear regression, $R^2=0.51$, $P<0.0001$; 6c linear regression, $R^2=0.53$, $P<0.0001$).
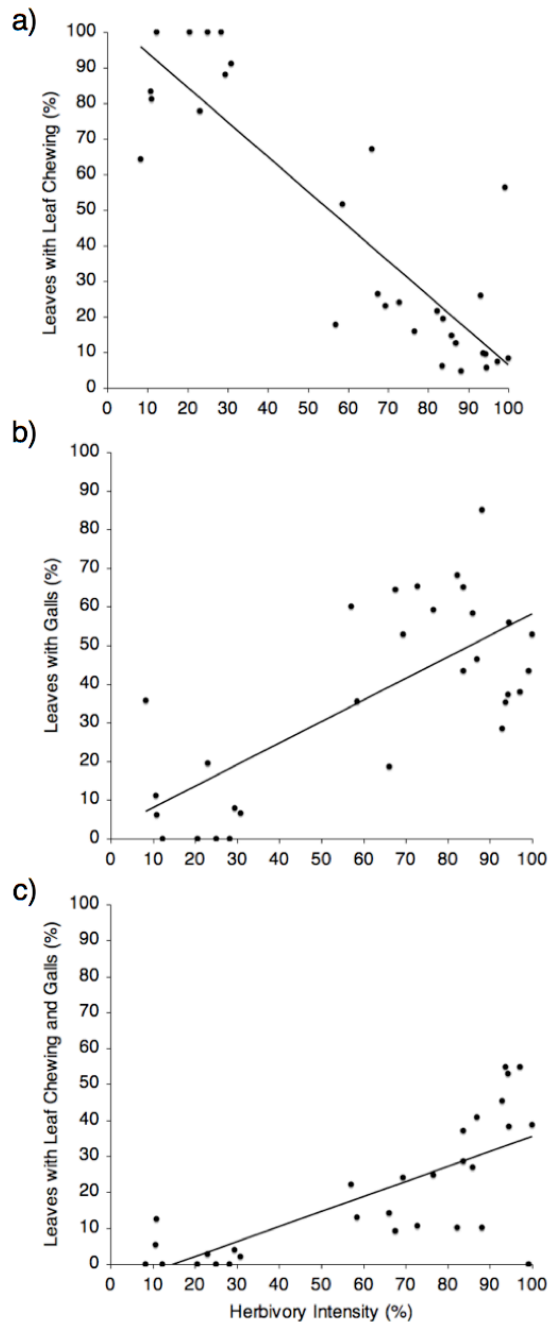

FIG. 7. Proportion of Leaf Herbivory Type as a function of Herbivory Intensity in *H. rosa-sinensis* (n=30). a) Proportion of leaves with leaf chewing as a function of Herbivory Intensity. The proportion of leaves with leaf chewing significantly decrease as Herbivory Intensity increases ($R^2=0.76$, $P<0.0001$). b) Proportion of leaves with galls as a function of Herbivory Intensity. The proportion of leaves with galls significantly increases as Herbivory Intensity increases ($R^2=0.51$, $P<0.0001$). c) Proportion of leaves with both leaf chewing

and galls as a function of Herbivory Intensity. The proportion of leaves with both significantly increases as Herbivory Intensity increases (R^2=0.51, P<0.0001).

DISCUSSION

The resulting variation in trends of herbivory across human impacted areas in this study most importantly shows that anthropogenic activity can have a significant influence on the population dynamics of herbivorous insects. The collective results of this study have consistently shown patterns that suggest the prevalence of herbivory is increasing in order from UCB Gump Station to the Belvedere to the Agriculture School. This is more accurately reflects the results for *H. tiliaceus*, whose insect herbivory estimates significantly increase across sites. In contrast, insect herbivory estimates for *H. rosa-sinensis* consistently showed no significant difference between the Belvedere and Agriculture School sites, and they will be referred to as the 'high impact sites' in this discussion.

The interspecific variation in insect herbivory estimates in conjunction with *H. rosa-sinensis* exhibiting two different insect herbivory types supports previous findings that non-invasive exotic plants suffer greater levels of insect herbivory (Cappuccino and Carpenter 2005). This may attributable to *H. rosa-sinensis* exhibiting characteristics associated with the Increased Susceptibility Hypothesis (Hokkanen and Pimentel 1989), which states that exotic plants will potentially suffer more insect herbivory in their area of introduction because they have not co-evolved with these indigenous herbivores, thus lack effective anti-herbivore defense mechanisms.

This interspecific variation in insect herbivory estimates can be explained by consequences of competition between both the leaf chewers and gall formers of *H. rosa-sinensis*. Niche partitioning (Schoener 1974) may be a potential consequence of these competitive interactions, and can be reflected in the data showing how leaf chewing herbivory decreases as Herbivory Intensity increases (Fig. 7), and if the relative Gall (Fig. 4) and Leaf Chewing Intensities (Fig. 3) are compared between the high impact sites and UCB Gump Station. Because the gall formers are much more prevalent at the high impact sites, perhaps this competitive pressure has driven leaf chewer dispersal to lowland sites like UCB Gump Station, which exhibit a higher prevalence of leaf chewers than gall

formers. It is also possible that the gall formers are not as tolerant to the low elevation and marine influenced changes in microclimate at UCB Gump Station. Although it may also be possible that the gall formers have not been heavily introduced to this area.

The results from this study have consistently shown that all measures of herbivory are the highest at the Agriculture School site to at least a small degree, and this trend is consistent with literature describing the influences of agriculture fields on herbivore activity. Previous studies have recorded agriculturally subsidized increases in herbivorous insects around the agricultural field natural edges (Kogan and Turnipseed 1987, McKone *et al.* 2001). The described mechanism driving this phenomenon is due to the utilization of agriculturally provided resources by herbivorous insects, which increase their populations, that spillover into the adjacent natural edges (Tscharntke *et al.* 2005). A similar mechanism has been described and recorded for insect natural enemies (Rand *et al.* 2006). It has also been shown that herbivorous insect spillover has the potential to detrimentally affect target vegetation occurring at natural edges, as was the case with sunflowers that were affected by agriculturally subsidized corn root-worm beetles at McKnight Prairie in Minnesota (McKone *et al.* 2001). This was not the case in this study, for there was no significant difference in leaf chewing damage between the high impact sites for both *H. tiliaceus* and *H. rosa-sinensis*, but limitations associated with the LDI method may be held accountable for this.

In addition to agricultural edges, there is a wide pool of literature describing similar phenomena occurring at forest edges, referred to as the edge effect principle (Wiens 1976, Harris 1988). A review evaluating 55 cases of herbivore patterns associated with forest edges showed that 82% of the cases were associated with higher herbivore diversity, abundances, and herbivory patterns (Wirth *et al.* 2008). An abiotic explanation for the edge effect principle is that forest edges create changes in microclimate conditions, which select for specific plant communities relative to the forest interior. Plant communities within tropical forest edges can vary as a function of edge structure, which also affects the magnitude of microclimate conditions (Didham 1999). It is difficult to determine holistic mechanisms behind such edge effects because they are likely a result of complex

ecological processes that can include top-down or bottom-up trophic cascades. For example, it has been shown that the prevalence of insectivorous birds and natural enemies also increase at forest edges and agriculture-natural edges (Strelke and Dickson 1980, Rand *et al.* 2006). Such edge effects may ultimately result in a top-down trophic cascade, where target herbivore populations will decrease thus plant community composition may be altered because of release from predation.

Comparable to forest edges, ecotones can induce similar mechanisms that result in changes in community composition. It has been shown that marine nutrient transfer to land through algal wrack and shorebirds can ultimately increase populations of arthropod secondary consumers around the marine-terrestrial interface (Polis and Hurd 1996). These hypothetical increases in arthropod secondary consumer densities can possibly explain why UCB Gump Station had the lowest prevalence of herbivory. A previous study showed that increases in arthropod secondary consumer densities on broccoli significantly decreased the abundances of several leaf chewing caterpillar genera as well as the magnitude of leaf chewing herbivory on the plant (Hooks *et al.* 2003). But, it is probable that the combination of the ocean and human infrastructure constitute a large enough barrier to pose as a dispersal challenge for herbivorous insects. There was also a relatively lower vegetation cover at UCB Gump Station relative to the high impact sites.

Aside from environmental and anthropogenic influences affecting herbivory patterns, plant secondary compound defense mechanisms may explain some of the variation we see in insect herbivory patterns across sites and between species. Many plants have evolved these secondary compound defense mechanisms to deter herbivores that can either be constitutively expressed or induced in response to herbivore attack (Stamp 2003). *H. rosa-sinensis* was introduced by the Polynesians for medicinal purposes (Florence 2004) and is known to contain secondary compounds (Cox 2008) but it is unknown as to what type or magnitude of resistance *H. rosa-sinensis* exhibited in this study.

A study involving cotton, a Malvaceae species closely related to *H. rosa-sinensis*, as well as gall inducing mites and leaf chewing caterpillars showed how constitutive and induced resistance mechanisms affected their survivorship. The mites exhibited a tolerance to both types of resistance and its population size remained the same while the caterpillars were severely affected by both types of resistance, reducing their survivorship by approximately 50% (Agrawal and Karban 2000). These findings may be relevant to why gall formers are much more prolific at the high impact sites. It may be possible that their tolerance to the secondary compounds of the cultivated varieties grown there has allowed them to thrive, while the leaf chewers are more sensitive to them.

In addition to secondary compound plant resistance, plant-insect anti-herbivore defense mutualisms may be responsible for some of the variation in herbivory patterns seen across sites and between species. *H. tiliaceus* is known for having extrafloral nectaries which ants tend and mutualistically provide anti-herbivore defenses for the plants (Pemberton 1998). It has been shown that the lack of extrafloral nectaries in a related species, *Hibiscus glaber*, shows higher rates of flower-bud herbivory than *H. tiliaceus*. So it is possible that variation in presence-absence of this anti-herbivore mutualism across sites may have contributed to some of the variation seen in *H. tiliaceus* insect herbivory estimates across sites. The lack of this anti-herbivore defense mutualism in *H. rosa-sinensis* may attribute to the interspecific variation in leaf chewing insect herbivory. Although leaf chewing estimates were often significantly greater in *H. tiliaceus*, the lack of an anti-herbivore mutualism in *H. rosa-sinensis* may have potentially contributed to its susceptibility to gall forming insects.

CONCLUSIONS

In conclusion, this study at least provided knowledge that herbivorous insect communities within a far removed archipelago may still be significantly affected by human activity, as shown by the variation in insect herbivory patterns of *H. tiliaceus* and *H. rosa-sinensis* across human impacted areas. These patterns support previous findings that forest and agriculture edges are often associated with changes in herbivory activity, thus supporting the edge effect principle.

The significant variation in interspecific insect herbivory patterns also support the Increased Susceptibility Hypothesis with respect to *H. rosa-sinensis*, and evidence that non-invasive exotic plants are more susceptible to insect herbivory.

With respect to future studies investigating anthropogenic impacts on herbivorous insects, it is important to note that the anthropogenic impacts in Mo'orea, French Polynesia are relatively low severity in comparison to the widespread deforestation in continental regions allowing for urbanization, suburban sprawl and extensive monoculture farming. Thus, these findings may highlight the hypersensitivity of herbivorous insect communities to human activity. It is recommended for future researchers to determine what degree of anthropogenic disturbance may still allow for the preservation of natural ecological processes in forests. Linking human-induced changes in herbivory patterns to its effects on forest ecosystem functioning, in the form of nutrient cycling would be novel direction to take in order to holistically understand the repercussions of human impacts on forest ecosystems.

LITERATURE CITED

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