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ORIGINAL PAPER

Does enemy release matter for invasive plants? evidence from a comparison of insect herbivore damage among invasive, non-invasive and native congeners

Hong Liu · Peter Stiling · Robert W. Pemberton

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Abstract One of the most popular single-factor hypotheses that have been proposed to explain the naturalization and spread of introduced species is the enemy release hypothesis (ERH). One ramification of the ERH is that invasive plants sustain less herbivore damage than their native counterparts in the invaded range. However, introduced plants, invasive or not, may experience less herbivore damage than the natives. Therefore, to test the role of natural enemies in the success of invasive plants, studies should include both invasive as well as non-invasive introduced species. In this study, we employed a novel three-way comparison, in which we compared herbivore damage among native, introduced invasive, and introduced non-invasive *Eugenia* (Myrtaceae) in South Florida. We found that introduced *Eugenia*, both invasive and non-invasive, sustained less herbivore damage, especially damage by oligophagous and endophagous insects, than native *Eugenia*. However, the difference in insect damage between introduced invasive and introduced non-invasive *Eugenia* was not significant. Escape from herbivores may not account for the spread of invasive *Eugenia*. We would not have been able to draw this conclusion without inclusion of the non-invasive *Eugenia* species in the study.

Keywords Biological invasion · Endophagous insect damage · Enemy release hypothesis · *Eugenia* · Herbivory · Introduced species · Invasive species · Non-invasive species · Oligophagous insect damage

H. Liu · P. Stiling
Department of Biological Sciences, University of South Florida, 4202 East Fowler Ave, Tampa, FL 33620-5200, USA

R. W. Pemberton
USDA, ARS, Invasive Plant Research Lab, 3225 College Ave, Fort Lauderdale, FL 33314, USA

Present Address:
H. Liu (✉)
IFAS, Ft. Lauderdale Education and Research Center, University of Florida, 3225 College Ave, Fort Lauderdale, FL 33314, USA
e-mail: hongliuf@ufl.edu

Introduction

The enemy release hypothesis (ERH), which states that introduced invasive species are successful because they left their co-evolved natural enemies behind, is one of the most cited explanations for the undesired success of introduced invasive species worldwide (Crawley 1997; Maron and Vila 2001; Keane and Crawley 2002). This hypothesis has received support from many studies comparing herbivore pressure on the invasive plants in their native versus introduced ranges (Wolfe 2002; Colautti et al. 2004; DeWalt et al.

2004; Liu and Stiling 2006). One ramification of the ERH is that invasive introduced plants sustain less herbivore pressure than their native counterparts in the introduced range. This hypothesis has received support from some studies (Schierenbeck et al. 1994; Siemann and Rogers 2003; Dietz et al. 2004; Liu and Stiling 2006), but not others (Agrawal and Kotanen 2003; Parker and Hay 2005). A modification of the ERH, which states that it is the escape from specialist insects (including endophagous species) that allow the introduced plants to be successful, has received increasing support (Wolfe et al. 2004; Joshi and Vrieling 2005; Stastny et al. 2005; Mitchell et al. 2006). However, studies comparing herbivory between sympatric introduced invasive plants and their native counterparts rarely distinguished damage from specialist versus generalist, or from endophagous versus ectophagous insects (e.g., Agrawal and Kotanen 2003; Dietz et al. 2004). In addition, since all introduced plants, regardless of their abundance or impact, may support a reduced insect herbivore fauna and experience less damage (Strong et al. 1984; Colautti et al. 2004), testing ERH would be more meaningful if such studies also included introduced non-invasive species (Colautti et al. 2004; Levine et al. 2004). Only three studies have performed such comparisons (Mitchell and Power 2003; Cappuccino and Carpenter 2005; Carpenter and Cappuccino 2005). All three found that the less invasive or non-invasive species had more pathogens (Mitchell and Power 2003) or suffered more herbivory than the more invasive species (Cappuccino and Carpenter 2005; Carpenter and Cappuccino 2005), which is consistent with the predictions of ERH.

A three-way comparison distinguishing specialist versus generalist, and endophagous versus ectophagous herbivore damage on congeneric native, introduced invasive, and introduced non-invasive (innocuous) species co-occurring in the same region would provide much insightful information on the validity of ERH by comparing the biotic resistances encountered by the invasive versus non-invasive plants in relation to the native species. The working hypothesis of this approach is that the introduced invasive plants experience greater relief (relative to the native congeners) from herbivory, particularly from specialist or endophagous herbivore pressure than do the introduced non-invasive plants. Endophagous herbivores are of interest because an internal feeding niche is likely to be correlated with dietary specialization (Frenzel and Brandl 1998).

In this study we compared herbivore damage levels among native (two species), introduced invasive (one species), and introduced non-invasive (three species) of *Eugenia* (Myrtaceae) living in South Florida. The *Eugenia* spp. we studied are small-medium sized trees native to Florida or Central-South America (Ruehle et al. 1958; Wunderlin and Hansen 2003). We predict that: (1) the total herbivore damage, and damage by specialist and/or endophagous insects, will be (a) greater for the native *Eugenia* species than for the introduced invasive and non-invasive congeners; and (b) greater for the introduced non-invasive *Eugenia* than for the introduced invasive congener and, (2) the herbivore damage by generalist and/or ectophagous insects will be (a) greater on the native *Eugenia* than the introduced congeners, and (b) greater on the introduced non-invasive *Eugenia* than the introduced invasive congener. The second prediction was made based on the predictions of Keane and Crawley (2002), which states that native species should experience higher impact by generalists than the co-occurring introduced congeners. The first portions of the two predictions are comparable to predictions made by the usual two-way (native versus introduced invasive plants) comparisons. For the ERH to be supported in the current three-way study system, the second portions of the predictions should be validated as well.

Materials and methods

Study species

Eugenia is a large, mostly neo-tropical genus in the family of Myrtaceae. *Eugenia axillaris* (Sw.) Willd. (white stopper) and *E. foetida* Pers. (Spanish stopper) are two common understory shrubs or small trees native to the subtropical evergreen forest in South Florida. They bear fleshy fruits that are potentially dispersed by birds and small mammals (H. Liu, personal observations). *Eugenia uniflora* L. (Surinam cherry), *E. aggregata* Kiaersk. (cherry of the Rio Grande), *E. brasiliensis* Lam. (grumichama), and *E. luschnathiana* Klotzsch (pitomba) are all large shrubs or small trees introduced to South Florida from Brazil in the late 1800s or early 1900s for home fruit gardens (Ruehle et al. 1958; Martin et al. 1987). *E. uniflora* is also a common hedge plant in South Florida, probably due to its robust and rapid growth. Since its introduction, *E. uniflora* has escaped cultivation and invaded hammocks (evergreen broad-leaved forests) in South Florida, growing side by side in some areas with the native congeners, including *E. axillaris* and *E. foetida* (Gann et al. 2001) (Table 1). The other three introduced *Eugenia* still remain in cultivation in some public and private gardens and nurseries.

Study sites

We carried out herbivore damage censuses at two subtropical hammocks in Broward County where *E. axillaris* (native), *E. foetida* (native), and *E. uniflora* (invasive) co-occur: Hugh Taylor Birch State Park (hereafter referred to as Birch Park), and the Bonnet House Museum and Garden (hereafter referred to as Bonnet House). The two sites were about 1.5 km apart. Subtropical hammocks in South Florida are evergreen, broad-leaved forests composed predominantly of trees common to the Bahamas and Greater Antilles (Snyder et al. 1990). They occupy limestone outcroppings that are elevated, rarely inundated, and relatively fire-free. In hammocks of both Birch Park and Bonnet House, the canopy trees are primarily composed of *Bursera simaruba* (gumbo-limbo), *Coccoloba unifera* (sea-grape), *Krugiodendron ferreum* (black iron wood), and *Ficus aurea* (strangler fig). The understory is dominated by *E. axillaris*, *E. foetida*, and *E. uniflora*. Sandy soil is characteristic of both sites.

For the introduced non-invasive *E. aggregata*, *E. brasiliensis*, and *E. luschnathiana*, we located up to 14 individuals per species in the following research, public, and private gardens in Miami Dade and Broward, two adjacent counties in South Florida: University of Florida—Tropical Research and Education Center, the Fruit and Spice Park, Plantation Heritage Park, and Fairchild Tropical Garden. These plants are referred to as cultivated aggregata, cultivated brasiliensis, and cultivated luschnathiana (Table 1). In addition, as a control for potential site related differences between these gardens and the natural subtropical hammocks, we also sampled nine, ten, and 28 individuals, respectively, of *E. axillaris* (native), *E. foetida* (native), and *E. uniflora* (invasive) at the above gardens. These individuals were referred to as cultivated axillaris, cultivated foetida, and cultivated uniflora. Census frequencies for the cultivated plants were the same as for the wild populations mentioned above.

Quantification of herbivore damage

Four and two 5×3 m^2 plots were established at the Birch Park and the Bonnet House, respectively, for quantification of foliar herbivore damage and demography on wild populations of *E. axillaris*, *E. foetida*, and *E. uniflora* (Table 1). Only the herbivore damage data are presented here. All individuals of the three species that were greater than 1.0 m in height within each plot were tagged. Within each plot, two circular subplots (1 m^2) were established and all individuals that were less than 1m in height were tagged. Since *E. uniflora* density was lower than either of the

Table 1 Summary of the study system. *n* is the number of plants included in the analyses. Plants that grow in Gardens are cultivated

Plant species	Status	Growing habitat in south Florida (*n*)
E. axillaries	Native	Natural hammocks (71) and garden (9)
E. foetida	Native	Natural hammocks (65) and garden (10)
E. uniflora	Introduced invasive	Natural hammocks (53) and garden (28)
E. aggregata	Introduced non-invasive	Garden (9)
E. brasiliensis	Introduced non-invasive	Garden (14)
E. luschnathiana	Introduced non-invasive	Garden (10)

native *Eugenia*, several individuals of *E. uniflora* were also tagged arbitrarily outside the sample plots to increase sample size. All these plants are hereafter referred to as wild axillaris, wild foetida, and wild uniflora. These plots were visited bimonthly during the dry season (October to April) and monthly during the wet season (May to September) of 2004. We quantified foliar herbivore damage by examining up to 100 leaves per plant and counting the number of leaves with herbivore damage. Since most foliar damage by oligophagous (defined as insects that feed on plants of one family only) and endophagous herbivores are distinctive, we were able to separate damage by oligophagous and endophagous herbivores from that by polyphagous and ectophagous herbivores. In this study the terms ''oligophagous'' and ''polyphagous'' were interchangeable with ''specialist'' and ''generalist,'' respectively. For fruit and seed feeders, we collected and examined random fruit samples from three to ten trees and 20–100 fruits per tree, depending on availability. Some non-rotten fruits on the ground, all of which may not belong to the tree directly above it if there is dispersal, were also included in the sample.

Data analyses

Data on herbivore damage level, i.e., proportion of leaves and seeds with herbivore damage were transformed using Anscombe's 1948 version of the arcsine transformation (Zar 1984, p240) that gives better results for extreme proportions (near to 0 or 1). We conducted an ANOVA on the average damage across all censuses as well as a repeated measures ANOVA to determine if the foliar herbivory among plant species were significantly different. Since results of these two analyses largely agreed with each other, we only present results on the average damage. Only plants that had more than 20 leaves at all censuses were included in this analysis. ANOVA was also used to determine the differences in seed damage among species. Four sets of planned contrasts were made to examine the differences in damage between (1) wild native *Eugenia* versus wild introduced invasive *Eugenia*, (2) cultivated native *Eugenia* versus cultivated introduced invasive *Eugenia*, (3) cultivated native versus cultivated introduced non-invasive *Eugenia*, and (4) cultivated invasive *Eugenia* versus cultivated non-invasive *Eugenia*. Samples from the two natural area sites were pooled because they had similar herbivory levels. Samples from the four garden sites were pooled because all gardens did not have adequate sample sizes for among site comparisons.

Results

Total foliar damage

Plant species exhibited significantly different total foliar damage levels ($F_{8,260} = 13.68$, $P < 0.001$) (Fig. 1a). Planned contrasts indicated that wild native *Eugenia* had significantly higher foliar damage than wild introduced invasive *Eugenia* ($F_{1,260} = 16.52$, $P < 0.001$). Similarly, cultivated native *Eugenia* had significantly higher foliar damage than cultivated invasive *Eugenia* ($F_{1,260} = 39.38$, $P < 0.001$) as well as non-invasive *Eugenia* ($F_{1,260} = 38.66$, $P < 0.001$). However, the foliar damage levels did not differ between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,260} = 0.06$, $P = 0.808$).

Foliar damage by ectophagous insects

Different species of *Eugenia* differed significantly in the foliar damage by ectophagous insects ($F_{8,260} = 10.62$, $P < 0.001$) (Fig. 1b). Planned contrasts indicated that wild native *Eugenia* had significantly higher ectophagous foliar damage than wild introduced invasive *Eugenia* ($F_{1,260} = 6.67$, $P = 0.010$). Similarly, cultivated native *Eugenia* had significantly higher foliar damage than cultivated invasive *Eugenia* ($F_{1,260} = 37.18$, $P < 0.001$) as well as non-invasive *Eugenia* ($F_{1,260} = 36.47$, $P < 0.001$). However, the foliar damage levels were not different between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,260} = 0.057$, $P = 0.811$).

Foliar damage by endophagous insects

Eugenia species differed significantly in the foliar damage by endophagous insects ($F_{8,260} = 27.58$,

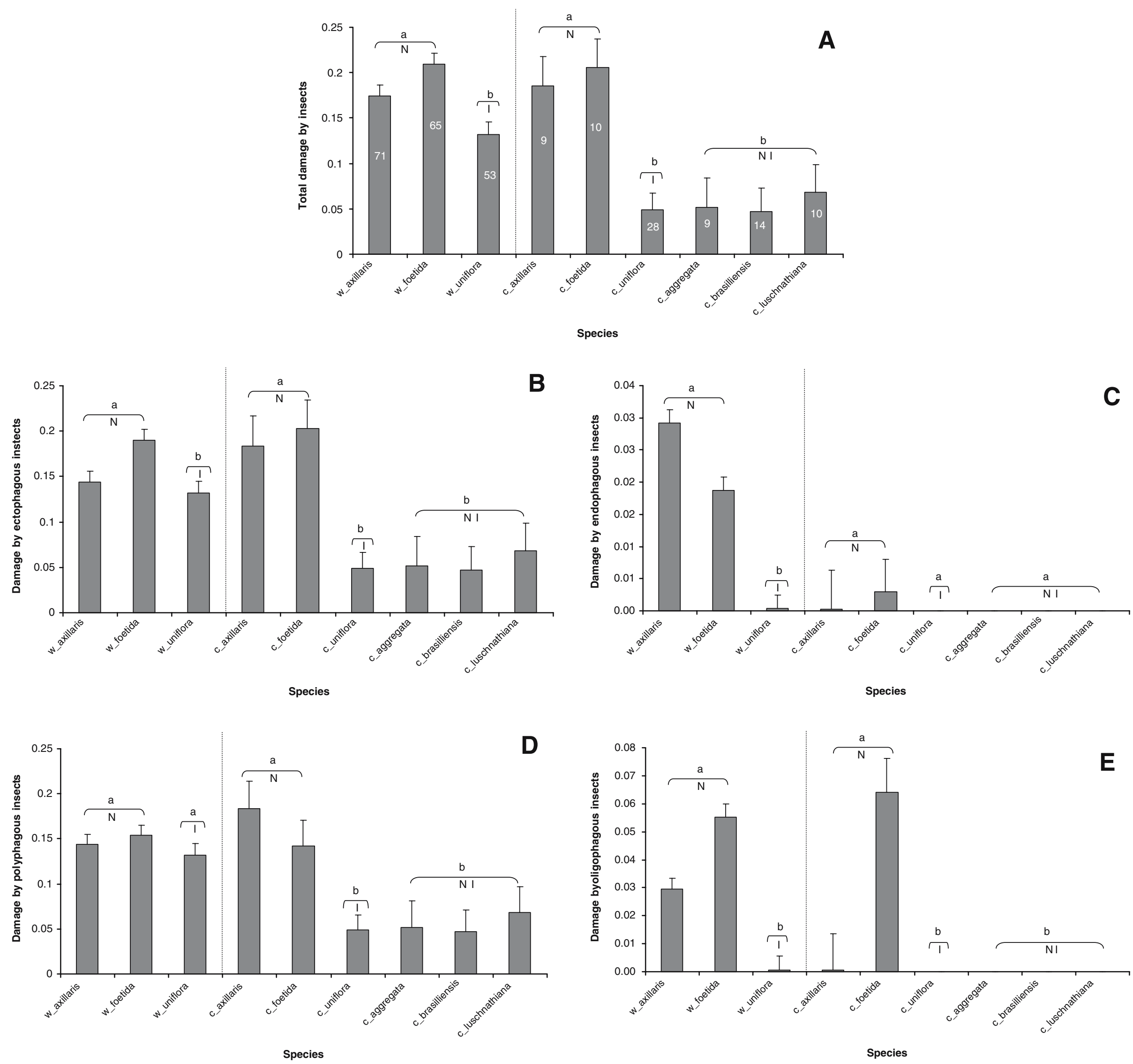

Fig. 1 Means and standard errors of foliar insect damage (in proportion) on six wild and/or cultivated *Eugenia* species in South Florida with seven censuses pooled. Numbers inside bars are sample sizes for each species. The *vertical dashed line* separates the wild from cultivated samples, with the former on the left. *W* wild growing and *C* cultivated plants. Species were grouped into three categories as indicated by letters below the grouping line: ''*N*'' indicates native *Eugenia*, ''*I*'' invasive introduced *Eugenia*, and ''*NI*'' non-invasive introduced *Eugenia*. *Different letters* above the group line indicates significant difference between groups of the same cultivation state (wild or cultivated). (**A**) Total damage. (**B**) Damage by ectophagous insects. (**C**) Damage by endophagous insects. (**D**) Damage by polyphagous insects. (**E**) Damage by oligophagous insects

$P < 0.001$) (Fig. 1c). Planned contrasts indicated that wild native *Eugenia* had significantly higher endophagous foliar damage than wild introduced invasive *Eugenia* ($F_{1,260} = 121.40$, $P < 0.001$). However, the endophagous foliar damage did not differ statistically between the cultivated native *Eugenia* and the cultivated invasive *Eugenia* ($F_{1,260} = 0.329$, $P = 0.567$) or the non-invasive *Eugenia* ($F_{1,260} = 0.346$, $P = 0.557$). In addition, the foliar damage levels were the same between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,260} = 0.00$, $P = 1.00$).

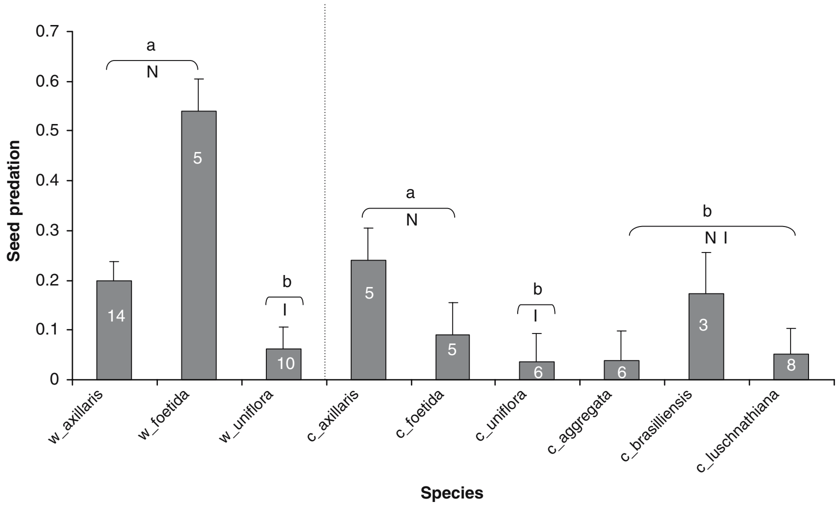

Fig. 2 Means and standard errors of seed predation (in proportion) of six wild and/or cultivated *Eugenia* species in South Florida. Numbers inside bars are sample sizes for each species. Each sample consists of 20–100 seeds. The *vertical dashed line* separates the wild from cultivated samples, with the former on the left. *W* wild growing and *C* cultivated plants. Species were grouped into three categories as indicated by letters below the grouping line: "*N*" indicates native *Eugenia*, "*I*" invasive introduced *Eugenia*, and "*NI*" non-invasive introduced *Eugenia*. *Different letters* above the group line indicates significant difference between groups of the same cultivation state (wild or cultivated)

Foliar damage by polyphagous insects

Different species of *Eugenia* differed significantly in the foliar damage by polyphagous insects ($F_{8,260} = 7.27$, $P < 0.001$) (Fig. 1d). The difference in polyphagous damage was only marginally significant between wild native *Eugenia* and wild introduced invasive *Eugenia* ($F_{1,260} = 2.98$, $P = 0.085$). In addition, cultivated native *Eugenia* had significantly higher foliar damage than cultivated invasive *Eugenia* ($F_{1,260} = 26.83$, $P < 0.001$) as well as non-invasive *Eugenia* ($F_{1,260} = 25.93$, $P < 0.001$). However, the foliar damage levels were not differ between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,260} = 0.060$, $P = 0.806$).

Foliar damage by oligophagous insects

Eugenia species differed significantly in the foliar damage by oligophagous insects ($F_{8,260} = 114.07$, $P < 0.001$) (Fig. 1e). Planned contrasts indicated that wild native *Eugenia* had significantly higher oligophagous foliar damage than wild introduced invasive *Eugenia* ($F_{1,260} = 114.07$, $P < 0.001$). Similarly, cultivated native *Eugenia* had significantly higher foliar damage than cultivated invasive *Eugenia* ($F_{1,260} = 13.41$, $P < 0.001$) as well as non-invasive *Eugenia* ($F_{1,260} = 14.09$, $P < 0.001$). However, the foliar damage levels were not differ between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,260} = 0.00$, $P = 1.000$).

Fruit and seed predation rate

Fruit predation (fruit galling) occurred only in the two native *Eugenia* species. The fruit predation rate ranged from 0 to 26% for *E. axillaris*, and 0 to 10% for *E. foetida*. No statistical analysis was carried out on fruit predation. ANOVA on transformed seed predation rates indicated that species were significantly different ($F_{8,53} = 7.25$, $P < 0.001$) (Fig. 2). Planned contrasts indicated that wild native *Eugenia* had significantly higher seed predation than wild introduced invasive *Eugenia* ($F_{1,53} = 27.83$, $P < 0.001$). Similarly, cultivated native *Eugenia* had marginally significantly higher foliar damage than cultivated invasive *Eugenia* ($F_{1,53} = 3.83$, $P = 0.056$), but the difference between cultivated native *Eugenia* and introduced non-invasive *Eugenia* was not significant ($F_{1,53} = 1.82$, $P = 0.184$). In addition, the seed predation levels did not differ between the cultivated invasive *Eugenia* and the non-invasive *Eugenia* ($F_{1,53} = 0.881$, $P = 0.352$).

Discussion

The first portion of our first prediction that the native species should sustain higher total herbivore damage, and damage by oligophagous and endophagous insects than introduced invasive and non-invasive species, was supported by the foliar and seed damage data, except for the endophagous damage comparison among the cultivated *Eugenia*. In addition, only the two native species sustained damage by the fruit gall maker, a devastating oligophagous and endophagous insect that ruins the whole infested fruit (H. Liu, personal observation). Our results are consistent with a meta-analysis of 21 pairs of native versus introduced invasive congeneric plants, in which the native species had significantly higher foliar damage than their introduced invasive congeners (Liu and Stiling 2006). In addition, in a community wide study, Dietz et al. (2004) found that the introduced invasive plants had less damage by insect herbivores than did co-occurring native species. However, in contrast to predictions from the ERH, a common garden study showed that several introduced invasive plants suffered less foliar insect damage than their native relatives (Agrawal and Kotanen 2003).

We found no support for the second portion of our first prediction, which states that introduced invasive *Eugenia* should have lower total, oligophagous, and endophagous insect damage than the non-invasive *Eugenia*. Instead, we found that the invasive and non-invasive *Eugenia* sustained similar levels of herbivore damage. In contrast, other studies had reported that non-invasive or less invasive plants had more leaf damage or pathogens than the invasive or more invasive plants (Mitchell and Power 2003; Cappuccino and Carpenter 2005; Carpenter and Cappuccino 2005). But none of these studies distinguished between polyphagous versus oligophagous or ectophagous versus endophagous herbivore damage.

Similarly, we found support for the first portion of our second prediction that herbivore damage by polyphagous and ectophagous insects will be greater in the native *Eugenia* than in the introduced congeners. The native *Eugenia* had higher levels of polyphagous and ectophagous insect damage than the introduced *Eugenia*, except in one case in which the polyphagous insect damage levels were similar between the wild native *Eugenia* and wild invasive *Eugenia*. However, we did not found support for the second portion of our second prediction as no difference in polyphagous or ectophagous insect damage was found between the invasive and non-invasive *Eugenia*.

There were differences in herbivore damage between wild and cultivated plants of the same species. For example, wild *E. uniflora* (the introduced invasive) had higher levels of total damage, and damage by external and generalist insects than its cultivated counterpart. But the damage caused by internal and specialist insects did not differ in the cultivated and wild *E. uniflora*. In contrast, wild *E. axillaris* (native) had less damage by external and generalist insects, but higher damage by internal and specialist insects than it's cultivated counterpart. Since the comparison of wild versus cultivated plants was not relevant to the ERH hypothesis testing, we are not presenting detailed results of these comparisons. The significant differences between the wild versus cultivated plants reinforced the need to restrict comparisons among different species to plants of the same cultivation status (wild or cultivated).

Interestingly, most of the foliar damage on wild invasive *E. uniflora* was done by the recently introduced polyphagous weevil *Mylloceras undatus* Marshall, a native of Sri Lanka (Schall 2000). This weevil attacked the invasive *E. uniflora* more heavily than it did the other studied *Eugenia* species and it was most abundant at the natural areas (Liu et al. 2006). However, we did not find any preference by native polyphagous insects. Our observations differed from a recent study in which the authors found that a native generalist herbivore preferred non-native plants and an exotic generalist had no preference in term of native versus introduced plants (Parker and Hay 2005). In another recent study, the native herbivores, mostly vertebrates, were found to suppress introduced plants, whereas exotic herbivores, also mostly vertebrates, promoted exotic plants (Parker et al. 2006).

In summary, we found support to ERH only from the conventional two-way comparison between the native versus invasive plants. However, because the insect damage levels of the introduced invasive and introduced non-invasive *Eugenia* are similar, escape from herbivores, including oligophagous and/or endophagous insects, is likely to account for only a small portion, if any, of the success of the invasive *Eugenia*. If we did not include the non-invasive *Eugenia* species in the study and only compared the herbivore damage levels between the native *Eugenia* and invasive *Eugenia*, we would have thought that release from the natural enemies may have played a larger role in the success of *E. uniflora*. Nevertheless, our study focused on damage by insects whereas the ERH is based on impact by natural enemies. Because damage does not necessarily correlate with impact, our study should be interpreted with caution. Future studies should take advantage of this unique three-way system to examine other competing but non-exclusive hypotheses. For example, differential competitive interactions of introduced invasive *Eugenia* versus native co-occurring plants and non-invasive introduced *Eugenia* versus native plants may be a factor in the success of *E. uniflora*. In addition, *E. uniflora*, as a common hedge plant, was sold and planted much more widely than the other three introduced *Eugenia* spp. The differential propagule pressures exerted by the invasive versus the noninvasive *Eugenia* to the urban forest fragments may well be a major player leading to the successful naturalization and invasion by *E. uniflora* in these natural areas.

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