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# INSECT HERBIVORE FAUNAL DIVERSITY AMONG INVASIVE, NON-INVASIVE AND NATIVE *EUGENIA* SPECIES: IMPLICATIONS FOR THE ENEMY RELEASE HYPOTHESIS

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Abstract

The enemy release hypothesis (ERH) frequently has been invoked to explain the naturalization and spread of introduced species. One ramification of the ERH is that invasive plants sustain less herbivore pressure than do native species. Empirical studies testing the ERH have mostly involved two-way comparisons between invasive introduced plants and their native counterparts in the invaded region. Testing the ERH would be more meaningful if such studies also included introduced non-invasive species because introduced plants, regardless of their abundance or impact, may support a reduced insect herbivore fauna and experience less damage. In this study, we employed a three-way comparison, in which we compared herbivore faunas among native, introduced invasive, and introduced non-invasive plants in the genus *Eugenia* (Myrtaceae) which all co-occur in South Florida. We observed a total of 25 insect species in 12 families and 6 orders feeding on the six species of *Eugenia*. Of these insect species, the majority were native (72%), polyphagous (64%), and ectophagous (68%). We found that invasive introduced *Eugenia* has a similar level of herbivore richness as both the native and the non-invasive introduced *Eugenia*. However, the numbers and percentages of oligophagous insect species were greatest on the native *Eugenia*, but they were not different between the invasive and non-invasive introduced *Eugenia*. One oligophagous endophagous insect has likely shifted from the native to the invasive, but none to the non-invasive *Eugenia*. In summary, the invasive *Eugenia* encountered equal, if not greater, herbivore pressure than the non-invasive *Eugenia*, including from oligophagous and endophagous herbivores. Our data only provided limited support to the ERH. We would not have been able to draw this conclusion without inclusion of the non-invasive *Eugenia* species in the study.

Key Words: biological invasion, endophagous insect, herbivore fauna, introduced species, invasive species, non-invasive species, oligophagous insects

Resumen

La hipótesis de escape del enemigo (HEE) ha sido frecuentemente utilizada para explicar la naturalización y extensión de especies introducidas. Una de las ramificaciones de la HEE es que las plantas invasoras soportan un grado de herbivorismo menor que el de las especies nativas. La mayor parte de los estudios empíricos para analizar la HEE han implicado comparticiones de dos-vías entre la especie invasora y su contraparte nativa del área de invasión. Estos análisis serían de mayor relevancia si los mismos también incluyeran especies no nativas que fueran no invasoras. Estas especies, independientemente de su abundancia e impacto, podrían tener una reducido fauna herbivora y por tanto experimentar un grado menor de daño. En este estudio nosotros usamos una comparación de tres vías en la cual se compara las fauna herbivoras de especies nativas, especies invasoras introducidas y especies introducidas no invasoras del género *Eugenia* (Myrtaceae) del Sur de La Florida. Observamos un total de 25 especies de insectos en doce familias y seis órdenes alimentandose sobre seis especies de *Eugenia*. Entre éstos, la mayoría son nativos (72%) polifagos (64%) y ectofagos (68%). Nosotros encontramos que especies invasoras introducidas de *Eugenia* tiene niveles similares de riqueza de herbívoros que los de las especies nativas e introducidas no invasoras. Sin embargo el número y el porcentaje de insectos oligofagos fue mayor en las especies nativas, aunque estas diferencias no fueron significativas entre las especies introducidas invasoras y no invasoras de *Eugenia*. Uno de los herbívoros oligofago y endofago es probable que haya cambiado desde la especie nativa a la invasora, pero ninguno de éstos a la especie no invasora de *Eugenia*. En resumen, la especie invasora de *Eugenia* ha encontrado la misma, o quizás mayor, presión por parte de herbivoros que la especie no invasora de Eugenia, incluyendo oligofagos y endofagos. Nuestros datos indican un apoyo muy limitado para la HEE. Nosotros no habriamos podido llegar a esta conclusión al menos que hubieramos incluido la especie no invasora de *Eugenia* en nuestro estudio.

Translation provided by the authors.

The enemy release hypothesis (ERH) states that introduced invasive species are successful because they left their co-evolved natural enemies behind. This idea makes intuitive sense and is the theoretical foundation of classical biological control. It is one of the most cited explanations for the undesired success of introduced invasive species worldwide (Williams 1959; Crawley 1997; Maron & Vilà 2001; Keane & Crawley 2002). Although empirical studies testing the ERH on invasive plants are limited in number (Maron & Vilà 2001; Keane & Crawley 2002; Liu & Stiling 2006) and vigor (but see Schierenbeck et al. 1994; Wolfe 2002; Siemann & Rogers 2003; DeWalt et al. 2004), there have been several syntheses to test the predictions stemming from ERH during the last decade (Maron & Vilà 2001; Keane & Crawley 2002; Colautti et al. 2004; Liu & Stiling 2006). One consensus generated from these syntheses and other more recent empirical studies is that the total number of insect herbivores, and the numbers of endophagous and oligophagous herbivores, are all reduced on introduced invasive species compared with conspecific populations in the native range or on co-occurring native congeners (Keane & Crawley 2002; Colautti et al. 2004; Hinz & Schwarzlaender 2004; Torchin & Mitchell 2004; Liu & Stiling 2006). In addition, 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).

All the empirical studies reviewed above were performed in one of two ways: first, insect herbivore diversity, load, or insect herbivore impact either on invasive plants in native vs. introduced ranges was examined (e.g., Wolfe 2002; DeWalt et al. 2004), or second, the same comparisons were made between invasive plants and their native counterparts in the new region (Schierenback et al. 1994; Agrawal & Kotanen 2003; Siemann & Rogers 2003). The latter approach is not a direct test of the ERH. Rather, it tests a ramification of the ERH that invasive introduced plants sustain less insect herbivore pressure than their native counterparts. However, all introduced plants, regardless of their abundance or impact, may support a reduced insect herbivore fauna and experience less damage simply because plants tend to lose their associated insect herbivores during the introduction (Colautti et al. 2004) and it takes time, on the ecological and/or evolutionary scale, for a new population to acquire its insect herbivore fauna (Strong et al. 1984). Testing the ERH would be more meaningful if such studies also included introduced plants which do not become invasive, or so-called innocuous species (Colautti et al. 2004; Levine et al. 2004). However, few studies have included introduced non-invasive plants (but see Mitchell & Power 2003; Cappuccino & Carpenter 2005; Carpenter & Cappuccino 2005).

A three-way comparison of insect herbivore faunas in a system in which congeneric native, introduced invasive, and introduced non-invasive (innocuous) plants that co-occur in the same region can provide insightful information on the validity of the ERH. If release from natural enemies is important in determination of the success of an introduced plant species, one would expect that invasive introduced plants escape more from herbivore pressure than do non-invasive introduced plants. One question of particular interest is whether there have been any shifts of oligophagous and/or endophagous herbivores from the native to the introduced plant congeners, and if such shifts occur more onto the non-invasive than to the invasive congeners. Endophagous herbivores are of interest because an internal feeding niche is likely to be correlated with dietary specialization (Frenzel & Brandl 1998). Plants that are closely related phylogenetically (i.e., congeners or confamiliers), as used in many ERH tests, offer a good chance to detect host shifts by herbivores to the introduced plants because herbivore host choice is often determined by plant relatedness.

In this study, we compared insect herbivore faunas among native (two species), invasive (one species), and non-invasive (three species) of *Eugenia* growing in South Florida. The *Eugenia* spp. studied here are small-medium sized trees native to Florida and Central-South America (Wunderlin & Hansen 2003; Ruehle et al. 1958). We predict that (1) the total number of herbivore species will be (a) greater on the native *Eugenia* species than on the introduced invasive and non-invasive congeners; and (b) greater on the introduced non-invasive *Eugenia* than on the introduced invasive congener; (2) the number and proportion of oligophagous and endophagous herbivores will be (a) greater on the native *Eugenia* species than on the introduced invasive and non-invasive congeners; and (b) greater on the introduced non-invasive *Eugenia* than on the introduced invasive congener, and (3) fewer herbivores, particularly oligophagous and endophagous herbivores, will be shared between the native *Eugenia* and the introduced invasive *Eugenia* than between the native and introduced non-invasive *Eugenia*. The first portions of the first two predictions are comparable to predictions made by the usual two-way (native vs. introduced invasive plants) comparisons. For ERH to be supported in the current three-way testing system, the second portion of the prediction should be validated. We believe this study represents the first known comparison of herbivore funna on native, invasive, and innocuous species of the same genus in the same geographic location.

## Material and Methods

### Study Plants

*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 with potentially animal-dispersed fleshy fruits that were introduced to south Florida from Brazil in the late 1800s or early 1900s for home garden fruit and ornamental purposes (Ruehle et al. 1958; Martin et al. 1987). *Eugenia uniflora* is 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 2 native congeners, *E. axillaris* (Sw.) Willd. (white stopper) and *E. foetida* Pers. (Spanish stopper) (Gann et al. 2001) (Table 1). The other 3 introduced *Eugenia* spp. still remain in cultivation in many public and private gardens and nurseries.

### Study Sites

We carried out most of our sampling 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). 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* (L.) Sarg. (gumbo-limbo), *Coccoloba unifera* L. (seagrape), *Krugiodendron ferreum* (Vahl) Urb. (black iron wood), and *Ficus aurea* Nutt. (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 4 research, public, and private gardens in Miami Dade and Broward, 2 adjacent counties in South Florida. These gardens include University of Florida, Tropical Research and Education Center, the Fruit and Spice Park, Plantation Heritage Park, and the Fairchild Tropical Garden. These plants are referred to as cultivated aggregata, cultivated brasiliensis, and cultivated lushnathiana (Table 1). In addition, as a control for potential site related differences between these gardens and the natural subtropical hammocks, we also sampled 9, 10, 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. Sampling frequencies for the cultivated plants were the same as for the wild populations mentioned above.

### Determination of Insect Herbivore Faunas

Four and two $5 \times 3\text{-m}^2$ plots were established at the Birch Park and the Bonnet House, respectively, for herbivore faunal surveys on wild populations of *E. axillaris*, *E. foetida*, and *E. uniflora* (Table 1). We tagged a total of 182, 202, and 97 wild plants of various sizes of *E. axillaris*, *E. foe-*

Table 1. Summary of the study system, including the number of plants sampled ($n$). Plants that grow in gardens are cultivated.

| Plant species | Status | Growing habitat in south Florida ($n$) |
|---|---|---|
| *E. axillaris* | Native | Natural hammocks (182) and garden (9) |
| *E. foetida* | Native | Natural hammocks (202) and garden (10) |
| *E. uniflora* | Introduced invasive | Natural hammocks (97) and garden (28) |
| *E. aggregata* | Introduced non-invasive | Garden (9) |
| *E. brasiliensis* | Introduced non-invasive | Garden (14) |
| *E. lushnathiana* | Introduced non-invasive | Garden (10) |

*tida*, and *E. uniflora*, respectively. All these plants were visited every other month during the dry season (Oct to Apr) and monthly during the wet season (May to Sep) from Jan to Dec 2004. Larval and adult insects were hand caught and brought back to the lab for rearing, specimen preparation, and identification. For fruit and seed feeders, we collected random fruit samples from 3-10 trees and 20-100 fruits per tree, depending on availability. Some non-rotten fruits on the ground directly beneath the trees were also included in the samples. Unidentified fruit/seed feeders were reared to maturity for identifications. We sent unknown specimens to specialists in the USA for identification. Information on insect immigration status (i.e., native or exotic) and diet breadth were provided by these insect specialists when possible. Insects were classified as native or exotic, oligophagous or polyphagous, and endophagous or ectophagous feeders. Oligophagous refers to insects which feed only on plants of 1 family while polyphagous indicates herbivores that feed on more than 1 family. Insects were "very important" if they were seen in every census, or were seen to cause 10% or more of leaf or seed damage on average in at least 1 census (Liu, unpublished data). Insects were "important" if they were seen in more than 1 census but caused less than 10% leaf or seed damage. Herbivores were "not important" if they were seen only once during the entire study period or caused very little plant damage. Determination of % damage to plants depended on the nature of the insect. For example, the % damage by a leaf miner was determined by counting the % of leaves with mines, while the % damage by a chewing caterpillar was by counting the % of leaves chewed.

### Data Analyses

In addition to the identity of the herbivores, the number of total insect herbivore species on each *Eugenia* species, the number and percentage of native insect herbivores, the number and percentage of endophagous vs. ectophagous feeders, and the number and percentage of oligophagous vs. polyphagous feeders were determined. The differences in these percentages among the native (average among the 2 species), invasive and non-invasive (average among the 3 species) plants were determined with chi-square tests (Zar 1984) in SPSS 13.0 (SPSS, Chicago, Illinois, USA). Because there may be differences in the herbivore fauna between wild and cultivated populations of the same species as the latter are in artificial settings, 2 sets of the chi-square tests were performed. One was a two-way test that included wild native plants and wild introduced invasive plants. The other was a three-way test that included cultivated native, invasive, and non-invasive plants. We also determined the number of herbivores, particularly oligophagous and/or endophagous, shared between the native, invasive and non-invasive plants. Samples from the two natural area sites were pooled because they had identical herbivore fauna for the three wild *Eugenia* populations. Samples from the four garden sites were pooled because all gardens did not have adequate sample sizes for among site comparisons.

## Results

We observed, collected, and reared a total of 25 insect species in 12 families and 6 orders feeding on the 6 species of *Eugenia* during the 1-year sampling period (Table 2). Among them, the majority were native (72%), polyphagous (64%), and external feeders (68%). There were 7 additional uncommon species of Lepidoptera reared from bagged branches of various *Eugenia* spp. that were not included in the results because herbivory by these species was not confirmed. The native wild *Eugenia* species had higher numbers of herbivore species than the wild introduced *E. uniflora* and most cultivated *Eugenia*. The only exception was that the cultivated *E. uniflora* had more herbivore species than the native *Eugenia* (Fig. 1A).

The introduced invasive and non-invasive *Eugenia* recruited fewer oligophagous insect herbivores than the native *Eugenia* (Fig. 1A). The difference in proportions of herbivore diet breadth (oligophagous vs. polyphagous) among the cultivated native, invasive, and non-invasive *Eugenia* was marginally insignificant (Pearson $\chi^2 = 5.76$, $df = 2$, $P = 0.056$). The difference in herbivore diet breadth was not statistically significant between the wild native *Eugenia* and wild invasive *Eugenia* (Pearson $\chi^2 = 1.94$, $df = 1$, $P = 0.163$). In addition, the proportions of herbivore feeding site (endophagous vs. ectophagous) were not different between the wild native *Eugenia* and wild invasive *Eugenia* (Pearson $\chi^2 = 0.003$, $df = 1$, $P = 0.960$), or among the cultivated plants (Pearson $\chi^2 = 1.91$, $df = 2$, $P = 0.385$) (Fig. 1B). Separate analyses (not reported here) incorporating the excluded uncommon Lepidoptera yielded similar results. Finally, all introduced *Eugenia* species attracted more exotic insect herbivores than the native *Eugenia* plants (Fig. 1C). However, the differences in the proportion of native herbivores were not significant between the wild native *Eugenia* and the wild invasive *Eugenia* (Pearson $\chi^2 = 1.02$, $df = 1$, $P = 0.311$), and among the cultivated native, invasive, and non-invasive *Eugenia* (Pearson $\chi^2 = 0.76$, $df = 2$, $P = 0.683$) (Fig. 1C).

The native *Eugenia* shared a total of 6 generalist herbivores, 4 with the invasive *Eugenia*, 4 with the non-invasive *Eugenia*, and 2 (the weevil *Diaprepes abbreviatus* L. and a kerriid scale *Paratachardina lobata* Chamberlin) with both kinds (Table 2). Among the shared herbivores, only 1 native weevil (*Artipus floridanus* Dietz) fed on the inva-

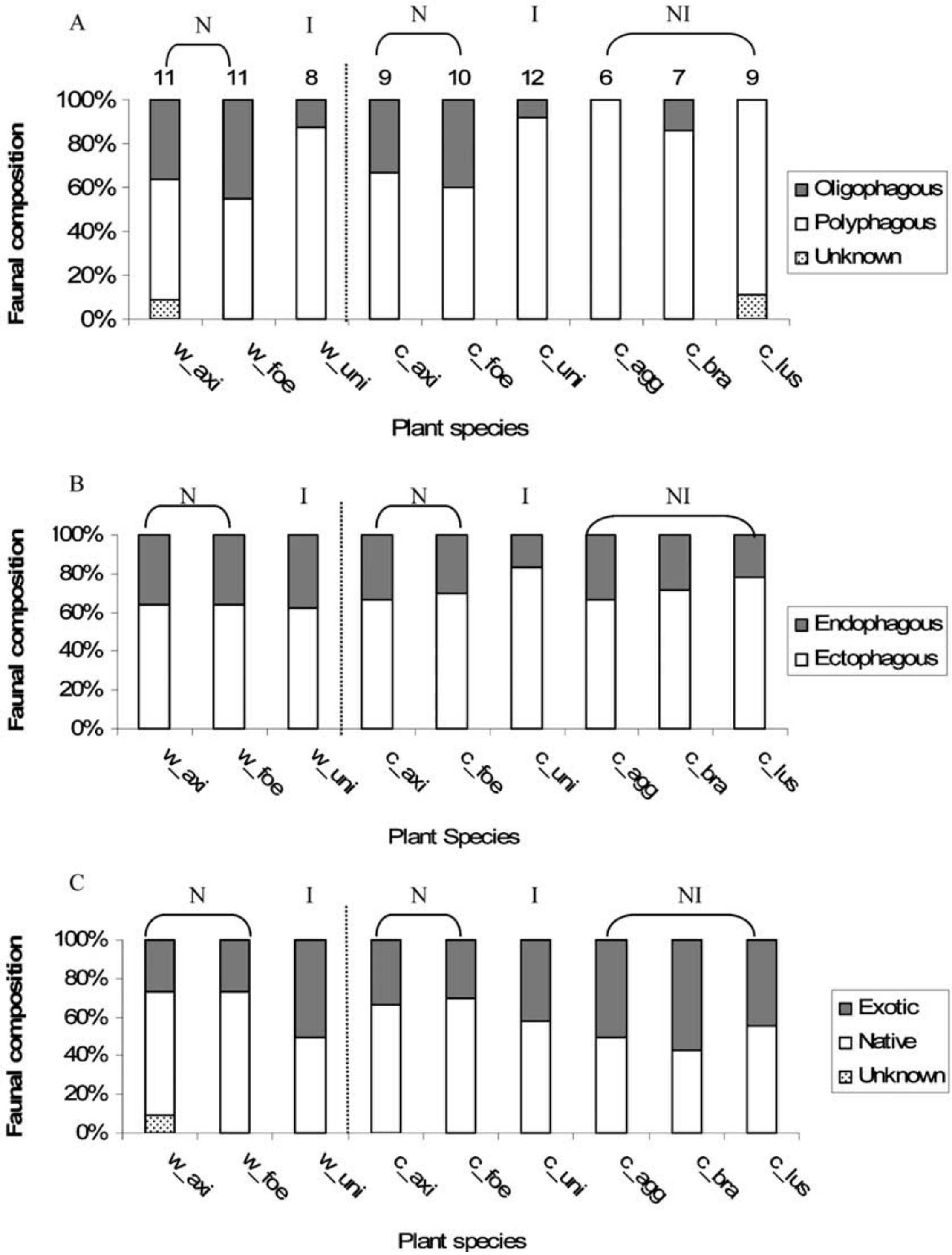


Fig. 1. Percentage of herbivore species found in different categories on six wild and/or cultivated *Eugenia* species in South Florida. The vertical dash lines separate wild plants from cultivated ones, with the former on the left. W_axi = wild *E. axillaris*, w_foe = wild *E. foetida*, w_uni = wild *E. uniflora*, c_axi = cultivated *E. axillaris*, c_foe = cultivated *E. foetida*, c_uni = cultivated *E. uniflora*, c_agg = cultivated *E. aggregata*, c_bra = cultivated *E. brasiliensis*, c_lus = cultivated *E. lushnathiana*. "N" indicate native plants, "I" the introduced invasive plant, and "NI" the introduced non-invasive plants. Numbers on top of the bars are the total number of herbivore species found.

TABLE 2. HERBIVOROUS INSECT SPECIES FOUND ON SIX WILD AND/OR CULTIVATED *EUGENIA* SPECIES IN SOUTH FLORIDA. NATIVE *EUGENIA* SPECIES ARE IN BOLD AND INVASIVE *EUGENIA* ARE IN ITALICS. W_AXI = WILD *E. AXILLARIS*, W_FOE = WILD *E. FOETIDA*, W_UNI = WILD *E. UNIFLORA*, C_AXI = CULTIVATED *E. AXILLARIS*, C_FOE = CULTIVATED *E. FOETIDA*, C_UNI = CULTIVATED *E. UNIFLORA*, C_AGG = CULTIVATED *E. AGGREGATA*, C_BRA = CULTIVATED *E. BRASILIENSIS*, C_LUS = CULTIVATED *E. LUSHNATHIANA*, POLY = POLYPHAGOUS OR GENERALIST. OLIGO = OLIGOPHAGOUS OR SPECIALIST. ENDO = ENDOPHAGOUS, ECTO = ECTOPHAGOUS. — DOES NOT OCCUR, + NOT IMPORTANT, ++ IMPORTANT, +++ VERY IMPORTANT. UNID = UNIDENTIFIED. ? INDICATES UNKNOWN OR UNCERTAIN INFORMATION.

| | | | | | Occurrence on *Eugenia* species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Insect species | Origins[b] | Diet breadth[b] | Feeding nich[b] | Guild /plant parts | **w_axi** | **w_foe** | *w_uni* | **c_axi** | **c_foe** | *c_uni* | c_agg | c_bra | c_lus |
| Coleoptera | | | | | | | | | | | | | |
| Curculionidae | | | | | | | | | | | | | |
| *Anthonomus alboannulatus* Boheman | Native | Oligo | Endo | Seed | ++ | +++ | — | — | — | — | — | — | — |
| *Anthonomus irroratus* Dietz | Native | Oligo | Endo | Seed | — | — | — | +++ | ++ | | | | |
| *Atractomerus punctipennis* Gyllenhal | Native | Oligo | Ecto | Leaf | + | — | — | — | — | — | — | — | — |
| *Artipus floridanus* Horn | Native | Poly | Ecto | Leaf, root? | + | + | + | + | + | + | — | — | — |
| *Diaprepes abbreviatus* L. | Exotic | Poly | Ecto | Leaf, root? | ++ | ++ | ++ | + | + | + | + | + | + |
| *Myctides imberbis* Lea | Exotic | Oligo | Ecto | Leaf, fruit? | — | — | — | — | — | ++ | — | + | — |
| *Myllocerus undatus* Marshall | Exotic | Poly | Ecto | Leaf, root? | + | + | +++ | ++ | ++ | ++ | — | — | — |
| *Pheloconus hispidus* LeConte | Native | Poly | Endo | Seed | — | — | ++ | — | — | ++ | ++ | ++ | ++ |
| Nitidulidae | | | | | | | | | | | | | |
| *Lobiopa insularis* Castlenau[a] | Native | Poly | Ecto | Fruit flesh | — | — | — | — | — | ++ | ++ | ++ | ++ |
| *Epuraea luteolus* Erichson[a] | Native | Poly | Ecto | Fruit flesh | — | — | — | — | — | ++ | ++ | ++ | ++ |
| Diptera | | | | | | | | | | | | | |
| Cecidomyiidae | | | | | | | | | | | | | |
| *Dasineura eugeniae* Felt | Native | Oligo | Endo | Leaf, fruit galler | +++ | +++ (fruit only) | — | ++ | ++ | — | — | — | — |
| *Stephomyia eugeniae* Felt | Native | Oligo | Endo | Leaf galler | — | +++ | — | — | — | — | — | — | — |
| Tephritidae | | | | | | | | | | | | | |
| *Anastrepha suspense* Loew[a] | Exotic | Poly | Endo | Fruit flesh | — | — | +++ | — | — | +++ | ++ | ++ | +++ |
| Hemiptera | | | | | | | | | | | | | |
| Coccidae | | | | | | | | | | | | | |
| *Pulvinaria psidii* Maskell | Native | Poly | Ecto | Stem and leaf | — | — | — | ++ | — | — | — | — | — |
| Flatidae | | | | | | | | | | | | | |
| *Melormenis basalis* Walker | Exotic | Poly | Ecto | Leaf | — | — | — | — | — | — | — | — | + |
| Kerriidae | | | | | | | | | | | | | |
| *Paratachardina lobata* Chamberlin | Exotic | Poly | Ecto | Stem | ++ | + | + | ++ | ++ | ++ | + | ++ | ++ |

[a]Herbivores with little fitness consequences because they only consume fleshy parts of the fruit without damaging the seed.
[b]unknown cases are assumed to be native, polyphagous, and external feeders for the chi-square tests.

TABLE 2. (CONTINUED) HERBIVOROUS INSECT SPECIES FOUND ON SIX WILD AND/OR CULTIVATED *EUGENIA* SPECIES IN SOUTH FLORIDA. NATIVE *EUGENIA* SPECIES ARE IN BOLD AND INVASIVE *EUGENIA* ARE IN ITALICS. W_AXI = WILD *E. AXILLARIS*, W_FOE = WILD *E. FOETIDA*, W_UNI = WILD *E. UNIFLORA*, C_AXI = CULTIVATED *E. AXILLARIS*, C_FOE = CULTIVATED *E. FOETIDA*, C_UNI = CULTIVATED *E. UNIFLORA*, C_AGG = CULTIVATED *E. AGGREGATA*, C_BRA = CULTIVATED *E. BRASILIENSIS*, C_LUS = CULTIVATED *E. LUSHNATHIANA*, POLY = POLYPHAGOUS OR GENERALIST. OLIGO = OLIGOPHAGOUS OR SPECIALIST. ENDO = ENDOPHAGOUS, ECTO = ECTOPHAGOUS. — DOES NOT OCCUR, + NOT IMPORTANT, ++ IMPORTANT, +++ VERY IMPORTANT. UNID = UNIDENTIFIED. ? INDICATES UNKNOWN OR UNCERTAIN INFORMATION.

| | | | | | Occurrence on *Eugenia* species | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Insect species | Origins[b] | Diet breadth[b] | Feeding nich[b] | Guild /plant parts | **w_axi** | **w_foe** | *w_uni* | **c_axi** | **c_foe** | *c_uni* | c_agg | c_bra | c_lus |
| Psyllidae | | | | | | | | | | | | | |
| *Katacephala tenuipennis* Tuthill | Native | Oligo | Ecto | Leaf | — | +++ | — | — | +++ | — | — | — | — |
| Lepidoptera | | | | | | | | | | | | | |
| Gracillariidae | | | | | | | | | | | | | |
| *Chilocampyla dyariella* Busck | Native | Oligo | Endo | Leaf miner | ++ | ++ | +? | ++ | + | — | — | — | — |
| Tortricidae | | | | | | | | | | | | | |
| *Ancylis* sp. | Native | Poly | Ecto | Leaf tier young leaves | — | +++ | — | — | +++ | — | — | — | +++ |
| *Platynota flavedana* Clemens | Native | Poly | Ecto | Leaf tier | — | — | + | — | — | + | — | — | — |
| *Sparganothis lentiginosana* Walsingham | Native | Poly | Ecto | Leaf tier young leaves | — | — | — | — | — | + | — | — | — |
| *Strepsicrates smithiana* Walsingham | Native | poly | Ecto | Leaf tier young leaves | +++ | +++ | — | +++ | +++ | — | — | — | — |
| Orthoptera | | | | | | | | | | | | | |
| Acrididae | | | | | | | | | | | | | |
| *Stenacris vitreipennis* Marshall | Native | Poly | Ecto | Leaf | — | — | — | — | — | + | — | — | — |
| Unid. Acrididae | Native? | Poly | Ecto | Leaf | + | — | — | — | — | — | — | — | — |
| Thysanoptera | | | | | | | | | | | | | |
| Phlaeothripidae | | | | | | | | | | | | | |
| *Elaphrothrips* sp. | Native | Poly? | Endo | Leaf galler | ++ | — | — | — | — | — | — | — | ++ |

[a]Herbivores with little fitness consequences because they only consume fleshy parts of the fruit without damaging the seed.
[b]unknown cases are assumed to be native, polyphagous, and external feeders for the chi-square tests.

sive *Eugenia*, while two native insects (*Ancylis* sp. and *Elaphrothrips* sp.) fed on the non-invasive *Eugenia*. The insect that caused substantial damage on the invasive *Eugenia* was an exotic weevil (*Myllocerus undatus* Marshall), while the insect that caused substantial damage on the non-invasive *Eugenia* was a native moth (*Ancylis* sp.). The native *Eugenia* also likely shared a specialist insect (a leaf blotch mining moth, *Chilocampyla dyariella* Busck) with the invasive congener (Table 2). However, it was not clear if the leaf miners were able to complete their development in *E. uniflora* leaves, because these incidents were rare and we were not able to rear any adults.

## DISCUSSION

Prediction 1—there will be greater numbers of herbivore species on native *Eugenia* than on introduced species.

There is limited evidence supporting our first prediction in relation to herbivore species richness on native vs. introduced non-invasive *Eugenia* because the cultivated native species had more insect herbivore species than 2 of the 3 introduced non-invasive species. This is consistent with the results found in a study comparing insect herbivore fauna between a native *Pinus* and a co-occurring introduced non-invasive congener (Lindelöw & Björkman 2001). There also was only limited support for the prediction in relation to the native vs. introduced invasive species in this study because the native *Eugenia* species had more insect herbivore species than the introduced invasive *Eugenia* in the wild, but not in cultivation. In the only other similar study (Bürki & Nentwig 1997), comparing the herbivore fauna between populations of the native *Heracleum sphonylium* L. and the co-occurring introduced invasive congeners, *H. mantegazzianum* Simmier & Levier, there was an equal number of insects associated with both plant species.

Furthermore, contrary to the second part of our first prediction that the invasive *Eugenia* should have a smaller number of herbivore species than the non-invasive congeners, the invasive *Eugenia* (*E. uniflora*), wild or in cultivation, had greater numbers of insect herbivore species than all 3 non-invasive *Eugenia*. This result is the opposite to that reported in a study on plant pathogens (Mitchell & Power 2003), in which the authors found that more invasive plants tended to have fewer pathogens. Nevertheless, differences in herbivore richness were small among the *Eugenia* species studied here. In addition, there is always the possibility that high number of herbivore species may not translate into high damage level (Liu, unpublished data).

Prediction 2—There will be greater numbers of oligophagous and endophagous herbivore species on native *Eugenia* than on introduced species.

The data support the first part of our second prediction that native *Eugenia* species should have the highest number and percentage of oligophagous insect herbivores. However, the statistical results should be interpreted with caution due to the small number of insect species on each *Eugenia* species. Our result is consistent with 1 congeneric native vs. introduced species comparison (Bürki & Nentwig 1997), but differs from another (Lindelöw & Björkman 2001). In addition, the native plants had higher number of internal feeders even though the percentage of endophagous herbivore species was not different between the native and introduced *Eugenia*. However, in contrast to the second part of our second prediction, the invasive *Eugenia* had as many or more oligophagous and/or endophagous feeders than non-invasive introduced *Eugenia*. No other studies were found to compare the number of oligophagous and endophagous insects between invasive and non-invasive plants.

Prediction 3—Fewer herbivores will be shared between native *Eugenia* and invasive *Eugenia* than between native *Eugenia* and non-invasive *Eugenia*.

The third prediction that native *Eugenia* should share fewer specialist and endophagous herbivores with invasive *Eugenia* than with non-invasive *Eugenia* was not supported by the data. While native *Eugenia* shared no oligophagous or endophagous herbivores with non-invasive *Eugenia*, they likely shared a leaf miner with *E. uniflora* (the invasive introduced *Eugenia*). However, because the blotch mines were only found on the wild individuals, it is possible that the host shift occurred after *E. uniflora* had invaded the natural areas. In addition, because the mines occurred at such a low rate the biotic resistance from this miner should be small. Host sharing by oligophagous herbivores largely depends on the taxonomic closeness of the host plants (Strong et al. 1984). A phylogeny of the genus *Eugenia* may help to explain and predict the shifts of specialists from the native to the introduced congeners.

No leaf galls were observed on any of the introduced *Eugenia* species in this study whereas one specialist galling fly, *Eugeniamyia dispar* Maia et al. (Diptera, Cecidomyiidae) (Maia et al. 1996) was found on *E. uniflora* in its native range. All introduced *Eugenia* studied here have probably escaped specialist insects that may be found in their native ranges. The lack of specialist insect attack may lead to a shift in plant resource allocation to growth (Blossey & Nötzold 1995; Siemann & Rogers 2001, Wolfe et al. 2004) and/or defense to generalist herbivores (Joshi & Vrieling 2005).

Native *Eugenia* plants in cultivation have a less diverse insect fauna than those in the wild, probably due to the differences in time since population establishment (Strong et al. 1984). Cultivated populations tend to be much younger and have less time to acquire insect fauna. Pesticide treatment in some horticulture or agriculture situations also may cause a decrease in herbivore fauna. However, all cultivated *Eugenia* individuals sampled in this study were not treated directly with pesticides (Jonathan H. Crane of TREC, Micheal Davenport of FTBG, Chris Rollins of FSP, personal communications). Nevertheless, our analyses and discussions are mostly limited to faunal comparisons among different species of the same source (wild or cultivated).

A result that is not related to the ERH testing but nonetheless interesting is the composition of native vs. exotic herbivores on the 3 categories of *Eugenia* plants. The native herbivores constituted about half of the insect herbivore fauna acquired by the introduced *Eugenia*. The numbers of exotic insects attacking the native, invasive, and non-invasive plants are similar (3-5 on each plant species). Since most of these exotic herbivores came from continents other than Central and South America, where the introduced *Eugenia* are native, it is unlikely that these exotic herbivores were associated with the exotic *Eugenia* in its native range. We did not observe any native insect herbivores having more importance on the introduced than on the native *Eugenia* plants. In contrast, it appeared that an exotic weevil (*M. undatus*), a new comer from Sri Lanka (Schall 2000), fed more heavily on *E. uniflora* (the invasive *Eugenia*) than on other congeners (Liu, personal observations). In addition, the only exotic oligophagous weevil (*Myctides imberbis,* an Australian native) found in this study also was observed on *E. uniflora* more than on the native or the non-invasive *Eugenia*. Together, our data suggested that the exotic herbivores provided as much, if not more, herbivore pressure as the native insects to the introduced *Eugenia*. Our finding was different from that of a recent study which found that the native herbivores, mostly vertebrates, suppressed introduced plants, whereas exotic herbivores, also mostly vertebrates, promoted exotic plants (Parker et al. 2006).

In summary, data on herbivore faunal diversity of *Eugenia* species provided limited support to the ERH. It is likely that other factors contribute to the success of *E. uniflora*. If we did not include the non-invasive *Eugenia* species in the study and only compared the herbivore fauna between the native *Eugenia* and invasive *Eugenia*, we would have thought that release from the insect herbivores was an important factor in the success of *E. uniflora*. We did not include pathogens, also recognized as natural enemies, in this study. Future study should take advantage of this unique three-way system to examine the effects of pathogens and other competing but non-exclusive hypotheses to help explain the success of *E. uniflora*. For example, competitive interactions of introduced invasive *Eugenia* vs. native co-occurring plants and non-invasive introduced *Eugenia* vs. native plants could be examined. The three- way comparison could also be used to examine the importance of relative seed numbers (the propagule pressure hypothesis (Williamson 1996), which states that the species with the greater number of propagules will be the most invasive). *Eugenia uniflora*, is much more abundant than the non-invasive Eugenia because it has long been used as a hedge plant, and probably produces more potentially invasive seeds.

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