Invasional conflict: Do invasive insect herbivores mediate the effects of enemy release for their invasive plant hosts?

Kerry R. Bohl and Peter Stiling

Department of Integrative Biology, University of South Florida, 4202 E. Fowler Avenue, Tampa, FL 33620 USA

Introduction

Most introduced plant species never become invasive, failing to establish a viable population in their new range. Although many factors have been proposed that potentially contribute to invasion success in plants, it remains unclear why some species successfully establish and become dominant while others do not. The most often cited explanation for the success of invasive plants worldwide is the enemy release hypothesis (ERH), which maintains that populations are kept in check by their co-evolved natural enemies in their native range and are released from this regulation in the new range (Keane and Crawley 2002). However, the role of enemy release in regulating plant population dynamics remains uncertain. Experiments excluding natural enemies in natural communities can be used to test the ERH empirically, although very few studies of this type have been conducted. Since its introduction from Brazil, *Eugenia uniflora* has escaped cultivation and has begun to invade natural areas in southern Florida, growing in some areas alongside two native congeners, *E. axillaris* and *E. foetida*. This system provides an opportunity to test the ERH and its possible effects on plant vital rates when herbivores are excluded from the system.

Materials and methods

Experimental protocol

Eugenia axillaris, *E. foetida*, and *E. uniflora* are found in high densities at Hugh Taylor Birch State Park in Ft. Lauderdale, Florida. Ten 3 X 3 m quadrats were established at this location in February 2008 in which height, leaf number, and proportion of leaves damaged by insect herbivores were measured for all adult individuals of all three *Eugenia* spp. Two 1m diameter sub-plots were also established in the quadrats, and the same measurements were taken for all seedlings and saplings of all three species growing within them. Five of the quadrats were treated with Merit® 75 WP Imidacloprid insecticide to exclude insect herbivores. The other five quadrats served as controls and were treated with an equal amount of water. The above variables were quantified again during three subsequent censuses for all existing and any newly emerged individuals, the last of which occurred in March 2009. More censuses are planned throughout 2009 and into 2010.

Data analysis

Effect of treatment on number of individuals exhibiting herbivore damage was assessed using logistic regression. When damage was present, two-factor ANOVA was used to determine the effect of treatment and species on change in proportion of leaves damaged. Two-factor ANOVA was also used to assess differences in change in relative height and leaf number for the three species under the two treatments.

Figure 2: Surinam cherry (*Eugenia uniflora*) fruit.

Results

Logistic regression indicates that both species and treatment have a significant effect on whether an individual experiences insect herbivore damage ($p<0.01$). Assuming damage occurs, two-way ANOVA demonstrates that the change in proportion of leaves damaged is affected by application of insecticide as well as by species ($p<0.01$, Figure 3). Two-way ANOVA also reveals a significant effect of treatment on change in leaf number ($p<0.05$, Figure 4) and height ($p<0.05$, Figure 5), with individuals treated with insecticide losing fewer leaves and growing taller than untreated individuals. Change in leaf number also differed among species ($p<0.05$, Figure 4). Figure 6 shows proportion of individuals surviving over one year, split into three time intervals. In general, application of insecticide resulted in higher survival rates for all three species. The largest difference can be seen when treated and untreated *E. uniflora* are compared.

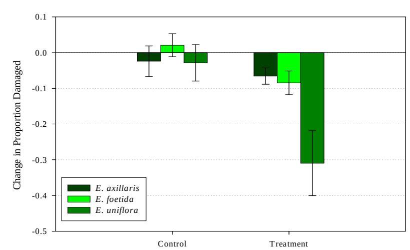

Figure 3: Mean change in proportion of leaves damaged for three *Eugenia* species from February 2008-March 2009. Error bars represent 1 SE.

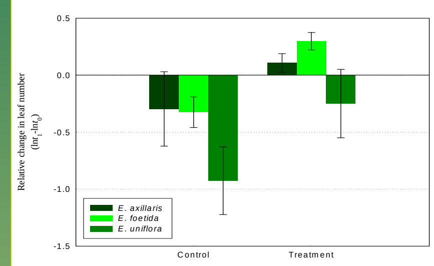

Figure 4: Mean relative change in leaf number ($\ln t_1 - \ln t_0$) from February 2008-March 2009 for three *Eugenia* species. Error bars represent 1 SE.

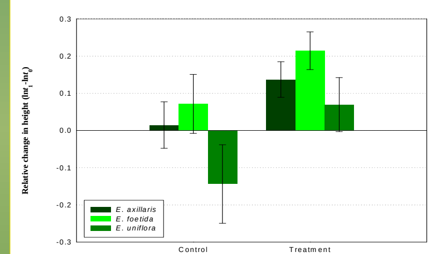

Figure 5: Mean relative change in height ($\ln t_1 - \ln t_0$) from February 2008-March 2009 for three *Eugenia* species. Error bars represent 1 SE.

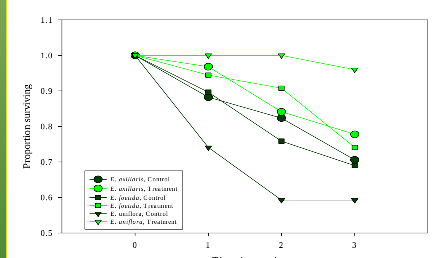

Figure 6: Lines indicate proportion of originally marked individuals surviving over three time intervals spanning from February 2008-March 2009. Black lines indicate treated individuals, whereas green lines represent the control group.

Conclusions

The results presented here indicate that the insecticide treatment is indeed having an effect on prevalence of damage for *Eugenia* spp. However, it is surprising that the effect was only significant for the invasive species, *E. uniflora*. This result contradicts the Enemy Release Hypothesis, which would suggest that *E. uniflora* should experience no herbivory by insects in its introduced range. Instead, *E. uniflora* has a greater proportion of damaged leaves and experiences a greater reduction in this damage when herbivores are excluded from the system. An additional result is that herbivores appear to affect vital rates in this system. Although not all of the results are significant, the trend exhibited by the data demonstrates that exclusion of enemies led to greater growth, both in leaf number and in height, and greater survival. All three species are relatively slow-growing, so these results may increase in significance as this experiment progresses over the course of one more year.

The insect herbivore fauna utilizing native *Eugenia* spp. is more diverse than that of *E. uniflora*. *E. uniflora* exhibits, with few exceptions, mostly damage characteristic of a notching weevil, *Myllocerus undatus*, a recent import from Sri Lanka (O'Brien *et. al* 2006). This is especially interesting given that *E. uniflora* is from Brazil, so these species share no evolutionary history. The results of this study indicate that *M. undatus* may have a negative effect on *E. uniflora*, potentially benefitting the native species by reducing competition. Negative effects of invasive species on other invasive species have not received much attention in the literature. Instead, most studies that address affects of invasive species on one another center around the idea of invasional meltdown (Simberloff and Von Holle 1999). This is a possible example of another type of interaction, which we have termed "invasional conflict". This interaction will undoubtedly become much more prevalent as more species are introduced, become established, and interact with one another, forming new biological associations.

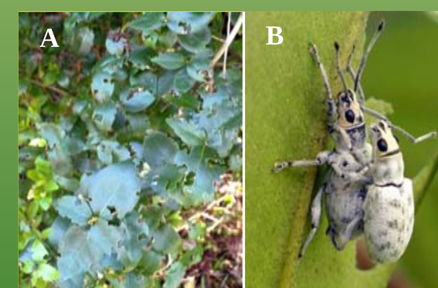

Figure 7: A) *Eugenia uniflora* leaves damaged by *Myllocerus undatus*. B) *M. undatus*.

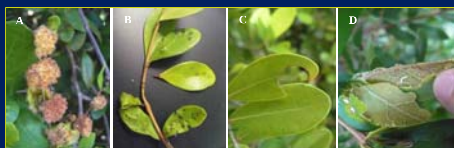

Figure 1: Some herbivore damage experienced by native *Eugenia*. A) and B) two types of galls, C) leaf chewing, D) blotch mine.

Literature cited

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O'Brien, C. W., M. Haseeb, and M. C. Thomas. 2006. *Myllocerus undecimpustulatus undatus Marshall* (Coleoptera: Curculionidae), a Recently Discovered Pest Weevil from the Indian Subcontinent. *Florida Department of Agriculture and Consumer Services Entomology Circular* 412: 1-4.

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For further information

Please e-mail *kbohl@mail.usf.edu*

USF
UNIVERSITY OF SOUTH FLORIDA