

Resistance to Plant Invasion? A Native Specialist Herbivore Shows Preference for and Higher Fitness on an Introduced Host

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ABSTRACT

The response of native herbivores to the introduction of a new plant to the community has important implications for plant invasion. Under the Enemy Release Hypothesis introduced species become invasive because of reduced enemy control in the new range, while under the New Association Hypothesis introduced species lack effective defenses against native enemies because they do not share an evolutionary history. I tested the response of a native South-American specialist herbivore *Utetheisa ornatrix* (Lepidoptera: Arctiidae) to a native (*Crotalaria incana*) and an introduced host (*Crotalaria pallida*) (Fabaceae: Papilionoideae). I compared seed predation rates between the two hosts in the field, and I tested preference and performance traits with common garden experiments. *Utetheisa ornatrix* caused much higher seed predation rates on the introduced host than on the native host. Females also preferred to oviposit on the introduced over the native host. Additionally, larvae feeding on the introduced host had higher fitness (higher pupal weight) than larvae feeding on the native host. I discuss how the response of this specialist herbivore to this introduced host plant contradicts the predictions of the Enemy Release Hypothesis and support the New Association Hypothesis. This study shows that the New Association Hypothesis can also be true for specialist herbivores.

Abstract in Portuguese is available at <http://www.blackwell-synergy.com/loi/btp>

Key words: coevolution; Enemy Release Hypothesis; herbivore fitness; host–parasite interaction; host-shift; New Association Hypothesis; plant invasion; rapid evolution; seed predation.

THE INTRODUCTION OF NONNATIVE SPECIES THREATENS NATIVE BIODIVERSITY by altering ecosystem structure and function (Pimentel 2002). However, only a small fraction of exotic species have become major pests or have formed monocultures and displaced native species (Rejmánek & Richardson 1996). Therefore, it is crucial to understand what determines the success of introduced species. One of the most accepted hypotheses attributes the difference in success of introduced species to natural enemies, the Enemy Release Hypothesis (Keane & Crawley 2002). These introductions of species to new communities also present a valuable opportunity to understand coevolution. Species coevolve with their natural enemies, and, in plant–herbivore interactions, plants are expected to evolve defense traits and herbivores are expected to evolve virulence traits (*i.e.*, traits that overcome the plant defense trait; Thompson 1982). With the introduction of a new species a mismatch between the plant defense traits and the herbivore virulence traits is likely to occur (Callaway & Maron 2006). In the new community, the native herbivores may not be able to consume the exotic plant or, alternatively, a native plant may not be well defended against the new herbivores.

The response of the native natural enemies to the introduced community member is a key aspect to determine whether they will facilitate or prevent invasiveness. The Enemy Release Hypothesis posits that introduced plant species become invasive because they are less affected by consumers in the new range (Darwin 1859, Elton 1958). Under this hypothesis, the introduced species will be less affected by both specialist and generalist herbivores; specialists on the exotic plant species will not be present in the new range and

the native generalists will preferentially consume native plants instead of the exotics (Maron & Vila 2001, Mitchell *et al.* 2006). The release from enemies will contribute to the success of the introduced species. However, an understudied alternative possibility is that introduced plants may be poorly adapted to avoid the native herbivores. Because exotic plants do not share an evolutionary history with the native herbivores, they have not experienced selection from these consumers and may lack effective defenses. This alternative possibility is called the Increased Susceptibility Hypothesis or New Association Hypothesis (Hokkanen & Pimentel 1989, Parker & Hay 2005). Under this scenario, natural enemies will limit the success of introduced species. However, these two hypotheses are not mutually exclusive as they address two ends of the spectrum of introduced species invasiveness.

Responses of a herbivore to an introduced plant depend on features such as behavior (preference for host plants), phenology, and physiological adaptations to features of the plant that affect the herbivore's growth, survival, and reproduction (performance). While some studies have reported correlations between preference and performance (Singer *et al.* 1988), in other cases these traits are independent (Forister 2005). In addition, the response to a new host is likely to differ between generalist and specialist herbivores because plants may employ different defense traits against generalists and specialists (van der Meijden 1996, Joshi & Vrieling 2005).

In this study, I investigate the response of a native specialist herbivore to the introduction of an exotic plant to the community. I used the specialist herbivore *Utetheisa ornatrix* L. (Lepidoptera: Arctiidae) feeding on a native (*Crotalaria incana* L.) and an introduced host (*Crotalaria pallida* Aiton) (Fabaceae: Papilionoideae). First, I compared damage caused by this specialist herbivore on the introduced and the native host plant in the field. Second, I used a

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common garden experiment to address the mechanisms responsible for the differences in seed predation rates. I tested how the introduction of the new host affects the herbivore preference and performance. Specifically, the following questions were investigated: (1) Are seed predation rates in the field different between the two hosts? (2) Do ovipositing females discriminate between the two hosts? If so, which host is preferred? (3) How do host species affect larval performance?

METHODS

STUDY SYSTEM.—*Crotalaria* is a pantropical genus of weeds with approximately 600 species (Polhill 1982). Most species are native to Africa and Asia and about 70 species occur in the Neotropics. In Brazil, for example, 42 species occur, of which 31 are native and 11 introduced (Flores 2004). Two *Crotalaria* species that are currently widely distributed in the New World and Old World tropics were used in this study: the native (in the New World) *C. incana* and the introduced *C. pallida*. *Crotalaria incana* is native to the Neotropics, while *C. pallida* is native to Africa and is now considered an invasive weed in the Neotropics (Lorenzi 2000, Flores 2004). In the New World both species are distributed from Argentina to the southern United States. Both species are abundant in sandy soils, near rivers, and in human-disturbed habitats, especially road sides (Flores 2004, Fonseca *et al.* 2006). There is no clear evidence about when *C. pallida* was introduced in the New World, but it is likely that it was transported from Africa during slavery trade in the sixteenth century (Polhill 1982). The two species contain pyrrolizidine alkaloids with very similar chemical structures and extrafloral nectaries that attract ants that may prey on herbivores (Flores 2004, Guimarães *et al.* 2006). *Utetheisa ornatrix* is a Neotropical moth species that specializes on the genus *Crotalaria* (Eisner 2003). Females lay eggs on the plant leaves, and the larvae eat leaves for a few days before entering into the fruit and preying on green seeds (Ferro *et al.* 2006).

FIELD SITE.—Fieldwork was carried out in Campinas (22°54'20" S, 47°03'39" W), São Paulo State, southeastern Brazil. The site consists of grassland where three *Crotalaria* species co-occur: the native *C. incana* and two introduced species, *C. pallida* and *Crotalaria lanceolata* E. Mey. The moth uses all three species as hosts in this area (Ferro 2001). Adult moths were collected in the site where the three species co-occur. Larvae were observed on the three hosts at the time of the collection. Seeds were collected in October 2005; moths were collected in January and July 2006. I collected seeds from at least 25 different individuals for each species. Thirty-six adult moths were collected in January and an additional 20 adults were collected in July.

HERBIVORE EFFECT ON PLANTS IN THE FIELD.—The use of the native *C. incana* and the introduced *C. pallida* by *U. ornatrix* and the impact that *U. ornatrix* cause on each host were quantified in the field. In December 2008, I collected all the fruit pods of 26 *C. incana* individuals and 28 *C. pallida* individuals that were distributed in an area of ca 0.5 km². Plants were randomly chosen, were at least 1 m

from each other, and had approximately similar sizes. *Crotalaria* fruits stay on the plant for several weeks before autochoric dispersion. I avoided plants that had already started seed dispersion to be able to calculate the entire seed set of individuals and to restrict sample to plants that have been exposed to *U. ornatrix* at approximately the same time. Each fruit pod was classified as attacked by *U. ornatrix* or unattacked. Pods attacked by *U. ornatrix* can be easily identified by the characteristic opening that the larvae make to enter the pod (Pereira 2008). The only other herbivore attacking *C. incana* and *C. pallida* seeds was *Etiella zinckenella* Treit. (Pyralidae). However, this herbivore does not leave the characteristic opening on the pod as *U. ornatrix* (Ferro 2001) and it occurred at extremely low frequency (7 of 2239 pods). I calculated the proportion of pods attacked by *U. ornatrix* per individual plant as the number of pods attacked divided by the total number of pods. I counted the number of seeds on unattacked pods (up to 10 pods/plant) to calculate the average number of seeds per pod. The total number of seeds per individual plant was estimated by multiplying the number of pods by the average number of seeds per pod. For each damaged pod, I counted the number of seeds that were not attacked. The number of seeds attacked was estimated by subtracting the number of seeds not attacked from the average number of seeds per pod. Finally, the proportion of seed set consumed was calculated by dividing the estimated number of seeds attacked by the estimated total number of seeds per plant. Differences in the proportion of attacked pods and the proportion of seed set consumed were compared between the two hosts by Mann–Whitney tests.

ORGANISM MAINTENANCE.—In May 2006, I placed seeds on Petri dishes with water-soaked filter paper and kept them in an incubator with 24 h light (four 32 W fluorescent lamps) at 26°C. After germination and the emergence of leaves, seedlings were transferred to trays (ca 650 mL volume) filled with standard potting soil (Sunshine Mix #1 by Sun Gro Horticulture, Vancouver, Canada). After 3 wk, I transferred seedlings to large pots (ca 7.6 L). Seedlings and plants were kept at a greenhouse at Stony Brook University, New York, under natural sunlight. Plants were watered daily with the minimum water amount to avoid wilting; standard fertilizer (15N:5P:15K at 300 ppm) was added weekly. These plants produced fruits from September to November, when all the experiments were carried out. Forty-five plants of each species were grown. I kept a large colony of moths (with > 25 adults at any single time) in the laboratory. I fed nonexperimental larvae on an artificial diet based on *Phaseolus* beans (Signoretta *et al.* 2008), to avoid maternal and paternal effects, and to avoid selection for the use of host plant available in captivity. I kept adults in paper cages (ca 3.2 l) where 5 percent honey solution was provided (as in Cogni & Futuyma 2009). All experiments were carried out in an incubator at 26°C.

PREFERENCE: OVIPOSITION EXPERIMENT.—An experiment was designed to test if females discriminate between a native (*C. incana*) and an exotic (*C. pallida*) host species for egg-laying. A single female and two males were kept in a paper cage (ca 3.2 l) for 48 h. All females used were 1–2 wk old and had previous contact with males.

In each cage 5 percent honey solution was provided. I placed two leaves (with three leaflets each) from each host species in the cage. The leaves were cut from the plants and the petiole was immediately inserted in a vial with water. The leaves remained fresh during the 48-h period. Leaves from each host were chosen to match in size. I counted the total number of eggs laid on the leaves of each host species after 48 h. The assay was repeated 43 times, each time with different females and different individual plants. The average number of eggs laid on each host species was compared by a paired t -test, after $\log(x+1)$ transformation of the data.

PERFORMANCE: LARVAE EXPERIMENT.—Another experiment was designed to test if host plant affects fitness components of *U. ornatix* larvae, such as survival, development time, and pupal weight. I fed larvae on each host plant from hatching to pupation. One hundred and forty larvae were reared on *C. pallida* and 130 on *C. incana*. Larvae were fed on fresh leaves for the first 4 d; after that, the larvae were fed with green fresh fruit. This was done to simulate condition in the wild, where neonates first consume leaf material for some days before entering the fruit pod to prey on seeds (Ferro 2001). Neonate larvae were put individually in a 1.5-mL microcentrifuge tube with a leaf-disk for 48 h. Leaf-disks were made from fresh leaves and were 1 cm diam. After 4 d of eating leaves, larvae were transferred to individual Petri dishes (5 cm diam.) with a moistened filter paper and green fruit. The fruits were opened with a razor blade to completely expose the seeds. On alternative days, I transferred the larvae to a clean dish and provided new fruit. The amount of fruit given to each larva was: 1/3 fruit on days 5 and 7, 1/2 on day 9, 1 on days 11 and 13, and 2 (every other day) after day 13. Each fruit was weighed (to the nearest 0.001 g) before and after each 48-h period to calculate the total weight of seeds consumed by individual larva. Fruits lost about 20 percent of weight due to water loss during the 48 h under the conditions used; however, water loss did not differ between the two host species. I recorded larval development time as the number of days each larva took from egg hatching to pupation. I recorded larval survival as the percent of neonate larvae that survived to pupation. Pupal weight was measured 5 d after pupation. Pupal weight is directly related to adult fitness in *U. ornatix* (see ‘Discussion’). I calculated efficiency by dividing pupal weight by the weight of fruits consumed. Growth rate was calculated by dividing pupal weight by development time. The proportion of larvae that survived to pupal stage was compared between the two hosts by a χ^2 test. Larval performance (pupal weight, larval development time, total weight of seeds consumed, efficiency, and growth rate) was compared by two-factor analyses of variance, with host species and sex as factors.

RESULTS

HERBIVORE EFFECT ON PLANTS IN THE FIELD.—The introduced host *C. pallida* suffered much higher levels of herbivore damage caused by *U. ornatix* than the native *C. incana* in the field (Fig. 1). Seventy-nine percent of *C. pallida* individuals were damaged, while for *C. incana* only 38 percent of individuals were damaged. The percent of pods attacked by *U. ornatix* was higher for *C. pallida* than

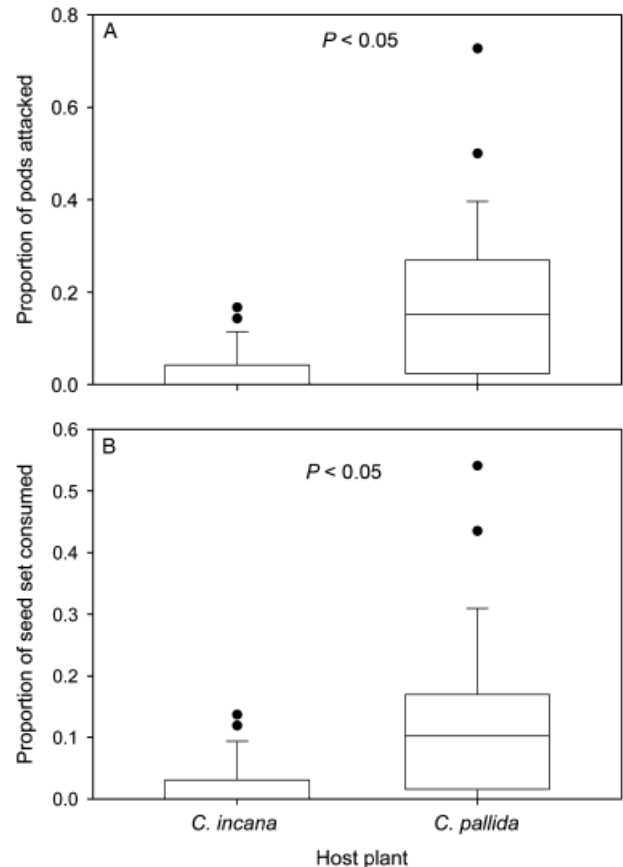


FIGURE 1. Herbivore damage caused by *Uetheisa ornatix* on the native host *Crotalaria incana* and the introduced host *Crotalaria pallida* in the field. (A) Proportion of pods attacked per plant. (B) Proportion of the seed set consumed by larvae per plant. Median, 10th, 25th, 75th and 90th percentiles. $P < 0.05$ = difference significant in Mann–Whitney U test. $N = 26$ for *C. incana* and 28 for *C. pallida*.

for *C. incana* ($U = 139$, $N_1 = 28$, $N_2 = 26$, $P < 0.001$; Fig. 1A). The percent of the plant seed set that was consumed by *U. ornatix* was also higher for *C. pallida* than for *C. incana* ($U = 154$, $N_1 = 28$, $N_2 = 26$, $P < 0.001$; Fig. 1B).

OVIPOSITION PREFERENCE IN THE LABORATORY.—Females preferred to oviposit on the introduced *C. pallida* plants over the native *C. incana* (Fig. 2). The mean number of eggs laid on *C. pallida* was more than double the number of eggs laid on *C. incana* ($t = 2.70$, $df = 42$, $P = 0.01$). Twenty-four females laid a higher number of eggs on *C. pallida* and just seven females laid more eggs on *C. incana*.

LARVAE PERFORMANCE IN THE LABORATORY.—The percentage of larvae that survived to pupation on *C. pallida* (15.7%) was not significantly different from *C. incana* (23.8%; $\chi^2 = 2.82$, $df = 1$, $P = 0.09$). Larvae that fed on the introduced *C. pallida* had higher pupal weight than those that fed on the native *C. incana* (Table 1A; Fig. 3A). Larvae feeding on *C. pallida* took on average 1 d longer to pupate than larvae feeding on *C. incana* (Table 1B; Fig. 3B). The

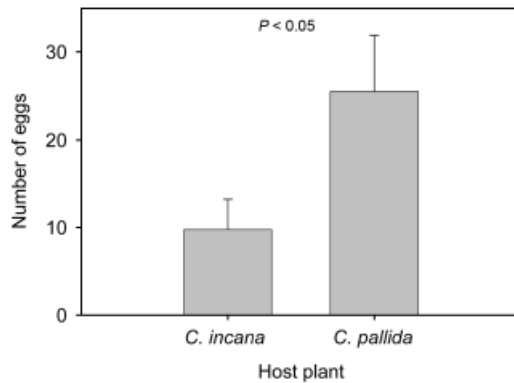


FIGURE 2. Mean (+SE) number of eggs laid by *Utetheisa ornatrix* on leaves of the native host *Crotalaria incana* and the introduced host *Crotalaria pallida* in laboratory choice tests. $P < 0.05$ = difference significant in paired t -test. $N = 43$.

total weight of fruits consumed by larvae, larval efficiency (pupal weight/weight of fruits consumed) and growth rate (pupal weight/development time) did not differ between the two hosts (Table 1C–E). Neither sex nor the interaction between sex and host species had a significant effect on any of the response variables (Table 1).

DISCUSSION

Seed predation rates in the field were much higher for the introduced host than the native host. The common garden experiment indicates that this difference in herbivory rate is caused by differences in the herbivore preference and performance. *Utetheisa ornatrix* showed higher larval performance on the introduced host *C. pallida* than on the native host *C. incana*. Even though survival did not differ between the two hosts, larvae feeding on *C. pallida* achieved higher pupal weight. Pupal weight in this species is a reliable correlate of adult body weight, and adult body weight is directly related to fitness (Iyengar & Eisner 1999). Larger females lay more eggs, and larger males copulate with more females because females prefer larger males (Iyengar & Eisner 1999). The small difference in development time (average of just 1 d) between the two hosts may not affect overall fitness significantly. Although longer development time may result in higher chance of attack by natural enemies (Schoonhoven *et al.* 1998), this small difference might not be biologically meaningful. *Utetheisa ornatrix* larvae are protected against predators by two mechanisms, mechanically by feeding inside the pod (Ferro *et al.* 2006), and chemically by the sequestration of pyrrolizidine alkaloids (Eisner 2003). Additionally, parasitoids are not an important mortality factor. Other researchers and I have collected thousands of eggs and larvae in the field to rear at the laboratory and we rarely found parasitoids (R. Cogni and J. R. Trigo, pers. comm.). Nonetheless, this difference in development time may be the explanation for larger pupae on the introduced host. Growth rate and efficiency did not differ between the two hosts, but, due to a longer development time, larvae feeding on the introduced host consume slightly more seeds (although not statistically significant), resulting in significantly larger pupae.

TABLE 1. Effect of host plant and moth sex on (A) pupal weight, (B) larval development time, (C) weight of seeds consumed, (D) larval efficiency and (E) larval growth rate. *Utetheisa ornatrix* larvae were fed with fruits of *Crotalaria pallida* and *Crotalaria incana* in the laboratory. * indicate significant effects.

Source	df	F-ratio	P
<i>(A) Pupal weight</i>			
Host plant*	1	7.29	0.009
Sex	1	0.02	0.88
Host plant × sex	1	0.84	0.36
Error	49		
<i>(B) Development time</i>			
Host plant*	1	10.13	0.003
Sex	1	0.32	0.57
Host plant × sex	1	0.86	0.36
Error	49		
<i>(C) Weight of seeds consumed</i>			
Host plant	1	0.68	0.41
Sex	1	0.00	0.96
Host plant × sex	1	0.62	0.43
Error	49		
<i>(D) Larval efficiency</i>			
Host plant	1	0.02	0.89
Sex	1	0.02	0.88
Host plant × sex	1	0.10	0.75
Error	49		
<i>(E) Larval growth rate</i>			
Host plant	1	1.42	0.24
Sex	1	0.03	0.87
Host plant × sex	1	0.09	0.76
Error	49		

Utetheisa ornatrix females also showed preference to oviposit on the introduced host (*C. pallida*) over the native host (*C. incana*). There are two possible explanations for the preference and performance results. It could be the result of rapid evolution (see, e.g., Carrol & Boyd 1992). Alternatively, preference and performance traits may be the result of a 'preadaptation' in the sense that the introduced host and the moth possess traits that evolved independent of the interaction, and incidentally those traits led to oviposition preference and higher larval performance when these species first encountered each other. As an example, Thomas *et al.* (1987) showed that all the studied populations of the butterfly *Euphydryas editha* were able to grow and survive in the introduced host *Plantago lanceolata*, but oviposition preference for the new host evolved only in communities where the introduced plant occurs.

Support to the Enemy Release Hypothesis or the New Association Hypothesis depends on the level of invasiveness of the species studied. For the species pair used in this study, the results contradict the predictions of the Enemy Release Hypothesis and support the New Association Hypothesis. It is possible that the

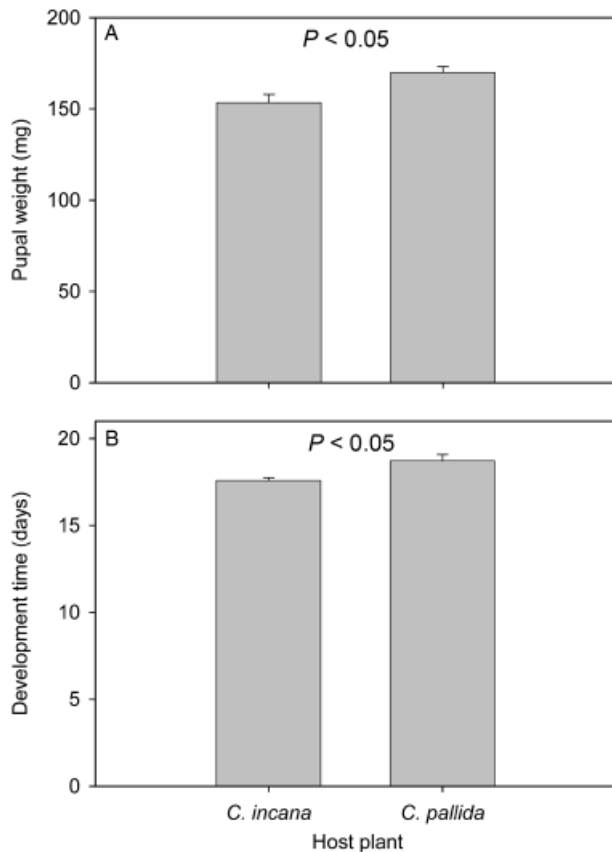


FIGURE 3. Differences in *Utehisia ornatrix* larval performance on the native host *Crotalaria incana* and the introduced host *Crotalaria pallida*. Larvae were reared on leaves for the first 4 d and on green fruits from day 5 until pupation. (A) Pupal weight. (B) Development time. $P < 0.05$ = difference significant in ANOVA tests. $N = 31$ for *C. incana* and 22 for *C. pallida*.

introduced host lacks effective defenses against the native herbivore because they do not share an evolutionary history. *Crotalaria pallida* is considered an invasive species in the Neotropics (Fonseca *et al.* 2006). It is widely distributed and abundant in several localities; however, this species does not form monocultures and does coexist with native *Crotalaria* species. It is likely that host range expansion of the specialist herbivore *U. ornatrix* makes *C. pallida* less invasive. In the Neotropics *U. ornatrix* is the main natural enemy of *Crotalaria* species and other herbivores or pathogens are rarely found in the field (Ferro 2001, Pereira 2008, Cogni & Futuyama 2009). Future studies can address how the differences in seed predation affect demography of both host species. Such a study is necessary to confirm if the great reduction in seed set caused by *U. ornatrix* makes *C. pallida* less invasive.

The Enemy Release Hypothesis has been challenged recently. For example, a recent study examining a large variety of plant taxa and diverse enemies reported a limited potential role for consistent enemy release in the success of introduced species (Agrawal *et al.* 2005). In addition, recent studies have reported that exotic plants are more palatable than native plants to generalist herbivores, and

that introduced plant species are especially susceptible to novel native generalist herbivores that they have not been selected to resist (Agrawal & Kotanen 2003, Parker & Hay 2005, Parker *et al.* 2006). My study shows that the New Association Hypothesis may also be true for a specialist herbivore. A host-range expansion of native specialist herbivores may be common when the introduced host has close relatives with similar chemical defenses in the native flora. A few other studies in natural environments have reported preference of specialist herbivores to introduced hosts (Thomas *et al.* 1987; Solarz & Newman 1996, 2001; Trowbridge & Todd 2001; Trowbridge 2004). Furthermore, in a meta-analysis study Strauss *et al.* (2006) found that introduced plants that were less phylogenetic related to community members were more invasive. The main mechanism responsible for such a pattern may be host shifts of native specialist herbivores and the lack of effective resistance traits on the introduced host, as reported here. My study shows the importance of considering host-expansion of native specialist herbivores as a resistance mechanism to plant invasion.

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