Testing the enemy release hypothesis: a review and meta-analysis

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Abstract

One of the most cited hypotheses explaining the inordinate success of a small proportion of introduced plants that become pests is the ‘natural enemies hypothesis’. This states that invasive introduced plants spread rapidly because they are liberated from their co-evolved natural enemies. This hypothesis had not been properly tested until recently. Previous reviews on this topic have been narrative and vote counting in nature. In this review, we carried out quantitative synthesis and meta-analysis using existing literature on plants and their herbivores to test the different components of the enemy release hypothesis. We found supporting evidence in that (1) insect herbivore fauna richness is significantly greater in the native than introduced ranges, and the reduction is skewed disproportionately towards specialists and insects feeding on reproductive parts; and (2) herbivore damage levels are greater on native plants than on introduced invasive congeners. However, herbivore damage levels are only marginally greater for plants in native than in introduced ranges, probably due to the small numbers of this type of study. Studies quantifying herbivore impacts on plant population dynamics are too scarce to make conclusions for either comparison of plants in native vs introduced ranges or of co-occurring native and introduced congeners. For future research, we advocate that more than two-way comparisons between plants in native and introduced ranges, or native and introduced congeners are needed. In addition, the use of herbivore exclusions to quantify the impacts of herbivory on complete sets of population vital rates of native vs introduced species are highly desirable. Furthermore, three-way comparisons among congeners of native plants, introduced invasive, and introduced non-invasive plants can also shed light on the importance of enemy release. Finally, simultaneously testing the enemy release hypothesis and other competing hypotheses will provide significant insights into the mechanisms governing the undesirable success of invasive species.

Introduction

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 theo-

retical foundation of classical biological control. It is one of the most cited explanations for the undesirable success of introduced invasive species worldwide (Crawley 1997; Maron and Vilà 2001; Keane and Crawley 2002). However, vigorous testing of the ERH did not start until very

recently. Maron and Vilà (2001) were the first review to evaluate the ERH from empirical studies. Since published direct comparisons were lacking, they evaluated the validity of ERH by examining studies on native herbivore and native plant interactions. The rationale behind this approach was that if ERH is valid, one should observe regulatory effects of native herbivores on native plant populations. They concluded that only short-lived perennials, which lack persistent seed banks and have to rely on current seed crops for recruitment, should be affected by enemy release. This conclusion constitutes a hypothesis itself.

Keane and Crawley (2002) tested three assumptions that they inferred from the ERH: (1) specialist enemies will be absent on exotic species; (2) host switching to exotic invasive species by specialists of native congeners will be rare; and (3) generalists will have a smaller impact on exotic species than on native congeners. The first prediction turned out to be false because there is evidence that some specialists feed on exotic invasive species, even though the phenomenon is probably rare. There were no adequate data to test the second assumption. The study found support for the third prediction, but the conclusion was based on 11 comparisons, only one of which involved herbivore exclusion experiments.

Colautti et al. (2004) conducted a wide-ranging review of studies testing ERH, which included data on diverse groups of organisms and their predators, parasites, herbivores, and/or pathogens. They categorized these studies into two broad categories: (1) comparative or correlative 'biogeographical' studies, in which native and introduced populations of the same species were compared; and (2) 'community' studies in which non-indigenous species were compared with native counterparts. They found that the conclusions drawn from these two types of studies were contradictory. 'Biogeographical' studies supported the ERH while 'community' studies did not.

All the above reviews were qualitative narrative summaries of empirical studies. A quantitative synthesis and analysis of published data is needed to more rigorously test the ERH. While quantifying biotic resistance to exotic plant invasion, Levine et al. (2004) carried out a meta-analysis on the effects of herbivore

exclusion on exotic invasive plants and found that herbivores did exert negative effects on establishment and performance of invasive plants. Their analysis focused mostly on mammalian herbivores (10 of the 12 studies included). In addition, they did not consider the effects of herbivores on co-occurring native species. As they pointed out, even though the negative impact of herbivores were significant, the relative abundance of invasive plants increases if herbivory impacts native species to a greater extent.

Here, we employ this quantitative approach using a meta-analysis on native and exotic plants and their insect herbivores. Herbivores, in this review, are defined as insects feeding on one or more parts of a plant. We have used 'introduced' and 'exotic' to indicate plants that have been brought to a new area (often a different continent), and 'invasive' for introduced plants that have become very common and are spreading (Myers and Basely 2003). Comparative studies on plants and insect herbivores are relatively abundant, but only a few fulfill the requirements (means, standard deviations, and sample sizes) of modern meta-analysis to allow calculation of effect size.

We hypothesize that liberation of invasive exotic plants from natural enemies may be interpreted in the following three ways:

- (1) insect herbivore fauna richness is reduced;
- (2) insect herbivore load, i.e. damage level or abundance of phytophagous individuals is reduced; and
- (3) impact of insect herbivory on plant population vital rates is reduced.

The first hypothesis on reduced insect herbivore richness in invasive exotic plants may be further divided into the following predictions:

- (a) the total number of phytophagous insect species is reduced;
- (b) the percentage of specialist insects is reduced;
- (c) the percentage of endophagous insects is reduced (since endophagous insects are more likely to be specialized); and
- (d) the percentage of phytophagous insects feeding on reproductive parts, which presumably have more direct impact on plant recruitment, is reduced.

Materials and methods

We carried out our literature search through Cambridge Scientific Abstracts, using data bases of Agricola, Biological Sciences (including Ecology Abstracts), Biology Digest, and Plant Science. We used various combinations of the keywords: herbivores, herbivore fauna, or herbivory, introduced or exotic or invasive species, natural enemy, and enemy release. Additional papers were obtained by examining the reference lists of original articles. Only plant species that have been introduced for >100 years were included. In addition, crops were excluded because of the highly artificial conditions they were usually subject to. Much of the published data were in graph form. We photographed those graphs with a digital camera and read them using the UTHSCSA Image Tool (<http://www.ddstdx.uthscsa.edu/dig/itdesc.html>) to extract these data for our quantitative synthesis.

Studies testing ERH have been done in two ways: examine herbivore diversity, load, and impacts either in plants native vs in introduced ranges, or between invasives and native counterparts in the same region. The second type of comparison is more informative if the pairs are close phylogenetically and similar ecologically because herbivory varies widely across plant families and genera (Agrawal and Kotanen 2003). We therefore only include studies that are carried out between congeners or confamiliers for the second type of study. These two types of data were kept separate when we compiled the data. When a group of compiled data fulfilled requirements of modern meta-analysis, with means, variation, and sample size, we used MetaWin (Rosenberg et al. 2000) to calculate Hedge's *d*, one type of effect size. When the compiled data did not fulfill meta-analysis requirements but we had more than five comparisons, we used paired *t*-tests to quantify the differences statistically using SPSS 10.0 (SPSS, Chicago, IL, USA). When multiple *t*-tests were performed for each set of data, we adopted Bonferroni corrections to adjust *P* values to ensure the overall statistical type I error was less or equal to 0.05.

Results

Insect herbivore richness

We found data on 15 plant species whose herbivore faunal diversity was compared in the native and introduced invasive range (Table 1). All these data came from field surveys of one or more populations except for one case, in which data were obtained from a literature survey (Blossey et al. 2001). A paired *t*-test indicated that plants have significantly higher numbers of phytophagous insect species in their native than in introduced ranges (Figure 1a). In addition, among these insect faunas, the percentage of specialist and endophagous insects were higher in the native than in introduced ranges (Figure 1b, c). There were also significant differences in feeding niches between the two ranges. Specifically, the percentage of insects feeding on plant reproductive parts was significantly larger in the native than in the introduced ranges (Figure 2). The opposite was true for insects feeding on vegetative parts. No significant difference was found in the percentage of insects feeding on roots in native vs introduced ranges (Figure 2).

We only found two reports comparing the herbivore faunas on introduced and native congeners in the same region (Table 2). In one case, Bürki and Nentwig (1997) surveyed the invertebrate herbivore communities of *Heracleum mantegazzianum*, an invasive weed introduced from the Caucasus, and *H. sphondylium*, a native to Switzerland. They found no difference in number of herbivorous insect species between the two congeners. However, the percentage of specialist insects was higher in the native than the introduced plant species (Table 2). In the other case, Lindelöw and Björkman (2001) compared insect herbivore fauna of lodgepole pine (*Pinus contorta* var. *latifolia*), a tree species introduced to Sweden from North America, with that of Scots pine (*Pinus sylvestris*), a native to Sweden. They found that the native pine had a higher number of herbivorous insect species than the introduced congener. In contrast, lodgepole pine had a higher percentage of specialists than the native congener (Table 2). No statistical test was possible for this comparison.

Table 1. Comparison of phytophagous insect fauna diversity of introduced invasive plant species at its native vs introduced ranges. Italic indicate an average between two locations.

Species	Study location	# of insect sp.	Specialist (%)				Endophagous (%)				Feeding niches (%)				Reference		
											Repro-ductive		Vegetative			Roots	
			N	I	N	I	N	I	N	I	N	I	N	I		N	I
<i>Alliaria petiolata</i>	Europe	39	10	85.7	33.3	44.0	30.0	13.3	0	68.3	100	18.3	0	Blossey et al. (2001), Hinz and Gerber (1998)			
<i>Amorpha fruticosa</i>	US	12	3	–	–	–	–	–	–	–	–	–	–	Szentesi (1999)			
<i>Betula pendula</i>	Britain	85	42	–	–	–	–	–	–	–	–	–	–	Southwood et al. (1982)			
<i>Carduus nutans</i>	Europe	57	22	–	–	41.8	5.3	33.1	19.2	57.9	76.3	9.8	0	Briese (1989), Zwölfer (1965)			
<i>Carduus pycnocephalus</i>	Europe	76	31	36.7	3.8	38.2	10.2	31.1	17.4	59.9	80.4	8.7	2.0	Briese (1989), Goeden (1973)			
<i>Cirsium vulgare</i>	Europe	56	19	–	–	64.9	11.7	31.6	20.7	41.7	77.7	26.7	2.1	Briese (1989), Zwölfer (1965)			
<i>Cytisus scoparius</i>	Europe	5.9	2.5	67.3	30	–	–	24.3	5.6	65.7	94.4	10.1	0	Mennott et al. 2000			
<i>Mimosa pigra</i>	Mexico	156	114	27.7	3.2	38.5	12.3	22.4	9.6	75.7	88.6	1.9	1.8	Wilson et al. (1990)			
<i>Onopordum acanthium</i>	Northern Mediterranean	77	12	31.1	8.3	35.1	16.7	31.4	33.3	57.0	58.34	11.63	8.3	Briese (1989), Briese et al. (1994)			
<i>Onopordum illyricum</i>	Northern Mediterranean	86	22	25.6	22.7	34.9	13.6	34.9	31.8	45.3	54.5	10.5	13.6	Briese (1989), Briese et al. (1994)			
<i>Quercus robur</i>	Britain	96	36	–	–	–	–	–	–	–	–	–	–	Southwood et al. (1982)			
<i>Sida acuta</i>	Mexico	39	20	–	–	41.0	10.0	25.6	30	74.4	70	0	0	Wilson and Flanagan (1990)			
<i>Silybum marianum</i>	Europe	13	29	–	–	21.6	6.5	39.7	14.1	54.2	86.4	7.1	0	Briese (1989), Goeden (1971), Zwölfer (1965)			
<i>Solidago altissima</i>	North America	314	55	25	3.6	17	9	19	1.8	78.0	96.4	3	1.8	Jobin et al. (1996)			
<i>Xanthium occidentale</i>	Southern US and Pakistan	60	60	15.4	3.8	15	8.5	10	8.6	85	90.7	5	0.7	Baloch et al. (1968), Hilgendorf and Geoden (1982), Wilson and Flanagan (1993)			

(N, native range; I, introduced range).

Figure 1. Comparison of insect herbivore fauna of introduced invasive species in their native vs introduced ranges. (a) Total number of species, (b) percentage of specialist, and (c) percentage of endophagous insects.

Herbivore load

Here we defined herbivory load as either the level of damage by insects on a per leaf, per individual or per population basis, or the number of phytophagous individuals per plant. For example, the herbivore load of *Silene latifolia* was the percentage of individuals with insect damage in a population (Wolfe 2002). Due to need of combined variables to boost sample size, we believed that it was reasonable to combine the above two types of variables because damage levels are often correlated with the number of phytophagous

insects present. For example, in our own study, the number of leaves chewed or rasped by caterpillars were found positively correlated with the number of caterpillars found on *Eugenia axillaries* ($r^2 = 0.91$, $F_{1,46} = 491.17$, $P < 0.001$) and *E. foetida* ($r^2 = 0.90$, $F_{1,45} = 382.47$, $P < 0.001$), two woody species native to South Florida (Liu and Stiling, unpublished data). We found seven comparisons on herbivore load of introduced plant species in their native vs introduced ranges, among which two comparisons were done on the same species (Table 3). We kept these two cases separate as was done by the original authors

Figure 2. Comparison of insect herbivore feeding niches on introduced invasive species in their native vs introduced ranges.

(Connor et al. 1980). Due to the incomplete information on variance, we performed a paired *t*-test, instead of a meta-analysis for this comparison. Since the measured variables were on scales of several magnitude differences (Table 3), we log transformed (base 10) the variables before we carried out the paired *t*-test. Herbivore load was greater for plants in their native than in their introduced ranges, but the difference was not statistically significant (Figure 3).

We found 21 comparisons of herbivore damage between congeners (20 cases) or confamiliar pairs (one case) (Table 4). When we used the vote counting technique to summarize the data, we found that among the 21 cases, only nine of

them were in support of ERH, which was less than 50% of the cases. However, when we performed a meta-analysis on these data, we found that the main effect size, Hedge's *d*, was -0.24 with a 95% confidence interval of -0.37 – -0.10 , a range which did not include zero. This indicates that herbivore damage to introduced invasive species is significantly smaller than damage to native species at $P < 0.05$ level. This is contrary to the vote counting results. However, the more conservative bootstrap confidence interval of the Hedge's *d* effect size did include zero (-0.48 – 0.10), so that the comparison of herbivore damage between native and introduced congeners was inconclusive.

Table 2. Comparison of insect herbivore fauna diversity between co-occurring native and introduced invasive congeners.

Native/introduced plant sp.	Location	# of insect sp.		% of specialists		Reference
		N	I	N	I	
<i>Heracleum sphondylium</i> / <i>H. mantegazzianum</i>	Switzerland	34	34	26.5	23.5	Bürki and Nentwig (1997)
<i>Pinus sylvestris</i> / <i>P. contorta</i> var <i>latifolia</i>	Sweden	57	19	57.9	78.9	Lindelöw and Björkman (2001)

(N, native plant species; I, introduced plant species).

Table 3. Comparison of insect herbivore load (damage or number of phytophagous individuals) of introduced species in their native and introduced ranges.

Plant species	Location		Herbivore load		Standard deviation		Sample size		Variable quantified	Reference
	N	I	N	I	N	I	N	I		
<i>Betula pendula</i>	Britain	South Africa	17,789	203	–	–	1	1	Number of phytophagous individuals	Southwood et al. (1982)
<i>Clidemia hirta</i>	Costa Rica	Hawaii	4.6	1.1	8.6	2.9	26	26	Percent leaf area missing	DeWalt et al. (2004)
<i>Quercus alba</i>	North America	Australia	10.5	4.6	–	–	4	1	% leaves mined	Connor et al. (1980)
<i>Quercus robur</i>	Britain	South Africa	4692	97	–	–	1	1	Number of phytophagous individuals	Southwood et al. (1982)
<i>Quercus virginiana</i>	North America	Australia	6.8	8.4	–	–	4	2	% leaves mined	Connor et al. (1980)
<i>Quercus virginiana</i>	North America	New Zealand	5.26	10.2	–	–	3	1	% leaves mined	Connor et al. (1980)
<i>Silene latifolia</i>	Europe	North America	14.7	2.8	15.9	15.9	50	36	% individuals with insect damage	Wolfe (2000)

(N, native range; I, introduced range).

Herbivore impacts

We found only two studies comparing the impacts of insect herbivory on population vital rates, (i.e. plant growth, survival, and/or reproduction) between plants in their native range (or native plants) and plants in their introduced range (or introduced congeners). Such impacts can only be quantified via herbivore exclusion experiments and documentation of plant population parameters over a relatively long period of time. Due to the low number of available studies, no statistical tests were possible. We thus verbally summarized each case.

Schierenbeck et al. (1994) was the first study quantifying effects of herbivory on invasive species and native congeners via herbivore exclusion experiment. They found that when herbivores were excluded, native *Lonicera* growth increased, but not the introduced invasive *Lonicera*. Their results support the ERH.

DeWalt et al. (2004) was so far the only published study that did a parallel herbivore exclusion experiment in the species' native range and its invasive range. They found that in Costa Rica, *Clidemia hirta*'s native range, exclusion of insect herbivores increased survival in understory habitat, but not in open habitat. No differences were seen in Hawaii, the introduced invasive range. This study showed conditional support for the Enemy Release Hypothesis, depending on the habitat. DeWalt et al. (2004) used this habitat dependency to explain habitat type expansion of *Clidemia hirta* in the invasive range. *Clidemia hirta* only occurs naturally in the open habitat in Costa Rica, but it can be found in both open and understory habitats in Hawaii, its invasive range.

Discussion

Our review shows strong evidence supporting our first prediction: that on introduced invasive plants the number of herbivore species is indeed lower. Furthermore, the escape from insect herbivores by the introduced invasive species is disproportionately skewed towards specialists, endophytophagous insects, and insects feeding on reproductive parts. Reduction of insect species

Figure 3. Comparison of insect herbivore load (damage or number of individuals) of introduced species in their native vs introduced ranges.

number on introduced host plants are somewhat expected due to ‘invasion bottleneck’ effects, which posit that because usually only a limited number of propagules are associated with an introduction event, only a subset of enemies are likely to be introduced as well (Colautti et al. 2004). On the other hand, introduced plants may recruit new herbivores from local insect pool in the introduced range to counter the initial loss of herbivores (e.g. Bürki and Nentwig 1997).

However, one should be cautious when interpreting species richness comparisons between two geographic ranges. There are many factors influencing the richness of phytophagous insect species, e.g. plant geographic ranges, the amount of time elapsed since a species has been introduced to an area, and sampling effort (Strong et al. 1984, Colautti et al. 2004). Nevertheless, we consider our results relatively robust for the following reasons. First, we only used data that were collected from field surveys of one or more populations of the target plant species, rather than compiled phytophagous species lists from literature surveys; with the exception of Blossey et al. (2001). The latter methodology usually gives a larger number of insect species that came from multiple survey efforts and covers the entire range of the species. In this way, we minimized the biases due to differences in the geographic ranges and survey efforts. In Blossey et al. (2001) the number of insect species in the introduced range was still much lower than that from field surveys in the native range. Second, each comparison was mostly done by the same research team such that

their survey methods were more or less the same. Third, we only included species that have been introduced for at least 100 years. Although this is still a very short time on an evolutionary scale, it is nonetheless workable ecologically. Our data are consistent with that presented by similar studies, which provide strong support of ERH from data of the number of pathogen and parasite species and their infestation frequency of exotic vs native populations (Mitchell and Power 2003; Torchin and Mitchell 2004).

Our second prediction, which states that herbivore load on introduced invasive species is lower, received positive support from our quantitative synthesis, even though this support was much weaker than that for insect fauna richness. Results seen in these studies vary much and are even contradictory. This may be due to the high individualistic nature of invasive species (i.e. each species may be unique in the success of invasion process). Interestingly, the conclusion drawn from this group of data would be somewhat different if one used the vote counting method. This discrepancy emphasizes the importance of quantitative synthesis, which can provide a different result than qualitative analysis. Nevertheless, it is apparent that the release in herbivore species richness is only partially translated into a release in herbivore load, (i.e. damage or number of herbivore individuals on the host plants), a conclusion similar to that drawn by Colautti et al. (2004).

Finally, our third prediction, that the impact of herbivores on plant population vital rates is reduced, may be true, but there is insufficient

Table 4. Comparison of phytophagous insect damage on native vs introduced congeners in the same range.

Native/introduced plant sp.	Location	Mean damage		Standard deviation		Sample size		Reference
		N	I	N	I	N	I	
<i>Artemisia campestris</i> /A. biennis	Ontario	0.81	3.70	0.62	4.66	18	5	Agrawal and Kotanen (2003)
<i>Asclepias syriaca</i> /Cynanchum rossicum	Ontario	2.86	0.89	2.58	1.22	14	14	Agrawal and Kotanen (2003)
<i>Bromus kalmii</i> /B. inermis	Ontario	1.36	1.22	3.00	2.30	11	16	Agrawal and Kotanen (2003)
<i>Campanula rotundifolia</i>	Ontario	0.23	7.2	0.41	5.87	11	10	Agrawal and Kotanen (2003)
<i>C. rapunculoides</i>								
<i>Cerastium arvense</i> /C. fontanum	Ontario	0.27	1.06	0.75	2.46	17	16	Agrawal and Kotanen (2003)
<i>Chenopodium simplex</i> /C. album	Ontario	7.50	10.5	8.63	7.98	6	14	Agrawal and Kotanen (2003)
<i>Elymus trachycylus</i> /E. repens	Ontario	1.87	4.50	3.80	6.28	15	16	Agrawal and Kotanen (2003)
<i>Eucalyptus gomphocephala</i>	Australia	34.6	22	29.4	15.4	10	10	Radho-Toly et al. (2001)
<i>E. botryoides</i>								
<i>Eucalyptus marginata</i>	Australia	16.0	18.8	7.15	8.57	10	10	Radho-Toly et al. (2001)
<i>E. cladocalyx</i>								
<i>Eugenia axillaries</i> /E. uniflora	Florida	32.6	14.6	28.6	17.1	188	94	Liu and Stiling unpublished
<i>Eugenia foetida</i> /E. uniflora	Florida	21.1	14.6	20.6	17.1	177	94	Liu and Stiling unpublished
<i>Galium boreale</i> /G. verum	Ontario	0.54	0	0.75	0	12	15	Agrawal and Kotanen (2003)
<i>Geum aleppicum</i> /G. urbanum	Ontario	3.30	6.77	3.39	8.17	15	11	Agrawal and Kotanen (2003)
<i>Lactuca Canadensis</i> /L. serriola	Ontario	13.4	3.77	18.9	6.11	18	11	Agrawal and Kotanen (2003)
<i>Lepidium densiflorum</i> /L. campestre	Ontario	32.2	39.7	35.2	28.0	15	15	Agrawal and Kotanen (2003)
<i>Lonicera sempervirens</i> /L. japonica	S. Carolina	8.74	1.99	9.91	6.96	30	30	Schierenbeck et al. (1994)
<i>Plantago rugelii</i> /P. major	Ontario	5.89	14.9	4.51	13.9	14	15	Agrawal and Kotanen (2003)
<i>Potentilla arguta</i> /P. recta	Ontario	1.68	2.83	1.67	1.53	14	3	Agrawal and Kotanen (2003)
<i>Quercus robur</i> /Q. cerris	England	0.83	0.71	0.79	0.76	10	10	Yela and Lawton (1997)
<i>Senecio pauperculus</i> /S. vulgaris	Ontario	4.41	7.5	12.1	3.54	16	2	Agrawal and Kotanen (2003)
<i>Silene antirrhina</i> /S. vulgaris	Ontario	0.37	0.91	0.81	1.56	15	16	Agrawal and Kotanen (2003)

(N, native plant species; I, introduced plant species).

data to demonstrate this. Herbivore impacts on plant population dynamics can only be quantified via herbivore exclusion experiments. This type of experiment is time- and labor-demanding, and as a consequence, rigorous field herbivore exclusion studies comparing native and introduced plants are seriously lacking. Yet, these types of studies will provide the most convincing evidence in terms of testing ERH.

It is apparent from this review that to draw more robust conclusions about the validity of ERH, we need more two-way studies comparing herbivore damage in a host plants' native and introduced range, and also on co-occurring native and introduced congeners. In addition, among the few available studies that quantified the impacts of herbivory on plant vital rates, all studied only one or two population parameters. Studies that quantify effects of herbivory on complete sets of population vital rates (including growth, survival, and reproduction rates) are needed. An excellent analytical tool for this is population matrix model analysis. Matrices may be built for plant populations with and without herbivore damage for comparison of their respective population growth rates. Furthermore, measuring impacts of herbivore damages on congeneric introduced and native plants at the same range will allow us to best measure biotic resistance (Levine et al. 2004) and thence its roll in the invasion processes. On the other hand, studies that measure impacts of herbivore damage on plants in their native vs introduced ranges, combined with common garden experiments, will shed light on the generality of evolution of increased competitive ability hypothesis (EICA, *sensu* Blossey and Nötzold 1995), which attribute the increased competitive ability of invasive species to the release of natural enemies. Furthermore, there exist plant systems in which congeneric native, introduced invasive, and introduced non-invasive co-occur in the same region. Such three-way comparisons can provide particularly insightful information on the validity of ERH. Finally, the three-way system is also ideal for simultaneously testing ERH and other competing, but not necessarily exclusive hypotheses, such as competition, and recruitment limitation.

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References

- Agrawal AA and Kotanen PM (2003) Herbivores and success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters* 6: 712–715
- Baloch GM, Mohyuddin AI and Ghani MA (1968) *Xanthium strumarium* L. – insects and other organisms associated with it in west Pakistan. Technical Bulletin of the Commonwealth Institute for Biological Control Technical Bulletin 10: 103–111
- Blossey B, Nuzzo V, Hinz H and Gerber E (2001) Developing biological control of *Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard). *Natural Area Journal* 21: 357–367
- Briese DT (1989) Natural enemies of carduine thistles in New South Wales. *Journal of the Australian Entomological Society* 28: 125–134
- Briese DT, Sheppard AW, Zwolfer H and Boldt PE (1994) Structure of the phytophagous insect fauna of *Onopordum* thistles in the northern Mediterranean basin. *Biological Journal of the Linnean Society* 53: 231–253
- Bürki CB and Nentwig W (1997) Comparison of herbivore insect communities of *Heracleum sphondylium* and *H. mantegazzianum* in Switzerland (Spermatophyta: Apicaceae). *Entomologia Generalis* 22: 147–155
- Colautti RI, Ricciardi A, Grigorovich IA and MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7: 721–733
- Connor EF, Faeth SH, Simberloff D and Opler PA (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 5: 205–211
- Crawley MJ (1997) *Plant Ecology*. Blackwell Science, Oxford
- DeWalt SJ, Denslow JS and Ickes K (2004) Natural-enemy release facilitates habitat expansion of the invasive tropical shrub *Clidemia hirta*. *Ecology* 85: 471–483
- Goeden RD (1971) The phytophagous insect fauna of milk thistle in southern California. *Journal of Economic Entomology* 64: 1101–1104

- Goeden RD (1973) Comparative survey of the phytophagous insect faunas of Italian thistle, *Carduus pycnocephalus*, in southern California and southern Europe relative to biological weed control. *Environmental Entomology* 3: 464–474
- Hilgendorf JH and Goeden RD (1982) Phytophagous insects reported worldwide from the noxious weeds spiny clotbur, *Xanthium spinosum*, and cocklebur, *X. strumarium*. *Bulletin of the Entomological Society of America* 28: 147–152
- Hinz HL and Gerber E (1998) Investigations on Potential Biological Control Agents of Garlic Mustard, *Alliaria petiolata* (Bieb.) Cavara & Grande. Annual Report for 1998. CABI Bioscience, Delemont
- Jobin A, Schaffner U and Nentwig W (1996) The structure of the phytophagous insect fauna on the introduced weed *Solidago altissima* in Switzerland. *Entomologia Experimentalis et Applicata* 79: 33–42
- Keane RM and Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164–169
- Levine JM, Adler PB and Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7: 975–989
- Lindelöw A and Björkman C (2001) Insects on lodgepole pine in Sweden – current knowledge and potential risks. *Forest Ecology and Management* 141: 107–116
- Maron JL and Vilà M (2001) When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95: 361–373
- Memmott J, Fowler SV, Paynter Q, Sheppard AW and Syrett P (2000) The invertebrate fauna on broom, *Cytisus scoparius*, in two native and two exotic habitats. *Acta Oecologica* 21: 213–222
- Mitchell CE and Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature* 421: 625–627
- Myers JH and Basely DR (2003) *Ecology and Control of Introduced Plants*, pp 20–23. Cambridge University Press, Cambridge 20–23
- Radho-Toly S, Majer JD and Yates C (2001) Impact of fire on leaf nutrients, arthropod fauna and herbivory of native and exotic eucalypts in Kings Park, Perth, Western Australia. *Australia Journal of Ecology* 26: 500–506
- Rosenberg MS, Adams DC and Gurevitch J (2000) *MetaWin: Statistical software for Meta-Analysis Version 2.0*. Sinauer Associates, Sunderland
- Schierenbeck KA, Mack RN and Sharitz RR (1994) Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* 75: 1661–1672
- Southwood TRE, Moran VC and Kennedy CEJ (1982) The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* 51: 635–649
- Strong DR, Lawton JH and Southwood R (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific Publications, Oxford
- Szentesi A (1999) Predispersal seed predation of the introduced false indigo, *Amorpha fruticosa* L. in Hungary. *Acta Zoologica Academiae Scientiarum Hungaricae* 45: 125–141
- Torchin ME and Mitchell CE (2004) Parasites, pathogens, and invasions by plants and animals. *Frontiers in Ecology and Environment* 2: 183–190
- Wilson CG and Flanagan GJ (1990) The phytophagous insect fauna of the introduced shrubs *Sida acuta* Burm. F. and *Sida cordifolia* L. in the northern territory, Australia. *Australian Entomological Magazine* 17: 7–15
- Wilson CG and Flanagan GJ (1993) Phytophagous insect fauna of the introduced noxious weed *Xanthium occidentale* in northern Australia and its relevance to biological control. *Biological Control* 2: 254–261
- Wilson CG, Flanagan GJ and Gillett JD (1990) The phytophagous fauna of the introduced shrub *Mimosa pigra* in northern Australia and its relevance to biological control. *Environmental Entomology* 19: 776–784
- Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. *American Naturalists* 160: 705–711
- Yela JL and Lawton JH (1997) Insect herbivore loads on native and introduced plants: a preliminary study. *Entomological Experimentalis et Applicata* 85: 275–279
- Zwölfer H (1965) Preliminary list of phytophagous insects attacking wild Cynareae (Compositae) in Europe. *Technical Bulletin of the Commonwealth Institute for Biological Control Technical Bulletin* 6: 81–154