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Evidence for the enemy release hypothesis in *Hypericum perforatum*

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Abstract The enemy release hypothesis (ERH), which has been the theoretical basis for classic biological control, predicts that the success of invaders in the introduced range is due to their release from co-evolved natural enemies (i.e. herbivores, pathogens and predators) left behind in the native range. We tested this prediction by comparing herbivore pressure on native European and introduced North American populations of *Hypericum perforatum* (St John's Wort). We found that introduced populations occur at larger densities, are less damaged by insect herbivory and suffer less mortality than populations in the native range. However, overall population size was not significantly different between ranges. Moreover, on average plants were significantly smaller in the introduced range than in the native range. Our survey supports the contention that plants from the introduced range experience less herbivore damage than plants from the native range. While this may lead to denser populations, it does not result in larger plant size in the introduced versus native range as postulated by the ERH.

Keywords Biological control · Herbivory · Plant invasions · Natural enemies hypothesis · St John's Wort

Introduction

Biological invasions are worldwide phenomena with often devastating effects on native species and natural

habitats (Cox 1999). The impact of alien species can depend largely on both the size of their introduced geographical range and their abundance where introduced (Parker et al. 1999). Traditionally, there has been a general perception that plant invaders are very abundant (i.e. large population sizes) and attain larger stature compared to conspecifics in the native range (Elton 1958). However, empirical evidence supporting these impressions is surprisingly scanty. Only recently have researchers begun to rigorously examine the demography of plant invaders in the introduced and in the native range. These studies have generally found higher seedling establishment and greater overall plant densities in the introduced than native range (Grigulis et al. 2001; Paynter et al. 2003). There is also some observational confirmation that certain plant species are larger in their introduced versus native range and that these differences are genetically based (Crawley 1987; Blossey and Nötzold 1995; Buckley et al. 2003). Nevertheless, when a large number of species have been compared this trend is not always found. For example, a screening of floras has shown that on average European plants invading California are not significantly taller than in Europe, and Californian plants invading Europe are even smaller than in California (Thébaud and Simberloff 2001). To fully establish whether plants from the introduced range perform better than those in the native range, extensive field surveys must be conducted where introduced and native populations are compared (Willis and Forrester 2000; Leger and Rice 2003).

When differences in plant size exist, the enemy release hypothesis (ERH) has been proposed as an explanation. The ERH posits that one of the leading causes of increased vigour of some invaders in the introduced range is liberation from co-evolved natural enemies (i.e. herbivores, pathogens and predators) (Maron and Vilà 2001). ERH predicts that plants in the introduced range are less damaged by natural enemies than in the native range and this reduction in herbivore pressure translates to demographic advantages that result in larger population and plant sizes than in the native range. The few

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studies that have compared levels of herbivory between the native and the introduced range have found that abundance and diversity of phytophagous insects (Memmott et al. 2000) and herbivory and pathogen damage is greater in native than in introduced populations (Mitchell et al. 2003; Wolfe 2001). Only one study has simultaneously compared herbivore pressure, population density and plant sizes between invaders in their native and introduced range (Jakobs et al. 2004).

We examined rates of herbivory, plant population densities, and plant sizes of the perennial herb *Hypericum perforatum* L. (Guttiferae), in its native range in Europe and in a portion of its introduced range in western North America. If the ERH is correct, we would expect to find introduced populations to be larger, denser and less damaged than native populations, and North American plants to be larger than European plants.

Materials and methods

Study species

Hypericum perforatum is a widespread noxious invader native to Europe, North Africa and Asia and introduced into America, Australasia and South Africa (Weber 2003). *H. perforatum* was first introduced into western North America in the mid 1800s. By 1943 it had spread to >200,000 ha of rangeland in California (Holloway and Huffaker 1951). *H. perforatum* contains secondary compounds that are phototoxic and can affect the tissues of grazing insects and mammals (Knox and Dodge 1985). To control this weed, in the mid 1940s, the defoliating chrysomelid beetle, *Chrysolina quadrigemina* Förster (Coleoptera: Chrysomelidae) was introduced as a biocontrol agent (Huffaker and Holloway 1949; Holloway and Huffaker 1951). In 1951, biological control beetles had successfully established colonies in all California counties and had markedly reduced *H. perforatum* populations (Holloway and Huffaker 1951).

Field survey

From mid June to mid July 2003 we simultaneously conducted a survey of 25 *H. perforatum* populations in the introduced range in California and southern Oregon, and 40 populations within the native range across Europe (Table 1). The survey was conducted at the stage of plant flowering. To overcome differences in phenology, we were careful to first survey populations in lower latitudes and altitudes, and with an acute Mediterranean climate. Within each region (Europe and North America), we sampled populations that were at least 20 km apart and <1,500 m in elevation. We sampled populations that consisted of groups of more than ten flowering plants interspaced within a 100 m radius within the same habitat type. In each population we counted the number

of live and recently dead *H. perforatum* plants per unit area. If the population was very large (>100 plants), we randomly sampled 30 plants from within the larger population. For each plant in the population we recorded whether individuals showed any evidence of aboveground herbivore damage. Herbivore damage was assessed by noting whether plants were defoliated or had other signs of insect damage such as browsed twigs.

In each population, we randomly selected 20 plants (or from ten to 20 if the population had <20 plants) that were 2 m from each other to ensure they were not connected underground. On each plant we measured the number of upright stems, the height of the tallest stem and two perpendicular diameters of the projected plant area.

We compared the proportion of populations with herbivore damage and the presence of dead plants between the two ranges (i.e. native and introduced) with a χ^2 -test. Differences in population size, plant density and the percentage of plants with herbivore damage and percentage plant mortality within a population were compared with a Mann-Whitney test. Differences in plant size (number of stems and plant volume) were compared with a nested ANOVA with region and population within region as random factors. Plant volume (V) was estimated as $V = H \times \pi \times (D_1 + D_2) / 4)^2$ where D_1 and D_2 are the two perpendicular diameters of the plant crown and H is the height of the tallest stem. Because plants grow as clumps of many upright stems, cylindrical volume is a reasonable measure of overall plant size and is strongly correlated with above-ground plant biomass (Maron et al. 2004). We transformed data to ln or arcsin if necessary. Means \pm SE are given.

Results

We found that 70% of the European populations had plants with signs of insect herbivore damage. In contrast, in western North America only 28% of the populations contained plants that showed evidence of herbivore damage ($X^2 = 10.92$, $P = 0.001$). The intensity of the damage within each population was also higher in Europe, where on average $23.39 \pm 4.26\%$ of the plants had clear signs of herbivory compared to $3.60 \pm 1.46\%$ of the introduced plants (Mann-Whitney, $z = 3.82$, $P = 0.0001$). In the introduced range, none of the *H. perforatum* plants were dead, while in Europe 32.5% of the populations had some dead plants ($X^2 = 3.28$, $P = 0.001$). On average, the percentage of dead plants within native populations was $5.45 \pm 1.98\%$.

Plant population density (Mann-Whitney, $z = 4.71$, $P < 0.0001$) but not population size (Mann-Whitney, $z = 0.32$, $P = 0.75$) was significantly different between regions. Populations in western North America had more plants per square metre (1.65 ± 0.56) than in Europe (0.17 ± 0.04). Plant volume was also significantly different based on the region of plant origin ($F_{1, 63} = 34.89$, $P < 0.0001$). On average, plants in western

Table 1 Information of

Range	Location	Code	Latitude (°)	Habitat
Introduced	Piercy	101	39.96	Grassland
	Miranda	102	40.24	Ruderal
	Hwy 101	103	40.45	Woodland
	Lake Shasta	104	40.66	Woodland
	Trinity Lake	105	40.69	Woodland
	Litte Brown's	106	40.70	Woodland
	Big Flat	107	40.74	Grassland
	Del Lane	108	40.81	Woodland
	Arcata	109	40.83	Ruderal
	Titlow	110	40.87	Ruderal
	Dunsmuir III	111	40.99	Woodland
	Dunsmuir II	112	41.24	Ruderal
	Dunsmuir I	113	41.25	Ruderal
	Gasket	114	41.42	Ruderal
	Edgewood	115	41.44	Grassland
	Hwy 3	116	41.62	Ruderal
	Hwy 199	117	41.84	Grassland
	Knoppi	118	41.92	Woodland
	Yreka	119	42.17	Grassland
	Sarape	120	42.42	Ruderal
	Rogue River	121	42.43	Ruderal
	Campjoy	122	42.50	Ruderal
	Frontage	123	42.70	Ruderal
	Elk Creek	124	42.85	Woodland
	Day's Creek	125	42.96	Ruderal
Native	Constantina (Spain)	1	37.92	Grassland
	Fte. Ovejuna (Spain)	2	38.27	Grassland
	Beneixida (Spain)	3	39.08	Ruderal
	Picassent (Spain)	4	39.37	Woodland
	Vall d'Uixó (Spain)	5	39.83	Orchard
	Torreblanca (Spain)	6	40.23	Orchard
	Ulldecona (Spain)	7	40.61	Old field
	Sant Cugat (Spain)	8	41.47	Grassland
	Igualada (Spain)	9	41.58	Grassland
	Callús (Spain)	10	41.73	Grassland
	Ponts (Spain)	11	41.91	Ruderal
	Solsona (Spain)	12	41.99	Grassland
	Barbastro (Spain)	13	42.05	Grassland
	Selva de Mar (Spain)	14	42.33	Grassland
	Castillo de Jaca (Spain)	15	42.67	Meadow
	Cuxac (France)	16	43.40	Woodland
	Les Sangsues (France)	17	43.61	Grassland
	Lacaune (France)	18	43.68	Woodland
	Sainte Affrique (France)	19	43.96	Ruderal
	Millau (France)	20	44.31	Woodland
	Rodez (France)	21	44.41	Ruderal
	Figeac (France)	22	44.64	Ruderal
	Rocamadour (France)	23	44.78	Grassland
	Uzerche (France)	24	45.43	Ruderal
	Saint Paul (France)	25	45.73	Grassland
Bessines (France)	26	46.12	Woodland	
Delemont (Switzerland)	27	47.37	Ruderal	
Bonhomme (France)	28	48.17	Ruderal	
Baccarat (France)	29	48.44	Ruderal	
Wettstetten (Germany)	30	48.82	Ruderal	
Seurenholz (Germany)	31	48.95	Old field	
Pans (France)	32	49.20	Ruderal	
St Saens (France)	33	49.64	Ruderal	
Foucarmont (France)	34	49.80	Woodland	
Verdun (France)	35	49.80	Ruderal	
Nouvion (France)	36	50.17	Ruderal	
Berec (France)	37	50.38	Grassland	
Wasserknoten (Germany)	38	50.70	Woodland	
Saltzer (Germany)	39	51.49	Ruderal	
Letwitz (Germany)	40	51.58	Old field	

Hypericum perforatum
populations surveyed in the
introduced range in western
North America and the native
range in Europe

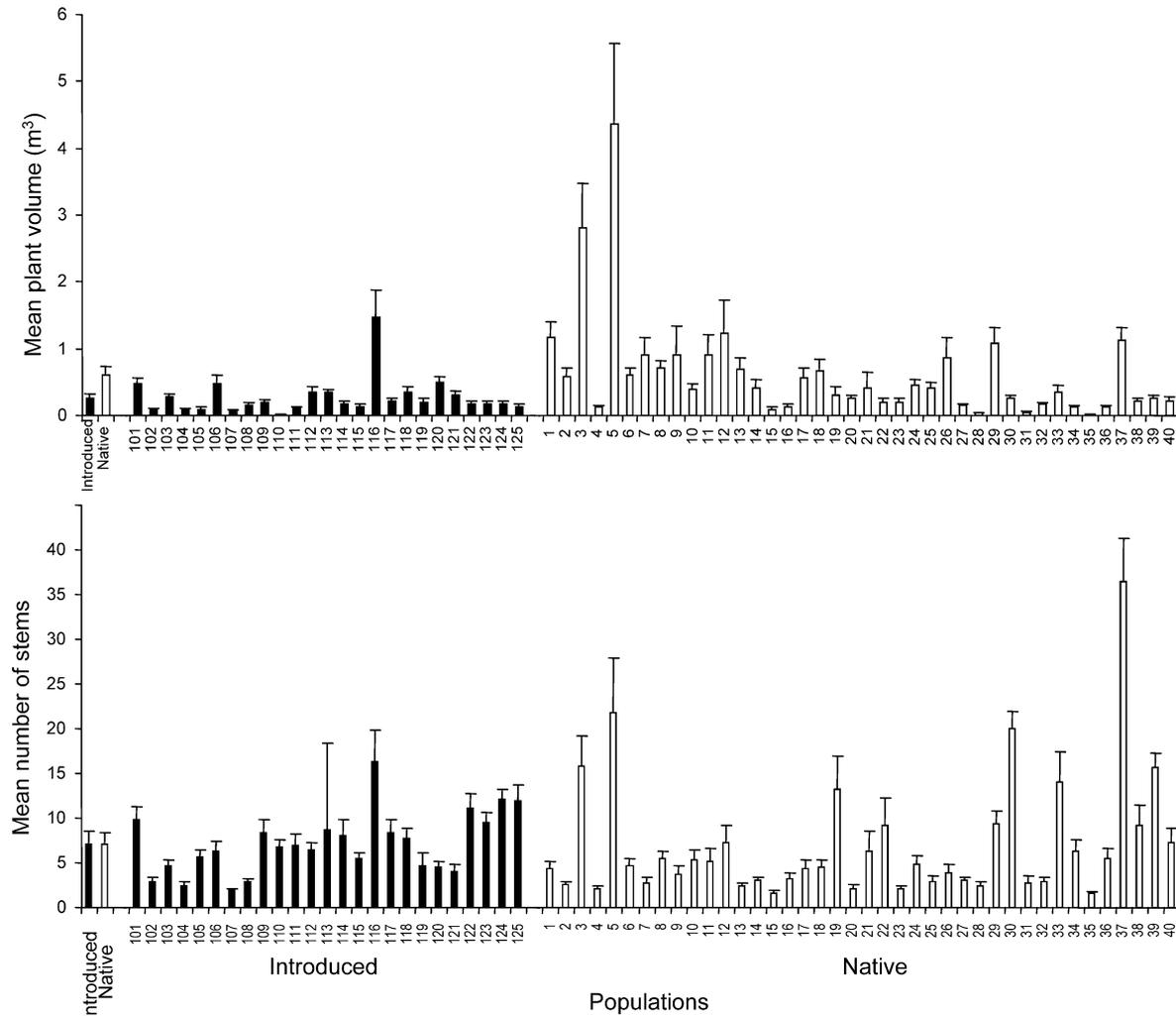


Fig. 1 Mean plant volume and mean number of stems (+SE) of *Hypericum perforatum* from introduced western North America (black bars) and native European (white bars) populations. Each

bar represents the mean of a population ordered according to Table 1. The two initial left-hand bars of the histograms are the regional means, i.e. the means of the population means for each region

North America were smaller than in Europe (Fig. 1) but plants did not differ in the number of stems per plant ($F_{1, 63} = 0.03$, $P < 0.86$) (Fig. 1). Within regions, there were significant differences in *H. perforatum* volumes ($F_{63, 1240} = 12.14$, $P < 0.0001$) and number of stems ($F_{63, 1240} = 11.53$, $P < 0.0001$) among populations (Fig. 1).

Discussion

Our study supports the ERH prediction in that *H. perforatum* are less damaged by insect herbivores in the introduced range than in the native range. Furthermore, in the native range 32% of populations contained at least one dead plant (and often more), whereas in the introduced range mortality was nil. While we cannot be certain, plant mortality in the native range was likely caused by pathogen attack or extensive root boring (Wapshere 1984; Julien and Griffiths 1998). Most dead plants had the same symptoms that plants infected by the generalist fungi *Colletotrichum* sp., *Alternaria* Nees

sp. and *Fusarium oxysporum* (Maron et al. *in press*). Other studies have also found that populations in the native range are more damaged and host more herbivores than in the introduced range (Memmott et al. 2000; Wolfe 2002; Jakobs et al. 2004).

H. perforatum form denser populations in western North American than in Europe. However, contrary to theory, plants from the introduced range were not larger than plants from the native range. In fact, even if they did not differ in the number of stems per plant, plants from the introduced range were smaller than in the native range. This suggests that the lower herbivore pressure in the introduced than in the native range did not translate into higher allocation to plant growth as predicted by the ERH. These results are in accordance with data we have collected from multiple common garden experiments in which we found no evidence that plants from North American populations are, on average, larger than plants from European populations (Maron et al. 2004). In another experiment we have also found that North American plants are not better interspecific

competitors than are European plants (Vilà et al. 2003). Not only did our survey provide no evidence of increased plant size in response to enemy release (as postulated by the ERH), but, in fact, plants in North America that supported insect herbivores were larger ($0.68 \pm 0.12 \text{ m}^3$) than herbivore-free plants ($0.2 \pm 0.01 \text{ m}^3$). In contrast, in Europe, there were no significant differences between plants with ($0.58 \pm 0.12 \text{ m}^3$) and without ($0.62 \pm 0.05 \text{ m}^3$) defoliation.

There are several possibilities for why we found larger variation in plant volume among European (coefficient of variation = 1.29) than North American (coefficient of variation = 1.05) plants. One possibility is that North American plants were founded by a small subset of European individuals and hence there has been a bottleneck that has resulted in decreased variation among introduced plants. However, our previous work has clearly indicated that there have been multiple introductions of *H. perforatum* into North America (Maron et al. 2004). Furthermore, based on amplified fragment length polymorphism molecular markers we found as much neutral genetic variation among introduced plants as we did among native plants. In addition to this, in common gardens introduced plants exhibit as much if not more phenotypic variation than native European plants (Maron et al. 2004). Thus a more likely possibility for the greater variation in size among European versus North American plants is that populations were surveyed across a greater latitudinal range in Europe than in North America.

It is probable that plants from the introduced range are smaller than native European plants due to greater intraspecific competition generated by higher plant densities in the introduced range. This is supported by a negative correlation between plant density and mean plant volume (Spearman rank correlation $r_s = -0.33$, $P = 0.009$). This explanation was also suggested for the invasive *Cytisus scoparius*. *C. scoparius* plants grow more densely where they have been introduced, in Australia and New Zealand, than in native European populations. High density appears to limit their growth (Sheppard et al. 2002).

From a management point of view, the ERH is the main theoretical foundation of classic biological control. Biological control assumes that the deliberate importation and establishment of specific natural enemies, usually phytophagous insects, from a plant's original geographical range will have a large impact limiting the growth of plants and populations in the areas where the plant has invaded. The success of biological control programs have been assessed by observations of host and prey performance before and after the biological control agent release (Huffaker and Holloway 1949; Hoffmann et al. 1998; Hoffmann and Moran 1998). Surprisingly, few studies have compared how populations between the introduced and the native range differ after biological control. In western North America the biological control of *H. perforatum* in the late 1940s and 1950s was considered a major success (Huffaker and Holloway 1949;

Holloway and Huffaker 1951), although there have been no recent re-assessments as to how well *H. perforatum* continues to be controlled. Given that *H. perforatum* has been under biocontrol in western North America, it is possible that our results could be influenced by some unknown history of biological control agent attack. In the introduced range, our observations suggest that at least some *H. perforatum* populations undergo boom-bust dynamics (J. L. Maron, personal observation). That is, plants erupt from a seedbank, grow in dense patches, and then are found by biocontrol agents which bring these incipient populations under control. In the native range, we have also witnessed the colonization of disturbed areas by large populations which subsequently crash due to pathogen attack (M. Vilà, unpublished data). As far as we know, no one has quantified differences in dynamics between native and introduced populations, so it is difficult to know precisely how our results might be influenced by biological control in western North America. Nevertheless, given that *H. perforatum* has been a target for biocontrol, our results represent an extremely conservative test of the ERH. In cases where introduced plants have been controlled by biocontrol agents for several decades, it might be expected that some of the ERH predictions (e.g. larger plant size among introduced plants) might fail.

Species invasions represent excellent ecological "experiments" that can be used to test hypothesis regarding the evolutionary and ecological mechanisms of colonization and the nature of interspecific interactions of founder populations. Our survey is the first to find that despite lower herbivore damage in the introduced than in the native range, introduced plants are smaller than natives.

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