



Presence of *Lythrum salicaria* enhances the bodyguard effects of the parasitoid *Asecodes mento* for *Filipendula ulmaria*

Johan A. Stenberg, Juha Heijari, Jarmo K. Holopainen and Lars Ericson

J. A. Stenberg (johan.stenberg@emg.umu.se) and L. Ericson, Dept of Ecology and Environmental Science, Umeå Univ., SE-901 87 Umeå, Sweden. – J. Heijari and J. K. Holopainen, Dept of Ecology and Environmental Science, Univ. of Kuopio, P.O. Box 1627, FI-70211 Kuopio, Finland.

This paper reports significant effects of a co-occurring plant species (*Lythrum salicaria*, Lythraceae) on the reproductive success of the perennial herb *Filipendula ulmaria* (Rosaceae). We studied 15 *Filipendula* populations in the Skeppsvik Archipelago; seven of which were monospecific and eight mixed with *Lythrum*. All the *Filipendula* populations studied harbored the chrysomelid beetle *Galerucella tenella*, and in 2005 seed set was strongly negatively correlated with the percentage leaf area consumed. Moreover, data from 2004 showed that 25–100% of the *G. tenella* larvae were parasitized by the hymenopteran parasitoid *Asecodes mento*, and we found a strong cascading top-down effect of parasitism in 2004 on *Filipendula* seed set in 2005. In 2004, parasitism (at the population level) was negatively correlated with percentage leaf area consumed and positively correlated with seed set in 2005. The parasitoid *Asecodes* also parasitized *G. californiensis*, which is monophagous on *Lythrum*. Mixed populations of *Filipendula* and *Lythrum* supported higher densities of their shared ‘bodyguard’ *Asecodes*. Further, Y-tube bioassays showed that floriferous *Filipendula* attracted more than twice as many gravid *Asecodes* females as floriferous *Lythrum*. Taken together, these findings suggest that coexistence of the two plants results in ‘associational resistance’ for *Filipendula* and ‘associational susceptibility’ for *Lythrum*. This scenario was supported for *Filipendula* since, for this species, we found lower leaf consumption followed by higher seed production in mixed than in monospecific populations. Considered together, our results show that bodyguards may increase the reproductive fitness of a perennial herb, and that the strength of the cascading ‘bodyguard’ effect can be strongly influenced by co-occurring plants through ‘apparent competition’. This is the first paper to demonstrate that, in the wild, plant species may use odors to compete for ‘bodyguards’, thereby causing asymmetrical ‘apparent competition’ between the herbivores involved. Our data emphasize the need to consider community factors in studies of trophic interactions.

The degree to which host plants are consumed by herbivores varies between sites because herbivores and their natural enemies (bodyguards) have patchy distributions (Thompson 2005). However, the distribution of herbivores and ‘bodyguards’ may, in turn, be highly dependent on the presence of coexisting plant species that provide alternative food sources for the interacting species (Callaway 1995, Zabel and Tschardt 1998, Rand 1999, Sessions and Kelly 2002, Rand 2003, Östergård and Ehrlén 2005, Hambäck et al. 2006). For example, damage to particular plant species by oligophagous herbivores has been shown to increase in cases where the herbivores also utilize

co-occurring plants, which provides scope for increases in the size of the herbivore populations. Such indirect interactions between plants have been called ‘apparent competition’ or ‘associational susceptibility’ and have been shown in a number of studies (Karban 1997, Zabel and Tschardt 1998, Rand 1999, White and Whitham 2000, Sessions and Kelly 2002, Rand 2003, Östergård and Ehrlén 2005). ‘Associational resistance’ may also occur if the ‘apparent competition’ is asymmetrical (Whelan et al. 2003, Hambäck et al. 2006) or if non-host plants interfere with herbivores’ ability to locate a host (Finch and Collier 2000, Hambäck et al. 2003).

A more complex indirect interaction between plants is competition for 'bodyguards'. Although few studies have been able to demonstrate that plant fitness (survival and seed set) is correlated with 'bodyguard' abundance, many studies have shown that 'bodyguards' can trigger top down effects by suppressing herbivore populations, thus increasing primary production (biomass) (reviewed by Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002).

Plants can probably compete directly for 'bodyguards' by emitting attractant VOCs (volatile organic compounds) or providing pollen resources, but the importance of such competition has never been tested before. However, the occurrence of 'apparent competition' between herbivores which feed on separate host plants while sharing a common enemy has been demonstrated in a number of studies (Morris et al. 2004, Hambäck et al. 2006), and intuitively the outcome of such competition seems likely to be of immense importance for the host plants involved, especially if the interaction is asymmetric.

One, recently studied, example of asymmetric 'apparent competition', mediated by a shared 'bodyguard', involves the parasitoid wasp *Asecodes mento* (Hymenoptera: Eulophidae), which attacks the larvae of *Galerucella tenella* (Coleoptera: Chrysomelidae) in *Filipendula ulmaria* (Rosaceae) populations. The parasitoid is more abundant in populations where *Filipendula* grows together with *Lythrum salicaria* (Lythraceae) than in monospecific *Filipendula* populations (Hambäck et al. 2006). This is because *Lythrum* harbors large populations of *G. calmariensis*, a species closely related to *G. tenella*, which functions as an alternative host for *Asecodes* (Hambäck et al. 2006). While more parasitoids are hatched from a single mummified *G. calmariensis* larva than from a single *G. tenella* larva, the latter is still the preferred host. Thus, *G. tenella* suffers higher parasitism when co-occurring with *G. calmariensis* than in monospecific populations (Hambäck et al. 2006).

In this study, we tested two main hypotheses. First, that the bodyguard *Asecodes* plays a key role in influencing seed set in the host plant *Filipendula*. Second, that in mixed stands of *Filipendula* and *Lythrum*, the increase in parasitism of *G. tenella* larvae associated with the latter is accompanied by lower rates of leaf consumption and higher seed set in mixed than in monospecific populations. As *Filipendula* has a strong and characteristic smell, we also tested the hypothesis that *Filipendula* attracts a higher proportion of gravid *Asecodes* females than *Lythrum*, and thus has superior ability to attract bodyguards. We tested these hypotheses in a series of field and laboratory studies. First, in 2004, we visited the major natural populations of *G. tenella* and *G. calmariensis* in the Skeppsvik Archipelago and estimated the parasitization rate in

each population. Second, the strength of the cascading bodyguard effect on *Filipendula* plants was assessed during the following year by determining leaf area consumed by *G. tenella* and seed set. Finally, we performed Y-tube bioassays in which we tested whether herbivore-damaged *Filipendula* attracts more gravid *Asecodes* females than herbivore-damaged *Lythrum*. We found marked correlations between parasitism in 2004 and both leaf damage (negative correlation) and seed set (positive correlation) in 2005. Concordantly, the increase in parasitism when *Lythrum* was present was followed by lower leaf consumption and higher seed production in *Filipendula*. Finally, the bioassays showed that *Filipendula* attracted more than twice as many gravid parasitoids as *Lythrum*.

Material and methods

Study system

The studies were performed in the Skeppsvik Archipelago, located on the western side of the Gulf of Bothnia, 20 km east of Umeå in northern Sweden (63°44–49'N, 20°34–40'E, Fig. 1). The archipelago is affected by isostatic rebound, resulting in an annual increase in land height of 0.85 cm. It consists of about 100 small islands at various stages of primary colonization.

Filipendula ulmaria (Rosaceae) (meadowsweet) and *Lythrum salicaria* (Lythraceae) (purple loosestrife) are both perennial herbs that are abundant on the shores of most areas of the northern Baltic Sea. In the study area, *Lythrum* has a more restricted distribution, occurring in high densities only on islands in the outer part of the archipelago, while *Filipendula* is abundant throughout most of the archipelago. The more restricted distribution of *Lythrum* is probably due to the dependence of the species on regular disturbance as a result of wave-wash during autumn and winter storms for successful seedling establishment. Both plant species are insect-pollinated in July–August and seedling establishment occurs in early June, typically on the lower, open part of the shore.

Galerucella tenella (Coleoptera: Chrysomelidae) is the main natural enemy of *Filipendula* in the central and outer parts of the archipelago. A previous field experiment in the area revealed that plants treated with insecticide exhibited five-fold higher seed sets than control plants in a natural *G. tenella*-infested *Filipendula* population (Stenberg and Ericson, unpubl.). Within the archipelago, *G. tenella* exhibits large variations in densities that are asynchronous in both space and time. Over-wintering adults emerge in late May to early June when they start feeding on *Filipendula* leaves. Oviposition starts in mid-June and the first larvae can be seen in early July. Larval

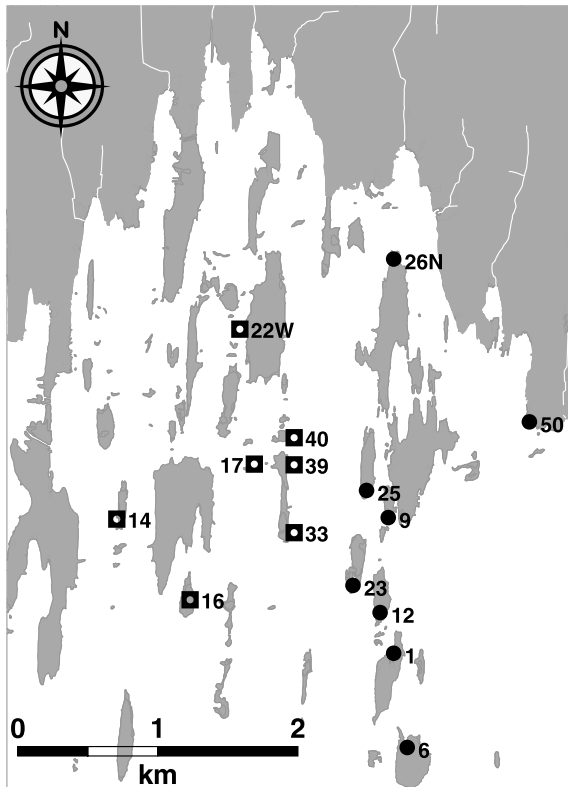


Fig. 1. The study area, Skeppsvik Archipelago, located on the western side of the Gulf of Bothnia, Sweden ($63^{\circ}44\text{--}49\text{N}$, $20^{\circ}34\text{--}40\text{E}$), showing the studied *Filipendula ulmaria* populations with (●) and without (□) *Lythrum salicaria*.

numbers peak after mid-July and no larvae are apparent after mid-August (Hambäck et al. 2006). Larvae are mostly found on floral plants and in particular in the inflorescences while feeding on the seed-embryos. They feed for about three weeks and pupate in the ground. The pupae hatch after about eight days and the new adults feed on the leaves. Over-wintering starts in mid-September. *G. tenella* also feeds on other species of Rosaceae; in the study area these include *Potentilla palustris* and *Rubus arcticus*. However, *Filipendula* is highly preferred (Stenberg and Ericson, unpubl.).

Ascodes mento (Hymenoptera: Eulophidae) is a koinobiont larval endoparasitoid that is known to attack young larval stages of all species in the *Galerucella* genus as well as species in related chrysomelid genera (Askew and Viggiani 1978, Dolgin 1979, Hippa and Koponen 1984, Hansson 1996). In the archipelago studied, its only hosts are *G. tenella* and *G. californiensis* L., the latter being monophagous on *Lythrum* (Hambäck et al. 2006). From a previous study we know that an average of 3.8 parasitoids hatch from a single parasitized *G. tenella* larvae, while considerably

more parasitoids (4.7) hatch from a single parasitized *G. californiensis*, the larger of the two chrysomelids (Hambäck et al. 2006).

Field study

In 2005, we visited all major *Filipendula* populations in the Skeppsvik archipelago (Fig. 1) that were known to have been colonized by the herbivore *G. tenella* in 2004. The islands are listed in Appendix 1. Populations of *Filipendula* that harbored other major herbivores apart from *G. tenella* were excluded from this study. Further, we only selected forested islands since low-lying (non-forested) islands may be submerged during autumn and winter storms, resulting in local extinctions of the chrysomelids. On eight of the islands *Lythrum* and *Filipendula* grew together in dense mixed populations, while *Lythrum* was absent from the remaining seven populations. The *Ascodes* parasitization rates on *G. tenella* and *G. californiensis* larvae were determined in 2004, when we collected 47–55 larvae from each population, fed them with fresh plant material until pupation and calculated the percentage that was mummified. The resulting data have been published elsewhere (Hambäck et al. 2006).

In order to collect data on leaf damage and seed set, on 5–6 July 2005 we marked 40 floral *Filipendula* plants in each of the 15 populations. On each island we used a transect, located on the upper part of the open shore, parallel to the shore line. The distance between sampled plants was 1.5 m. The plants were numbered and marked with white plastic bands tied around the middle part of the floral shoot. The same day, we visually scored the marked plants for percentage leaf area consumed by *G. tenella*. Leaf damage was assessed independently by two persons and the mean values were used.

All islands were revisited on 19 or 20 September, 2005. At this time, the inflorescences were removed and placed individually in paper bags before being returned to the laboratory. In order to estimate seed set, we first counted the number of flowers that had produced seeds, then extracted 15 fruits and scored the number of seeds per fruit. The mean value thus derived was multiplied by the number of seed-producing flowers to obtain an estimate of total seed set. Some plants produced only a few seeds, and in such cases the total number of seeds was counted.

Since inflorescence size varied between populations, we also calculated the proportion of intact seeds for each plant (number of mature seeds divided by the number of seed embryos). Each flower forms nine seed embryos.

Bioassays

For this experiment we used *Asecodes* females that hatched from mummified *Galerucella* larvae sampled in the archipelago in 2005 then overwintered. The response of gravid *Asecodes* females to herbivore-damaged floriferous *Filipendula* and *Lythrum* was tested in a two-arm Y-tube olfactometer (Vuorinen et al. 2004). The Y-tube, measuring $10.5 \times 10 \times 10$ cm for the stem and arms, was made of transparent glass; it had an internal diameter of 1.6 cm and the angle between the two arms was 90° . Filtered air was directed towards two 20 l glass vessels, each containing one herbivore-damaged (48 h) *Filipendula* or *Lythrum* plant. The air flow, containing the odor from the appropriate vessel was directed down one of the arms of the Y-tube at a rate of 0.35 l min^{-1} (airflow was measured using an M-5 mini-Buck calibrator). Floriferous plants of both species were used. *Lythrum* plants were obtained by sowing seeds, collected from population 50 in the Skeppsvik archipelago (Fig. 1) in March 2006, and grown in a greenhouse at the Univ. of Kuopio Botanical Research garden. Undamaged *Filipendula* plants were dug up from a natural population close to the Univ. of Kuopio. Four plant pairs (*Filipendula*/*Lythrum*) were used; all plants were about 1 m tall. Five third-instar larvae (*G. tenella* resp. *G. calmaricensis*) larvae were placed (on the stem leaves) of each experimental plant 48 h prior to the Y-tube trials. The larvae were removed from the foliage just before the trials started. Since the plants were too large to fit into the olfactometer, the upper 30 cm of each floral shoot was cut off and placed in a 0.75 l glass vessel with water, which in turn was placed in the 20 l glass vessel.

In total, 113 parasitoids were tested in the Y-tube setup, with approximately the same number tested on each of the four plant pairs. The testing procedure was as follows: Each parasitoid was placed at the end of the Y-tube and observed for 5 min or until it made a decisive choice. The choice was recorded when the parasitoid had reached a “finish line” two-thirds up one of the arms of the Y-tube and had stayed there for at least 5 s. We recorded “no-choice” in cases when the finish line had not been reached within 5 min. The Y-tube was rotated 180 degrees after each trial. Each Y-tube was used for 10 trials, after which it was replaced with a new sterile one (heated at 120°C for 30 min and cooled to room temperature). The 20 l glass vessels were used with two sets of plant pairs before they were replaced with new sterile (heated at 120°C for 1 h and cooled to room temperature) vessels.

Statistical analyses

Three ‘analyses of covariance’ (Ancovas) were performed to evaluate the field data. In the first Ancova the ‘mean consumed leaf-area in 2005 (at the population level)’ was used as the response variable and ‘co-occurrence with *Lythrum*’ (categorical), and ‘parasitism 2004 (%)’ (continuous) were used as explanatory variables. In the second Ancova the ‘mean seed production’ was used as the response variable and ‘co-occurrence with *Lythrum*’ (categorical), and ‘mean consumed leaf-area in 2005 (at the population level)’ (continuous) were used as explanatory variables. In the third Ancova the ‘mean seed production’ was again used as the response variable and ‘co-occurrence with *Lythrum*’ (categorical), and ‘parasitism 2004 (%)’ (continuous) were used as explanatory variables.

An ‘exact binomial test’ (sign test) was used to determine whether the number of gravid *Asecodes* females choosing floriferous *Filipendula* or *Lythrum* in the Y-tube bioassay differed significantly from a random choice of direction (50% chance of selecting each arm).

The computer package R 2.2.0 (The R Development Core Team 2005) was used for all statistical analysis.

Results

Cascading bodyguard effects

Our July 2005 data describing the mean leaf damage to *Filipendula ulmaria* (at the population level) showed wide variation: from very low levels of around 0–5% consumed leaf area on islands where levels of parasitism were high in 2004 to $\sim 30\%$ on islands with low parasitism (Figs. 2 and 3). The first Ancova (Table 1) showed that herbivory was lower on *Lythrum* islands ($p < 0.001$) and, although we found a negative correlation between parasitism and herbivory, this relationship fell just outside the level of significance ($p = 0.075$). This high p-value for the effect of parasitism on herbivory is due to a single outlier: island 12, in the year that the data were collected, had a much lower parasitization rate (40%, Appendix 1) than usual (Stenberg and Ericson, unpubl.). When island 12 is removed from the data set, the Ancova shows a strong significant effect of parasitism on herbivory ($p = 0.019$).

Data relating to total seed production in 2005 showed that plant fecundity was highest (~ 5000 seeds plant^{-1}) in the population with the least herbivory, while populations with mean consumed leaf areas exceeding 25% produced very few seeds, or no seeds

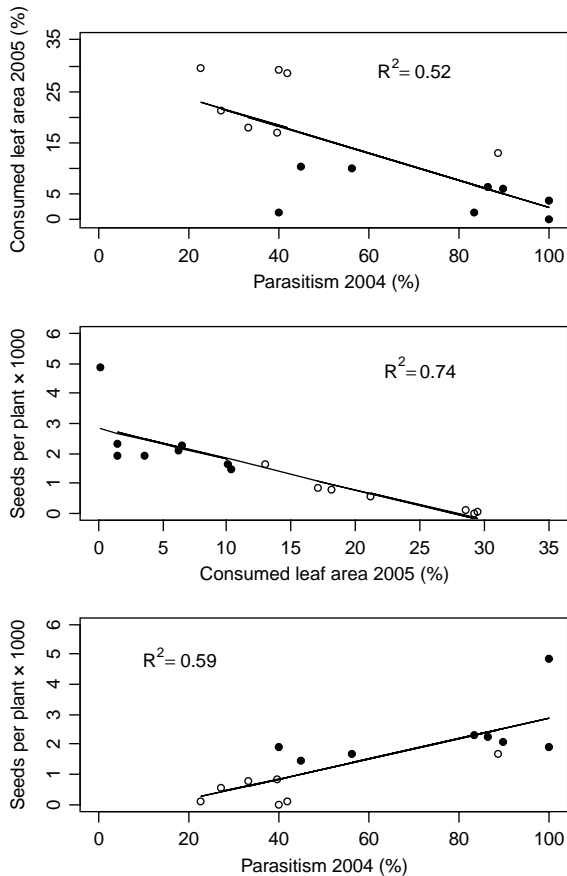


Fig. 2. Mean percentage leaf area of *Filipendula ulmaria* consumed in 2005 by the specialist leaf beetle herbivore *Galerucella tenella* plotted against the percentage *G. tenella* larvae parasitized by *Asecodes mento* during the previous summer (2004) (top graph); mean seed set in 2005 plotted against mean leaf damage (middle graph); and mean seed set in 2005 plotted against parasitism the previous summer (2004) (bottom graph). Mean values (leaf damage and seed set) are based on 40 replicates per population and the number of parasitized larvae (from Hambäck et al. 2006) was calculated from 47–55 sampled larvae per population. Open circles denote monospecific *F. ulmaria* populations, while filled circles denote populations where both *F. ulmaria* and *Lythrum salicaria* were present.

at all (Fig. 2 and 3). The second Ancova (Table 2), similarly, showed that seed production was significantly correlated with herbivory in 2005 ($p = 0.009$) and that seed production was higher on *Lythrum* islands ($p < 0.001$). The proportion of intact seeds exhibited the same pattern as total seed set; it was highest (maximum 75%) in populations with high levels of parasitism and lowest (less than 3%) in populations with low levels of parasitism (Appendix 1). The third Ancova (Table 3) confirmed that seed production was significantly

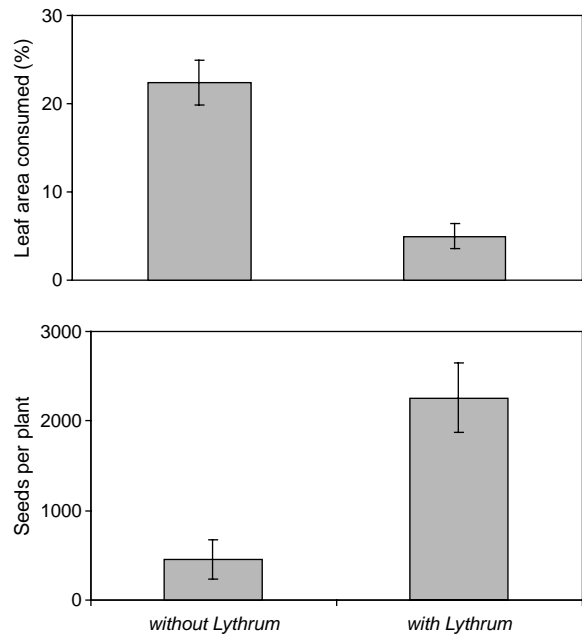


Fig. 3. Leaf area consumed ($\% \pm \text{SE}$) by the specialist leaf beetle herbivore *Galerucella tenella* (upper) and seed set (lower) of *Filipendula ulmaria* plants in island populations where *F. ulmaria* occurs with, and without *Lythrum salicaria*. *Lythrum* is the only host plant for *G. californiensis*, which in turn shares the parasitoid *Asecodes mento* with *G. tenella*. The mean values were calculated from eight and seven island populations, respectively, and $n = 40$ plants for each population.

correlated with parasitism ($p = 0.029$) and that seed production was higher on *Lythrum* islands ($p < 0.001$).

Bioassays

An ‘exact binomial test’ showed that the number of gravid *Asecodes* females that were attracted to *Filipendula* (78 individuals, 69%) compared to *Lythrum* (35 individuals, 31%) was significantly higher ($p < 0.001$) than expected if the selection of direction of movement in the Y-tube had been random (50% chance of selecting each arm).

Table 1. Analysis of covariance of the effects of *Lythrum* (presence/absence) and parasitism (%) in 2004 on the percentage *Filipendula* leaf area consumed by *Galerucella tenella* in 2005.

Source	DF	Sum of squares	F	p
Lythrum (L)	1	1125	46.96	<0.001
Parasitism (P)	1	92.19	3.85	0.075
L × P	1	22.70	0.95	0.351

Table 2. Analysis of covariance of the effects of *Lythrum* (presence/absence) and herbivory (%) on the number of seeds produced by *Filipendula*.

Source	DF	Sum of squares	F	p
Lythrum (L)	1	11.35	25.33	<0.001
Herbivory (H)	1	4.53	10.12	0.009
L × H	1	0.62	1.38	0.265

Discussion

Cascading bodyguard effect

All the *Filipendula* populations studied were colonized by *Galerucella tenella*, which consumed large proportions of both leaves and seed embryos, thereby markedly reducing seed set, when present at high abundance. Furthermore, high parasitization rates of *G. tenella* larvae in 2004 were followed by both lower levels of leaf damage and increased seed set for *Filipendula* in 2005. Contrary to contemporary ecological theory, which suggests that trophic cascades should be uncommon in natural terrestrial systems (Strong 1992, Persson 1999, Polis 1999, Halaj and Wise 2001, Shurin et al. 2002, but see Gomez and Zamora 1994, van Loon et al. 2000, and Crabb and Pellmyr 2006), our data reveal a strong top-down effect of arthropod bodyguards on host plant fitness. We only know of a few studies where the presence of parasitoids has been shown to increase seed set of host plants, and they all involve systems where parasitization leads to early death of the larva, thus preventing further direct loss by the parasitized larva (Gomez and Zamora 1994, van Loon et al. 2000, and Crabb and Pellmyr 2006). However, in the *Asecodes–Galerucella–Filipendula* system studied here, parasitized larvae are not mummified until the pre-pupal stage and, hence, parasitized larvae consume just as much plant biomass as unparasitized larvae. The direct effects of parasitism are manifested in the population dynamics of the herbivore, and the indirect effects on the host plant species can be observed in the following year, as indicated by the positive correlations between parasitism in 2004 and leaf consumption and seed set in 2005.

Although many previous studies have demonstrated effects of bodyguards on plant damage and plant

Table 3. Analysis of covariance of the effects of *Lythrum* (presence/absence) and parasitism (%) in 2004 on the number of seeds produced by *Filipendula* in 2005.

Source	DF	Sum of squares	F	p
Lythrum (L)	1	11.35	19.53	0.001
Parasitism (P)	1	3.67	6.31	0.029
L × P	1	0.02	0.03	0.860

biomass, these effects have not usually translated into real fitness effects in terms of enhanced survival or seed set (Schmitz et al. 2000, Halaj and Wise 2001). The strong effect shown in our study is probably due to the system being relatively simple, despite being terrestrial, including only one major herbivore acting on the plant and only one important bodyguard. It has been proposed that strong herbivores must be coupled with effective bodyguards for trophic cascades to take place in terrestrial systems (Polis 1994, 1999, Borer et al. 2005). This prerequisite seems to be met within the *Asecodes–Galerucella–Filipendula* system, where *G. tenella* commonly consumes over 30% of the leaf area and reduces seed set by up to 100% (Fig. 2, Appendix 1) when there is little parasitism. In addition, more than 90% of the *Galerucella* larvae may be parasitized in some populations, reducing leaf consumption and increasing seed set markedly (Fig. 2). It is also possible that host plant apparency significantly affects the chance of strong bodyguards occurring. *Filipendula* is a dominant plant along the shores of the study islands, and it is intriguing that the two earlier studies (Gomez and Zamora 1994, Crabb and Pellmyr 2006) that have demonstrated fitness effects in natural populations also both relate to dominant plants.

Effects of co-occurring *Lythrum salicaria*

The other main findings of this study are the marked spatial patterns across the archipelago with respect to *Filipendula* leaf damage and seed set, which coincide with the distribution of *Lythrum salicaria*. We have previously found parasitism of *Filipendula*-associated *G. tenella* larvae to be higher in populations where *Filipendula* and *Lythrum* co-occur (Fig. 4, Hambäck

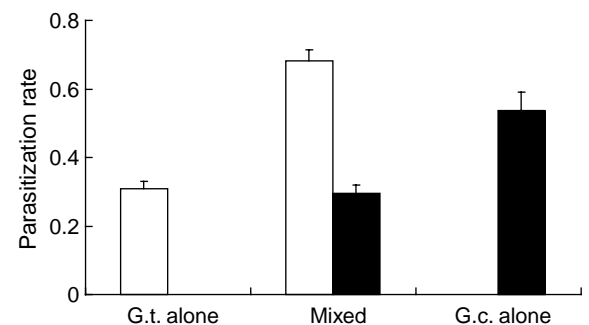


Fig. 4. From Hambäck et al. (2006). Parasitism (% ± SE) of the leaf beetle herbivores *Galerucella tenella* (white bars), a specialist on the host plant *Filipendula ulmaria*, and *Galerucella calmariensis* (black bars), a specialist on the host plant *Lythrum salicaria*. Data are from 2004. The parasitoid is *Asecodes mento*, which is specific to *Galerucella*. Results from populations both with and without the parasitoid.

et al. 2006). Concordant with the increased parasitism of *G. tenella* in mixed populations, this study shows that leaf damage to *Filipendula* was significantly lower in mixed than in monospecific populations, and that seed set was significantly higher in mixed populations (Fig. 3). One possible interpretation of these results is that *Lythrum* mediates a fitness increase in *Filipendula* by facilitating a higher abundance of bodyguards dwelling among *Filipendula* plants, thus maintaining *G. tenella* densities at low levels. However, as the populations with *Lythrum* that were studied are mainly located in the eastern part of the archipelago while those without are mainly located in the western part, it could be argued that the observed spatial pattern may be due to some environmental factor operating in the archipelago.

Baltic archipelagos show a number of marked abiotic gradients that govern distribution patterns of organisms (Häyrén 1940, Ericson 1981). Among the most important are outward-inward gradients of decreasing wave exposure and salinity and increasing duration of ice cover (Ericson 1981). The latter two factors can be ignored here, but the first is important. However, within each of the two island categories 'Lythrum present' and 'Lythrum absent' the islands sampled represent a similar gradient from strongly wave-washed shores (island 1 and 33, respectively) to those with intermediate wave-wash to very sheltered shores in the inner part of the archipelago (islands 26N and 22W, respectively; see also Fig. 12F in Ericson 1981 showing the spatial distribution of damage due to late autumn and winter storms). Since our data show no trend within the two island categories with regard to parasitism, we feel that it is safe to conclude that our results do not mirror any abiotic factor.

Two major findings support our interpretation that *Lythrum* mediates increased parasitism of *G. tenella*. First, as reported by Hambäck et al. (2006), higher densities of the parasitoid can be supported by mixed populations of *G. tenella* and the *Lythrum*-associated herbivore *G. californiensis* than by monospecific *G. tenella* populations. Second, the Y-tube bioassay performed in this study provides a further mechanistic explanation for the asymmetric 'apparent competition' between the herbivores; namely that floriferous *Filipendula* has a more attractive odor (containing *inter alia* benzyl alcohol, phenethyl alcohol, salicylaldehyde and anisaldehyde, which are not found in *Lythrum*, Heijari et al. unpubl.) than floriferous *Lythrum*. This odor gradient that spreads out from floriferous *Filipendula* is easily detected, even by humans, and as evidenced by the bioassay by *Asecodes*. In recent years it has become widely accepted that herbivore-damaged plants commonly emit volatile organic compounds (VOCs) that attract various natural enemies of herbivores. Recent studies have shown that this occurs even in natural

populations with all their environmental complexity (Kessler et al. 2004). This paper, however, is the first to suggest that complex ecosystem phenomena (such as 'apparent competition' between herbivores) may be directed by herbivore-induced VOCs.

Given the parasitoid's preference for *Filipendula*, one would also predict an 'associational susceptibility' for *Lythrum* in the presence of *Filipendula*. We have no experimental field data allowing us to address this issue. However, based on data on plant population dynamics collected since the beginning of the 1970s in the study archipelago, (Ericson unpubl.), it is striking that *Lythrum* has been unable to expand in the western part of the archipelago in spite of the frequent occurrence of suitable wave-washed sites; the few isolated populations that do occur are severely damaged by *G. californiensis*. This suggests that associational susceptibility may be a factor and that the virtual absence of *Lythrum* in this area can be explained by apparent competition.

The mechanism of bodyguard-mediated associational resistance was proposed and tested by Stiling et al. (2003), who showed that the number of galls on the maritime plant *Iva frutescens* was significantly lower when it grew together with the closely related *Borrchia frutescens*, with which it shared bodyguards. The fitness effect of reduced gall numbers was, however, not quantified for *I. frutescens*. However, given the frequency of shared bodyguards, we believe that this mechanism is more prevalent in nature than the literature reflects, and may involve cases of both closely related host plants (as in the study of Stiling et al. 2003) or, as in our study, closely related herbivores.

The same fundamental theory dealing with bodyguard-mediated associational resistance and susceptibility is likely to be of immediate interest in the growing field of studies of invasive plants. For example, *Lythrum* is an important invasive in North America (Blossey et al. 2001) and, in order to combat its spread, *G. californiensis* has been introduced to several areas as a biocontrol agent to slow the spread of this species. The biocontrol program for *Lythrum* has had successes (Landis et al. 2003, Lindgren 2003) and failures (Albright et al. 2004) as regards slowing the spread. Our results suggest that one reason for the different outcomes may be found in local differences in plant species composition and/or their native herbivores, since the effects of parasitism/predation may be dependent on species composition. It would be interesting to examine whether the reported differences in the success of this program coincide with the spatial distribution of native 'apparent competitors' to *G. californiensis*.

Concluding remarks

Our data show that *G. tenella* has a strong fitness effect on its host. We have previously shown that, in the archipelago studied, the strength of *Filipendula* resistance to *G. tenella* reflects the past history of leaf beetle exposure, suggesting that these leaf beetles drive the evolutionary increase in host resistance (Stenberg et al. 2006). The present study shows that the strength of selection also has a second spatial scale within the archipelago, linked to plant community composition. The evolutionary implications of this remain to be studied. However, our findings strongly suggest that studies addressing plant-herbivore interactions should take into account community-level features.

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Appendix 1

Data collected from *Filipendula ulmaria* populations in the Skeppsvik Archipelago. Columns (from left to right) contain data on: island id number; co-occurrence of *Lythrum salicaria*; percentage of *Galerucella tenella* larvae parasitized by *Asecodes mento*, from Hambäck et al. (2006) – based on field samplings of 47–55 larvae per population; mean percentage leaf area (\pm SE) consumed by *G. tenella* (n = 40 plants for each population); mean number of seeds (\pm SE) produced per plant (n = 40 plants for each population); and the percentage (\pm SE) of intact seeds (the number of harvested mature seeds divided by the number of premature seed embryos originally produced). Within each of the two *Lythrum* categories, absent and present, respectively, the islands are listed from south to north (Fig. 1).

Island id	<i>Lythrum</i>	Parasitism 2004 (%)	Consumed leaf area 2005 (%)	Seeds per plant 2005	Intact seeds 2005 (%)
16	Absent	89	12.95 \pm 0.73	1670.50 \pm 304.45	32.29 \pm 3.89
33	Absent	42	28.5 \pm 0.78	104.20 \pm 38.16	2.74 \pm 1.06
14	Absent	40	17.05 \pm 0.74	836.05 \pm 155.81	20.58 \pm 3.20
17	Absent	23	29.48 \pm 0.79	88.90 \pm 45.03	2.96 \pm 1.65
39	Absent	27	21.13 \pm 1.14	551.50 \pm 113.93	17.31 \pm 3.37
40	Absent	40	29.2 \pm 1.05	0	0
22W	Absent	33	18.08 \pm 0.79	786.40 \pm 173.39	15.54 \pm 3.08
6	Present	100	0.15 \pm 0.1	4863.65 \pm 410.56	74.71 \pm 2.36
1	Present	45	10.28 \pm 1	1470.09 \pm 201.96	36.12 \pm 3.57
12	Present	40	1.5 \pm 0.55	1939.08 \pm 163.54	59.83 \pm 2.69
23	Present	56	10.05 \pm 1.1	1674.28 \pm 193.27	46.59 \pm 4.25
9	Present	100	3.63 \pm 0.69	1906.55 \pm 178.31	60.69 \pm 2.35
25	Present	87	6.5 \pm 0.74	2276.69 \pm 276.68	53.38 \pm 3.41
50	Present	90	6.2 \pm 0.73	2098.94 \pm 239.62	54.66 \pm 3.08
26N	Present	83	1.53 \pm 0.43	2334.24 \pm 224.12	64.36 \pm 2.67