Oecologia (2016) 180:1175–1182
DOI 10.1007/s00442-015-3532-y

PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Plant patch structure influences plant fitness via antagonistic and mutualistic interactions but in different directions

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Received: 14 November 2014 / Accepted: 16 December 2015 / Published online: 29 December 2015

Abstract Plant patch structure and environmental context can influence the outcome of antagonistic and mutualistic plant–insect interactions, leading to spatially variable fitness effects for plants. We investigated the effects of herbivory and pollen limitation on plant reproductive performance in 28 patches of the self-compatible perennial herb *Scrophularia nodosa* and assessed how such effects varied with plant patch size, plant density and tree cover. Both antagonistic and mutualistic interactions had strong effects on plant reproductive performance. Leaf feeding from herbivores reduced both fruit production and seed germination, and leaf herbivory increased with plant patch size. Experimentally hand-pollinated flowers produced more seeds than open-pollinated flowers, and pollen limitation was more severe in patches with fewer plants. Our study on *S. nodosa* is one of few which documents that plant patch structure influences the outcome of both antagonistic and mutualistic plant–insect interactions. The results thus provide an example of how variation in plant patch structure and environmental factors can lead to spatially variable fitness effects from mutualistic and antagonistic interactions.

Keywords Habitat context · Patch size · Plant density · Plant–insect interactions · Pollen limitation

Introduction

Variation in the intensity of mutualistic and antagonistic interactions with other organisms is an important source of spatial variation in fitness (Thompson 2005). In plants, the reproductive output is commonly affected by interactions with antagonists and mutualists, such as plant–herbivore and plant–pollinator interactions (Morris et al. 2007). The strength of these interactions often varies spatially as a consequence of heterogeneity of habitats and landscape structures (Diekotter et al. 2007; Dauber et al. 2010), resulting in a spatial variation in plant mean fitness (Thompson 2005). The spatial structure of host plant patches is known to affect both mutualistic and antagonistic interactions, and some of the attributes commonly considered important include the patch size, plant density, presence of other plant species in the neighbourhood and corridors facilitating dispersal (Root 1973; Rosenberg et al. 1997; Kunin 1999). When interacting with the same host plant, herbivores and pollinators may respond to the same or to different aspects of the context, and changes in habitat or landscape characteristics may shift the relative importance of herbivores and pollinators for fitness. Hence, understanding the ways in which herbivores and pollinators respond to variation in spatial structures of plant patches could be important for understanding among-patch variation in plant fitness and selection on plant traits.

The responses of insects to spatial attributes of plant patches and environmental context have previously been studied, both for herbivores and pollinators. For example, some studies suggest that the density or visitation rates are higher in large or dense patches, whereas other studies suggest that density or visitation rates are higher in small and sparse patches (Sih and Baltus 1987; Kunin 1999; Elzinga et al. 2005; Hambäck and Englund 2005; Feldman 2006;

Communicated by Katherine L. Gross.

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Ward et al. 2013). Various explanations for such variation have been proposed, such as differences in the degree of specialization in the relationship between the insect and the plant, behavioural differences in patch searching behaviour between different insects and differences in the relative importance of local and regional processes for local insect density (Aguilar et al. 2006; Englund and Hambäck 2007; Gonzalez-Varo et al. 2009; Andersson and Hambäck 2012). In addition, intensity of antagonistic and mutualistic plant–insect interactions can be altered by environmental variation. For example, variation in canopy cover may create spatial variation in microclimatic conditions or affect host searching, with consequences for plant–insect interactions. Such effects have been shown for insect herbivores, where attack rates on plants may be either higher or lower in shaded habitats as a result of habitat preferences of the insect herbivores (Arvanitis et al. 2007; Kolb et al. 2007). Hence, there is a potential for the reproductive performance of plants in heterogeneous landscapes to be affected by spatial variation in plant patch structures and environmental variation, such as tree cover, via the intensity of antagonistic and mutualistic plant–insect interactions. However, studies linking both these plant–insect interactions to patch structure and environmental variation are rare.

In the study reported here, we examined spatial variation in the effects of herbivores and pollinators on the reproductive performance of the perennial self-compatible figwort *Scrophularia nodosa.* Figwort has a naturally fragmented distribution, and we recorded the reproductive performance of plants in 28 figwort patches varying in size, density and amount of canopy cover. In all patches, we estimated leaf damage caused by the monophagous weevils *Cionus scrophulariae* and *C. tuberculosus* and performed supplemental hand-pollination experiments on a subset of all plants. This setup allowed us to assess the effects of spatial structure and canopy cover on herbivory and pollen limitation. To assess the simultaneous effects of herbivores and pollinators on plant fitness, we estimated fruit and seed production as well as seed quality in terms of germinability.

Materials and methods

Study system

Figwort *Scrophularia nodosa* L. (Scrophulariaceae) is a self-compatible perennial herb which usually grows in discrete patches of varying sizes along roadsides, forest edges, grasslands and clear-cuttings. The plant is a pioneer species where seedlings may be common in disturbed sites and where adult plants may be less apparent in closed plant communities. As a consequence, even though firm data are lacking, seed set and seedling establishment are likely to be important phases for population persistence and growth. The plants emerge in early spring, and the flowering period starts in late June and continues throughout July. The flowers produce nectar rewards and are visited by a wide variety of insects, including syrphids and other flies, bees, bumblebees and wasps (P. Andersson, personal observation). However, the flowers of figwort and other *Scrophularia* species appear to be particularly adapted to wasp pollination (Lagerberg 1938; Devos 1983; Brodmann et al. 2012). Earlier observations on the pollination of figwort revealed that the number of pollen grains attached to the stigma differs substantially depending on the type of flower-visitor, with wasps (*Dolichovespula sylvestris*) attaching an average of 632 pollen grains onto the stigma, bumblebees (two *Bombus* species) an average of 35–90 pollen grains and honey bees (*Apis mellifera*) an average of 55 pollen grains (Devos 1983). Although pollen appears to be most efficiently transferred by wasps, visits from wasps are fairly rare compared to those from bumblebees and flies (P. Andersson, personal observation). In the absence of pollinator visits, flowers are capable of self-pollination (Lagerberg 1938).

The weevils *Cionus scrophulariae* L. and *C. tuberculosus* Scop. (Coleoptera: Curculionidae) are the most abundant herbivores on figwort. In Sweden, *Cionus* weevils are monophagous on figwort, but they have been observed feeding on other *Scrophularia* species elsewhere in Europe (Morris 1991). These weevils occur sympatrically in figwort patches from mid-May and feed and oviposit on the plants throughout summer. Adults and larvae feed externally on the plants, mainly on the leaves but also on flower buds, and may therefore have both direct and indirect effects on plant reproductive output. The grazing of adults and larvae of *Cionus* weevils can cause severe damage, with strong negative effects on fruit production (Hambäck et al. 2011).

Data collection, supplemental hand pollination experiment and seed germination study

The field study was conducted in 2009 on the island Mörkö (51 km^2), which is situated 40 km southwest of Stockholm, Sweden. We defined a patch as a group of plant individuals separated by $\geq$30 m from another group of figwort plant individuals. In June, we located 28 patches of figwort plants (average patch size 21.5 plants, range 1–159 plants).

In all patches, we counted the total number of flowering plants and used this value as a measure of plant patch size. Vegetative plants are quite rare, fairly small and almost never attacked by *Cionus*; therefore, they were not counted. In patches with <20 plants we marked all plant individuals, and in patches with $\geq$20 plants we randomly selected and marked 20 individuals. In total, we marked 270 plants. For all marked plant individuals we measured the distance (in centimetres) to the nearest plant neighbour and used this distance as a measure of plant density. We estimated tree cover for all sites by taking photographs using a digital camera directed perpendicular upwards from the ground within the plant patch. The number of photographs taken per site varied: one to two photographs were taken for small patches (covering a small area), and two to four photographs were taken for larger patches, which often covered a larger area and therefore may vary more in tree cover. To quantify tree cover, we converted the photos to binary images in the software ImageJ (National Institutes of Health, Bethesda, MD) and obtained the area fraction of the photo that was covered by tree branches and canopies. We calculated an average for the photos from each site as a proxy for tree cover. Figworts seldom grow inside forests, and a high tree cover in this study implies that patches were located at forest edges.

To investigate pollen limitation, we conducted a hand-pollination experiment during the first 2 weeks in July on all marked plants within all figwort patches. On each plant individual, we marked one flower on each of two branches by sewing the flowers with threads of different colours. One flower was left unmanipulated as a control flower, and the other was subject to a pollen-supplement treatment. On the stigma of the treated flower, we gently brushed pollen until the stigma was covered by pollen. The stamens used for hand-pollination were collected from plants at the site growing no less than 5 m from the focal plant or from a nearby site. A potential problem with hand-pollination experiments is that plants may allocate resources from flowers adjacent to flowers receiving a surplus of pollen. To minimize these effects, control and hand-pollinated flowers were located on different branches. In order to examine if re-allocation still occurred, we marked one additional control flower located on the same branch in the inflorescence as the hand-pollinated flower. Our reasoning was that re-allocation effects should be stronger for flowers located close to hand-pollinated flowers (on the same branch) than for flowers located on other branches within the inflorescence (Knight et al. 2006). We found no significant difference in the number of seeds between the two categories of control flowers (analysis of variance, $F = 0.11$, $P = 0.74$) and therefore concluded that potential effects of resource allocation should be negligible.

In August, when the fruits had matured, we relocated 233 of the marked individuals. Some plants could not be located or had been cut during the summer. In all individuals, we measured plant height (in centimetres) and estimated the percentage leaf area consumed by *Cionus* weevils by pooling the percentage damage on all leaves on the plant. We also counted the total number of fruits on each individual plant, as well as the number of flowers that did not develop into fruits. The stalks of figwort flowers which do not develop into fruits remain on the plant and can be counted. The sum of the flower and fruit numbers was then used as a measure of total flower number for each plant. We collected all fruits from flowers that had been subject to supplemental hand-pollination or used as open-pollinated controls and transported these to the lab where the number of seeds per fruit was counted. After counting, the seeds from each fruit were stored for 11 months in plastic boxes in a refrigerator (approx. 4 °C).

To assess the quality of seeds from hand-pollinated flowers and the open-pollinated controls, we conducted a seed germination study in which 50 randomly chosen seeds from each fruit were placed on a wet filter paper in a petri dish (diameter 90 mm). When a fruit contained <50 seeds, we used all seeds from that fruit. All germinated seeds were recorded at weekly intervals, up to 4 weeks after sowing. Of the seeds which germinated, most germinated during the first 2 weeks after sowing, with very few seeds germinating thereafter. The seeds were watered two to three times per week by gently spraying the filter paper with water. The laboratory temperature was 23–25 °C throughout the study. We were not able to sow seeds from all fruits at the same date, and sowing dates therefore differed between seed cohorts. We controlled for sowing date in the analyses but found no significant effect of sowing date on the proportion of germinated seeds [generalized linear model (GLM) with binomial error distribution: $t = 0.76$, $P = 0.45$]. A considerable proportion (22 %) of the seeds were overgrown by fungi (unidentified species), but the incidence was not explained by treatment, plant patch size, distance to nearest plant, or tree cover ($P \geq 0.19$; data not shown). For all appearances the fungal attack was randomly distributed across the fruits, and we therefore concluded that the likelihood of confounding effects on the overall patterns of seed germination should be small.

Statistical analysis

We used a series of analyses to investigate the effects of mutualistic and antagonistic interactions in figwort, as well as the effects of interactions on fitness components. First, we investigated the factors influencing the leaf herbivory by *Cionus* weevils. To do so, we used a linear mixed-effects model and analysed the fixed effects of plant patch size (ln-transformed), distance to nearest neighbouring plant (in centimetres, ln-transformed), the proportion of tree cover (arcsine square root-transformed) and plant height (in centimetres, ln-transformed) on the percentage of consumed leaf area (+0.5; ln-transformed). The site identity was included as a random effect.

Second, we investigated the effects on fruit set (no. mature fruits/total no. flowers) using a linear mixed-effects model with binomial error distribution with the command 'glmer' in package lme4 (Bates et al. 2014). In the model, we included as fixed factors plant patch size (ln-transformed), distance to nearest plant (in centimetres, ln-transformed), proportion of tree cover (arcsine square root-transformed), percentage of leaf area consumed (+0.5; ln-transformed) and plant height (in centimetres ln-transformed). We also included the site identity as a random effect. The initial model was found to be overdispersed, and we therefore included an observation-level random intercept (Zuur et al. 2014).

Third, we investigated the effects of mutualistic and antagonistic interactions on the probability of a fruit developing seeds, using a GLM model with binomial error distribution. The underlying rationale for performing this analysis was that a fairly large proportion (18 %) of the fruits collected from the hand-pollination experiment and examined in the laboratory were small and did not contain seeds. We analysed the effects of treatment (hand- vs. open-pollinated), percentage of leaf area consumed (+0.5; ln-transformed), plant patch size (ln-transformed), distance to nearest plant (in centimetres, ln-transformed), proportion tree cover (arcsine square root-transformed), and plant height (in centimetres, ln-transformed). In order to test if the probability of seed development was explained by variation in pollen limitation in relation to patch structures and habitat context, we included the two-way interactions between treatment and plant patch size, distance to nearest plant and tree cover. The site and plant identities (nested within site) were included as random effects.

Fourth, we investigated the effects of mutualistic and antagonistic interactions on seed production (no. seeds per fruit) of figwort using a GLM model. Because the initial analysis using a Poisson error distribution indicated overdispersion, we modelled a negative binomial error distribution using 'glmmadmb' in R (Fournier et al. 2012; Zuur et al. 2014). We analysed the fixed effects of treatment (hand- vs. open-pollinated), plant patch size (ln-transformed), distance to nearest plant (in centimetres, ln-transformed), proportion tree cover (arcsine square root-transformed), percentage of leaf area consumed (+0.5; ln-transformed) and plant height (in centimetres, ln-transformed) on the number of seeds in fruits that contained at least one seed in the hand-pollination experiment. To test whether the effect of the hand-pollination treatment did depend on plant patch size, distance to nearest plant and tree cover, we included the two-way interactions between these factors and treatment in the model, with site and plant identities (nested within site) included as random effects.

Finally, we investigated the effects of mutualistic and antagonistic interactions on seed germination (the proportion of seeds germinating) using a GLM model with binomial error distribution. We analysed the effects of treatment (hand- vs. open-pollinated), plant patch size (ln-transformed), distance to nearest plant (in centimetres, ln-transformed), proportion tree cover (arcsine square root-transformed) and the percentage of leaf area consumed (+0.5; ln-transformed). We also included the fungal attack (as a categorical variable) and plant height (cm, ln-transformed). In order to test whether seed germination was affected by variation in pollen limitation in relation to patch structures and habitat context, we included the two-way interactions between treatment and plant patch size, distance to nearest plant and tree cover in the model. We included the site identity and plant identity (nested within site) as the random effects. The initial model was found to be overdispersed, and we therefore included an observation-level random intercept (Zuur et al. 2014). All statistical analyses were performed using R 3.11.1 ® Core Team 2014).

Results

The leaf area consumed by the *Cionus* weevils increased with increasing plant height and with patch size (Table 1; Fig. 1). Fruit set was negatively correlated with consumed leaf area, and positively correlated with plant height (Fig. 2; Table 2). Plant patch size, tree cover and distance to nearest neighbouring plant were not associated with fruit set.

The probability of developing fruits with seeds tended to be negatively related to the percentage of leaf area consumed and positively related to plant height (Table 2). The proportion of open-pollinated flowers that developed fruits was lower than that of hand-pollinated flowers (78 vs. 86 %, respectively; Table 2). We also found an interactive effect between treatment and plant patch size, indicating that the probability of seed development for open-pollinated and hand-pollinated flowers was differently related to the plant patch size. This interaction occurred because the probability of developing seeds was higher in

Table 1 Results of the linear mixed effects model for leaf area of figwort (*Scrophularia nodosa* L.) plants consumed by the weevils *Cionus scrophulariae* and *C. tuberculosis*

Effect	Estimate ± SE	Δ*df*	Likelihood ratio	*P*
Intercept	−1.82 ± 1.28			
Plant patch size (no. plants)[a]	0.44 ± 0.19	1	5.1	0.02
Distance to nearest plant (cm)[a]	−0.64 ± 0.65	1	1.0	>0.3
Tree cover (%)[b]	0.07 ± 0.04	1	2.6	>0.1
Plant height (cm)[a]	0.56 ± 0.25	1	5.0	0.02

SE standard error; *df* degrees of freedom

[a] ln-transformed

[b] Asin-square-root transformed

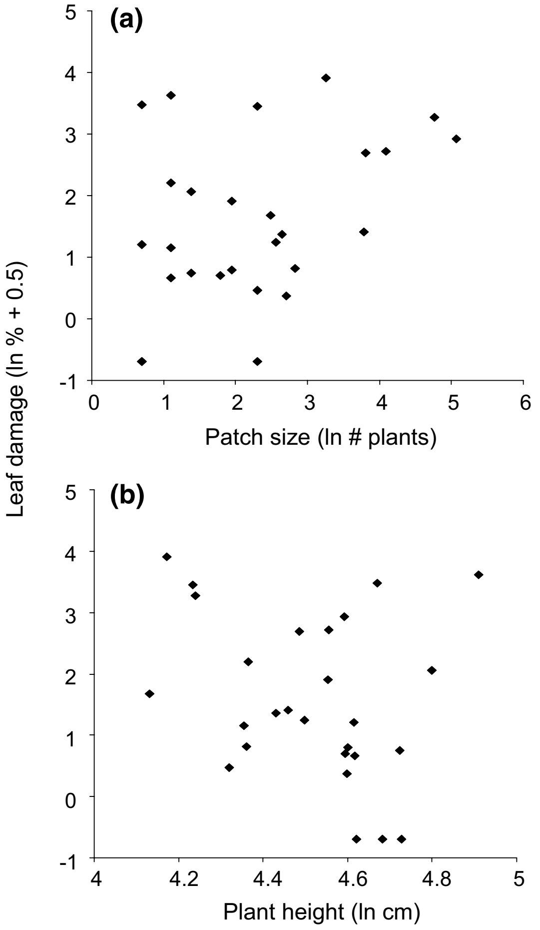

Fig. 1 Damage caused by the weevils *Cionus scrophulariae* and *C. tuberculosus* to leaves of figwort (*Scrophularia nodosa* L.) plants in relation to patch size (number of plants; **a**) and plant height (**b**). Leaf damage was measured as the ln (percent leaf area removed + 0.5) summed over all leaves of the plant

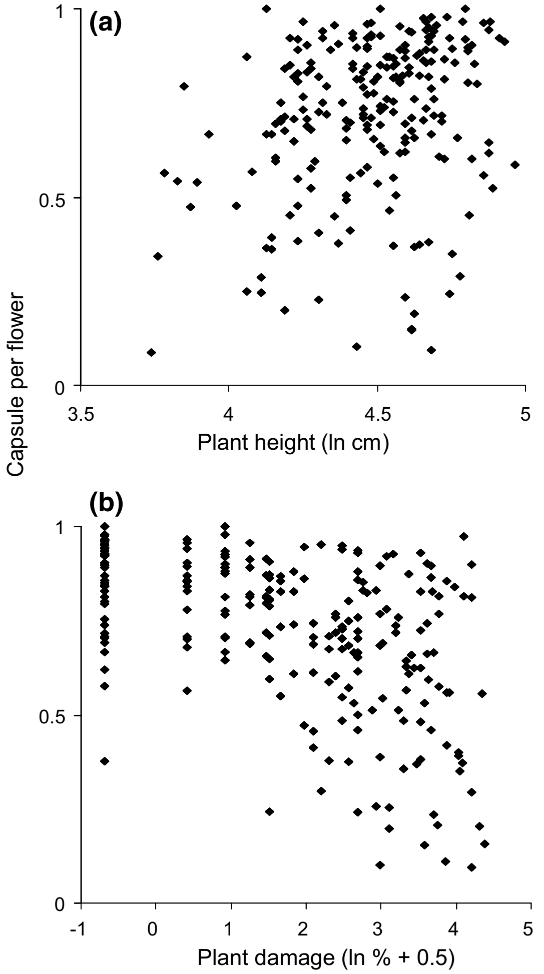

Fig. 2 Proportion of figwort flowers that matured to fruits in relation to plant height (**a**) and leaf damage by *C. scrophulariae* and *C. tuberculosus* (**b**). Leaf damage measured as in Fig. 1

hand-pollinated than in open-pollinated fruits in small but not large patches (Table 2; Fig. 3). Other interactions were not significant and are not presented.

The number of seeds per fruit was negatively related to the leaf area consumed and positively affected by the hand-pollination treatment (Fig. 4; Table 3). Hand-pollinated flowers produced on average more seeds than open-pollinated flowers [mean ± 95 % confidence interval (CI) 131.2 ± 8.3 vs. 111.1 ± 8.0 seeds, respectively]. Pollen limitation of seed number per fruit did not differ with patch size, with the distance to nearest plant or with tree cover, as indicated by non-significant interactions (Table 3). The number of seeds per fruit also increased with plant height. The proportion of seeds that germinated was 0.23 % (95 % 0.21–0.27 %) for hand-pollinated flowers and 0.23 % (75 % CI 0.21–0.27 %) for open-pollinated flowers and was not related to any of the investigated factors (results not shown).

Discussion

The results of this study showed that spatial variation in both leaf herbivory and pollen limitation in the perennial self-compatible herb figwort (*Scrophularia nodosa*) was associated with differences in patch size but not with environmental variation. Both herbivores and pollinators had strong effects on plant seed set, implying that effects of patch properties and plant performance are mediated by a combination of mutualistic and antagonistic interactions.

Patch size influenced the probability of fruits producing seeds through differences in pollen availability. Surprisingly, the probability of seed set was roughly constant (at 70–75 %) for open-pollinated fruits, while it varied with patch size for hand-pollinated fruits. In small patches, almost all hand-pollinated fruits produced seeds, but in large patches the probability of setting seed was not higher for hand-pollinated fruits than for open-pollinated ones. Other

Table 2 Results of the linear mixed effects model for fruit production on *S. nodosa* plants accounting for proportion of flowers developing into fruits and proportion of fruits developing seeds

Effect	Estimate ± SE	Δ*df*	χ2	*P*
Proportion of fruits				
Intercept	−2.54 ± 0.94			
Plant patch size (no. plants)[b]	−0.05 ± 0.10	1	0.26	>0.6
Tree cover (%)[a]	−0.13 ± 0.33	1	0.15	>0.7
Distance to nearest plant (cm)[b]	0.06 ± 0.03	1	2.82	0.09
Consumed leaf area (%, +0.5)[b]	−0.29 ± 0.04	1	57.3	<0.001
Plant height (cm)[b]	0.94 ± 0.19	1	22.8	<0.001
Proportion of seeds				
Intercept (hand-pollinated flowers)	−0.32 ± 3.12			
Treatment (open-pollinated flowers)	−2.74 ± 0.94			
Plant patch size[b]	−0.65 ± 0.25			
Tree cover (%)[a]	0.38 ± 0.56	1	0.5	>0.4
Distance to nearest plant (cm)[b]	0.03 ± 0.13	1	0.05	>0.8
Consumed leaf area (%, +0.5)[b]	−0.23 ± 0.13	1	3.3	0.07
Plant height (cm)[b]	1.15 ± 0.67	1	3.0	0.08
Treatment × plant patch size[b]	0.60 ± 0.26	1	5.7	0.02

For seeds, a binomial error distribution model was used in which the intercept corresponds to the central tendency for hand-pollinated fruits. The estimated probability for open-pollinated fruits can be determined by adding this parameter estimate to the intercept. Similarly, the slope for plant patch size is for hand-pollinated fruits; the slope for open-pollinated fruits can be determined by adding the parameter estimate for the treatment-by-plant patch size interaction to this value

[a] Asin-square-root transformed

[b] ln-transformed

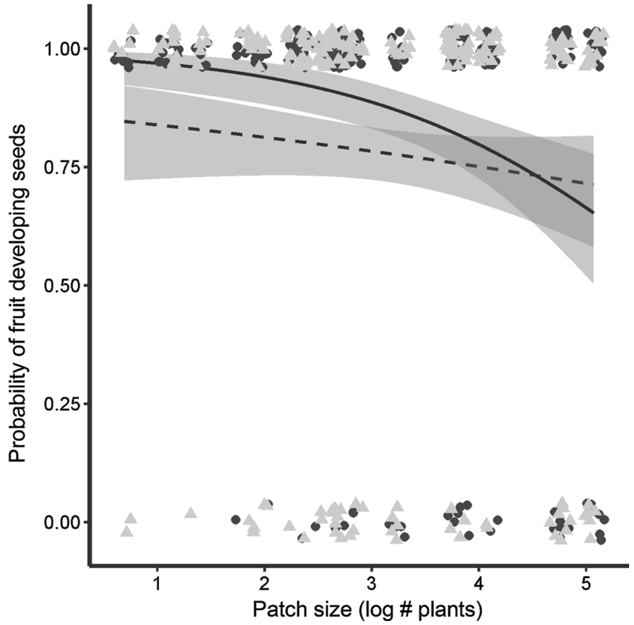

Fig. 3 The probability of developing seeds in fruits for hand-pollinated (*solid line*, *filled circles*) and open-pollinated (*dotted line*, *grey triangles*) fruits. Values are slightly jittered vertically and horizontally to prevent overplotting. The linear regression lines and their 95 % confidence interval (as determined in stat_smooth, package 'ggplot2' within R software) are provided for illustration (*shaded area*)

components of fitness were not affected by interactions between hand-pollination and environmental factors. These patterns of seed set suggest two things: (1) the probability of seed set is pollen limited, with the magnitude of this limitation decreasing with increasing patch size; (2) some unmeasured factor affects the level of seed set that is attainable, with pollen supplementation lower in larger patches. For the control plants, such negative effects appeared to exactly balance the positive effects of patch size on pollen availability. The mechanism underlying such a patch size-dependent limiting factor cannot be determined without further experiments, but it is possible that variation in the competitive environment for the plant or variation in some other interacting species, such as soil micro- or macrobiota, play a role. Previous studies on variation in hand-pollination have focussed on the effect of patch size on pollinator behaviour and pollen transfer. For example, the effect of hand-pollination may vary with patch size due to shifts in the relative proportions of intra- and interspecific pollen transfer with plant density (Jakobsson et al. 2009). The hypothesis is that while flowers on single isolated plant individuals may receive mostly inter-specific pollen during pollinator visits, plants of the same species growing aggregated should receive a higher proportion of intra-specific pollen. Alternatively, pollen limitation may arise because the spatial configuration of plants mediates variation in pollinator movement. An increased flower-visitation for aggregated plants, such as in dense (and large) patches, has often been attributed to an attraction of pollinators to high-rewarding flower resources (Sih and Baltus 1987; Ågren 1996; Lazaro and Totland 2010). Our results suggest that pollen limitation may be related to patch size also through other factors, making experimental manipulations necessary to unravel the underlying mechanism. (Stout et al. 1998; Goulson 2000; Waddington and Holden 1979; Dukas 2008; Lihoreau et al. 2011).

Leaf herbivory from the two herbivores *C. scrophulariae* and *C. tuberculosus* also varied with patch size, and in this case leaf damage was highest in large plant patches. Similar to the effects on pollinators, we found no effect of environmental variation on the attack rates. The fact that weevil herbivory was associated with plant patch size—but not with plant neighbour distance—suggests that the spatial

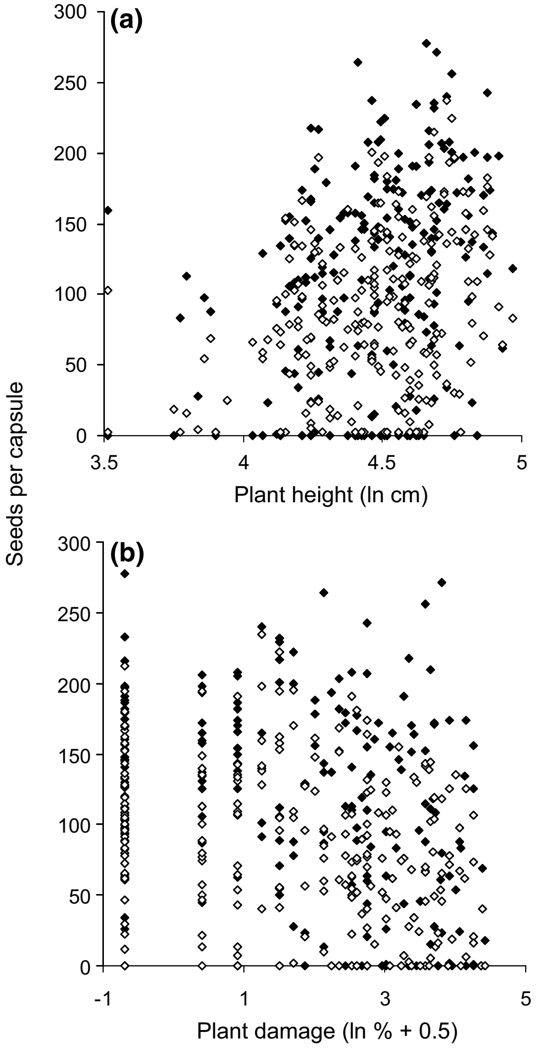

Fig. 4 Number of seeds per fruit (excluding fruits with no seeds) in individual figwort plants in relation to plant height (**a**) and leaf area consumed by *C. scrophulariae* and *C. tuberculosus* (**b**). Data for hand-pollinated (*filled diamonds*) and open-pollinated (*open diamonds*) flowers are indicated. Leaf damage measured as in Fig. 1

Table 3 Results of the generalized linear mixed model (negative binomial error distribution) for the number of seeds per fruit of *S. nodosa*

Effect	Estimate ± SE	Δ*df*	Deviance	*P*
Intercept (hand-pollinated)[a]	2.48 ± 0.62			
Treatment (open-pollinated)	−0.15 ± 0.06	1	6.82	<0.01
Plant patch size	−0.01 ± 0.04	1	0.06	>0.8
Tree cover (%)[b]	−0.09 ± 0.13	1	0.58	>0.4
Distance to nearest plant (cm)[c]	−0.02 ± 0.02	1	0.86	>0.3
Consumed leaf area (%, +0.5)[c]	−0.06 ± 0.02	1	6.64	<0.01
Plant height (cm)[c]	0.58 ± 0.13	1	18.9	<0.001

[a] The intercept corresponds to the central tendency for hand-pollinated fruits; the estimated probability for open-pollinated fruits can be determined by adding this parameter estimate to the intercept

[b] Asin-square-root transformed

[c] ln-transformed

configuration of plants within patches was relatively less important for herbivore attack on the plants. We know from recent experiments that both emigration and immigration rates, per plant, for adult weevils are negatively related to patch size and that field densities of adults are also often negatively related to the figwort patch size, at least in the early season (Andersson and Hambäck 2011, 2012). While this may seem to contradict the pattern found in this study, where attack rates increased with patch size, the relative importance of local reproduction and movement processes for weevil densities may also differ between large and small figwort patches (Andersson and Hambäck 2012). A positive relationship between leaf herbivory and plant patch size is likely the result of weevil reproduction being relatively more important than movement processes for their population size in large patches compared to in small patches, resulting in a higher number of *Cionus* larvae and a higher attack on plants in larger figwort patches (Andersson and Hambäck 2012).

The results of our study suggest that similar attributes of plant patches can be important for antagonistic and mutualistic plant–insect interactions and that the effects of these interactions can have opposite directions, with consequences for among-patch variation in plant reproductive performance. In our study system, both pollination limitation and the level of herbivore attack were associated only with plant patch size. Herbivore attacks translated into negative effects on several reproductive variables, such as the proportion of flowers developing into fruits, the probability of the fruits developing seeds, and the proportion of seeds germinating. In contrast to conclusions from studies addressing effects of fragmentation on plant fitness (reviewed and analysed in Aguilar et al. 2006), a small patch size did not necessarily affect figwort plants negatively as plants in small patches escaped attacks from herbivores more often. On the other hand, pollen limitation had more negative effects on seed set in smaller patches. In an ephemeral plant such as figwort, effects on seed set may have direct effects on demography and trait selection. The results of our study suggest that because antagonistic and mutualistic plant–insect interactions both depend on environmental context but in different ways, interactions form important pathways through which habitat heterogeneity translates into spatially variable selection on plant traits and spatially variable plant population dynamics.

Acknowledgments We thank Cecilia Lind Lindkvist for field assistance and Johanne Ericson, Caroline Essenberg and Tove Porseryd for lab assistance. We also thank Steven D. Johnson for helpful comments on earlier versions of the manuscript. The experiments comply with the current laws of the country Sweden in which the experiments were performed.

Author contribution statement PA, JE and PAH conceived and designed the experiments. PA performed experiments and collected data. PA and PAH analysed the data. PA, JE, and PAH wrote the manuscript.

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