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Neighbourhood of host plants influences oviposition decisions of a stem-boring weevil

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Spatial distribution

Summary

The spatial arrangement of suitable host plants in the field may significantly constrain insects to find optimal hosts. Plant neighbours around a focal host plant can either lead to lower (associational resistance) or higher (associational susceptibility) herbivore loads. We tested whether the spatial arrangement of hosts of different suitability for the larval development of the shoot-base boring weevil *Apion onopordi* affects oviposition decisions in the field. Host plants in our study were healthy creeping thistles (*Cirsium arvense*; suboptimal hosts) and thistles infected by a rust pathogen (*Puccinia punctiformis*; optimal hosts). For analysis, we used nearest neighbour methods that disentangle the spatial distribution of organisms that are dependent on the position of other species (e.g. phytophagous insects and their host plants). Although theory predicts that the small-scale spatial infestation pattern can have major consequences for the population dynamics in insect–plant systems, field studies quantifying spatial pattern of phytophagous insects are rare.

The spatial arrangement of host plants clearly influenced oviposition pattern in *A. onopordi*. In contrast to previous studies, we demonstrated that not the rust infection itself determined if a plant was infested by weevils, but rather the density of rusted shoots within a certain neighbourhood. We found strong indications for associational susceptibility of healthy thistle shoots to weevil oviposition when growing in the neighbourhood of rusted thistles. Weevil-infested plants were spatially aggregated, indicating that *A. onopordi* is limited in its dispersal ability within patches. Other stem-boring insects on creeping thistle were affected in their oviposition decisions by other factors than *A. onopordi*. Thus, it may be difficult to find general rules for oviposition choice in phytophagous insects.

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Our study showed that the spatial arrangement of host plants in the field critically determines oviposition choice and should thus be included as constraint in theories of optimal host selection.

Zusammenfassung

Die räumliche Anordnung von Wirtspflanzen im Feld kann für Insekten das Auffinden optimaler Wirte stark einschränken. Die benachbarten Pflanzen einer Zielpflanze können so entweder zu einem niedrigeren („assoziierte Resistenz") oder höheren („assoziierte Empfänglichkeit") Herbivorenbefall führen. Wir haben in Feldexperimenten getestet, ob die räumliche Anordnung von Wirtspflanzen, die sich in ihrer Eignung zur Larvenentwicklung des Stängel minierenden Rüsselkäfers *Apion onopordi* unterscheiden, die Eiablageentscheidungen der Käferweibchen beeinflussen. Wir verwendeten in unserer Arbeit gesunde Ackerkratzdisteln (*Cirsium arvense*; suboptimale Wirte) und Disteln, die mit einem Rostpilz befallen waren (*Puccinia punctiformis*; optimale Wirte). Zur Analyse verwendeten wir Nearest-Neighbour-Verfahren, die räumliche Verteilungen von Organismen, die von der Position anderer Organismen abhängen (z.B. phytophage Insekten und ihre Wirtspflanzen), getrennt berücksichtigen. Obwohl theoretische Vorhersagen die Wichtigkeit kleinräumiger Verteilungsmuster für die Populationsdynamik von Insekten-Pflanzen-Systemen betonen, gibt es nur wenige Feldstudien, die die räumliche Verteilung von phytophagen Insekten quantifiziert haben.

Die räumliche Verteilung der Wirtspflanzen zeigte einen deutlichen Einfluss auf das Eiablagemuster bei *A. onopordi*. Im Gegensatz zu früheren Arbeiten konnten wir zeigen, dass nicht der Rostbefall selbst bestimmt, ob eine Pflanze vom Käfer zur Eiablage ausgewählt wird, sondern vielmehr die Dichte Rost befallener Sprosse in der Nachbarschaft. Es gab starke Hinweise für das Auftreten von assoziierter Empfänglichkeit von gesunden Distelnsprossen gegenüber Rüsselkäferbefall, wenn sie in der Nachbarschaft von rostinfizierten Disteln wuchsen. Käfer befallene Disteln traten räumlich aggregiert auf, was darauf hinweist, dass *A. onopordi* sich nur begrenzt innerhalb eines Standorts zu verbreiten vermag. Andere Stängel minierende Insekten an der Ackerkratzdistel wurden in ihren Eiablageentscheidungen von anderen Faktoren gelenkt als *A. onopordi*. Es wird daher schwierig sein, generelle Regeln für Eiablageentscheidungen für phytophage Insekten zu finden.

Unsere Arbeit zeigt, dass die räumliche Verteilung von Wirtspflanzen im Feld einen starken Einfluss auf Eiablageentscheidungen haben kann und daher in Theorien zur optimalen Wirtswahl eingebunden sein sollte.

Introduction

Oviposition, i.e. the decision by the mother where her offspring will develop, is a crucial step in the life cycle of phytophagous insects (e.g. Meiners & Obermaier, 2004; Price, 2005). In many phytophagous insect species and particularly in species that develop inside their host plants, the larvae are restricted in their mobility and cannot change the host. In these species, the ovipositing female selects the food source for their offspring (Mayhew, 1997). The preference–performance hypothesis (PPH) (Jaenike, 1978) has been central to the approach for studying host selection by phytophagous insects. The PPH predicts that oviposition preference should correlate with host suitability for offspring development because females are assumed to maximize their fitness by ovipositing on high-quality hosts. However, evidence for females to behave according to the PPH is mixed; some studies found strong positive correlations between host preference and larval performance, but many found only poor correlations (Mayhew, 1997). A major factor responsible for the failure of insects to find optimal hosts may be the spatial arrangement of suitable host plants in the field (Kareiva, 1982).

The susceptibility of a plant to be attacked by herbivores can depend on the surrounding vegetation, i.e. the identity and proximity of neighbouring plants (Atsatt & O'Dowd, 1976; Vehviläinen, Koricheva, Ruohomäki, Johansson, & Valkonen, 2005; White & Whitham, 2000). Plant neighbours can either lead to lower (associational resistance) or higher (associational susceptibility) herbivore loads on a focal plant. Thus, depending on plant neighbours, phytophagous insects may fail to find a preferred host among less preferred vegetation (Andow, 1991). On the other hand, a preferred host plant may act as a source of herbivores for the surrounding non-favoured hosts (White & Whitham, 2000). Reasons for these patterns are likely restricted search and dispersal capabilities of the herbivores (Bernays, 2001; Raffa, Havill, & Nordheim, 2002). Constraints on host choice imposed by the spatial arrangement of host plants in the field may therefore lead to a distribution of offspring among host plants that is suboptimal for larval development, and may thus at least partly explain the lack of general evidence for the PPH.

We tested whether the spatial arrangement of hosts affects oviposition in the shoot-base boring weevil *Apion onopordi* Kirby (Coleoptera, Apionidae) and one of its host plants, the creeping thistle *Cirsium arvense* L. Scop. (Asteraceae). We knew from previous studies that when given the choice between a healthy thistle and a thistle systemically infected by the biotrophic rust fungus *Puccinia punctiformis* (Str.) Röhl., the weevil prefers to oviposit into rust-infected plants (Bacher & Friedli, 2002; Friedli & Bacher, 2001a). Moreover, weevils developing in rusted thistles grow larger, produce more offspring and have a higher survival during winter diapause (Bacher, Friedli, & Schär, 2002). However, in the field, even when the preferred rusted plants are abundant, a significant proportion of eggs are laid in suboptimal, healthy hosts (Bacher & Friedli, 2002). The distribution of weevil eggs over healthy and rust-infected thistles has important consequences for the population dynamics of thistles (Bacher & Friedli, 2002), because the weevil transmits the rust when ovipositing in healthy thistles (Friedli & Bacher, 2001a, b), and systemically rust-infected thistles die in the same year before flowering. A limited dispersal of weevils, indicated for example by an aggregated distribution of weevils among host plants, may lead to the observed partial preference for the optimal host plant.

Aggregated distributions of organisms are widespread in nature. However, spatial distributions are inherently scale-dependent, and traditional methods to study the spatial distribution of a species (e.g. by quadrate counts; Leiss & Klinkhamer, 2005) are limited to one scale only, namely the size of the quadrate. Moreover, since herbivores depend on their host plant, the study of the distribution pattern of herbivores has to disentangle the distribution of the plants from the distribution of the herbivores on the plants. We used nearest neighbour methods developed by Casas (1990) to study clumping in our system. The advantage of these methods is that the natural distribution of an organism in the field can be investigated at different spatial scales and that the distribution of organisms that are dependent on other species (e.g. phytophagous insects and their host plants) can be disentangled from each other. While nearest neighbour techniques have often been used in the study of the spatial distribution of plants, they have been rarely applied to animals living on plants (but see Casas, 1990). Thus, the patterns of the spatial distribution of plant-dwelling animals and the consequences for population dynamics are poorly understood.

In this paper, we studied whether the local environment of a host plant affects its choice for oviposition by the weevil *A. onopordi*. In particular, we investigated the hypothesis that a suboptimal distribution of eggs should be due to associational susceptibility of healthy thistles growing in the vicinity of rusted thistles. If this was the case, then healthy plants in the neighbourhood of rust shoots should have a higher probability of being selected for oviposition. Because host plant choice is a multi-factorial process, other factors (e.g. host plant characteristics, occurrence of other phytophagous insects, environmental factors) were also considered. Finally, we investigated whether the same factors that are important for host choice of one stem-boring insect species are also important for other stem-boring insects of creeping thistle.

Material and methods

Field collection

Six 3 × 3 m plots and one 6 × 6 m plot (Figs. 1 and 2) were installed during summer 2003 in the south west of Sierre (Canton of Valais, Switzerland) on a triangle-shaped xerotherm site of about 120 m length and 50 m width at its widest point. The spatial positions of the seven plots on the site were first randomly drawn and then slightly adjusted in order to maximize the number of rusted thistles inside plots.

In each plot, all creeping thistle shoots were assigned *x*- and *y*-coordinates to the nearest cm. The basal stem diameter and height of each shoot was recorded. In addition, we recorded whether a shoot was systemically infected by the rust fungus *P. punctiformis*. All shoots including parts of the root system were collected and dissected for eggs and mining early instar larvae of *A. onopordi* and other stem-boring insects under a binocular. By

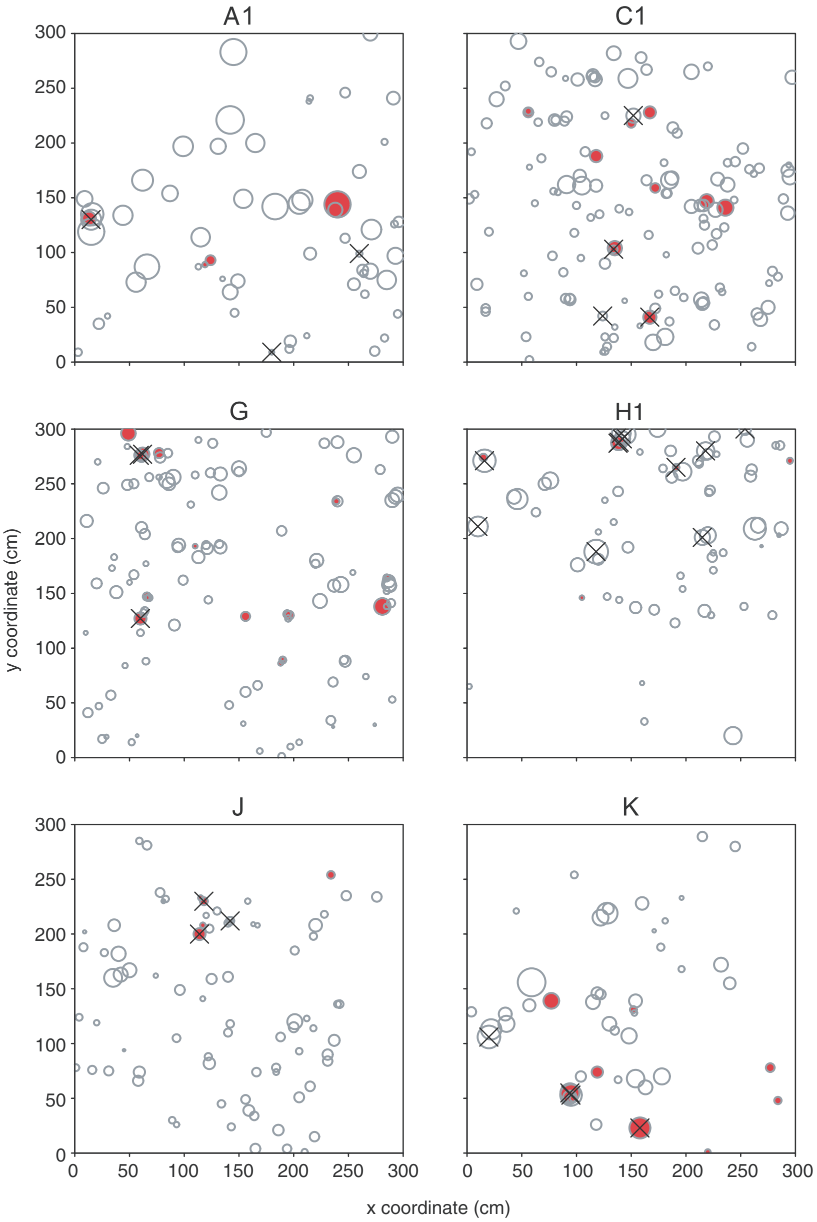

Figure 1. Location of thistles and weevils on the 3 × 3 m sample plots. Open circles represent healthy and filled circles rusted thistles. Circle diameter is proportional to the thistle stem diameter. Black crosses indicate plants infested by weevils.

adjusting our sampling and data collection to early developmental instars (eggs and young larvae), we assume that plant characteristics and environment did not change much since oviposition and that the parameters recorded thus represent true estimates of oviposition choice factors.

Spatial pattern

For each individual plot, we analysed the spatial distribution of thistles infested by *A. onopordi* (regardless of how many weevils were found inside the thistles) using nearest neighbour methods. We first focussed on the distance between an infested thistle and the nearest infested thistle in order to test for deviations from a random distribution (i.e. aggregation or regularity) of thistles selected by weevils for oviposition. Then we considered the distance between infested thistles and their nearest rusted thistle in order to investigate attraction of ovipositing weevils by rusted thistles. In each case, we computed the empirical distribution function for the distance to the nearest neighbour of all infested thistles in a plot. These functions give for different distances the proportion of infested thistles with a nearest infested/rusted neighbour closer than these distances. For each

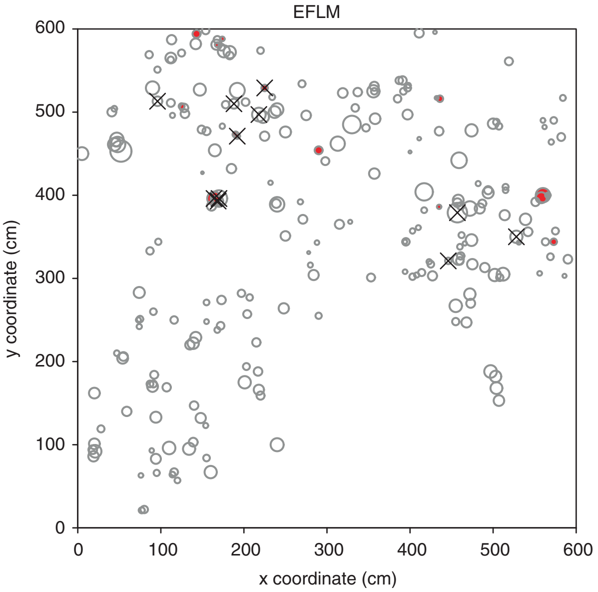

Figure 2. Location of thistles and weevils on the 6 × 6 m sample plot. Open circles represent healthy and filled circles rusted thistles. Circle diameter is proportional to the thistle stem diameter. Black crosses indicate plants infested by weevils.

plot, the empirical distribution functions were compared with 90% confidence intervals built under the hypothesis of random selection of thistles by the weevil. Given that we had k infested plants over n in the plot, the confidence interval was built by 10,000 times randomly selecting k plants from the n available and calculating the respective distribution function. For details on the method see Casas (1990). The results are combined in one graph for each plot showing the observed empirical distribution F^* and the confidence interval built under the null hypothesis H_0 = "plants for oviposition are randomly selected". If, at a particular distance, F^* lies inside the confidence interval, then the empirical distribution does not differ significantly from a random distribution at that distance, otherwise there is either aggregation (F^* above the confidence limit) or regularity (F^* below the confidence limit). For some plots, the number of infested thistles k was very low (e.g. $k = 3$ for plot A1). Although the empirical distributions in such cases were not very smooth and the confidence intervals quite wide, the statistical test remained valid, but was not very powerful in detecting deviations from randomness.

Statistical analysis

We used multiple logistic regression in order to explain the occurrence of the weevil (present or absent) on thistles. We refrained from analysing the factors determining the number of eggs laid in a shoot, because we cannot decide whether all eggs in one shoot stem from a single female (that chose the shoot only once) or from different females (choosing independently). The analyses were performed on thistles from all plots pooled. The response variable was the binary variable infested/not-infested. Explanatory variables related either to the plot, the plant itself (basal shoot diameter, rust status, presence of other insects) or to its neighbourhood (density of thistles within the plot, density of healthy and/or rusted thistles at different radii around the focal thistle). We used a stepwise approach based on the Akaike Information Criterion (AIC) to select the significant variables (procedures glm and stepAIC in the statistical software R; www.r-project.org). Estimation of densities of all, healthy or rusted thistle shoots around a focal shoot required the definition of a relevant neighbourhood radius. In order to select such a radius, we performed logistic regression between the occurrence of the weevil in a thistle shoot and the thistle densities estimated for different neighbourhood radii around the focal shoot ranging from 5 to 100 cm. For a first analysis, we considered only 181 thistle shoots situated in the centre of the plots, at least 100 cm away from the plot borders. Relative deviance of the models was used to measure goodness of fit: the model with the lowest deviance was considered to fit best (Dobson, 2002). In this analysis, distances above 50 cm proved non-significant (Fig. 3, left column). Analyses were then repeated considering only distances from 5 to 50 cm and working on all thistles situated at least 50 cm away from plot borders (447 thistles; Fig. 3, right column). For each variable (density of all, of healthy and of rusted thistles), we then selected the neighbourhood radius that minimized the relative deviance. All the analyses were performed with the R software (http://www.r-project.org).

Results

Global pathogen infection and insect infestation rates

Density of thistles varied between plots from 5 to 15 m^{-2} (Table 1). The percentage of thistles infected by the rust was below 23%. The percentage of thistles infested by *A. onopordi* varied between plots from 3% to 16%. Apart from *A. onopordi*, larvae of two other stem-boring species

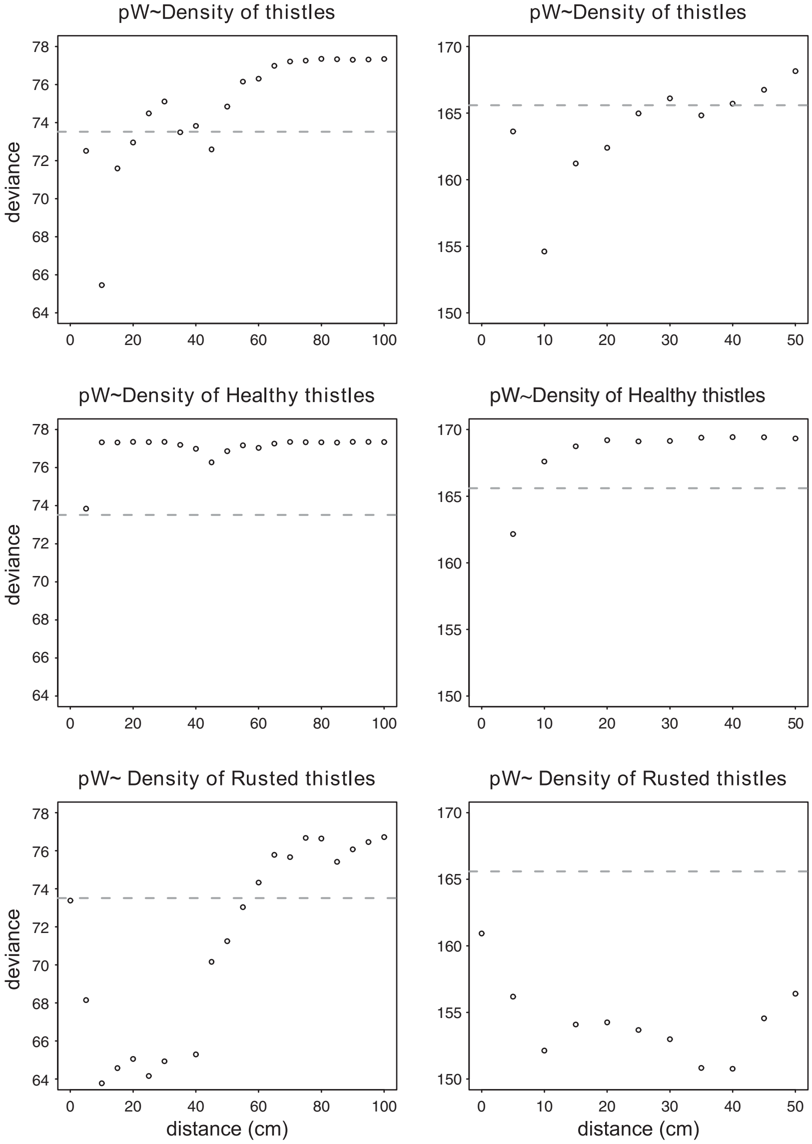

Figure 3. Selection of relevant neighbourhood radii for local density estimation. Deviance of logistic regressions between presence of weevils and density of thistles estimated for different neighbourhood radii (dots). Deviance below the dashed line indicates a significant relationship. The plots in the left column were estimated excluding thistles that were situated less than 1 m from the plot borders. Densities of thistles can thus be estimated without bias for the thistles in the core zone. The three plots in the right column show the same analyses with a 50 cm buffer zone. Neighbourhood radii were varied from 5 to 100 cm at steps of 5 cm. For the density of rusted thistles (lower row), a radius of 0 cm was also considered: the density at 0 cm indicates that the rust was on the thistle. pW: presence of weevils.

were considered, as they occurred quite often in the dissected plants: *Lixus angustatus* (Fabricius 1775) (Coleoptera, Curculionidae) and an unidentified beetle of the family Mordellidae (*Mordellia* sp.). Other species were found only sporadically feeding inside thistles and were not considered further in the analyses. Overall, rusted thistle shoots ($N = 79$) had a higher probability of being infested by *A. onopordi* (17.7%) than healthy shoots ($N = 754$; 3.3%; χ^2 test, $p < 0.001$).

Nearest neighbour analyses

Weevil-infested thistles proved aggregated in five of seven plots (Fig. 4). Aggregation was observed at different distances ranging from 5 cm (plots G, H1, K) to 40 cm and more (plots J and EFLM). Plots A1 and C1 showed no particular patterns, the observed distributions lying within the confidence interval over all distances. In all plots, we found an association between

Table 1. Characteristics of the sampling plots

	Area (m^2)	Thistles	Rusted thistles		Thistles infested by weevils		Shoot diameter (mean $\pm$ SD)
		$n\,m^{-2}$	$n\,m^{-2}$	%	$n\,m^{-2}$	%	
Plot A1	9	6.6	0.56	8.5	0.33	5.1	7.8 ± 3.8
Plot C1	9	14.9	1.11	7.5	0.44	3.0	5.7 ± 1.8
Plot G	9	12.6	2.11	1.7	0.33	2.7	5.2 ± 1.9
Plot H1	9	7.8	0.56	7.1	1.22	15.7	6.2 ± 2.8
Plot J	9	8.8	0.56	6.3	0.33	3.8	4.7 ± 1.6
Plot K	9	5.3	1.22	22.9	0.44	8.3	6.9 ± 3.1
Plot EFLM	36	6.7	1.53	7.9	0.31	4.6	6.4 ± 2.4

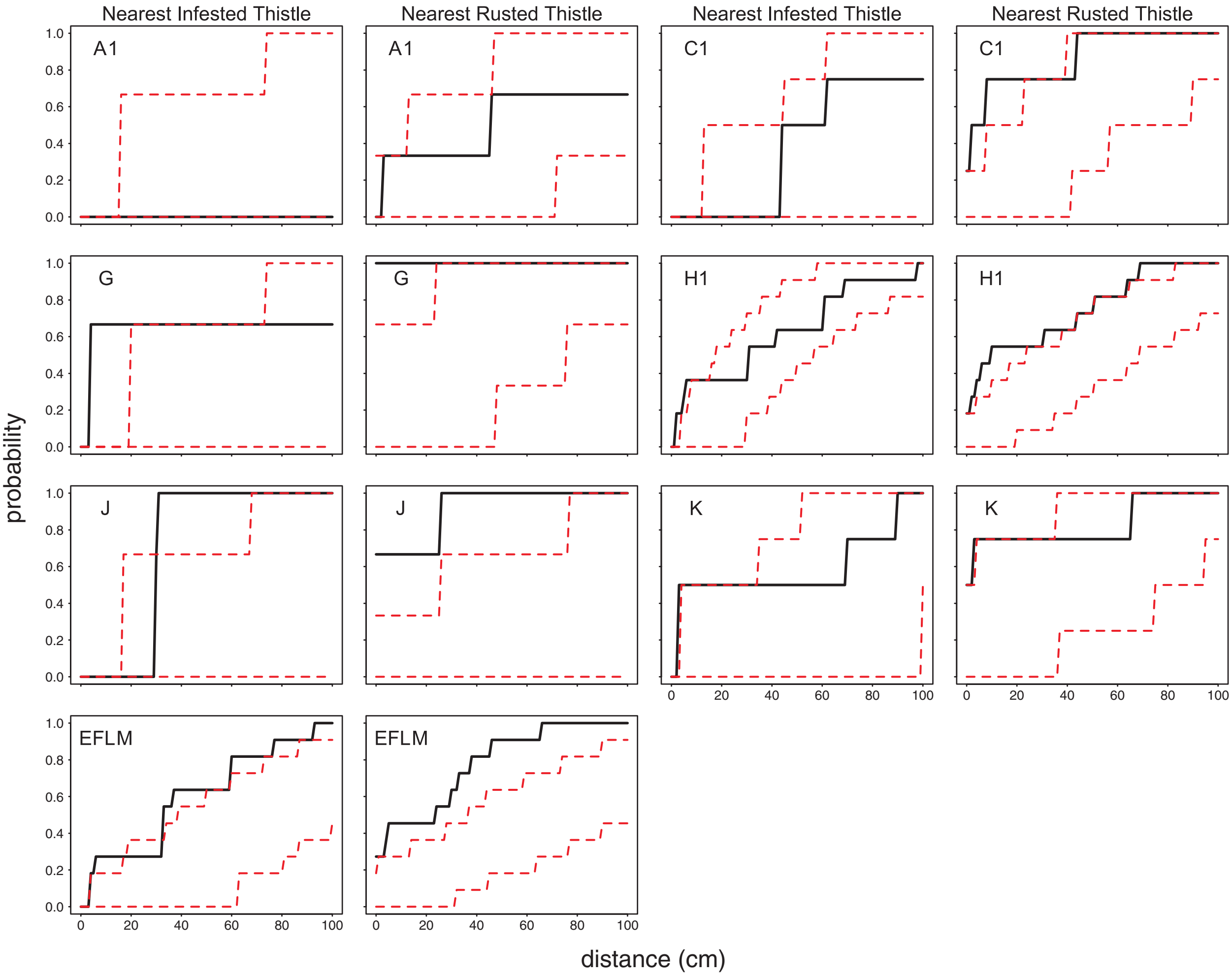

Figure 4. Observed and expected distributions from the nearest neighbour analyses. For each plot, the left-side graph presents the observed and expected distributions of the distance from infested thistles to the nearest infested thistle. The right-side graph presents the distributions of the distance from infested thistles to the nearest rusted thistle. Solid lines represent observed distributions calculated from the sample plot and dashed lines represent confidence intervals of the expected distribution under the hypothesis of random selection of thistles by weevils (90% confidence interval from 10,000 simulations).

weevil-infested plants and rusted plants at short distances (less than 20 cm) and in some cases even at larger distances (up to 100 cm for plot EFLM; Fig. 4).

Regression analyses

The search procedure for neighbourhood radii revealed distances with highest explanatory capability of 10 cm for the density of all thistles, of 5 cm for the density of healthy thistles and of 40 cm for the density of rusted thistles (Fig. 3, right column). The stepwise regression including plot identity, stem diameter, presence of the rust and presence of the two others species (*L. angustatus* and *Mordellia* sp.) as additional explanatory variables led to a final model with three explanatory variables: stem diameter of thistles, density of rusted thistles in a radius of 40 cm and presence of *Mordellia* sp. all correlated positively with the presence of *A. onopordi*. The same analyses were performed for the other two stem-boring insect species (Table 2). The occurrence of *L. angustatus* was positively correlated with stem diameter and negatively correlated with the presence of *Mordellia* sp. The occurrence of *Mordellia* sp. was negatively correlated with the presence of *L. angustatus*, and also dependent on the plot.

Discussion

The spatial arrangement of host plants clearly influenced oviposition pattern in *A. onopordi*. In accordance with earlier studies (Bacher & Friedli, 2002; Friedli & Bacher, 2001a), rust infection of thistles played a major role for oviposition decisions in *A. onopordi*, together with the plant size and the presence of other stem-boring insects. However, nearest neighbourhood analysis and logistic regression revealed that it was not the rusted plant itself that determined whether a plant was infested by weevils, but rather the density of rusted shoots within a certain neighbourhood. In this way, not only rust-infected thistles but also healthy host plants growing in the neighbourhood of rusted thistles were infested by *A. onopordi*, although healthy thistles provide only suboptimal food for *A. onopordi* larvae (Bacher et al., 2002). Thus, we found strong indications for associational susceptibility of healthy thistle shoots to weevil oviposition. This may explain the increasing proportion of weevil-infested healthy thistles with increasing rust densities observed in the field (Bacher & Friedli, 2002).

The small-scale spatial aggregation of weevil-infested plants provides a mechanistic explanation for the suboptimal distribution of offspring among hosts of different quality. Moreover, for a female to behave optimally during host choice, she needs accurate information on her environment. Because the perception and memory capabilities of phytophagous insects are limited (Bernays, 2001; Raffa et al., 2002), females most likely do not have an accurate overall image of the occurrence and location of optimal host plants in the field. Rather, they are likely to infer the probability of encountering optimal hosts for oviposition from their previous host plant encounters. In an environment, in which optimal hosts are rare, the probability of a female to accept a suboptimal host for oviposition will increase with the time since the last encounter with an optimal host and with each encounter of a

Table 2. Explanatory variables for the presence of insects on thistles

Dependent variable	Explanatory variables selected		
	Shoot diameter	Density of rusted thistles in 40 cm radius	Presence of *Mordellia*
Presence of *Apion* ($k = 21$, $N = 447$)	+, $p < 0.0001$	+, $p < 0.0001$	+, $p = 0.0276$
	Shoot diameter	Presence of *Mordellia*	
Presence of *Lixus* ($k = 69$, $N = 447$)	+, $p < 0.0001$	$-$, $p = 0.0005$	
	Presence of *Lixus*	Plot	
Presence of *Mordellia* ($k = 134$, $N = 447$)	$-$, $p < 0.0001$	$p = 0.0039$	

N = total number of thistles situated less than 50 cm from the plots borders; k = number of thistles infested by the insect; + and $-$ signs indicate, respectively, positive or negative correlations.

suboptimal host (hierarchical threshold model for host plant choice; Courtney, Chen, & Gardner, 1989). The spatial arrangement of host plants in the field can thus critically affect oviposition decisions of phytophagous insects by affecting the encounter probability of host plants of different suitability. The mechanism involved is likely to be a limited search and memory capability of the weevils, resulting in an aggregated distribution around rust plants.

The imperfect host plant choice of *A. onopordi* has important consequences for the population dynamics of the herbivore–pathogen–plant system (Bacher & Friedli, 2002), because the propagation of the rust fungus largely depends on vector-mediated transport to healthy thistle shoots (Friedli & Bacher, 2001a, b). If *A. onopordi* females were able to locate rusted hosts, which are optimal for larval development, and oviposit exclusively on them, the rust population would die out locally, and the thistle population would be released from one of its enemies. However, the attraction of weevils to the vicinity of rusted thistles will tend to concentrate rust infections in places where they are already present, creating patches of rusted thistles rather than randomly distributed rusted thistles, as would be expected if the weevils chose thistles at random for oviposition. Spatial aggregation of pathogen infections in turn tends to mitigate the negative effects on thistle host population densities by creating spatial refuges (Crawley, 1991). Thus, the effectiveness of *P. punctiformis* as a biocontrol agent against creeping thistle under natural conditions will likely be less than expected from a model where the weevil chooses plants at random (Bacher & Friedli, 2002). We expect that similar processes are at work and should be considered also in other insect-mediated plant pathogen systems (Harris & Maramorosch, 1980).

Apart from host plant quality and neighbourhood, the size of the host and the presence of other stem borers were important determinants for infestation probability in *A. onopordi*. However, results of our study suggest that there are no general rules for oviposition choice in phytophagous insects. The other stem-boring insects on creeping thistle were affected by different factors than *A. onopordi*. For example, rust infection was of no importance to the other species. It has been shown in previous work that the reaction norms of thistle-feeding insects towards rust-infected shoots are very heterogeneous (Kluth, Kruess, & Tscharntke, 2001). Moreover, while all species were generally affected by the presence of other stem borers, each species was sensitive to the occurrence of a different species. Thus, the apparent lack of common rules even among members of the same feeding guild on a shared host plant calls for studies of oviposition choice in phytophagous insects of each species individually.

In summary, our study showed that the spatial arrangement of host plants in the field critically determines oviposition choice and should thus be included in theories of optimal host plant selection. Constraints of host choice in the field due to spatial heterogeneity of hosts and limited dispersal ability of insects may be responsible for the currently observed imbalance of optimal oviposition theory and field data.

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