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Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape

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Summary

Habitat fragmentation can disrupt communities of interacting species even if only some of the species are directly affected by fragmentation. For instance, if parasitoids disperse less well than their herbivorous hosts, habitat fragmentation may lead to higher herbivory in isolated plant patches due to the absence of the third trophic level. Community-level studies suggest that parasitoids tend to have limited dispersal abilities, on the order of tens of metres, much smaller than that of their hosts, while species-oriented studies document dispersal by parasitoids on the scale of kilometres. In this study the distribution patterns of three parasitoid species with different life histories and their moth host, *Hadena bicruris*, a specialist herbivore of *Silene latifolia*, were compared in a large-scale network of natural fragmented plant patches along the rivers Rhine and Waal in the Netherlands. We examined how patch size and isolation affect the presence of each species. Additionally, experimental plots were used to study the colonisation abilities of the species at different distances from source populations.

In the natural plant patches the presence of the herbivore and two of the parasitoids, the gregarious specialist *Microplitis tristis* and the gregarious generalist *Bracon variator* were not affected by patch isolation at the scale of the study, while the solitary specialist *Eurylabus tristis* was. In contrast to the herbivore, the presence of all parasitoid species declined with plant patch size. The colonisation

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experiment confirmed that the herbivore and *M. tristis* are good dispersers, able to travel at least 2 km within a season. *B. variator* showed intermediate colonisation ability and *E. tristis* showed very limited colonisation ability at this spatial scale. Characteristics of parasitoid species that may contribute to differences in their dispersal abilities are discussed.

Zusammenfassung

Habitatfragmentierung kann Gemeinschaften von interagierenden Arten auseinander reißen, auch wenn nur einige der Arten direkt von der Fragmentierung beeinflusst werden. Wenn sich z. B. Parasítoide weniger leicht ausbreiten als ihre herbivoren Wirte, kann Habitatfragmentierung zu einer stärkeren Herbivorie in isolierten Pflanzenvorkommen aufgrund der Abwesenheit der dritten trophischen Ebene führen. Untersuchungen auf der Ebene der Gemeinschaften lassen vermuten, dass Parasitoide dazu tendieren eine geringe Ausbreitungsfähigkeit zu haben, die sich auf einen Bereich von mehreren zehn Metern beschränkt und viel geringer ist als die ihrer Wirte. Dagegen dokumentieren Untersuchungen, die sich an Arten orientieren, die Ausbreitung von Parasitoiden auf einer Skala von Kilometern. In dieser Untersuchung wurden die Verbreitungsmuster von drei parasitoiden Arten mit unterschiedlichen Eigenschaften und ihrem Wirtsschmetterling *Hadena bicruris*, einem spezialisierten Herbivoren auf *Silene latifolia*, in einem großräumigen Netzwerk von natürlichen, fragmentierten Pflanzenvorkommen entlang der Flüsse Rhein und Waal in den Niederlanden verglichen. Wir untersuchten, wie die Bestandsgröße und Isolation die Anwesenheit einer jeden Art beeinflusst. Darüber hinaus wurden experimentelle Anordnungen genutzt, um die Besiedlungsfähigkeit der Arten in unterschiedlichen Entfernungen zu den Quellpopulationen zu untersuchen.

In den natürlichen Planzenbeständen wurde die Anwesenheit des Herbivoren und zweier seiner Parasitoide, des gregären Spezialisten *Microplitis tristis* und des gregären Generalisten *Bracon variator* durch die Isolation des Bestandes innerhalb der Skala dieser Untersuchung nicht beeinflusst, während der solitäre Spezialist *Eurylabus tristis* beeinflusst wurde. Im Gegensatz zum Herbivoren verringerte sich die Anwesenheit aller Parasitoiden Arten mit der Größe des Pflanzenbestandes. Das Besiedlungsexperiment bestätigte, dass sich der Herbivore und *M. tristis* gut ausbreiten und mindestens zwei 2 km pro Saison zurücklegen können. *B. variator* zeigte eine mittlere und *E. tristis* eine sehr begrenzte Besiedlungsfähigkeit auf dieser räumlichen Skala. Es werden die Eigenschaften der parasitoiden Arten diskutiert, die zu den Unterschieden in der Ausbreitungsfähigkeit beitragen.

Introduction

Many insect species live in naturally patchy environments where dispersal processes may play a key role in regional dynamics (Eber, 2001; Halley & Dempster, 1996; Hanski, 1999; Harrison, 1994). Currently, the scale of human-induced habitat fragmentation increases the importance of dispersal for species persistence. The size of habitat fragments has been reduced by, e.g. deforestation, agriculture, and urbanisation, that lead to small population sizes and secondly, increased isolation leads to larger distances to be traversed between fragments (Groombridge, 1992; Henle, Lindenmayer, Margules, Saunders, & Wissel, 2004; Saunders, Hobbs, & Margules, 1991). Habitat fragmentation can disrupt whole communities even if only some of the species respond directly to fragmentation. This is because species interact with one another, so the chance of a particular species persisting in a habitat patch can be strongly affected by the presence or absence of other species. Examples are flowering plants whose reproduction depends on the presence of specific pollinators (Steffan-Dewenter & Tscharntke, 1999), and plant–herbivore–parasitoid systems, in which all three trophic levels can influence the population dynamics of one another.

Several studies have shown that fragmentation differentially affects the number of insect species in different guilds and trophic levels, potentially disrupting communities (Golden & Crist, 1999; Kareiva, 1987; Komonen, Penttila, Lindgren, & Hanski, 2000; Kruess & Tscharntke, 1994; Zabel & Tscharntke, 1998). For example, abundance and

diversity of predators and parasitoids are often more strongly affected by habitat fragmentation than the abundance and diversity of the herbivorous hosts, even at the scales of a few hundred metres (Komonen et al., 2000; Kruess & Tscharntke, 1994; Zabel & Tscharntke, 1998), suggesting that third-trophic-level insects disperse or colonise less well than second-trophic-level insects. In general, it is noted that higher levels of fragmentation lead to increased herbivore incidence, in part because predatory insects and parasitoids can only colonise patches already occupied by their hosts (Holt, 2002; Van Nouhuys, 2005; Weisser, 2000) or perhaps because they do not disperse as well as their host (Roland, 1993). Small-scale studies, in which dispersal within a habitat patch has been observed, indeed suggest that only a small fraction of released individual parasitoids disperse up to the maximum measured distance (100 m at most) (Ellers, Van Alphen, & Sevenster, 1998; Fournier & Boivin, 2000; Hagler, Jackson, Henneberry, & Gould, 2002).

Interestingly, the few studies of both parasitoid and host dispersal in naturally fragmented habitat do not support a general pattern of low dispersal of parasitoids relative to their hosts. Van Nouhuys and Hanski (2002) found that the parasitoid Hyposoter horticola could colonise patches up to several kilometres from a source population within a year, whereas the second parasitoid Cotesia melitaearum, did not colonise habitat patches further than 1 km during the same period (see also Lei & Hanski, 1998). The host Melitaea cinxia, showed intermediate dispersal ability. Antolin and Strong (1987) found that the very small egg parasitoid Anagrus and its host regularly disperse 1 km or more, even to off-shore islets, crossing the water. Dempster, Atkinson, and French (1995) studied colonisation of plant patches by several herbivorous insects and their parasitoids and found that all species were highly mobile, colonising patches up to 800 m from a source, and moving up to 3 km outside the study area within a year. Also, observations of dispersal by parasitoid species released for biological control in agricultural or managed habitats show rates of spread in the order of tens of kilometres over a few generations (see refs. in Godfray, 1994; Jones, Godfray, & Hassell, 1996).

These contrasting studies confirm that the actual dispersal abilities and spatial patterns of occurrence of insect species in general (Stein, Price, Craig, & Itami, 1994), and particularly of parasitoids in relation to their hosts, are not well understood (Jones et al., 1996), partly due to logistic and practical difficulties (Hagler et al., 2002). However, to understand the effects frag-

mentation may have on plant–herbivore–parasitoid interactions, it is essential to consider the dispersal and colonisation abilities of both hosts and parasitoids.

In this study, we investigate the impact of isolation and patch size of the host plant Silene latifolia on the distribution of the specialist noctuid herbivore moth, Hadena bicruris and three of its parasitoids with differing life histories in a natural rural landscape. The natural distribution patterns of all these species are compared with their colonisation patterns in experimental plots with different degrees of isolation. We expect that the noctuid moth is a very good disperser, as has been shown for similar noctuids (Schneider, 1999), but that the parasitoids species differ in their dispersal abilities. Therefore, the presence of the different parasitoid species are expected to be differently affected by patch size and isolation. Similarly, we hypothesise that the herbivore can colonise experimental plant plots up to large distances from a source population, whereas the distance from source populations at which parasitoid species can colonise experimental plant plots will depend on their biology (small specialist gregarious, large specialist solitary, small generalist gregarious). Specifically, we hypothesise that the large parasitoid disperses greater distances than the small ones and is less affected by the level of fragmentation (Tscharntke & Brandl, 2004). The generalist is not expected to be strongly affected by patch size or isolation because it probably uses alternate hosts in the surrounding habitats. Other life history characteristics that might contribute to differences in dispersal behaviours among parasitoids, and the possible consequences of habitat fragmentation in the system are discussed.

Material and methods

Study species

Plant

S. latifolia Poiret (= S. alba (Miller) Krause = Melandrium album (Miller) Garcke), the white campion, is a dioecious, weedy, short-lived perennial occurring in open disturbed habitats such as fallow fields, field margins, and roadsides (Goulson & Jerrim, 1997). In north-western Europe, S. latifolia flowers from the end of April until the end of October, with two distinct peaks at the end of May and in the beginning of August (Biere & Honders, 1996; Bopp & Gottsberger, 2004). After pollination of the female flower, mainly performed

by noctuid moths (Jürgens, Witt, & Gottsberger, 1996), the ovule expands and develops into a seed capsule containing several hundreds of seeds (Jürgens et al., 1996). In Europe the most important herbivore consuming the developing seeds is the noctuid *H. bicruris* (Brantjes, 1976b, 1976c; Elzinga, Turin, van Damme, & Biere, 2005; Wolfe, 2002).

Herbivore

H. bicruris Hufn. (Lepidoptera: Noctuidae), the Lychnis, is a night-active moth with a wingspan of 30–40 mm. Caterpillars can be found in the Netherlands from May until October, with peaks in June and at the end of August (J. Elzinga, pers. obs.), indicating that there are two overlapping generations. Although it strongly prefers *S. latifolia*, it can use a few other closely related caryophyllaceous plant species (Wirooks & Plassmann, 1999) but no signs of *H. bicruris* or other *Hadena* species have been observed on other Caryophyllaceous plant species in the study area (J. Elzinga, pers. obs.). After pollination and nectar feeding, the female moth may oviposit a single egg on the ovary of female flowers (Brantjes, 1976a). Upon eclosion, the first-instar larva (L1) enters the young fruit and feeds on the ovules and developing seeds. The larva will stay in the seed capsule (here: 'primary capsule') until it has consumed all the seeds, which usually occurs when the larva has reached the fourth or fifth (last) (hereafter L4 and L5, respectively) instar. At this stage, it moves to other seed capsules (here: 'secondary capsules'). Late-instar larvae are usually too large to fit entirely within a seed capsule, and thus the caudal appendages usually protrude during feeding, exposing it to parasitoids (Biere, Elzinga, Honders, & Harvey, 2002). At maturity the larva leaves the food plant and pupates in the soil, either developing into an adult or diapausing, depending on the season (Elzinga, Biere, & Harvey, 2002).

Parasitoids

Microplitis tristis Nees (Hymenoptera: Braconidae) is a small gregarious koinobiont endoparasitoid with a wingspan of 3.5 mm, that is specialised on larvae of *H. bicruris* (Shenefelt, 1978). It usually attacks L4 and L5 larvae when they are too large to be protected by the seed capsule (Elzinga, Harvey, & Biere, 2005). Upon maturation, the on average 18 parasitoid larvae leave the dying host larva (Elzinga, 2005). Parasitised caterpillars can be found throughout the summer, suggesting that there are several overlapping generations during a year.

Eurylabus tristis (Hymenoptera: Ichneumonidae) is a large solitary larval–pupal endoparasitoid with a wingspan of 16 mm. It is a specialist on *Hadena* species, attacking L4 and L5 *H. bicruris* larvae and egressing from the host pupa approximately 2 weeks after pupation or diapause (Elzinga, 2005).

Bracon variator (Hymenoptera: Braconidae) is a very polyphagous gregarious ectoparasitoid with a wingspan of 4 mm. It is known as a parasitoid of larvae of a wide range of insects. However, we do not know the hosts and habitat range it uses in the study area. *B. variator* paralyses its host before depositing on average 6 eggs on L4, L5, or rarely L3 *H. bicruris* larvae (Elzinga, 2005).

Study area

Our study was performed on both riversides of the Rhine and the Waal in the Netherlands, from the German border to near the city of Gorinchem, spanning a distance of ca. 100 km. We searched for *S. latifolia* in the floodplains and along the river dikes. *S. latifolia* patches are mainly found on elevated sandy places in the floodplains, on river dikes, along roadsides, in field margins or in disturbed areas near industrial sites. Vegetation management of the patches is highly variable, ranging from mowing twice a year (on dikes and along roadsides) to low-intensity grazing by horses and cattle (floodplains) or no obvious management at all (field margins and disturbed areas). Due to the clear borders, and the linear structure that made it efficient to survey, the riversides were very suitable for this study. The surrounding area was also surveyed, but *S. latifolia* was found to be largely absent due to heavy agriculture and unsuitable soil.

Patch location

In May and early June of 2000 and 2001, the whole study area was scanned by foot or bicycle to locate flowering *S. latifolia* plants and map the distribution of host plant patches. The minimum distance to distinguish between separate plant patches was defined as 100 m. In every patch the coordinates of plants along the edges of the patches were recorded using a GPS system with a resolution of a few metres (GIS*backpack*, Commetius, Leiderdorp, NL). With these data the distances between patches were calculated.

Measurements

The number of reproductive male and female plants (plants with flowers, seed capsules, or flower

buds) in every patch was counted in August 2001, early June 2002, and early June 2003. Occupancy of the herbivore was determined by observation of any life stage or its typical damage to fruits at one or more visits during the 3-year study period. Similarly, for the parasitoid occupancy was determined by observation of its presence in any of the collected caterpillars or by sighting of adults during a visit. At each visit, female plants were searched for eggs, larvae, or signs of herbivory until presence of *H. bicruris* was observed or all plants in the patch had been carefully checked. Damaged seed capsules were recognised by a small entrance hole at the side (a primary capsule) or by a large entrance hole at the top (a secondary capsule).

In September 2001, June and September 2002, and June and September 2003 all plant patches were visited to collect *H. bicruris* caterpillars. All female plants in a patch were examined (except if patch size exceeded 1000 plants) by checking each seed capsule. Caterpillars that were inside secondary capsules or moving freely on plants were collected and reared in the laboratory on artificial diet (Elzinga et al., 2002) to assess parasitism. Caterpillars were collected only twice a year to avoid disrupting local population dynamics. The range of maturation times was wide in each generation, so that sampling probably had little impact on population size.

Fragmentation estimates

The two estimates of fragmentation used in this study are the size and the connectivity of the patches. Patch size was calculated as the maximum number of reproducing plants present in a patch during any of the 3 years of the study. Both male and female plants were included in the estimate of patch size since both male and female flowers are supposed to attract female moths (Brantjes, 1976b, 1976c; Dötterl, Wolfe, & Jürgens, 2005). Although the number of flowering plants differed from year to year, the overall pattern of fragmentation of patches was relatively constant over the study period. Our fragmentation estimates probably slightly underestimate actual fragmentation as we consider the maximum number of observed plants and three of the patches (with less than three flowering plants) actually disappeared since 2001 and four, discovered only in 2003, may have been newly founded during the study period.

Connectivity of patches can be estimated in many ways (Moilanen & Nieminen, 2002). In this study we used distance to the nearest neighbouring *S. latifolia* patch (NND$_{plant}$) and the connectivity

index S_i (Hanski, 1999). NND is a good estimate of isolation in situations where the landscape has a linear structure (Moilanen & Nieminen, 2002). To avoid extremely small populations strongly affecting the estimate, we excluded patches of fewer than 10 plants, although results based on NND estimates using all patches were qualitatively similar. For each of the species we also analysed NND$_{spec}$, i.e. the distance to the nearest patch occupied by that species.

The second estimate of connectivity that we used takes into account the distance of a patch from all other occupied (and unoccupied) patches and their sizes (Hanski, 1999). Here the connectivity (S_i) of a patch i can be calculated as follows:

$$S_i = \sum_{j \neq i} p_j N_j e^{-\alpha d_{ij}},$$

where α is a constant determining the effect of distance on isolation, d_{ij} is the distance between population i and j (in km) and N_j is the number of (male and female) plants in population j. The p_j stands for presence of a species and is either 1, when this species is present, or 0 when it is absent from patch j.

The constant α characterises how steeply the number of migrants from patch j decline with increasing distance (Hanski, Alho, & Moilanen, 2000). More generally, $1/\alpha$ is considered as the average dispersal distance of a species (Moilanen & Nieminen, 2002). α can be estimated using mark-recapture data (Hanski, 1999). Because these data are not available for the species in this study, the appropriate values for α are unknown. Therefore, S was calculated for α's ranging from 0.2 to 50. Because this study is investigating fragmentation effects for each species separately, S_i was calculated using all plant populations ($p_j = 1$) ($= 'S_{plant}'$) as well as using only plant populations occupied by the species whose presence was analysed ($p_j = 1$ or 0) ($= 'S_{spec}'$).

Whereas it is logical to use plant patch size in estimates of fragmentation for the herbivore, herbivore population size might be better to use in estimates of fragmentation for the parasitoid (Van Nouhuys & Hanski, 2002). However, in the study area, the number of caterpillar-damaged plants linearly increases with the number of plants in a patch (Elzinga, Turin et al., 2005), suggesting that herbivore population size is in fact highly correlated with plant patch size.

Colonisation experiment

In 2002 and 2003, an experiment was performed to investigate the colonisation abilities of the

insect species using experimental plots. First, six locations were selected where it was possible to establish experimental plots at different distances up to 2000 m from a natural source population. The selected source populations were known to be occupied by the herbivore and the parasitoid *M. tristis* in 2001 or 2002. Experimental plots were established in 2002 at 125, 250, 500, 1000, and 2000 m from each source population (except for one 2000 m plot at one location), giving a total of 29 plots (Fig. 1). Thorough searching around each plot made sure that within a radius of the distance to the source patch, no other natural patches were present in 2002 (in one location a patch of 2 females was, however, observed in 2003).

In July 2002, 14 plants (7 males and 7 females) were transplanted into each plot. The plants were grown from seedlings in a garden in Heteren, the Netherlands, in 5 l pots containing potting soil. Flowers were removed daily to ensure that they would not be colonised by *H. bicruris* before the experiment. After removing the pots, plants were transplanted into small holes, about 30 cm apart, in the natural vegetation.

Weekly censuses of the plots began 4 weeks after transplantation and continued until late September 2002. At each census the plants were checked for eggs or signs of herbivory by *H. bicruris* and adult parasitoids. When encountered, L4 or L5 caterpillars visible on the plant or inside secondary seed capsules were collected and reared through in the lab. In early 2003, approximately half of the plots had disappeared and these were re-established. Where necessary, plants were added to remaining plots to restore a number of 14 plants. All plots were visited regularly during the rest of the year.

Analyses

Logistic regression (McCullagh & Nelder, 1989) was used to test effects of patch size and isolation on the presence or absence of herbivore and parasitoid species using the statistics software package R v.1.8.1 (Venables & Smith, 2003). Four measures of isolation were tested, NND_{plant}, NND_{spec}, S_{plant}, and S_{spec} in combination with patch size (maximum number of *S. latifolia* plants). Since the probability that a parasitoid species (especially if it occurs at low frequency) is detected increases with number of collected caterpillars and since small populations provide smaller sample sizes, analyses were repeated with the number of caterpillars collected as an offset variable, i.e. a component of the linear predictor that is known and requires no coefficient (McCullagh & Nelder, 1989) and allows evaluation of the contribution of size and isolation effects while holding fixed the already fit caterpillar sample size effect. Since results of analyses with and without the offset variable were qualitatively similar, we only present analyses without offset for simplicity. All fragmentation parameters were log-transformed prior to analysis. For the colonisation experiment, impact of distance to the source population on the presence of parasitoid species was analysed using logistic regression. First, for each species separately, we analysed the effect of log-transformed distance (continuous variable) to the source population on the presence or absence of the species, using each patch as an independent observation. Second, comparisons between species were made by analysing the observations of species, with species entered as a class variable.

Results

Natural distribution pattern

In total, 85 patches of *S. latifolia* were found with a maximum number of plants ranging from 1 to over 13,000 and with different degrees of isolation (Fig. 2). Patch size was not correlated with any connectivity parameter (all $P > 0.05$). Eight patches consisted of only one or two male plants, unsuitable for the larval stage of the herbivore. Of the
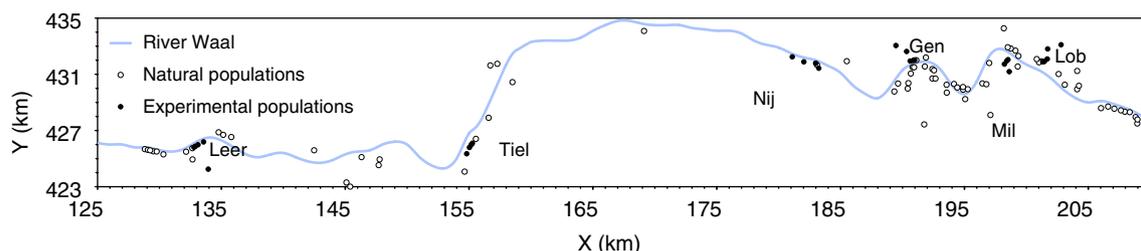
Figure 1. Map showing the locations of the natural patches (open circles) and experimental plots (filled circles) of *S. latifolia* in the study area. Names of the source locations are shown. Numbers on the *x* and *y* axes give the official Dutch geographical coordinates.
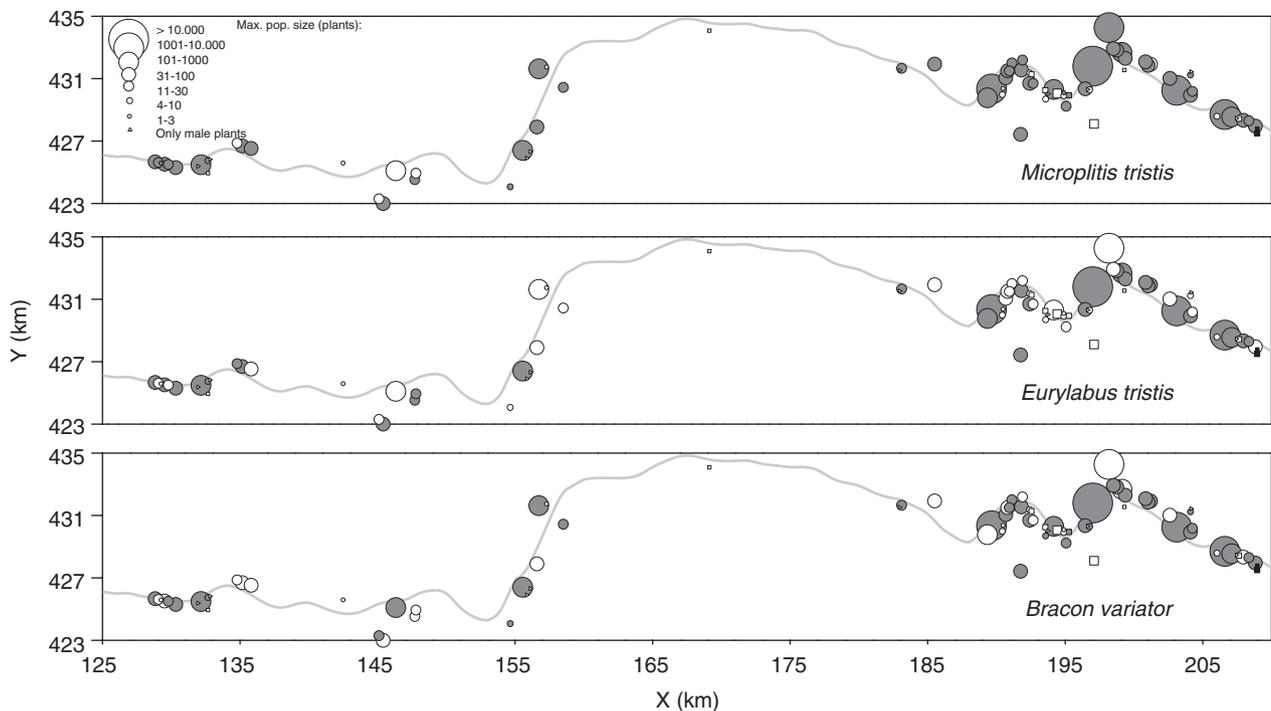
Figure 2. Maps showing the distribution of the herbivore *H. bicruris* and its parasitoids *M. tristis*, *E. tristis*, and *B. variator* along the river. In all three maps the size of natural plant patches of *S. latifolia* is indicated by the size of the symbol: grey circles: patches with caterpillars parasitized by the respective parasitoid species; open circles: patches from which the respective parasitoid species was not recorded; open squares: patches in which herbivory was observed, but no caterpillars were collected; black squares: patches in which no herbivory was observed. Numbers on the *x* and *y* axes give the official Dutch geographical coordinates.

remaining patches only two did not show any signs of herbivory by *H. bicruris* (NND_{moth} and S_{moth} were therefore not further considered). Both were not extremely isolated, but rather small (Fig. 2). We were able to collect caterpillars from 66 patches. Because of our searching strategy and because host population size may be strongly correlated with plant patch size, the number of caterpillars collected from a patch depended strongly on the number of plants in the patch (Pearson correlation, $P < 0.001$). The number of caterpillars collected was independent of any isolation parameter (all $P > 0.05$).

Based on parasitoids reared from the caterpillars we collected (and the sighting of an adult *M. tristis* in one patch), we detected *M. tristis*, *E. tristis*, and *B. variator* in 53, 31, and 40 patches, respectively (Fig. 2). In total, these parasitoids were found in 22.9%, 11.7%, and 4.9% of the 1773 caterpillars that were collected during the study, respectively. Because some larvae could have been superparasitised (with only one parasitoid species developing successfully), these numbers probably slightly underestimate the number of larvae actually parasitised by each species (Elzinga, 2005).

Table 1. Regression coefficient estimates from two logistic regression models explaining the observed presence of the parasitoids *M. tristis*, *B. variator,* and *E. tristis* in natural *S. latifolia* patches

	M. tristis	*B. variator*	*E. tristis*
Patch size	2.02[**]	0.95[*]	2.07[***]
Isolation (NND_{plant})	—	—	−2.50[**]
Patch size	2.07[**]	0.88[*]	2.08[***]
Isolation (NND_{spec})	—	—	−1.83[**]

Factors included in the models are patch size (maximum number of *S. latifolia* plants) and a measure of isolation of the patch, either NND_{plant} or NND_{spec} (see text).
[*]$P < 0.05$, [**]$P < 0.01$, [***]$P < 0.001$.

The probability of observing *M. tristis* increased with the number of plants in a patch (Table 1), with a 50% probability of observation in patches consisting of five plants (Fig. 3A). The probability to observe *M. tristis* was not related to any of the isolation estimates based on NND (Table 1) or on S ($P > 0.05$ for all models). The distribution of *B. variator* was similar to that of *M. tristis*. The probability of observing *B. variator* increased with
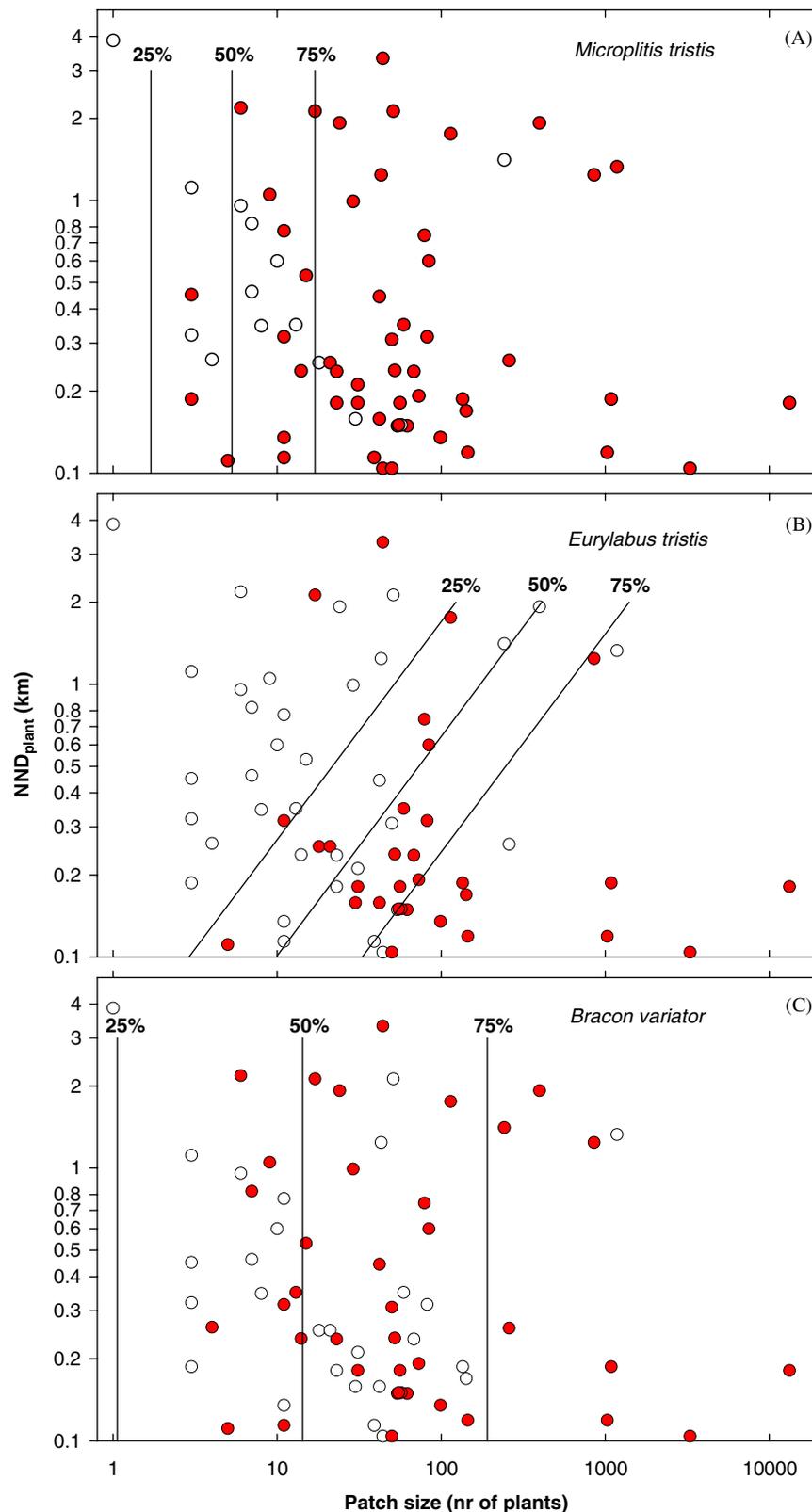
Figure 3. Effects of the number of *S. latifolia* plants observed in 2001–2003 and the distance to the nearest neighbouring patch with at least 10 plants (NND) on the observed presence (closed symbols) or absence (open symbols) of the parasitoids *M. tristis* (A), *E. tristis* (B), and *B. variator* (C). The 25%, 50%, and 75% probabilities of occurrence were obtained from the logistic regression models (Table 1). Note that there was a significant effect of NND only for *E. tristis*.

the number of plants in a patch, although less strongly than for *M. tristis*, as can be observed from the wider range between the 25% and 75% probability of observation (Fig. 3C). None of the isolation estimates significantly affected the presence of *B. variator*, either based on NND (Table 1) or on S (*P*>0.05 for all models).

The occupancy pattern of *E. tristis* was different from that of the other two parasitoids. The probability of occurrence increased strongly with patch size, with only a few observations in patches of less than 50 plants (Table 1, Fig. 3B). Additionally, the presence of *E. tristis* significantly decreased with increasing distance to the nearest neighbouring patch, both when estimates were based on all neighbouring plant patches (NND$_{plant}$), and for estimates based on patches with *E. tristis* only (NND$_{spec}$) (Table 1, Fig. 3B). Presence of *E. tristis* also significantly increased with increasing connectivity (S), but only when this estimate was based on the non-species specific connectivity measurement (S$_{plant}$) and for values of α larger than 4.5. The best fit for both the models with (minimum $P = 0.004$) and without (minimum $P = 0.016$) patch size included, was obtained for values of α around 10 (based on the lowest *P*-values and the highest regression coefficient estimates). Connectivity measures based on patches that contained *E. tristis* only (S$_{spec}$) could not significantly explain the presence or absence of *E. tristis* in a patch for any value of α.

Colonisation experiment

Although at least one female plant flowered in each of the experimental plots, the total number of flowering plants in most plots was less than 10. Nevertheless, over the 1.5 years of the study, colonisation by all species was observed. The herbivore, *H. bicruris* (observed either as eggs, herbivory, or caterpillars present) colonised all but one (at 250 m) of the 29 plots. The one exception might be due to a very low number of female flowers in that plot. Despite the high number of plots that were colonised, only few caterpillars could be found in most of the plots (mean = 3.7 ± 0.8). In 13 plots only one or two caterpillars could be collected and in four plots no caterpillars were found.

The gregarious specialist *M. tristis* was observed in 15 out of the 28 plots in which the herbivore was observed to be present on all investigated distances from the source populations. On three occasions an adult *M. tristis* was observed in a plot where no host larvae were yet found. Although the number of

observed colonisations by *M. tristis* was significantly lower than for *H. bicruris* (logistic regression, *P*<0.001), no relation was found between colonisation and distance from the source patches (logistic regression, n.s.). *E. tristis* and *B. variator* were both observed significantly less than *M. tristis* (logistic regression, *P*<0.001). Only one plot, at 1000 m from the source population, was colonised by the specialist parasitoid *E. tristis* and only five (at all distances except 2000 m) out of the 28 suitable plots were colonised by the generalist *B. variator*.

From the colonisation data it is clear that, within the study period of 1.5 years, all species could reach a plot 1 km from a source population, and that *M. tristis* could go farther, as it was observed even in three out of the five plots 2 km from the sources.

Discussion

Natural distribution patterns

Since *H. bicruris* was observed in almost all natural *S. latifolia* patches, we conclude that the presence of this herbivore was not negatively affected by the current level of fragmentation. The natural distribution patterns of the parasitoids indicate that the different species attacking *H. bicruris* are differently affected by habitat fragmentation. In fact, only one parasitoid, the solitary specialist *E. tristis*, showed a distribution that was related to the degree of isolation of plant patches. For this species a lower occurrence was observed in patches that were more isolated based on both nearest neighbour estimates and on connectivity values (S). The patterns of occupancy of the two gregarious parasitoids, the specialist *M. tristis* and the generalist *B. variator* were not related to isolation at the scale of this study. All three parasitoids however, occurred with lower frequency in small patches. This effect was strongest for *E. tristis* where parasitoids were almost completely absent from patches of less than 50 plants, whereas *B. variator* and especially *M. tristis*, were regularly observed in patches consisting of 10 plants or less.

Values of α that improve the fit of the logistic models for occupancy should represent biologically significant spatial information. The value of α for *E. tristis* with the largest regression coefficient and lowest *P*-value was around ten. If the number of *E. tristis* dispersers is diluted with distance at a rate described by the negative exponential, as is

assumed by the incidence function model (Hanski, 1994), the average dispersal distance is $1/\alpha$ (Moilanen & Nieminen, 2002). This would mean a typical dispersal distance for *E. tristis* of about 100 m. In general however, in our attempts to detect effects of isolation we gained little by using connectivity estimates instead of estimates based on nearest neighbouring populations. Perhaps the linear structure of the habitat makes the use of estimates that incorporate all patches and their sizes less applicable in our study (Moilanen & Nieminen, 2002).

The effect of plant patch size on occupancy is apparent for all of the parasitoid species. However, the chance of finding parasitoids depends on the number of caterpillars collected, and in small patches few caterpillars are available so effects of patch size cannot easily be distinguished from effects of sample size. Incorporating an offset in the model for the number of hosts collected indicates whether plant number in a patch has an effect over and above sample size, but the two are still confounded. In fact, the number of small patches occupied by a parasitoid might be underestimated due to small host sample sizes. For *M. tristis* and *B. variator* a higher incidence would strengthen the conclusion that their presence is not strongly affected by fragmentation. For *E. tristis*, the conclusions might change but the very low incidence of the parasitoid in the experimental plots suggests that small host populations are indeed unlikely to be colonised.

The colonisation experiment

Whereas the presence of herbivores and parasitoids in the natural patches may reflect local population dynamics, extinctions, the age of the patches, and long-term persistence, the colonisation experiment singles out the colonisation abilities of the species. In fact, the results of the colonisation experiment correspond well with the results obtained from the natural distribution patterns, suggesting that dispersal among patches is probably an important part of the maintenance of the system regionally. As might be expected by its distribution among the natural patches, the herbivore, *H. bicruris*, colonised virtually all of the experimental plots, independent of the distance from a potential source population, within the first year. This indicates a strong dispersal capacity and a good plant patch locating ability because even the smallest patches of only one flowering plant were inhabited. Presumably the moth, as a nectar feeder, pollinator and herbivore on *S. latifolia*, is

attracted over long distances by the strong odour that the flowers produce (Dötterl et al., 2005). It is known that many other moths locate odour sources, especially pheromone sources over a distance of several kilometres (see Cardé & Millar, 2003). Furthermore, noctuid moths of similar size and shape have been shown to be strong fliers capable of dispersing hundreds of kilometres (Förare & Solbreck, 1997; Schneider, 1999).

The parasitoid *M. tristis* was also very efficient in colonising the experimental plots, even though the number of hosts was very low. Colonisation by *M. tristis* was observed in more than half of the plots within 1.5 years, including three plots at 2000 m. *B. variator* colonised only a few experimental plots, and *E. tristis* was observed in only a single plot. Analysis of the natural distribution patterns showed that the occurrence of *E. tristis* and *B. variator* was lower in small patches, which might explain why colonisation by these species was not observed more frequently, even at short distances, in the small experimental plots. In fact, our experiment may underestimate the colonisation abilities of the parasitoids due to the small number of available hosts.

The natural distribution pattern and the results from the colonisation experiment both show that the herbivore, *H. bicruris*, basically saturates the host plant in this landscape. The parasitoids differ in their occupancy and dispersal abilities, with the solitary specialist *E. tristis* being most affected by fragmentation. The gregarious specialist *M. tristis* is a good disperser. The gregarious generalist, *B. variator*, may be a good disperser but is probably also responsive to alternative hosts in the surrounding environment.

Differences in dispersal abilities between parasitoid species

Our results are in agreement with those of several other studies showing that different species of parasitoids using the same herbivore host species can respond differently to the spatial distribution of host habitat patches (Brodmann, Wilcox, & Harrison, 1997; Doak, 2000; Kankare, Van Nouhuys, Gaggiotti, & Hanski, 2005; Roland & Taylor, 1997; Van Nouhuys & Hanski, 2002). Several factors may underlie the wasp distribution patterns, and explain why different species of parasitoid using a single host species react differently to fragmentation.

First of all, the number of dispersers (potential colonisers) may differ because total population sizes differ. In a study on colonisation of fragmented

clover habitats, Kruess and Tscharntke (1994) observed that the number of colonised plots corresponded with the number of individuals of particular species in the source habitat (for both herbivores and parasitoids). This might explain why the solitary specialist *E. tristis* seems to be more affected by fragmentation than the other parasitoids. Although the parasitism rate of *E. tristis* is only 2.4 times smaller than that of the gregarious *M. tristis*, the latter produces on average 18 individuals per host, leading to potentially 45 times more progeny. When we consider that the sex ratio of *M. tristis* is female biased and that of *E. tristis* is 0.5, the difference might be even larger. In addition, small population sizes of *E. tristis* might leave them more prone to local extinctions (Van Nouhuys & Tay, 2001).

A second factor that has often been suggested to explain differences in distribution patterns among species in fragmented landscapes, is the level of resource specialisation (Thomas, Thomas, & Warren, 1992; Zabel & Tscharntke, 1998). Highly generalist parasitoid species are not expected to respond strongly to isolation of habitat patches of the host if alternative hosts are available in the surroundings. This might explain why we did not find any effects of isolation in *B. variator* in our study area. Alternative hosts for *B. variator* in the region are unknown but might have led to a larger overall population size and a weak relationship between its occurrence and the population sizes of *S. latifolia* and *H. bicruris*. Studies addressing host range of parasitoids and predators have indeed reported that, in general, specialist species are more vulnerable to isolation than generalists (Kruess & Tscharntke, 2000), but whether this is due to a larger number of dispersers in the source habitat or due to the availability of alternative hosts, or both is unknown.

Third, differences in colonisation ability and patterns of occupancy between parasitoids can also be explained by differences in dispersal behaviour (Brodmann et al., 1997; Van Nouhuys & Hanski, 2002). For several parasitoid life history traits, we can speculate about their role in causing differences in dispersal between parasitoids in a fragmented landscape. First, it might be expected that large parasitoid species are stronger fliers and thus disperse better than small parasitoids (Tscharntke & Brandl, 2004). This has been shown for a small parasitoid species at a scale of 20 m (Ellers et al., 1998). Also, Van Nouhuys and Hanski (2002) show that the largest of two parasitoid species has a better dispersal ability and Roland and Taylor (1997) show that the spatial scale at which parasitism rate responds to forest structure

is positively correlated with the relative body size of four tachinid parasitoids. However in this study, we found that the smaller parasitoid species are less affected by isolation than the large *E. tristis*. Other studies also have shown that even very small egg parasitoids do regularly cross at least 1 km of water (Antolin & Strong, 1987). Perhaps active dispersal, which might be facilitated by large sizes or wingspan, is not always the most important mode of parasitoid dispersal. Studies performed in the first half of the 20th century report many small Hymenopterans in air samples taken at tens to thousands of metres by airplanes and balloons (Freeman, 1945; Glick, 1939), suggesting that passive dispersal is a common phenomenon for small parasitoids. Lifespan can also contribute to the distance travelled by a parasitoid. Unfortunately, the lifespan of parasitoids in the field is unknown. In addition, realised dispersal is not only a function of the distance moved but also of the tendency to leave a patch in the first place. Perhaps, parasitoids specialised on solitary hosts with low local abundances, as is the case with *H. bicruris*, have higher dispersal tendencies compared with specialists on aggregated and abundant hosts (Fournier & Boivin, 2000). Frequency-dependent dispersal has been found in parasitoids, suggesting that also intraspecific competition is likely to affect dispersal tendency (French & Travis, 2001). Gregarious parasitoids such as *M. tristis*, occurring in small patches with few hosts available, may avoid competition between females and also avoid inbreeding due to sibling mating, by having a strong dispersal tendency.

Effect of habitat fragmentation for the plant–herbivore–parasitoid system

Although the herbivore *H. bicruris* is a strong disperser, it does not escape from the most abundant parasitoid in the study area, *M. tristis*, even in isolated patches. The generalist *B. variator* has a relatively low rate of parasitism (4.7%) and in the surrounding habitats is probably independent of the level of fragmentation of *S. latifolia* patches. Consequently, for these two parasitoids habitat fragmentation should have little or no effect on the parasitoid–host–plant dynamics. However, in the extreme case that all of the plant patches would be very small, regardless of their isolation, *H. bicruris* could avoid parasitism and have a greater negative impact on the plant. Indeed, analyses of the level of herbivory in the system showed an increase in *H. bicruris* herbivory with decreasing patch

size (Elzinga, Turin et al., 2005) and this was accompanied by a decrease in parasitism rate and number of parasitoid species present. However, experiments with different plant patch sizes suggest that not the absence of the parasitoids but rather alterations in oviposition behaviour, leading to increased oviposition in smaller patches, may explain the increased herbivory in smaller patches (Elzinga, Turin et al., 2005). Only the specialist *E. tristis* seems to be seriously affected by the current level of fragmentation in the system.

Our results show that different parasitoid species using the same host species have different distribution patterns in a fragmented habitat. This possibly reflects differences in dispersal and colonisation ability due to their differences in life histories. When studying effects of fragmentation on plant–herbivore–parasitoid systems, careful consideration should be given to the biology of the actual parasitoid species involved.

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