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Does fragmentation of *Urtica* habitats affect phytophagous and predatory insects differentially?

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Abstract Effects of habitat fragmentation on the insect community of stinging nettle (*Urtica dioica* L.) were studied, using 32 natural nettle patches of different area and degree of isolation in an agricultural landscape. Habitat fragmentation reduced the species richness of Heteroptera, Auchenorrhyncha, and Coleoptera, and the abundance of populations. Habitat isolation and area reduction did not affect all insect species equally. Monophagous herbivores had a higher probability of absence from small patches than all (monophagous and polyphagous) herbivore species, and the percentage of monophagous herbivores increased with habitat area. Abundance and population variability of species were negatively correlated and could both be used as a predictor of the percentage of occupied habitats. Species richness of herbivores correlated (positively) with habitat area, while species richness of predators correlated (negatively) with habitat isolation. In logistic regressions, the probability of absence of monophagous herbivores from habitat patches could only be explained by habitat area (in 4 out of 10 species) and predator absence probability only by habitat isolation (in 3 out of 14 species). Presumably because of the instability of higher-trophic-level populations and dispersal limitation, predators were more affected by habitat isolation than herbivores, while they did not differ from herbivore populations with respect to abundance or variability. Thus increasing habitat connectivity in the agricultural landscape should primarily promote predator populations.

Key words Island biogeography · Predation · Trophic interactions · Diversity · Monophagy

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Introduction

Habitat fragmentation is a major threat to biodiversity in the agricultural landscape (Diamond and May 1976; Saunders et al. 1991; Tscharntke 1992; Rosenzweig 1995). Some species are systematically disadvantaged in small or isolated habitats, thereby changing both community structure and ecosystem function. Disruption of species interactions may affect pollination, seed predation, decomposition of dung or litter, and mutualistic mycorrhizal associations or antagonistic fungal infections (Matthies et al. 1995; Didham et al. 1996). For example, isolated clover and vetch islands are characterized by reductions in both numbers of parasitoid species and percent parasitism, thereby releasing prey populations from possible biocontrol (Kruess and Tscharntke 1994, 1998; Tscharntke and Kruess 1998). These results confirm theoretical predictions that natural enemies should generally be more susceptible to disturbance and go extinct more readily than their phytophagous prey in fragmented habitats (Pimm 1991; Lawton 1995; Holt 1996). Theoretical analyses by Andrén (1994) show that where suitable habitat covers less than 50% of the landscape, the area of habitat fragments decreases disproportionately, and where suitable habitat covers less than 20% of the landscape, the distance between fragments increases disproportionately. In general, the relative importance of (1) pure habitat loss (without patch area or isolation effects), (2) patch area, (3) patchisolation, including a measure of the hostility of the surrounding landscape, and (4) patch quality (e.g, age) for herbivores and predators is unclear in most studies on island ecology (see Saunders et al. 1991).

In this paper, we analyze the effects of habitat fragmentation on insect diversity in nettle (*Urtica dioica*) habitats. These habitats cover much less than 5% of the agricultural landscape in Germany. Hence, patch area and isolation could be expected to be the most important variables influencing insect diversity in habitat fragments.

We tested the hypotheses that (1) fragmentation of nettle habitats reduces the diversity of nettle-inhabiting insects and results in the well-known species-area relationship (e.g., Ward and Lakhani 1977; Rey 1981; MacGarvin 1982), (2) specialized insects suffer more than unspecialized species, resulting in differential slopes of the species-area relationships (a rarely tested theoretical generalization, e.g., Lawton 1995), (3) density is negatively and population variability positively related to the probability of absence in nettle patches (Kruess and Tscharntke 1994), and (4) isolation and area of habitats affect predators and herbivores differentially. The last hypothesis is derived from food web theory which predicts that species at higher trophic levels should be more susceptible to habitat disturbance than those at lower trophic levels (the Volterra effect; see Wilson and Bossert 1971; Kareiva 1987, 1990; Kruess and Tscharntke 1994; Tscharntke 1997; Tscharntke and Kruess 1998)

Stinging nettle is a vigorous, perennial plant that often occurs in dense stands producing a distinctive habitat. Its natural occurrence in northern Europe is probably restricted to open woodland on peaty soils, but the plant has reached widespread distribution in central Europe due to accumulation of organic matter provided by human habitation and agriculture. Therefore, stinging nettle patches are not usually isolated by large distances, although recent papers have stressed the importance of small-scale isolation in agricultural systems (Kareiva 1987, 1990; Kruess and Tscharntke 1994). The insect community on stinging nettle has been described by Davis (1973, 1991) who found 31 phytophagous species to be virtually restricted to *U. dioica* or other Urticales, while predators are generally not confined to nettles.

Materials and methods

Thirty-two naturally occurring patches of stinging nettle in the Leine River valley near Göttingen (northern Germany) were sampled in 1994 to study the diversity and abundance of the insect fauna. Sunny sites in an agricultural landscape were chosen: (1) "isolated" habitats, 75–300 m from the nearest nettle bed of at least 50 m^2, and (2) "connected" habitats, isolated by only 10–20 m. The two isolation classes contained a graded series of habitats of 5–1000 m^2. Sites measuring 5–50 m^2 were designated as "small" ($n = 21$), those measuring more than 50 m^2 as "large" (75–1000 m^2, $n = 11$). Thus, the 32 sites could be grouped into four types: (a) isolated and small (14 sites), (b) isolated and large (7 sites), (c) connected and small (7 sites), (d) connected and large (4 sites).

Distances of isolation were calculated in different ways. We only show results with the distance to the nearest nettle patch of at least 50 m^2, but we also tested the distance (1) to the nearest nettle patch of at least 20 m^2, and (2) to the nearest patch of at least the same area. Further, we (3) tested a correction of distances by −33%, when the nettle patches were enclosed by species-rich old fields, and by + 33% when they were habitat islands within crop monocultures. The outcome of the statistical results and the main conclusions (in particular the different response of monophagous and polyphagous herbivores, and the differential effects of area and isolation on herbivores and predators) were almost identical in all four calculations of the distance of isolation.

Insects were sampled three times at each site, in May, July, and September 1994, using a Univac portable suction sampler (Henderson and Whitaker 1977). A gauze cage 1 m in height, covering $0.50 \times 0.50 = 0.25$ m^2, was placed on a randomly chosen part of the nettle patch, and for 3 min, insects inside the cage were captured. On each sampling date, five such samples were collected at each site, representing a total sample area of 1.25 m^2 per sampling date. Therefore, species richness and abundance of each site and for all three dates is based on 3.75 m^2. Only Heteroptera, Auchenorrhyncha, and Coleoptera were identified (with the help of experts, see Acknowledgements), so species richness was based on these three insect orders.

In addition to the isolation and area of the site, average height (cm), density (percent of estimated maximum), and dominance (percent of all plant species) of *U. dioica* on each site were evaluated. In stepwise multiple regression, these five site variables were tested against species richness and population abundance. Independent variables which did not significantly contribute to the regression were excluded from models. Variables were tested to be virtually normally distributed; percentages were arcsin square root transformed. Dependence of species absence probabilities on area and isolation were analyzed with logistic regressions for the 10 monophagous herbivores (2 of the 11 species could not be separated, see Table 1) and the 14 (polyphagous) insect predators (Table 1). Furthermore, the four habitat types were compared using ANOVA. Data were analyzed with Statgraphics software (Manugistics 1994) or, in logistic regressions, with SAS software (SAS 1988).

Results

Habitat area and isolation of the 32 nettle patches were not significantly intercorrelated ($F = 1.5$, $r^2 = 0.049$, $P = 0.22$). Plant height, density, and dominance of *U. dioica* were positively intercorrelated, but did not correlate with area or isolation of habitats with the exception of area versus density ($F = 8.8$, $r^2 = 0.22$, $P = 0.006$). The average plant height was 102 cm (SD = 15, $n = 32$).

A total of 45 800 insects were sampled. Three major groups were identified to species level: Heteroptera (2900 specimens), Auchenorrhyncha (9200), and Coleoptera (2000) comprised 69 species (see Table 1). We captured all eleven herbivore species that Davis (1991) considered to be restricted to nettles (but the lygaeid bug *Heterogaster urticae* was found only in an extra sample), as well as the monophagous *Macrosteles variatus*. In addition to these 11 monophagous species, 44 polyphagous herbivorous species were sampled. Of the 14 principal insect predators found on nettles (Davis 1991), only the ladybird *Coccinella 11-punctata* and the damsel bug *Nabis rugosus* were missing from our samples, but we additionally found two cantharid beetles (*Rhagonycha limbata, Cantharis livida*). Accordingly, our samples very much resembled the UK samples (for a European survey, see Davis 1989).

Site characteristics other than habitat area and isolation were correlated with abundance of each of the 25 species in only four cases, so there was obviously little relationship between insect density and plant attributes (density, height, dominance): plant height (cm) was negatively correlated with both *Cidnorhinus quadrimaculatus* densities ($r^2 = 0.19$, $n = 32$, $P = 0.01$) and *Phyllobius pomaceus* density ($r^2 = 0.11$, $n = 32$, $P = 0.07$), but positively with *Anthocoris nemorum* densities ($r^2 = 0.47$, $n = 32$, $P < 0.001$), while the

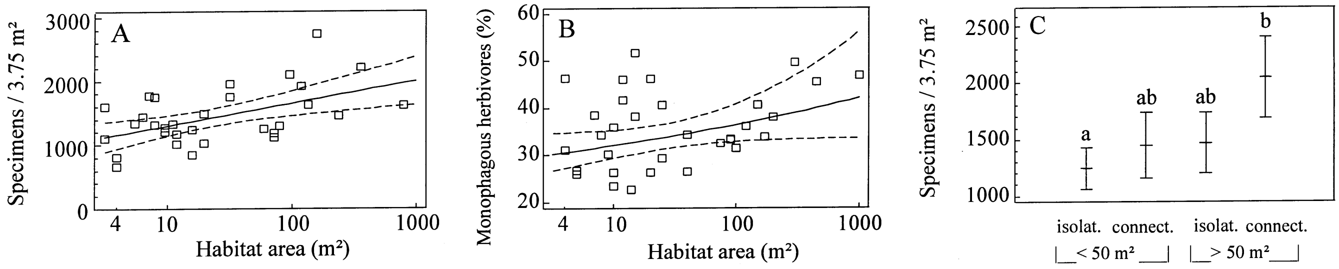

Fig. 1A–C Dependence of arthropod (insect and spider) abundance on habitat size and habitat type ($n = 32$ nettle habitats). Regression lines and 95% confidence limits are given. **A** Arthropod density in relation to habitat size: $y = 917.4 + 349.1 \log x$, $F = 10.8$, $r^2 = 0.26$, $n = 32$, $P = 0.003$. **B** Percentage of herbivore specialist individuals in relation to all herbivores: $y = 1/(0.035–0.004 \log x)$, $F = 4.3$, $r^2 = 0.13$, $n = 32$, $P = 0.04$. **C** Arthropod density in relation to habitat type: $F = 5.0$, $n = 32$, $P < 0.01$. Homogenous groups have *identical letters* (Tukey test)

Table 1 Plant bugs, leaf hoppers, and beetles on stinging nettle (*U. dioica*): the monophagous herbivores and the (polyphagous) predators

	Mean abundance ± SE (n/3.75 m^2)	Occupied habitats (% of 32)
Monophagous herbivores		
Plant bugs		
Liocoris tripustulatus	19.7 ± 17.1	93.8
Leaf hoppers		
Eupteryx cyclops and *E. urticae*	187.4 ± 174.5	100.0
Eupteryx aurata[a]	83.1 ± 73.7	100.0
Macropsis scutellata	0.4 ± 1.8	18.8
Macrosteles variatus	0.1 ± 0.08	9.4
Beetles		
Apion urticarium	0.1 ± 0.0	6.3
Parethelcus pollinarius	0.4 ± 1.3	18.8
Cidnorhinus quadrimaculatus	3.3 ± 6.0	65.6
Phyllobius pomacaeus	4.7 ± 7.8	59.4
Brachypterus urticae	17.7 ± 27.8	81.3
Predators		
Plant bugs		
Himacerus apterus	0.4 ± 0.5	28.1
Nabicula limbata	0.6 ± 0.6	40.6
Anthocoris nemorum	3.3 ± 3.7	75.0
Orius minutus	29.2 ± 22.1	100.0
Deraeocoris ruber	0.1 ± 0.0	9.4
Beetles		
Coccinella septempunctata	1.3 ± 1.2	62.5
Adalia bipunctata	0.5 ± 1.6	21.9
Adalia decempunctata	<0.1	3.1
Propylaea 14-punctata	1.4 ± 1.4	62.5
Tachyporus sp.	<0.1	3.1
Demetrias atricapillus	<0.1	3.1
Rhagonycha fulva	1.2 ± 2.9	28.1
Rhagonycha limbata	0.1 ± 0.5	6.3
Cantharis livida	0.5 ± 2.5	18.8

[a] Only the monophagous first generation was taken into account (89% of all individuals), since the second generation is polyphagous (Davis 1991)

dominance of nettles (%) was negatively correlated with *Coccinella septempunctata* density ($r^2 = 0.19$, $n = 32$, $P = 0.01$).

Total arthropod (insects and spiders) abundance was positively correlated with habitat area (Fig. 1A). In a multiple regression model, habitat area explained 27% of the variance of arthropod abundance (positively correlated), and isolation contributed a further 11.6% (negatively correlated, *Urtica* characteristics did not enter the model). The percentage of monophagous herbivore individuals in relation to all herbivores was also positively correlated to habitat area, but only weakly (Fig. 1B). Small, isolated sites had the lowest arthropod density, averaging only 58% of the density of large, connected sites (Fig. 1C).

Fragmentation of nettle habitats significantly reduced insect species numbers: total species richness (of Heteroptera, Auchenorrhyncha, and Coleoptera) was positively correlated with habitat area (Fig. 2A), but not significantly influenced by isolation or *Urtica* characteristics. This relationship was dominated by specialized herbivores: the number of species of monophagous herbivores was more closely correlated with habitat area (Fig. 2B) than was the number of all species, explaining 39.3% of the variance (while habitat isolation and *Urtica* characteristics did not significantly contribute to the model).

A comparison of monophagous and polyphagous herbivores showed that monophagous nettle specialists were much more affected by habitat area than polyphagous non-specialists. For monophagous herbivores, we found a z-value of 0.11 (Fig. 2B), whereas for all herbivores, the z-value was only 0.05 (log all herbivore species = $1.13 + 0.05 \log$ area; $F = 5.7$, $r^2 = 0.40$, $n = 32$, $P = 0.02$). Both the z-values ($F = 2.9$, $P = 0.09$) and the intercept ($F = 547$, $P < 0.001$) were statistically different. z is a constant in MacArthur and Wilson's (1967) equation $S = cA^z$, measuring the slope of the logarithmic species-area relationship, with A = area and S = species richness of a habitat. Regression of only the polyphagous herbivore species on area was not significant ($r^2 = 0.025$, $P = 0.38$).

In contrast to herbivore species richness, the number of predator species (of Heteroptera, Auchenorrhyncha, and Coleoptera) was not affected by habitat area (or *Urtica* characteristics), but only by habitat isolation (Fig. 2C). Furthermore, the percentage of predator species (of all 69 species) decreased with habitat isolation (Fig. 2D). A much smaller percentage of predator spe-

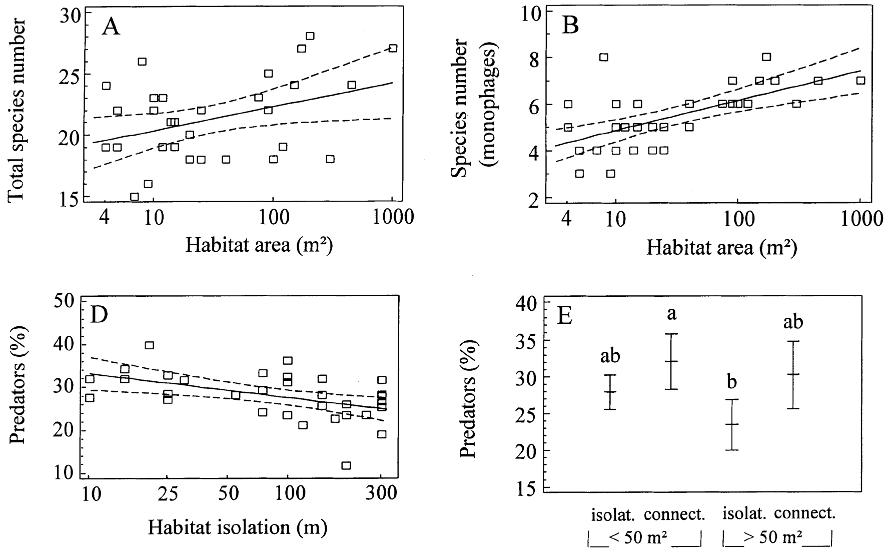

Fig. 2A–E Effects of habitat fragmentation on species numbers of phytophagous and predatory nettle insects, based on all Heteroptera (18 species), Auchenorrhyncha (20 species), and Coleoptera (31 species) ($n = 32$ nettle habitats). Regression lines and 95% confidence limits are given. **A** Dependence of total species number on habitat size: $y = 18.4 + 1.93 \log x$, $F = 4.9$, $r^2 = 0.14$, $n = 32$, $P < 0.05$. **B** Dependence of species number of monophagous herbivores (11 species) on habitat size: $y = 3.6 + 1.3 \log x$, $F = 19.4$, $r^2 = 0.39$, $n = 32$, $P < 0.001$. **C** Dependence of species number of predators (14 species) on habitat isolation: $y = 7.7-1.55 \log x$, $F = 7.2$, $r^2 = 0.19$, $n = 32$, $P = 0.01$. **D** Percentage of predator species in relation to habitat isolation: $y = 38.7 - 5.6 \log x$, $F = 9.7$, $r^2 = 0.24$, $n = 32$, $P = 0.005$. **E** Dependence of percentage of predator species on habitat fragmentation: $F = 3.9$, $n = 32$, $P < 0.05$. Homogenous groups have *identical letters* (Tukey test)

cies could be found on isolated than on connected habitats, independent of habitat area (< 50 m^2 versus > 50 m^2, Fig. 2E).

In logistic regressions, absence probabilities of monophagous herbivores could only be explained by habitat area (in 4 out of 10 species), whereas probability of predator absence could only be explained by habitat isolation (in 3 out of 14 species, Fig. 3). The incidence curves show that even relatively small distances to the nearest nettle bed affect survival of local predator populations.

Calculations of mean abundance and coefficient of variation for each species were based on the samples of the 11 largest habitats, since these ‘control’ habitats should give reliable estimates of the species’ performance in “near-natural”, little-fragmented habitats. Less abundant species occupied fewer nettle patches than did more abundant species (Fig. 4A). Abundance explained 78% of the variation in the percentage of occupied habitats. Coefficients of variation (CV), as a measure of the species’ variability in abundance, were also related to percentage of occupied habitats (Fig. 4B), explaining 71% of the variance. Abundance and variability (CV) were negatively correlated ($r^2 = 0.62$, $P < 0.001$). In contrast to expectations, herbivore species were not more abundant or less variable than predator species (Fig. 4).

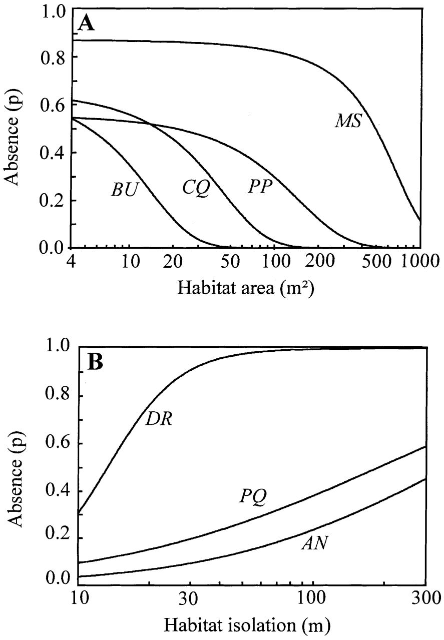

Fig. 3A, B Percentage absence of nettle insects on fragmented nettle patches (logistic regressions based on $n = 32$ habitats). **A** Monophagous herbivores in relation to habitat area (log-transformed m^2). *Macropsis scutellata* (*MS*): $a = 1.97$, $b = -0.004$, $X^2 = 3.7$, $P = 0.05$; *Cidnorhinus quadrimaculatus* (*CQ*): $a = 0.66$, $b = -0.042$, $X^2 = 11.2$, $P < 0.001$; *Phyllobius pomacaeus* (*PP*): $a = 0.24$, $b = -0.011$, $X^2 = 4.9$, $P < 0.05$; *Brachypterus urticae* (*BU*): $a = 0.71$, $b = -0.135$, $X^2 = 9.2$, $P < 0.005$. **B** Predatory species in relation to habitat isolation (log-transformed distance to the nearest *Urtica* habitat of at least 50 m^2). *Deraeocoris ruber* (*DR*): $a = 7.36$, $b = -6.57$, $X^2 = 9.9$, $P < 0.005$; *Propylaea 14-punctata* (*PQ*): $a = 4.0$, $b = -1.76$, $X^2 = 4.1$, $P < 0.05$; *Anthocoris nemorum* (*AN*): $a = 5.29$, $b = -2.06$, $X^2 = 3.8$, $P = 0.05$

Discussion

The results of this study emphasize that even small-scale habitat fragmentation of a widespread plant like *U dioica* causes a significant decrease in the diversity and popu-

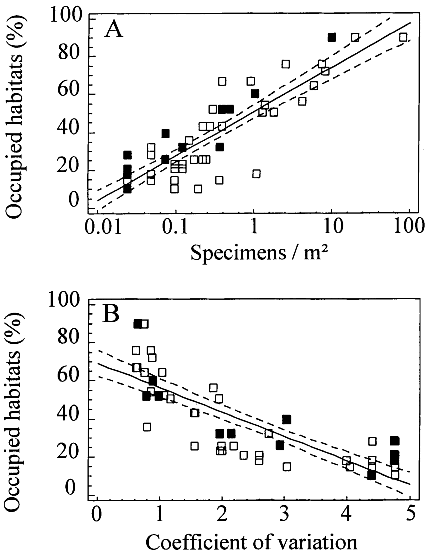

Fig. 4 Percentage of occupied habitats in relation to mean density of insect species (**A**): $y = 50.8 + 23.4 \log x$, $F = 200$, $r^2 = 0.78$, $n = 56$, $P < 0.001$; and coefficients of variation (**B**) (SD/X): $y = 69.1 - 12.8\ x$, $F = 132$, $r^2 = 0.71$, $n = 56$, $P < 0.001$. Analyses included the 56 species that occurred on at least one of the 11 largest (control) habitats and was based on their densities in these 11 largest habitats. Regression lines and 95% confidence limits are given (*open squares* herbivores, *filled squares* predators)

lation densities of associated insects. Small and isolated nettle habitats showed a reduced insect diversity and their total arthropod (insect and spider) density was only 58% of the density of large, connected sites. Such a decline in local abundance could well be a precursor to local extinction (Gaston 1994). Davis (1975) found that experimentally established nettle plots some 800 m from the nearest large nettle bed were colonized by only 50% of the local insect fauna within 3 years. In our study on naturally occurring nettle patches, monophagous herbivores could cope with fairly small habitats. Some species occupied 90% of nettle habitats when habitat area was 1000 m^2 (*Macropsis scutellata*), 200 m^2 (*P. pomaceus*), 70 m^2 (*C. quadrimaculatus*) or 20 m^2 (*Brachypterus urticae*) (Fig. 3A). Minimum area requirements, calculated for a 90% performance (related to the performance on the largest sites, i.e., on 1000 m^2 habitats), were 274 m^2 in total abundance (Fig. 1A), 230 m^2 in the percentage of monophagous herbivores (Fig. 1B), 56 m^2 in total species number (Fig. 2A), and 265 m^2 in the number of monophagous herbivore species (Fig. 2B). These results support similar findings from insects on *Spartina alterniflora* (Rey 1981), *Chamerion angustifolium* (MacGarvin 1982), *Helianthemum chamaecistus* (Davis and Jones 1986), and *Juniperus communis* (Ward and Lakhani 1977).

The species richness of monophagous nettle herbivores was more affected by decreasing habitat area than that of all herbivores, i.e., of both monophagous and polyphagous species: the slope of the log-log species-area relationship was much steeper (*z*-value: 0.11 versus 0.05). In addition, the percentage of monophagous herbivores increased with area. Similarly, the percentage of butterflies with monophagous caterpillars significantly increased with the area of 33 chalk grasslands in Germany (Rengelshausen et al. 1997), and Nieminen (1996) found in an analysis of island occupancy of moths in Finland that the extinction risk was lower for habitat generalists than specialists. Fragmentation of habitats can be generally expected to be of greater importance for monophages or other habitat specialists than for polyphages or generalists (see Lawton 1995), because they depend on conditions that are less likely to occur on small patches. For monophagous or otherwise specialized insects, the landscape produces a pattern of isolated habitat islands, whereas for polyphagous species, these islands may be connected by usable habitat patches, thereby producing a habitat continuum.

The main result of this study is the differential susceptibility of herbivores and predators to habitat fragmentation. In logistic regressions, the absence probability of monophagous herbivores could only be explained by habitat area (in 4 out of 10 species), and in predators only by habitat isolation (in 3 out of the 12 species). Furthermore, herbivore species richness correlated with habitat area and that of predators only with habitat isolation.

Four hypotheses may explain the observed patterns. (1) Rarity: the fact that predator populations may be smaller than those of their prey makes them more vulnerable to stochastic extinctions (Kruess and Tscharntke 1994, 1998), (2) Variability: population variability is often higher for natural enemies and thereby causes a higher extinction risk (Kruess and Tscharntke 1994, 1998; Tscharntke and Kruess 1998). (3) Dispersal power: predators may fail to colonize isolated habitats because they are bad dispersers (Turin and den Boer 1988). (4) Trophic level: colonizers from higher trophic levels are principally disadvantaged due to their dependence on successful establishment of prey populations (Schoener 1989; Pimm 1991; Lawton 1995; Holt 1996).

Predator populations did not prove to be generally smaller (hypothesis 1) or more variable (hypothesis 2) than their phytophagous prey (Fig. 4). In contrast, studies on clover and vetch insects showed that parasitoids had smaller and more variable populations than their hosts (Kruess and Tscharntke 1994, 1998). In general, parasitoids differ from predators in that they are much more specific and have very low population densities, even on a large-scale, landscape basis (see Greiler et al. 1991).

The predators found in this study appeared to have the dispersal power to connect local populations (hypothesis 3), since they are not restricted to prey items on nettles, but also use, for example, field margins in the agricultural landscape. Nevertheless, Walde and Nachman (1998) showed in *Tetranychus urticae-Phytoseiulus persimilis* dynamics that as inter-plant distance decreased and thereby predator dispersal was enhanced, density of prey decreased, and density of predators increased. Such promotion of between-habitat dispersal and biological control is also shown in results on aphid-predator interactions (Kareiva 1987, 1990; Müller and Godfray 1997).

Most convincing is the theoretically (Pimm 1991; Lawton 1995; Holt 1996) and empirically (Kareiva 1987, 1990; Kruess and Tscharntke 1994; Tscharntke and Kruess 1998) supported trophic-position hypothesis (hypothesis 4) that populations at the top of food chains are more likely to become extinct than those at lower trophic levels. Plant populations are a more stable and predictable resource for herbivores than are herbivore populations for predators. A greater susceptibility to extinction should make frequent colonization of habitat fragments more important for predators than for herbivores. Accordingly, the instability of higher-trophic-level populations should make dispersal limitation a major factor in local predator survival. Only predators with a rapid response to decreasing local prey populations, in that they quickly switch to the next prey population, may be able to survive. The susceptibility of polyphagous predators to fragmentation is ambiguous: they should suffer disadvantages from their trophic-level position, but they gain an advantage by being generalists when they colonize islands (see Becker 1992), so the mostly specialized and monophagous parasitoids should be more affected than generalist predators (Tscharntke and Kruess 1998).

Predators on nettle herbivores were greatly affected by habitat isolation of only small distances (up to 300 m). The threshold distance, calculated for a 90% performance (related to a minimum distance between *Urtica* habitats of 10 m), was 25 m for the number of predator species (Fig. 2C) and 39 m for the percentage of predator species (Fig. 2D). These distances already appeared to affect polyphagous predators due to the frequent incidences of disappearance and recolonization.

In conclusion, nettle patches may be particularly important as reservoirs of natural enemies attacking pest insects (Perrin 1975) so long as they are not isolated. Habitat connectivity appears to be important for increasing predator populations in the agricultural landscape for possible biocontrol of actual or potential pests.

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