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## Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*

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**Abstract** Effects of habitat fragmentation on species diversity and herbivore-parasitoid interactions were analyzed using the insect community of seed feeders and their parasitoids in the pods of the bush vetch (*Vicia sepium* L.). Field studies were carried out on 18 old meadows differing in area and isolation. The area of these meadows was found to be the major determinant of species diversity and population abundance of endophagous insects. Effects of isolation were further analyzed experimentally using 16 small plots with potted vetch plants isolated by 100–500 m from vetch populations on large old meadows. The results showed that colonization success greatly decreased with increasing isolation. In both cases, insect species were not equally affected. Parasitoids suffered more from habitat loss and isolation than their phytophagous hosts. Minimum area requirements, calculated from logistic regressions, were higher for parasitoids than for herbivores. In addition, percent parasitism of the herbivores significantly decreased with area loss and increasing isolation of *Vicia sepium* plots, supporting the trophic-level hypothesis of island biogeography. Species with high rates of absence on meadows and isolated plant plots were not only characterized by their high trophic level, but also by low abundance and high spatial population variability. Thus conservation of large and less isolated habitat remnants enhances species diversity and parasitism of potential pest insects, i.e., the stability of ecosystem functions.

**Key words** Island biogeography · Insect diversity · Herbivore-parasitoid interactions · Trophic levels · Biological control

### Introduction

Habitat fragmentation following increasing intensity of land use in the landscape (Burgess and Sharpe 1981) has been perceived as a major threat to biological diversity (Wilcove et al. 1986; Noss 1991; Saunders et al. 1991; Tschardtke 1992; Rosenzweig 1995). The effects of habitat fragmentation on species diversity can be mainly assigned to three processes: reduction of total habitat area within a region, loss of area within each single habitat, and increase in isolation between habitats (Andr en 1994). These three processes are interrelated in a non-linear way (Gustavson and Parker 1992). Theoretical models such as the equilibrium theory of island biogeography (MacArthur and Wilson 1967) predict the number of species on islands as a function of island size and isolation. Loss of species may lead to changes in ecosystem functions such as decomposition, pollination, parasitism, or predation (Kareiva 1987, 1990; Klein 1989; Kruess and Tschardtke 1994, 1999; Didham et al. 1996; Burkey 1997; Steffan-Dewenter and Tschardtke 1997; Didham 1998; Dubbert et al. 1998; Tschardtke and Kruess 1999). Ecosystem functions based on trophic structure were theoretically analyzed by Holt (1996), who investigated the general effects of area loss and isolation on food chain length and species of different trophic rank. He predicted that (1) food chain length should increase with area and decrease with isolation, and (2) that the slope of species-area and species-isolation curves should increase with trophic rank, either due to direct effects (e.g., decline of population size with trophic rank) or indirect effects (dependence of high-rank species on the presence of low-rank species). Not only trophic position but also feeding type may be differentially influenced by fragmentation, and several studies have examined the effects of fragmentation on both ectophagous (e.g., Davis 1975; Ward and Lakhani 1977; Rigby and Lawton 1981; Tschardtke 1992; Matter 1997; Zabel and Tschardtke 1998) and endophagous insect communities on plants (MacGarvin 1982; Davis and Jones 1986; Tschardtke 1992; Kruess 1996; Dubbert et al. 1998).

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**Table 1** List of landscape, meadow and host plant characteristics used in multiple regression analyses

Field studies on meadows	Field experiment with <i>Vicia sepium</i> plots
<i>Landscape characteristics</i>	<i>Landscape characteristics</i>
Number of meadows within a radius of 250 m	Total area of the “source meadow” (m <sup>2</sup> )
Number of meadows within a radius of 500 m	Distance to the source meadow (m)
Total area of meadows within a radius of 250 m (m <sup>2</sup> )	Distance to the nearest near-natural habitat <sup>c</sup> (m)
Total area of meadows within a radius of 500 m (m <sup>2</sup> )	Distance to the nearest fallow (m)
Distance to the nearest meadow (m)	Distance to the nearest hedge (m)
Distance to the nearest meadow (>2 ha) (m)	<i>V. sepium</i> plants m <sup>-2</sup> on source meadows
	<i>V. sepium</i> pods m <sup>-2</sup> on source meadows
<i>Meadow characteristics</i>	<i>Plant plot characteristics</i>
Meadow size (m <sup>2</sup> )	Mean plant height (cm)
Center/edge ratio <sup>a</sup>	Number of plants m <sup>-2</sup>
Number of vascular plant species per 49 m <sup>2</sup>	Number of pods m <sup>-2</sup>
Cover of vegetation (%) <sup>b</sup>	Mean pod length (cm)
Mean vegetation height (cm)	Mean number seeds pod <sup>-1</sup>
<i>Host plant characteristics</i>	
Number of legume species	
Cover of legume species (%)	
Number of <i>Vicia</i> species	
Cover of <i>Vicia</i> species (%)	
Cover of <i>V. sepium</i> (%)	
Pods m <sup>-2</sup> of <i>V. sepium</i>	
Mean pod length of <i>V. sepium</i> (cm)	
Mean seeds pod <sup>-1</sup> of <i>V. sepium</i>	

<sup>a</sup> Edge was defined as the 5 m wide margin. Center/edge ratio was calculated from the center area (m<sup>2</sup>) and the edge area (m<sup>2</sup>)

<sup>b</sup> Estimated by eye

<sup>c</sup> Including hedges, forest edges, and fallows

We analyzed the effects of fragmentation on the endophagous insects inhabiting the pods of bush vetch (*Vicia sepium*), including herbivores and parasitoids. Since endophagous insect communities are more likely to comprise specialized mono- or oligophagous species than ectophagous insects (Cornell 1989), area and isolation of habitats can be defined by the distribution of the host plant populations. Moreover, plant-insect systems with endophagous species seem to be more likely to show changes in diversity and abundance due to environmental changes since they are more host-specific and less mobile (Cornell 1989).

Previous experimental studies on the effects of isolation on colonization success of endophagous insect herbivores and their insect parasitoids on red clover (Kruess and Tscharrntke 1994, 1999; Kruess 1996) found that food-web interactions were disrupted: on isolated plant patches, parasitoid populations were more reduced than their phytophagous hosts. In this paper, results are presented from field samples and from a field experiment on the endophagous insect community in the pods of another legume, the bush vetch (*Vicia sepium*). Bush vetch is a very abundant and widely distributed plant species in old meadows in south-west Germany. The pods are easily collected and rearing success of the insects is high. Regional data on the range of host plants and hosts of the expected insects were available from Garbe (1996), who investigated the endophagous herbivores inhabiting the pods of 27 leguminous plant species in the Kraichgau region. Field samples were taken on extensively managed old meadows, to analyze the effects of habitat characteristics (e.g., area, vegetation, surrounding landscape). The field experiment tested the effects of isolation using small and isolated plots of potted vetches.

We addressed the following questions:

1. Are species richness and abundance affected by habitat area, habitat isolation, or other landscape, meadow, or host plant characteristics?
2. Are parasitoids more affected than herbivores?
3. Does higher susceptibility of parasitoid species lead to a reduction in parasitism?
4. How can species that are susceptible to habitat fragmentation be characterized?

## Material and methods

Field samples were taken in a region called Kraichgau, situated near Karlsruhe in south-west Germany. In the first half of this century, this landscape was dominated by extensively used meadows with scattered standard cherry and apple trees. Most of these meadows had areas of several hectares, often surrounding villages like “green belts”. Intensification of agricultural land use since the 1930s has led to a dramatic loss and fragmentation of these meadows. Nowadays, most of the remaining meadows are only small fragments of less than 1 ha. Few meadows of more than 10 ha still exist. Within a region of 400 km<sup>2</sup>, 18 meadows with areas ranging from 300 m<sup>2</sup> to 70 ha were selected to analyze the effect of habitat area. Selection criteria were similarity in age, management, vegetation, exposition, and soil type (Loess). All meadows were at least 30 years old and were mown annually in mid-July. They were scattered with apple trees and slightly exposed to the south or south-east. In June, vegetation of the meadows was mapped in 49-m<sup>2</sup> plots (1×49 m<sup>2</sup> on meadows <1000 m<sup>2</sup>, 2×49 m<sup>2</sup> on meadows of 1000–10,000 m<sup>2</sup>, and 4×49 m<sup>2</sup> on meadows >10,000 m<sup>2</sup>). The parameters used to characterize the landscape surrounding the meadows, the meadows and the host plants and considered in the statistical analyses are shown in Table 1. From 3 to 6 July, 200 pods of the bush vetch *V. sepium* were collected randomly from each meadow. The field experiment comprised 18 plots of potted *V. sepium* plants, each consisting of 12 pots, covering an area of 1.0 m<sup>2</sup>. Since this experiment was carried out to analyze the ef-

fects of isolation on colonization processes, we used five old meadows (area >2 ha) with naturally growing *V. sepium* as “sources”. One plant plot was placed in the center of each meadow (controls), and the other 13 plant plots were established in the same local environment (old field margins adjacent to cereal fields) in the area surrounding the meadows, separated by 100–500 m from the meadows. To avoid effects of plant variety, and nutrient and water availability, we used the same variety of *V. sepium* and the same potting compost for all plant plots. All plots were watered twice a week. Spatial arrangement of the plots was identical to that of an experiment done in 1992 with red clover plants (see Kruess and Tscharnke 1994 for details), but in June, two of the isolated plots were destroyed, so results are based on only 16 *Vicia* plots. Pods were collected six times between 7 June and 7 July, since only a few ripened pods were available at the same time. All together 2032 pods were collected, with the total number of pods per plot ranging from 101 to 155. Out of these, 100 pods per plot were randomly selected for dissection, in order to have equal sample sizes. Abundances (e.g., specimens m<sup>-2</sup>, pods m<sup>-2</sup>) were calculated on a total sampled area of 6 m<sup>2</sup> per plot (six sample times, plot size 1 m<sup>2</sup>).

The pods from both the meadow samples and the field experiment were individually separated in small plastic tubes for rearing insects. After 5 months, the pods were dissected, and pod length and number of seeds were measured. Species number and species composition of herbivores and parasitoids were recorded. Unknown insect species were sent to experts for identification (see Acknowledgements).

Statistical analyses (simple and multiple regression analyses, logistic regression analyses, and one-way ANOVA) were performed with Statgraphics Plus for Windows 3.0 (Manugistics 1996). Data were tested for normality, and if necessary log-transformed. Percentages were always arcsine-transformed.

## Results

### Meadow vegetation

Altogether the 18 meadows supported 126 plant species that occurred in at least one meadow). Species diversity ranged between 14 and 61 species of vascular plants per 49 m<sup>2</sup>. Multiple regression showed that plant species richness was positively correlated with the meadow area for both total number of vascular plant species [ $y=0.86+3.3\times\ln(x)$ ,  $F=20.4$ ,  $P=0.003$ ,  $r^2=0.56$ ,  $n=18$ ] and number of leguminous plant species [ $y=-0.2+0.61\times\ln(x)$ ,  $F=13.23$ ,  $P=0.002$ ,  $r^2=0.45$ ,  $n=18$ ]. Abundance (% plant cover) of *V. sepium* increased slightly from small to large meadows [ $\ln(y)=2.26+0.025\times\ln(x)$ ,  $F=5.0$ ,  $r^2=0.24$ ,  $P=0.04$ ,  $n=18$ ], but neither pod (pods m<sup>-2</sup>) nor seed abundance (seeds m<sup>-2</sup>) was correlated with meadow area (pods:  $F=1.88$ ,  $r^2=0.19$ ,  $P=0.19$ ; seeds:  $F=0.39$ ,  $r^2=0.02$ ,  $P=0.54$ ) or other habitat characteristics. Thus, resource abundance for seed-feeding herbivores did not change significantly from small to large meadows.

In the isolation experiment, seed set was negatively correlated with isolation of the plots, slightly decreasing from 3.8 seeds pod<sup>-1</sup> on the meadow plots to 3.3 seeds pod<sup>-1</sup> on the most isolated plots ( $y=3.81-9.9\times 10^{-4}x$ ,  $F=10.3$ ,  $r^2=0.43$ ,  $P=0.006$ ,  $n=16$ ). However, the abundance of pods (pods m<sup>-2</sup>) and seeds (seeds m<sup>-2</sup>) were not negatively affected by isolation (pods:  $F=0.07$ ,  $r^2=0.005$ ,  $P=0.79$ ; seeds:  $F=1.48$ ,  $r^2=0.09$ ,  $P=0.24$ ). Thus, resource availability did not differ between isolated and non-isolated plant plots.

### Insect community

The endophagous insects found in the pods of *V. sepium* comprised 4 phytophagous and 10 parasitoid species (Table 2). In the meadows, the herbivores were, from highest to lowest abundance, the weevil *Oxystoma ochropus*, the seed-beetle *Bruchus atomarius*, the weevil *Tychius quinquepunctatus* and the tortricid moth *Cydia nigricana*. The most abundant parasitoids were a pteromalid wasp *Pteromalus sequester*, two braconid wasps *Pigeria piger* and *Triaspis thoracicus*, and an eupelmid wasp *Eupelmus vesicularis*. All other parasitoids had low abundances ( $\leq 1$  individuals per 100 m<sup>2</sup>) and were found on only one or two meadows.

Five parasitoid species attacked the tortricid moth *C. nigricana*, four species parasitized the weevil *O. ochropus*, and one species, *T. thoracicus*, parasitized the seed-beetle *B. atomarius*. The weevil *Tychius quinquepunctatus* was not attacked by parasitoids (Table 2). In the field experiment, the number of insect species that successfully colonized the small plots of potted *V. sepium* plants was lower because there were fewer parasitoids: only four parasitoids were found on the control plots (see Table 2).

### Species diversity

The distribution of the insect species among the 18 different-sized meadows is shown in Table 2. Three of the herbivores (*O. ochropus*, *B. atomarius*, and *C. nigricana*) were recorded on meadows of all size classes while the weevil *T. quinquepunctatus* was absent from meadows smaller than 0.3 ha. This absence on small meadows was significantly different from an equal distribution of this species on all meadows ( $\chi^2=6.33$ ,  $P=0.05$ ). In contrast to their hosts, the parasitoids were more scattered. Species diversity of parasitoids was highest on both the largest and the smallest meadows, but species composition differed. Three parasitoids were found only on large meadows (*Scambus annulatus*, *Glabrobracon* sp. 1, *Entedon* cf. *procioni*) or the smallest meadows (*Pristomerus vulnerator*, *Glabrobracon* sp. 2, *Trichomalus repandus*), respectively.

Regression analyses showed that species diversity of both herbivores and parasitoids increased with habitat area (Fig. 1a,b), but the slope of the species-area relationship was steeper for parasitoids than for herbivores. Only two of the small meadows (<1 ha) supported more than two parasitoid species, whereas in large meadows (>1.6 ha) at least four parasitoid species were always found. Nevertheless, even in each of the large meadows, species richness of parasitoids was only 50% of the total richness of parasitoids. In the field experiment, multiple regression analyses showed a significantly negative species-isolation relationship for both herbivores and parasitoids. Number of herbivores decreased from four species on the control plots to two species on the most isolated plots (Fig. 1c). Number of parasitoids was approxi-

**Table 2** The insect community in pods of *Vicia sepium*. Hosts of the parasitoids are indicated by *superscript arabic numerals* corresponding with herbivore numbers. Meadow study: mean ( $\bar{x}$ ), minimum and maximum abundance, and the number of meadows of different size classes with insect populations are given. Field experiment: mean ( $\bar{x}$ ), minimum and maximum abundance on colonized plots are given for control plots and isolated plots. The numbers of colonized plots are listed for isolated plots and for all plots. For range of host plants and hosts see footnotes

	Meadow study				Field experiment				
	Specimens per 100 m <sup>2</sup> on all meadows $\bar{x}$ (min./max.), n=18	>10 ha n=6	>1 ha n=2	>0.1 ha n=6	>0.01 ha n=4	All meadows n=18	Specimens per 100 m <sup>2</sup> on control plots $\bar{x}$ (min./max.), n=5	Specimens per 100m <sup>2</sup> on isolated plots with populations $\bar{x}$ (min./max.)	Number of isolated plots with populations n=11 (n=16)
<b>Phytophagous insects</b>									
1. <i>Oxytoma ochropus</i> (Germ.) (Col., Apionidae) <sup>a</sup>	363 (156/709)	6	2	6	4	18	576 (450/783)	225 (67/383)	4 (9)
2. <i>Bruchus atomarius</i> (L.) (Col., Bruchidae) <sup>a</sup>	261 (26/1286)	6	2	6	4	18	377 (250/700)	312 (66/517)	11 (16)
3. <i>Tychius quinquepunctatus</i> (L.) (Col., Curculionidae) <sup>b</sup>	128.7 (0/665)	6	1	3	–	10	450 (300/850)	–	0 (5)
4. <i>Cydia nigricana</i> (F.) (Lep., Tortricidae) <sup>c</sup>	81.7 (0/397)	6	2	6	3	17	127 (100/167)	112 (16/300)	11 (16)
<b>Parasitoids</b>									
<i>Pteromalus sequester</i> (Walk.) (Hym., Pteromalidae) <sup>d,1</sup>	228.3 (0/516)	6	2	6	3	17	293 (217/383)	33 (33/33)	1 (6)
<i>Eupelmus vesicularis</i> (Retz.) (Hym., Eupelmidae) <sup>e,1</sup>	9.1 (0/36)	6	2	2	1	11	10 (0/17)	–	0 (3)
<i>Trichomalus repandus</i> (Walk.) (Hym., Pteromalidae) <sup>1</sup>	0.13 (0/2)	–	–	–	1	1	–	–	–
<i>Entedon cf. procioni</i> (Erd.) (Hym., Eupelmidae) <sup>1</sup>	0.05 (0/0.7)	1	–	–	–	1	–	–	–
<i>Triaspis thiracicus</i> (Curt) (Hym., Braconidae) <sup>2</sup>	16.1 (0/81)	6	1	–	1	8	3.3 (0/17)	–	0 (3)
<i>Pigeria piger</i> (Wesm.) (Hym., Braconidae) <sup>1,4</sup>	21.3 (0/190)	6	2	–	1	9	90 (0/150)	–	0 (4)
<i>Glabrobracon</i> sp. 1 (Hym., Braconidae) <sup>4</sup>	4.2 (0/49)	1	1	–	–	2	–	–	–
<i>Scambus annulatus</i> (Kiss) (Hym., Ichneumonidae) <sup>§,4</sup>	1.0 (0/18)	1	–	–	–	1	–	–	–
<i>Pristomerus vulnerator</i> (Pz.) (Hym., Ichneumonidae) <sup>§,4</sup>	1.0 (0/3)	–	–	–	1	1	–	–	–
<i>Glabrobracon</i> sp. 2 (Hym., Braconidae) <sup>4</sup>	0.3 (0/6)	–	–	–	1	1	–	–	–

Range of hosts or host plants (Peck et al. 1964; Horstmann 1990; Garbe 1996)

<sup>a</sup> Feeding on *V. sepium* only

<sup>b</sup> Also feeding on seeds of *Lathyrus pratensis*, but very occasionally

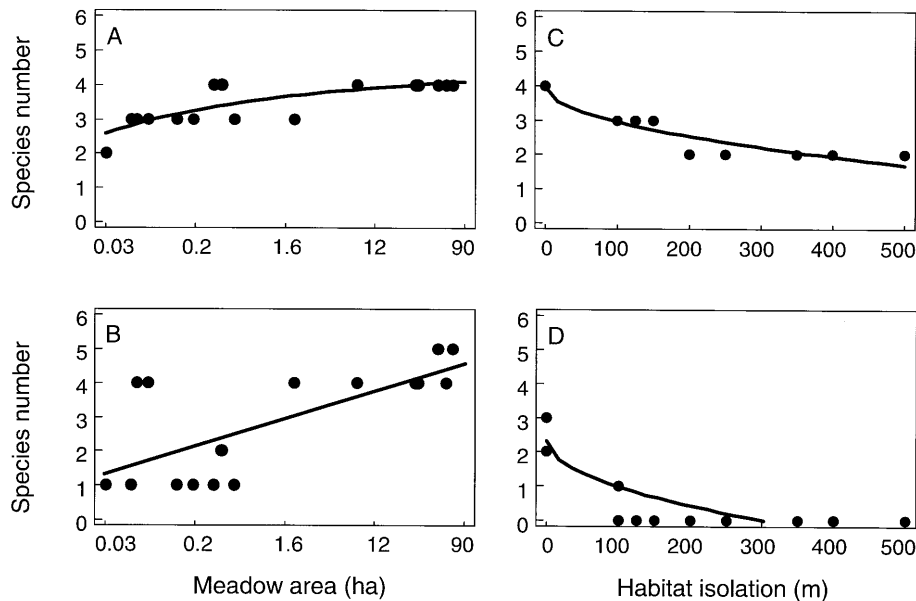
<sup>c</sup> Feeding on seeds of *Lathyrus aphaca*, *L. pratensis*, *L. niger*, and *Vicia tetrasperma*

<sup>d</sup> Also attacking hosts in the pods of *Astragalus glycyphyllos*, *Cytisus scoparius*, *Genista tinctoria*, *Lathyrus pratensis* and *Vicia cracca*

<sup>e</sup> A polyphagous ectoparasitoid with a broad range of hosts

<sup>f</sup> Also attacking hosts in pods of *A. glycyphyllos*, *Lathyrus aphaca*, *L. pratensis*, *Lotus corniculatus* and *Vicia cracca*

<sup>§</sup> Attacking tortricid moths.



**Fig. 1A,B** Dependence of species richness on habitat size of old meadows. **A** Number of phytophagous insect species:  $y=5.19-14.86/\ln(x)$ ,  $F=28.7$ ,  $r^2=0.64$ ,  $P<0.001$ ,  $n=18$ . **B** Number of parasitoid species:  $y=-1.00+0.41/\ln(x)$ ,  $F=17.7$ ,  $r^2=0.53$ ,  $P<0.001$ ,  $n=18$ . Comparison of regression lines of phytophagous and parasitoid species showed significant differences in both slope ( $F=5.4$ ,  $P=0.026$ ) and intercept ( $F=4.8$ ,  $P=0.037$ ). **C,D** Depen-

dence of species richness on isolation of small *Vicia* plots. **C** Number of phytophagous insect species:  $y=3.97-0.10\sqrt{x}$ ,  $F=179.3$ ,  $r^2=0.93$ ,  $P<0.001$ ,  $n=16$ . **D** Number of parasitoid species:  $y=2.31-0.13\sqrt{x}$ ,  $F=52.13$ ,  $r^2=0.79$ ,  $P<0.001$ ,  $n=16$ . Comparison of regression lines of phytophagous and parasitoid species showed no difference in the slopes but significant differences in the intercepts ( $F=152$ ,  $P<0.001$ )

**Table 3** Results from logistic regression analyses on the relation between species presence and meadow area [ $y=e^{a+bx}/(1+e^{a+bx})$ ,  $x=\ln(\text{meadow area})$ ,  $y=\text{species presence}$ ]. Estimated minimum areas required for 90% occupancy of meadows for insect herbivores and parasitoids are given

Species	<i>a</i>	<i>b</i>	<i>P</i>	PD <sup>a</sup>	$\chi^2$	Minimum area (m <sup>2</sup> )
<i>Cydia nigricana</i>	-14.7119	2.4691	0.0185	0.73	5.5	942
<i>Tychius quinquepunctatus</i>	-8.98899	1.0322	0.0004	0.52	12.7	50881
<i>Eupelmus vesicularis</i>	-8.56803	1.0428	0.0007	0.48	11.5	30437
<i>Triaspis thoracicus</i>	-5.50586	0.5819	0.0056	0.31	7.7	561190
<i>Pigeria piger</i>	-6.27436	0.6233	0.0034	0.35	8.6	799300

<sup>a</sup>Percentage of deviance (similar to  $r^2$  statistic)

mately 2.5 species on the control plots and decreased to no species on the isolated plots (Fig. 1d).

The presence-absence pattern of the insect species on the meadows was analyzed by logistic regression. Both ubiquitous species (*Bruchus atomarius*, *Oxystoma ochropus*, *Pteromalus sequester*) and rare species (Table 2) were excluded from analysis. For the two remaining herbivores (*Cydia nigricana*, *Tychius quinquepunctatus*) and the three parasitoids (*Eupelmus vesicularis*, *Pigeria piger*, *Triaspis thoracicus*), the best-fit regression was obtained using log area (Table 3). Using the equations from the logistic regressions, the minimum area requirement for a 90% probability of site occupancy was calculated (Table 3). In pairwise comparison, area requirements were higher for parasitoids than for their hosts. For example in *T. thoracicus*, the calculated minimum area for 90% meadow occupancy was 56 ha, but its host, *B. atomarius*, was distributed from the largest to the smallest meadows. The area requirement of *P. piger* was highest at 80 ha, but its host *C. nigricana* had a 90% oc-

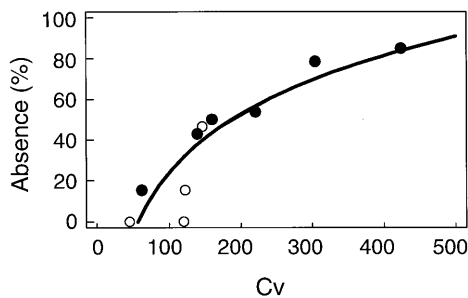
cupancy of habitats at only 942 m<sup>2</sup>. The polyphagous parasitoid *E. vesicularis* required 3 ha for 90% probability of site occupancy, whereas its host *O. ochropus* colonized all meadows. Host abundance did not significantly contribute to the explanation of the presence-absence pattern of these parasitoids in logistic regression.

#### Species abundance and population variability

Only for one herbivore species was abundance related to habitat area. Number of specimens m<sup>-2</sup> of *Tychius quinquepunctatus* was positively correlated with meadow area [ $y=-1.12+0.46/\ln(x)$ ,  $F=13.2$ ,  $r^2=0.45$ ,  $P<0.01$ ,  $n=18$ ]. Host plant abundance (plant cover, pods m<sup>-2</sup>, seeds m<sup>-2</sup>) had no effect. The other herbivore species did not show any correlation between abundance and habitat characteristics (area, isolation) or host plant abundance. In the field experiment, abundances of two herbivores were found to be negatively affected by isolation. Density of

the weevil *O. ochropus* decreased from 525 specimens per 100 m<sup>2</sup> on the control plots to 225 specimens per 100 m<sup>2</sup> on plots isolated by 100–150 m ( $y=5.55-0.29\sqrt{x}$ ,  $F=67.5$ ,  $r^2=0.83$ ,  $P<0.001$ ,  $n=16$ , see also Table 2). More isolated plots were not successfully colonized. Abundance of the weevil *T. quinquepunctatus* was affected by isolation in that this species did not colonize any of the isolated plant plots, though density of this weevil (488 specimens per 100 m<sup>2</sup>) on the control plots was very similar to that of *O. ochropus*.

Two additional variables, the absence rate, and the population variability, were calculated to characterize the species. Absence rate of a species was defined as percentage of the 18 meadows on which this species was not found. Population variability was calculated as coefficient of variation ( $CV=100 s/\bar{x}$ ) of species abundance on all 18 meadows. We used CV since it is insensitive against differences between means and low abundances (Sokal and Rohlf 1995). We also included different calculations of CV (including or excluding zeros) in the regression analyses but did not find differences in the re-



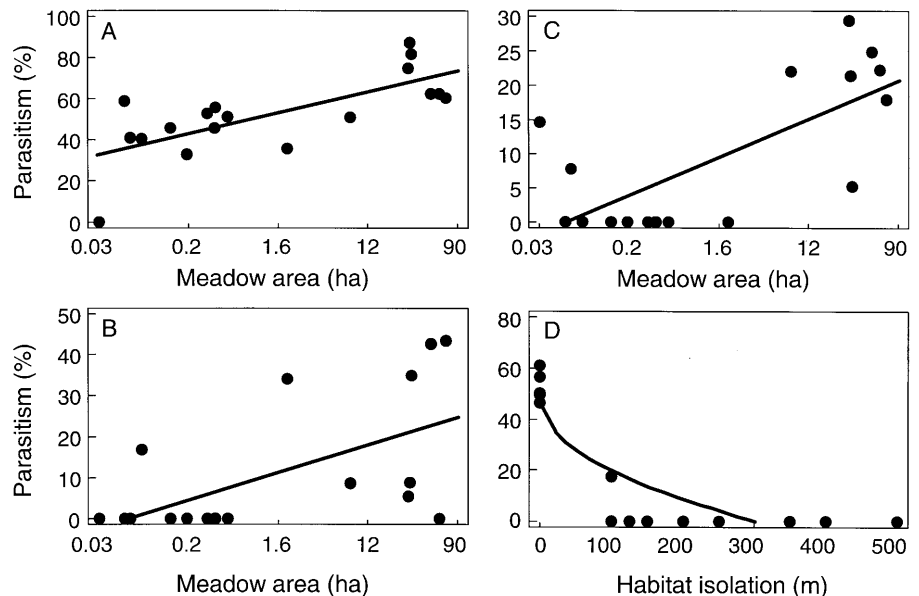
**Fig. 2** Percent absence of the herbivore (open circles) and parasitoid (filled circles) species on the meadows depending on population variability (Cv):  $y=-40.01+6.17\sqrt{x}$ ,  $F=102.5$ ,  $r^2=0.89$ ,  $P<0.001$ ,  $n=14$

sults. Multiple regression analyses showed that absence rate was significantly correlated only with the coefficient of variation (CV, see Fig. 2), but the coefficient of variation and the mean species abundance were negatively correlated [ $y=335.86-45.72 \ln(x)$ ,  $F=107.4$ ,  $r^2=0.90$ ,  $P<0.001$ ,  $n=14$ ]. Thus, species that showed a high absence rate, were characterized by both low abundance and higher population variability. Moreover, species with a high absence rate on the meadows also showed a high absence rate on the small plant plots and vice versa (Spearman's rank correlation:  $r_s=0.8$ ,  $P=0.034$ ,  $n=8$ , species found in the isolation experiment).

### Parasitism

Changes in percent parasitism were also analyzed with regard to habitat fragmentation as well as plant and host characteristics. For the three parasitized herbivores percent parasitism on the meadows was only affected by habitat size (Fig. 3a,b,c), whereas habitat isolation, host abundance, and plant characteristics had no significant effects. The weevil *O. ochropus* suffered most from parasitism, with a parasitism rate between 60% and 80% on large meadows, compared to 40% on the smallest meadows (Fig. 3a). Percent parasitism of the seed beetle *Bruchus atomarius* decreased from 25% on the largest meadows to nearly zero on the smallest meadows (Fig. 3b). Similarly, parasitism of the pea moth decreased from more than 20% on large meadows to nearly zero on the smallest meadows (Fig. 3c). In the field experiment, parasitism of the weevil *O. ochropus* was negatively affected by isolation (Fig. 3d). Though four isolated (by 100–150 m) *Vicia* plots were successfully colonized by *O. ochropus* (see Table 2), parasitoids attacked this weevil on only one plot. Percent parasitism on this isolated plot was very low (19%) compared to parasitism on the control plots (53%).

**Fig. 3A–C** Dependence of percent parasitism on habitat size of old meadows. **A** *Oxystoma ochropus*:  $y=56.03+5.64/\ln(x)$ ,  $F=16.8$ ,  $r^2=0.51$ ,  $P<0.001$ ,  $n=18$ . **B** *Bruchus atomarius*:  $y=-17.51+2.79 \ln(x)$ ,  $F=16.6$ ,  $r^2=0.51$ ,  $P<0.001$ . **C** *Cydia nigricana*:  $y=-22.71+3.49 \ln(x)$ ,  $F=7.3$ ,  $r^2=0.32$ ,  $P=0.01$ ,  $n=18$ . **D** Dependence of percent parasitism on isolation of small *Vicia* plots. *Oxystoma ochropus*:  $y=46.53-2.68\sqrt{x}$ ,  $F=62.72$ ,  $r^2=0.82$ ,  $P<0.001$ ,  $n=16$



## Discussion

The hypothesis that habitat area is an important determinant of species diversity (Williams 1964; MacArthur and Wilson 1967; Brown 1971; Wilson and Willis 1975; Diamond and May 1976; Wilcox 1980; Wilcox and Murphy 1985; Thornton et al. 1993) was supported by our studies. These species-area effects may be explained by the area-per-se hypothesis or the habitat-heterogeneity hypothesis. In general, area-per-se effects can be caused by: (1) a higher random extinction probability due to smaller population sizes in smaller areas (Shaffer 1981; Gilpin and Soulé 1986; Have 1993; Baur and Erhardt 1995; Lei and Hanski 1997), or (2) the random-sample effect in that larger samples have a higher probability of containing more species (Connor and McCoy 1979; Haila 1983; Haila and Järvinen 1983). According to the habitat-heterogeneity hypothesis species richness is positively linked to habitat heterogeneity. On larger areas different habitat types are more likely to be included, and different habitats support different communities, thus supporting higher species richness (Williams 1964; Lack 1969, 1976; Johnson and Simberloff 1974; Williamson 1981; Rosenzweig 1995). Sample effects can be excluded because the sample size was equal in all habitats. Since the herbivorous insects in this study are almost completely restricted to one plant species, the bush vetch *V. sepium*, habitat heterogeneity should have a low impact on species diversity of these herbivores. This is also supported by the results from multiple regression analyses in that meadow characteristics (species richness of vascular plants, legumes and *Vicia* species, percent cover of total vegetation, legumes, and *Vicia* species) could not be related to species diversity. Further, resource concentration (Root 1973; e.g., pods  $m^{-2}$ , and seeds  $pod^{-1}$ ) were independent of area. Since the field experiment (where landscape and habitat variables were kept constant) gave similar results to the meadow analyses, we argue that possibly confounding landscape effects were of minor importance. Therefore, the species-area relationships found in this study are likely to be caused by the high extinction probability of small populations. In fact, the probability of a species being absent was associated with small populations, but even more with spatial population variability (as in Kruess and Tscharrntke 1994). Since the small meadows were remnants of former large meadows, it is most likely that historically species richness of the former large meadows had been similar to species richness of the large meadows of this study. Thus decline in species richness on the small meadows can be attributed to extinction processes. According to the results from our field experiment, only the most abundant species colonized small meadows. Decline in species richness with decrease in habitat area was steeper for parasitoids than for their phytophagous hosts. In logistic regression analyses of the percent absence of species and meadow area, minimum area requirements were up to 10 times higher for parasitoids than for herbivores. Species on the third trophic level,

characterized by small and variable populations, were more affected by fragmentation than species on the second trophic level. This has been theoretically predicted (Pimm 1991; Lawton 1995; Holt 1996) and empirically supported by field studies (Kareiva 1987, 1990; Kruess and Tscharrntke 1994, 1999; Lei and Hanski 1997; Roland and Taylor 1997; Zabel and Tscharrntke 1998; Dubbert et al. 1998). In addition to the trophic-level position, parasitoids were less abundant and had more variable populations, which is generally found to be a major characteristic of species prone to extinction. As shown in the field experiment with isolated *Vicia* plots, large insect populations on large meadows functioned as "source populations", whereas less abundant species failed to colonize plant plots isolated by 100 m or more (see also Kruess and Tscharrntke 1994; Tscharrntke and Kruess 1999). Percent parasitism of the weevil *O. ochropus* was an increasing function of area, doubling from 35% on the smallest to 70% on the largest meadows. A similar pattern was found for parasitism of two other herbivores, the seed-beetle *B. atomarius*, and the pea moth *C. nigricana*. This disruption in food-web interactions can be explained by a decline of both parasitoid species richness and abundance of parasitoids caused by reductions in habitat area. Habitat isolation also negatively affected herbivore-parasitoid interactions, as shown in the field experiment: (1) on the isolated plant plots only one phytophagous species (*O. ochropus*) was attacked by parasitoids compared to three species on the old meadows, (2) percent parasitism of *O. ochropus* was at least 50% lower on the isolated plots than on the control plots and decreased to zero on the most isolated plots. The high susceptibility of the third trophic level to habitat fragmentation supports previous results (Kruess and Tscharrntke 1994, 1999; Zabel and Tscharrntke 1998). These results give support to the general conclusion that habitat fragmentation in the agricultural landscape releases herbivores from parasitism. Since pest populations are often limited by top-down control of parasitoids (LaSalle and Gauld 1991; Hawkins and Gross 1992; LaSalle 1993), decreases in percent parasitism (shown in this study) may sometimes favour pest outbreaks. This has been shown by Kareiva (1987) for an aphid-predator system in which population explosions of aphids were more frequent on small than large patches of goldenrod. Roland and Taylor (1997) found that outbreaks of the tent caterpillar *Malacosoma disstria* lasted longer in fragmented forest due to low parasitism. In bush vetch *V. sepium*, changes in herbivore abundance with area did not show a general pattern. Only in the weevil *T. quinquepunctatus* were abundance and area correlated. But this species was not attacked by parasitoids and, opposite to the findings of Kareiva (1987), abundance was positively correlated with area. Since *T. quinquepunctatus* did not occur on meadows smaller than 3000  $m^2$ , it is likely that a critical threshold in minimum area requirement (Kareiva and Wennergren 1995; With and Christ 1995; Andrén 1996; Bascompte and Solé 1996) caused this abundance-area pattern.

In conclusion, the results of this paper indicate that remnant large habitats play an important role in (1) the conservation of species richness of insect communities, and (2) the enhancement of parasitoid populations relative to herbivore populations, and thereby, in the preservation of herbivore-parasitoid interactions. Habitat isolation of only a few hundred meters negatively affected the colonization process of insects and destabilized herbivore-parasitoid interactions. Species that were most likely to be negatively affected by habitat fragmentation could be characterized by their trophic position, which was associated with small and variable populations.

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