Oecologia (2000) 125:559–572
DOI 10.1007/s004420000483

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Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation

Received: 16 November 1999 / Accepted: 27 June 2000 / Published online: 22 July 2000

Abstract The fragmentation of natural habitats is generally considered to be a major threat to biodiversity. We investigated short-term responses of vascular plants (grasses and forbs) and four groups of invertebrates (ants, butterflies, grasshoppers and gastropods) to experimental fragmentation of calcareous grassland in the north-western Jura mountains, Switzerland. Three years after the initiation of fragmentation – which was created and maintained by mowing the area between the fragments – we compared species richness, diversity and composition of the different groups and the abundance of single species in fragments of different size (area: 20.25 m^2, 2.25 m^2 and 0.25 m^2) with those in corresponding control plots. The abundances of 19 (29%) of the 65 common species examined were affected by fragmentation. However, the experimental fragmentation affected different taxonomic groups and single species to a different extent. Butterflies, the most mobile animals among the invertebrates studied, reacted most sensitively: species richness and foraging abundances of single butterfly species were lower in fragments than in control plots. Of the few other taxonomic groups or single species that were affected by the experimental fragmentation, most had a higher species richness or abundance in fragments than in control plots. This is probably because the type of fragmentation used is beneficial to some plants via decreased competition intensity along the fragment edges, and because some animals may use fragments as retreats between foraging bouts into the mown isolation area.

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Keywords Biodiversity · Calcareous grassland · Habitat fragmentation · Species richness

Introduction

Due to human pressures, many terrestrial habitats are being rapidly changed, destroyed and fragmented, species are becoming extinct and gene pools are reduced – and all this at an increasing and historically unprecedented rate. Habitat fragmentation is generally considered to be one of the major threats to biodiversity (Quinn and Hastings 1987; Bolger et al. 1991; Harrison 1991; Saunders et al. 1991; Seitz and Loeschcke 1991; Margules and Milkovits 1994; Diffendorfer et al. 1995b). Fragmentation reduces the total area of original habitat, creates isolated subpopulations, thus disrupting individual behaviour (e.g. Davies and Margules 1998), the exchange of genes between populations (e.g. Lacy and Lindenmayer 1995; Gaines et al. 1997), species interactions (e.g. Kruess and Tscharntke 1994; Arango-Velez and Kattan 1997; Lei and Hanski 1997) and ecological processes (e.g. Robinson et al. 1992). Thus, habitat fragmentation can influence an entire suite of processes, ranging from individual behaviour through population dynamics to ecosystem fluxes.

The response of plant and animal species to habitat fragmentation depends on their dispersal behaviour, their demography, their competitiveness, and on the size of the fragments (Kareiva 1987; Saunders et al. 1991; Tilman 1994). Furthermore, habitat fragmentation occurs on many different spatial scales (Simberloff 1988; Lord and Norton 1990; Kareiva and Wennergren 1995), and ranges from small breaks in an otherwise homogeneous habitat to widely scattered fragments in a surrounding area (Wiens 1989). For each species, the relevant spatial scale is different (Forman and Godron 1986; Wiens 1994).

Up to now, few studies have simultaneously examined effects of habitat fragmentation on different taxo-

nomic groups (Robinson et al. 1992). However, only multispecies approaches covering different groups of organisms allow an assessment of species interactions at higher trophic levels. For example, changing plant diversity due to fragmentation may also influence parasite and predator foraging efficiency and the interactions between herbivores and their predators (e.g. Strong et al. 1984; Golden and Crist 1999). Furthermore, most earlier studies of habitat fragmentation have focused on conspicuous animals like large mammals (Bowers et al. 1996; Peacock and Smith 1997), birds (Schmiegelow et al. 1997) and butterflies (Cappuccino and Martin 1997; Sutcliffe et al. 1997), or plants (Holt et al. 1995). Experimental studies of the effect of small-scale fragmentation on less conspicuous animal species are scarce.

The unfertilised calcareous grassland of the north-western Jura mountains in Switzerland harbours a variety of invertebrates and vascular plants (Zoller 1954; Baur et al. 1996). This sensitive habitat type has diminished dramatically during recent decades due to changes in agricultural practices, such as increased fertilisation (Fischer and Stöcklin 1997) or abandonment and reforestation (Zoller and Bischof 1980; Küchli et al. 1999). For example, in the Passwang region 24 km south of Basel, unfertilised grasslands decreased by 78% between 1950 and 1985 (Zoller et al. 1986). The rapid habitat change and fragmentation of the grasslands have resulted in significant losses of specialist plant species (Fischer and Stöcklin 1997) and the same may be true for invertebrates as well (Baur et al. 1996).

The aim of this study was to examine effects of habitat fragmentation under experimental, controlled conditions. Large-scale fragmentation, such as occurs on the landscape level, is hardly amenable to experimental investigations. However, findings obtained in a controlled small-scale experiment may to some degree give important insights into the effects of fragmentation at the landscape level.

We investigated the short-term responses of vascular plants (grasses and forbs) and four groups of invertebrates (ants, butterflies, grasshoppers and gastropods) to small-scale experimental grassland fragmentation. In particular, we compared species richness, diversity and composition, and the abundance of single species between fragments of various sizes and corresponding control plots 3 years after the initiation of the fragmentation experiment. We also examined how microclimate and productivity (above-ground biomass) were influenced by fragmentation, and whether productivity was correlated with species richness in plants and four invertebrate groups in the fragments and control plots.

Material and methods

Study sites

The fragmentation experiment was carried out in three calcareous grasslands situated in the region of Basel (47°34′N, 7°35′E) in the north-western Swiss Jura mountains: in Nenzlingen (13 km south of Basel), Movelier (26 km south-west of Basel) and Vicques (26 km south-south-west of Basel). Originally covered by beech forest, these grasslands have been grazed by cattle for many centuries, leading to the characteristic vegetation of the *Teucrio-Mesobrometum* (Zoller 1947; Schläpfer et al. 1998).

The study site in Nenzlingen is situated on a south-west-facing slope with an inclination of 19–22° at an altitude of 510 m. A deciduous forest borders the study area to the north-east. Mean annual temperature is around 8.5–9.0°C (the average July temperature is approximately 17°C) and annual precipitation is 900 mm (Ogermann et al. 1994). Snow usually covers the area for less than 1 month. Soils are of the rendzina type with an A horizon varying in depth from 2 to 27 cm (for details on soil properties and profiles see Ogermann et al. 1994). Until 1993, the site was grazed by cattle from May to September with a high stocking rate. The lower part of the slope was moderately fertilised by cattle dung.

The study site in Movelier is situated on a south-south-east-facing slope (inclination 20–22°) at an altitude of 770 m. Half of the site is surrounded by deciduous forest. Snow usually covers the site for more than 1 month. The humus layer is thicker than in Nenzlingen, contains some clay and is moister than at the other two sites. Until 1993, the site was grazed by cattle and a moderate amount of artificial fertiliser was used.

The study site in Vicques is situated on a south-east-facing slope (inclination 15–27°) at an altitude of 590 m. Snow usually covers the area for a few days only. The humus layer is extremely thin and there are several patches of exposed bedrock (this type of habitat is absent at the other sites). There is mixed deciduous forest at the south-west border of the area. Until 1993, the site was exposed to a low grazing pressure by cattle.

Fragmentation experiment

The experimental fragmentation of the grasslands was created in spring 1993 by mowing the vegetation around the experimental fragments. One experimental unit ("block"), contains one large (4.5×4.5 m), one medium (1.5×1.5 m) and two small (0.5×0.5 m) fragments, all of them separated by a 5-m-wide strip of mown vegetation, as well as the corresponding control plots, which are mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Within each block, the positions of the different sizes of fragment-control plot pairs as well as the control and fragment halves were randomised. The experimental set-up consists of 12 blocks with 48 fragments (24 small, 12 medium and

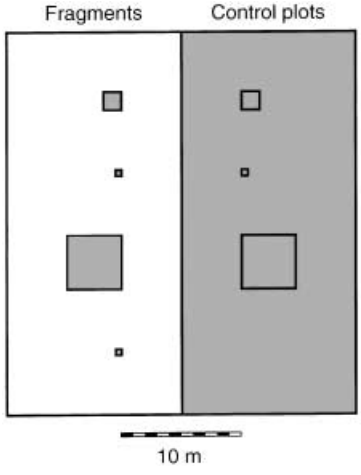

Fig. 1 Diagram of one block of the fragmentation experiment. A block contains two small (0.5×0.5 m), one medium (1.5×1.5 m) and one large (4.5×4.5 m) fragment and corresponding control plots. The isolation area between the fragments (*open*) is frequently mown

12 large) and 48 corresponding control plots distributed over the three study sites. Five blocks are situated at Nenzlingen, three blocks at Movelier and four blocks at Vicques. The distances between blocks within the sites range from 25 to 135 m. The distance between sites ranges from 9 to 19 km. At each site, the blocks are part of a larger study area (1.5–2 ha) enclosed by a fence to exclude large herbivores. The experimental fragmentation has been maintained since April 1993 by frequently (6–12 times per year) mowing the area between the fragments in the period from March to October. The entire experimental area is mown in late autumn every year to prevent succession (Kienzle 1979).

Field methods

Abundance data on vascular plants, ants, butterflies, grasshoppers and gastropods were collected between March and October 1996 in all fragments and control plots of every block. We used exclusively non-destructive methods, i.e. no plants or animals were removed.

To estimate the abundance of the various plant species, the number of grass and graminoid culms and the number of rooting shoots and rosettes of herbaceous plants were counted in each plot. A grid (0.5 m×0.5 m) laid over the plots facilitated the counting. Woody plants were regularly removed and are therefore not considered. Each plot was examined three times: in May/June, June/July and August/September. Nomenclature of the vascular plants follows Binz and Heitz (1990). The term "grasses" includes all true grasses (Poaceae) as well as sedges (*Carex* spp.) and rushes (Juncaceae).

Nest counts were used as a measure for ant abundance. Nests were detected by carefully searching the whole area of the plots and by setting baits (sugar solution offered in small plastic caps) and following the attracted ants back to their nests. The plots were searched on consecutive days until no further nests were detected. Behavioural clues like fighting helped to distinguish between colonies (nests) of the same species. Ant surveys were made between 12 March and 18 April in Nenzlingen, between 22 April and 17 May in Vicques and between 20 May and 12 June in Movelier. Consequently, seasonal differences in ant activity cannot be excluded during the period of mapping; however, fragments and their corresponding controls were mapped on the same or on succeeding days. Nomenclature of ants follows Bolton (1995).

Butterfly diversity and abundance were recorded at intervals of 10–14 days during the peak flight period between 3 June and 16 August 1996. In each block, butterflies were observed during 13 periods of 30 min. Both the number of butterflies and the species were recorded. Observations were conducted only between 10 a.m. and 4.30 p.m. and under the following weather conditions: cloudiness < 30%, air temperature > 18°C and wind speed ≤2 m s^{-1}. Within sites, observation periods were randomised with respect to time of day to avoid any bias due to time-dependent butterfly activity. Nomenclature of butterflies follows Koch (1991) and Lepidopterologen-Arbeitsgruppe (1987).

A direct census method was used to record the relative abundance of the different grasshopper species (including bush crickets). The entire vegetation of the plots was carefully searched for grasshoppers. Plants were slightly moved with a bamboo rod for easier detection of the insects. The number of individuals observed was recorded for each species. Monitoring was repeated three times in all blocks between July and early September 1996. Nomenclature of grasshoppers follows Bellmann (1993).

Wet sheets of cardboard placed in the grassland vegetation attract gastropods (Boag 1981; Oggier et al. 1998). We used this technique to assess the relative abundance of gastropod species. In the evening of a rainy day, sheets of cardboard (measuring 10×10 cm) were placed 50 cm apart in the vegetation of the plots (1 cardboard sheet in small plots, 9 in medium plots and 81 in large plots). In the morning of the following day (between 6 and 8 a.m.) the cardboard sheets were checked for adhering gastropods. Specimens were identified in the field and the numbers of individuals were recorded for each species. Animals were released at the same spot where they were found. Field work was done in autumn when gastropods are most active in dry grasslands (in Nenzlingen on 24–25 September, in Movelier on 6–7 October and in Vicques on 1–2 October 1996). Nomenclature of gastropods follows Kerney et al. (1983).

The above-ground plant biomass was used as a measure of productivity. When the whole study site was mown in late autumn, the plant biomass was clipped at a height of 5 cm above ground level (to preserve the rosettes of several plant species) in all 12 blocks between 6 and 15 October 1996. In the small plots, the entire vegetation was collected. In the other plots, subsamples covering 0.25 m^2 (5 subsamples in medium sized plots and 20 subsamples in large plots) were randomly chosen and the plants harvested. A total of 648 samples were harvested, oven-dried and weighed to the nearest 0.1 g.

The effect of fragmentation on the ground air temperature was measured using Tinytalk temperature loggers (Gemini Data Loggers, Chichester, UK). Loggers were placed along six transects across the edge of large fragments in Vicques. In each transect, nine loggers were placed at distances of 0, 5, 10, 15 and 25 cm on both sides of the edge of the fragment, i.e. into the vegetation of the fragment and onto the mown area. Temperature was recorded every 10 min for 12 days from 31 August to 12 September 1995, a period with no rain and little cloud cover. Loggers placed in the mown area measure temperatures which are close to the surface temperature of the ground (S. Zschokke, unpublished work). For comparison, measurements of air temperature were obtained from a recording thermometer in a standard shaded box, 2 m above the ground, situated 30 m away from the fragments.

Data analysis

Two different methods were used to examine possible effects of the grassland fragmentation on species richness, species diversity and productivity. First, species richness (square-root transformed), species diversity (Shannon diversity index) and productivity (dry weight of above-ground biomass, log-transformed) were compared between fragments and control plots using a four-way ANOVA (Table 1). Statistical analyses were performed using SAS 6.08 (SAS Institute 1990). Second, fragments and control plots were compared for each plot size separately using paired *t*-tests. Because of the great variation in the field, we set α=0.10 for all statistical tests. Bonferroni-corrected significance levels for the

Table 1 ANOVA model (type III) used to analyse the effects of fragmentation on species richness, species diversity and productivity (*MS* mean square). The interaction Fragmentation×Plot size was omitted when P>0.20

Source of variation	Abbreviated as:	*df*	*F*	Remark
Site	S	2	MS S/MS B(S)	
Fragmentation	F	1	MS F/MS F×B(S)	
Block(Site)	B(S)	9	MS B(S)/MS F×B(S)	Random factor
Plot size	P	2	MS P/MS Residual	
Fragmentation×Block(Site)[a]	F×B(S)	11	MS F×B(S)/MS Residual	Random factor
Fragmentation×Plot size	F×P	2	MS F×P/MS Residual	

[a] This term also includes the interaction Fragmentation×Site

ANOVAS were set at 0.10/7=0.0143. Similarly, Bonferroni-corrected significance levels for the *t*-tests were set at 0.10/21= 0.0048. All *P* values presented are uncorrected.

To determine the effect of fragmentation on species composition, we calculated the similarity of species composition (log-transformed abundance data) among all large and among all medium plots (fragments and control plots) using the percentage similarity or Renkonen index (Renkonen 1938; Krebs 1999). The percentage similarity is defined as the sum of the shared importance values (percentage within a sample) of each species found in both samples. We compared the percentage similarities between fragments and control plots of the same block with the similarities among all plots with the same treatment and with the similarities among all plots with different treatments, excluding the plots of the same block. Bonferroni-corrected significance level was set at 0.10/6=0.0167 .

The effect of fragmentation on the abundance of the 65 common species distributed over all groups of organisms (i.e. species present in at least 10 of the 12 blocks) was assessed using a sign test. The differences were classified as either "strong" (equivalent to a $P<0.01$, sign test), "moderate" (equivalent to $P<0.05$, sign test) or "no difference". This analysis is descriptive, and therefore no Bonferroni correction was applied. Consequently, differences found in species abundance cannot be considered as a proof of a real difference. A list of all species found in this study is given in the Appendix.

The relationships between productivity and species richness and species abundance of the common invertebrates were examined using a two-way ANCOVA with site and fragmentation as factors and productivity (log-transformed) as covariate. For this analysis, only large plots were used, because many species were too rare in medium and small plots. Bonferroni-corrected significance levels were set at 0.10/7=0.0143 for the relationships with species richness and at 0.10/22=0.0046 for the relationships with species abundance.

Air temperatures were analysed in two ways. First, to evaluate edge effects, the average temperatures and the average minima and average maxima along the transects were compared between neighbouring loggers using unpaired *t*-tests. Second, to assess the microclimatic differences between fragments and the surrounding mown area, data from loggers inside the fragments were pooled and compared with those from loggers in the mown area using unpaired *t*-tests.

Results

Species richness and diversity

Species richness differed between fragments and control plots in two taxonomic groups. Considering all plot sizes, more grass species and fewer butterfly species were found in fragments compared to the corresponding control plots. Fragments and control plots did not differ in species richness of forbs, ants, grasshoppers and gastropods (four-way ANOVAs, fragmentation effect, in all cases $P>0.18$).

Considering plots of the same size, small fragments contained more grass species ($t=3.26$, $n=24$, $P=0.004$) than small control plots. In all plot sizes, fragments contained fewer butterfly species than the corresponding control plots (small: $t=3.47$, $n=24$, $P=0.002$; medium: $t=4.47$, $n=12$, $P<0.001$; large: $t=4.20$, $n=12$, $P=0.002$). In the other taxonomic groups, fragments did not differ in species richness from the corresponding control plots (paired *t*-test, in all cases $P>0.11$). Plot size per se significantly affected species richness in all taxonomic groups (Table 2 , Fig. 2).

Table 2 Summary of ANOVAs testing the effects of different sites (*S*), experimental fragmentation (*F*), block (*B*) and plot size (*P*) on species richness (square-root transformed) in all taxonomic groups. For details of the model see Table 1 . Bonferroni-corrected significance levels were set at 0.10/7=0.0143

Source of variation	*df*	Grasses		Forbs		Ants		Butterflies		Grasshoppers		Gastropods		Vascular plants combined	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
S	2	14.02	0.002	10.75	0.004	9.12	0.007	4.55	0.043	2.24	0.162	5.01	0.035	3.09	0.095
F	1	9.13	0.009	2.02	0.183	0.26	0.622	34.23	<0.001	2.07	0.178	0.03	0.874	4.24	0.060
B(S)	9	1.47	0.268	4.45	0.012	1.63	0.221	3.48	0.028	3.67	0.023	0.63	0.753	2.84	0.053
P	2	174.46	<0.001	811.73	<0.001	81.22	<0.001	275.33	<0.001	176.43	<0.001	126.48	<0.001	921.95	<0.001
F×B(S)	11	0.85	0.595	1.05	0.417	0.54	0.866	0.73	0.709	0.86	0.585	1.45	0.169	1.35	0.219
F×P	2	1.72	0.188											2.32	0.106

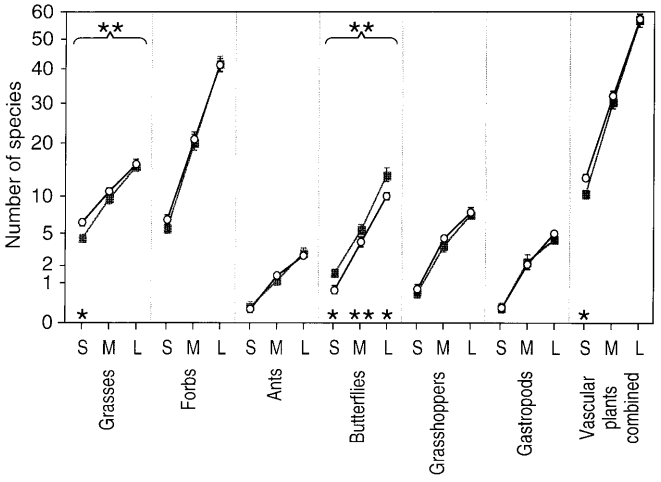

Fig. 2 Species richness (mean±1 SE, $\log_{10}(x+1)$ scale) in grasses, forbs and four groups of invertebrates in small (*S*, *n*=24), medium (*M*, *n*=12) and large (*L*, *n*=12) fragments (*open circles*) and the corresponding control plots (*filled squares*). *Asterisks* indicate differences between fragments and control plots. Those in the *upper line* refer to the overall difference (ANOVA), those in the *lower line* to plot-size-specific differences (paired *t*-test); **P*<0.10, ***P*<0.01 (Bonferroni-corrected)

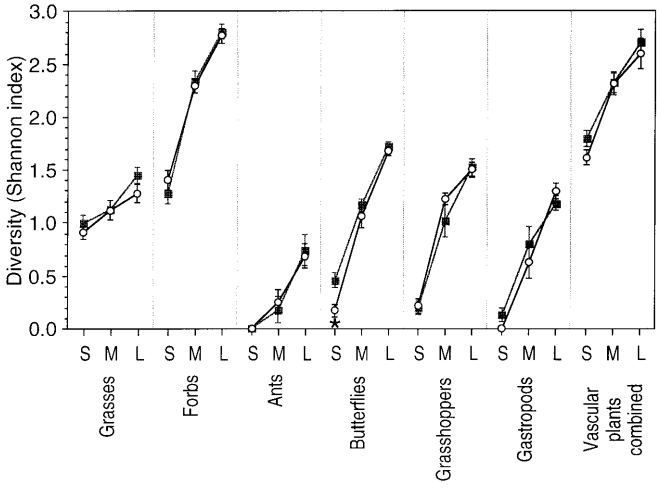

Fig. 3 Species diversity (mean±1 SE) in grasses, forbs and four groups of invertebrates in small (*S*, *n*=24), medium (*M*, *n*=12) and large (*L*, *n*=12) fragments (*open circles*) and in the corresponding control plots (*filled squares*). *Asterisks* indicate differences between fragments and control plots. Those in the *upper line* refer to the overall difference (ANOVA), those in the *lower line* to plot-size-specific differences (paired *t*-test); **P*<0.10, ***P*<0.01 (Bonferroni-corrected)

We found no significant differences in species diversity between fragments and control plots (Table 3, Fig. 3). Considering plots of the same size, the diversity of butterflies was lower in small fragments than in the corresponding control plots (t=3.51, n=24, P=0.002). In the other taxonomic groups, diversity did not differ significantly between fragments and control plots (paired *t*-test, in all cases P>0.02). Plot size per se significantly affected species diversity (Table 3 , Fig. 3).

Table 3 Summary of ANOVAs testing the effects of different sites (*S*), experimental fragmentation (*F*), block (*B*) and plot size (*P*) on species diversity (Shannon index) in all taxonomic groups. For details of the model see Table 1 . Bonferroni-corrected significance levels were set at 0.10/7=0.0143

Source of variation	*df*	Grasses		Forbs		Ants		Butterflies		Grasshoppers		Gastropods		Vascular plants combined	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
S	2	2.75	0.117	7.66	0.011	0.83	0.467	0.90	0.440	0.50	0.621	3.73	0.066	12.38	0.003
F	1	2.17	0.169	0.30	0.598	0.01	0.921	7.21	0.018	1.10	0.317	0.99	0.341	5.20	0.044
B(S)	9	1.04	0.469	1.80	0.177	2.27	0.100	3.26	0.034	5.21	0.006	0.70	0.699	3.28	0.034
P	2	13.81	<0.001	239.39	<0.001	51.18	<0.001	258.83	<0.001	177.49	<0.001	120.78	<0.001	94.87	<0.001
F×B(S)	11	0.84	0.598	1.93	0.049	0.95	0.501	1.05	0.418	0.70	0.732	1.56	0.130	0.73	0.708
F×P								2.23	0.115						

Species composition

In general, species composition was more influenced by location of the block than by the experimental fragmentation. In all taxonomic groups, except in ants, the similarity in species composition was higher between large fragments and corresponding control plots than among all large plots with identical treatment (pairwise comparisons among all large fragments and among all large control plots; Fig. 4, $t>3.66$, $df=22$, $P<0.0014$ in all cases). This means that the heterogeneity in species composition within and between the study sites was stronger than the fragmentation effect. The average similarity of all pairs of large plots with identical treatments was higher than the average similarity of all pairs of large plots with different treatments (excluding those within the same block) for the butterflies ($t=2.96$, $df=22$, $P=0.007$), indicating that fragmentation had some influence on the species composition only in this group, even though this effect was much smaller than that of the geographic location. For medium plots, the results were similar (data not shown). For small plots, no comparisons were made (not enough data).

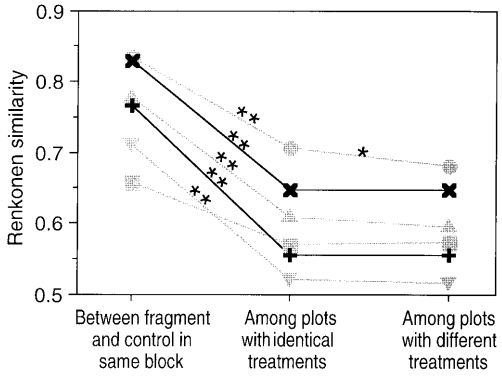

Fig. 4 Comparison of percentage similarities between different large plots for grasses (✕), forbs (✚), ants (■), butterflies (●), grasshoppers (▲) and gastropods (▼); **P*<0.10, ***P*<0.01 (Bonferroni-corrected)

Abundances and densities of single species

Our results suggest that the abundances of 19 (29%) of the 65 common species examined were influenced by habitat fragmentation (Table 4 , Fig. 5). Butterflies were most affected: all nine species considered in this analysis foraged less frequently in fragments than in control plots. The two most abundant species, *Melanargia galathea* and *Maniola jurtina*, showed a decrease in foraging activity of 65% and 81% respectively in the small plots. Of the six grasshopper species, three (50%) were affect-

Table 4 List of all common species (present in at least 10 of the 12 blocks) which showed a difference in abundance between fragments and control plots. An *asterisk* (*) indicates species on the Red List for Switzerland (Landolt 1991; Duelli 1994)

Taxonomic group	Species	Small plots[a]	Medium plots[a]	Large plots[a]	Overall trend[a]
Grasses[b]	*Bromus erectus*	+ +	+		+ +
	Dactylis glomerata	+ +			+
	Danthonia decumbens	+			
	Luzula campestris			–	
	Phleum pratense				+
Forbs[c]	*Ranunculus bulbosus*	+ +		+	+ +
	Sanguisorba minor		+	+ +	+ +
Butterflies	*Coenonympha pamphilus*			–	
	Cynthia cardui				–
	Macroglossum stellatarum			– –	– –
	Maniola jurtina	– –	– –	– –	– –
	Melanargia galathea	– –	– –	– –	– –
	Ochlodes venatus			– –	– –
	Polyommatus icarus				–
	Thymelicus sylvestris			– –	
	Zygaena filipendulae			– –	– –
Grasshoppers[d]	*Chorthippus biguttulus*				+
	*Platycleis albopunctata**		+ +	+	+ +
	Stenobothrus lineatus			–	–

[a] +/++ Higher abundance in fragments (moderate/strong); –/– – lower abundance in fragments (moderate/strong)

Species which did not differ in abundance between fragments and control plots:

[b] Grasses: *Agrostis tenuis, Brachypodium pinnatum, Briza media, Carex caryophyllea, C. flacca, Cynosurus cristatus, Festuca ovina, F. pratensis, Koeleria pyramidata*, Poa pratensis*

[c] Forbs: *Achillea millefolium, Agrimonia eupatoria, Betonica officinalis, Centaurea jacea, Cirsium acaule, Daucus carota, Helianthemum nummularium, Hieracium pilosella, Hypericum perforatum, Lathyrus pratensis, Linum catharticum*, Lotus corniculatus, Medicago lupulina, Plantago lanceolata, P. media, Potentilla erecta, Prunella grandiflora, P. vulgaris, Teucrium chamaedris, Trifolium medium, T. montanum*, T. ochroleucon*, T. pratense, T. repens, Veronica officinalis, Vicia hirsuta*

Ants: *Lasius paralienus, Myrmica scabrinodis*

[d] Grasshoppers: *Chorthippus parallelus, Metrioptera bicolor*, Omocestus rufipes**

Gastropods: *Cochlicopa lubrica, Deroceras reticulatum, Limax* spp., *Trichia plebeia, Vertigo pygmaea*

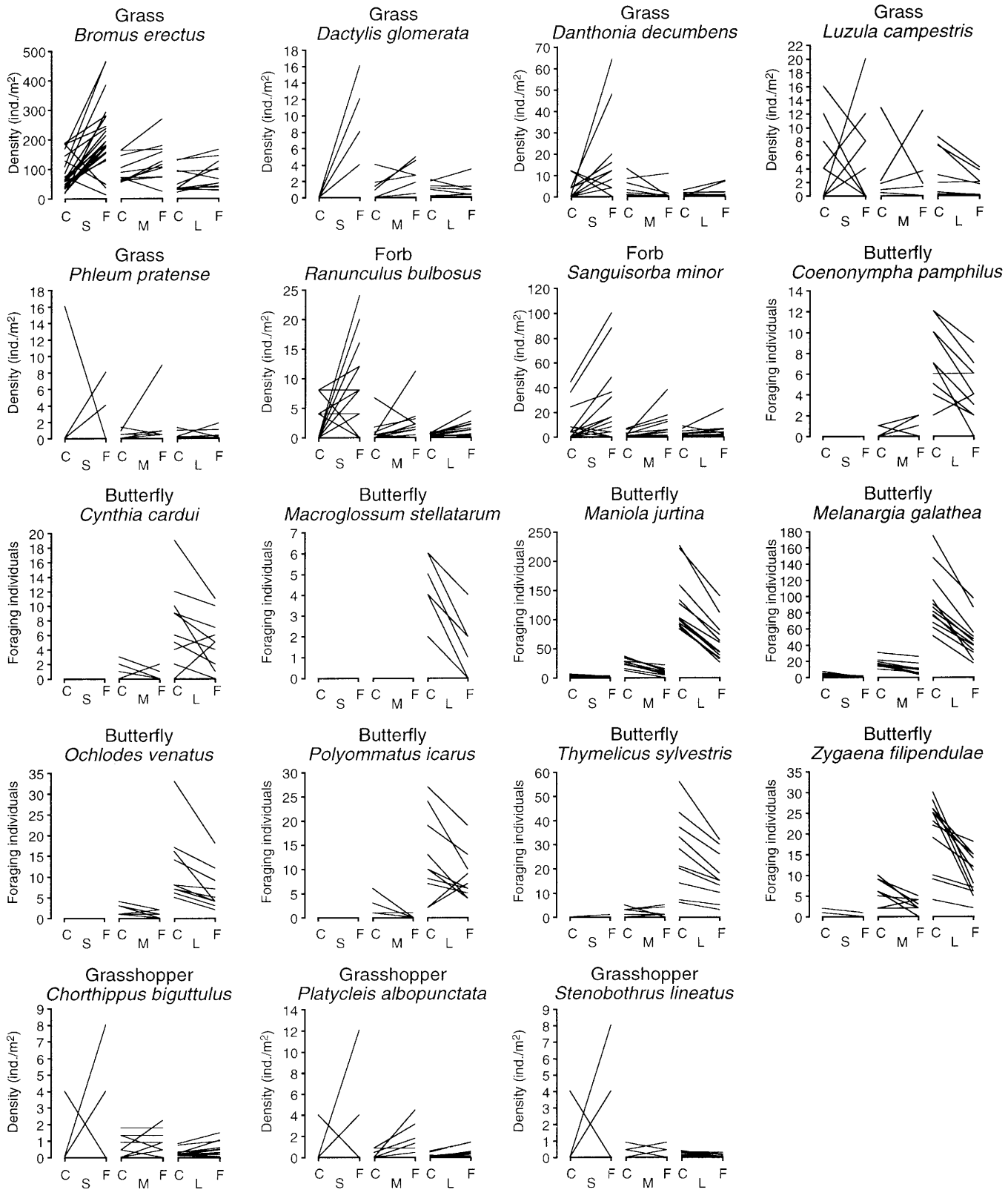

Fig. 5 Pairwise comparison of the density of all common species (present in at least 10 of the 12 blocks) which showed a difference in abundance between fragments (*F*; *S* small, *M* medium, *L* large) and corresponding control plots (*C*). *Lines* connect fragments with the corresponding control plots in the same block. For butterflies the total number of foraging individuals observed over 6.5 h is shown

ed by the fragmentation: two of them showed a higher density in fragments than in control plots, whereas one species showed a lower density in the fragments. Of the 15 grass species 5 (33%) were also affected by the experimental fragmentation. One of them had a lower density in fragments than in control plots, whereas four had a higher density in the fragments. The density of *Bromus erectus* was 159% higher in small fragments compared with control plots. Of the 28 common forbs, however, only 2 (7%) were affected. Both occurred at a much higher density in the fragments (*Ranunculus bulbosus*, small fragments: +236%; *Sanguisorba minor*, small fragments: +184%).

Plant productivity

The productivity measured as above-ground biomass was significantly higher in fragments of all three sizes than in corresponding control plots (Tables 5 , 6). Small fragments had on average 80.8% (pairwise comparison) more biomass than the corresponding control plots. In the medium and large plots, the difference was smaller (30.2% and 22.4% respectively), but still highly significant.

Table 5 Summary of ANOVAs testing the effects of different sites (*S*), experimental fragmentation (*F*), block (*B*) and plot size (*P*) on above-ground biomass (g m^{-2}, log-transformed)

Source of variation	*df*	MS	*F*	*P*
S	2	0.714	3.98	0.058
F	1	2.130	30.51	<0.001
B(S)	9	0.179	2.54	0.074
P	2	0.103	1.67	0.196
F×B(S)	11	0.071	1.15	0.336
F×P	2	0.257	4.20	0.019

Table 6 Above-ground biomass (mean±SE, g m^{-2} dry weight) in small, medium and large fragments and the corresponding control plots; *t*-values were calculated using a paired *t*-test on log-transformed data

Plot size	Control plot	Fragment	*n*	*t*	*P*
Small	227.4±15.7	379.0±25.9	24	5.89	<0.001
Medium	261.8±18.7	336.4±29.4	12	3.74	0.003
Large	234.6±13.3	284.7±17.5	12	5.89	<0.001

Productivity was negatively correlated with species richness of forbs and with that of vascular plants (Table 7, Fig. 6). There was no relationship between productivity and species richness in any other group (grasses: P=0.25, ants: P=0.51, butterflies: P=0.45, grasshoppers: P=0.18, gastropods: P=0.82). Furthermore, there were no significant relationships between productivity and the abundance of any invertebrate species (P>0.02).

Air temperature on ground surface

Along the transect across the edge of a large fragment, the average ground air temperature did not differ significantly within distances of 5–10 cm (Fig. 7). When temperature data measured in the mown area were pooled and compared with those measured in the fragment vegetation, the average temperature in the mown area (15.6°C, SD=0.3) was slightly (0.7°C) higher than that in the fragment vegetation (14.9°C, SD=0.3; t=7.13, n=22, P<0.001). However, average daily maximum ground air temperatures differed strongly between the fragments and the surrounding mown area with a sharp change at

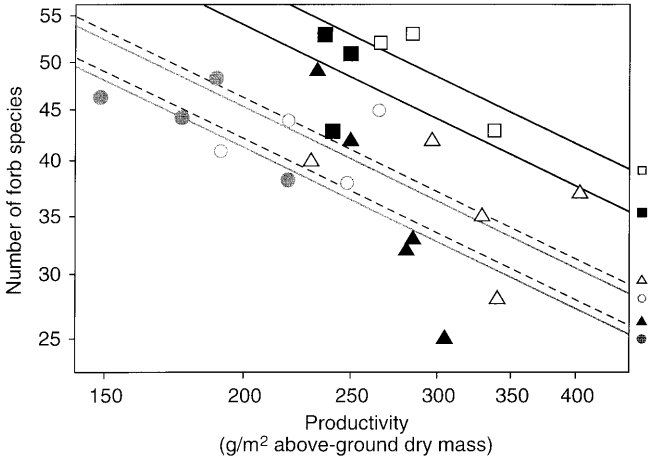

Fig. 6 Relationship between forb species richness (square-root transformed) and productivity (log-transformed) in large patches. *Open symbols* refer to fragments, *filled symbols* denote control plots. *Triangles* refer to patches in Nenzlingen, *squares* to patches in Movelier and *dots* to those in Vicques. The *lines* shown are the regression lines based on the two-way ANCOVA (Table 7). The *small symbol* at the *right hand side* indicates to which group each line belongs

Table 7 Results of a two-way ANCOVA examining the relationship between productivity (*R*, measured as above-ground dry biomass, log-transformed) and species richness of forbs and of vascular plants combined (square-root transformed). The factors site (*S*) and fragmentation (*F*) were considered. Bonferroni-corrected significance levels were set at 0.10/7=0.0143

Source of variation	*df*	Forbs			Vascular plants combined		
		MS	*F*	*P*	MS	*F*	*P*
S	2	1.70	10.06	0.001	1.36	9.10	0.002
F	1	0.37	2.21	0.153	2.83	3.17	0.091
R	2	1.22	7.28	0.014	0.40	8.03	0.011

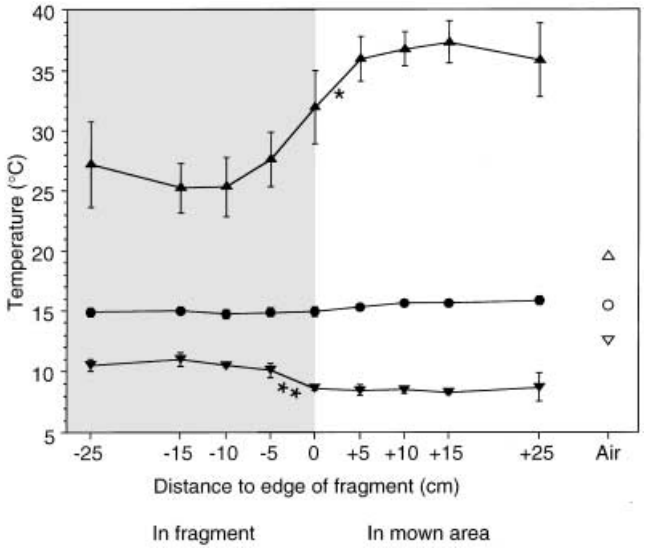

Fig. 7 Ground air temperature (*filled symbols*, mean±1 SD) along six transects across the edge of large fragments and air temperature (*open symbols*) measured 2 m above ground in a standard shaded box (▲ average daily maximum temperature, ● average temperature, ▼ average daily minimum temperature, **P*<0.05, ***P*<0.01, *t*-test)

the edges of the fragments (Fig. 7). Overall, the average daily maximum temperature was lower inside the fragments (pooled data: 26.2°C, SD=2.6) than in the mown area (36.5°C, SD=1.9; t=14.92, n=22, P<0.001). Similarly, the average daily minimum temperatures changed abruptly at the edge of the fragment (Fig. 7). The daily minimum temperature in the fragment (pooled data: 10.5°C, SD=0.6) was higher than the corresponding value in the mown area (8.5°C, SD=0.5; t=12.48, n=22, P<0.001). The minimum temperatures measured on the ground surface were lower than the minimum air temperatures recorded under standard conditions, whereas the maximum temperatures on the ground surface were higher than those measured under standard conditions, indicating the large temperature variations at the ground surface.

Discussion

This study shows that the experimental fragmentation over three years affected different species and groups to a different extent. Butterflies, the most mobile group examined, reacted most sensitively: both species richness and foraging abundance of single species were lower in fragments than in corresponding control plots. Most of the other groups or species that were influenced by the fragmentation had a higher species richness or abundance in the fragments. This can be explained by a so-called "retreat effect". For several animal species, the mown area surrounding the fragments is no longer the preferred habitat, but it may still function as foraging area. Thus the animals spend most of their life in a fragment, but leave it to forage. Ambush predators like the sand lizard *Lacerta agilis* and workers of various ant species are examples (G.H. Thommen, unpublished work; B. Braschler, unpublished work). As a consequence, the species richness and abundance in the fragments will increase in these species. Reactions to habitat fragmentation were in most cases species-specific, as found in other studies (Margules and Milkovits 1994; Diffendorfer et al. 1995a; Davies and Margules 1998).

Habitat patches are parts of a landscape mosaic and the presence of plant species may depend on the initial composition of the plant community, history of the patch, patch size, type of neighbouring habitat, isolation, and other factors (Andrén 1996). The calcareous grasslands at the three study sites had similar numbers of coexisting plant species (Baur et al. 1996). However, the composition of the plant communities differs among sites with only 53.8% of all species occurring at all three sites (Baur et al. 1996). Diversity indices assessed in the first year of the experiment (1993) were also similar for the three sites, indicating that similar environmental and ecological factors were influencing these communities (Joshi 1994; J. Joshi, personal communication).

Three years after the initiation of the experiment, we recorded more grass species in fragments, especially in the small ones, than in the corresponding control plots. No such differences were found in forbs. This suggests that fragmentation influenced plant communities at the level of the smallest plots within a period of 3 years. The abundance of 5 of the 15 common grasses differed between fragments and control plots. This difference was most pronounced in *Bromus erectus* which seems to benefit from the conditions in the fragments, most probably because of a reduced competition for light. Another factor that could positively influence *B. erectus* is the change of grassland management from grazing to mowing at the beginning of the experiment. Tufts of *B. erectus* grow better on mown than on grazed grasslands (Zoller 1954; Schläpfer et al. 1998). *Dactylis glomerata* also occurred in higher densities in fragments than in control plots. However, in contrast to *B. erectus*, the density of *D. glomerata* decreased in the control plots since the beginning of the experiment in 1993 (Joshi 1994; J. Joshi, personal communication).

Only two forb species, *Sanguisorba minor* and *Ranunculus bulbosus*, both typical species of calcareous grasslands, differed in abundance between fragments and control plots. Both occurred in higher densities in fragments than in control plots. Compared with the densities at the beginning of the experiment, the densities of *S. minor* increased in the fragments, whereas the density of *R. bulbosus* decreased in the control plots. The increase of the density of *S. minor* in the fragments can be explained by better light conditions in the fragments in combination with the ability of *S. minor* to overcome summer droughts with its long tap-root (Grime et al. 1988). In contrast, *R. bulbosus* prefers grasslands where shading is prevented by heavy grazing (Grime et al. 1988), a situation no longer present in the control plots.

In ants and gastropods, we neither detected any difference in species richness and diversity nor in the abundance of single species between fragments and control plots. A few ant species (e.g. *Lasius paralienus* and *Solenopsis fugax*) seemed to benefit from mowing, but most ant species are too rare in the study sites (of three species only a single nest was found) to allow statistical analysis. In gastropods, between-site differences in species composition were more pronounced than the effects of habitat fragmentation. A more detailed study using mark-release-recapture techniques showed that habitat fragmentation affected plot occupancy, extinction and colonisation rates and population sizes in land snails (Oggier 1999). Three of six snail species were found less frequently in fragments than in control plots, whereas three other species were not affected by the experimental fragmentation.

A total of 19 butterfly species were recorded foraging in the fragments and 29 species in the control plots. This indicates that even small-scale fragmentation reduces butterfly species richness. The decline in species richness in the fragments was rather unexpected, since butterflies are the most mobile species investigated in the present study. Of the 29 species 14 were rare, with less than 20 individuals recorded during the entire observation period. Individuals of these rare species were patchily distributed in the investigation area, but preferred to forage in the continuous grassland (control plots). Since species richness of butterflies is mainly determined by rare species, the observed decline in species richness in the fragments concerns particularly rare species. Thus, fragmentation had a particularly adverse effect on rare butterfly species.

Several studies have shown that the abundance and distribution of larval host plants and nectar source plants determine the abundance and distribution of butterfly species (Murphy et al. 1983; Lörtscher et al. 1995). In our study, however, the composition and abundance of larval food plants and nectar plants did not differ between fragments and control plots and we recorded an increase in flower offer (forbs had more flowers per individual) in the fragments (H.-P. Rusterholz, unpublished work). Consequently, we expected to observe more butterflies in the fragments. The smaller number of foraging butterflies observed in the fragments was probably caused by behavioural inhibition of the butterflies crossing the mown isolation areas or by reduced attractiveness of the fragments as a result of their small size compared with the control area. Even though butterflies have the physical ability to disperse over long distances, their reduced flower visitation rate in spite of an increased flower offer in the fragments shows that an unsuitable matrix surrounding the fragments can become an effective barrier for the movement of butterflies as well as of other animals (Mader 1984).

Separate analyses of the nine common butterfly species showed reduced foraging abundance in the fragments. Moreover, different butterfly species differed in the observed response to fragmentation. In the statistical analysis, the most abundant species *Maniola jurtina* and *Melanargia galathea* showed the strongest reaction, whereas the less abundant species *Cynthia cardui* and *Coenonympha pamphilus* exhibited the weakest responses to the experimental fragmentation (Table 4). However, this difference may well be the result of a sample-size artefact. The among-species difference in response to fragmentation is partly due to differences in foraging abundance (cf. Fig. 5). Detailed field observations revealed that butterflies exhibit different foraging behaviours in the fragments and the control plots (H.-P. Rusterholz, unpublished work). Our results parallel findings in the skipper butterfly *Hesperia comma*, which showed an increasing probability of re-colonisation of suitable habitat (and a declining probability of extinction) with increasing patch size (Thomas and Jones 1993). Furthermore, the observed response of butterflies to small-scale fragmentation may well be an example of the foraging patterns of other animals that need larger areas for foraging, such as migrating birds. Thus, fragmentation and reduction of foraging grounds will generally affect and reduce foraging in animals and hence reduce their fitness and population size, which in turn might lead to inbreeding and the accompanying deleterious effects, as recently observed in Glanville fritillary butterflies (*Melitaea cinxia*; Saccheri et al. 1998). Island size and the degree of plant specialisation also affected pollination success in hummingbird-pollinated plants. Pollination in a generalised plant (*Justicia secunda*, Acanthaceae) was not affected by island size, whereas in the specialised *Mandevilla hirsuta* (Apocynaceae) pollination and hence fruit set were significantly reduced in a small compared with a large island (Linhart and Feinsinger 1980). Jennerston (1988) also found reduced pollinator activity and hence reduced seed sets in fragmented, small populations of *Dianthus deltoides* in Sweden.

A significant effect of fragmentation was also found in the bushcricket *Platycleis albopunctata*, the most efficient flier among the orthopterans studied. In contrast to butterflies, however, *P. albopunctata* occurred more frequently in the fragments. Since *P. albopunctata* was somewhat more abundant in plots with low productivity, we can conclude that it does not prefer fragments because of their higher productivity. We rather suggest that this species uses the fragments as retreats and forages in the mown isolation area. *P. albopunctata* is a thermophilic species that prefers dry habitats with a mosaic of varying plant densities and heights (e.g. Harz 1957). This type of diverse habitat is better represented in fragments surrounded by mown area than in the more homogeneous control area. A similar, but less pronounced influence of fragmentation was observed in the grasshopper *Chorthippus biguttulus* in 1994–1996. This very common species occupies a much wider niche (temperature, air humidity and vegetation structure) and was also found in relatively high densities in the mown area between the fragments.

Habitat fragmentation affects the ecology of plants in many ways. For example, rain forest fragments in central

Amazonia were found to experience a dramatic loss of above-ground tree biomass that was not offset by recruitment of new trees (Laurance et al. 1997). In our experiment, fragments had an increased above-ground biomass which was most likely the result of an edge effect. In large and medium fragments, the above-ground biomass was on average 6% higher in samples collected at the edge than in samples from the centre of the fragments (C. Dolt, unpublished work). Plants at the edge may experience less competition for light and nutrients. It is also possible that interactions among plants are altered at the fragment edge due to differences in microclimatic conditions. The observed negative correlation between productivity and species richness of forbs can be explained by competitive interactions between grasses and forbs. High productivity was associated with a high density of grasses which displaced many forbs.

The average air temperatures differed only slightly between fragments and the surrounding mown area. However, temperature fluctuations were more pronounced in the mown area than in the fragments. We found no differences among the temperatures measured inside the fragment or among those measured inside the mown area. This indicates that the temperature change at the edge of the fragment occurred within less than 5 cm from the fragment edge. Inside the fragments, temperature was mainly influenced by the vegetation cover.

To summarise, taxonomic groups and single species which benefited from the conditions in the mown isolation area (e.g. some plants and grasshoppers) were more abundant in the fragments, whereas species for which the isolation area was disadvantageous (e.g. butterflies) occurred less frequently in fragments. Within groups of organisms, reactions to experimental habitat fragmentation were species-specific. For many species, the period of 3 years between the initiation of the experiment and the present study was probably too short to show a detectable reaction.

The extremely low abundance of rare species does not allow statistical analysis of a single rare species. However, since rare species are the main determinant of species richness, we may conclude that the experimental fragmentation had an adverse effect on rare invertebrates, especially butterflies.

In conclusion, despite the short time frame of this study, we did find some changes in plant and invertebrate abundance and species richness. The study also revealed pronounced edge effects which could cause the increase in plant productivity in the fragments. Interestingly, the most mobile organisms investigated in our study, the butterflies, showed the strongest negative effect of small-scale habitat fragmentation. This shows (1) that butterflies are sensitive indicators of habitat change, and (2) that they may serve as model organisms for potential reactions of other species (e.g. birds) to large-scale habitat fragmentation.

Acknowledgement We are grateful to Christoph Seibert, Stephan Ledergerber, Salome Schüpbach, Michel Wurtz and numerous students for field assistance and to Bernhard Seifert and Cesare Baroni Urbani for help with species determination of ants. We thank Paul Jordan for statistical advice, and Ann Rypstra, Christoph Jäggi, Ian Sanders and two anonymous reviewers for helpful comments on the manuscript. This work is part of the Swiss Priority Programme Environment supported by the Swiss National Science Foundation (grants 5001–44620 to B. Baur and 5001–46622/1 to A. Erhardt).

Appendix

Species list

Each line contains the species name (with authority). Asterisks (*) indicate species on the Red Lists of Switzerland (Landolt 1991; Duelli 1994). The number of blocks (out of 12) in which each species was found and the sites (*N* Nenzlingen, *M* Movelier, *V* Vicques) are also indicated.

Grasses

- *Agrostis stolonifera* L. 1 M
- *A. tenuis* Sibth. 12 N,M,V
- *Anthoxanthum odoratum* L. 7 N,M,V
- *Avenula pubescens* Dumortier 5 N
- *Brachypodium pinnatum* P. B. 12 N,M,V
- *Briza media* L. 12 N,M,V
- *Bromus erectus* Hudson 12 N,M,V
- *Carex caryophyllea* La Tourrette 12 N,M,V
- *C. flacca* Schreber 12 N,M,V
- *C. pilulifera* L. 1 M
- *Cynosurus cristatus* L. 12 N,M,V
- *Dactylis glomerata* L. 12 N,M,V
- *Danthonia decumbens* DC. 12 N,M,V
- *Festuca ovina* L. 12 N,M,V
- *F. pratensis* Hudson 10 N,M,V
- *F. rubra* L. 5 N,M
- *Holcus lanatus* L. 5 N
- *Koeleria pyramidata* P. B. * 10 N,M,V
- *Lolium perenne* L. 9 N,M,V
- *Luzula campestris* DC. 11 N,M,V
- *Phleum pratense* L. 11 N,M,V
- *Poa compressa* L. 7 N,M,V
- *P. pratensis* L. 12 N,M,V
- *P. trivialis* L. 6 N,M,V

Forbs

- *Achillea millefolium* L. 10 N,M,V
- *Acinos arvensis* Dandy 2 V
- *Agrimonia eupatoria* L. 12 N,M,V
- *Ajuga reptans* L. 1 N
- *Alchemilla* agg. L. * 1 M
- *Allium oleraceum* L. 2 M,V
- *Anacamptis pyramidalis* Rich. * 3 M
- *Anemone nemorosa* L. 1 N
- *Anthericum ramosum* L. 1 M
- *Anthyllis vulneraria* L. 3 N,V
- *Asperula cynanchica L.* * 6 M,V
- *Aster amellus* L. 1 M
- *Bellis perennis* L. 4 N
- *Betonica officinalis* L. 12 N,M,V
- *Campanula glomerata* L. * 3 M
- *C. rotundifolia* L. 5 N,M,V
- *Cardamine hirsuta* L. 1 N
- *Carlina acaulis* L. 3 M
- *C. vulgaris* L. * 1 V
- *Centaurea jacea* L. 11 N,M,V
- *Centaurium erythraea* Rafn * 4 N,V
- *Cerastium fontanum*, Baumg. 7 N,M

- *Chamaespartium sagittale* P. Gibbs 7 N,M,V
- *Cirsium acaule* Scop. 12 N,M,V
- *Colchicum autumnale* L. 2 N, M
- *Convolvulus arvensis* L. 1 V
- *Crepis biennis* L. 3 N, M
- *C. taraxacifolia* Thuill. 2 M
- *Daucus carota* L. 11 N, MY
- *Euphorbia cyparissias* L. 9 N,V
- *E. verrucosa* L. * 1 M
- *Galium album* Miller 4 N,M,V
- *G. pumilum* Murray 1 M
- *G. verum* L. 9 N,M,V
- *Genista tinctoria* L. * 1 V
- *Gentiana cruciata* L. * 1 V
- *G. verna* L. * 1 M
- *Gentianella ciliata* Borkh. * 1 M
- *G. germanica* Börner * 2 M
- *Geranium dissectum* L. 1 N
- *Gymnadenia conopsea* R. Br. 3 M
- *Helianthemum nummularium* Miller 11 N,M,V
- *Hieracium pilosella* L. 12 N,M,V
- *Hippocrepis comosa* L. 6 N,V
- *Hypericum perforatum* L. 12 N,M,V
- *Hypochoeris radicata* L. 7 N,M,V
- *Knautia arvensis* Duby 9 N,M,V
- *Lathyrus pratensis* L. 10 N,M,V
- *Leontodon hispidus* L. 7 N,M,V
- *Leucanthemum vulgare* Lam 8 N,M,V
- *Linum catharticum* L. * 12 N,M,V
- *Lotus corniculatus* L. 12 N,M,V
- *Medicago lupulina* L. 10 N,M,V
- *Ononis repens* L. 9 N,M,V
- *Orchis militaris* L. * 1 M
- *O. morio* L. * 1 M
- *O. ustulata* L. 3 N,M
- *Origanum vulgare* L. 5 N,M,V
- *Pimpinella saxifraga* L. 6 N,V
- *Plantago lanceolata* L. 12 N,M,V
- *P. major* L. 2 N, M
- *P. media* L. 12 N,M,V
- *Platanthera chlorantha* Rchb. * 1 M
- *Polygala amarella* Crantz 4 N,M,V
- *P. comosa* Schkuhr * 6 N,M,V
- *Potentilla erecta* Räuschel 11 N,M,V
- *P. neumanniana* Rchb. 8 N,M,V
- *P. reptans* L. 1 N
- *P. sterilis* Garcke 8 N,M,V
- *Primula veris* Hudson 9 N,M,V
- *Prunella grandiflora* Scholler 11 N,M,V
- *P. vulgaris* L. 12 N,M,V
- *Ranunculus acris* L. 1 N
- *R. bulbosus* L. 12 N,M,V
- *R. repens* L. 2 N,V
- *Rumex acetosa* L. 4 N
- *Salvia pratensis* L. * 8 N,V
- *Sanguisorba minor* Scop. 12 N,M,V
- *Scabiosa columbaria* L. * 8 N,M,V
- *Sedum sexangulare* Grimm 5 N,V
- *Senecio erucifolius* L. 9 N,M,V
- *Silaum silaus* Sch. et Th. * 2 M
- *Spiranthes spiralis* Chevallier * 1 M
- *Succisa pratensis* Moench 4 N,M
- *Taraxacum officinale* Weber 1 N
- *Tetragonolobus maritimus* Roth * 3 M
- *Teucrium chamaedrys* L. 10 N,M,V
- *T. montanum* L. 1 M
- *Thlaspi perfoliatum* L. 1 M
- *Thymus serpyllum* L. 9 N,M,V
- *Trifolium campestre* Schreber 8 N,V
- *T. medium* L. 11 N,M,V
- *T. montanum* L. * 11 N,M,V
- *T. ochroleucon* Hudson * 11 N,M,V
- *T. pratense* L. 12 N,M,V
- *T. repens* L. 11 N,M,V
- *Veronica arvensis* L. 5 N, M
- *V. chamaedrys* L. 7 N,V
- *V. officinalis* L. 12 N,M,V
- *V. prostrata* L. * 3 N
- *V. serpyllifolia* L. 8 N,M,V
- *V. teucrium* L. * 1 V
- *Vicia cracca* L. 1 M
- *V. hirsuta* S. F. Gray 11 N,M,V
- *V. sativa* L. 6 N,V
- *Viola hirta* L. 2 V

Ants

- *Formica cunicularia* Latreille 1798 3 N,M,V
- *F. rufibarbis* Fabricius 1793 3 N,M,V
- *Lasius flavus* (Fabricius 1781) 6 N,M
- *L. paralienus* Seifert 1992 12 N,M,V
- *Myrmecina graminicola* (Latreille 1802) 1 N,
- *Myrmica sabuleti* Meinert 1860 1 M
- *M. scabrinodis* Nylander 1846 10 N,M,V
- *M. schencki* Emery 1894 2 N,M
- *M. specioides* Bondroit 1918 * 1 V
- *Solenopsis fugax* (Latreille 1798) 3 N,M
- *Tapinoma ambiguum* Emery 1925 2 V
- *T. erraticum* (Latreille 1798) 6 N,M
- *Tetramorium caespitum* (L. 1758) 4 N,M,V

Butterflies

- *Aphantopus hyperantus* (L. 1758) 1 N
- *Argynnis paphia* (L. 1758) * 4 M,V
- *Aricia agestis* (Denis & Schiffermüller 1775) 1 V
- *Brintesia circe* (Fabricius 1775) * 7 N,M,V
- *Clossiana dia* (L. 1767) * 3 M
- *Coenonympha pamphilus* (L. 1758) 11 N,M,V
- *Cupido minimus* (Fuesslin 1775) * 4 N,M,V
- *Cynthia cardui* (L. 1758) 11 N,M,V
- *Erebia aethiops* (Esper 1777) * 1 M
- *Gonepteryx rhamni* (L. 1758) 1 N
- *Hesperia comma* (L. 1758) 6 N,M,V
- *Inachis io* (L. 1758) 3 M,V
- *Lasiommata megera* (L. 1767) * 4 N,M,V
- *Lycaena tityrus* (Poda 1761) * 1 M
- *Lysandra coridon* (Poda 1761) * 8 N,M,V
- *Macroglossum stellatarum* (L. 1758) 11 N,M,V
- *Maniola jurtina* (L. 1758) 12 N,M,V
- *Melanargia galathea* (L. 1758) 12 N,M,V
- *Mellicta parthenoides* (Keferstein 1851) * 2 M
- *Ochlodes venatus* (Bremer & Grey 1803) 10 N,M,V
- *Papilio machaon* (L. 1758) 1 M
- *Pieris brassicae* (L. 1758) 6 N,M,V
- *P. rapae* (L. 1758) 9 N,M,V
- *Plebicula dorylas* (Denis & Schiffermüller 1775) * 1 M
- *Polyommatus icarus* (Rottemburg 1775) 10 N,M,V
- *Pyronia tithonus* (L. 1771) * 1 M
- *Spialia sertorius* (Hofmannsegg 1804) 6 N,M,V
- *Thymelicus sylvestris* (Poda 1761) 10 N,M,V
- *Zygaena filipendulae* (L. 1758) 12 N,M,V

Grasshoppers

- *Chorthippus biguttulus* (L. 1758) 12 N,M,V
- *C. parallelus* (Zetterstedt 1821) 12 N,M,V
- *Chrysochraon brachyptera* (Ocskay 1826) 7 N,M
- *Decticus verrucivorus* (L. 1758) * 6 M,V
- *Gomphocerus rufus* (L. 1758) 8 N,M,V
- *Gryllus campestris* L. 1758 * 2 N
- *Metrioptera bicolor* (Philippi 1830) * 12 N,M,V
- *M. brachyptera* (L. 1761) * 1 M
- *M. roeselii* (Hagenbach 1822) 5 N,M
- *Omocestus rufipes* (Zetterstedt 1821) * 10 N,M,V
- *Pholidoptera griseoaptera* (De Geer 1773) 6 N,M

- *Platycleis albopunctata* (Goeze 1778) * 11 N,M,V
- *Stenobothrus lineatus* (Panzer 1796) 11 N,M,V
- *Tettigonia cantans* (Fuessly 1775) 1 M
- *T. viridissima* L. 1758 5 N,M,V

Gastropods

- *Arion rufus* (L. 1758) 2 N
- *Cochlicopa lubrica* (O.F. Müller 1774) 11 N,M,V
- *Cochlodina laminata* (Clessin 1882) 1 N
- *Deroceras reticulatum* (O.F. Müller 1774) 11 N,M,V
- *Helicella itala* (L. 1758) 5 N,M,V
- *Limax* spp. 10 N,M,V
- *Punctum pygmaeum* (Draparnaud 1801) 5 M,V
- *Pupilla muscorum* (L. 1758) 5 N,V
- *Succinea oblonga* (Draparnaud 1801 1 M
- *Trichia plebeia* (Draparnaud 1805) 12 N,M,V
- *Vertigo pygmaea* (Draparnaud 1801) 12 N,M,V
- *Vitrina pellucida* (O.F. Müller 1774) 4 M,V

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