

# Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study

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**Abstract.** 1. Habitat fragmentation is considered one of the major threats to invertebrate diversity in semi-natural grassland. However, the effects of habitat fragmentation through mowing on the rich insect fauna of these grasslands have not been sufficiently investigated and experiments are especially rare.

2. We studied the impact of small-scale grassland fragmentation on orthopterans over 7 years in an experiment which allowed us to additionally investigate the effect of frequent mowing on Orthoptera communities.

3. Overall, Orthoptera density and species richness increased over time. This was likely a result of increased small-scale habitat heterogeneity and the provision of a short-turf habitat suitable for xerophilous species. The fragmentation affected orthopteran density and species composition but not species richness whose response lagged behind the changes in abundance.

4. Responses differed between suborders. Ensifera density was higher in fragment than in control plots. Caelifera density did not differ between fragment and control plots. The mown matrix was an unsuitable habitat for most of the species, particularly within the Ensifera.

5. Our experiment shows that even small-scale fragmentation can affect Orthopteran communities and that the effects became more pronounced over time. As the mown matrix was unsuitable for many Ensifera species, they may go locally extinct when large areas are mown simultaneously.

**Key words.** Bush crickets, calcareous grasslands, crickets, disturbance, grasshoppers, habitat fragmentation, isolation, Jura mountains.

## Introduction

Habitat fragmentation is considered one of the major threats to invertebrate diversity in semi-natural grassland (Collinge, 2000). Fragmentation reduces the area suitable to the organisms and tends to create isolated metapopulations by reducing the exchange of individuals, and thus the gene flow between grassland

patches (Hanski, 1998). The effect of fragmentation on population dynamics of invertebrate taxa depends on species' ecological traits, such as movement behaviour and habitat specialization, as well as on size and spatial configuration of the fragments (Saunders *et al.*, 1991). Furthermore, grassland fragmentation occurs at many different spatial scales, ranging from small breaks in a homogeneous sward (Collinge, 2000) to widely scattered grassland fragments in an unsuitable matrix (Wiens, 1989). In the long term, fragmentation may lead to higher extinction, not only as a result of increased demographic and genetic stochasticity of populations, but also via indirect effects. These include altered abiotic conditions or the disruption of biological interactions (Goverde *et al.*, 2002; Braschler & Baur, 2003; Braschler *et al.*,

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2003). Dry calcareous grasslands are species-rich, semi-natural habitats whose area has decreased dramatically during recent decades as a result of changes in agricultural practices, causing a high degree of fragmentation (Strijker, 2005).

Among the different taxonomic groups associated with calcareous semi-natural grasslands, the populations of grasshoppers, bush crickets, and crickets are declining across Europe, and more than half of these species are now considered endangered (e.g. Ingrisch & Köhler, 1998; Reinhardt *et al.*, 2005; Monnerat *et al.*, 2007; Steck *et al.*, 2007). The conservation of these grasslands is thus a necessary measure to prevent further species extinctions. For hundreds of years, these grasslands have been used for pasture and for harvesting hay. Among the different management options, mowing without any fertiliser input is a common practice (Knop *et al.*, 2006). However, while effects of this management practice on plant diversity have been assessed, its impact on invertebrate communities has not been sufficiently investigated and experiments are especially rare (but see Chambers & Samways, 1998; Gardiner & Hassall, 2009). In particular, it remains unclear how the sward- and soil-dwelling invertebrates use the mown areas after cutting. The disturbance caused by mowing is mainly related to machine trampling, direct mortality, and periodic removal of the standing biomass, causing strong fluctuations in resource availability and habitat stability (Wagner, 2004; Gardiner & Hill, 2006; Johst *et al.*, 2006). On the one hand, the mown areas are considered an unsuitable matrix for orthopterans, in which individuals are more exposed and thus, at increased risk from predation (Ingrisch & Köhler, 1998), overheating, and desiccation (Willott, 1997; Gardiner & Hassall, 2009). On the other hand, the mown areas can provide suitable thermal and physical environments for those species which lay eggs in the soil, thus affecting the population dynamics in the long term (Van Wingerden *et al.*, 1991).

In this study, we examined the effect of small-scale fragmentation and mowing on population dynamics and community structure of orthopterans in a 7-year experiment carried out in three semi-natural calcareous grasslands. We created and maintained the fragmentation by frequently mowing the sward around unmown fragments (With *et al.*, 1999; Collinge, 2000). We separated the analyses for Ensifera (crickets and bush crickets) and Caelifera (grasshoppers), which we expected to react differently to the treatment according to their ecological traits. The specific aims of our study are: (i) to test the effects of small-scale grassland fragmentation and mowing on orthopteran density and species composition, and (ii) to test how these factors affect population dynamics and community structure over time in a controlled experiment.

## Materials and methods

### Study sites

The study was carried out in three sites in the Swiss Jura mountains near the villages of Nenzlingen (Ne), Movelier (Mo), and Vicques (Vi). The sites selected were nutrient-poor, dry calcareous grasslands of the *Teucrio-Mesobrometum* association (Ellenberg, 1986). The slope varied from 15 to 27° and the

aspect was SW–SE. All three sites were initially used as extensive pasture for cattle, but were fenced off at the beginning of the experiment. Throughout the experiment, the whole sites including the experimental plots were mown annually in autumn, whereas woody plants were removed regularly. A detailed description of the sites can be found in Zschokke *et al.* (2000).

### Experimental fragmentation

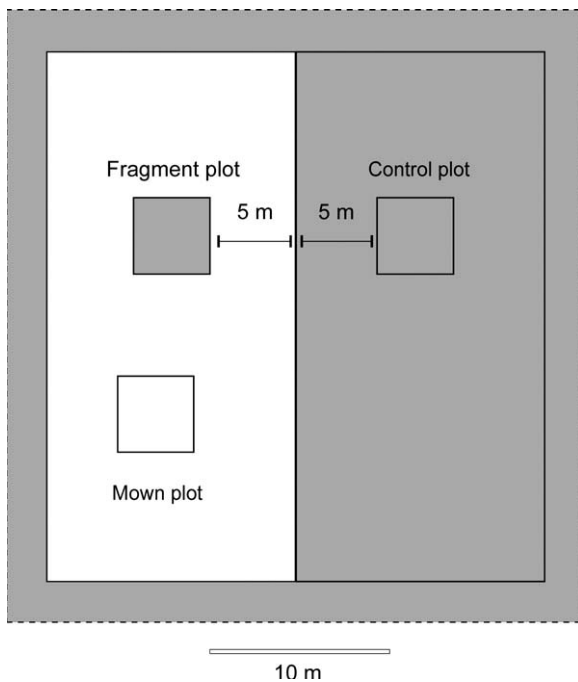
To test the effect of fragmentation and mowing on Orthopterans, we set a series of experimental grasslands in three sites. To account for heterogeneity within the sites, a blocked design was used. One experimental unit ('block') was a rectangle of 32 × 29 m embedded in undisturbed grasslands. Each block was divided into two halves, one unmown and one mown. The mown area contained one (4.5 × 4.5 m) unmown fragment plot and one mown plot. Fragment plots were isolated by frequently mowing the vegetation around them and removing the biomass. The number of cuts varied between years and sites, mainly according to the weather conditions (mean across sites and years: 7) to keep the sward height at *c.* 8 cm and to prevent the plants from flowering. However, the number of cuts did not differ between sites (means values: Ne = 7, Mo = 6, Vi = 6; NS) and was not correlated with the duration of the experiment ( $r_s = 0.04$ ; NS). The mowing was carried out with a lawn-mower moving slowly to reduce orthopteran mortality. The fragment plot was separated by a 5-m-wide strip of mown vegetation, as well as the corresponding control plot, which was mirror-symmetrically arranged (Fig. 1). Within each block, the positions of the fragment-control plot pairs as well as the control mown plot and mown–unmown halves were randomised. As a result of field site size, five blocks were located in Nenzlingen, three in Movelier, and four in Vicques. The experimental fragmentation was created in spring 1993 and maintained for 7 years until the end of 1999.

### Orthoptera surveys

All Orthopterans were directly surveyed in the three experimental plots per block with an 'open quadrat' method. In each year, two surveys were done between August and the beginning of September. The abundance of the different species was recorded by carefully searching the three plots per block. We moved the vegetation using a bamboo rod to cause any Orthopteran present to jump (similar to the 'flushing' method described in Gardiner *et al.*, 2002). The method allowed us to record species abundance without capturing or injuring any individuals. Surveys took place between 11.00 and 17.00 hours on warm sunny days that did not follow a day of rainfall. Nomenclature follows Coray and Thorens (2001).

### Statistical analyses

*Density and species richness.* Our response variables were the cumulative number of species per plot (species found in the



**Fig. 1.** Diagram of one block of the fragmentation experiment. A block ( $32 \times 29$  m) contained three plots ( $4.5 \times 4.5$  m): one unmown plot (fragment plot) and one mown plot in the fragmented area, and one control plot in the unmown area. The position of the fragment–control plot pairs and the mown plot was randomly placed within blocks. Mown areas are white, whereas unmown areas are grey.

two surveys) and abundance quantified as density (sum of individuals in the two surveys divided by the plot area). Treatment effects (fragment, control, and mown plots) were examined using repeated measurement general linear mixed models (GLMM) followed by post-hoc multiple comparisons (Tukey–Kramer tests). Duration of the experiment (Time) was the repeated variable, whereas Site and Block nested in Site were entered in the model as random factors to account for environmental heterogeneity in the landscape. A Time-by-Treatment interaction was also entered in the model as a further fixed factor. Preliminary, several different co-variance structures were tested for the repeated factor, and unstructured was found to be the best in all cases. Similar models were used to test the treatment effect for the separate years. All analyses were done for all orthopterans, as well as for the two suborders (Ensifera and Caelifera) separately. To avoid type-I errors, the  $P$ -values were adjusted using Bonferroni's correction. In mixed anovas, the critical  $P$ -value was set to  $P = 0.05/6 = 0.0083$ . The Time effect could potentially have been confused with the effect of temperature over years. However, as the correlation between mean annual temperature and Time was not significant ( $r_s = 0.04$ ; NS), effects of Time should be related only to the time since the beginning of the experiment. Data on density and species richness were  $\log_e(x+1)$ -transformed for analyses using raw data. For analyses using means, no transformation was necessary. GLMM analyses were done using procedure mixed in SAS 9.1 (Littell *et al.*, 1996).

**Species composition.** Our response variables were the species by plot matrix of the  $\log_{10}$ -transformed abundance [ $\log_{10}(x+1)$ ]. According to the abundance and species richness analyses, we considered Treatment (control plots in unmown areas, fragment plots, and mown plots), Site and the duration of the experiment (Time). A preliminary detrended correspondence analysis (DCA) was performed. The largest gradient length, expressed in standard deviation (SD) units of species turnover, of the first four DCA axes were always below 3 SD units. Thus, the use of linear-based ordination models was appropriate for these data (ter Braak & Šmilauer, 2002). First, we performed a principal component analysis (PCA) to extract the main part of the variability related to species composition irrespective of our factors. Second, we performed several redundancy analyses (RDA), and used a separate Monte Carlo permutation test with 999 permutations (at  $P < 0.05$ ) to test our three factors. As the factors in our experiments were completely uncorrelated between each other, the total variation explained by a full model including all factors was equal to the sum of the variation explained by the single factors, i.e. the factors did not share any proportion of explained variation. Thus, we did not perform partial RDAs to extract the pure effects of our factors. All the analyses were carried out in CANOCO version 4.5 (ter Braak & Šmilauer, 2002).

## Results

### *Density and species richness over time*

In total, 7838 individuals belonging to 19 orthopteran species were observed in the experimental plots in the 7 years (1993–1999) (Table 1). Species richness differed between sites (Movelier: 21 species, Nenzlingen: 17 species, Vicques: 12 species). Eighteen species were found in control plots and 19 in fragments, whereas only 12 species were observed in the mown matrix. Overall species richness and abundance increased with the duration of the experiment (Fig. 2), despite variations between years (untransformed data: overall density:  $r^2 = 0.62$ ,  $F_{1,5} = 8.30$ ,  $P = 0.035$ ; overall species richness:  $r^2 = 0.63$ ,  $F_{1,5} = 8.33$ ,  $P = 0.034$ ). The species richness increase was related mainly to appearance of three rare species not presented at the beginning of the experiment (*Chorthippus dorsatus*, *Pholidoptera griseoaptera*, and *Tettigonia viridissima*). Abundance of Ensifera did not change over time (untransformed data: overall density:  $r^2 = 0.15$ ,  $F_{1,5} = 0.89$ ,  $P = 0.39$ ). In contrast, the abundance of several species belonging to the suborder Caelifera increased (untransformed data: overall density:  $r^2 = 0.64$ ,  $F_{1,5} = 9.01$ ,  $P = 0.030$ ). In neither of the groups did species richness change over time when analysed separately. The patterns for the different groups were similar when treatments were considered separately (Figs 2 and 3). Overall Ensifera were much less abundant than Caelifera (Table 1).

### *Effect of fragmentation and mowing on density and species richness*

Orthopteran density differed between the three treatments and there was a significant interaction between Treatment and

**Table 1.** Orthopteran species found in the three study sites in the Swiss Jura mountains (Ne, Nenzlingen; Mo, Movelier; and Vi, Vicques) during the period 1993–1999.

Species	Code	Disp.†	Site			Treatment		
			Ne	Mo	Vi	C	F	M
Suborder Ensifera								
Family Gryllidae								
<i>Gryllus campestris</i> Linnaeus, 1758	Grycam	1	+	+	+	0.007	0.004	0.059
Family Tettigoniidae								
<i>Decticus verrucivorus</i> (Linnaeus, 1758)*	Decver	1	+‡	+	+	0.026	0.017	
<i>Metrioptera bicolor</i> (Philippi, 1830) *	Metbic	3	+	+	+	0.233	0.343	0.014
<i>Metrioptera brachyptera</i> (Linnaeus, 1761)*	Metbra	2		+		0.034	0.011	0.005
<i>Metrioptera roeselii</i> (Hagenbach, 1822)	Metroe	2	+	+		0.017	0.015	0.002
<i>Platycleis albopunctata</i> (Goeze, 1778)*	Plaalb	2	+	+	+	0.086	0.345	0.039
<i>Pholidoptera griseoaptera</i> (DeGeer, 1773)	Phogri	1	+	+		0.005	0.002	
<i>Tettigonia cantans</i> (Fuessly, 1775)	Tetcan	2		+			0.002	
<i>Tettigonia viridissima</i> (Linnaeus, 1758)	Tetvir	3	+	+	+	0.003	0.006	
Family Phaneropteridae								
<i>Phaneroptera falcata</i> (Poda, 1761)*	Phafal	3	+‡	+			0.001	
Suborder Caelifera§								
Family Acrididae								
<i>Chorthippus biguttulus</i> (Linnaeus, 1758)	Chobig	3	+	+	+	0.238	0.340	0.270
<i>Chorthippus dorsatus</i> (Zetterstedt, 1821)	Chodor	3		+		0.013	0.002	
<i>Chorthippus parallelus</i> (Zetterstedt, 1821)	Chopar	3	+	+	+	0.286	0.324	0.134
<i>Chrysochraon dispar</i> (Germar, 1834)*	Chrdis	2		+		0.002	‡	
<i>Euthystira brachyptera</i> (Ocskay, 1826)	Eutbra	2	+	+		0.486	0.597	0.118
<i>Gomphocerippus rufus</i> (Linnaeus, 1758)	Gomruf	2	+	+	+	0.198	0.167	0.008
<i>Omocestus rufipes</i> (Zetterstedt, 1821)*	Omoruf	1	+	+	+	0.012	0.076	0.100
<i>Stenobothrus lineatus</i> (Panzer, 1796)	Stelin	2	+	+	+	0.165	0.180	0.155
Family Tetrigidae								
<i>Tetrix tenuicornis</i> (Sahlberg, 1893)	Tetten	1	+	+	+	0.001	0.002	0.012

Treatments are control plots (C), fragment plots (F), and mown plots (M) in the matrix around fragment plots. Densities (individuals per m<sup>2</sup> per year) for treatments are given based on counts from two surveys and are calculated for the sites in which a species occurred.

\*Species marked with asterisks are listed in the red-list of Switzerland as endangered or potentially endangered (Monnerat *et al.*, 2007).

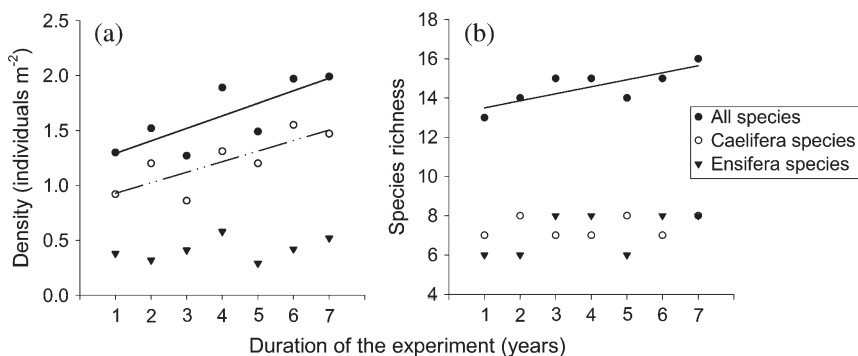
†Dispersal scores from Reinhardt *et al.* (2005): 1 – low, 2 – moderate, 3 – highly mobile species.

‡Species observed in additional surveys not included in the analyses.

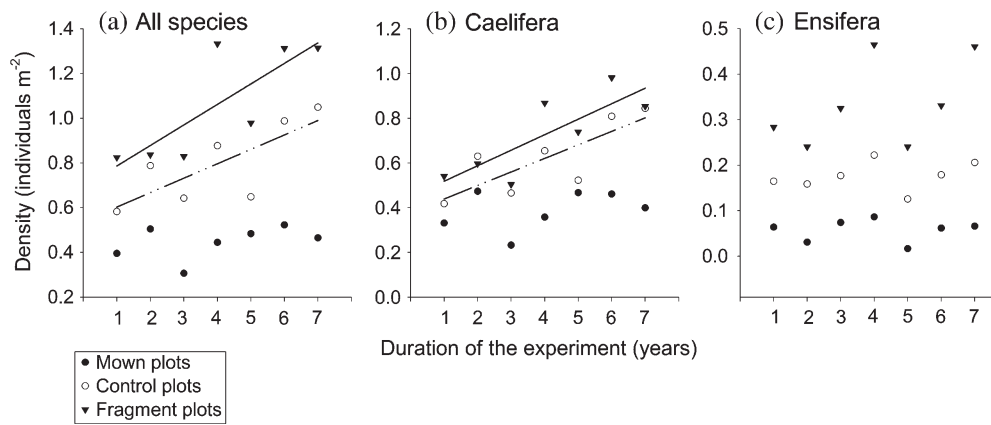
§Young juveniles of some species could not be identified to species level and are thus not included here.

Time (Table 2; Fig. 3). The response differed between the two suborders. The significant interaction between Treatment and Time for the Ensifera was a result of non-directional variation between years. In contrast, Caelifera density increased over time in both fragments and in control plots, whereas it remained steady in the mown areas. Ensifera density was higher in fragments than in control plots. This was partly as a result of the most abundant Ensifera species *Platycleis albopunctata*, which

was very abundant in fragments, but had a similar low density in control plots as in the mown matrix (Table 1). However, Ensifera density was significantly higher in fragments than in control plots, even when this species was removed from the dataset. In contrast, Caelifera density did not differ between fragments and control plots. Densities of both suborders were significantly lower in the mown matrix than in either fragments or control plots. Half of the Ensifera species were never observed



**Fig. 2.** Variation in mean (a) density and (b) overall species richness in experimental plots over the lifetime of the experiment. Results are presented for all orthopteran species (filled circles), Caelifera (open circles), and Ensifera species (inverted triangles), separately. Only significant regression lines are shown (all species, solid line; Caelifera, solid-dot line). In (b) at year seven the species richness of both Caelifera and Ensifera is eight.



**Fig. 3.** Variation in mean density of (a) all species, (b) Caelifera, and (c) Ensifera over the lifetime of the experiment in the three treatments. Only significant regression lines are shown (fragment plots, solid line; control plot, solid-dot line).

in the matrix, whereas most Caelifera species did at least use the matrix, even if not all were abundant there (Table 1). This may indicate that the isolation effect experienced by many Ensifera species in the fragments was much greater than for the Caelifera species.

Species richness was not different between fragments and control plots, either overall or when the suborders were considered

separately. In contrast, overall species richness was reduced in the mown matrix (Table 2). This was mostly as a result of the lower Ensifera species richness in the matrix than in either fragments or control plots. Ensifera species richness was higher in fragments and control plots than in the matrix in all years. In contrast, Caelifera species richness in the matrix did not differ significantly from that in either fragments or control plots in 5 out of 7 years.

**Table 2.** Summary of repeated measurement general linear mixed models (GLMM) testing the effect of the fragmentation on orthopteran groups (a) density and (b) species richness. Density and species richness were  $\log_e(x+1)$ -transformed.

	Num d.f.	Den d.f.	<i>F</i>	<i>P</i>	Tukey–Kramer*
<b>(a) Density</b>					
All species					
Treatment	2	220	63.44	<0.001	F > C > M
Time	6	220	18.52	<0.001	
Treatment × Time	12	220	3.26	<0.001	
Ensifera species					
Treatment	2	220	49.66	<0.001	F > C > M
Time	6	220	21.34	<0.001	
Treatment × Time	12	220	2.87	0.001	
Caelifera species					
Treatment	2	220	15.11	<0.001	F, C > M
Time	6	220	17.09	<0.001	
Treatment × Time	12	220	3.28	<0.001	
<b>(b) Species richness</b>					
All species					
Treatment	2	220	36.07	<0.001	F, C > M
Time	6	220	3.80	0.001	
Treatment × Time	12	220	1.54	0.120	
Ensifera species					
Treatment	2	220	47.44	<0.001	F, C > M
Time	6	220	7.13	<0.001	
Treatment × Time	12	220	1.72	0.064	
Caelifera species					
Treatment	2	220	2.94	0.055	
Time	6	220	2.70	0.015	
Treatment × Time	12	220	1.51	0.123	

\*The last column gives significant differences ( $P < 0.05$ ) between treatments: C (control plots), F (fragment plots), M (plots in mown matrix). To avoid type-I errors the *P*-values were adjusted using Bonferroni's correction ( $P = 0.05/6 = 0.0083$ ).

**Table 3.** Ordination summary of principal component analysis (PCA) and different redundancy analyses (RDA) for orthopteran species composition.

Analysis	Explanatory variables*	P	$\lambda_1$	$\lambda_2$	$\lambda_3$	$\lambda_4$	$\lambda_5$	$\Sigma$ all canonical eigenvalues (TVE)
PCA	–	–	0.367†	0.169†	0.132†	0.079†	0.032†	–
RDA	Treatment, Time, Site	0.001	0.279	0.098	0.077	0.025	0.010	0.489 (48.9%)
RDA	Treatment	0.001	0.135	0.019	–	–	–	0.154 (15.4%)
RDA	Site	0.001	0.191	0.076	–	–	–	0.267 (26.7%)
RDA	Time	0.001	0.068	–	–	–	–	0.068 (6.8%)

$\lambda_i$ : Indicate the first five eigenvalues. In parentheses the proportion of total variation explained (TVE) is indicated.

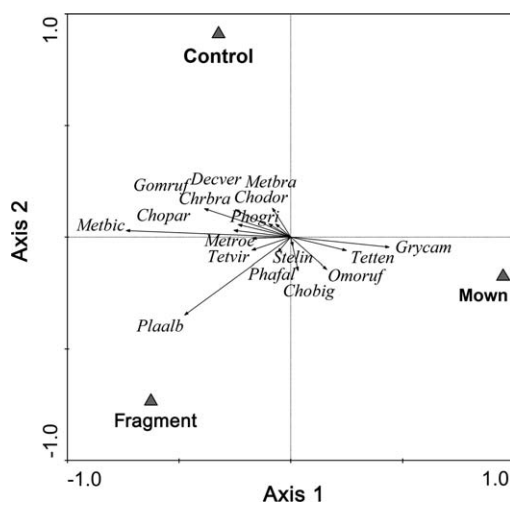
\*All variables were significant at  $P < 0.01$  (Monte Carlo Permutation Test,  $n = 1000$ ).

†Indicates non-canonical eigenvalues (PCA).

In the overall analysis, there is a borderline non-significant trend towards a lower Caelifera species richness in the matrix (Table 2).

### Species composition

The first four eigenvalues obtained from the PCA were 0.367, 0.169, 0.132, and 0.079. Considering the RDA model, orthopteran species composition responded significantly to Site, Treatment, and Time (Table 3). The full RDA model with all the variables explained 48.9% of the total variation. The largest proportion of explained variation was related to differences among sites (26.7%) and between treatments (15.4%), whereas the time since the start of the fragmentation experiment had a relatively small effect (6.8%). Most of the species were least abundant in the plots in the mown matrix, with the exception of *Gryllus campestris*, *Tetrix tenuicornis*, and *Omocestus rufipes* (Fig. 4). Both Ensifera and Caelifera showed a similar response to

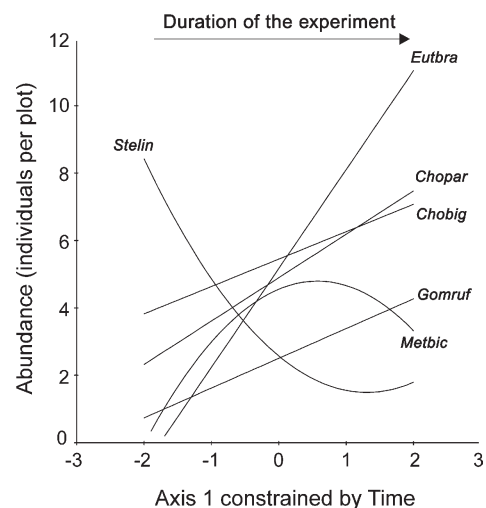


**Fig. 4.** Redundancy analysis (RDA) biplot showing the pure effect of Treatment on orthopteran species composition. The first two axes explained 15.4% of the total variation. Triangles indicate the different treatments (mown plots, control plots, and fragment plots). Species abbreviations are according to Table 1.

mowing. *Platycleis albopunctata* seemed to prefer the fragments. Considering the duration of the experiment, we found contrasting responses among the different species. *Stenobothrus lineatus* showed an evident decrease in abundance over time, whereas *Euthystira brachyptera*, *Chorthippus parallelus*, *C. biguttulus*, and *Gomphocerippus rufus* all became more abundant (Fig. 5). Several species did not show a clear response to time since fragmentation. The species' response to time did not differ between control and fragment plots, i.e. species abundance either declined or increased in a similar manner in both treatments.

### Discussion

In our study, we found significant effects of small-scale grassland fragmentation and mowing on orthopteran population



**Fig. 5.** Predicted curves of species abundance against the constrained axis scores from a redundancy analysis (RDA) model including Time as an explanatory variable. Predicted curves were obtained from a model testing the linear, quadratic, and cubic terms with a stepwise backward deletion (F-test,  $P < 0.05$ ). Only species with a significant response are shown (at least the linear term significant at  $P < 0.05$ ). Species abbreviations are according to Table 1.

density and community structure. Overall, density and to a lesser degree, species richness also increased over time, possibly as a result of the presence of the mown matrix which represented a novel habitat type. There was a marked difference between the two suborders.

In our experiment, the fragmentation had a stronger effect on orthopteran abundance than on species richness. Ensifera density was higher in fragment plots than in control plots, whereas Caelifera density did not differ. Particularly, the bush-cricket *P. albopunctata* showed higher density in fragment plots as this species is able to use both open habitats and small grassland patches (Gottschalk *et al.*, 2003; Hein *et al.*, 2003). Uncut areas have demonstrated to be particularly important as shelters for this species (Harvey & Gardiner, 2006). An increased density in fragment plots was also observed for some other taxonomic groups in the same fragmentation experiment (e.g. grasses, Dolt *et al.*, 2005; aphids, Braschler *et al.*, 2003; ants, Braschler & Baur, 2003, 2005; although other groups showed decreased abundance in fragment plots: e.g. bumblebees, Goverde *et al.*, 2002). Our results confirm the tendency of some large Ensifera, such as *P. albopunctata* and *Metrioptera bicolor* to be reluctant to leave isolated small patches (With *et al.*, 1999). Considering the mobility of our Ensifera species (Table 1), we did not find any clear patterns with response to fragmentation, although low mobility has been demonstrated to be a key factor in explaining orthopteran extinction at a regional scale (Reinhardt *et al.*, 2005). As orthopterans are supposed to be one of the most resilient insect groups (Joern & Pruess, 1986; Collins, 2000), it is likely that the duration of the experiment was too short to cause important changes in species richness, which should be expected to lag behind changes in abundance. It is thus likely that the experimental fragmentation would with time have led to stronger differences also in species richness, especially for the Ensifera, which for the most part seemed reluctant to cross the mown area. However, our experiment did not allow us to quantify local extinction and recolonisation processes in the fragments plots. The relatively weak effect of fragmentation we observed could have been due to the fact that mown areas were less suitable for orthopterans, but not completely unsuitable (Collinge, 2000). We hypothesised that small-scale dispersal between plots might have smoothed the fragmentation effects (see also Chambers & Samways, 1998).

In general, the mown area was an unpreferred habitat for a large proportion of the investigated species. This confirms the results of Guido and Gianelle (2001), who found that mowing in a small-scale experiment seemed to cause a redistribution of species across mown and unmown areas with a significant decrease in overall orthopteran abundance in the cut areas (Wagner, 2004; Gardiner & Hill, 2006). Such a decrease could be a result of mortality induced by mowing and by the migration of species to adjacent undisturbed microhabitats. For example, this process has been observed for populations of *Chorthippus mollis* (Thorens, 1993) and *C. parallelus* (Guido & Gianelle, 2001). Most Ensifera were rarely found in the mown matrix around the fragment plots. The reluctance of the Ensifera to venture into the matrix and their resulting lower overall species richness and abundance in fragment plots, is likely a result of the reduced cover offered by the mown matrix (Diekötter *et al.*, 2007).

Larger Ensifera especially, such as *Decticus verrucivorus*, *Pholidoptera griseoptera* or *P. albopunctata* would have been exposed to predators, particularly birds, when moving through the matrix (Harvey & Gardiner, 2006). Most Ensifera species are larger than the Caelifera species included in this study, and thus would have been even more exposed. Considering the species found in our sites, adult Ensifera are 14–37 mm in length, whereas adult Caelifera are only 9–26 mm in length. Frequent cutting regimes may lead to higher mortality as a result of injuries from blades and machine movements (Gardiner & Hill, 2006). Direct mortality due to mowing is supposed to be one of the most detrimental factors reducing orthopteran species richness in managed grasslands (Detzel, 1985; Wagner, 2004; Marini *et al.*, 2008). The mown matrix did not only provide little cover from predators for the orthopterans, but also strongly affected the microclimate. In general, minimum surface temperatures in our experimental grasslands were lower in the mown matrix than in the unmown vegetation, whereas maximum temperatures were higher in the matrix (Zschokke *et al.*, 2000). Orthopteran individuals venturing out into the matrix thus risked surpassing critical thermal thresholds on sunny days when solar irradiation was high (Willott, 1997; Gardiner & Hassall, 2009). These results conform to the findings of Pitt (1999), who found that orthopterans utilise different microhabitats to balance the trade-off between reducing mortality from predators and experiencing greater food availability, and suitable thermic conditions.

The presence of the frequently mown matrix in the otherwise undisturbed experimental grasslands might explain the significant change over time in some species' abundance. Orthopterans are generalist herbivores and they have been previously shown to be strongly affected by sward structural differences between grasslands (Gardiner *et al.*, 2002; Marini *et al.*, 2008). Although frequent mowing was detrimental for most of the species in the short term, the presence of the mown matrix offered a novel short-turf habitat with a comparatively high percentage of bare ground at the whole-site scale. This change in vegetation structure at the block scale might have provided suitable conditions for species that required short turf for egg deposition, such as *Chorthippus parallelus* and *C. biguttulus*, or species related to the presence of bare ground such as *Tetrix* sp. or *Gryllus campestris* (Van Wingerden *et al.*, 1991; Guido & Gianelle, 2001). Although Dolt *et al.* (2005) found that the vegetation also slightly changed at the plot scale, these changes should be of less importance than the presence of the mown matrix for population dynamics at our temporal scale. According to this interpretation, after the suspension of the former grazing management and the creation of the mown matrix, most of the species that showed an increase in population density were mainly species dwelling in mown grasslands (Gerstmeier & Lang, 1996; Marini *et al.*, 2008). On the contrary, *E. brachyptera*, as a typical inhabitant of undisturbed grasslands (Ingrisch & Köhler, 1998), probably increased its density because of the suspension of the former grazing management regime. In long-term studies, the creation of small mown patches surrounded by undisturbed grasslands can enhance species abundance and diversity for some species, particularly Acrididae such as *Chorthippus* sp., by providing more favourable thermic conditions for reproduction (Van Wingerden *et al.*, 1991) or higher quality of food resources, as a result of

the presence of higher live grass biomass and new growth (Chambers & Samways, 1998).

## Conclusions

Although the ecological processes related to fragmentation as a result of mowing usually operate at the landscape scale at which experiments are generally impossible, our findings obtained in a controlled small-scale experiment may permit initial assessment of the effects of fragmentation on species diversity patterns and abundance (With *et al.*, 1999; Zschokke *et al.*, 2000). On the one hand, the reluctance to cross the mown matrix shown by many Ensifera species suggests that this group could be more easily prone to local extinctions in response to mowing of large areas and habitat fragmentation. On the other hand, some Caelifera species demonstrated an ability to cope better with mowing, although most species exhibited a decreased abundance in the mown matrix. The relatively weak effect of fragmentation on community structure should be considered with prudence, as might have been mitigated by small-scale dispersal movements between treated plots. The stability of orthopteran communities could be a further element explaining the weak response to fragmentation. The negative effect of frequent mowing was much clearer on both population density and species diversity. The detrimental effects of frequent mowing at the landscape scale could be related to both direct mortality and creation of an unsuitable matrix perceived as an unpreferred habitat, particularly by Ensifera species. Frequent mowing such as that applied in parks or intensive hay meadows, can be considered one of the main threats to orthopteran communities in managed grasslands. Hence, the presence of habitat refugia (e.g. woody vegetation or unmown areas) close to grassland patches, might enhance the persistence of species-rich communities as it might compensate for the detrimental effect of mowing.

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