Abstract
Finding an optimal balance between livestock production and grazing impact on animal diversity is important for the development of sustainable grazing systems. This paper tests the hypothesis that extensification of grazing management enhances animal diversity. Similar treatments were applied over a period of three years to sites in the UK, France, Germany and Italy. There were three treatments at each site: moderate grazing intensity with a commercial breed (MC), lenient grazing intensity with a commercial breed (LC) and lenient grazing intensity with a traditional breed (LT). Animal diversity was studied at the species level for birds, hares, butterflies and grasshoppers, and at higher taxonomic level for ground-dwelling arthropods. Bird and hare numbers were low and showed no overall treatment effects. Species richness and abundance of butterflies and grasshoppers were higher for treatment LC than for treatment MC, both for species preferring short open grasslands and those preferring tall grasslands. There was no difference in the impact of commercial or traditional breeds. Most ground-dwelling arthropod groups did not show consistent treatment effects but some taxa showed site-specific responses, generally indicating a greater abundance at lenient grazing intensity. Overall, the study showed that lenient grazing intensity enhanced animal diversity on grasslands at a small scale within 3 years. By comparison, the effect of livestock breed differences was negligible. Follow-up research is needed to elucidate the processes leading to increased biodiversity in patch mosaics and to establish the generality of these findings at larger spatial scales and longer time scales.

Keywords: biodiversity, grazing, stocking rate, livestock breeds, butterflies, grasshoppers, arthropods, birds

Introduction
The Council of the European Union has set a target of stopping the ongoing loss of biodiversity by 2010. However, due to changes in land use over recent decades, there has been a high loss of biodiversity, especially on farmland in Europe (Krebs et al., 1999; De Heer et al., 2005). This loss is a consequence both of abandonment of marginal farmland (Balmer and Ehrhardt, 2000; Laiolo et al., 2004; EEA, 2004) and intensification of agriculture on potentially productive land (Donald et al., 2000; Benton et al., 2003; EEA, 2004). One solution for preserving and enhancing biodiversity is to implement a more extensive form of agriculture on ‘high nature-value farmland’ (Green et al., 2005). On agricultural land, a large part of European biodiversity is found in semi-natural grasslands (Bignal and McCracken, 1996; EEA, 2004). There is a lack of insight about adequate management strategies and insufficient evaluation of outcomes on the basis of reliable data (Kleijn et al., 2001; Kleijn and Sutherland, 2003). In particular, targeted experiments in a grassland context are lacking (Rook and Tallowin, 2003; Rook et al., 2004).

This paper tests the hypothesis that extensification of grazing management enhances animal diversity on semi-natural grasslands. Grazing by large herbivores can dramatically influence the structure and composition of animal communities (Van Wieren, 1998). Research to determine the impact of grazing has mostly
The same experimental design was used in four countries: UK (Devon), Germany (Solling Uplands), France (Massif Central uplands) and Italy (Pordenone foothills). Each treatment was replicated three times according to a randomized block design. Data were collected over a period of 18 months at the end of which subsamples were taken for analysis. The results are presented in Table 1: a moderate grazing intensity with a commercial breed designed to optimize livestock productivity without fertilizer use (MC), a lenient grazing intensity with a commercial breed (LC), and a lenient grazing intensity with a traditional breed (LT).

Materials and methods
Experimental sites

Table 1 Main characteristics of the experimental sites and treatments.

<table>
<thead>
<tr>
<th>Country</th>
<th>United Kingdom (UK)</th>
<th>Germany (D)</th>
<th>France (F)</th>
<th>Italy (I)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>North Devon 50°53’N 3°W</td>
<td>Solling Uplands 52°N 9’E</td>
<td>Auvergne 45°N 3’E</td>
<td>Pordenone 46°N 12’E</td>
</tr>
<tr>
<td>Altitude</td>
<td>100 m</td>
<td>250 m</td>
<td>1100 m</td>
<td>400 m</td>
</tr>
<tr>
<td>Initial conditions</td>
<td>Mesotrophic grassland</td>
<td>Mesotrophic hill grassland</td>
<td>Semi-natural upland grassland</td>
<td>Calcareous grassland</td>
</tr>
<tr>
<td>Moderate grazing intensity treatment (treatment MC)</td>
<td>Continuous variable stocking with growing cattle; herbage mass maintained at 3000 kg ha⁻¹</td>
<td>Continuous variable stocking with growing cattle; compressed sward height maintained at 6 cm</td>
<td>Continuous set stocking (May–October: 12 LU ha⁻¹) with growing cattle</td>
<td>Rotational stocking with growing sheep (12.5 sheep ha⁻¹; 10 grazing days, 20-d rest)</td>
</tr>
<tr>
<td>Lenient grazing intensity treatments (treatments LC and LT)</td>
<td>Same as above but herbage mass maintained at 4500 kg ha⁻¹</td>
<td>Same as above but compressed sward height maintained at 12 cm</td>
<td>Same as above but stocking rate reduced to 0.85 LU ha⁻¹</td>
<td>Same as above but at 75 sheep ha⁻¹</td>
</tr>
<tr>
<td>Commercial breeds</td>
<td>Charolais × Friesian steers</td>
<td>Simmental steers</td>
<td>Charolais heifers</td>
<td>Finnish Romanov sheep</td>
</tr>
<tr>
<td>Traditional breeds (treatments MC and LC)</td>
<td>Devon steers</td>
<td>German Angus steers</td>
<td>Salers heifers</td>
<td>Karst sheep</td>
</tr>
<tr>
<td>Paddock size</td>
<td>1.5 ha</td>
<td>1 ha</td>
<td>3.6 ha</td>
<td>0.4 ha</td>
</tr>
</tbody>
</table>

MC, moderate grazing intensity with a commercial breed; LC, lenient grazing intensity with a commercial breed; LT, lenient grazing intensity with a traditional breed; LU, livestock unit.
three summer grazing seasons between spring 2002 and autumn 2004.

Measurements
At each site, animal diversity in each paddock was recorded at a species level for butterflies, grasshoppers, birds and hares, but at higher taxonomic levels only for ground-dwelling arthropods (Table S4). Number of sampling dates varied somewhat between sites and years, mainly caused by unfavourable weather conditions, but there was no variation in sampling effort between treatments within sites because all paddocks were surveyed at each sampling date.

Butterflies were surveyed at each paddock using the ‘Pollard walk’ (Pollard and Yates, 1993). All the butterflies encountered on a transect were counted and identified. Weather conditions permitting, 10 counts were carried out at approximately 14-d intervals between early May and late September of each year.

Grasshoppers were recorded along the same transects as the butterflies, using sweep-net sampling with 25 sweeps per transect at 2-m intervals. In addition, at the F site acoustic observations of singing males were recorded (proportionately 0·08 of all grasshoppers recorded at the F site). Four counts at approximately monthly intervals were carried out between June and October, the exact timing depending on differences in timing of life cycles of the insects at the different sites. Fewer counts than for butterflies were judged adequate in view of the longer life span of grasshoppers. Only adults were counted on all occasions; nymphs were counted separately only on some occasions. Cricket (Gryllidae) numbers were also counted in pitfall traps (see below).

Birds and hares (Lepus europaeus L.) were counted early in the morning at approximately 14-d intervals between May and October, using two methods: 7-min observations of each paddock from a fixed point outside the paddock followed by walking of a transect though the paddock in order to disturb any individuals that may have been hidden in the vegetation. Only birds residing in the paddocks or flying low over the paddocks were counted. Among the bird species the focus was on those associated with grassland; woodland birds were only recorded frequently at the I site. Using the same method, counts were also carried out on two to four occasions during winter at the I and UK sites, as these sites could also offer valuable habitat outside the grazing season.

Ground-dwelling arthropods were sampled during three periods of pitfall trapping each year, in late spring, summer and early autumn. Twelve traps were placed in each paddock, four traps at regular intervals along each ‘buttermilk transect’. Traps were provided with about 1-cm depth of a 4% formalin solution or with a mixture of 80% alcohol, ethylene glycol and acetic acid. Trap design varied slightly between sites, but all traps were approximately 10 cm in diameter, covered with a plate to prevent ingress of rain and protected against trampling by a cage-like construction. The traps were emptied after 2 weeks and the samples stored in alcohol for later identification. Identification and counts of individuals were carried out at higher taxonomic level for adults of 28 arthropod groups with a minimum size of 2 mm (see Table S4). At the UK site, earthworms (Lumbricidae) and slugs (Mollusca and Stylommatophora) were also recorded. Numbers within each transect series were adjusted for traps missing caused by trampling or flooding.

Statistical analysis
Data analysis focused on the effects of the treatments on species richness (S) and individual abundance within each paddock in a given year. Moreover, abundance data for butterflies and grasshoppers were analysed in relation to habitat affinity with species assigned to the following habitat types: bare ground (grasshoppers only), short grassland, tall grassland and wide-ranging generalists (butterflies only) (based on, among others, Bellmann and Luquet, 1995; Tolman and Lewington, 1997; Fontana et al., 2002). As a measure of the evenness of the distribution of individuals among species, the Shannon index ($H' = - \sum p_i \ln p_i$, where $p_i$ is the proportion of individuals of species $i$ relative to the total number of individuals of all species) and Pielou’s Specific Evenness ($J = H'/\ln S$) (Magurran, 2004) were computed.

Results were pooled over transects within each paddock for each year prior to analysis. Species groups for a particular site were left out of the analysis when the total number of individuals was <100, to avoid high frequencies of zero values. Log-transformation ($\ln N$ or $N + 1$, when 0 values occurred) was applied to abundance data. In addition to a fixed treatment factor, the mixed ANOVA model included a fixed factor nested within sites, a random block factor within each site, a year factor, and three two-way interactions between sites, treatments and years; the contribution of the three-way interaction was explored but proved insignificant and was therefore omitted from the final model. Whenever treatment effects or site × treatment effects were found to be marginal with respect to significance ($0.05 < P < 0.10$), the site × year and treatment × year interactions were left out of the statistical model to gain degrees of freedom. Pairwise treatment effects were compared by Tukey’s HSD, with a focus on the two
most relevant treatment comparisons, i.e. LC vs. MC and LC vs. LT, using a Bonferroni correction for multiple comparisons. All statistical analyses were carried out using JMP Version 5 with REML estimation of random effects (SAS, 2002).

Results

Butterflies and grasshoppers

In total, 6193 butterflies from 66 species were observed, including, at the F site, seven individuals of Maculinea arion, a species listed in Annex IV of the European Habitats Directive (Table S1). The most abundant species were associated with tall vegetation (Maniola jurtina, Coenonympha pamphilus, Polyommatus icarus, Thymelicus lineola), followed by flower-seeking generalists (Vanessa cardui, Aglais urticae, Pieris brassicae, P. napi, P. rapae). Characteristic butterflies of short grasslands (mainly Lycaena phlaeas, Spialia sertorius, Pyrgus malvae, Pyrgus malvoides, Aricia agestis) were less abundant and almost restricted to the F and I sites. Woodland butterflies were only frequent at the I site (especially Melitaea athalia). Grasshoppers were more numerous than butterflies (14,895 individuals) but there were fewer species (34) (Table S2). Species associated with tall vegetation were the most abundant (Chorthippus dorsatus, Chorthippus parallelus, Chorthippus albomarginatus and Pezotettix giornai) but characteristic species of short grassland (mainly Chorthippus biguttulus and Euchorthippus declivus) and bare patches (mainly Omocestus rufipes and Stenobothrus stigmaticus) were almost as numerous. Across all sites, species richness was negatively related to herbage mass. The highest number of species occurred at the I site (46 butterfly and 21 grasshopper species), followed by the F site (34 butterfly and 12 grasshopper species) and the rather species-poor D site (23 butterfly and nine grasshopper species) and UK site (17 butterfly and only three grasshopper species).

The abundance and species richness of both butterflies and grasshoppers were significantly different between treatments (Tables 2 and 3), with higher values for butterflies ($P < 0.05; P < 0.10$ for LC vs. MC treatment contrast) and grasshoppers ($P < 0.01$) at the lenient (treatments LC and LT) than at the moderate (treatment MC) grazing intensity. Differences between commercial and traditional breeds at the lenient grazing intensity (treatments LC and LT, respectively) were not significant for either butterflies or grasshoppers. The absence of significant treatment × year interactions indicated that treatment effects did not change during the experiment.

A higher abundance on the lenient grazing intensity was apparent for species characteristic of tall vegetation ($P < 0.05$ for butterflies with a marginally significant LC vs. MC treatment contrast, $P < 0.10$ and $P < 0.001$ for grasshoppers), for species from short grasslands ($P < 0.01$ for butterflies and $P < 0.05$ for grasshoppers; sufficiently abundant for inclusion in the data analysis for F and I sites only) and for grasshoppers associated with bare patches ($P = 0.05$; sufficiently abundant for inclusion in the data analysis for F and I sites only, but not for generalist butterflies (Figure 1). Woodland butterflies were only found at the I site, but their numbers were not significantly affected by the experimental treatments. Nymphs from Chorthippus grasshoppers were counted at the D site in 2003 and 2004 and were also significantly more abundant at the lenient grazing intensity ($P < 0.05$; log $(N + 1)$, treatment MC, $1:53$; treatment LC, $2:14$; treatment LT, $2:12$; s.e. of mean, 0:11).

Piezou’s specific evenness was not significantly different between treatments for butterflies but significant ($P < 0.05$) for grasshoppers (Table 3). Evenness was similar between treatments LC and LT and highest on treatment MC. Grasshopper data from the UK were excluded from this analysis, because of insufficient numbers of species. Data on the Shannon index are not presented separately, as they were (by their nature) highly correlated with species richness ($r = 0.91$ for butterflies and $r = 0.96$ for grasshoppers) and, hence, did not provide additional information.

Birds and hares

A total of 1930 birds from 29 species associated with grassland were observed in the various sites during the summer season (Table S3). Meadow pipit (Anthus arvensis) and Skylark (Alauda arvensis) were by far the most abundant. In addition 126 birds belonging to six different woodland species were observed, mostly at the Italian site (mainly Jay Garrulus glandarius and Blackbird Turdus merula). Winter observations at the I and UK sites totalled 637 birds from 15 grassland species and 141 birds from nine woodland species. Typical meadow birds and geese were absent from the sites, with the exception of Snipe (Gallinago gallinago) during winter at the UK site. Hares were present at all sites, but only recorded with some frequency at the UK site. Their abundance was insufficient for statistical analysis, but the total number of hares did not indicate any treatment effect (UK site: treatment MC, 12; treatment LC, 14; treatment LT, 15).

Mean abundance and species richness of birds were low and not significantly affected by grazing treatment (Tables 2 and 3). Treatment effects did not vary between years. Piezou’s Specific Evenness did not differ between treatments (Table 3). As for butterflies and grasshoppers, the Shannon index was highly correlated with species richness ($r = 0.87$).
Table 2 Least square means for individual abundance (log N individuals per paddock per year) of butterflies, grasshoppers, birds and arthropod groups from pitfall catches for the treatments MC, LC and LT (for description of treatments see Table 1) with the level of significance of treatment and site × Treatment effects, and the sites (D, Germany; F, France; I, Italy; UK, United Kingdom) included in the statistical analysis.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>MC</th>
<th>LC</th>
<th>LT</th>
<th>s.e. of mean</th>
<th>Treatment</th>
<th>Site × treatment</th>
<th>Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Butterflies</td>
<td>1·49&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1·62&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1·67&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0·05</td>
<td>*</td>
<td>NS</td>
<td>all</td>
</tr>
<tr>
<td>Grasshoppers</td>
<td>1·53&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1·78&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1·75&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0·06</td>
<td>**</td>
<td>NS</td>
<td>all</td>
</tr>
<tr>
<td>Birds</td>
<td>0·65</td>
<td>0·15</td>
<td>0·51</td>
<td>0·08</td>
<td>NS</td>
<td>NS</td>
<td>all</td>
</tr>
</tbody>
</table>

Pitfall catches

A total of 284 051 arthropods were recorded from the 28 target groups (Table S4). In addition, 515 earthworms and 6706 slugs were counted at the UK site. A meaningful statistical analysis was possible for 23 of the 28 target groups, but only occasionally for all sites (Table 2).

Where significant differences between treatments occurred, they were mostly site-specific but generally showed a greater abundance at the lenient grazing intensity. Higher numbers at the lenient grazing intensity were found for Carabidae at the UK site (Figure 2a; P < 0·05 for the treatment LC vs. MC contrast), Staphylinidae at the UK site (Figure 2c; P < 0·10 for the treatment LC vs. MC contrast), Heteroptera at the UK site (Figure 2e; P < 0·05 for the treatment LC vs. MC contrast), and also for slugs at the UK site (P < 0·01; log(N + 1)), treatment MC = 1·97; treatment LC = 2·48; treatment LT = 2·40; s.e. of mean, 0·07). A significant

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Table 3  Species richness and Pielou’s specific eveness for butterflies, grasshoppers and birds for the treatments MC, LC and LT (for description of treatments see Table 1) with the level of significance of treatment and site x treatment effects, and the sites (D, Germany; F, France; I, Italy) included in the analysis. Numbers reflect annual means per paddock.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Species richness</th>
<th>Level of significance</th>
<th>Site x treatment</th>
<th>Sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>MC</td>
<td>LC</td>
<td>LT</td>
<td>s.e. of mean</td>
</tr>
<tr>
<td>Butterflies</td>
<td>80a</td>
<td>96b</td>
<td>101b</td>
<td>0.5</td>
</tr>
<tr>
<td>Grasshoppers</td>
<td>38a</td>
<td>52b</td>
<td>45b</td>
<td>0.3</td>
</tr>
<tr>
<td>Birds</td>
<td>2.3</td>
<td>2.2</td>
<td>2.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Pielou’s specific evenness</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Butterflies</td>
<td>0.75</td>
<td>0.69</td>
<td>0.69</td>
<td>0.02</td>
</tr>
<tr>
<td>Grasshoppers</td>
<td>0.77a</td>
<td>0.72b</td>
<td>0.71b</td>
<td>0.02</td>
</tr>
<tr>
<td>Birds</td>
<td>0.72</td>
<td>0.75</td>
<td>0.69</td>
<td>0.09</td>
</tr>
</tbody>
</table>

MC, moderate grazing intensity with a commercial breed; LC, lenient grazing intensity with a commercial breed; NS, not significant.
Different letters indicate significant differences between treatments, *P < 0.05, Tukey’s HSD test.
**P < 0.01.

Discussion
Methodological considerations
From the multitude of possible diversity indicators of animals, a number of taxonomic groups to represent the above-ground grassland fauna were chosen. For an adequate indication of biodiversity a species group should (i) have been studied sufficiently to have adequate knowledge of its distribution status and ecological relations; (ii) reflect the environmental variation in the habitat under study; (iii) be sensitive to environmental change and (iv) be able to be monitored by an established quantitative method (Thomas, 2005). Butterflies are one of the few taxonomic groups that satisfy all these conditions.

Although grasshoppers performed similarly in their response to the treatments, less is known about their ecology and distribution. Moreover, there is no standard and quantitatively sound methodology for monitoring grasshopper abundance (see Fontana et al., 2002). Nevertheless, the sweepnet sampling adopted in this study appears to give an adequate quantitative assessment of the abundance of most grasshopper species in grasslands. However, rarer and more elusive species are better surveyed by acoustic recording but such results are quantitatively less reliable.

The fixed-point and transect counts used in this study to survey birds and hares followed established methods and are suitable for application at small spatial scales (Bibby et al., 1992). However, the lack of treatment effects may have been precluded by the generally low abundance of birds and hares. Nevertheless, treatment effects remained absent even at the F site where there were higher densities of larks and pipits. In general, birds and hares are probably more sensitive to changes at the landscape scale than at the scale of a few hectares examined in this study (Söderström et al., 2001; Benton et al., 2003). Invertebrates, such as butterflies, can also respond strongly to landscape features (e.g. Weibull et al., 2000; Söderström et al., 2001; Bergman et al., 2004) but they are especially sensitive to small-scale variation in vegetation structure, botanical composition and management (e.g. Oates, 1995; Mortimer et al., 1998; Morris, 2000). Hence, invertebrates appear more promising candidates than birds or hares to evaluate the paddock-scale treatments examined in this study.
treatment effects were as evident in ground-dwelling groups as in vegetation-dwelling groups. The second explanation is that the pitfall samples were identified at higher taxonomic levels rather than at the species level. It is clear that species differ in ecological requirements and may therefore show contrasting responses to different types of management (e.g. Morris, 1990; 2000; Bourn and Thomas, 2002; Dennis et al., 2004). The overall effect at higher taxonomic level might then be small because of species effects cancelling one another out. Nevertheless, various studies have reported consistent effects of management at higher taxonomic levels in arthropods (e.g. Morris, 1968; King and Hutchinson, 1976; Hutchinson and King, 1980; Morris and Rispin, 1987; Dennis et al., 1998; 2004). It may be that the treatment effects were not distinct enough to result in more significant changes in the abundance of invertebrates caught in the pitfalls. Further examination of the samples at species level could shed more light on this issue.

**Effects of grazing intensity**

There was a consistent effect of grazing intensity on butterflies and grasshoppers across the sites in four countries. The lenient grazing intensity (treatments LC and LT) increased butterfly numbers and species richness, resulting in an uneven abundance of individuals for a greater number of species. Two-way interactions in the statistical model were generally not significant, with the exception of site × year interactions (results not shown) showing different effects of certain years at the various sites. Treatment effects were thus consistent across sites, despite a wide variation in animal community structure and composition between sites.

There was little evidence of an effect of grazing intensity on abundance of birds and hares. The difference between grazing intensities in vegetation height was small at the F site (Isselstein et al., 2007) and apparently not large enough to result in changes in the abundance of meadow pipits and skylarks, although these species could be expected to benefit from tall grass during the breeding season (Milsom et al., 2000).

The lenient grazing intensity treatments (treatments LC and LT) increased the abundance of Carabidae, Staphylinidae and also slugs at the UK site and Heteroptera and Homoptera at the D site. The moderate grazing intensity (treatment MC) raised the abundance of some arthropods: Curculionidae and Dermaptera at the D site and Staphylinidae at the F site. The effect of grazing intensity on the predatory carabid and staphylinid beetles in the UK site could reflect increased forage resources in the taller, heterogeneous vegetation on treatments LC and LT, but might also reflect a more favourable microclimate (Tscharntke and Greiler, 1995;
Dennis et al., 1998; 2004). Heteroptera and Homoptera at the D site are likely to have benefited from the more complex vegetation structure and lesser disturbance under the lenient grazing treatments (Morris and Rispin, 1987; Tschamntke and Greiler, 1995; Kruess and Tschamntke, 2002a). The contrasting responses in abundance of Staphylinidae to the lenient grazing intensity treatments at the F (negative) and UK (positive) sites may be due to the less productive soil and climatic conditions at the F site, which could have had a negative impact on staphylinid species from short and, hence, more productive swards (see Morris, 1990). The negative effect of the lenient grazing treatments (treatments LT and LC) on the abundance of Curculionidae and Dermaptera at the D site is not easily explained: studies on the relationship between Dermaptera populations and grassland management are lacking and many Curculionidae are closely linked to specific food

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**Figure 2** Individual abundance of (a) Carabidae, (b) Curculionidae, (c) Staphylinidae, (d) Dermaptera and (e) Heteroptera (least square means per paddock per year) for treatments moderate grazing intensity with a commercial breed (MC) (●), lenient grazing intensity with a commercial breed (LC) (■) and lenient grazing intensity with a traditional breed (LT) (□) (descriptions of treatments are given in Table 1) between in different countries sites (D, Germany; F, France; I, Italy; UK, United Kingdom) for arthropods from pitfall catches. Bars represent s.e. of mean.
plants so that changes in, for example, the availability and quality of clover could have affected some abundant species (see Dennis et al., 2004).

The significant effects of the treatments did not increase over the three years of the experiment, with the exception of leaf hopper (Homoptera: Auchenorrhyncha) abundance at the D site (Figure 3). This indicates that grazing intensity may already have had a great impact in the short term through the alteration of vegetation structure. The absence of further change may partly be due to the spring and summer drought in 2003, when grazing had to be stopped for part of the season and treatment differences could not diverge further. Also, the small size of the paddocks (<4 ha) may have masked some effects because of the movement of, for example, butterflies between paddocks. In any case, three years is still a very short period over which to evaluate the temporal effect of grazing.

An overview of the impact of reduced grazing intensity on animal diversity from other studies has shown a predominance of positive effects on the abundance of butterflies and grasshoppers, supporting the results of this study. For butterflies increased abundance associated with a reduction in grazing intensity has been found by Söderström et al. (2001), Krueß and Tscharntke (2002b), Ellis (2003); Franzén and Ranius (2004) and Pöyry et al., 2004; 2005) and for grasshoppers a similar effect has been found by Cherrill and Brown (1992); Van Wingerden and Dimmers (1993); Fartmann and Mattes (1997); O’Neill et al. (2003); Schuhmacher and Fartmann (2003) and Hjermann and Ims (2005). For butterflies and grasshoppers there also are some notable exceptions to these effects of a reduction in grazing intensity on their abundance (Thomas et al., 1986; Bourn and Thomas, 2002; Dolek and Geyer, 2002), concerning especially species associated with short swards, bare patches or the presence of dung (Morris, 1968; 1990; Gibson et al., 1992b; Bourn and Thomas, 2002; Dennis et al., 2004). Among these, are species with high conservation priorities in temperate Europe, mainly because of their dependence on warm microclimates found in open vegetation on low-productivity sites (Bourn and Thomas, 2002; Dolek and Geyer, 2002). It should be noted that, under such marginal conditions for agriculture, reduction of grazing pressure can be detrimental to biodiversity.

Positive effects of a reduction in grazing intensity have also been reported for the abundance of many groups of ground-dwelling arthropods, such as spiders (Morris, 1968; Hutchinson and King, 1980; Gibson et al., 1992a,b; Dennis et al., 1998; Bonte et al., 2000), Chilopoda (Hutchinson and King, 1980), Coleoptera (Morris, 1968; 1990; Dennis et al., 1998; 2004; Krueß and Tscharntke, 2002a), CollemboIa (King and Hutchinson, 1976; King et al., 1976), Dermaptera (Hutchinson and King, 1980), DiplopoIoda (Hutchinson and King, 1980), Hemiptera (Morris, 1967; 1968; 1969; 1973; Gibson et al., 1992b; Dennis et al., 1998; Di Giulio et al., 2001; Krueß and Tscharntke, 2002a) and Isopoda (Morris, 1968).

The importance of structural heterogeneity

Several mechanisms have been suggested to explain the greater biodiversity at reduced grazing intensities. The greater architectural complexity of lightly grazed swards appears to be a main driver of insect diversity (Tscharntke and Greiler, 1995; Dennis et al., 1998; Morris, 2000; Krueß and Tscharntke, 2002a,b). This complexity not only concerns the vertical dimension but also the horizontal dimension, in the form of patchiness (e.g. Dennis et al., 1998). The benefit of this variation lies not only in a greater number of ecological niches, but also in increased habitat quality for species requiring buffered microclimates (Tscharntke and Greiler, 1995; Willott, 1997) and relying on low levels of disturbance from large herbivores (Krueß and Tscharntke, 2002a; Berggren, 2004). In addition, tall vegetation lowers predation risk for large insects (Schuhmacher and Fartmann, 2003). Conversely, tall vegetation provides more food resources, in the form of nectar for butterflies (e.g. Loertscher et al., 1995), plant and insect biomass for herbivorous and carnivorous insects, respectively (Tscharntke and Greiler, 1995; Krueß and Tscharntke, 2002a,b) and dead biomass for detritivores (King and Hutchinson, 1976; King et al., 1976; Morris, 1990).

Interestingly the effect of a lenient grazing intensity was not only found for the abundance of butterfly

<table>
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Figure 3 Change in treatment effects during the experiment for Homoptera (Auchenorrhyncha) at the German site (least square means per paddock per year) for treatments moderate grazing intensity with a commercial breed (MC) ( ■ ), lenient grazing intensity with a commercial breed (LC) ( ■ ) and lenient grazing intensity with a traditional breed (LT) ( □ ) (descriptions of treatments are given in Table 1). Bars represent s.e. of mean.
and grasshopper species characteristic of tall vegetation, but also for those associated with short vegetation and grasshoppers associated with bare ground (Figure 1), despite a greater availability of short vegetation on the moderate grazing intensity treatment (treatment MC). The answer to this discrepancy could well lie in the more pronounced mosaic of short and tall patches at the lenient grazing intensity (treatments LC and LT) (Scimone et al., 2007). For the butterflies, this result might be explained by increased nectar availability in tall vegetation. However, this does not agree with the finding that the flower-seeking generalist butterflies were not affected by grazing intensity. Moreover, as the nectar-independent grasshoppers from short vegetation and bare patches were also favoured by the lenient grazing treatments, increased patchiness appears to be a better explanation for greater abundance of butterflies and grasshoppers at the lenient grazing intensity. Indeed, other studies have also shown the benefit of increased structural heterogeneity through patchiness in a variety of arthropods, e.g. butterflies (Dennis, 2004), grasshoppers (Fartmann and Mattes, 1997; Willott, 1997; Guido and Gianelle, 2001), spiders (Bonte et al., 2000) and other arthropods (Morris, 1990; 2000; Kruess and Tscharntke, 2002a,b). Patchiness may increase species richness by providing habitat for species characteristic of short as well as tall vegetation (habitat heterogeneity). But patchiness may also be essential for species requiring both short and tall vegetation (symbiosis between patches). Dennis et al. (1998) found support for the first hypothesis, but not for the second. Nevertheless, there are good examples of species relying on a mosaic of short and tall patches or early and mid-successional stages (butterflies: Wallis De Vries, 2001; 2004; Dennis, 2004; grasshoppers: Cherril and Brown, 1992; Fartmann and Mattes, 1997; Willott, 1997; birds: Milsom et al., 2000; Perkins et al., 2000; Benton et al., 2003). Short patches provide warmer microclimates and different food resources than tall patches that, in turn, provide cooler refuges and shelter against predation and trampling. It may thus be suggested that the observed increases in butterflies and grasshoppers, associated with short vegetation or bare patches, could be a result of improved habitat quality through greater patchiness. Further research on microhabitat use and survival in relation to patchiness is necessary to confirm this hypothesis.

Effects of livestock breed

The effects of breed on abundance and species richness were negligible compared with the effects of grazing intensity. Only the indistinct category of ‘other Coleoptera’ at both the D and I sites was significantly more abundant under lenient grazing intensity with traditional breeds than with commercial breeds. Hence, this study does not support a generally positive effect of traditional breeds on animal diversity. Differences between livestock breeds could emerge when there is greater variation in size and physiology of breeds. In that case, however, it is those factors rather than breed differences per se that should be considered (Rook et al., 2004).

Conclusions

The two main messages from this study are that the effects of livestock breeds on animal diversity are negligible and that, in the short term, a lenient grazing intensity is preferable from the viewpoint of butterfly and grasshopper diversity. When this results in the encroachment of competitive plants, however, as observed in the more productive UK and D sites (Scimone et al., 2007), insect diversity is likely to become compromised. Further research is needed to evaluate the effects of grazing intensity over a longer period and at the larger farm scale that is relevant to sustainable land-use practices. On the other hand, a scaling-down to the level of patches is necessary to improve the understanding of the processes leading to increased biodiversity in patch mosaics.

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Supplementary material
The following supplementary material is available for
this article:
Table S1. Number of butterflies for each species
recorded during the experiment at the four different
sites for the different habitats.
Table S2. Number of grasshoppers for each species
recorded during the experiment at the four different
sites for the different habitats.
Table S3. Number of grassland birds and hares
recorded during the experiment at the four different
sites during summer season.
Table S4. Total number of arthropods recorded in
pitfall traps during the experiment for each site.

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