Plant species richness in montane grasslands affects the fitness of a generalist grasshopper species

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Abstract. Theory predicts negative effects of increasing plant diversity on the abundance of specialist insect herbivores, but little is known about how plant diversity affects the performance and abundance of generalist insect herbivores. We studied oviposition rates and offspring numbers in females of the generalist grasshopper *Chorthippus parallelus* that were collected in 15 montane grasslands in 2005 and 2007 along a gradient of plant species richness in central Germany. In addition to plant species richness, we determined evenness and plant community composition in the grasslands and measured aboveground plant biomass and other habitat variables such as leaf area index, vegetation height, and solar radiation. There was substantial variation among sites in grasshopper fecundity and the number of nymphs that hatched from the egg pods. Both fitness measures were positively influenced by plant species richness at the sites, while female fitness did not correlate with any of the other habitat parameters. Abundance of *C. parallelus* in the grasslands was positively correlated with plant species richness, plant community composition, and incident solar radiation of the sites. There were no phenological differences between grasshoppers from the different study sites. Our results suggest that decreasing biodiversity threatens the persistence not only of specialist, but also of generalist insect herbivores via a variety of mechanisms including a decrease in diversity of the generalists' food plants.

Key words: *Chorthippus parallelus; extensively managed montane grasslands; fecundity; Germany; grasshoppers; plant community composition; reproduction.*

Introduction

Recently, increasing attention has been paid to the community-level effects of biodiversity (Loreau et al. 2001, Hooper et al. 2005). While earlier studies on the relationship between biodiversity and ecosystem functioning mostly focused on primary producers (e.g., Schulze and Mooney 1993), more recent studies have started to address the effects of species diversity on trophic interactions (e.g., Duffy 2002, Cardinale et al. 2003, Schmitz 2003), for example, between plants and herbivorous insects (Weisser and Siemann 2004, van Ruijven et al. 2005). With respect to herbivorous insects, research has focused on the effects of plant diversity on herbivore diversity or abundance (e.g., Andow 1991, Sieman 1998, Jactel et al. 2005). These studies were motivated by the work of Root (1973), who predicted that the abundance of herbivores will be lower in diverse plant communities than it is in simple communities ("resource concentration hypothesis"). The mechanism

underlying this assumption is that herbivores find and remain on plants more often in pure stands than in diverse plant communities (Root 1973). Tests of Root's hypothesis have thus focused on the response of specialist insect herbivores to changes in plant diversity (e.g., Schellhorn and Sork 1997, Otway et al. 2005), often in agricultural systems (Andow 1991, Tonhasca and Byrne 1994). However, it is essential to also understand the effects of plant diversity on generalist herbivore species, as they are an important part of natural ecosystems.

In contrast to the many theories about specialists, there is no general theory of how increasing plant diversity might affect the abundance of generalist herbivores. Predictions can be derived from ecophysiological studies investigating the effects of mixed diet on the performance of generalist insect herbivores (e.g., Bernays and Chapman 1994, Simpson and Raubenheimer 2000). In most of these laboratory studies, the performance (e.g., survival, growth rate, fecundity, etc.) of generalist herbivores was better on mixtures of food plant species than on diets containing single plant species (e.g., Bernays and Bright 1993, Unsicker et al.

2008), although there were exceptions in which no general benefits of dietary mixing were measurable (e.g., Bernays and Minkenberg 1997, Singer 2001).

Based on our results from these ecophysiological studies with generalist herbivores in the laboratory, we can predict that under natural conditions in the field, generalist herbivores perform better in more diverse habitats where they can take advantage of many species of potential food plants. Experimental tests of this prediction in biodiversity experiments involving grasshoppers reared outdoors on mixtures of different diets have led to conflicting results (Pfisterer et al. 2003, Specht et al. 2008). Plant diversity in natural habitats is often a function of land use and abiotic conditions, all of which are likely to affect herbivore performance. To separate the effects on herbivore fitness of land use and climate (e.g., vegetation structure and solar radiation) from the effects on herbivore fitness of diet (e.g., diversity and abundance of food plant species), it is essential to make simultaneous measurements of variation in all these parameters.

In Central European grasslands, grasshoppers (Orthoptera, Acrididae) are an important component of the phytophagous insect community and are responsible for a considerable part of total herbivory (Köhler et al. 1987). One of the most common acridid species in Central Europe is the meadow grasshopper *Chorthippus parallelus* Zetterstedt 1821 (Acrididae, Gomphocerinae), which has been the subject of several classical studies on diet selection in herbivorous insects (Bernays and Chapman 1970*a, b*) as well as of studies relating to the consumption and use of food (Köhler and Schäller 1981).

We tested the influence of plant species richness on the fitness and the abundance of *C. parallelus* by collecting females in meadows that were selected along a gradient of plant species richness (Kahmen et al. 2005). In addition to plant species richness, we recorded plant community composition, plant community biomass, vegetation height, leaf area index, and solar radiation, parameters that can affect grasshopper performance. The main questions we asked were: (1) Is there variation in fitness measures such as fecundity and number of hatched offspring of female *C. parallelus* among the different grassland sites? (2) Does grasshopper fitness correlate with plant species richness? (3) What are the effects of other habitat variables for grasshopper performance, compared to the influence of plant species richness?

MATERIALS AND METHODS

Study sites

The study was conducted in 15 hay meadows in Frankenwald and Thüringer Schiefergebirge (50°21′–50°34′ N, 11°00′–11°37′ E), a low mountain range at the Bavarian/Thuringian border in Central Germany with a maximum elevation of 841 m above sea level. The 15 grassland sites are part of an interdisciplinary research project. Selection criteria for the sites were (1) no fertilization and (2) no grazing during the last 15 years

and (3) soil pH higher than 5.0 (Kahmen et al. 2005). All of the meadows have been extensively managed for at least the last 15 years with two mowings per year (June/July and August/September). Sites were chosen to represent a gradient of plant species richness from ~20 species (species in four plots of 1 m^2 each) in the species-poor meadows to ~41 species in the most diverse mountain hay meadows.

Habitat variables

All habitat variables were measured in June 2005 in a 5-m^2 plot in each of 15 field sites. Aboveground community biomass was sampled in four 0.1-m^2 rectangles (total 0.4 m^2 for each plot) quadrats within the 5 × 5 m plot, by cutting the vegetation 3 cm above ground. The community biomass samples were dried at 70°C for 48 h and weighed. All plant species were identified in four 1 × 1 m quadrats that were placed close to the center of the 5 × 5 m plot and percent cover was visually estimated using a modified Londo scale (Londo 1976). We use plant species richness as the mean species richness in these four quadrats.

The leaf area index (LAI) of each study site was measured four times in a 5 × 5 m plot with an LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebraska, USA) and the maximum height of the plant community at each site was determined by placing a quadratic piece of polystyrene (30 × 30 cm) on top of the vegetation. The height at which the quadrat rested on top of the vegetation was measured. This measure was repeated at four points with a distance of 1.5 m from one another and averaged. To characterize the sites, geographic position (GPS coordinates), altitude (range = 595–685 m above sea level), exposition (range = pure north to pure south), and inclination (range = 0–20°) were determined. Based on exposition and inclination, we calculated mean potential direct solar insolation (PDSI; R. Hohmann, J. Schumacher, and J. Perner, *unpublished program*, algorithm based on Volz [1959]). In addition to species richness, we calculated Carmargo's evenness as another relevant plant diversity measure (Krebs 1999).

Grasshopper abundances in the study area

On 17 and 18 June 2005, abundances of *C. parallelus* in 11 study sites were classified based on the sampling success of two people performing sweep netting for 30 min within a 300-m^2 portion of each meadow. Eight categories were used to measure grasshopper abundances: 0, no record; 1, 1–4 individuals; 2, 5–10; 3, 11–20; 4, 21–30; 5, 31–40; 6, 41–50; 7, 51–60; 8, 61–70 individuals. For all subsequent statistical analyses, the highest number of each category was picked (10, 20, 30, 40, 50, 60, and 70).

Experimental setup and grasshopper size

In order to determine fitness parameters in *C. parallelus* along the gradient of plant species diversity, we collected 20 adult females of *C. parallelus* in each of

the 15 meadows (=300 females) at the end of July 2005 (26 and 28 July). Females of one site were placed in plastic boxes (27 × 17 × 18 cm; Savic, Heule, Belgium), together with 5–10 males that were caught additionally at each site. Mating of grasshoppers caught in the same site was allowed to take place until the start of the experiment. Twenty-four hours after the grasshoppers were caught, each female was placed individually in a cage, 14 cm in diameter and 17 cm in height, consisting of aluminium mesh (aperture size, 1.5 mm) fixed to the lid of a Petri dish (14.5 cm in diameter) with hot-melt adhesive, thus forming a cylinder that slides over the bottom part of the Petri dish. Each cage contained a plastic cup (diameter, 5 cm; height, 3 cm) filled with a 50:50 mixture of moistened sand and soil for egg-laying and a small plastic vial for holding the food plant.

Throughout the experiment, all grasshoppers were fed with *Dactylis glomerata* (Poaceae), a grass species known to be an adequate food source for *C. parallelus* (Ingrisch and Köhler 1998, Köhler 2001, Unsicker et al. 2008). The freshly cut grass leaves were put in a plastic vial that was filled with water to prevent the grass from wilting. In order to provide sufficient food throughout the experiment, the cages were checked daily and if necessary, freshly cut *D. glomerata* leaves were added. The cups with the sand/soil mixture were also kept moist throughout the experiment. As not all females could be handled within one day, 144 females (50.2%) were kept individually in cages for six days and 143 females (49.8%) for seven days. Thereafter females were anesthetized with CO_2 and the length of the left hind femur was measured under a binocular microscope with the aid of an object slide engraved with measuring units. As landmark points for the measurement, we chose the most distant points of the outer rim of the upper, larger lobe of the notched base and the outer rim of the upper one of the two genicular lobes at the apex (Jentzsch et al. 2003).

Grasshopper reproduction

In 2005, grasshopper fecundity (number of egg pods) and the number of hatchlings from the egg pods were taken as fitness measures. Egg pods laid by each female until the end of the experiment (after 6–7 days) were counted by carefully washing the egg pods out of the egg-laying soil. After counting, the egg pods were buried again in an autoclaved sand and soil mixture (50:50), keeping the same orientation as they had before with the narrow part of the egg pod facing upwards. The pods laid by a single female were placed together in one cup covered with conventional fly mesh to prevent grasshopper progeny from escaping after hatching. For two months the egg pods were kept in the laboratory at room temperature so that the embryos could develop to blastokinesis. Throughout this time, the sand and soil mixture in the cups was regularly watered to prevent drying out. At the beginning of October 2005 all cups with egg pods were transferred to the refrigerator at 6°C.

On January 26 all cups were removed from the refrigerator and kept under laboratory conditions with a diurnal room temperature of 22°C ± 1.6°C (mean ± SD). All pots containing egg pods were checked daily for hatchlings and were watered when necessary. Freshly hatched grasshoppers were collected with an aspirator and immediately killed by freezing at −20°C. As the experiment was not terminated on the same day for all female grasshoppers, the rates per day for both pods laid and hatched offspring were calculated. Thus for each female, egg pods per day and number of offspring per day (number of hatchlings divided by time of oviposition) were calculated as variables measuring fecundity and reproductive success, respectively.

In 2007, we repeated our study with slight modifications in order to test whether the relationship between grasshopper fecundity and plant species richness is reproducible. In mid-July 2007 (13 and 17 July) 10–30 juvenile grasshoppers (nymphal stages 3 and 4) were caught in nine of the 15 study sites from 2005. The investigation of grasshopper abundance in 2007 was part of another research project, which is the reason why the number of field sites investigated differed from 2007. The nymphs that were caught in each site were kept in separate cages (30 × 30 × 30 cm; MegaView Science, Taiwan) under laboratory conditions. In 2007 the grasshoppers were fed with a food plant mixture consisting of the grass species *D. glomerata* and the legume *Trifolium pratense*. After maturity moult (end of July until middle of August) grasshopper males and females that were originally caught in the same study site were allowed to mate and oviposit in cups filled with a sand and soil mixture, as in the previous experiment. The oviposition experiment in 2007 lasted until the grasshoppers died. Thereafter the number of egg pods laid by the females in each cage was counted. By dividing the total number of egg pods by the number of female grasshoppers present in the cages (cages represent study sites), the number of egg pods per female grasshopper was calculated. In 2005 12 female grasshoppers died during the experiment and one escaped; hence the number of valid replicates for the statistical analyses was 287.

Grasshopper phenology

Because in 2005 grasshoppers were only counted without determining the nymphal stages of each individual, another survey was conducted in 2007 in order to test for differences in grasshopper phenology between sites. We caught *C. parallelus* grasshoppers by sweep netting along a transect in each of the study sites at the beginning of July 2007 (7 July). Ten beats with the sweep net were performed in each site, and the developmental status of each *C. parallelus* grasshopper caught was then recorded (all instars but the first could be found in the study sites). Thus the phenological status of each grasshopper population could be determined.

TABLE 1. Summary of data for eight habitat variables that were measured in the 15 study sites in central Germany in June 2005.

Parameter	Mean ± SE	Range	n
Plant species richness	30.4 ± 1.58	20–41	15
Community biomass (g/m^2)	298.49 ± 36.53	120.74–652.04	14
NMDS1	0.02 ± 0.12	−0.85–0.96	15
NMDS2	−0.03 ± 0.24	−1.68–1.06	15
Camargo's evenness	0.32 ± 0.015	0.23–0.45	15
Leaf area index (LAI)	3.68 ± 0.37	1.18–5.92	14
Vegetation height (cm)	30.57 ± 6.7	16.0–108.0	14
Solar radiation in site (J/cm^2)	2055.68 ± 32.1	1796.97–2353.15	15

Notes: The difference in the number of replicates for the habitat variables is due to early accidental mowing of one study site in June 2005. Thus none of the parameters except plant species richness and solar radiation could be investigated at this time.

Grasshopper diet breadth experiment

To test the diet breadth of *C. parallelus* and to verify the fact that this grasshopper species is a generalist feeder rather than a specialist, we performed a cage experiment in which six grasshopper females were continuously provided with food plants of a species-rich meadow typical for the study area. Thirteen plant species were selected as food plants based on their abundance in the study site. All plant species in the grassland that had a cover over 1% (plant cover was estimated in four 1-m^2 plots) were integrated in the feeding experiment. The selected plant species were seven grass species (*Agrostis tenuis*, *Anthoxanthum odoratum*, *Dactylis glomerata*, *Festuca rubra*, *Holcus lanatus*, *Phleum pratense*, and *Trisetum flavescens*), four herbaceous species (*Alchemilla vulgaris*, *Hypericum maculatum*, *Plantago lanceolata*, and *Veronica chamaedrys*), and two legumes (*Trifolium pratense* and *Trifolium repens*).

Grasshoppers were reared from oothecae laid in the laboratory by females collected from a field population near Jena in 2004. Individuals were kept singly in 6-L fauna boxes (Savic) from within three days after hatching until death. Freshly cut food plants were randomly arranged in a plastic box (115 × 15 × 60 mm) placed in the fauna box, filled with water, and covered with plastic foil to prevent plants from desiccation and grasshoppers from drowning. Plants were offered ad libitum.

Every fourth day, the leaf area (in square millimeters) of each plant species consumed by the grasshoppers was measured with the help of graph paper. To convert the leaf area eaten into dry mass consumed, 10 1-cm^2 leaf discs of each plant species were cut, dried for 48 h in a drying oven at 70°C, and weighed. Here, we only present data on food plant consumption of females during their four nymphal instars.

Statistical analysis

All count data were square-root transformed prior to analyses. Means are displayed with standard errors (SE).

To account for the effects of plant community composition on the fitness of *C. parallelus*, we used nonmetric multidimensional scaling (NMDS) ordination of the plant communities in the 15 study sites, using the square-root-transformed plant cover data. Nonmetric multidimensional scaling is an ordination method that has been shown to deliver robust results for vegetation data (Faith et al. 1987, Minchin 1987). From a matrix of resemblances (similarities or dissimilarities) between pairs of objects, here plant communities, NMDS constructs a configuration of points in a specified number of dimensions, such that the rank order agreement between the inter-point distances and the resemblance values is maximized. As a distance measure, the Bray-Curtis coefficient was used, and NMDS analyses were conducted using the program PC-ORD (McCune and Mefford 1997). We tested whether a two-dimensional solution gives a sufficiently good fit to the data, indicated by a low "stress" value (Faith et al. 1987, Minchin 1987).

Because we investigated eight habitat variables (plant species richness, community biomass, Camargos's evenness, NMDS1, NMDS2, LAI, vegetation height, and solar radiation; Table 1) we tested for correlations among the independent variables using a principal components analysis (PCA).

Multiple linear regressions in a stepwise selection procedure were carried out using SPSS 15.0 for Windows (SPSS, Chicago, Illinois, USA) to analyze the effects of habitat variables on grasshopper fitness parameters and abundances. In addition to the models presented by the stepwise procedure, models were tested by using the forward and backward procedure implemented in SPSS. The Akaike information criterion (AIC) values of the best model are reported.

RESULTS

Grasshopper diet breadth experiment

Female grasshoppers in the experiment lived on average for 97.5 ± 0.89 days. Fig. 1 shows the larval food consumption of six female grasshoppers from the first nymphal instar to the time of maturity molt (45.0 ± 0.97 mg). During their development, the grasshoppers consumed all offered plant species except the herbaceous species *Alchemilla vulgaris* (Fig. 1). There were significant differences in the amount of food consumed from individual plant species (ANOVA, $F_{12,5} = 25.4$, $P = 0.001$). The bulk of biomass consumed during the four larval stages was grasses (87.4%) and, to a lower extent, herbs (12.6%). The two legume species, *Trifolium pratense* and *Trifolium repens*, comprised 12.5% of the total nymphal food consumed. According to these results, *C. parallelus* can be termed a true generalist feeding on food plants from more than one plant family.

Multivariate analysis of plant communities

In total 89 plant species occurred in the 15 study sites, and their abundances were used for the ordination of the plant communities. The NMDS analysis showed that a
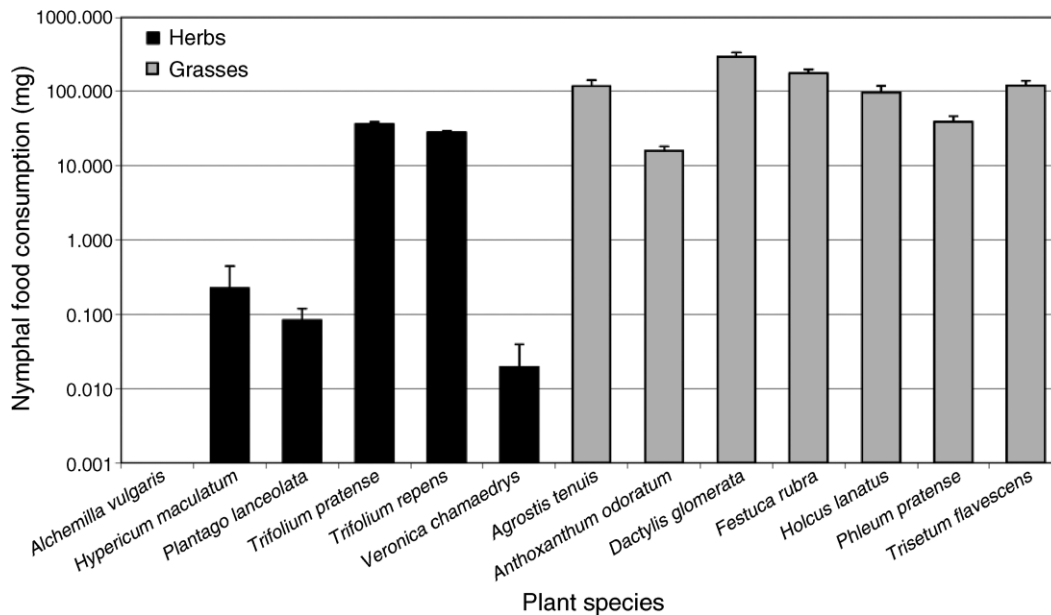
Fig. 1. Food consumption of six females (mean + SE) of the grasshopper *Chorthippus parallelus* during the four nymphal instars in a food plant mixture with seven grasses and six herbs. Note that the *y*-axis is a log scale.

two-dimensional solution was sufficient to achieve low stress values explaining plant species composition in the 15 sites (first axis/dimension = 34.7, second axis/dimension = 9.0). Thus for all future analyses, we used the two main axes, labelled NMDS1 and NMDS2, to represent plant community composition. For a more detailed description of the occurrence of particular plant species along the NMDS gradients, see Kahmen et al. (2005). The relationships between the plant species that were tested in the grasshopper diet breadth experiment and the two NMDS axes are shown in the Appendix.

Multivariate analysis of habitat variables

The means, standard errors, and ranges of all measured habitat variables are given in Table 1. Community biomass decreased with increasing plant species richness, with 652.04 g/m^2 and 120.74 g/m^2 at the site with the lowest (20 species) and highest diversity (41 species), respectively. However, this relationship was not significant ($r^2 = 0.26$, $P = 0.062$). There was no relationship between plant species richness and Camargo's evenness ($r^2 < 0.01$, $P = 0.736$). The number of grass species was positively correlated with the total number of plant species ($r^2 = 0.734$, $P < 0.001$). Community biomass was correlated with LAI, vegetation height, and NMDS1, whereas NMDS1 was correlated with Camargo's evenness.

We included the two NMDS axes NMDS1 and NMDS2 into a PCA analysis of all habitat variables. The resulting first two PCA axes explained 70% of the total variance in habitat variables (Table 2). The first axis was closely positively correlated with community biomass, LAI, and vegetation height and negatively

correlated with NMDS2. Thus, the composition of the plant community, expressed by NMDS2, affected productivity and structural parameters of the plant community (biomass, LAI, height). The second axis was mainly determined by NMDS1 and Camargo's evenness.

To reduce the number of parameters in further multiple regressions, community biomass was selected instead of the closely correlated vegetation height and LAI. While NMDS2 was correlated with community biomass (Table 2), both NMDS1 and NMDS2 were kept for future analyses as plant species composition represents the host plant combinations in the plant communities, i.e., resource quality, whereas productivity is a measure of resource quantity. The six parameters plant species richness, Camargo's evenness, community biomass, NMDS1, NMDS2, and solar radiation were

TABLE 2. Eigenvalues and eigenvector coefficients (loadings) of a standardized principal component analysis (PCA) of the eight independent variables.

Variable	PCA1	PCA2
Eigenvalues	0.5062	0.1904
Plant species richness	**−0.573**	−0.161
Community biomass	**0.943**	0.089
Camargo's evenness	0.002	**−0.865**
NMDS1	0.126	**0.800**
NMDS2	**−0.914**	0.046
Leaf area index (LAI)	**0.893**	−0.150
Solar radiation	**−0.592**	0.271
Vegetation height	**0.914**	0.066

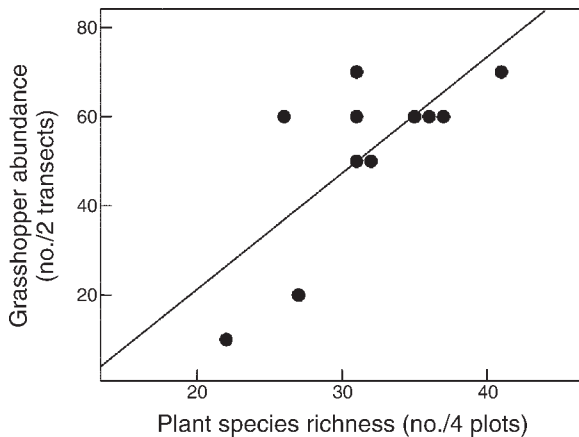*Note:* Loadings >0.5 appear in boldface to emphasize the impact of the representative axes.

FIG. 2. Relationship between plant species richness and the abundance of *Chorthippus parallelus* in 11 study sites in central Germany ($r^2 = 0.53$, $F_{1,9} = 10.12$, $P = 0.011$). Abundance is the number of grasshoppers caught in 30 min by two people sweep-netting along two transects in the respective study site. Plots were 1 m² each.

used as independent variables in all multiple regressions on grasshopper abundance and fitness-related variables.

Grasshopper abundances

There was a positive relationship between plant species richness and grasshopper abundance in June 2005 ($r^2 = 0.53$, $F_{1,9} = 10.12$, $P = 0.011$; Fig. 2). Increasing community biomass tended to decrease the abundance of grasshoppers, but the relationship was marginally significant ($r^2 = 0.40$, $F_{1,8} = 5.29$, $P = 0.05$). There was no relationship between grasshopper abundance and Camargo's evenness ($r^2 = 0.02$, $F_{1,9} = 0.2$, $P = 0.663$) or NMDS1 ($r^2 = 0.09$, $F_{1,9} = 0.86$, $P = 0.377$), but *C. parallelus* abundances were influenced by NMDS2 ($r^2 = 0.55$, $F_{1,9} = 11.05$, $P = 0.009$) and solar radiation ($r^2 = 0.42$, $F_{1,9} = 6.46$, $P = 0.032$) in the sites. There was a positive relationship between grasshopper abundance and solar radiation. In a multiple linear regression with the six selected habitat variables, only plant species richness and NMDS2 remained in the final model (species richness alone, $r^2 = 0.70$, $F_{1,8} = 18.74$, AIC = 51.04, $P = 0.003$; plant species richness and NMDS2, $r^2 = 0.85$, $F_{2,7} = 20.44$, AIC = 45.88, $P = 0.001$).

Grasshopper body size

Mean female femur length was independent of overall plant species richness ($r^2 < 0.001$, $F_{1,13} < 0.001$, $P = 0.988$), community biomass ($r^2 = 0.03$, $F_{1,12} = 0.32$, $P = 0.581$), NMDS1 ($r^2 = 0.001$, $F_{1,13} = 0.01$, $P = 0.911$), NMDS2 ($r^2 = 0.01$, $F_{1,13} = 0.2$, $P = 0.658$), and solar radiation ($r^2 = 0.004$, $F_{1,13} = 0.05$, $P = 0.833$), but there was a significant positive relationship between Camargo's evenness and mean femur length in females of *C. parallelus* ($r^2 = 0.55$, $F_{1,12} = 16.12$, $P = 0.001$). In a multiple regression the best model included Camargo's evenness and NMDS1 as explanatory variables (Ca-

margo's evenness alone, $r^2 = 0.55$, $F_{1,12} = 14.74$, AIC = -43.76, $P = 0.002$; Camargo's evenness and NMDS1, $r^2 = 0.71$, $F_{2,11} = 13.96$, AIC = -48.23, $P = 0.001$).

Grasshopper reproduction 2005

Females laid between zero and two egg pods within the time frame of seven days, and 52.3% of the 287 grasshoppers laid at least one egg pod (193 eggs pods by $n = 150$ females). The percentage of females laying zero egg pods was negatively correlated with plant species richness of the study sites ($r^2 = 0.33$, $P = 0.025$). There was a significant positive relationship between mean egg pod number per day and overall plant species richness across sites ($r^2 = 0.39$, $F_{1,13} = 8.39$, $P = 0.012$; Fig. 3a). In a multiple regression with the six habitat variables only plant species richness emerged as significant predictor variable ($r^2 = 0.426$, $F_{1,12} = 8.891$, AIC = -85.76, $P = 0.011$).

Hatching started 18 days after the egg pods were removed from the refrigerator. Offspring hatched from 134 of the 193 egg pods laid by 99 of the 150 females. Altogether 716 nymphs hatched from the 134 egg pods (3.68 ± 0.28 individuals per egg pod). Grasshopper abundances of *C. parallelus* in the field did not influence the number of offspring per day ($r^2 = 0.113$, $P = 0.312$, n
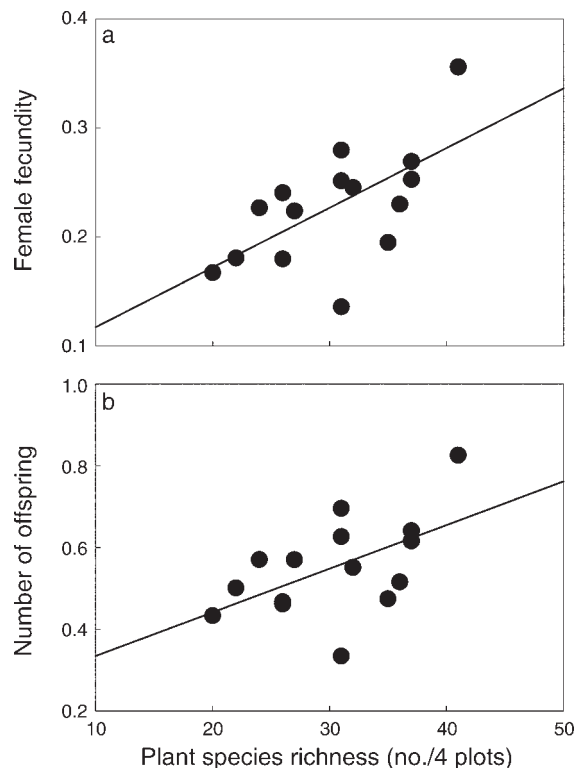

FIG. 3. Relationship between plant species richness and (a) female fecundity (mean number of egg pods per day, square-root transformed) in 15 study sites ($r^2 = 0.39$, $F_{1,13} = 8.39$, $P = 0.012$) and (b) mean number of offspring per day (square-root transformed; $r^2 = 0.30$, $F_{1,13} = 5.52$, $P = 0.035$) of *Chorthippus parallelus*. Plots were 1 m² each.

= 11). There was a significant positive relationship between plant species richness and the mean number of offspring per day ($r^2 = 0.30$, $F_{1,13} = 5.52$, $P = 0.035$; Fig. 3b). In a multiple regression with the six selected habitat variables, only plant species richness was significant ($r^2 = 0.30$, $F_{1,12} = 5.10$, AIC $= -61.42$, $P = 0.043$).

Grasshopper reproduction 2007

There was a significant positive relationship between mean egg pod numbers per female grasshopper and overall plant species richness in their original habitats ($r^2 = 0.56$, $F_{1,7} = 7.624$, $P = 0.028$). In a multiple regression with the six habitat variables, only plant species richness was retained as a significant predictor variable ($r^2 = 0.56$, $F_{1,6} = 6.535$, AIC $= 2.876$, $P = 0.043$).

Grasshopper phenology

The phenology of *C. parallelus* in the study sites in 2007 was not related to the local plant species richness, i.e., there were no systematic differences in developmental speed between the study sites. When individual regressions were performed with percentage of grasshoppers in the respective developmental stage vs. plant species richness in the study sites, plant species richness did not explain the variability in the abundances of any of the nymphal instars (nymphal stage 2, $F_{1,9} = 0.039$, $P = 0.848$; nymphal stage 3, $F_{1,9} = 1.203$, $P = 0.301$; nymphal stage 4, $F_{1,9} = 2.156$, $P = 0.176$; adults, $F_{1,9} = 0.050$, $P = 0.828$).

DISCUSSION

The fitness of the grasshopper *C. parallelus*, measured as the number of egg pods laid by females and by the number of hatching offspring, greatly varied between different grassland sites investigated. The variation in grasshopper fitness was best explained by plant species richness in the different study sites. This was true for both years (2005 and 2007) in which grasshopper fecundity was investigated. Furthermore, grasshopper abundances were positively affected by increasing plant species richness and, to a lesser extent, plant species composition in the study sites. Our results show that in addition to effects of plant diversity on specialist insect herbivore fitness, there are also measurable effects of plant diversity on the abundance of these generalist insect herbivores. We will discuss possible mechanisms underlying the observed patterns in female grasshopper fitness, in particular the role of a diverse diet for generalist herbivores.

Host specificity of C. parallelus

There is clear evidence from our feeding experiments that the grasshopper *C. parallelus* is a true generalist feeder, sensu Schoonhoven et al. (2005), that feeds on grass and legume species, but largely avoids the consumption of forbs. Feeding behavior of acridid grasshoppers including *C. parallelus* in the field has been studied by observations and gut analyses (see

Chapman and Joern 1990). Differences between grasshopper species belonging to different species within one subfamily could be found with respect to the relative amount of grasses and forbs in their diet (Joern 1979). The consumption of food plants was not exclusively determined by the abundance of food plant species in the grasshoppers' habitats (e.g., Bernays and Chapman 1970b), which is an indirect proof that grasshoppers exert active food choice.

Grasshopper abundance and fitness in relation to habitat variables

The abundances of *C. parallelus* in the field and female fitness were higher in sites with higher plant species richness, and none of the other habitat parameters tested in our study was significantly correlated with grasshopper fitness. The abundances of *C. parallelus* were additionally influenced by plant community structure (NMDS) and by solar radiation in the sites. Plant community composition has already been shown to explain a large portion of the variance in insect abundances (e.g., Perner et al. 2005). Plant community composition is a surrogate for a number of effects the plant community exerts on herbivorous insects that are difficult to identify, because they include effects on grasshopper diet (i.e., combinations of particularly suitable or unsuitable food plants), microclimatic effects, and structural effects such as refuges from natural enemies (Perner et al. 2005). Our study sites are at elevations up to 685 m above sea level with high annual precipitation and low mean temperatures. In grasshoppers, like in most ectothermic animals, both activity and growth are temperature-dependent. It is thus conceivable that sunshine is a major restriction for *C. parallelus* activity in the study area, which may explain why there are more grasshoppers in sites more exposed to sunshine. Data on the relative abundances of *C. parallelus* nymphal instars in the different study sites in 2007 show, however, that the phenology of the grasshoppers was not correlated with plant species richness. Thus, the positive effect of plant species richness on grasshopper fitness is not confounded by systematic differences in phenology, i.e., a systematic difference in female grasshopper age among sites at the time of capture.

The consistent effect of plant species richness on herbivore fitness and the absence of significant correlations with other habitat parameters suggest that the plant diversity per se has positively affected female nutrition, which resulted in the observed differences in fecundity and the number of offspring among sites. There are at least three possibilities for the positive affect of plant species richness on grasshopper performance: (1) an increase in the diversity of food plant resulting in a better diet, (2) a decrease in top-down control of grasshoppers by natural enemies with increasing plant species richness, and (3) a positive effect of plant species richness on other, unmeasured,

abiotic variables that also positively influence grasshopper fitness. In our view, most evidence points to explanation 1, a positive effect of plant species richness on grasshopper fitness via the increased possibility of dietary mixing. Dietary mixing has repeatedly been shown to increase fitness in generalist grasshoppers, including *C. parallelus* (e.g., Bernays et al. 1994, 1997, Unsicker et al. 2008). Plant species richness and hence the number of potential food plants for *C. parallelus* doubled along the plant diversity gradient in this study. Although the results from the feeding experiment with *C. parallelus* show that this species predominantly feeds on grass and legume species, we observed some feeding on other forbs. As we cannot exclude the possibility that feeding on these forbs affects grasshopper fitness despite the low amounts consumed, we used overall plant species richness in the statistical model presented here rather than species richness based only on grass and legume species. Multiple regressions using grass and legume species richness gave the same results for the number of grasshopper egg pods and grasshopper abundance, only the number of offspring was not significantly affected (data not shown). Experiments that tested feeding strategies in generalist grasshoppers to date have mostly tested a restricted number of plant species offered in monocultures or as mixtures, and to our knowledge, only one study observed beneficial effects of a plant community containing more than 20 plant species in the field (Pfisterer et al. 2003). Pfisterer et al. (2003) found positive effects of plant species richness on mass gain of the generalist grasshopper *Parapleurus alliaceus* in a setting in which grasshoppers were caged on experimental mixtures of one, two, four, eight, and 32 plant species, all of which included at least one grass species. While the difference was mainly due to a higher mass gain in 32-species mixtures compared to mixtures of eight or fewer species, this study in an artificial grassland system also indicated positive effects of plant diversity on generalist herbivore performance. Interestingly, Specht et al. (2008) caged *C. parallelus* in artificial mixtures of 1–60 plant species, half of which did not included grasses and found an overwhelming effect of grass presence on grasshopper fitness while the effect of plant species richness per se was not significant. While a cage experiment may not mimic natural conditions entirely, our correlative study therefore cannot rule out additional effects of plant species richness on grasshopper fitness that are mediated by factors other than diet composition, i.e., possibilities 2 and 3. The risk of predation for grasshoppers, in particular by spiders, has been shown to greatly influence grasshopper foraging behavior (e.g., Schmitz 2003), with possible consequences for nutrition and fitness. Unsicker et al. (2006) found in a study in the same area a general increase in spider abundances with increasing grasshopper abundances, suggesting that top-down control does not decrease with increasing plant species richness. While we do not have information on other predators such as passerine birds,

it appears that the generally lower vegetation in the more species-rich meadows (Kahmen et al. 2005, Unsicker et al. 2006) would increase rather than decrease foraging success of birds. Similarly, we cannot exclude the possibility that other abiotic factors, such as the structure of the vegetation, favor grasshopper reproduction more in the more diverse sites. Overall, however, the results from our correlative study suggest that both grasshopper abundance and fitness are controlled bottom-up, mediated by food plant availability.

On the other hand, there are also top-down effects of grasshoppers on the plant community itself. Grasshoppers are important components of arthropod assemblages in grassland ecosystems and it has already been shown experimentally that they can alter plant populations and community dynamics by, e.g., suppressing abundant, highly competitive grass species and thus facilitating the eveness in grasslands (e.g., Schmitz 2003). Although we have no experimental evidence in our study sites, it is conceivable that *C. parallelus* populations that mainly feed on grasses also affected plant species richness and plant community composition in the study sites. Grasshopper abundances are highest in species-rich meadows, and as these grasshoppers mainly feed on grasses and some legumes, it is likely that they prevent highly competitive grass species from dominating these sites. This in turn would benefit the competitively inferior forb species. Long-term grasshopper exclusions could shed light on the question of whether bottom up forces shape grasshopper communities or grasshopper populations sustain high levels of plant diversity through top-down effects.

The results from our study imply that the fitness of polyphagous herbivores may be diminished in low-diversity plant communities. Therefore, declines in biodiversity pose a threat to the persistence of generalist herbivores by inhibiting optimal feeding patterns.

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APPENDIX

Linear regressions for the grasses and forbs that were investigated in the grasshopper feeding experiment with respect to the two nonmetric multidimensional scaling axes (NMDS) (*Ecological Archives* E091-076-A1).