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Effects of management practices on ant species richness and community composition in grasslands (Hymenoptera: Formicidae)

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Abstract

The aim of our study was to evaluate the impact of four types of grassland management (silage meadows, hay meadows, meadow pastures and cattle pastures) on species richness and composition of ant communities. No impact of management type on ant species richness and community composition could be revealed. In contrast, moisture and total nitrogen content of the soil had a strong influence on the number of ant species. We could not find a relationship between species richness of ant communities and plant diversity. It is concluded that differences in intensity between the four management types were probably not strong enough for affecting ant communities differentially. Thus, assuming the maintenance of low intensity agriculture, a mosaic of different regimes of grassland management seems not to be imperative for maintaining ant diversity in mesic grasslands of marginal regions of Central Europe. In contrast, environmental conditions are important and should be considered in grassland management schemes aiming at protecting ant diversity.

Key words: Grassland, marginal region, low-intensity management, species richness

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Introduction

Most grasslands of Central Europe are shaped by human impacts (BLAB 1993), with their structure being the result of dynamic forces such as management and succession (MORRIS 2000). For example, cutting generates a homogeneous habitat by reducing the vegetation to a uniform height and by deleting or reducing topographical structures in the sward as ant mounds and tussocks (BONESS 1953, CURRY 1994). Grazing, in contrast, is a selective process that strongly depends on kind and density of the animals involved (MORRIS 2000).

Although low-intensity farming is believed to be crucial for maintaining biodiversity in agricultural landscapes of Europe (BIGNAL & MCCRACKEN 1996), little is known about the contribution of mosaics resulting from different grassland management types to invertebrate biodiversity. Thus, the aim of our study was to examine the impact of four types of grassland management on a key invertebrate group. Ants were chosen because of both their ecological role in grasslands and their suitability as indicators for environmental change (STEINER & SCHLICK-STEINER 2002). They are ubiquitous in agroecosystems (PECK & al. 1998) and are important predators in grasslands (KAJAK & al. 1972). As "ecosystem engineers", ants directly and indirectly affect the flow of energy and material in ecosystems (FOLGARAIT 1998), for instance by modifying physical and chemical soil properties (BLOMQVIST & al. 2000, PETAL & al. 2003). Moreover, they are closely bound to their habitat by perennial nests and by limited mobility (ALONSO 2000).

Management may affect ant communities of grasslands in various ways (Fig. 1). Direct effects are comparatively rare (ANDERSEN & MAJER 2004), and inter alia relate to the reduction of ant biomass or to the destruction of nests (HELLER & ROHE 2000). Indirect effects are considered to be much more important. They are basically caused by changes in vegetation structure and soil conditions (BONESS 1953), which are mediated through alterations in habitat structure, microclimate or food supply (CURRY 1994). Since the microclimate strongly depends on height and density of vegetation (PETAL 1976, ELMES & WARDLAW 1982), management of plant communities may induce changes in faunal communities (KRUESS & TSCHARNTKE 2002, NASH & al. 2004). However, vegetation and soil also affect ants independently from management (Fig. 1). For example, high plant species-richness and plant diversity are considered to be important factors for the development of a diverse ant community (MAJER 1983, MORRISON 1998, ARMBRECHT & al. 2004). Moreover, ant communities are additionally structured by geographical and topographical variables (DAUBER & WOLTERS 2000) as well as by complex relationships between management and community effects via changes in prey abundance or intra- and interspecific competition. However, the analysis of such complex interactions was beyond the scope of this paper.

It was hypothesised that ant community structure would significantly differ among the four types of grassland management investigated in our study due to the varying microhabitat and microclimate requirements of the constituting species. We thus determined the influence of management via vegetation and soil. The following questions were addressed concerning the effects of grassland

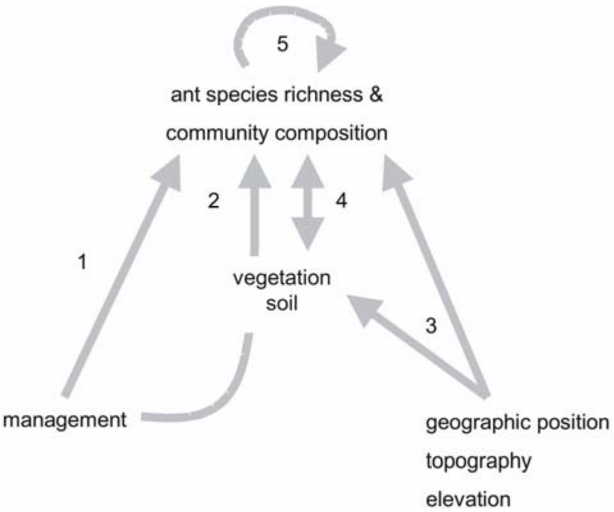

Fig. 1: Drivers of ant species richness and community composition in grasslands. 1 = direct management effects, 2 = indirect management effects, mediated by soil and vegetation, 3 = influence of geographical and topographical site conditions, 4 = effects of vegetation and soil on ant communities (independent from management) and vice versa, 5 = intra- and interspecific competition.

management on ant communities: I) Do different types of extensive management differ in their impact on ant species richness and community structure? II) How strong are direct management effects as compared to management-induced differences in vegetation and soil? III) Are there any overarching effects of site characteristics? IV) Do different management types contribute to species richness? V) Is a high diversity of plants accompanied by a species-rich ant community?

Materials and methods

Study area and study sites

The study was carried out in the "marginal region" (sensu BALDOCK & al. 1996) of the Lahn-Dill-Bergland (Hesse, Germany), in which the land cover of managed grassland has continuously increased since the 1950s and now replaces both the traditionally small-scaled crop production and the crop/grassland rotation (HIETEL & al. 2004). The region covers about 900 km² and is characterised by climate unfavourable for arable farming, poor soil conditions and small farm sizes (FREDE & BACH 1999). The mean annual temperature of the study region is about 8 °C with an average precipitation of 700 - 1100 mm per year (DEUTSCHER WETTERDIENST 1981, FREDE & BACH 1999). Together with historical, political and social reasons the unfavourable environmental conditions have lead to an ongoing abandonment of arable farming, whereas the proportion of grassland and fallow-land increased over the last decades (WALDHARDT & OTTE 2003, HIETEL & al. 2004).

Four types of managed grasslands were distinguished according to both time and intensity of mowing or grazing:

- H hay meadows, cut once or twice a year, with a late first mowing in mid June
- M meadow pastures, involving late mowing in mid June and subsequent grazing
- S silage meadows, characterised by three times mowing per year, an early first cut in May and a fertilizer application of up to 30 kg NPK ha^{-1} $year^{-1}$
- P cattle pastures, grazed during several short periods and with < 1.5 individuals ha^{-1} between May and September

Hay meadows, meadow pastures and pastures have no fertilizer input. All of the 30 grassland sites included in this study (H: n = 7, M: n = 10, S: n = 8, P: n = 5) had their management regime established at least 20 years before the investigation commenced. The sites were located in nine political districts, which were widely scattered across the Lahn-Dill-Bergland. Management types were almost evenly distributed among these districts. The elevation of the study sites ranged between 270 and 525 m a.s.l.

Sampling and species determination

Ants were sampled using small pitfall-traps (diameter: 3 cm) filled with approximately 15 ml of an ethylene-glycol-water-solution (1:1). A few drops of a detergent were added to reduce surface tension. At each site, 16 traps were placed with a minimum distance of two meters to the border zones of the sites to avoid edge effects (DAUBER & WOLTERS 2004). Traps were separated by 10 m, and arranged in either a 4 x 4 or 8 x 2 grid, according to shape and size of the site. Ants were collected during a six-day period in May 2004. All individuals were determined to species level according to SEIFERT (1996), but only workers were considered in statistical analysis. Total frequency of ants (TF) was calculated as the percentage of ant occurrence in the 16 traps per site. Furthermore, the frequency of each species was calculated to describe ant community structure.

Site characteristics

The following vegetation variables were measured: total number of vascular plant species (TP), Shannon diversity of plants (DP), total vegetation coverage (TC), coverage of the moss layer (ML), and plant density (PD). TP of each study site was estimated on a modified Braun-Blanquet-scale on plots with a standard size of 5 m x 5 m during the period from May to September in 2003 and 2004. DP was calculated by means of the program Sort 4.0 (ACKERMANN & DURKA 1998). PD was estimated according to SEIFERT (1986) by multiplying the height of three vegetation layers (lower and upper grasses, herbs) with the total coverage. For each site mean cover-weighted ELLENBERG (1992) indicator values for nutrient (nutrient value = NV), moisture (moisture value = MV) and temperature (temperature value = TV) were determined to characterise habitat conditions. Furthermore total nitrogen (N), carbon (C) and plant available phosphorus (P, using the CAL method) content as well as acidity (pH, in H_2O) of the soil were measured (according to STEUBING & FANGMEIER 1992). Geographical position and topographical site characteristics (i.e., elevation, slope and aspect) were identified. Aspect was characterised by Northness (cosine of aspect) and Eastness (sine of aspect).

Data analysis

The impact of management and habitat characteristics on vegetation, soil and ant species richness was tested by means of General Regression Models (GRM), using the forward stepwise procedure to eliminate non-significant parameters from the models. GRM implements stepwise and best-subset regression for Analysis of Covariance (ANCOVA) design with categorical and continuous predictor variables (STATSOFT 2001). Interactions between management type and the continuous variables were also considered.

GRMs with vegetation and soil as dependent variables included management type as categorical predictor and geographical position, elevation, slope and aspect as continuous predictors. Geographical position was included in the model by adding all terms for cubic trend surface analyses to control for spatial auto-correlation (LEGENDRE & LEGENDRE 1998). Models with number of ant species per site and total frequency of ants per site as dependent variables included management type as categorical predictor variable and soil characteristics (N and pH), all vegetation variables except TP as well as geographical and topographical variables as continuous predictors. Carbon and phosphorus content were not considered because of a significant correlation with the nitrogen content and total number of plants was not included in models because it was strongly correlated with Shannon diversity. The percentage of variance explained by each variable was estimated from the sums of square errors. Homogeneity of variances was checked prior to analyses by means of Levene's Test and data were log-transformed when necessary.

To test the efficiency of the trap sampling on the sites of different management we calculated rarefaction curves using the first order Jackknife richness estimator. Similarity of ant communities between sites or between the four types of grassland management was estimated using the Morisita Horn index. Multidimensional Scaling (MDS) was conducted to test whether ant communities were more similar among sites of one management type than between different types. GRMs and MDS were performed using the STATISTICA for Windows package (STATSOFT 2001). Similarity indices and rarefaction curves were calculated with the program EstimateS 5.0.1 (COLWELL 1997).

Canonical ordination technique was used to examine species responses to environmental variables. For the final analysis only environmental variables with the highest predictive power were selected (ML, PD, N and MV). DCCA was carried out to decide whether species response of the five most frequently sampled species was corresponding to a linear or unimodal model. Since a gradient length of 1.1 indicated a linear species response (LEPS & SMILAUER 2003), an RDA was conducted. Only species which occurred at least on more than 20 percent of the study sites were included, because rare species may have an unduly large influence on the analysis (TER BRAAK & SMILAUER 1998). DCCA and RDA were carried out by means of the CANOCO for windows 4.5 software package (TER BRAAK & SMILAUER 1998).

Results

Management effects on vegetation and soil

Plant species richness and Shannon diversity of plants were affected by management (Tab. 1). Plant species richness (TP) was lowest on the silage meadows and plant diversity (DP) was highest on hay meadows. Management type accounted for one third of total variance in each case. In addition, geographical and topographical parameters affected vegetation either dependently (diversity of plants, plant density, moisture value and nutrient value of the vegetation) or independently from management (number of plant species, moisture value). While management had no direct effect on soil conditions, soil acidity varied in relation to the joint effect of aspect and management type (Tab. 1). Geographical and topographical factors did not affect nitrogen, carbon or phosphorus content.

Ants

A total of 1607 ants belonging to 13 species of four genera were sampled at the 30 study sites (Tab. 2). With the exception of *Formica polyctena* FÖRSTER, 1850, which visited the grassland from a nearby forest edge, all species are typical of open habitats. Mean species richness and total species richness were almost identical among management types (3.2 to 4.0 and 7 to 8 respectively; Fig. 2). The species richness obtained by the Jackknife estimation showed that the estimated numbers of species quite well resembled the numbers of species caught. Estimated species richness was nine on H and M, eight on P and only for S the curve did not reach saturation but rose above 12 species. Moisture value and total nitrogen content of the soil together explained almost one third of the variance in ant species richness (Tab. 3), with both variables having negative effects. Moreover, the total frequency of ants per site was negatively related to moisture and additionally influenced by the geographical site position. The GRMs did not reveal any relationship between plant diversity and species richness of ants.

No effect of management type on the structure of ant communities could be established. The calculation of the Morisita-Horn index revealed only intermediate degrees of similarity between sites of different management (means: 0.49 - 0.60; Tab. 4), but the similarity among sites of identical management was even lower in some cases (means: 0.41 - 0.68). Frequencies of the individual species were also not related to management (Tab. 2). Multidimensional Scaling of species similarities among sites confirmed that sites of the same management type were not more similar among each other than sites of different management types.

Redundancy analysis revealed a species-specific response to some environmental variables (Fig. 3). The first two axes had cumulative eigenvalues of 0.2, with the sum of all eigenvalues being 1.0. This indicates that the first two axes represented comparatively weak gradients. Together they explained only 20.4 % of total species variance. The first axis (eigenvalue: 0.15) was positively related to moss layer and nitrogen content, the latter being also positively correlated to axis two (eigenvalue: 0.05). The moss layer accounted for 11 % of total variance, followed by nitrogen content (8 %), moisture value (4 %) and plant density (3 %). Frequency of *Myrmica scabrinodis* NYLANDER, 1846 increased with an increasing moss

Tab. 1: Variance explanation (VE), p-level and sign of influence of the continuous variables (I) revealed by the general regression models for vegetation and soil variables: TP = total number of plant species per site, DP = Shannon diversity of plants per site, PD = plant density, MV = moisture value and NV = nutrient value according to ELLENBERG (1992), pH = acidity of the soil. R^2 and p of the whole regression model are listed at the bottom of the table (*: $p < 0.05$, **: $p < 0.001$, ***: $p < 0.0001$).

	Vegetation															Soil		
	TP			DP			PD			MV			NV			pH		
	VE	p	I	VE	p	I	VE	p	I	VE	p	I	VE	p	I	VE	p	I
Management	32.3 %	*		33.7 %	*													
x-coordinate	30.3 %	**	–															
y-coordinate^3																24.3 %	*	–
Northness										22.7 %	*	–						
Elevation																8.2 %	*	–
Slope										8.6 %	*	–						
Managment x Northness										20.6 %	*		48.9 %	**		26.5 %	*	
Management x Slope				25.4 %	*		28.7 %	*										
R^2	0.57			0.55			0.43			0.25			0.43			0.51		
p	***			**			**			*			**			**		

Tab. 2: Frequency (i.e., percentage of traps in which the respective species was found) of all ant species and number of species per site sampled on differently managed grasslands.

Species	Hay Meadow (H)							Meadow Pasture (M)										Silage Meadow (S)								Pasture (P)				
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	8	9	10	1	2	3	4	5	6	7	8	1	2	3	4	5
Myrmica scabrinodis NYL., 1846		31	25	5	25	38	19	19	56	6	19	5	19	38	44	25		31	44	13	6	19	47		6		6	7	44	87
Lasius niger (L., 1758)	13	5	25	13		6		25	13	38	13	31	38	13	44			13	19	6	25	25	7	13	6	25		73	38	
Myrmica rubra (L., 1758)	56	5		31	44	69	56	13		6	44		38		31		31	6	56	25		63	7		5	38		7	25	
Myrmica sabuleti MEINT., 1861		6	19		6	6	13	6		6	19	6			6		81	25	19						6			7		
Myrmica schencki VIER., 1903	6	6					6				19						6	25							19	6			6	
Myrmica ruginodis NYL., 1846			6						6						6			6					7							
Formica rufibarbis FABR., 1793							19				6																			
Lasius flavus (FABR., 1782)																										6			6	
Formica fusca L., 1758																													13	
Formica polyctena FÖRST., 1850																									6					
Lasius alienus (FÖRSTER, 1850)																			6											
Myrmica lobicornis NYL., 1846											13																			
Tapinoma erraticum (LAT., 1798)							19																							
Number of species per site	3	5	4	3	3	4	6	4	3	4	7	3	3	2	5	1	3	6	5	3	2	3	4	1	6	4	1	4	6	1

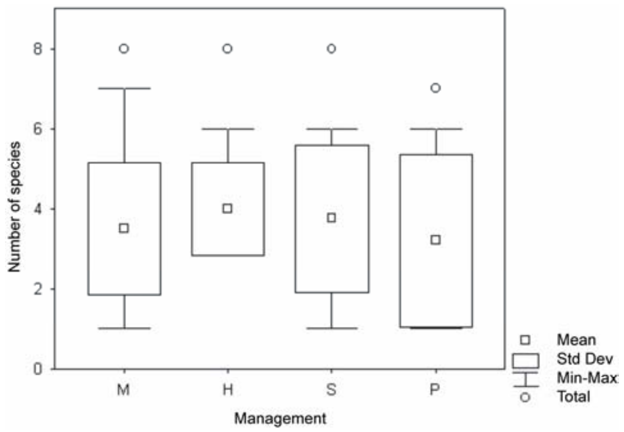

Fig. 2: Mean number of ant species per site (Mean), standard deviation (Std Dev), minimum and maximum number of ant species per site (Min-Max) and total number of ant species per management type (Total).

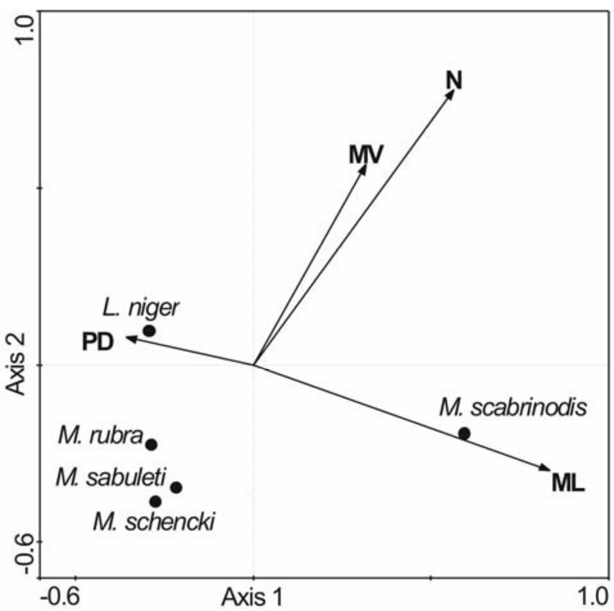

Fig. 3: RDA ordination diagram with species (dots) and environmental variables (arrows). ML = moss layer, N = total nitrogen content, PD = plant density, MV = moisture value.

layer, while *Lasius niger* (LINNAEUS, 1758) was almost independent from the environmental variables studied. *Myrmica rubra* (LINNAEUS, 1758), *Myrmica schencki* VIERECK, 1903 and *Myrmica sabuleti* MEINERT, 1861 were grouped together all being negatively affected by high moisture values of the vegetation and nitrogen contents of the soil.

Discussion

The four types of grassland management investigated in our study considerably differed in management intensity. However, neither direct nor indirect effects of management on ant communities were found. These results contrast to the results of other studies. PETAL (1976) demonstrated that long-term fertilisation leads to reduced ant species richness and decreased nest density. HELLER & ROHE (2000) also showed that management of pastures and meadow pastures adversely affects ant species richness. Compared to our sites, however, grasslands of these studies were more intensively managed and thus differed more strongly in vegetation and soil characteristics. The surprisingly small differences, especially the limited variation of vegetation in relation to management, among the grassland types of our study most probably reflect the moderate impact of low intensity farming on grassland conditions within the study region (WELLSTEIN & al. unpubl.). Variations in both timing and frequency of management may have additionally added to the strong internal variability of the data set.

Ant communities nevertheless strongly responded to management-independent effects of environmental, geographical and topographical conditions, with moisture and nitrogen content having particular strong negative effects. Increasing nitrogen content can increase both shading by vegetation and soil humidity (PETAL 1976). Since ants are generally thermophilic (SEIFERT 1996, ANDERSEN 1997), abundance decreases with decreasing temperature (KASPARI & al. 2000) and soil moisture. Although diverse veg-

Tab. 3: Variance explanation (VE), p-level and sign of influence (I) of the general regression models calculated for the total number of ant species (TA) and total frequency of ants (TF) per site. MV = moisture value according to ELLENBERG (1992), N = total nitrogen content of the soil. R^2 and p of whole regression model are shown at the bottom of the table. *: $p < 0.05$, **: $p < 0.001$.

	TA			TF		
	VE	p	I	VE	p	I
WS	18.2 %	*	–	26.0 %	*	–
N	13.9 %	*	–			
x-coordinate^3				20.9 %	*	–
R^2	0.44			0.43		
p	**			**		

Tab. 4: Mean and standard deviation (in brackets) of Morisita Horn similarity indices for ant communities of different grassland management types.

	Hay Meadow	Meadow Pasture	Silage Meadow	Pasture
Hay Meadow	0.68 (± 0.23)	0.55 (± 0.24)	0.60 (± 0.30)	0.50 (± 0.26)
Meadow Pasture		0.56 (± 0.30)	0.53 (± 0.25)	0.54 (± 0.32)
Silage Meadow			0.49 (± 0.28)	0.49 (± 0.28)
Pasture				0.41 (± 0.34)

etation should provide a greater variety of microhabitats and food sources (BOOMSMA & VAN LOON 1982), we did not find a correlation between ant species richness and vegetation diversity. This is consistent with results from complementing investigations carried out in the same study region (DAUBER & WOLTERS 2005). A possible explanation might be that managed grasslands have a comparatively low structural diversity anyway.

Ant species richness was typical of the studied area. DAUBER & WOLTERS (2000) found a total of 17 ant species in grasslands in the Lahn-Dill-Bergland, with an average of seven species per site. The 12 open habitat-species found in this study therefore appear to be representative for the regional species pool of managed grasslands. Furthermore, the observed number of species was almost similar to species richness predicted from rarefaction curves for hay meadows, meadow pastures and pastures, indicating a sufficient sampling effort. For silage meadows predicted species richness did not reach saturation due to heterogeneous occurrence of single species in individual traps, with several traps containing no ants at all, influencing the rarefaction calculation. Although a comparison with other regions of Central Europe might be limited by differences in geographical and topographical site conditions, study designs and management schemes, the grasslands of our study seem to be of medium ant species richness. SEIFERT (1986) reports 3 - 11 ant species for comparable grassland sites in Germany, whereas ROHE (2003) found up to 23 species in different extensively managed meadows and pastures. CZECHOWSKI & al. (1990) detected a total of 13 ant species, PETAL (1974, 1980) 4 - 14 and WOYCIECHOWSKI & MISZTA (1976) 11 species in extensive mesic grasslands in Poland.

The frequency of individual species strongly varied among sites. These differences were caused by site characteristics that were independent from management. This is consistent with our results from the calculation of similarity indices. The effects of vegetation and soil parameters on the frequency of the five most abundant species reflect species-specific differences in ecological requirements. Nevertheless, the four selected explanatory variables accounted only for a relatively small part of species variance. Other major explanatory factors, as there might be for example competitive interactions, were not included in the analysis or rather were not measured.

The dominant species *M. scabrinodis* is typical to grasslands and thus occurred on almost any management type (cf. HELLER & ROHE 2000). The frequency of this species was positively related to the coverage of the moss layer, which in turn was positively related to insolation and temperature of the soil. According to SEIFERT (1996), moss provides suitable nesting sites for this species. The frequency of the ubiquist *L. niger* was almost independent from vegetation structure. This species even occurs in homogenous, intensively managed grasslands (HELLER & ROHE 2000). *Myrmica rubra*, *M. sabuleti*, and *M. schencki* were also not related to vegetation structure, but their frequency was negatively affected by moisture and temperature. The former is an ubiquitous species, whereas the latter two species are thermophilic (SEIFERT 1996, ELMES & al. 1998). The frequency of *Lasius flavus* (FABRICIUS, 1782) was underestimated by pitfall-trapping, due to the hypogaeic foraging ecology of this species.

Conclusion

Despite the differences in the intensity of mowing, grazing and fertilisation, all four management types of our study basically are varieties of low intensity grassland management that equally contribute to the species richness of ant communities in the study region. In contrast to our expectations, maintaining a mosaic of different regimes of grassland management seems thus not to be imperative for protecting ant diversity. This offers new perspectives to grassland management in the Lahn-Dill-area and probably in many other marginal regions of Central Europe. Referring to the results of other studies, however, we nevertheless expect an intensification of management to adversely affect ant communities. Thus, sustaining low intensity farming will significantly contribute to the conservation of biodiversity in marginal regions. In any case, environmental conditions have turned out to be important and should therefore be considered when aiming at protecting ant diversity of grasslands.

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Zusammenfassung

Ziel unserer Untersuchung war es, den Einfluss verschiedener Formen der Grünlandbewirtschaftung (Silagewiesen, Heuwiesen, Mähweiden und Rinderweiden) auf den Artenreichtum und die Zusammensetzung von Ameisengemeinschaften zu beurteilen. Die Ergebnisse zeigten keinen Einfluss des Nutzungstyps auf die Ameisengemeinschaften. Dagegen stellten sich die Feuchte und der Gesamtstickstoffgehalt des Bodens als wichtigste Einflussgrößen für die Zahl der Ameisenarten heraus. Darüber hinaus konnten wir ebenfalls keinen Zusammenhang zwischen dem Artenreichtum von Ameisengemeinschaften und der pflanzlichen Diversität feststellen.

Möglicherweise waren die Intensitätsunterschiede zwischen den vier Nutzungstypen nicht groß genug um die Ameisengemeinschaften in unterschiedlichem Maße zu beeinflussen. Ausgehend von der Erhaltung der extensiven Landwirtschaft, scheint ein Mosaik von verschiedenen Grünlandbewirtschaftungsformen für den Schutz der Ameisendiversität in mesophilem Grünland in marginalen Regionen Mitteleuropas nicht von Bedeutung zu sein. Hingegen sind standörtliche Faktoren wichtig und sollten in Landnutzungskonzepten mit dem Ziel der Bewahrung von Ameisendiversität in Grünländern berücksichtigt werden.

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