Tuexenia 31: 301–315. Göttingen 2011.

Vegetation structure, ecological stability, and low-disturbance regime of abandoned dry grasslands support specific ant assemblages in Central Slovakia

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Abstract

Compared to other grassland types across Slovakia, dry grasslands harbour species-rich and specialised ant communities. High diversity and species richness of ants may be seen as a consequence of (i) the specific structure of dry grassland vegetation, (ii) long-term ecological stability, and (iii) currently low or absent management-induced disturbance. With special regard to dry grasslands, we report on structural characteristics of vegetation and low-disturbance regime, which contribute to ant assemblage structure. Our study was carried out in the Štiavnické Vrchy Mts. (Central Slovakia), a region with a historically well-developed grassland area. We established a set of 25 research plots within south-orientated grassland habitats representing five different grassland types: wet managed and wet abandoned grasslands, mesic managed and mesic abandoned grasslands (*Arrhenatherion elatioris*), and dry abandoned grassland habitats (*Asplenio-Festucion glaucae*). Each habitat type was represented by five plots. At each plot, a set of ten pitfall traps was used to sample ground-foraging ant assemblages. Around each trap, structural characteristics of vegetation and microhabitat were assessed. Dry grasslands were shown to have a specific microhabitat structure, characterised by the presence of a well-developed moss and lichen layer, exposed bedrock, bare soil, and significantly lower, although species-rich vegetation. Besides the specific microhabitat structure, the absence of management may have contributed to the distinctiveness of these ant assemblages compared to those associated with other grassland categories. Ant assemblages were more species-rich, and the activity of ants was higher in recently abandoned grassland habitats. The effect of abandonment was quite opposite for plants, whose species-richness was, contrary to ants, higher within managed sites.

Zusammenfassung: Vegetationsstruktur, ökologische Stabilität und Störungsregime geringer Intensität im aufgelassenen Trockengrasland begünstigen spezifische Ameisengesellschaften in der Mittelslowakei

Im Vergleich mit anderen Graslandtypen der Slowakei beherbergt Trockengrasland artenreiche und spezialisierte Ameisengesellschaften. Die hohe Diversität sowie der Artenreichtum an Ameisen können als eine Folge (i) der spezifischen Struktur der Trockengrasland-Vegetation, (ii) langfristiger ökologischer Stabilität und (iii) aktueller geringer oder ganz fehlender Störungsintensität durch Bewirtschaftung angesehen werden. Mit besonderer Berücksichtigung des Trockengraslandes berichten wir über strukturelle Charakteristika der Vegetation und Störungsregime niedriger Intensität, welche zur Struktur der Ameisengesellschaften beitragen. Unsere Studie wurde in den Schemnitzer Bergen (Štiavnické Vrchy, Mittelslowakei) durchgeführt, einer Region mit historisch gut entwickelten Graslandflächen. Ein Set von 25 Untersuchungsflächen (Plots) wurde in südexponierten Graslandhabitaten eingerichtet, welche fünf unterschiedliche Graslandtypen repräsentieren: Bewirtschaftete und aufgelassene Feuchtwiesen, bewirtschaftetes und aufgelassenes mesisches Grasland (*Arrhenatherion elatioris*) sowie aufgelassenes Trockengrasland (*Asplenio-Festucion glaucae*). Jeder Habitattyp ist durch fünf Plots repräsentiert. Auf jedem Plot wurde ein Set von zehn Barber-Fallen (Bodenfallen) benutzt, um am Boden jagende Ameisengesellschaften zu beproben. Rund um jede Falle wurden strukturelle Vegetations- und Mikrohabitat-Charakteristika erfasst. Es wurde gezeigt, dass Trockengrasland eine spezifische Mikrohabitatstruktur besitzt, die durch das reichliche Vorhandensein einer Moos- und Flechtenschicht, anstehendes Gestein, offenen Boden und eine signifikant niedrigere wiewohl artenreiche Vegetation charakterisiert ist. Neben der spezifischen Mikrohabitatstruktur trägt wohl das Fehlen von Bewirtschaftung zur Besonderheit dieser Ameisengesellschaften im Vergleich mit denjenigen der anderen Graslandkategorien bei. Jüngst aufgelassene Graslandhabitate wiesen artenreichere Ameisengesellschaften und eine höhere Aktivität der Ameisen auf. Der Effekt der Stilllegung war recht gegensätzlich für Pflanzenarten, welche, im Gegensatz zu Ameisenarten, mehr Arten in bewirtschafteten Flächen aufwiesen.

Keywords: Carpathians, *Formicidae*, habitat structure, management, Štiavnické Vrchy Mts.

1. Introduction

Dry grasslands represent a characteristic yet extremely threatened and declining feature of the sub-mountain landscape in Slovakia (David et al. 2007). Having been integrated into agricultural landscapes of Central Europe for centuries, dry grasslands have experienced a strong decline and loss of connectivity during the last hundred years (van Dijk 1991). This specific biotope type is considered a remnant of the late Pleistocene steppe formation (Bredenkamp et al. 2002) or a land form resulting from long-term agricultural activities in submontane areas (Ellenberg 1996). Besides direct devastation including urbanization, establishment of stone quarries, conversion to farmland and encroachment of invasive woody species, the change of traditional use and abandonment are among the main risks for both dry grassland habitats and associated species (Willems 2001, Luoto et al. 2003, Dekoninck et al. 2007, Rūsiņa & Kiehl 2010).

The abandonment of dry grassland may not cause rapid successional changes and overgrowth similar to the rate recorded from mesic or wet grasslands (Öckinger et al. 2006); however, the lack of traditional use usually contributes to the loss of open patchy vegetation patterns. Consequently, although the general open nature of a dry grassland habitat may remain relatively stable, the building of a dense and compact vegetation layer may have an adverse effect on the majority of specialised xerophilic species (Dekoninck et al. 2007). Traditional or sustaining management is hence being recognised as vital for conservation and restoration of dry grasslands (Bobbink & Willems 1993).

Generally, dry grasslands exhibit extreme habitat conditions, mainly due to relatively dry and nutrient-poor soils. Nevertheless, communities of plants and animals associated with these habitats are among the most species-rich, harbouring dozens of specialised, stenotopic and endemic species (David et al. 2007).

Ants (*Hymenoptera*: *Formicidae*) are classified as ecosystem engineers (Jones et al. 1994, Folgarait 1998). Considering their important role in soil engineering, distribution of plant seeds, and predation (Folgarait 1998), investigations on ant communities are essential for the assessment of biodiversity change in the cultural landscapes of Europe. Dry grasslands in Slovakia support a relatively diverse ant fauna with a number of unique species (Wiezik 2008). However, relatively little is known about the factors influencing dry grassland ant communities. Vegetation structure is recognised as an important factor affecting ant populations in temperate habitats (Retana & Cerdá 2000), mainly due to the regulation of microclimate conditions, which influence, in the form of environmental stress, ant activity and ant community composition (Andersen 2000). Furthermore, vegetation can directly and indirectly affect availability and quality of food and nesting sites, as well as interaction between particular ant species (Andersen 2000, Retana & Cerdá 2000, Lassau & Hochuli 2004).

The aim of this study was to analyse, with special regard to dry grasslands, the variation in habitat structure along a humidity and management gradient within grassland habitats in the Štiavnické Vrchy Mts., Central Slovakia, and to identify how these structural and management patterns are reflected in the structure of associated ant assemblages.

2. Study area

The study was conducted in the Štiavnické Vrchy Mts. in the western Carpathians, Slovakia. This region has a mean annual precipitation of 895 mm and a mean annual temperature of 7.6 °C (Hlavaček 1985). The soils of the area are of volcanic origin; rich brown soils overlaying andesite bedrock are most frequent (Konečný et al. 1998). The region has been used intensively for mining of metals since the 13th century. Human settlement, mining, and associated intensive timber production left a large portion of this area deforested, paralleling a general decline of low elevation forests in Slovakia (Korpeľ 1989) and elsewhere in Europe (Gilg 2005). The proportion of grassland habitats has hence been artificially increased and today represents about 30% of the region's total area (Kunca et al 2005).

The study was carried out on a set of managed and abandoned grassland habitats in the Štiavnické Vrchy Mts. (Fig. 1). We selected 25 grasslands at altitudes of 260–655 m a.s.l.

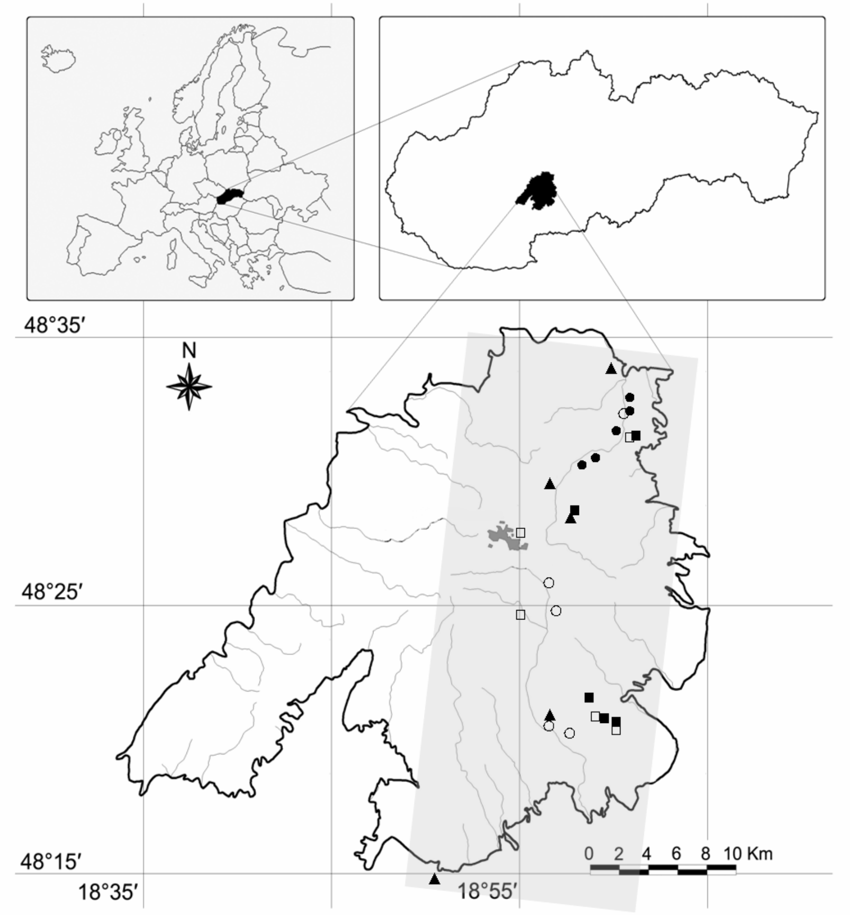

Fig. 1: Location of research plots. Grassland categories: ● wet abandoned, ○ wet managed, ■ mesic abandoned, □ mesic managed, ▲ dry abandoned.

Abb. 1: Lokalisierung der Untersuchungsflächen (Plots). Graslandkategorien: ● feucht, aufgelassen; ○ feucht, bewirtschaftet; ■ mesisch, aufgelassen; □ mesisch, bewirtschaftet; ▲ trocken, aufgelassen.

representing grassland categories typically occurring across the study area: wet abandoned (WA), wet managed (WM), mesic abandoned (MA) and mesic managed (MM) grasslands (*Arrhenatherion elatioris* Koch 1926, class *Molinio-Arrhenatheretea*), and dry abandoned (DA) grasslands (*Asplenio-Festucion glaucae* Zolyómi 1936, class *Festuco-Brometea*). Each type was represented by five individual plots. Except humid grasslands located in inundation zones with no apparent sloping, all plots were selected on SE, S, or SW facing slopes. Dry managed grasslands were not included in the study, as this particular grassland type is currently absent in the studied region (KUNCA et al. 2005). Wet and mesic abandoned grassland represented sites that have been abandoned during the last 15 years. A well-preserved open feature and no or only weak woody species overgrowth (not exceeding 10% of the total grassland area) were typical for all abandoned sites including dry grasslands that have been abandoned for at least 30 years. All managed sites were mown annually in early summer; within the majority of wet managed sites, cattle grazing was conducted during late summer.

3. Methods

3.1. Ant sampling

In each plot, a line of 10 traps, spaced at 3 m intervals, was established. The traps consisted of plastic cups (diameter 3 cm) buried at soil level and filled with about 50 ml of a 4% solution of formaldehyde. Each trap was left in place for 7 days before being opened in order to reduce digging-in effects (Greenslade 1973). In total, 250 traps were placed in the field during late May 2008, and each trap remained open for 7 days. Sampling was repeated in late September 2008. The number of individuals trapped per plot or grassland category depends on the activity of ants, which is not directly related to ant abundance; however, ant activity is a widely accepted measure in comparative analyses (Bestelmeyer et al. 2000, Goméz et al. 2003, Ottonetti et al. 2006). Ants were identified at the species level according to Seifert (2007); only workers were considered in the statistical analyses.

3.2. Vegetation and microhabitat measurements

The following vegetation and microhabitat variables were measured: total number of vascular plant species, maximum vegetation height, mean vegetation height (based on five randomly placed measurements), total vegetation coverage (including the coverage of vascular plants, bryophytes, and lichens), coverage of particular vegetation layers (e.g. woody species, grasses, herbs, bryophytes + lichens (growing on soil)), proportion of exposed bedrock and plain soil. All variables were measured in May 2008 before the mowing season, on a plot of 1 m × 1 m placed around each trap used for ant sampling. These microhabitat variables have been used in previous studies assessing the influence of vegetation on ants (Dahms et al. 2005), as they reflect the complexity of vegetation, which is considered a significant stress-related factor affecting ant communities (Andersen 2000).

3.3. Statistical analyses

Multiple regression analysis was used to examine the effect of vegetation variables (total species richness, mean vegetation height, total grass cover, total herb cover) on ant species richness. Best-subset regression based on Mallow's C_p criterion was employed to build the most parsimonious models (StatSoft 2004). The primary aim of our study was to separate the effects of humidity and management on ant assemblages; however, because of immanent correlations in explanatory variables, we fitted separate linear models for plant characteristics and grassland categories. The separate fitting of models allows for quantifying the individual and joint effects of humidity and management as the dominant forces hypothesised to shape ant diversity. Prior to the analyses, seasonal data were pooled over traps. Assumptions of normality and homoscedasticity were carefully checked using diagnostic plots of residuals. Variables were log transformed when necessary.

Differences in ant assemblages and vegetation characteristics between grassland categories were analysed according to the hierarchical ANOVA design. Mixed models, which included the fixed effect of grassland category (for categories cf. section 2) and the random effects of plot, nested within grassland category, were fitted to the data. A nested ANOVA allows partitioning of residual variance of the pooled model into the variance explained by the differences among particular plots and pure residual variance.

In order to separate the effects of habitat humidity and management, a hierarchical factorial ANOVA was employed. A mixed model, which included the fixed effects of management (managed, abandoned), habitat humidity (wet, mesic), and their interaction and the random effects of plot, nested within interaction, was fitted to the ant richness and activity and plant characteristics, respectively. Because of the absence of dry managed grasslands in the studied region, abandoned dry grasslands, and hence a dryness factor, could not be subjected to this mixed model analysis. For significant effects, relevant pairwise comparisons were made using Tukey's HSD tests. Assumptions of each model were screened in diagnostic plots, and data were log transformed when necessary. However, untransformed data are displayed in figures to facilitate interpretation.

A list of ant species and their activity was compiled for each trap to get a community data matrix. The same linear models were fitted to the ant assemblage data matrix using distance-based MANOVA (Anderson 2001). These multivariate analyses were based on Bray-Curtis distance (Bray & Curtis 1957). Species activities were log transformed to reduce asymmetrical influence of the dominant species. P values were based on 9999 permutations of raw data using correct permutable units (Anderson & ter Braak 2003) in DISTLM package (Anderson 2004). Non-metric multidimensional scaling (NMDS; Kruskal 1964) was used to visualise differences in assemblage composition. Relationships between species and NMDS configuration were examined by Spearman rank correlation.

4. Results

4.1. Microhabitat structure

The field assessment of microhabitat structure, based on measurements of selected vegetation and terrain surface characteristics, showed several unique structural features of dry grassland habitats. Structural patterns like exposed bedrock, plain soil, and a well-developed layer of mosses and lichens (Table 1) were recorded exclusively from dry grasslands.

Besides these patterns, marked differences in vegetation height and plant species richness between the grassland habitats were revealed by the hierarchical ANOVA (Table 2). Dry grasslands were characterised by the lowest mean vegetation height, being only about one third to one half of the vegetation height recorded from other grassland categories (Table 1). All grassland categories, except mesic managed, had significantly lower mean plant species richness compared to dry grasslands. In general, the lowest plant species richness was recorded from wet abandoned grasslands. Within all grassland categories (except wet abandoned), a moderate dominance of grass cover was typical; woody species occurred almost exclusively in mesic abandoned grasslands, where their overall coverage exceeded 10%.

We also observed a significant effect of management and its absence reflected in plant species richness: When comparing managed and abandoned grasslands within the same humidity category, the abandoned sites were significantly poorer in recorded plant species (Table 1).

Table 1: Selected microhabitat characteristics of studied grassland categories.
Mean values per 1 m^2 ± SE are displayed.

Tab. 1: Ausgewählte Mikrohabitat-Charakteristika der untersuchten Graslandkategorien.
Es sind Mittelwerte pro 1 m^2 ± Standardfehler angegeben.

	WM Wet managed	**WA** Wet abandoned	**MM** Mesic managed	**MA** Mesic abandoned	**DA** Dry abandoned
Total vegetation [%]	100 -	100 -	100 -	100 -	79 ± 18.4
Herb species [%]	39 ± 14.2	50 ± 17.6	47 ± 18.4	35 ± 12.5	27 ± 11.6
Grass species [%]	61 ± 14.2	50 ± 17.6	53 ± 18.4	50 ± 14.0	40 ± 18.9
Woody species [%]	- -	0.04 ± 0.08	- -	14 ± 14.0	0.22 ± 0.4
Bryophytes + Lichens [%]	- -	- -	- -	- -	13 ± 15.6
Bedrock [%]	- -	- -	- -	- -	7 ± 6.6
Bare soil [%]	- -	- -	- -	- -	14 ± 15.5
Plant species richness	10.2 ± 1.8	7.6 ± 1.6	14.5 ± 4.0	12.5 ± 2.3	14.1 ± 2.1
Max. vegetation height [cm]	118.9 ± 12.2	116.8 ± 19.1	121.4 ± 12.4	127.1 ± 18.1	73.7 ± 18.6
Mean vegetation height [cm]	72.8 ± 18.2	69.4 ± 18.5	66.0 ± 20.2	68.1 ± 25.6	30.2 ± 15.8

Table 2: Results of hierarchical ANOVA on vegetation characteristics.
Degrees of freedom (DF), mean sum of squares (MS), and *F* statistics with accompanying probabilities (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) are displayed for each source of variance. Plot was a nested random factor within management.

Tab. 2: Ergebnisse der hierarchischen Varianzanalyse (ANOVA) der Vegetations-Charakteristika.
Freiheitsgrade (DF), Mittlere Summe der Quadrate (MS), und *F*-Statistik mit zugehörigen Signifikanzwerten (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) sind für jede Quelle der Varianz angezeigt. Plot war ein genesteter, zufälliger Faktor innerhalb der Landnutzung.

Source of variance	DF	Total herb cover		Total grass cover		Plant species richness		Mean vegetation height	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*
Management	4	4368	2.62^{ns}	2815	1.37^{ns}	424	6.59**	15447	14.46***
Plot (Management)	20	1669	6.94***	2061	7.29***	64	13.93***	1068	7.63***
Trap	225	240		283		5		140	

4.2. Variation in ant assemblages

We collected a total of 6689 workers belonging to 35 different ant species from the 25 research plots. The total number of recorded ant species was highest at dry grasslands and decreased with increasing habitat humidity, being the lowest at wet managed grasslands (Table 3). The higher ant species richness of dry grasslands was partially attributed to a number of species recorded exclusively from this habitat (*Ponera testacea*, *Messor structor*, *Plagiolepis* spp., *Camponotus* spp.); however, those differences were not statistically significant (Table 4). On the other hand, significant differences were found for total epigaeic activity. The four most common ant species (*Myrmica scabrinodis*, *M. rubra*, *Formica pratensis*, and *Lasius niger*) accounting for 84.9% of the total number of sampled workers were recorded from wet and mesic grasslands only.

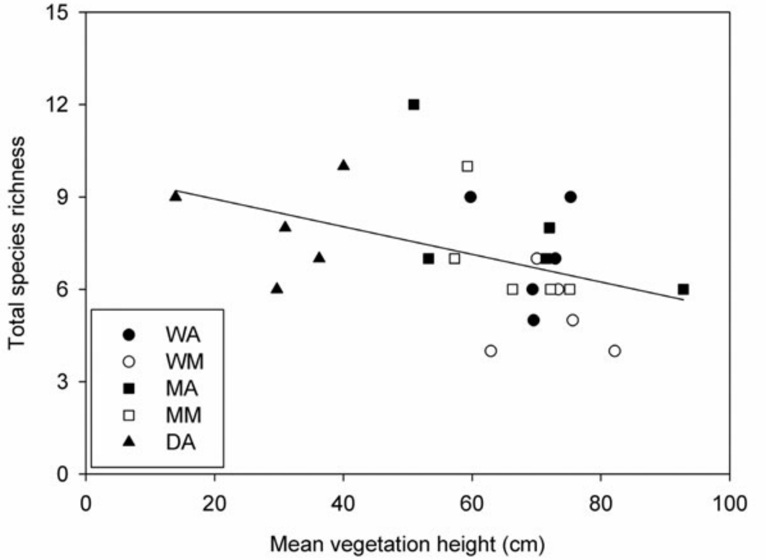

Fig. 2: Significant linear relationship between mean vegetation height and ant species richness ($F_{(1,23)} = 5.28$; $p < 0.05$; $R^2 = 0.19$). The symbols correspond to the grassland categories (see Table 1).

Abb. 2: Signifikanter linearer Zusammenhang zwischen mittlerer Vegetationshöhe und Artenreichtum der Ameisen ($F_{(1,23)} = 5.28$; $p < 0.05$; $R^2 = 0.19$). Die Symbole entsprechen den Graslandkategorien (siehe Tab. 1).

The assessment of relations between ants and vegetation structure showed a significant correlation between mean vegetation height and ant species richness ($F_{(1,23)} = 5.28$; $p < 0.05$). Across all grassland sites, the ant species richness was negatively related to the vegetation height (Fig. 2); this relation, however, was relatively weak, as it explained only about 19% of the total variance.

Composition of ant assemblages differed significantly among grassland categories (Table 4). Sites from dry grasslands and the remaining grassland categories tended to occupy different sections of the ordination space, suggesting that the composition of ant assemblages differed distinctly between these two groups (Fig. 3). The observed differences in ant assemblage composition among grassland categories corresponded to changes in proportions of several ant species (Fig. 3).

The dry grasslands were characterised by an increased proportion of *Tetramorium caespitum* and *Tapinoma ambiguum* and by the exclusive occurrence of *Tetramorium moravicum*. The remaining grassland categories, except mesic abandoned grasslands, grouped together to build a centroid characterised by affinity of several common eurytopic ant species. Mesic abandoned grasslands built a separate centroid, distinguished by an

Table 3: Total epigaeic activity of ants (number of workers trapped per grassland category and 50 traps during 2 × 7 days of trap exposure) and presence of species at replicated sites (superscript index representing the number of plots).
ZGe – Zoogeographical element (according to CZECHOWSKI et al. 2002): AP – Amphipalaearctic, CE – Central-European, E – European, EC – Euro-Caucasian, ES – Euro-Siberian, MD – Mediterranean, NP – North-Palaearctic, SE – South-European, SP – South-Palaearctic; Ee – Ecological element: e – eurytopic, p – polytopic, o – oligotopic, s – stenotopic; land use: m – managed, a – abandoned.

Tab. 3: Absolute epigäische Aktivität von Ameisen (Anzahl der gefangenen Arbeiter pro Graslandkategorie und 50 Fallen während 2 × 7 Tagen Fallenexposition).
ZGe – Zoo-Geographisches Element (nach Czechowski et al. 2002): AP – amphipaläarktisch, CE – mitteleuropäisch, E – europäisch, EC – euro-kaukasisch, ES – euro-sibirisch, MD – mediterran, NP – nord-paläarktisch, SE – süd-europäisch, SP – süd-paläarktisch; Ee – Ökologisches Element: e – eurytop, p – polytop, o – oligotop, s – stenotop; Nutzungstyp: m – bewirtschaftet, a – aufgelassen.

	ZGe	Ee	Wet		Mesic		Dry
			m	a	m	a	a
Ponerinae							
Ponera testacea (Emery, 1895)	MD	s	-	-	-	-	2^{2}
Myrmicinae							
Myrmica gallienii Bondroit, 1920	ES	o	3^{1}	-	2^{1}	-	-
M. lobicornis Nylander, 1846	BM	o	-	-	-	5^{1}	-
M. rubra (Linnaeus, 1758)	NP	e	200^{3}	338^{5}	12^{2}	-	-
M. rugulosa Nylander, 1849	ES	o	4^{1}	2^{1}	-	-	-
M. sabuleti Meinert, 1861	ES	o	-	-	16^{1}	53^{3}	4^{3}
M. scabrinodis Nylander, 1846	ES	p	3^{2}	103^{4}	118^{4}	2489^{5}	-
M. schencki Viereck, 1903	SP	o	3^{2}	11^{2}	-	21^{4}	4^{2}
Messor structor (Latreille, 1798)	MD	s	-	-	-	-	6^{2}
Myrmecina graminicola (Latreille, 1802)	AP	o	-	-	-	-	1^{1}
Solenopsis fugax (Latreille, 1798)	MD	o	-	-	4^{2}	-	3^{2}
Leptothorax acervorum (Fabricius, 1793)	BM	o	-	4^{1}	-	-	-
Temnothorax interruptus (Schenck, 1852)	E	s	-	-	-	-	4^{1}
Tetramorium caespitum (Linnaeus, 1758)	SP	p	2^{1}	41^{3}	3^{2}	14^{4}	44^{5}
T. ferox Ruzsky, 1903	MD	s	-	-	-	-	1^{1}
T. impurum (Förster, 1850)	CE	o	-	-	1^{1}	-	-
T. moravicum Kratochvíl, 1941	CE	o	-	-	-	-	46^{4}
Dolichoderinae							
Tapinoma ambiguum Emery, 1925	SE	s	-	-	-	6^{1}	5^{2}
T. erraticum (Latreille, 1798)	MD	s	-	2^{1}	4^{1}	4^{2}	9^{2}
Formicinae							
Plagiolepis pygmaea (Latreille, 1798)	MD	s	-	-	-	-	8^{2}
P. vindobonensis Lomnicki, 1925	MD	s	-	-	-	-	2^{1}
Lasius flavus (Fabricius, 1782)	SP	e	3^{3}	22^{4}	2^{1}	2^{2}	-
L. jensi Seifert, 1982	ES	s	-	-	-	-	1^{1}
L. alienus (Förster, 1850)	SP	o	10^{2}	-	126^{3}	92^{3}	565^{2}
L. niger (Linnaeus, 1758)	NP	p	228^{5}	437^{5}	193^{4}	6^{1}	-
L. psammophilus Seifert, 1992	E	o	8^{1}	-	20^{2}	7^{2}	-
Camponotus vagus (Scopoli, 1763)	ES	o	-	-	-	-	1^{1}
C. piceus (Leach, 1825)	MD	s	-	-	-	-	2^{1}
C. aethiops Latreille, 1798	MD	s	-	-	-	-	3^{1}
Formica cunicularia Latreille, 1798	EC	p	3^{3}	71^{4}	8^{3}	15^{4}	1^{1}
F. gagates Latreille, 1798	MD	o	-	-	-	-	50^{1}
F. pratensis Retzius, 1783	SP	p	-	201^{2}	478^{3}	347^{4}	-
F. rufa Linnaeus, 1761	NP	o	-	5^{1}	-	-	-
F. rufibarbis Fabricius, 1793	ES	o	4^{2}	2^{2}	7^{5}	4^{3}	1^{1}
F. sanguinea Latreille, 1798	SP	p	-	-	-	1^{1}	156^{1}
		Species richness	12	13	15	15	23

Table 4: Results of hierarchical ANOVA and MANOVA on ant assemblage characteristics.
Degrees of freedom (DF), mean sum of squares (MS), and *F*/pseudo-*F* statistics with accompanying probabilities (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) are displayed for each source of variance. Plot was a nested random factor within management.

Tab. 4: Ergebnisse der hierarchischen ANOVA und MANOVA der Charakteristika der Ameisengesellschaften.
Freiheitsgrade (DF), Mittlere Summe der Quadrate (MS), und *F*/pseudo-*F*-Statistiken mit zugehörigen Signifikanzwerten (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) sind für jede Quelle der Varianz angezeigt. Plot war ein genesteter, zufälliger Faktor innerhalb der Landnutzung.

Source of variance	DF	Ant species richness		Total epigaeic activity		Assemblage composition	
		MS	*F*	MS	*F*	MS	pseudo-*F*
Management	4	0.287	2.28^{ns}	3.252	2.92*	53800	3.21***
Plot (Management)	20	0.126	4.8***	1.115	7.42***	16780	8.38***
Trap	225	0.026		0.150		2003	

increased proportion of *Myrmica scabrinodis*. These results further corroborate our observation that ant assemblages of dry grasslands differ distinctly from other grassland categories, bearing features of a separate and specific ant community.

4.3. Impact of humidity and management

We tried to separate the effects of humidity and management on ants and plants through the hierarchical factorial ANOVA models (Table 5). We found a significant effect of management on total species richness of ants in wet and mesic grassland habitats (Fig. 4). The number of ant species collected per trap in recently abandoned grassland sites was significantly higher than in annually managed grasslands. This trend occurred along the grassland categories regardless of habitat humidity. The trend was opposite, although not significant, in plants, where the number of plant species recorded per square meter was higher at managed sites (Fig. 4). Contrary to the situation for ants, plant species richness was significantly related to grassland humidity: Wet grasslands contained ~40% less plant species compared to mesic sites.

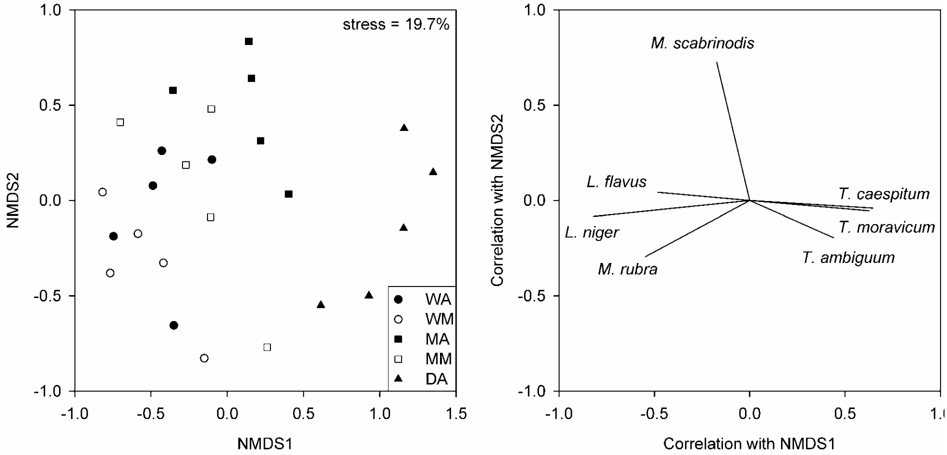

Fig. 3: NMDS ordination plot of Bray-Curtis dissimilarities in ant assemblages (left). Spearman correlation coefficients of species activities with ordination axes (right). Only species with higher correlation (> 0.4) are displayed. The symbols correspond to the grassland categories (see Table 1).

Abb. 3: NMDS Ordinationsdiagramm der Bray-Curtis Unähnlichkeiten in Ameisengesellschaften (links). Spearman Korrelationskoeffizienten der Aktivität der Arten mit den Ordinationsachsen (rechts). Nur Arten mit höherer Korrelation (> 0.4) sind gezeigt. Die Symbole entsprechen den Graslandkategorien (siehe Tab. 1).

Table 5: Results of hierarchical factorial ANOVA on ant and plant species richness
Degrees of freedom (DF), mean sum of squares (MS), and F statistics with accompanying probabilities (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) are displayed for each source of variance. Plot was a nested random factor within Humidity   Management interaction.

Tab. 5: Ergebnisse der hierarchischen faktoriellen ANOVA des Artenreichtums der Pflanzen und Ameisen
Freiheitsgrade (DF), Mittlere Summe der Quadrate (MS), und F-Statistik mit zugehörigen Signifikanzwerten (^{ns} > 0.05; * < 0.05; ** < 0.01; *** < 0.001) sind für jede Quelle der Varianz angezeigt. Plot war ein genesteter, zufälliger Faktor innerhalb der Interaktion Feuchtigkeit × Landnutzung.

Source of variance	DF	Ant species richness		Plant species richness	
		MS	*F*	MS	*F*
Humidity	1	0.038	0.39ns	1100	14.80**
Management	1	0.850	8.87**	235	3.17^{ns}
Humidity × Management	1	0.249	12.51ns	3	0.70^{ns}
Plot (Humidity × Management)	16	0.096	4.82***	74	16.65***
Trap	180	0.020		4	

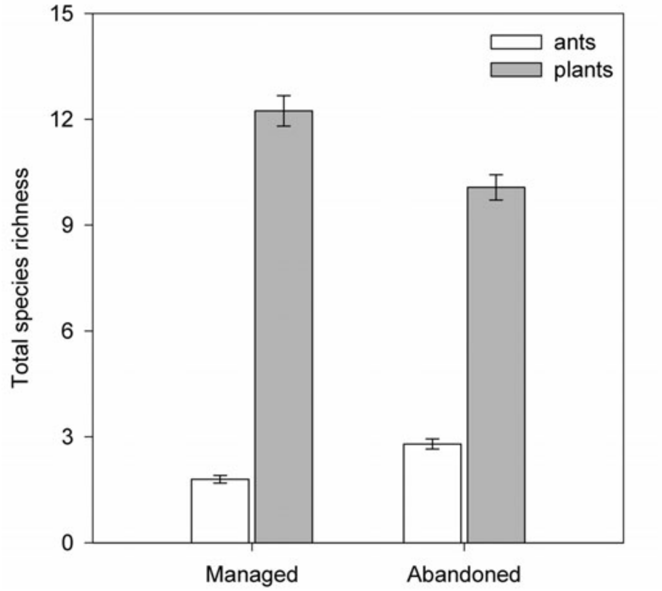

Fig. 4: Comparison of ant species richness ($F_{(1,16)}$ = 8.87; p < 0.01) and plant species richness (n.s.) across grassland management types in the Štiavnické Vrchy Mts.

Abb. 4: Vergleich des Artenreichtums der Ameisen (F(1,16) = 8.87; p < 0.01) und Pflanzen (n. s.) über alle Landnutzungstypen des Graslands in den Schemnitzer Bergen (Štiavnické Vrchy).

5. Discussion

Our results generally suggest that dry grasslands represent a specific habitat type. Compared to wet and mesic grasslands of the alliance *Arrhenatherion elatioris* (class *Molinio-Arrhenatheretea*), dry grasslands of the alliance *Asplenio-Festucion glaucae* (class *Festuco-Brometea*) were distinct in vegetation structure and consequently in associated ant assemblages. The habitat structure was characterised by species-rich, structurally divergent yet relatively short vegetation and a high proportion of patches without plant cover, as opposed to the dense and tall vegetation of wet and mesic grasslands. As shown in our study, the composition of ant assemblages from dry grasslands diverged strongly from assemblages from wet and mesic grassland habitats. Assemblages from dry grasslands were rich in species and hosted a number of exclusive Mediterranean zoogeographical elements (Table 3).

Several characteristics of dry grasslands may have contributed to unique ant assemblages, namely habitat structure, ecosystem stability, and low management-related disturbance. Even though we tend to interpret the effects of these characteristics separately, they in fact represent a group of interdependent patterns and processes jointly influencing the associated ant assemblages. As we did not assess any independent gradients linked to these characteristics in the present study, it is not possible to divide the impacts among them. In the following chapters we discuss these characteristics in detail.

5.1. Effect of habitat structure

As shown in our study, ant richness was negatively related to vegetation height. Nevertheless, only 19% of the variation in ant species richness was explained by vegetation height; hence a major portion of the variation remained unexplained. Several habitat traits, such as exposed bedrock and bare soil, were restricted to the dry grasslands and hence, as an exclusive structural pattern, were not considered in the statistical analyses. In the environment of Central Europe, such features are believed to determine the occurrence of the majority of the ant species recorded from dry grassland habitats (see SEIFERT 2007).

In the majority of invertebrate groups, high complexity habitats support high biodiversity. A more complex environment increases available microhabitats, food, and shelter, and thus increases the diversity of associated species (NIEMELÄ 1997, SIMILÄ et al. 2003, LASSAU et al. 2005). In ants, the situation may be different as they tend to show higher affinity for habitats with less complex vegetation structure (LASSAU & HOCHULI 2004).

From an ant's perspective, the main advantage of lower vegetation complexity is that it contributes to a low-stress environment (ANDERSEN 2000). Environmental stress is generally defined as any factor limiting productivity (GRIME 1979). The primary stressors for ants are, among others, low temperature and microhabitat structure. Low temperature is considered to be the primary stressor controlling global patterns of ant productivity and community structure (ANDERSEN 1995); together, climate and habitat structure determine the degree of surface insolation (ANDERSEN 2000). Densely covered habitats with structurally complex, high vegetation forming shaded and cool microclimate are generally poor in ants; on the other hand, warm and open habitats host the majority of ant species (ANDERSEN 1995). The structural complexity of the foraging surface exerts a major influence on the ability of ants to capture food resources. Dense or tall vegetation, for instance, dramatically reduces the efficiency of locating, retrieving and defending resources (ANDERSEN 2000).

Besides the overall affinity of ants to less shaded habitats, the patchy vegetation structure and presence of bare substrates within dry grasslands (Fig. 5) play an important role in structuring ant communities by widening the thermal range of the habitat. In general, vegetation alters the habitat microclimate in terms of reducing the diurnal and annual temperature and humidity variation. Areas that are exposed to wind and direct sunlight are drier and warmer than those that are protected by canopy cover. Thus, variations in vegetation structure may either enhance or reduce ant diversity by increasing or reducing habitat heterogeneity, microclimate suitability, or the activity of dominant species (RETANA & CERDÁ 2000). The combination of vegetation and bare substrate patches within dry grasslands creates

Fig. 5: Dry abandoned grasslands (*Asplenio-Festucion glaucae*, class *Festuco-Brometea*) in the Štiavnické Vrchy Mts. host unique ant assemblages even after decades of cessation (Photo: M. Wiezik 2008).

Abb. 5: Aufgelassene Trockenrasen des Verbandes *Asplenio-Festucion glaucae* (Klasse *Festuco-Brometea*) in den Schemnitzer Bergen (Štiavnické Vrchy) beherbergen besondere Ameisengesellschaften selbst Jahrzehnte nach der Nutzungsaufgabe (Foto: M. Wiezik 2008).

a mosaic of sunny and shaded microhabitats. A wider thermal range may increase species diversity, because different species are favoured by different thermal conditions. Gradual changes in the environment alter competition between species (ANDERSEN 2000). In particular, behaviourally dominant ant species are heat intolerant, and their external activity is limited by high temperatures. In areas with high vegetation cover, dominants benefit from lower temperatures by extending their periods of activity. This results in a decrease in the abundance of subordinate species (RETANA & CERDÁ 2000). Dominant species reach the maximum foraging activity at 20–30 °C and lower their activity distinctly at higher temperatures (RETANA & CERDÁ 2000). This allows the subordinate ant species to occupy the habitat during the high-temperature period of a day without taking a risk of encountering the behaviourally dominant ant species. In open habitats, ant communities are primarily ordered by thermal variations and hence show few effects of interactions. On the other hand, more complex habitats, where thermal variation is limited by lush vegetation, usually favour dominant ant species (ANDERSEN 2000, RETANA & CERDÁ 2000).

This temperature-driven niche partitioning in ants has been well documented from Mediterranean and steppe regions (HEATWOLE & MUIR 1989, RETANA & CERDÁ 2000). However, in tropical and boreal areas, the response of dominant and subordinate species to temperature is similar (ANDERSEN 1992); thus, dominant species may also dominate open habitats (SAMWAYS 1990). This, however, is not the case in the dry grasslands of our study. High richness and increased proportion of Mediterranean ant species (Table 3) suggest high temperature and strong thermal variation at assessed habitats. It is possible that the microclimate at the dry grasslands formed the current ant assemblages in a way observed in the Mediterranean. This would further explain why abundant ant species, which dominated a wide range of wet and mesic grassland habitats, were virtually absent from dry grasslands.

5.2. Effect of ecosystem stability

High species richness may increase ecosystem stability (Tilman et al. 1996) and, conversely, long-term ecosystem stability may promote and maintain biodiversity (Fjeldså et al. 1997). The dry grasslands in our study could be characterised by such long-term ecosystem stability. In contrast to wet and mesic grasslands, whose open structure is maintained (and has been created) by direct human intervention, dry grasslands tend to undergo less rapid successional changes after abandonment. In fact, the extreme soil and humidity conditions typical for dry grasslands may prevent excessive overgrowth after abandonment for several decades. The management of dry grasslands has traditionally been moderate to relatively extensive; however, its role in the preservation of open dry grassland structure is recognised as vital (Dekoninck et al. 2007, Schrautzer et al. 2009). Several authors suggest that a part of dry grasslands may be considered as natural, hence management-independent (Vera 2000, Bredenkamp et al. 2002, Ložek 2007); however, even in this case the grazing of large mammals (both wild and domestic) represents a significant disturbance factor. Although the overall open character of extreme dry grasslands may remain relatively stable, changes in plant composition (mainly a decrease in light-demanding dry grassland species) were reported after abandonment (Moog et al. 2002). In general, when compared to other grassland categories, dry grasslands have higher ecological stability, especially in relation to secondary succession.

In our study, a large proportion of species richness in dry grasslands was due to stenotopic steppe specialists (such as *Ponera testacea*, *Messor structor*, *Tetramorium ferox*, and *Camponotus piceus*). In Central Europe, these species are characterised by limited occurrence within steppe and forest-steppe habitats (Czechowski et al. 2002, Csősz & Seifert 2003, Seifert 2007). The dominance of these highly specialised species within dry grasslands and, on the other hand, their absence from semi-natural habitats of wet and mesic grasslands refer to a distinct community, paralleling the differences between the alliance *Arrhenaterion elatioris* (moist and mesic grasslands) and the alliance *Asplenio-Festucion glaucae* (dry abandoned grasslands) and higher rank plant syntaxa: the class *Molinio-Arhenatheretea* comprising fertilised meadows and pastures, and the class *Festuco-Brometea* comprising dry and semi-dry grasslands and basiphilous oligotrophic grasslands.

5.3. Effect of low disturbance

Dry grasslands in our study included abandoned sites only. As currently managed dry grasslands are not present in the studied region (Kunca et al. 2005), abandonment could not be compared to management for the dry sites. However, comparison with wet and mesic sites allows for insight into the disturbance-related variation.

Disturbance is defined as a factor removing biomass (Grime 1979). In Central Europe, management in the form of mowing and grazing represents the main disturbance regime for the majority of grasslands (Morris 2000). Although management is generally recognised as a principle tool for protection and restoration of dry grasslands, target species have to be recognised, and consequently, specific management treatments have to be applied, as the response of different groups of plants and animals to a particular management may differ (Morris 2000, Schrauzer et al. 2009). As shown by Englisch et al. (2005), ants and vascular plants of Central European dry grasslands respond to habitat structure in different ways. The results of our study demonstrate similar differences in response to management, suggesting that annual mowing is a suitable practice for preservation of rich plant communities, whereas the same treatment tends to decrease the species richness of associated ants. The positive effect of cutting on plant diversity is mainly due to its support of annual and biennial species, while dominant perennial species are rather impaired by the treatment (Bonanomi et al. 2006). By preventing woody encroachment, mowing maintains the structure and composition of grassland vegetation, and hence, from the perspective of the grassland plant community, is regarded as vital and positive. From the perspective of invertebrates, however, the effect of mowing is considerably different (Morris 2000). Cutting is non-selective and reduces the vegetation on a site level to a uniform height. It strongly reduces topographical features in the sward such as anthills and tussocks; by removing plant biomass it reduces the food resources and shelter, and by exposing the soil surface it rapidly alters the microclimate. Hence, repeated annual cutting does appear to result in impoverishment of grassland fauna (Morris 1990, 2000). The response of ants to cutting is even more pronounced, as sessile ant colonies have only limited opportunities to take evasive action. Besides the mentioned negative effects, direct destruction of anthills and reduction of flowering plants and phytophagous insects during cutting contribute to increased management-related disturbance of ant communities.

The overall decrease in disturbance is considered the main reason why the majority of arthropod groups experience rejuvenation during the cessation period between two management treatments or in the early stage of grassland abandonment (Morris 2000). After abandonment, this regenerative effect of management absence appears to be only temporary and is most pronounced during the initial period of secondary succession, after which the increasing encroachment of woody species distinctly alters the structure and composition of abandoned grasslands. As shown by Wieziková et al. (2010), the negative effect of secondary succession on grassland ant assemblages initially appeared after woody species encroachment exceeded 10–30% of the grassland area, which, depending on various environmental variables and management history, occurred several years to several decades after grassland abandonment. As discussed earlier in this paper, shrub encroachment may be strongly limited by the extreme soil and humidity conditions in dry grasslands. Thus, even though the dry grassland habitats in the Štiavnické Vrchy Mts. have been abandoned for a longer period, the rich and specialised ant assemblages found there may have benefited from the combined effects of open structure and low disturbance persisting at this specific grassland habitat.

Acknowledgements

The study was funded by research grants nos. 1/0026/08, 1/0529/09, and 1/0557/10 of the Slovak Grant Agency for Science (VEGA). We would like to acknowledge Anne Dovčiak and Aiko Huckauf for English language editing. The manuscript was greatly improved by the comments of Camilla Wellstein and two anonymous reviewers.

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Co-ordinating editor: Camilla Wellstein
Manuscript received: 15.10.2010; accepted: 31.01.2011.