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Differential responses of ant assemblages (Hymenoptera: Formicidae) to long-term grassland management in Central Germany

Antonio J. Pérez-Sánchez, Dorit Zopf, Sebastian Klimek & Jens Dauber

Abstract

Biodiversity decreases in response to either intensive management or land abandonment in permanent grasslands of Central Europe. Here, we evaluated the long-term impacts of different management regimes on ant richness, nest abundance, assemblage structure, and food resource use in three experimental grassland sites in Thuringia, Germany. Each experimental site comprised identical management regimes established in 2000/2001. Grassland sites differed with respect to plant community type and abiotic conditions. Ants were assessed in four treatments representing a gradient in management intensity: intensive mowing (four-five cuts per year), traditional mowing (two cuts per year), mulching (mulched once per year), and abandonment (no management). A total of fourteen species belonging to three genera were recorded. Overall, ant responses to management treatments were site dependent. Mean species richness did not vary across treatments but sites. Nest abundance was high in the intensive and traditional treatment but strikingly low in the mulching treatment. Assemblages were more diverse in the traditional and abandonment treatment in sites representing semi-dry conditions, while the intensive treatment enhanced ant diversity under mesic site conditions. Higher rates of food monopolization were detected in the intensive and traditional treatment in drier conditions. Our results show that long-term management affected ant assemblages in different ways, but these effects were strongly related to local climate and soil conditions. The responses of ants to grassland management, that is mowing, can be explained by how these management practices (or their absence) affect the microclimatic conditions under a local context. Hence, the interplay of these factors along with the species requirements is of key importance to determining the impact of the land management on ant assemblages in German and Central European grasslands.

Key words: Community structure, microclimate, mowing regimes, monopolization, mulching, nest abundance, traditional management, upland meadows.

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Introduction

Permanent grasslands are key elements of European agricultural landscapes, highly relevant for the establishment of a sustainable bio-based economy (Osoro & al. 2016). About 40% of the agricultural area in Europe and at least 13% in Germany constitute permanent grasslands, providing fodder for livestock, renewable raw materials for industry and energy production (FAO 2014, Statistisches Bundesamt 2016). Permanent grasslands are important in regulating climate and hazards like erosion and flooding, function as recreational areas, and shelter a high proportion of Europe's endangered biodiversity (Peeters 2009). Nevertheless, grasslands have been threatened by intensification of management or land abandonment in the past 50 years across Europe (Poschlod & al. 2005, Peeters 2009). These processes are known to cause changes in plant community composition and a loss of biodiversity in grasslands (Klimek & al. 2007, Poláková & al. 2011, Socher & al. 2013).

Ants are an important and omnipresent component of biodiversity in Central European grasslands (Curry 1994), being the major generalist predators in meadows (Kajak & al. 1972, Sanders & van Veen 2011). They are considered ecosystem engineers, directly or indirectly controlling many ecosystem processes by altering physical, chemical, and biological soil properties at their nesting sites (Dauber & al. 2008, Frouz & Jilková 2008, Sanders & van Veen 2011). From a nature conservation perspective, ants are key elements in the life cycle of flagship species of European grasslands such as endangered *Maculinea* butterflies (Elmes & al. 1998). Although ants are sensitive to anthropogenic disturbance and land-use changes (Crist 2009), the effect of different management regimes on the myrmecofauna of European grasslands is still a matter of debate (Dahms & al. 2005, Grill & al. 2008, Pihlgren & al. 2010).

The relationship between different mowing regimes and ant assemblages provides a paradigm to investigate the impact of grassland management (or lack thereof) on species richness and community structure. Prolonged and frequent mowing leads to habitat homogenization as a consequence of uniform plant height, cover, and the reduction of topographic structures such as mounds and grass tussocks (Curry 1994, Morris 2000). In contrast, the complete abandonment of

management practices allows natural succession leading to the establishment of tall grasses, litter accumulation, and shrub encroachment in the long run (Öckinger & al. 2006). Although the initial stages of natural succession may promote habitat heterogeneity and benefit grassland biodiversity (Öckinger & al. 2006), further advancement of succession can result in the loss of specialized and thermophilic ant species (Dahms & al. 2010, Dekoninck & al. 2010). Therefore, the effect of abandonment of grassland management on ant diversity is time dependent and further driven by site specific characteristics such as management legacy and grassland types (Dauber & Simmering 2006, Dahms & al. 2010, Dekoninck & al. 2010, Wiezek & al. 2011). In any case, both management extremes cause changes in habitat structure, microclimate, and food resources, affecting ant diversity and interspecific interactions within the assemblages (Curry 1994, Braschler & Baur 2005, Dahms & al. 2010). It has been proposed that regular use of traditional low-intensity mowing or livestock grazing is essential to preserve grassland biodiversity in Central Europe (Isselstein & al. 2005, Poláková & al. 2011). Traditional mowing can maintain high plant species richness by suppressing tall-statured dominant plant species, thereby decreasing light competition and enabling short-statured species to coexist (Hautier & al. 2009). Additionally, mulching has also been suggested as low-cost alternative management for the conservation of species-rich grasslands (Doležal & al. 2011). This management involves cutting the grassland without herbage removal, where the plant biomass subsequently decomposes and releases mineral nutrients into the ecosystem (Doležal & al. 2011, Gaisler & al. 2013).

Previous studies investigating the effects of grassland management on ants report ambiguous results (Dahms & al. 2005, Grill & al. 2008, Wiezik & al. 2011, Pech & al. 2015), perhaps because the intensity gradients of the considered management practices were not distinct enough (e.g., Dahms & al. 2005). In this study, a well-defined mowing gradient on permanent grasslands was investigated with intensive mowing and land abandonment as the outer limits. We evaluated the effects of different long-term grassland management regimes (intensive mowing, traditional mowing, mulching and abandonment) on ant fauna in three experimental grassland sites in Thuringia, Central Germany. The long-term experimental grasslands were established in 2000 / 2001 by the Thuringia Institute of Agriculture and covered different grassland plant community types and abiotic conditions representative of a large fraction of Germany and Europe. We hypothesized that ant diversity would be significantly reduced in both intensively managed and abandoned grasslands compared to traditionally managed or mulched grasslands. Furthermore, since land use imposes changes in habitat structure and alters community composition (Braschler & Baur 2005, Hillebrand & al. 2008, Philpott & al. 2009), we would also expect that such practices alter the biotic interactions within ant assemblages by promoting either dominance at food resources in intensively managed grasslands or coexistence in less disturbed habitats such as the abandoned grasslands. Hence, the following questions were addressed: i) Do different management regimes have an impact on ant assemblages in terms of species richness, nest abundance and assemblage structure?, ii) Are ant responses to management regimes consistent among grassland sites?, iii) Do the species associated with food resources differ between management regimes? Considering bait monopolization as a measurement of ant dominance and bait sharing as a measurement of species coexistence (Stuble & al. 2017), the additional question was addressed: iv) Do the management regimes affect competitive interactions by promoting changes in the monopolization or sharing of food resources? Here we focus on potential effects of management regimes on the resource usage rather than on establishing activity pattern, behavioral categorization or hierarchies within ant assemblages (sensu Cerdá & al. 2013, Stuble & al. 2017).

Materials and methods

Study area: The study was carried out in Thuringia, Central Germany, a region with heterogeneous landscapes, strong gradients in environmental conditions, management, and agricultural productivity. Its elevation ranges from 100 to 982 m, with annual precipitation between 500 mm and 1000 mm (Profft & al. 2009). Mean annual temperatures vary between 4 and 10 °C. Soils in the region include Brown soils, Rendzinas and Luvisols (Profft & al. 2009). Traditional and low input farming practices have created a range of different grassland types in the region. Long-term experimental grasslands at three different sites were selected: Wechmar, Hessberg and Oberweissbach (Tab. 1). The experimental grasslands were established in 2000/2001. The grassland sites are representative of the geological and climatic variation of Thuringia, and comprise different plant community types (Tab. 1). In Wechmar, the plant community consists of tall oat-grass meadows dominated by *Arrhenatherum elatius* with *Poa pratensis*, *Dactylis glomerata*, and *Trisetum flavescens*, and the herbaceous species *Galium mollugo* and *Geranium pratense* being also important. The site at Hessberg is characterized by foxtail meadows dominated by *Alopecuretum pratensis*, with *Ranunculus repens*, *P. pratensis*, *P. trivialis*, and *Elytrigia repens* as important species. The site at Oberweissbach contains golden oat meadows dominated by *T. flavescens*, with high abundances of *D. glomerata*, *Holcus lanatus*, *P. pratensis* and the herbaceous species *Taraxacum officinale*.

Long-term grasslands experimental design: At each grassland site, four different management regimes were applied representing a gradient in management intensity. Experimental treatments were: intensive mowing (intensive), traditional mowing (traditional), mulching once per year (mulching) and no management (abandonment) (Tab. 1). The intensive treatment represents intensively used grasslands with four to five cuts per year from mid-May until late-September. The traditional treatment represents extensively used grasslands with two cuts per year, the first in June-July and the second in September. The mulching treatment represents an alternative management for nature conservation with one cut in July without hay removal. The abandonment treatment includes grassland plots with natural succession and without mowing or fertilization. Mineral fertilizers (NPK) were only applied in the intensive treatment to balance the continued biomass removal by frequent mowing (Tab. 1). All treatments reflect common management regimes in temperate European grasslands. The experimental grasslands were rectangular vegetation plots of 20 to 30 m² in size (Tab. 1), isolated and separated by regularly mown extensions of 0.5 to 2 m distance. A randomized block design was applied with four plots per treatment at each site, except for Oberweissbach, where

Tab. 1: Characteristics of the sites, grassland experiments and management treatments in Thuringia, Central Germany. NPK indicates fertilization [kg / ha] with nitrogen (N), phosphorus (P) and potassium (K).

	Wechmar	Hessberg	Oberweissbach
Site features			
Bedrock	upper Muschelkalk	alluvial clay	Argillite
Elevation [m a.s.l.]	350	380	690
Mean annual temperature [°C]	8.0	7.4	5.7
Annual precipitation [mm]	541	773	861
Soil moisture regime	dry	moist	moderately moist
Soil type (German classification)	Mountain clay (Bergton-Rendzina)	Meadow / alluvial clay (Auenton-Amphigley)	Mountain loam (Berglehm-Braunerde)
Soil pH	6.8	6.2	6.1
Grassland experiments			
Plant community type	Tall oat-grass meadows (*Arrhenatheretum*)	Fox tail meadows (*Alopecuretum*)	Golden oat meadows (*Trisetetum*)
Site area (km^2)	2.9	2.7	2.8
Plot size (m^2)	25	30	20
Year of establishment	2001	2001	2000
Geographic location	50° 52' N, 10° 45' E	50° 25' N, 10° 46' E	50° 34' N, 11° 8' E
Management treatments			
Intensive	Annual cuts: 4 NPK: 200N 30P 220K	Annual cuts: 5 NPK: 260N 30P 220K	Annual cuts: 4 NPK: 200N 25P 200K
Traditional	Annual cuts: 2 NPK: None	Annual cuts: 2 NPK: None	Annual cuts: 2 NPK: None
Mulching	Annual cuts: 1 NPK: None	Annual cuts: 1 NPK: None	Annual cuts: 1 NPK: None
Abandonment	Annual cuts: None NPK: None	Annual cuts: None NPK: None	Annual cuts: None NPK: None

only two replicates were established for the mulching and abandonment treatment.

Ant sampling: Since all the plots constitute ongoing grassland experiments, non-intrusive methods had to be applied for the ant survey. Therefore, ant assemblages were assessed by direct sampling and baiting within a 6 m^2 rectangular area at each replicated plot (BESTELMEYER & al. 2000, SEIFERT 2017). The sampling areas were set at least 1 m from the plots' borders to avoid edge effects (DAUBER & WOLTERS 2004). Direct sampling consisted of an intensive search of ant workers and nests on the soil surface, in the litter and the vegetation (turf) during 30 minutes per sampling area at each plot (one person). All surface-active ants were collected and fixed in 80% ethanol, and only workers were considered for relative abundance analyses. All ant nests were recorded and marked during the direct sampling, and up to 10 workers were collected from each nest after the sampling period. The time invested in direct sampling per plot corresponds to the sampling effort of other ground-dwelling ant surveys in Central European grasslands (WYHNHOFF & al. 2011, SEIFERT 2017). Direct sampling was performed between 09:00 and 17:00 under standard weather conditions (air temperature over 15 °C without rain; SEIFERT 2007). The direct sampling was performed twice, in May – June and July – August 2016, and data from both surveys were pooled for further analyses.

Baiting procedures were employed in order to complement the direct sampling and to evaluate the food resource use by ants among treatments. Two bait stations, each consisting of a plastic platform of 8 cm in diameter with tuna (~ 4 g) or honey-rum (4 ml solution in cotton balls) bait, were installed at 2 m distance in each plot. The numbers of species, individuals and dominance-coexistence events were recorded during a 30-s period at each bait station. Dominance was measured as events where one species drove another away from the bait by aggressive behavior or numerical displacement; while coexistence was measured as events where two or more species shared the resource without engaging in antagonistic interactions (CERDÁ & al. 2013, STUBLE & al. 2017). Each observation was repeated six times (after 10 min and then at 20 min intervals) in a baiting session. Bait sessions were evenly distributed between 09:00 and 17:00, and repeated eight times per plot with a minimum separation time of 18 hrs from late-May to early-August 2016. A total of 64 baits were used per treatment at each site, 32 baits for the mulching and the abandonment treatment in Oberweissbach. All individuals collected were determined to species level according to SEIFERT (2007), and the nomenclature of RADCHENKO & ELMES (2010) was followed for the *Myrmica* species.

Since microclimate for ants strongly depends on height and density of the vegetation (SEIFERT 2017), temperature and humidity were assessed within management treatments. At each plot, the daily mean, maximum, and minimum temperatures (T_{mean}, T_{max} and T_{min}), and relative humidity (%RH) were recorded using Tinytag Plus 2 TPG-4500

Tab. 2: Subsets of candidate models, global and null model explaining ant species richness and nest abundance. The table shows the Akaike's Information Criterion (AIC), the delta AIC values (ΔAIC), the Akaike's weight (w_i) and the relative importance of predictor variables ($w + (j)$) in the whole subset (BURNHAM & ANDERSON 2002). *Treat* = management treatment; *Site* = grassland site; *%RH* = percentage of relative humidity; "x" indicates interaction between two predictor factors, "X" indicates variable included in the model, and "-" parameter not included in the model. Only models with ΔAIC < 4 are considered as candidates.

Models	Predictors	AIC	ΔAIC	w_i	Variables' relative importance		
					Site	*Treat*	*%RH*
Species richness							
Candidate 1	*Site*	144.2	0	0.57	X	-	-
Candidate 2	*Site + %RH*	145.9	1.63	0.25	X	-	X
Candidate 3	*Treat + Site*	147.9	3.63	0.09	X	X	-
Global	*Treat + Site + %RH*	149.8	5.63	0.03	X	X	X
Null	*1*	160.2	16	< 0.01	-	-	-
Distribution family: Poisson				$w + (j)$	**0.95**	**0.13**	**0.29**
Nest abundance							
Candidate 1	*Treat + Site*	136.2	0	0.40	X	X	-
Global	*Treat + Site + %RH*	136.7	0.46	0.32	X	X	X
Candidate 2	*Treat x Site*	138.7	2.47	0.12	X	X	-
Candidate 3	*Treat x %RH + Site*	139.7	3.55	0.07	X	X	X
Null	*1*	159	22.8	< 0.01	-	-	-
Distribution family: Negative binomial				$w + (j)$	**0.90**	**0.90**	**0.38**

sensors installed 10 cm above the soil from May to August 2016.

Statistical analysis: All data analyses were performed using the statistical program R 3.3.1 (R DEVELOPMENT CORE TEAM 2016). Pearson correlation coefficients were calculated to explore the relationships among the microclimatic measurements T_{mean}, T_{max}, T_{min} and %RH. Positive correlations between T_{max}, T_{min}, and T_{mean} were found (r > 0.69, p < 0.001), but no significant relationship between T_{mean} and %RH was detected (r = 0.12, p = 0.453) when the whole data set was compared. However, negative correlations between T_{mean} and %RH were found in Wechmar (r = -0.68, p = 0.004) and Hessberg (r = -0.73, p = 0.001), but not in Oberweissbach (r = -0.17, p = 0.58). Linear models were used to evaluate the variations of T_{mean} or %RH among grassland sites and management treatments. Based on the correlations mentioned before and depending on the scope of the analysis (between or within sites), either T_{mean} or %RH was used as an explanatory variable in further analyses.

Generalized linear models (GLMs) were used to evaluate the effects of treatment, site and microclimatic variables on species richness and nest abundance. Species richness was calculated as the total number of species recorded by direct sampling and baits sampling per plot. Models were constructed using treatment (henceforth *Treat*) and grassland site (henceforth *Site*) as categorical explanatory variables and the mean temperature (henceforth T_{mean}) or percentage of relative humidity (henceforth *%RH*) as continuous explanatory variable. For each response variable a subset of candidate models was generated by fitting i) a global model that contained all explanatory variables or factors, and ii) candidate models with all possible factor combinations and interactions. The models selection was based on the delta

AIC values (ΔAIC; Akaike's Information Criterion) and the Akaike weights (w_i) estimation (BURNHAM & ANDERSON 2002). The w_i values can be interpreted as the probability that the selected model is the best model of those considered. The ΔAIC procedure extracts delta AIC values of each model (global and candidates) against the best-fitted model, the one with the lowest AIC value (BURNHAM & ANDERSON 2002). The candidate models subsets were defined as models within a range of ΔAIC < 4. In addition, the relative importance of each explanatory variable (*j*) was calculated by summing the w_i values across all the models within the subset where such variable occurs ($w + (j)$). Therefore, the larger $w + (j)$, the more important is the variable compared to other variables (BURNHAM & ANDERSON 2002). Models were fitted using Poisson distribution family since the response variables were counts. In case of obtaining overdispersed Poisson models, negative binomial distribution was used. Multicollinearity among continuous (T_{mean} and *%RH*) and categorical variables (*Treat* and *Site*) was evaluated by calculating the variance inflation factor (VIF) for each model (FOX & WEISBERG 2002). Model assumptions were visually inspected through diagnostic plots of residuals and normal QQ-plots (ZUUR & al. 2010). All analyses were performed with the MASS version 7.3 - 45, car version 2.1 - 6, and MuMIn version 1.15.6 packages (VENABLES & RIPLEY 2002, FOX & WEISBERG 2002, BARTON 2009).

Cluster heat maps were used to explore the variation of ant assemblages between treatments and sites based on the workers and nest relative abundance data (ln[x + 1] transformed) recorded by direct sampling. The hierarchical clustering was done with Euclidean distances and the complete agglomeration method using the heatmap.2 function of the gplots version 3.0.1 package (WARNES & al. 2016).

The incidence of ant species on baits was measured as the proportion of baits visited by ants during the whole observation period. Monopolization (Mo) was calculated as the proportion of times (n = 6) a single species was dominant over the bait session. Sharing (Sh) was defined as the proportion of times (n = 6) more than one species coexisted without antagonistic interactions over the bait session. GLMs were fitted using treatment (*Treat*) and microclimatic data (T_{mean} or %*RH*) as explanatory variable with the ΔAIC procedure of Burnham & Anderson (2002). Binomial distribution was assumed for the incidence of ant species on baits (presence, absence) and Poisson distribution for Mo and Sh counts with an offset term equal to the total number of observations per bait session (log transformed). *Post-hoc* comparisons were performed using least-square means with Tukey's HSD (LSM Tukey) at α = 0.05. Pairwise contrasts were calculated for treatment within each site. LSM Tukey was performed using the lsmeans version 2.25 - 5 package (Lenth 2016).

Results

The microclimatic conditions of the plots varied between treatments and grassland sites (Fig. S1 as digital supplementary material to this article, at the journal's web page). A general decrease of T_{mean} was observed from Wechmar to Hessberg and Oberweissbach experimental grasslands. The highest T_{mean} records were generally observed in the traditional treatment while the lowest values were always detected in the abandonment treatment (Fig. S1). The variation of T_{mean} was explained by a joint effect of grassland site and treatment ($F_{11, 32}$ = 49.22, P < 0.001, R^2 = 0.93; Fig. S1). Further GLM analyses revealed collinearity of T_{mean} with the grassland sites (whole data set) and the treatments within each site (VIF > 3 to 10). Therefore, T_{mean} was not considered within the GLM analysis in order to avoid redundancy in the results. On the other hand, the variation of %RH values was also associated to the treatments of each site ($F_{11, 32}$ = 5.29, P < 0.001, R^2 = 0.52; Fig. S1). Hessberg showed the highest values of %RH in almost all treatments (95%; Fig. S1), while Oberweissbach showed the highest variation of %RH (53 - 94; Fig. S1).

Overall, 14 species from three genera were recorded with a total of 11 species detected in Wechmar, five in Oberweissbach, and four in Hessberg (Tab. S1). The mean number of species per plot varied significantly between sites but not between treatments (Fig. 1a). Nest abundance within treatments varied between sites (Fig. 1b). The intensive and traditional treatment showed the highest nest abundance in Wechmar and Hessberg, while the number of nests was generally low in all treatments of Oberweissbach (Fig. 1b). The mulching treatment showed the lowest number of nests at all grassland sites, and in some mulching plots no nests were found (Fig. 1b). In agreement with the model approach, the model containing *Site* as a single factor was better in explaining the variation in species richness among treatments (Fig. 1a, Tab. 2). Although the models subset suggested an additional effect of %*RH*, *Site* showed the highest relative importance value among the predictor variables for species richness (Tab. 2). In the case of nest abundance, the models with higher w_i indicate an independent effect of *Site*, *Treat*, and %*RH* on the response variable (Candidate 1 and Global, Tab. 2). The most important factors to predict nest abundance were *Site* and *Treat* (Tab. 2; Fig. 1b). A list of all
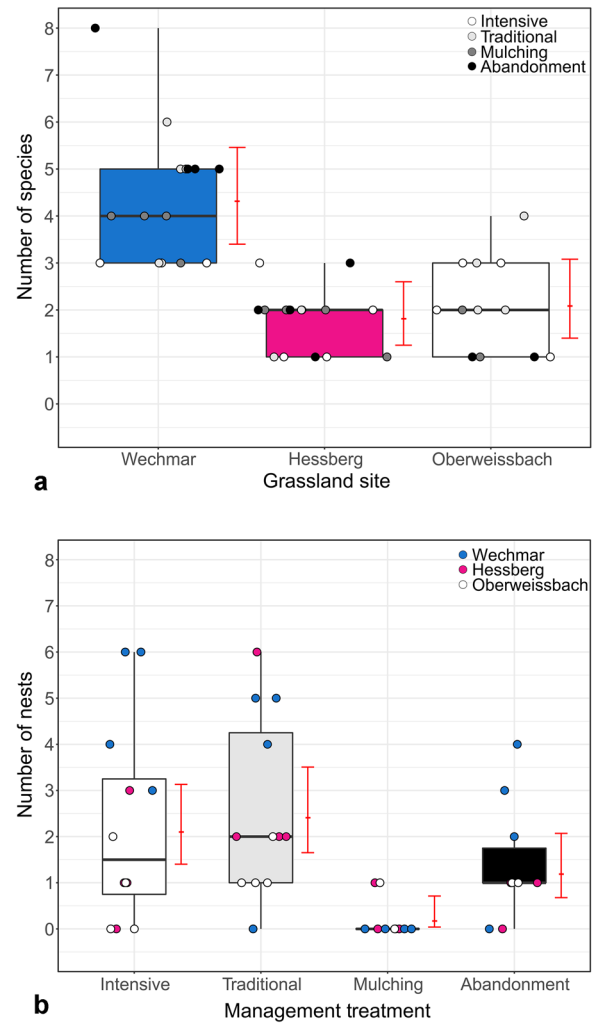

Fig. 1: Ant richness and nest abundance within grassland sites and management treatments. (a) Mean number of species per site, the jittered dots show the raw values per replicate (treatments color coded), and the error bars indicate the mean predicted values ± confidence intervals according with the candidate model 1 for ant richness (see Tab. 2). (b) Mean number of nests per treatment, the jittered dots show the raw data per replicated plot (sites color coded), and the error bars indicate the mean predicted values ± confidence intervals for the factor *Treat* according to the candidate model 1 for nest abundance (see Tab. 2).

candidate models fitted for both variables is provided in the supplement (Tab. S2).

The composition and structure of ant assemblages depended on the grassland site (Fig. 2). Wechmar experimental grassland had a diverse ant assemblage with high relative abundance of *Lasius niger* (Linnaeus, 1758) and the presence of exclusive elements of *Formica* and *Myrmica* species (Fig. 2a). At this site, the highest nest counts of *L. niger* and *L. flavus* (Fabricius, 1782) occurred at the intensive and traditional treatment, while *Myrmica sabuleti* Meinert, 1861 and *M. rubra* (Linnaeus, 1758) nests were detected only in the abandonment treatment (Fig. 2b). On the other hand, the Hessberg and Oberweissbach grasslands had less diverse ant assemblages with *M. scabrinodis* Nylander, 1846 as the most abundant species in all cases (Fig. 2a, b).
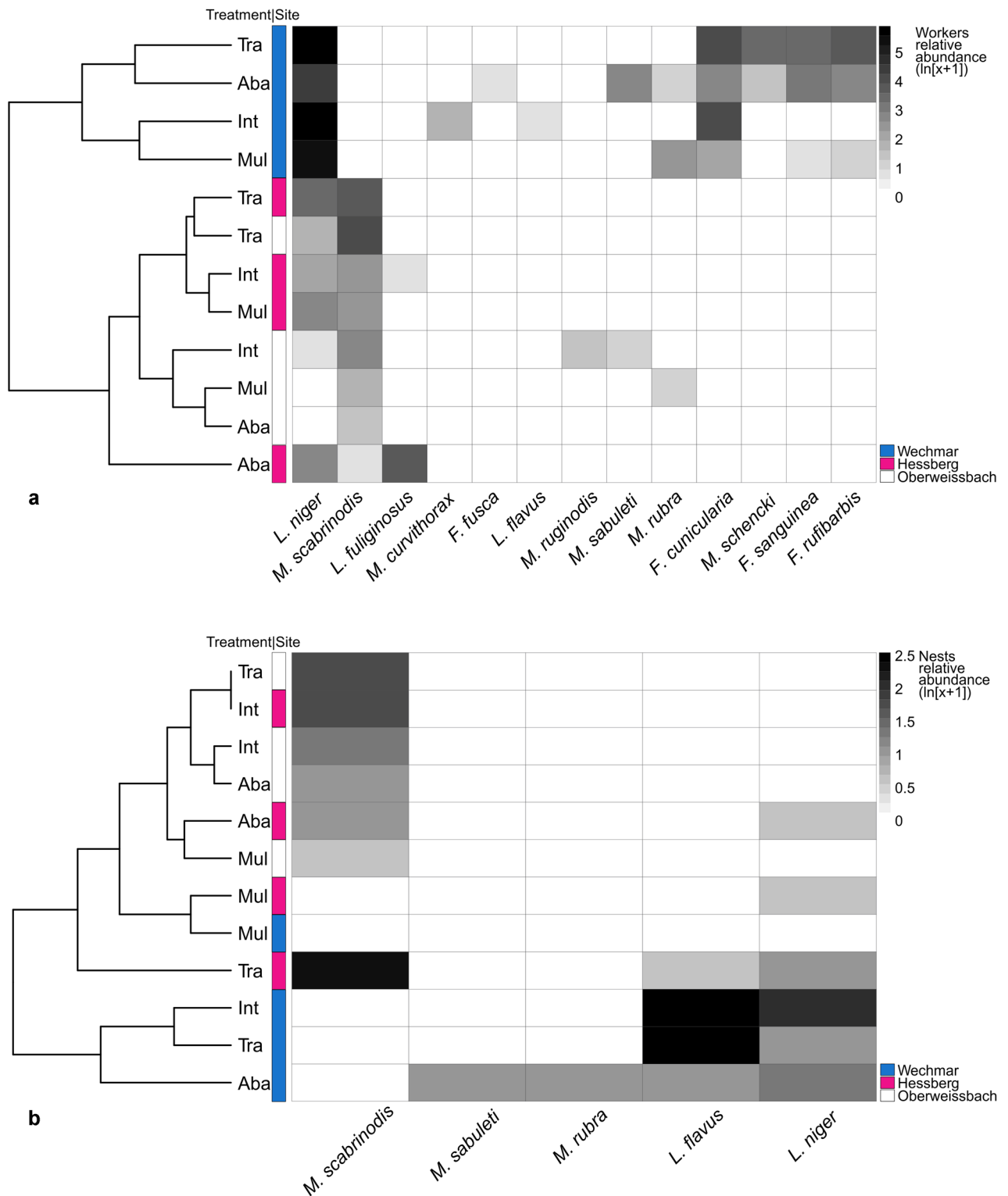
Fig. 2: Ant assemblage composition and structure based on (a) workers and (b) nest counts per species. In both cases the heat map plot shows the relative abundance of each species (ln [x + 1] transformed) at intensive (Int), traditional (Tra), mulching (Mul) and abandonment (Aba) treatment. The cluster heat map is based on similarity measures of the relative abundance of species per treatment.

Overall, cluster analyses showed high similarities on assemblage structure within the traditional, the abandonment and the intensive-mulching treatment (Fig. 2a), and confirmed the effect of the mulching treatment on nests counts in all sites (Fig. 2b).

Bait occupancy varied between grassland sites (Fig. 3). In Wechmar, more than 95% of the baits were occupied (Fig. 3a). Eight species were detected at this site, with *Lasius niger* occupying more than 80% of the baits (Fig. 3a). Baits at the intensive treatment of this site were mainly used by *L.*

niger, while the proportion of baits occupied by this species decreased in the abandonment treatment (Fig. 3a). Besides *L. niger*, the baits were partially used by *Formica sanguinea* LATREILLE, 1798 in the traditional and abandonment treatment at Wechmar. At this site, *F. cunicularia* LATREILLE, 1798 and *F. rufibarbis* FABRICIUS, 1793 occurred in low numbers in all treatments, while *Myrmica* species were restricted to the traditional and abandonment treatment (Tab. S1). The candidate model approach confirmed the effect of *Treat* on the bait occupancy by *L. niger*, and suggested that %RH explained the presence of this species on baits to a lesser extent (Tab. 3, Fig. 3a). On the other hand, three species were found on the baits in Hessberg, and four species in Oberweissbach (Tab. S1). At both sites, between 48 and 52% of the baits were occupied, with *M. scabrinodis* as the main species (Fig. 3b, c). In Hessberg, *M. scabrinodis* occupied a higher proportion of baits in the traditional and intensive treatment (Fig. 3b). In agreement with the model analysis, the incidence of *M. scabrinodis* on baits was affected by *Treat* and %RH, with both predictors having high relative importance within the subset (Tab. 3). Besides *M. scabrinodis*, *L. niger* was observed on baits in all treatments while *L. fuliginosus* (LATREILLE, 1798) was found only on baits in the abandonment treatment (Fig. 3b, Tab. S1). In Oberweissbach, a higher proportion of baits were occupied by *M. scabrinodis* in the traditional and abandonment treatment, while a lower proportion was detected in the intensive treatment (Fig. 3c). In this case, the model with the highest w_i value indicates that the presence of *M. scabrinodis* on the baits is mainly explained by *Treat* (Tab. 3). However, the models subset and the $w + (j)$ values also suggest an effect of %RH on the incidence of this species on the baits (Tab. 3). Additionally, *L. niger*, *M. lobicornis* NYLANDER, 1846 and *M. ruginodis* NYLANDER, 1846 were detected in low proportions on baits in the intensive and traditional treatment (Fig. 3c, Tab. S1).

Antagonistic or coexistence interactions among species were low, and the monopolization of baits was driven by numeral displacement. Baits shared by different species were scarcely recorded in Wechmar and Hessberg, and absent in Oberweissbach. Overall, Sh values were strikingly low among treatments and sites (Sh ≤ 0.1). On the other hand,
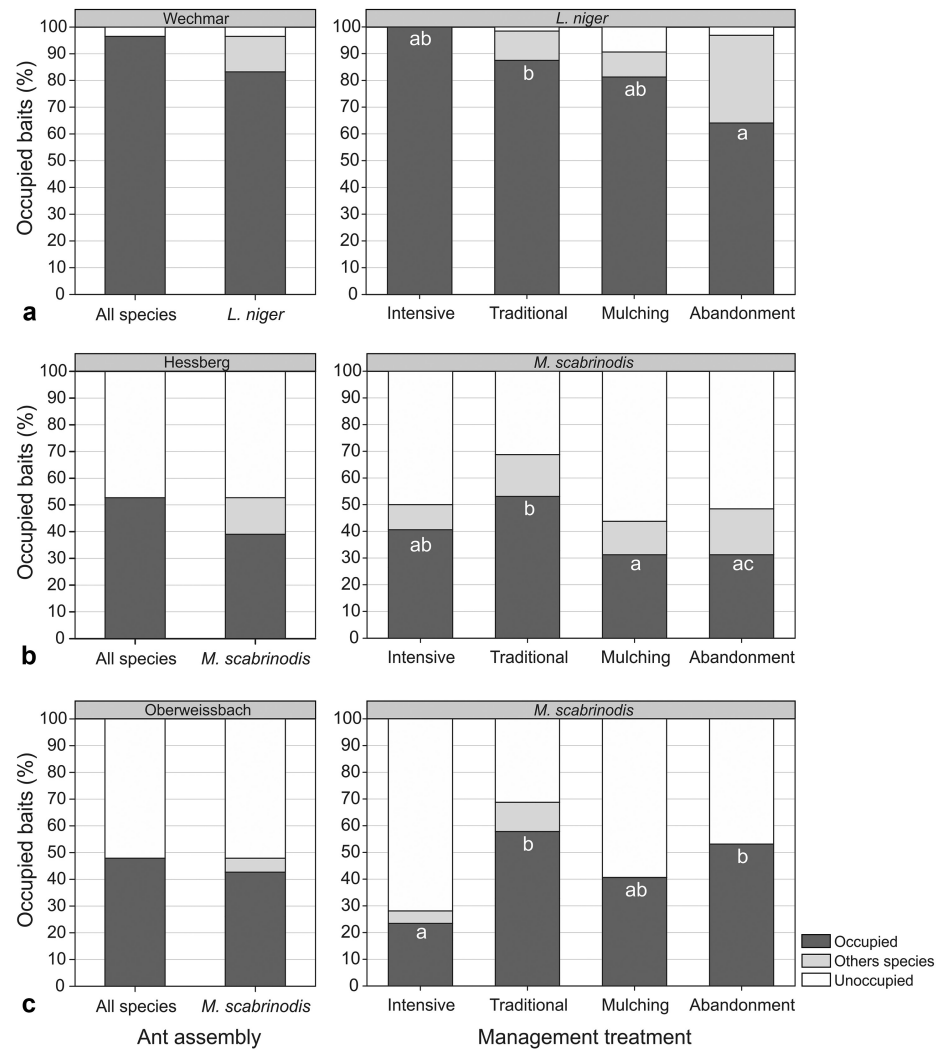

Fig. 3: Food resources occupancy by ants. An overview of the proportion of occupied baits by the assembly of species and most common species is provided for Wechmar (a), Hessberg (b), and Oberweissbach (c). Detail of the bait occupancy per treatment by the main species is also provided. [a, b, c] *post hoc* comparisons of each species incidence on baits among treatments (LSM Tukey, P > 0.05; Tab. 3).
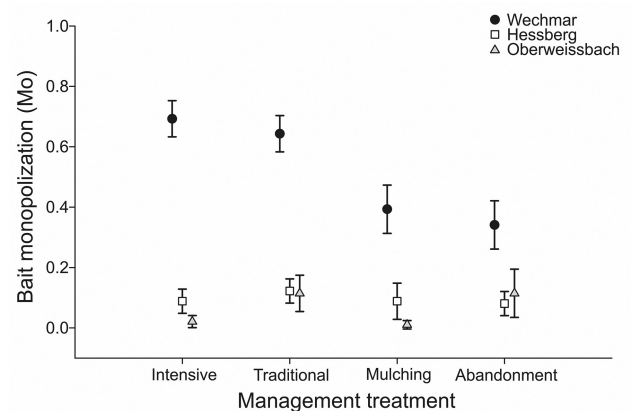

Fig. 4: Monopolization (Mo) of food resources by ants. Symbols show the Mo mean ± confidence intervals (2×SE) per treatment. Mo is the proportion of times (n = 6) at which a single species was dominant over a bait session.

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Tab. 3: Subsets of candidate models, global and null model explaining the incidence of *Lasius niger* and *Myrmica scabrinodis* on food resources per grassland site. The table shows the Akaike's Information Criterion (AIC), the delta AIC values (ΔAIC), the Akaike's weight (w_i) and the relative importance of predictor variables ($w + (j)$) in the whole subset (BURNHAM & ANDERSON 2002). *Treat* = management treatment; *%RH* = percentage of relative humidity; "x" indicates interaction between two predictor factors, "X" indicates variable included in the model, and "-" parameter not included in the model. Only models with ΔAIC < 4 are considered as candidates.

Models	Predictors	AIC	ΔAIC	w_i	Variables' relative importance	
					Treat	*%RH*
Site Wechmar: *L. niger*						
Candidate 1	*Treat*	201.59	0.00	0.70	X	-
Global	*Treat* + *%RH*	203.25	1.66	0.30	X	X
Null	*1*	233.76	32.17	< 0.001	-	-
Distribution family: Binomial				$w + (j)$	**1**	**0.30**
Site Hessberg: *M. scabrinodis*						
Global	*Treat* + *%RH*	340.16	0	0.50	X	X
Candidate 1	*Treat*	341.11	0.95	0.31	X	-
Candidate 2	*%RH*	343.45	3.29	0.10	-	X
Null	*1*	343.64	3.48	0.09		
Distribution family: Binomial				$w + (j)$	**0.81**	**0.60**
Site Oberweissbach: *M. scabrinodis*						
Candidate 1	*Treat*	252.32	0	0.70	X	-
Global	*Treat* + *%RH*	254.25	1.93	0.27	X	X
Null	*1*	264.07	19.08	< 0.001		
Distribution family: Binomial				$w + (j)$	**0.97**	**0.27**

the dominance events were detected mainly in Wechmar (Fig. 4). At this site, the higher Mo values were observed in the intensive and traditional treatment compared to the mulching and abandonment treatment (Fig. 4). The model subset for this site indicates that monopolization of baits was affected mainly by *Treat* (AIC = 1121.82, ΔAIC = 0, w_i = 0.71). An additional effect of *%RH* was also detected (AIC = 1123.6, ΔAIC = 1.78, w_i = 0.29). Overall, *Treat* had higher relative importance ($w + (j)$ = 1) in predicting the variation of Mo. The results of the Mo models at Hessberg and Oberweissbach are presented in the supplement (Tab. S3).

Discussion

We found that ant assemblages are sensitive to management within permanent grasslands of Thuringia, Central Germany. However, the responses of ant community composition and structure to long-term management regimes were affected by the grassland site. We detected diverse ant assemblages in Wechmar but impoverished assemblages in the experimental grasslands of Hessberg and Oberweissbach. This may be related to variations in climatic and soil conditions affecting the ant species pool of each site (DAUBER & al. 2005, DAUBER & SIMMERING 2006). It has been suggested that soil temperature and moisture along with their interplay with vegetation are important limiting factors for ant assemblages, where warm and dry conditions tend to be favorable for ants (KASPARI & al. 2000, SANDERS & al. 2007, SEIFERT 2017). Likewise, ant species richness tends to be negatively associated with elevated soil moisture levels in temperate grasslands (SEIFERT 2017). In our case, Wechmar

is characterized by semi-dry conditions with higher temperatures and drier soils than the other sites having more humid conditions (Tab. 1, Fig. S1). Such variation in soil conditions and microclimate may explain the ant diversity variation found among grassland sites. This is in accordance with the pattern described for Central European grasslands, where high ant diversity was found at hot and dry grasslands with well drained soils, while lower diversity was detected in more humid meadows (SEIFERT 2017). However, it is important to consider that our results are limited to the experimental plots and may not be representative for the overall regional diversity of each site. In any case, the patterns detected in the long-term and stable experimental systems of our study support the finding that the effects of land use on ants cannot be assessed independently of the site conditions (DAHMS & al. 2005, DAUBER & SIMMERING 2006, WYNHOFF & al. 2011).

Along with the site effect mentioned above, ant assemblages vary between treatments but not consistently from management extremes to extensive practices as we had expected. Mean species richness did not vary significantly among treatments, which is in line with previous studies in Central European grasslands (DAHMS & al. 2005, PECH & al. 2015, KORÖSI & al. 2014). However, the abandonment treatment at Wechmar harbored twice the number of species than the intensive treatment. In this particular situation, the abandonment of management practices at the scale of small plots could generate heterogeneous microhabitats with transitions from cooler conditions of tall vegetation in the plot center towards warmer microhabitats of short vegetation in the grassland matrix surrounding the plots

(Fig. S1). Such small-scale heterogeneity may provide wider resource availability for ant foraging and suitable nesting conditions for less thermophilic species (DAUBER & WOLTERS 2004, DAUBER & SIMMERING 2006). The fact that four species (*Myrmica sabuleti*, *M. rubra*, *Lasius niger*, *L. flavus*) with different nesting requirements were well established in this treatment supports this statement.

Nest abundance showed a differential response to the management regimes. The positive effects of the intensive and traditional treatment were site specific and related to the nesting preferences of the most abundant species: *Lasius niger* and *L. flavus* in Wechmar, and *Myrmica scabrinodis* in Hessberg. The first two species are well known for being resistant to and even favored by anthropogenic disturbance, while *M. scabrinodis* tends to be associated with less disturbed but warm and wet habitats, and is even favored by extensive management (ELMES & WARDLAW 1982, GRILL & al. 2008, WYNHOFF & al. 2011, SEIFERT 2017; but see KORÖSI & al. 2014). On the other hand, the total absence or low nest abundance within the mulching treatment at all sites might be attributed to changes in soil moisture and fertility. DOLEŽAL & al. (2011) showed that continuous mulching management over nine years increases water and nitrogen content within soils of upland meadows in Central Europe. This soil fertility improvement has also been reported in similar mulch-managed meadows of Thuringia (HOCHBERG & ZOPF 2011). Although such changes in soil may benefit plant communities, high levels of moisture and nitrogen in soil have a negative impact on ant composition (DAHMS & al. 2005), and long-term fertilization decreases species richness and nest density in managed grasslands (PETAL 1976, PIHLGREN & al. 2010). Therefore, we may expect that a continuous mulching management over 15 years alters the soil moisture and nitrogen levels within the studied plots, turning them into less suitable habitats for ant colonization and establishment. Although this explanation requires experimental verification, it may offer a starting point for formulating further research questions about the effect of mulching on ant diversity.

The effect of the management regimes at assemblage level was observed mainly in Wechmar, and to a lesser extent at the other sites. More complex ant assemblages were found in the traditional and abandonment treatment at Wechmar, which basically differ in the abundance of workers of either *Formica* or *Myrmica* species. The high T_{mean} and wide %RH in traditionally managed plots could benefit thermophilic species such as *F. cunicularia* and *F. rufibarbis* (Fig. S1). Both species tolerate high temperatures and are barely affected by extensive management like sheep grazing or traditional cutting (SEIFERT 2017). The heterogeneous vegetation structure of abandoned plots may favor species with different or wider requirements such as the thermophilic species *M. sabuleti* and *M. schencki*, or the phytodensity tolerant *M. rubra* (see DAHMS & al. 2005, SEIFERT 2017). In contrast, less impoverished assemblages were associated with the intensive treatment in Hessberg and Oberweissbach. Considering the moist soil conditions at these sites, one could expect that the intensive mowing practices might improve the microclimate for ants by means of decreasing humidity and increasing temperature. This situation seems to be plausible in Oberweissbach, where the intensively managed plots showed the lowest levels of humidity but not important changes in temperature (Fig. S1).

Food resource usage between treatments was affected by local variations of ant assemblages, which corresponds to our previous results. However, these results highlighted the fact that almost all resources were exploited at Wechmar, while the bait use in the other grassland sites was two times lower. Although this situation might be a consequence of the differences in relative abundance between species at each site, this difference does not completely explain the pattern observed between sites. An alternative explanation may be related to the behavioral and colony features of the most abundant species at each site. In terms of behavioral interaction *Lasius niger* has been categorized as a subdominant species due to its non-territorial but aggressive behavior when defending or trying to take over resources (CERDÁ & al. 2013). *Myrmica scabrinodis*, in contrast, has been considered as a subordinate species with a simple recruitment system that tends to avoid physical contact with workers of other colonies (CERDÁ & al. 2013). The higher colony size and foraging distances of *L. niger* (≈ 7000 workers, ≈ 18 m; ELMES 1971, SEIFERT 2007) may allow them to cover and use a higher proportion of food resources when compared to *M. scabrinodis* which have smaller colonies and restricted foraging areas (600 workers, up to 2 m; ELMES & al. 1998). Some studies have reported relatively low frequencies ($\approx 50\%$) of *Myrmica* species on baits, and it has been suggested that competition among this group is more related to nest site availability than food limitation (ELMES & al. 1998, GRILL & al. 2008, KORÖSI & al. 2014). Hence, all these aspects could explain why *M. scabrinodis*, despite showing higher number of nests at Hessberg than *L. niger* at Wechmar, occurs in a lower proportion on baits.

It could be expected that changes in the habitat structure caused by management alter the biotic interactions within ant assemblages (CERDÁ & al. 2013), promoting either the dominance of single species in intensively managed grasslands or the coexistence of several species in less disturbed habitats (BRASCHLER & BAUR 2005, PHILPOTT & al. 2009). Contrary to such expectations, no significant results on species coexistence on baits were detected in this study. In Hessberg and Oberweissbach, this absence of coexistence events was not related to an increase of dominance events but to the low usage of the food resources by less diverse assemblages dominated by *Myrmica scabrinodis*. In contrast, the significant dominance events detected at intensively and traditionally managed plots in Wechmar might partially support our hypothesis about how a decrease of habitat structure promoted by management contributes to ant dominance. *Lasius niger* dominated all baits in the open and homogenous plots of the intensive treatment, and partially in the traditional managed plots where they share roles with *Formica sanguinea*. Both species were less frequent on baits in the abandonment treatment, which might allow other species to have access to the resources. This indicates that intensive mowing practices may not only promote the colonization by subdominant species as our nest results suggested (e.g., *L. niger*), but also contribute indirectly to a displacement of less competitive and subordinate species on food resources (e.g., *Myrmica* and *Formica* (*Serviformica*)). Similarly, BRASCHLER & BAUR (2005) found that changes of habitat structure caused by fragmentation can alter the competitive interaction within ant assemblages by promoting nest densities of the dominant species *L. paralienus* SEIFERT, 1992. The study by BRASCHLER & BAUR (2005), despite of being focused on fragmentation effects on ants, showed

a response of the ants to long-term and constant mowing management versus land abandonment (fragment vs control plots) within experimental grasslands.

Conclusions

Due to the enormous variety of plant community types, management regimes and local environmental conditions, it is difficult to elucidate the direct effect of management regimes on ant communities in European grasslands. Nonetheless, in this study we demonstrated that long-term grassland management affects ant communities in different ways, but those effects are strongly related to local climate conditions and soil attributes. We detected that in experimental plots under semi-dry conditions (Wechmar), traditional management and land abandonment can harbor diverse ant assemblages; while in mesic conditions (Hessberg and Oberweissbach) some ants can be favored by either intensive or traditional management practices. Additionally, despite of being considered an alternative grassland management for nature conservation, annual mulching affects ant nest abundance negatively. Habitat complexity mediated by management regimes also differently affected the success of ant species on baits, for example the intensive mowing management favored dominance within assemblages while abandonment enhanced more subordinate species. Overall, ant response to management regimes can be explained by how these practices (or absence of them) affected the microclimatic conditions under a local context. The interplay of those factors along with the ant species requirements are key elements for determining the impact of the land management. Against this background, new approaches that take into account the local climatic context and how this potentially affects ant species must be considered in order to evaluate the ant assemblage - management relationship and thus preserve this important group of insects in German and Central European grasslands.

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