

Shrub encroachment alters composition and diversity of ant communities in abandoned grasslands of western Carpathians

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Abstract Invasions of woody species into grasslands abandoned by agriculture are a global phenomenon, but their effects on diversity of other taxa have been rarely investigated across both regional and local scales. We quantified how shrub encroachment affected the activity, composition, and diversity of ant communities in managed and abandoned grasslands in western Carpathians of Central Europe across four regions and four shrub encroachment stages in each region. We surveyed ant communities on 48 sites in total, with each encroachment stage replicated three times in each region and twelve times overall. We used pitfall traps to sample ants over three years (2008, 2009, 2011) and identified 9,254 ant workers belonging to 33 species in total. Although the epigeic activity and composition of ant communities varied with region, abandoned grasslands supported a greater species richness of ants than managed grasslands regardless of the region, and especially so in more advanced shrub encroachment stages. Since the woody colonization within grasslands was moderate even in the advanced encroachment stages (on average ~40 % of grassland colonized by woody species), it allowed coexistence of forest specialists (e.g. *Temnothorax crassispinus*) with species typical of open grasslands, thus increasing overall ant diversity. Managed grasslands were not only less species rich compared to abandoned grasslands, but they were characterized by different species (e.g. *Lasius niger*, *Myrmica rugulosa*). The differences in ant communities between managed and abandoned grasslands are likely to cause differences in ecological functions mediated by ants (e.g. predation of arthropods or plant seed dispersal).

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Introduction

Changes in land-use or land-management practices can be a major driver of changes in the diversity and composition of biological communities (e.g. Sala et al. 2000; Wiezik et al. 2007; Halpern et al. 2012). Semi-natural grasslands used by traditional low-intensity agriculture (such as mowing for hay or grazing) are known for their large species richness and they are considered to be one of the most important habitats for biodiversity conservation in Europe (e.g. Peet et al. 1983; Pärtel et al. 1996; Knops et al. 1999; Dengler 2005). Since continuous low-intensity management is important for maintaining the diversity and unique biological communities of these semi-natural grasslands (Morris 2000; Marriott et al. 2004; Dekoninck et al. 2007; Schrautzer et al. 2009), the abandonment of their traditional land-use over the last few decades has threatened their biodiversity throughout Europe (van Dijk 1991). The lack of disturbance after cessation of agricultural use tends to lead to the colonization of grasslands by woody species (Dovčiak et al. 2005, 2008), posing a significant threat for grassland diversity (Pärtel et al. 2005).

Invasions of woody species into abandoned grasslands have been increasingly documented globally (Eldridge et al. 2011) and in Europe (MacDonald et al. 2000; van Dijk et al. 2005), but our current understanding of their effects on grassland biodiversity and ecosystem functioning across regional and local scales is still limited. Grassland colonization by woody species alters above ground biomass, net primary productivity, solar radiation and light reaching the ground surface, microclimatic conditions, and water and nutrient availability, and thus it negatively affects grasses and other grassland plant and animal species typically dependent on open grassland environments (Reich et al. 2001; Mitlacher et al. 2002; Dierschke 2006; Van Auken 2009). However, moderate amount of woody colonization of grasslands can increase their spatial heterogeneity and structural complexity and thus positively affect grassland biodiversity (Duelli 1997; Reyes-López et al. 2003; Bestelmeyer 2005). The positive effects of management cessation and subsequent moderate woody colonization can be especially pronounced in arthropods (such as ants), which constitute a major component of grassland biodiversity (Morris 2000). However, grassland arthropod and ant communities can considerably vary across different regions, and thus their responses to woody colonization of grasslands can potentially dramatically vary across regions as well (Bestelmeyer and Wiens 2001).

Ants are a particularly important group in the arthropod communities of temperate grasslands in terms of their overall biomass and their ecological function as ecosystem engineers (Folgarait 1998; Jouquet et al. 2006). Ants are involved in a vast number of ecological relationships with plants and animals (Hölldobler and Wilson 1990), they actively alter soil chemical and physical properties (Eldridge 1994; Frouz et al. 2003), and they have been implicated in accelerating grassland secondary succession towards forest (Vlasáková et al. 2009). Consequently, ants have been used as bioindicators of ecosystem conditions and environmental quality to monitor environmental changes in various ecosystems throughout the world (King et al. 1998; Peck et al. 1998; Perfecto and Vandermeer 2002). The effects of woody colonization on grassland ant communities have been studied especially in the Mediterranean (e.g. Gómez et al. 2003; Reyes-López et al. 2003; Ottonetti et al. 2006), with smaller number of studies in temperate grasslands (Gallé 1991;

Dauber and Simmering 2006; Dekoninck et al. 2007; Wiezik et al. 2011) and with relatively little attention to potential regional variability in the effects of woody encroachment. Understanding the effects of woody colonization on ant communities in Central European grasslands is of particular importance because the diversity of Central European grassland ant fauna is considerable (Seifert 2007) and because much of this diversity is threatened by accelerating trends in the abandonment of traditionally managed semi-natural grasslands in this region (Van Dijk 1991; Hopkins and Holz 2006).

In order to improve our current understanding of the effects of woody colonization on the ant communities of abandoned semi-natural grasslands in Central Europe across regional and local scales, we addressed two main objectives in our study. First, we quantified how epigeaic activity, species composition, and species richness of ant communities varies across different regions and different levels of woody colonization of grasslands (shrub encroachment stages). We then proceeded to identify ant species sensitive to land abandonment and shrub encroachment (or “indicator” species for managed and abandoned grasslands and for the individual shrub encroachment stages), in order to determine what species are the most likely winners or losers under the observed dynamics of land-abandonment and subsequent woody colonizations in Central European semi-natural grasslands.

Methods

Study area

The study was conducted in four different regions (*R*) in western Carpathians, Slovakia (*R1*-Revúcka vrchovina Hills, *R2*-Turčianska kotlina Basin, *R3*-Strážovské vrchy Hills, *R4*-Zvolenská kotlina Basin). These regions were chosen to span a range of environmental conditions characteristic of submontane landscapes of western Carpathians. The study regions are located between 48°38' to 49°36.5'N and 18°14.5' to 20°08'E and encompass elevations between 300 and 600 m above sea level. Mean annual precipitation and mean annual temperature range between 700 to 800 mm and 7.0 to 7.8 °C, respectively, and geologic substrates vary from granodiorites to calcareous claystones to andesites with corresponding differences in soil types (Hrnčiarová 2000, Table 1). Grasslands in these

Table 1 Geographic locations and main environmental characteristics of study regions located in western Carpathians in Central Europe (based on Hrnčiarová 2000)

	R1	R2	R3	R4
Latitude (N)	48° 38.0'	49° 01.3'	48° 50.0'	49° 36.5'
Longitude (E)	20° 08.0'	19° 03.0'	18° 14.5'	19° 16.1'
Elevation (m)	350–450	550–600	300–350	350–500
Precipitation (mm/yr)	750	800	700	700
Temperature (°C) ^a	7.5	7.0	7.7	7.8
Bedrock	Granodiorites	Calc. claystones	Calc. claystones	Andesite
Soils	Dystric cambisoils	Stagni-eutric cambisoils	Eutric cambisoils	Eutric cambisoils

R1 Revúcka vrchovina Hills, *R2* Turčianska kotlina Basin, *R3* Strážovské vrchy Hills, *R4* Zvolenská kotlina Basin

^a Annual mean temperature

regions represent a characteristic land-use form, traditionally managed as hay meadows and pastures, with mowing as a predominant more recent management. We studied sub-xerophilous and mesic grasslands (*Arrhenatherion elatioris*, Koch 1926, class *Molinio–Arrhenatheretea*) which cover large areas of agricultural submontane landscapes in Slovakia (Janišová et al. 2010) with many of them abandoned during the last few decades and subsequently colonized to various degrees by woody species (mostly shrubs). The main colonizing woody species were common shrubs such as blackthorn (*Prunus spinosa*), dog rose (*Rosa canina*), hawthorn (*Crataegus* ssp.), and common juniper (*Juniperus communis*), with a smaller component of tree species such as Scots pine (*Pinus sylvestris*), field maple (*Acer campestre*), Turkey oak (*Quercus cerris*), and silver birch (*Betula pendula*) (Michal Wiezik, personal observation).

Study design and data collection

In order to assess the effect of progressive shrub encroachment on ant communities across different grassland regions, we selected 48 grassland sites in total, with twelve sites in each of the four study regions (see [Study area](#), Table 1) and three replicate sites for each of the four shrub encroachment stages in each region. All sites were situated on south facing slopes and at least 20 m from grassland borders to avoid edge effects. Any two sites within the same region were at least 500 m apart and separated by a different habitat (e.g. forest or field); any two sites from different regions were at least 57 km apart (with the maximum distance of 140 km). The shrub encroachment stages were defined by the extent of woody (mostly shrub) colonization of the grasslands as follows: (A) managed grassland without woody species, (B) abandoned grassland in initial woody encroachment stage (i.e. woody cover <5 %), (C) abandoned grassland in intermediate woody encroachment stage (i.e. woody cover ~ 25 %), and (D) abandoned grassland in advanced encroachment stage (i.e. woody cover ~ 50 %).

Within each site, we established a 30 m long transect with 10 pitfall traps placed at 3 m intervals. The traps consisted of plastic cups with a seal (3 cm in diameter) buried at the soil level and filled with about 50 ml of 4 % solution of formaldehyde as a fixative. A detergent was also added to lower surface tension. Each trap was left in place for at least 7 days before it was opened for sampling (i.e. trap seals were removed once ants became accustomed to the traps) in order to reduce digging-in effects (Greenslade 1973). In total, 480 traps were placed in the field and each trap remained open for 7 days before samples were collected. Sampling was conducted during the last week of May during each of the 3 years of the study (in 2009 at both *R1*-Revúcka vrchovina Hills and *R2*-Turčianska kotlina Basin, in 2008 at *R3*-Strážovské vrchy Hills, and in 2011 at *R4*-Zvolenská kotlina Basin). The data were pooled across all traps at each individual site for analyses. Ants were identified at the species level in the laboratory according to Seifert (2007) and only ant workers were considered in statistical analyses following Dahms et al. (2005). To corroborate and more fully quantify shrub encroachment stage for each site, we visually estimated woody plant cover (%) in the field on 1 × 1 m plots centered on each pitfall trap.

Statistical analyses

We constructed ant community matrix from the list of ant species and their epigaeic activity at each site. Total species richness (the number of species found at a site), total epigaeic activity (the number of individuals collected at a site per week; ind.wk⁻¹), and community composition (species presence/absence matrix) were used as response

variables. Ant community responses were analyzed using a generalized randomized block design (Quinn and Keough 2002) with a fixed effect model that included shrub encroachment stage (A–D), geographic region (R1–R4), and the two-way interaction of encroachment stage and geographic region.

Ant species richness and overall epigeaic activity were modeled using analysis of variance (ANOVA). In addition, we conducted rarefaction analysis (Hurlbert 1971) to ensure that the results of ANOVA on species richness were not confounded by differences in epigeaic activity. Samples were rarefied down to the smallest sample size (i.e. epigeaic activity of 5 ind.wk⁻¹) and the mean number of species in rarefied samples was used in ANOVA. Homoscedasticity was checked for each model using diagnostic plots of residuals. Epigeaic activity was log transformed to stabilize variance, but we report untransformed data in figures for the ease of interpretation. We employed permutational ANOVA to ensure that non-normality did not affect the results. Probability values were based on 9,999 permutations of residuals under a reduced model (Anderson and ter Braak 2003). Significant results of the overall tests ($\alpha = 0.05$) were followed by pair-wise comparisons using Tukey's HSD tests. Mean values were plotted along with 95 % confidence intervals derived by 10,000 bootstrap replications. Confidence limits were obtained using bias-corrected accelerated percentile method (Efron and Tibshirani 1986).

Ant community composition (species presence/absence matrix) was analyzed using the same fixed effects model as in the ANOVA described above. Since the traditional multivariate techniques that use Euclidean or Chi squared distances (such as RDA or CCA) are not always appropriate for the analysis of community data (e.g. Legendre and Legendre 1998; Legendre and Anderson 1999; Legendre and Gallagher 2001), we used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) which allows fitting linear models with interaction terms to any distance matrix (McArdle and Anderson 2001). We used Sørensen dissimilarity measure (Sørensen 1948) to construct the distance matrix. Overall significance was tested using the same permutation procedure described above for richness and epigeaic activity, followed by relevant pair-wise comparisons. Canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) was used to visualize the results of multivariate analysis to display the differences among groups in multivariate space. We used modified implementation of CAP with the axes weighted by eigenvalues and full dimensional solution (all axes with positive eigenvalues) to best approximate original dissimilarities (Oksanen et al. 2011). To facilitate the interpretation of CAP ordination, 95 % confidence ellipses (Murdoch and Chow 1996) were calculated for each shrub encroachment stage using the standard deviations of site scores. Species characteristic for individual encroachment stages were identified using indicator species analysis using species presence data (Dufrêne and Legendre 1997). The indicator value (IndVal) of each species was tested using Monte Carlo permutation test with 9,999 permutations. Species with higher indicator values (IndVal ≥ 20 %) were regarded as characteristic species for the shrub encroachment stage in question. Scores of those species were added into ordinations as weighted sums of incidence matrix.

The analyses were conducted in R language (R Development Core Team 2011) or PERMANOVA (Anderson 2005).

Results

We collected a total of 9,254 workers of ants belonging to 33 species from 3 subfamilies (See in Table 5 Appendix) with five species accounting for almost 85 % of all sampled

Table 2 Effects of shrub encroachment stage and geographical region on the total epigeaic activity, species richness, and composition of ant communities in semi-natural grasslands of western Carpathians

Source of variability	DF	Total epigeaic activity			Species richness			Community composition		
		MS	F	<i>p</i>	MS	F	<i>p</i>	MS	pseudo-F	<i>p</i>
Encroachment stage	3	1.49	1.43	0.248	20.50	3.45	0.027	7756.3	5.06	<0.001
Geographical region	3	6.31	6.05	0.002	8.72	1.47	0.236	4720.8	3.08	<0.001
Encroachment × region	9	2.12	2.04	0.069	12.37	2.08	0.058	2123.3	1.39	0.077
Plot	32	1.04			5.94			1531.5		

ANOVA and PERMANOVA outputs below show degrees of freedom (DF), mean sum of squares (MS), and F/pseudo-F statistics with accompanying probabilities (*p*) based on 9,999 permutations for each source of variability

individuals (*Lasius psammophilus*, *L. niger*, *Formica pratensis*, *Myrmica sabuleti*, and *M. scabrinodis*). These species were present in all four shrub encroachment stages, except for *F. pratensis*, which was not found in managed grasslands without woody species (encroachment stage A). Abandoned grasslands (encroachment stages B–D) varied in their colonization by woody species, reflecting our stratified sampling approach; woody cover was 1.5 ± 2.4 % in the initial encroachment stage B with sparse woody colonization, 21.8 ± 11.9 % in the intermediately colonized stage C, and 41.5 ± 20.8 % in the advanced encroachment stage D.

Overall epigeaic activity was statistically indistinguishable among encroachment stages, however differences were found among regions (Table 2). The ant communities at R2-Turčianska kotlina Basin were ~ two times more active compared to the remaining three regions (including R1-Revúcka vrchovina Hills sampled in the same year) (Fig. 1a). In contrast, species richness varied significantly with encroachment stage but not with geographical region (Table 2). Abandoned grasslands (encroachment stages B–D) consistently appeared to contain ~ 30 % more species compared to managed grasslands (stage A), but only grasslands with the most contrasting encroachment (A vs D) showed statistically significant differences (Fig. 1b). ANOVA on rarefied species richness confirmed the significant effect of encroachment stage ($F_{3, 32} = 4.33$, $p = 0.011$) that were independent of geographical region (interaction term: $F_{9, 32} = 1.55$, $p = 0.176$).

Unlike epigeaic activity and species richness, the composition of ant communities was significantly affected by both encroachment stage and geographical region (Table 2). Pair-wise comparisons and CAP ordination revealed significant differences in species composition between managed grasslands (encroachment stage A) and all abandoned grasslands (stages B–D) as well as between abandoned grasslands with sparse versus high woody cover (stage B vs D) (Table 3, Fig. 2a). Indicator species analysis identified *L. niger* and *M. rugulosa* as characteristic species for the managed grasslands (stage A), while *F. pratensis* was characteristic species for the initial encroachment stage B and *Temnothorax crassispinus* had a significant preferences for the advanced encroachment stage D (Table 4, Fig. 2b). Intermediate encroachment stage C appeared to be a transitional stage with species from both initial and advanced encroachment stages and without any stage-specific species (Table 4). In addition, several other species had increased frequencies in particular encroachment stages (i.e. *M. scabrinodis*, *F. rufibarbis*, and *L. psammophilus* in stage B, *M. sabuleti* and *F. sanguinea* in stage C, and *L. alienus* and *Tetramorium caespitum* in stage D; Table 4, Fig. 2b).

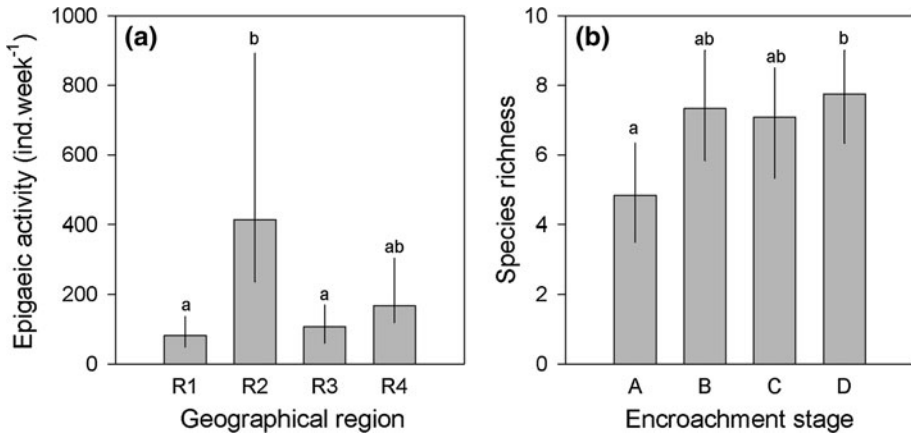


Fig. 1 Effects of geographical region and shrub encroachment stage on the total epigaic activity (a) and species richness (b) of ant communities in semi-natural grasslands of western Carpathians. Only significant effects are shown (i.e. epigaic activity did not vary with shrub encroachment stage and species richness did not vary with geographical region). Mean values \pm 95 % bootstrapped confidence intervals are displayed. Means with the same *lowercase letters* are not significantly different (Tukey’s HSD test, $\alpha = 0.05$). Data on epigaic activity were back-transformed. Regions: R1 Revúčka vrchovina Hills, R2 Turčianska kotlina Basin, R3 Strážovské vrchy Hills, R4 Zvolenská kotlina Basin, all in Slovakia. Encroachment stages were characterized by mean woody cover: (A) no woody cover, (B) 1.5 % (± 2.4), (C) 21.8 % (± 11.9), and (D) 41.5 % (± 20.8) woody cover

Table 3 Pair-wise comparison of the composition of ant communities among shrub encroachment stages (A–D) in semi-natural grasslands of western Carpathians

Stage	A	B	C	D
A	–	<0.001	<0.001	<0.001
B	2.62	–	0.149	0.043
C	3.11	1.30	–	0.375
D	2.85	1.56	1.05	–

Pseudo-t statistics are displayed below the table diagonal and corresponding probabilities above the diagonal

Discussion

We found that land abandonment and moderate woody plant invasions (shrubs encroachment) positively affected diversity and composition of ant communities in the temperate semi-natural grasslands in western Carpathians of Central Europe, irrespective of the study region. Thus the effects of woody invasions on ant communities in our study appear robust and corroborate previous findings from other ecosystem types (e.g. Mediterranean or arid; Reyes-López et al. 2003; Bestelmeyer 2005). The abandonment of the traditional management practices that maintain semi-natural grasslands of western Carpathians free of woody vegetation does not appear to immediately lead to negative effects on ant diversity. As long as woody colonization of the abandoned grasslands remains rather moderate (i.e. does not exceed ~50 %), ant diversity is likely to benefit from such land abandonment (potentially unlike some other taxa; cf. Miltacher et al. 2002). However, ant community diversity may not

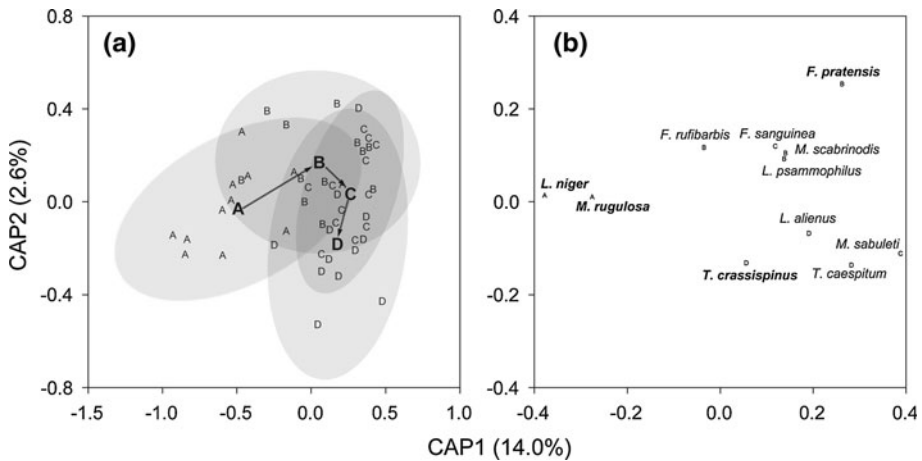


Fig. 2 Ordination illustrating compositional changes in ant communities in semi-natural grasslands of western Carpathians with shrub encroachment stage **(a)**, and indicator scores for species characteristic of individual encroachment stages (IndVal $\geq 20\%$) with significant indicator species ($p < 0.05$) in **bold (b)**. Ordination method was canonical analysis of principal coordinates (CAP) with Sørensen dissimilarity measure. In **a** site scores are plotted using *small uppercase letters* of their corresponding encroachment stage (A–D), overall centroids of each stage are plotted using *large bold uppercase letters* with *arrows* suggesting potential directional (successional) trend toward high colonization by shrubs, and 95 % confidence ellipses are shown for each stage in grey. The variation explained by the first two coordinates is given in parentheses. Encroachment stages are as in Fig. 1

Table 4 Characteristic species associated with individual shrub encroachment stages in semi-natural grasslands of western Carpathians

Species	Encroachment stage	IndVal (%)	<i>p</i>
<i>L. niger</i>	A	40	0.006
<i>M. rugulosa</i>	A	37	0.007
<i>F. pratensis</i>	B	31	0.050
<i>M. scabrinodis</i>	B	26	0.281
<i>L. psammophilus</i>	B	23	0.562
<i>F. rufibarbis</i>	B	20	0.577
<i>M. sabuleti</i>	C	31	0.135
<i>F. sanguinea</i>	C	22	0.112
<i>T. caespitum</i>	D	29	0.128
<i>T. crassispinus</i>	D	25	0.049
<i>L. alienus</i>	D	20	0.411

Indicator values (IndVal) are shown for all species with IndVal $\geq 20\%$ with corresponding probabilities based on 9,999 permutations

be the most important conservation objective; for example, grassland ant species became progressively replaced by forest ant species with increasing woody colonization.

Effect of shrub encroachment on species richness and epigeaic activity

Our results suggest that the cessation of grassland management (mowing) can lead to the increase in species richness of ant communities. However, ants generally tend to occupy more open habitats with increased exposure of soil to direct sunlight (Lassau and Hochuli 2004), and consequently, they are expected to be sensitive to microclimatic changes

resulting from shrub encroachment and to exhibit a general decline with increasing woody cover (consistent with the corresponding plant diversity decline in grasslands colonized by woody species; Mítlacher et al. 2002). The relatively moderate amount of woody cover even in the most advanced shrub encroachment stage in our study (stage D), however did not have such negative effect on ant diversity or the presence of many grassland ant species. The presence of the grassland species even in the areas most heavily colonized by woody species was likely facilitated by the significant amount of remaining patches of relatively open grassland. For example, we observed a relatively high frequency of the genus *Tapinoma*, typical of open grassland habitats (Gómez et al. 2003; Wiezik et al. 2011), in the most advanced shrub encroachment stage.

The number of ant species that can coexist within a temperate grassland has been shown to be strongly limited and relatively constant; grassland ant communities in Central Europe are typically saturated at approximately seven species per site (Dauber and Wolters 2004, 2005). We recorded slightly lower richness levels in managed grasslands, but the observed number of ant species in abandoned grasslands was close to this saturated species richness. The increase in species richness toward species saturation was due to the co-occurrence of original open grassland species with forest specialist species such as *Stenamma debile*, *T. unifasciatum*, *T. crassispinus*, or *L. fuliginosus*. These observed forest species are dependent on leaf litter layer and woody debris and represent a typical component of forest ant communities in Central Europe (Czechowski et al. 2002; Seifert 2007). We observed these forest species especially in the more advanced shrub encroachment stages, where patches of woody species with specific microclimate and copious leaf litter layer were sufficiently large. The presence of forest ant species within grasslands colonized by woody species further indicates that successional processes of grassland conversion toward forest are well under way (cf. Ottonetti et al. 2006), ultimately leading toward the collapse of original grassland ant community in more advanced successional stages (e.g. Gómez et al. 2003).

Unlike species richness, our results suggest that epigaic activity of ants can vary more with region than encroachment stage. Although, epigaic activity of ants derived from pitfall trap sampling cannot be directly related to ant abundance across different ant taxa (Greenslade 1973) or habitats (Adis 1979), epigaic activity can be efficiently used for comparing species composition of various ant communities (Bestelmeyer et al. 2000). In our study, the lack of any differences in the overall epigaic activity across shrub encroachment stages suggests that our observed response of species richness to shrub encroachment is not an artifact of different species behavior (activity) across the shrub encroachment gradient.

Compositional differences between ant communities of managed and abandoned grasslands

Our analyses suggest that abandoned grasslands host distinctly different ant communities than managed grasslands. On our sites, management in the form of mechanized mowing was the prevailing disturbance regime, well representing the land use in the majority of grasslands in Central Europe (Morris 2000). Although active management is generally recognized as a principle tool for sustaining and restoring semi-natural grasslands, responses of different biological taxa within grassland communities to a particular management regime may differ (Morris 2000; Söderström et al. 2001; Schrautzer et al. 2009). By preventing woody encroachment, mowing maintains the structure and composition of grassland vegetation, and thus it is regarded as an appropriate management strategy for the

conservation of semi-natural grasslands. However, mowing may effect various grassland taxonomic groups negatively, especially if the form, scale, or frequency of mowing is not appropriate. Mowing is a non-selective management that uniformly reduces all vegetation to the same height, removes various topographical features within the sward (e.g. mounds), reduces the food resources and shelter by removing plant biomass, and abruptly alters micro-climate and causes microclimatic stress by exposing the soil surface to direct solar radiation (Morris 2000). Hence, repeated annual cutting can result in impoverished grassland fauna (Morris 1990; Volkl et al. 1993; Baines et al. 1998; Vickery et al. 2001; Wiezik et al. 2011; but see Grill et al. 2008 for differing results). Direct destruction of anthills and the reduction of flowering plants and phytophagous insects during mowing operations pose additional negative effects on grassland ant communities.

The composition of ant communities in managed grasslands in our study seemed to reflect this high level of management-induced disturbance. Both characteristic species of managed grasslands *L. niger* and *M. rugulosa* are highly tolerant to human pressure and have synanthropic tendencies (Czechowski et al. 2002). *L. niger* is found frequently on arable land or on formerly farmed land (Dauber and Wolters 2005). On the other hand, typical grassland ant species such as *F. pratensis* and open habitat specialists such as the genus *Tapinoma*, were completely absent from managed grasslands in our study. Especially mound building ants of the *F. rufa* group (such as *F. pratensis*) are ecologically sensitive to succession and land-use change (Ellison 2012); they are sensitive to mowing, mainly due to the destruction of their nests by this management practice (Morris 2000), and hence they tend to avoid intensively managed grasslands (e.g. Dauber and Wolters 2005; Wiezik et al. 2011). Thus, the increased disturbance in managed grasslands allows for mowing-tolerant species to dominate the ant community, while more sensitive grassland species tend to benefit from the cessation of mowing in abandoned grasslands.

Compositional differences among ant communities of encroachment stages

The individual encroachment stages of abandoned grasslands hosted different ant communities in our study, especially when comparing the initial encroachment stage (B) with the advanced encroachment stage (D). These compositional differences were due to the characteristic species of these two stages, but they also reflected differences in others species which showed affinities to one of these two stages. Thus, shrub encroachment appears to be a major driver of compositional changes in ant communities in abandoned grasslands. Habitat (vegetation) structure influences the exposure of ground surface to direct solar radiation (Andersen 2000); dense and structurally complex habitats provide shaded cool microclimates that are generally poorly suitable for ants (Lassau and Hochuli 2004) while warm open habitats tend to host the majority of ant species (Andersen 1995). Low temperature has been shown to be the primary environmental stressor for ants and to control global patterns of ant productivity and community structure (Andersen 1995). Dense woody canopy induces environmental stress (*sensu* Grime 1979) for ant communities in general (and for grassland ants in particular) by negatively affecting surface temperature, and thus it can negatively affect ant community structure (Gómez et al. 2003).

However, early successional shrub encroachment may have positive effects on grassland biodiversity (Pihlgren and Lennartsson 2008). Pykälä et al. (2005) reported the highest richness of plant species at woody cover of ~5 %. Small to medium amount of woody canopy may be favorable for ants because it increases habitat structural heterogeneity and can thus increase ant species richness by providing niches for additional edge or shade-tolerant species (Reyes-López et al. 2003; Azcárate and Peco 2012). Our results extend

these findings since our advanced shrub encroachment stage (with ~41 % woody cover) was most species rich due to the retention of the original grassland species and their co-occurrence with forest species (such as *S. debile*, *T. unifasciatus*, *L. fuliginosus*, *Camp-onotus ligniperdus*). However, the original grassland species were less common (i.e. less commonly sampled) in the advanced (D) than in the initial (B) encroachment stage, suggesting deterioration of the environmental condition for grassland ants as woody colonization progressed. Thus, the initial encroachment stage supported diverse and abundant ant communities that consisted predominantly of grassland species due to the positive effects of lacking management-related disturbance and low woody encroachment-related environmental stress. With progressing succession in the advanced encroachment stage, the effect of increased woody cover and related environmental stress is likely to overcome the benefits that the absence management-related disturbance offers for the conservation of grassland ant species (and overall ant diversity) after grassland abandonment. Moreover, even without succession to woodland, number of grassland ants would likely decrease with increased height of the grassland vegetation and thickness of the grass litter layer in later stages of grassland succession (e.g. Dekoninck et al. 2007). It has to be expected that the more thermophilous species of ants would disappear from grasslands with long-term abandonment of management (Azcárate and Peco 2012), unless environmental properties such as very low soil fertility, dry microclimate or intensive grazing by wild herbivores would keep the grassland vegetation naturally low (Wiezik et al. 2011).

Conclusions

The overall effects of land abandonment on ant communities of semi-natural grasslands in western Carpathians appear positive, especially in the initial stages of abandonment. Unmanaged grasslands in this study hosted different and more diverse ant communities compared to managed (mowed) grasslands which were characterized by the dominance of synanthropic species and the absence of characteristic grassland species of ants. Thus, abandoned grasslands can play a crucial role for the preservation of temperate grassland ant communities in Central Europe (see also Wiezik et al. 2011). However, the challenge in using abandoned grasslands for the conservation of grassland ant species remains in the need to limit the natural woody plant encroachment to relatively low levels (<20 %) (see also Reyes-López et al. 2003; Dahms et al. 2010), perhaps by low frequency mowing (i.e. biannual or less frequent), grazing, or by targeted removal of the colonizing woody plants from more invaded areas (Dekoninck et al. 2007; Dahms et al. 2010). Prolonged periods of unchecked woody species colonization of grasslands are likely to lead to the conversion of the original grassland ant community to community dominated by forest ants (Gómez et al. 2003). Thus, while land abandonment favors grassland ants, it is the early shrub encroachment stage that offers the best conservation potential for grassland ant species (Decaëns et al. 1998). On the other hand, later shrub encroachment stages can offer conservation opportunities for a larger number of ant species (but less so for grassland ants) as long as the colonizing woody species remain under a threshold cover (likely < 50 %) when the ant community composition would become dominated mostly by forest ants (Gómez et al. 2003). Thus, the most appropriate conservation strategy for temperate ant communities of semi-natural grasslands will depend on the actual conservation goal—to conserve predominantly grassland ants, or to conserve the largest number of ant species—these two goals would lead to different management prescriptions for the amount of woody cover allowed to colonize abandoned grasslands. Both of these two goals

can be met at landscape scales by conservation and management approaches that retain and promote a mosaic of different successional stages of grasslands (including managed), thus increasing the overall ant diversity by supporting a variety of ant groups within the landscape.

Our results underline the importance of maintaining moderately overgrown grasslands as an important tool in the conservation of grassland arthropod diversity. However, managing for landscapes that contain these early successional shrub encroachment stages is hindered by the current structure of EU agricultural subsidies that cannot be applied to grasslands with woody cover above certain threshold (e.g. 5 % in Slovakia; TRINET 2010). This ecologically arbitrary threshold for allotting agricultural subsidies is counterproductive in terms of biodiversity conservation; it encourages both the abandonment of moderately overgrown grasslands that are above the threshold as well as the intensification of agricultural use of grasslands below the threshold, essentially promoting the loss of the intermediately overgrown grasslands and the loss of biological diversity associated with them.

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Appendix

See in Table 5 Appendix.

Table 5 Total epigeic activity of ants in semi-natural grasslands of western Carpathians

Subfamily and species	Habitat	% Sample	Encroachment stage			
			A	B	C	D
<i>Myrmicinae</i>						
<i>Myrmica gallieni</i>	G	<1	–	–	7 ¹	–
<i>M. lobicornis</i>	U	<1	2 ¹	2 ¹	17 ²	6 ¹
<i>M. lonae</i>	G	<1	1 ¹	–	–	–
<i>M. rubra</i>	U	1.1	8 ⁴	8 ³	55 ²	32 ³
<i>M. ruginodis</i>	F	<1	–	2 ¹	1 ¹	22 ³
<i>M. rugulosa</i>	G	1.5	103 ⁶	37 ¹	1 ¹	–
<i>M. sabuleti</i>	U	7.8	31 ³	300 ⁷	188 ¹¹	201 ¹¹
<i>M. scabrinodis</i>	G	7.8	67 ⁴	308 ⁸	261 ⁶	81 ⁷
<i>M. schencki</i>	U	1.5	18 ⁴	55 ⁷	51 ⁷	16 ⁴
<i>Stenammina debile</i>	F	<1	–	–	–	1 ¹
<i>Myrmecina graminicola</i>	F	<1	1 ¹	3 ²	15 ²	11 ³
<i>Solenopsis fugax</i>	G	<1	–	1 ¹	–	18 ¹
<i>Temnothorax crassispinus</i>	F	<1	–	–	–	11 ³
<i>T. interruptus</i>	G	<1	1 ¹	–	–	–
<i>T. unifasciatus</i>	F	<1	–	–	–	1 ¹
<i>Tetramorium cf. caespitum</i>	G	1.0	16 ²	30 ⁵	25 ⁷	23 ⁹

Table 5 continued

Subfamily and species	Habitat	% Sample	Encroachment stage			
			A	B	C	D
Dolichoderinae						
<i>Tapinoma erraticum</i>		<1	–	6 ³	16 ³	3 ³
<i>T. subboreale</i>		<1	–	2 ¹	4 ¹	35 ³
Formicinae						
<i>Lasius flavus</i>	U	<1	–	1 ¹	8 ⁴	7 ³
<i>L. fuliginosus</i>	F	<1	–	–	–	2 ¹
<i>L. jensi</i>	G	<1	1 ¹	–	1 ¹	1 ¹
<i>L. mixtus</i>	U	<1	–	–	–	1 ¹
<i>L. alienus</i>	U	1.4	2 ¹	30 ³	43 ⁴	50 ⁶
<i>L. niger</i>	G	17.5	1095 ¹¹	122 ⁷	17 ²	390 ⁵
<i>L. psammophilus</i>	G	36.3	320 ⁵	1954 ⁹	988 ⁸	95 ⁷
<i>Camponotus ligniperdus</i>	F	<1	–	1 ¹	–	12 ²
<i>Formica cunicularia</i>	G	1.3	15 ⁵	63 ⁷	31 ⁷	9 ⁵
<i>F. fusca</i>	U	<1	1 ¹	7 ¹	–	4 ²
<i>F. pratensis</i>	G	15.4	–	428 ⁸	585 ⁶	411 ³
<i>F. rufa</i>	F	2.1	190 ¹	–	1 ¹	–
<i>F. rufibarbis</i>	G	<1	15 ⁵	20 ⁷	16 ⁴	6 ⁴
<i>F. sanguinea</i>	G	2.2	–	144 ²	62 ⁴	–
<i>Polyergus rufescens</i>	G	<1	1 ¹	–	–	–
Total activity			1888	3524	2393	1449
Total richness			19	22	22	26

Total epigeaic activity was defined as the total number of ant workers trapped in each shrub encroachment stage. Upper index indicates the total number of sites where species was observed. Habitat preference according to Czechowski et al. (2002)

U ubiquitous species, F forest species, G grassland specialists, % sample percent of all sampled individuals

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