Abandonment of crop lands leads to different recovery patterns for ant and plant communities in Eastern Europe

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Abstract: Significant proportion of crop lands have been abandoned as management strategies have changed in Central and Eastern Europe in the past decades. The study of insect versus plant communities in such areas could help us understand how these processes take place, and whether these communities return to a semi-natural state maintained by human activities. Amongst insects ants, as ecosystem engineers, are a perfect target group in this respect. We studied epigaeic ant and plant communities of abandoned old-fields in Romania. Contrary to our expectations, the total number of ant species did not increase with time during succession on old-fields contrary to plants, where an increase was registered in the total number. Disturbance-tolerant ant species dominated the ant communities throughout the successional gradient, while in the case of plants a transition was found from weed-dominated to semi-natural communities. The diversity of both ant and plant communities increased after the 1-year stage, but the patterns were different. While a return to semi-natural state could be observed in plants during old-field succession, such a definite change did not occur in ants. This might be caused by the landscape context: the lack of connectivity of old-fields to larger natural areas. While plant propagules of semi-natural and natural habitat species can still successfully colonize the old fields even under such conditions, ant colonizers are mainly disturbance-tolerant species typical for agricultural areas, which can be hardly replaced by typical grassland species. Our findings underline the existence of important discrepancies between plant and ant community succession, mostly treated as paralleling each other. This is the first study to handle the effect of abandonment on ant and plant communities simultaneously in Eastern Europe.

Introduction

The Central and Eastern European landscape is generally characterized by ecosystems that have been formed through centuries due to the persistence of traditional agriculture (Tryjanowski et al. 2011, Fischer et al. 2012). During the past century, in several European countries traditional land use strategies (e.g. rotational land use, low intensity grazing, hand mowing, and use of horse-driven carts) have been abandoned (Ciaian and Pokrivcak 2007) in favor of more intensive and motorized agricultural management techniques. This poses a severe threat to biodiversity, already recognized in Western Europe, e.g. the decline of farmland bird species (e.g. Tryjanowski et al. 2011) and pollinators (e.g. Batáry et al. 2010). The opposite tendency could also be detected, specifically in Transylvania, Romania: smaller or bigger parcels regained by their former owners after the fall of the communism were abandoned due to financial unsustainability of old agrarian techniques in new structural circumstances (Fischer et al. 2012, Csergő et al. 2013). The persistence of traditional land use techniques contributes essentially to the existence of world-record meadows in plant diversity (Wilson et al. 2012), and of areas with unique cohabitation of several

flagship Large Blue butterfly species (e.g. *Maculinea* spp.) (Czekes et. al. 2014), but also to the maintenance of large populations of the threatened amphibians (e.g. *Bombina variegata*) (Hartel et al. 2014), birds (e.g. *Crex crex*) (Moga et al. 2010), and large carnivores (e.g. *Ursus arctos*) (Dorresteijn et al. 2014), and to the persistence of wide areas of unique landscape elements, as wood pastures, that offer shelter to many protected species (Hartel et al. 2013, Plieninger et al. 2015). Severe constraints are acting, though, upon traditional land use strategies. The collapse of the communism (1989) caused a relaxation in agrarian policies, while the implementation of new agrarian policies (CAP) with joining the European Union (2007) again led to the intensification of agriculture, enlargement of crop lands, and also to the application of forbidden, but efficient, land cleaning methods, as arsenic (see Ruprecht et al. 2015), in order to meet the communitarian requirements of hayfield and pasture management. Amongst these changes, the abandonment of crop lands is generally seen as beneficial, specifically when it involves the return to the application of traditional techniques as low intensity grazing and/or haymaking (Ruprecht 2006, Fischer et al. 2012). It can be considered as a chance for animal and plant communities to return to a semi-natural state maintained by human activities.

While these processes are traditionally studied based on plant assemblages, there is a need to apply a multi-angle approach, since different organisms, e.g., mobile vs. sessile (insects vs. plants) may reveal different aspects of the same process (see Batáry et al. 2010, Sutcliffe et al. 2014).

Ants are widely used group for monitoring ecological communities because (a) ant communities are typically rich in species and functional traits (see Agosti et al. 2000), (b) they act as ecosystem engineers (Folgarait 1998, Underwood and Fisher 2006), and keystone species at local and landscape scale (Mills et al. 1993), and (c) ants are often used as indicators of the success of restoration projects programs (e.g. Majer 1996, Holec and Frouz 2005, Wiezik et al. 2010). As revealed by many studies, ant communities are influenced to a variable extent by changes in vegetation structure and composition during secondary succession (e.g. Gallé et al. 1998). By being the primary producers, plants constitute the base of any community. Thus, it is important to document the regeneration of plant communities after major disturbances, like in the case of secondary succession on abandoned agricultural lands (e.g. Prach and Pyšek 2001, Ruprecht 2005, 2006). Thus, in the frame of the current study we address the following questions: (1) How do the species composition and diversity of ant and plant communities change after abandonment of crop lands? (2) Are these changes similar between the two groups? The current study is the first to treat the effect of abandonment on ant and plant communities in parallel in Eastern Europe.

Materials and methods

Study sites

During our study, we applied the space-for-time substitution method due to the limited time frame available. Four old-fields of different ages (1-year, 8-, 16-, and 30-years old) were selected for the purpose of the study and two reference stages of semi-natural vegetation maintained by human activities, typical for the study region's cultural landscape: grassland and shrubland. The study sites were located in the surroundings of Suatu (Cluj County) in Transylvania, Romania (Fig. 1). The climate in this area is temperate continental with an average yearly precipitation of ca. 550–600 mm, and a mean annual temperature of 8.5°C (Kun et al. 2007). The natural vegetation is forest-steppe/forest (Kun et al. 2007), but at present most of the area is used for agricultural crops.

The plant community of the 1-year old field (N 46.800114, E 23.962095, 377 m a.s.l.) was characterized by short-lived species. The percentage of perennial species was low, and the vegetation cover was also low, almost 30% of the soil surface was bare.

The vegetation cover of the 8-years old field (N 46.779962, E 23.975984, 372 m a.s.l.) was substantially higher; it could reach values like 95-98%. The cover of short-lived species was still quite high in patches, but the vegetation was characterized mostly by long-lived herbaceous species

The vegetation cover of the 16-years old field (N 46.798897, E 23.957664, 371 m a.s.l.) was almost 100%, it was rich in species and most of the species were characteristic of semi-natural grasslands. The moss cover was also quite high.

The 30-years old field (N 46.776145, E 23.974281, 372 m a.s.l.), used as hayfield by the locals, had 100% vegetation cover and also high moss cover. The vegetation was rich in species.

The more than 100 years-old semi-natural grassland (N 46.798842, E 23.955521, 342 m a.s.l.) was used as low intensity grazing site for cattle by locals. The vegetation was dense and rich in species, and the field had very low amount of bare soil surface, but also low cover of mosses. The high abundance of herbs (dicotyledonous species) was characteristic.
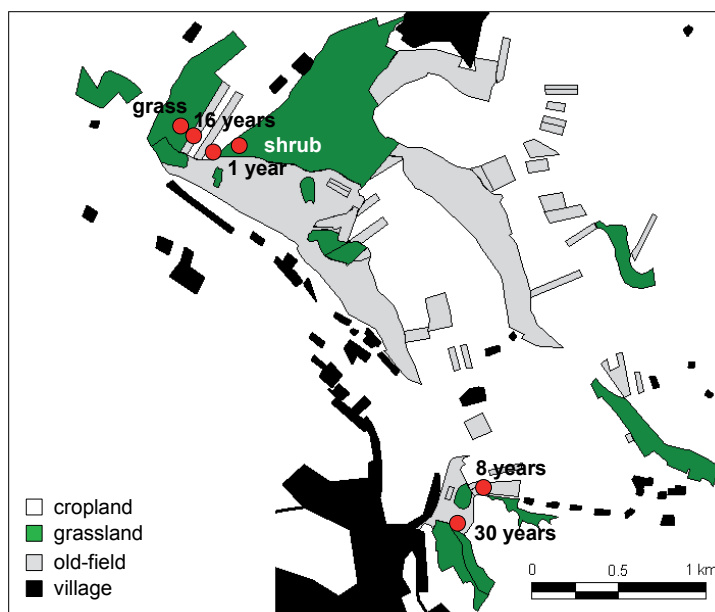

Figure 1. Detailed map of the study region according to main land use categories. Circles mark the studied old fields.

The shrubland (N 46.800945, E 23.964492, 382 m a.s.l.) can be considered as an alternative reference stage of grassland succession if the grassland is not grazed or mowed. The site sampled by us was characterized by the high cover of shrubs that altogether had 30% cover. Litter was present with high cover (37%) probably due to the entire abandonment of land use.

Sampling methods

Ant and plant communities were assessed by pitfall trap and vegetation plots. Pitfall trapping is a common and well-proven method used for the study of epigaeic ant communities (Agosti et al. 2000, Santos et al. 2007), but also for insects, generally (e.g. Magura et al. 2015). At each study site 15 traps (200 ml, 8 cm diameter), filled with ethylene glycol solution as conserving material, were placed arranged in a 3×5 grid, where each trap was separated by 5 m. Traps were active for 10 days during spring (from 14th May), summer (from 14th July) and autumn (from 14th September) in 2006. Just a few traps were destroyed during the sampling periods by grazing animals: (a) 1st period: one in the 1 year-old and 30-years old fields, and three in the 16-years old field, respectively; (b) 2nd period: one in the 8-years old field; (c) 3rd period: one at the 8-years old field, two in the 1-year old field and in the grassland, and four in the shrubland.

Randomly selected six vegetation plots of 2 m × 2 m were set up in the case of vegetation survey at each site in June, 2006. Percent cover was visually estimated for each plant species rooted in, or in the case of shrubs, overhanging each plot. We estimated the structural parameters of the vegetation as well: total vegetation cover (%), cover of bare ground (%), mosses (%) litter (%), and of woody perennials (%). We also recorded the maximum height of the vegetation (cm) around each pitfall trap in a 1 m² plot at each site.

Data analysis

Ant and plant species were classified in functional groups based on their disturbance tolerance and habitat affiliation. Ant species are frequently classified into functional groups but mostly based on their habitat affiliation or behaviour (e.g. Andersen 1997, Ottonetti et al. 2006, Bernadou et al. 2013). During our classification previous information on the Romanian (see Markó et al. 2006, Czekes et al. 2012), and generally the European (Czechowski et al. 2012) myrmecofauna was taken into consideration. Four groups have been established: disturbance-requiring, disturbance-tolerant, typical grassland and typical forest species (see Appendix 1). Plant species were classified into three groups based on Sanda et al.'s comprehensive work (1983): weeds (species of ruderal habitats), species common to ruderal and semi-natural or natural habitats, and species of semi-natural and natural habitats (see Appendix 2).

The site types were compared in terms of overall ant and plant species richness, and in terms of species richness and abundance of functional groups using Kruskal-Wallis test,

with subsequent multiple pairwise comparisons with Tukey and Kramer post-hoc test after Nemenyi (Pohlert 2014).

The diversity of ant and plant communities was expressed based on the Shannon general entropy ($\log_2$). The diversity index was calculated for each pitfall trap and vegetation survey plot, separately. The different fields were compared with Kruskal-Wallis test with subsequent Tukey and Kramer post-hoc tests. In addition, the diversity of ant and plant communities was also calculated separately for each site (site diversity further on). In the case of ants the across season average (3 periods) of the mean no. of individuals per trap per season for each site and for each species was taken into consideration (N_{ants} = 259 traps). The relationship between the site diversity of plants and ants was assessed with Spearman rank-correlation (N = 6 sites).

Data regarding the abundance of the slave-maker amazon ant (*Polyergus rufescens*) was excluded from the analyses regarding ant abundance and ant diversity, as their sometimes high number in the pitfall traps (see Results) could be attributed to seasonal slave-making raids and not to their regular epigaeic activity.

The structure of communities was analyzed with multivariate methods. In the case of ants we considered only those species which occurred with at least five specimens during the whole sampling period. Thus, *Camponotus atricolor, Myrmecina graminicola, Myrmica curvithorax*, and *Tapinoma erraticum* were excluded from the analyses, while *Polyergus rufescens* was also excluded for previously presented reasons. The abundance of different plant species was $\log_2(x+1)$-transformed prior to analysis to handle large differences within the dataset.

Differences among sites in ant and plant communities, and vegetation structure were analyzed with permutational multivariate ANOVA (perMANOVA, 5000 permutations). Individual data was used for vegetation structure and for plant communities. In the case of ants, the across season average of each ant species for each trap was taken into consideration.

The similarities between the successional pathways of ant and plant communities, ant communities and vegetation structure, and plant communities and vegetation structure were analyzed by pairwise Mantel-tests (max 1000 tries) between the Bray-Curtis distance matrices obtained separately for ant and plant communities, and vegetation structure of different sites. Non-metric multidimensional scaling (NMDS) was applied to visualize the distribution of old-fields based on ant and plant communities, and vegetation structure, respectively. For both Mantel-tests and NMDS the across season average (3 periods) of the mean no. of individuals per trap per season for each site and for each species was taken into consideration (N_{ants} = 259 traps) in the case of ants. For plants the average cover of each plant species was taken into account for each site (N_{plants} = 36 plots), while for vegetation structure the mean values for each site of recorded characters was used (N_{vegstr} = 36 plots), with the exception of the vegetation height were the the across season average (3 periods) of the mean height per sampling plot (N =15) for each site was taken into consideration.

Table 1. Distribution of ant and plant species according to functional groups in the studied old fields: total number of species and their mean abundance.

Functional groups	1-year	8-years	16-years	30-years	grassland	shrubland
Ants						
disturbance-requiring	4	4	4	5	3	3
	33.66	46.4	68.26	22.26	39.4	102.6
disturbance-tolerant	3	2	2	3	1	3
	20.16	29.83	0.25	64.25	1.66	4.08
grassland	7	7	9	7	8	9
	2.24	12.36	12.15	10.21	15.48	8.54
forest	-	-	-	-	1	1
	-	-	-	-	0.67	0.33
Plants						
ruderal	24	10	4	8	4	4
	34.48	8.6	0.33	1.3	0.26	0.86
ruderal and semi-natural/natural	10	23	22	21	19	11
	41.53	21.11	14.36	23.71	24.85	6.61
semi-natural/natural	2	29	39	44	46	56
	0.73	67.41	77.21	103.88	87.76	123.1

All statistical analyses were carried out using the R statistical environment version 2.12.0. (R Core Team 2013). Pairwise Tukey and Kramer post-hoc comparisons were performed with the PMCMR R-package (Pohlert 2014). In the case of perMANOVA and NMDS the vegan R-package (Oksanen et al. 2011) was applied, while for Mantel-tests the ecodist R-package (Goslee and Urban 2007).

Results

Changes in species number and functional groups during succession

Altogether 22 ant species were collected, most of them were frequent in all sites (see Appendix 1). The total number of ant species was almost the same in the 1-year old-field as in the shrubland, and even higher than that in the semi-natural grassland. However, the comparison of the species number/ traps yielded significant differences among fields (Kruskal-Wallis $\chi^2 = 23.66$, $P < 0.001$): the species number/trap was significantly lower in the 1-year old field than in the 8-, 16-year old field and the shrubland ($P < 0.05$), showing that there is an increase in species number/plot after abandonment.

A total of 312 plant species were identified in the study sites (see Appendix 2). Contrary to ants, the total number of plant species increased along the successional gradient, the lowest species number was identified in the 1-year old-field, while the highest number being recorded in the shrubland stage. The comparison of species number/plot yielded significant differences (Kruskal-Wallis $\chi^2 = 25.5$, $P < 0.001$): there was a significant increase in species number/plot from the 1-year and 8-years old fields to the 30-years old field and the shrubland ($P < 0.05$ pairwise post-hoc comparisons). The rest of the fields had intermediate positions in this respect, and no other significant differences were found.

There were clear differences between ant and plant communities with regards to the distribution of species among different functional groups (Table 1). The number of disturbance-requiring ant species was almost stable along the successional gradient, while their mean abundance was very high even in reference stages (e.g. *Lasius paralienus*, see Appendix 1, Table 1), and only a slight increase was registered in the total number of typical grassland species, which were registered in low abundance throughout the successional gradient. On the contrary, clear trends were revealed in plants: the total number and abundance of weed species decreased along the successional gradient, while that of semi-natural and natural habitat species increased (Table 1).

The analysis of the detailed datasets, where the number of ant species/trap was considered yielded significant differences among fields for all functional groups (Kruskal-Wallis $\chi^2 \geq 22.41$, $P < 0.001$) with the exception of forest species. However, pairwise post-hoc comparisons did not reveal any clear trends. In the case of disturbance requiring ant species, significant differences were discovered only in the case of shrubland, which contained significantly more such species, than the 16- and 30-years old fields and the grassland ($P < 0.05$ pairwise post-hoc comparisons). For disturbance tolerant ant species, significant differences were found at the 16-years old field, which contained significantly less such species than the 8-, and 30-years old fields ($P < 0.05$), the same being valid for the comparison of grassland and 30-years old field as well ($P < 0.01$). Typical grassland ant species, as expected, were significantly less numerous in the 1-year field than in all other fields ($P < 0.001$) with the exception of the 30-years field, which contained even lower species number than the 16-year field as well ($P < 0.05$).

A clear-cut pattern was detected in the case of the detailed analysis regarding number of plant species/plot. Significant differences were registered among fields for all functional groups (Kruskal-Wallis $\chi^2 \geq 20.6$, $P < 0.001$ for all groups), and the number of species of semi-natural and natural habi-
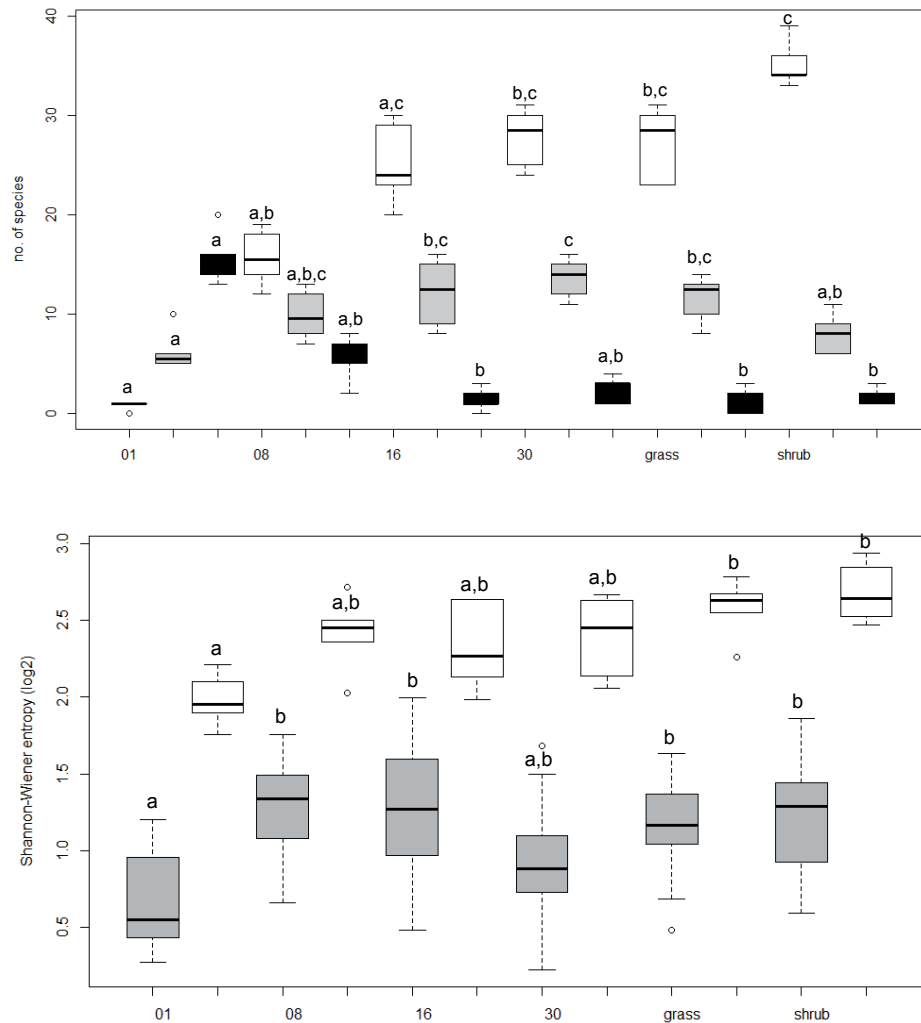
Figure 2. Distribution of the number of plant species/ plot according to functional groups along the successional gradient (black – weed, gray – natural + weed, white – natural).

Figure 3. The diversity of ant and plant communities along the successional gradient of old fields (grey – ants, white – plants).

tats/plot constantly grew along the successional gradient, while the number of weed species/plot decreased (Fig. 2).

Diversity and community structure

Significant differences were detected both in the case of ant and plant communities with regards to Shannon diversity (Kruskal-Wallis $\chi^2 \geq 18.49$, $P < 0.01$; Fig. 3). There was a significant increase in the diversity of ant communities after the 1-year stage, which differed from every other stage in this respect ($P < 0.05$) with the exception of the 30-years old field. In the case of plant communities significant differences were revealed only between the 1-year field and the two reference stages ($P < 0.01$). Generally, ant and plant communities differed from each other in this respect: no correlation was found between the overall diversities of ant vs. plant communities (Spearman R = 0.6, P = 0.24).

The structure of ant communities differed significantly among sites (perMANOVA F = 5.84, R^2 = 0.25, P < 0.001), as well as the composition of plant communities (perMANOVA F = 2.36, R^2 = 0.37, P < 0.01), and the structure of vegetation (perMANOVA F = 2.56, R^2 = 0.13, P < 0.01). In the case of the ant communities, the 1-year, the 30-years stage and

the shrubland seemed to differ slightly from the rest (Fig. 4), whereas in the case of the plant communities the 1-year stage definitely separated from the rest of the stages (Fig. 5). The patterns of ant and plant community development were clearly different (Mantel-test, Pearson r = 0.36, P = NS; Figs. 4-5), and there was no resemblance in the changes of ant communities and the changes registered in vegetation structure either (Mantel-test, Pearson R = 0.44, P = 0.08; Figs. 4, 6). As expected though, successional stages and reference stages were grouped in a similar manner according to the plant communities and vegetation structure (Mantel-test, Pearson R = 0.78, P = 0.004; Figs. 5-6). The 1-year stage is characterized by the bare ground cover, while the older sites are determined by the moss cover, the vegetation cover and the height of the vegetation. The separation of the shrub-land site is determined by the high abundance of woody perennials (Fig. 6).

Discussion

Major changes have been registered in the land use strategies in Eastern Europe in the past decades after the fall of the communism due to the sudden disruption of centralized agricultural activities and the reinstatement of former small

Figure 4. NMDS graph of the study sites based on ant species abundance (stress = 0.01). (Abbreviations: 1 – 1 year, 8 – years, 16 – 16 years, 30 – 30 years, grass – grassland, shrub – shrubland, ant species see in App. 1.).
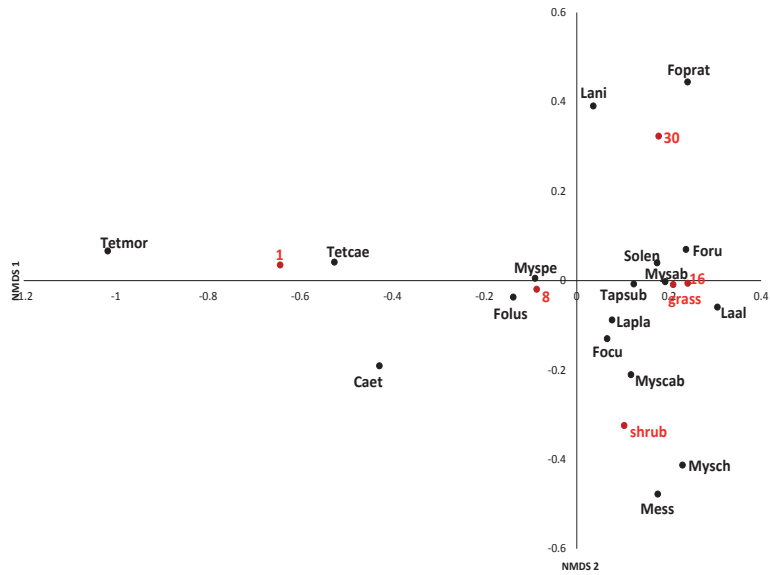
Figure 5. NMDS graph of the study sites based on plant species cover (stress = 0.0001). (Abbreviations: 1 – 1 year, 8 – years, 16 – 16 years, 30 – 30 years, grass – grassland, shrub – shrubland).
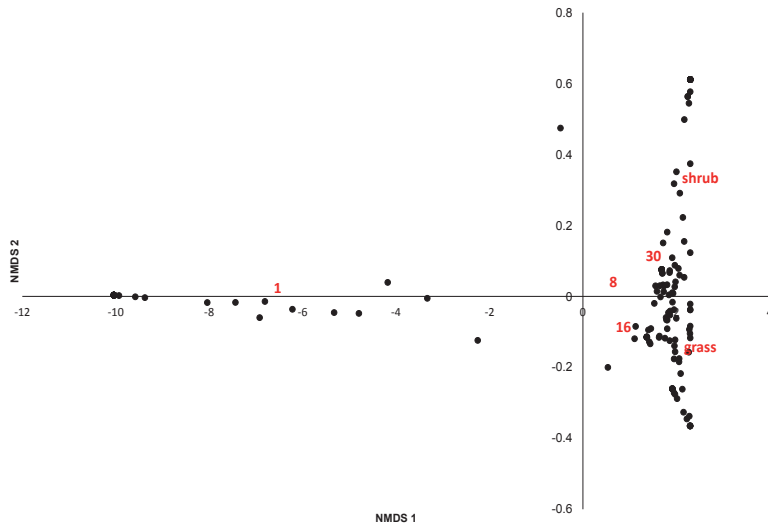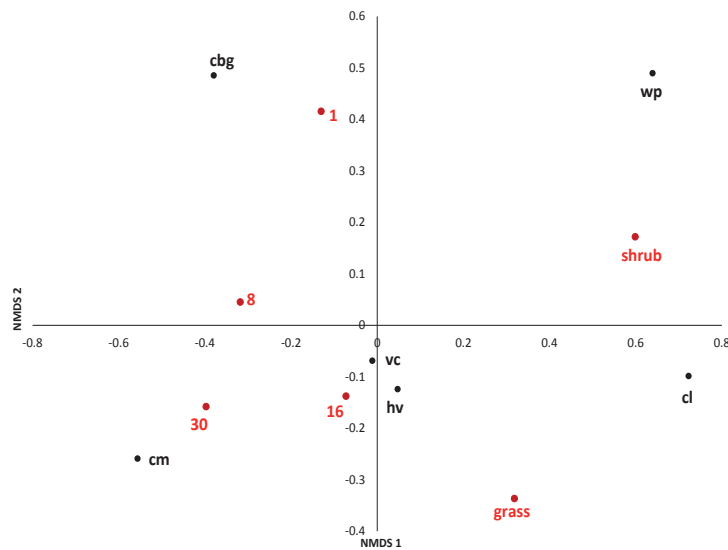
Figure 6. NMDS graph of the study sites based on the vegetation structure (stress = 0.001). (Abbreviations: 1 – 1 year, 8 – years, 16 – 16 years, 30 – 30 years, grass – grassland, shrub – shrubland, vc – vegetation cover, cbg – cover of bare ground, cm – cover of mosses, cl – cover of litter, wp – cover of woody perennials, hv – height of the vegetation).

ownerships. These implied mostly the abandonment of previously applied management techniques, and ultimately the abandonment of significant proportions of croplands, which then offered the chances of recovery for plant and animal communities (e.g. Ruprecht 2006, Tryjanowski et al 2011). This natural experimental setup makes possible the study of succession processes in order to validate or invalidate the generality of the expected return-to-natural-state pattern after cessation of the disturbance. The results of our study show that: (a) the ant fauna is relatively poor and it is dominated throughout the succession by disturbance requiring and tolerant species, while (b) the number of plant species is high and there is an increase in the number and abundance natural habitat species, thus (c) ant and plant communities do not follow the same pattern throughout the succession.

The number of ant species identified (22) during our survey indicates a relatively poor fauna compared to the more than 110 ant species known in Romania (e.g. Markó et al. 2006, Czekes et al. 2012). However, it is similar to the ant fauna of other temperate grasslands (Dauber and Wolters 2005, Englisch et al. 2005). Contrary to expectations, and to similar studies performed on ant community succession (e.g. Majer 1996, Gallé et al. 1998) the overall species number did not increase along the successional gradient, only the number of species/plot, which indicates that there is a homogenization in the spatial distribution of ant species during succession. Similar pattern was detected in other grassland ant communities as well (Dauber and Wolters 2005, Englisch et al. 2005). Opportunists characterize mostly the first phase of the succession (Dauber and Wolters 2005, Gallé et al 1998, Ottonetti et al. 2006) however, in our case, their quantitative dominance did not diminish at all, thus invalidating the return-to-natural-state scenario.

Contrary to ants, the total number of recorded plant species in the study sites was quite high (312 species), as the regional grassland species pool is also high (see e.g. the reported world records of species richness in Transylvanian grasslands by Wilson et al. [2012]). The number of species, and specifically that of natural habitat species, increased along the successional gradient as found in previous studies as well (e.g. Ruprecht 2005, 2006).

In light of these differences it is not surprising that overall changes in the ant community are not correlated with compositional changes in plant community throughout succession. Not even alterations in the structural properties of the vegetation seem to be connected to ant community succession patterns, whereas usually changes in vegetation during succession affect ant community transformations through their structural changes (e.g. Gallé et al. 1998), but also in other insects, as e.g. orthopterans (Baur et al. 2006, Sutcliffe et al. 2014).

Dispersal limitation was demonstrated to be the most important factor influencing the success of spontaneous succession and restoration programs in various grassland habitats in most of Europe and worldwide (Molnár and Botta-Dukát 1998, Stampfli and Zeiter 1999). Biodiversity in arthropods, or its simplest proxy, the species number, is not independent

of landscape context, but it is strongly dependent on patch size, patch connectivity and other landscape structural features (e.g. Gallé and Torma 2009, Rosenthal 2010), which could be valid in our specific case as well. However, in ants only the 1-year stage differed from the others in almost every aspect, whereas all other stages were quite similar irrespective of age, or other features, suggesting the stability of revealed patterns. In plants, the success of grassland species in colonizing abandoned croplands has been found to be affected by their frequency in the landscape (Ruprecht 2006). Thus, availability of propagules has a strong influence on the recovery success of old-fields. If former grasslands are farmed only for several years, diaspores of some grassland plants can persist in the seed bank and germinate after farming ceases (Jongepierová et al. 2004). However, after a longer farming history, soil seed bank may be depleted in grassland species and contains mainly the diaspores of weed or generalist species. Thus, in such cases, the regeneration of seminatural vegetation cannot rely on seed bank stores (e.g. Matus et al. 2003). In the case of ants, the life of propagules, that is young inseminated gynes, is ephemeral, and even in normal conditions their colony funding success is very low (ca. 2%) (Hölldobler and Wilson 1990). Therefore those ant species that are already present in the surrounding areas have higher chances of successfully colonizing abandoned areas. Given the fact that the most abundant ant species, which is also disturbance-requiring, *Lasius paralienus*, is also an aggressive species, thus competitively superior to many ant species it is not surprising that other ants have slim chances of displacing it.

We expected that after land abandonment similar return-to-natural-state-like processes would occur in the case of ants and plants. Nevertheless, the fact that these two different communities are linked only by loose connections, where ants react mostly to changes occurring in the structural properties of vegetation and not to species specific changes (Dauber and Wolters 2005), already predicts the existence of potential discrepancies with respect to community level responses (Dauber and Wolters 2005, Sutcliffe et al. 2014). While in the case of plants a certain recovery is revealed, ants differ in this respect, and disturbance-requiring species still dominate quantitatively even at potential end stages. It is important to admit that ant communities do not follow the steps of the plant communities' succession and they do not show the same characteristics in all cases even in temperate grasslands (Dauber and Wolters 2005, Englisch et al. 2005). The inclusion of more replicates from the same age category would have yielded probably a more accurate picture. However, since the patterns observed in plants are confirmed by previous studies on similar topics from the same region (e.g. Ruprecht 2005, 2006), while with the exception of the differences registered in 1-year old stage there are no trends detectable in the case of the ant communities, we think that more replications would not likely change the outcomes of our study.

Over centuries, the practice of traditional farming maintained a biodiversity, that now needs active support to be sustained (e.g. Plieninger at al. 2015, Fischer et al. 2012). As

lately revealed, the current intensification of agriculture has a net negative effect on many different organisms (Baur et al. 2006, Batáry et al. 2010, Tryjanowski et al. 2011, Csergő et al. 2013, Sutcliffe et al. 2014). It is important to acknowledge that increasing mosaicity, and patch connectedness within a cropland 'sea' could ensure the successful recolonization of temporarily abandoned land stripes with natural species, particularly in ants, and generally in arthropods. Ultimately, the findings of our study draw attention to the existence of quite large differences between changes in vegetation and ant, or implicitly arthropod, communities after land abandonment, which should be considered when evaluating the recovery success of old fields solely on the basis of vegetation during nature conservation actions.

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Electronic supplements

Appendix 1. List of identified ant species, their classification according to functional groups, and average number of individuals for each study site.

Appendix 2. Identified plant species on the study sites with their mean cover (%), and their classification into functional groups.

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