Original investigation

Responses of small mammal communities to environment and agriculture in a rural mosaic landscape

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ABSTRACT

Intensification of agriculture is an increasing threat for biodiversity. Central Romania still preserves a traditional rural landscape with a matrix of small plots of crops and large surfaces covered by grasslands and forests, but its biodiversity is very poorly studied. Small mammals are key components of agrarian and semi-natural ecosystems but rodents are also viewed as major pests. Knowledge of the driving factors of small mammal communities in agricultural landscapes may enable taking management measures that pursue both conservation and economic goals. Here we evaluate the response of small mammals to environmental variables, including vegetation characteristics, land use and geographic position. We conducted live trapping between June and October in habitats with different environmental characteristics and land uses. We found that vegetation traits were the most important factors influencing small mammal communities. Species composition was shaped mainly by tree cover, shrub cover had strong effects on community diversity and abundance, while the height of the herbaceous layer significantly influenced all the parameters. Among the agrarian land uses maize crops stood out for the abundance of mice, especially *Mus musculus*, and hayfields for *Microtus arvalis*. Land fallowing was linked to the increase of diversity and total abundance to the maximum values but did not significantly alter species composition. Species with low tolerance to tree cover were more prone to be abundant in agricultural lands, whereas the habitat generalists prevailed in non-agrarian lands. Our results suggest that preservation of the mosaic of farmed and semi-natural habitats and actions targeted for vegetation management, such as interspersing woody vegetation in the crop matrix and mowing the herbaceous vegetation in semi-natural habitats adjacent to crops, may together achieve the balance between biodiversity conservation and crop protection.

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Introduction

Turning grasslands and forests into arable land for the expanding needs of agriculture is a main cause of habitat loss and biodiversity impoverishment. Further, the mechanization, intensification and expansion of modern agriculture are increasing threats to biodiversity worldwide (Michel et al., 2006; Panzacchi et al., 2010). The modern methods have meant an increase in field size and monoculture methods; reduction of grassy field margins, hedgerows and tree-rows; increased mechanization; heavy use of herbicides and pesticides and a general reduction of permanent vegetative cover (Burel and Baudry, 1990; Robinson and Sutherland, 2002; Stoate et al., 2001). As a result, wildlife on farmland has declined all over Europe (Butler et al., 2007, 2010; Green et al., 2005).

The effects of agricultural land management on wildlife are relatively well studied in Western Europe (Robinson and Sutherland, 2002; Butler et al., 2010; Butet et al., 2006), but by comparison little research has been conducted during the past 25 years on the wildlife diversity on agricultural landscapes of Eastern Europe, and especially in Romania, Bulgaria and Croatia (Sutcliffe et al., 2015). Most small mammal studies conducted in Central Europe were undertaken some years ago and do not reflect recent changes in crop and landscape composition; hence, little information is available for small mammals in fallow fields (Janova and Heroldová, 2016) or in mosaic agricultural landscapes.

Unlike other parts of Europe affected by the agricultural intensification leading to habitat loss of semi-natural habitats and expansion of monocultures, central Romania presents high landscape heterogeneity. Large areas are still covered with pastures and forests, and arable land is still a mosaic of small crop fields. Following the political changes in 1989, most of the land was returned to former owners who cultivate different crops on small plots (frequently less than a hectare). The small size of crop fields favoured

the persistence of traditional farming methods. However, the economic inefficiency of this agricultural system has resulted in a high level of field abandonment and an increase in the frequency of fallow fields.

Hedgerows are important for preserving diverse small mammal communities in Western Europe (Michel et al., 2007), but in Romania they are absent. In our study area forest patches are connected by riparian forests and the shrubby vegetation along the ditches separating the fields. Roads, ditches and fields are bordered by unmown margins with medium to tall herbaceous vegetation. These semi-natural habitats act as dispersal corridors, which promote connectivity between patches, colonization and population maintenance (Fischer and Lindenmayer, 2007; de Redon et al., 2015), and thus are important for maintaining biodiversity (Ernoult et al., 2013). Moreover, these habitats are refuges for burrowing herbivores, such as *Microtus* voles (Rodríguez-Pastor et al., 2016).

Although the repeated agricultural activities of ploughing, sowing, cultivating and harvesting produce continual changes, farmland provides good food resources for many species during most of the growing season (Kozakiewicz and Kozakiewicz, 2008). Because most small mammals (rodents) are usually considered as pests, causing significant damage to agricultural products, they are seldom the focus of biodiversity studies (Butet et al., 2006). The increasing understanding of their ecological importance and their key roles in the energy flow through the ecosystem has led to recent studies on small mammal communities in agrarian ecosystems and their responses to environment factors (Bonnet et al., 2013; Fischer and Schröder, 2014; Gentili et al., 2014; Jareño et al., 2015; Michel et al., 2006, 2007; Rodríguez-Pastor et al., 2016). However, in Central and Eastern Europe such studies are still few in number (Heroldová et al., 2007; Janova and Heroldová, 2016).

Unveiling the factors that determine the distribution of species is one of the key objectives of ecological studies. In addition, a better understanding of the places in the agricultural landscape where the different small mammal species are most abundant would provide important information for more targeted management, biodiversity conservation and pest control. Our study focused on the relationships between the communities and the habitat characteristics in a typical forest-agricultural landscape in central Romania. Our aim was to answer the following questions: (1) which factors shape the structure, abundance and diversity of small mammal communities in rural mosaic landscapes? (2) do the habitat factors drive significant seasonal changes (from summer to autumn) in community composition? (3) what are the effects of agricultural land use and fallowing? (4) is the tolerance of habitat conditions by small mammals related to their preferences of different land use types?

Study area and methods

Landscape description and metrics

Our survey was conducted in the Hârtibaciu Plateau, southern Transylvania (Romania), between 45°56.190′ – 46°02.759′ N and 24°27.460′ – 24°46.040′ E. The research area is a highly patchy landscape, characteristic for this region (Appendix 1, Fig. A1a), and is part of the special protection area ROSPA0099 Hârtibaciu Plateau, designated under the European Union Directive on the Conservation of Wild Birds.

Crops, mostly cereals (maize and wheat) and alfalfa, covered between 2% and 34% of the open land surface in different parts of our study site. Maize is sown in widely spaced rows, often invaded by weeds. In some plots weeds are removed mechanically or by hand, in some herbicides are used, while others are left weedy (Appendix 1, Fig. A1b). Land fallowing induces significant changes in the vegetation, favouring the establishment of invasive species such as *Solidago canadensis, S. gigantea* and *Erigeron annuus* (Appendix 1, Fig. A1c), widespread on wet habitats along rivers and ditches. In our study area fallow lands commonly present tall vegetation throughout summer and autumn. Hayfields are mown 2–4 times a year at 5–6 weeks interval, beginning in June, and are used only for hay production; there is no aftermath grazing. Traditional mowing using the scythe is still done, especially in smaller hayfields. Field boundaries are represented by road verges, grassy field margins and ditches with tall hygrophilous vegetation. Pastures cover the largest surface among the open habitats and have low vegetation, often being overgrazed. Where the ligneous plants are not removed, pastures are quickly invaded by shrubs and trees (Appendix 1, Fig. A1d), inducing a secondary succession to broadleaf forests. Broadleaved (mainly oak and hornbeam, beech in the highest areas) forests are well represented in our study area, covering especially the hill tops. Most forests are connected or nearly so, with few isolated fragments.

Survey methods

The traps were set in lines within a single habitat, to avoid intersecting ecotones. For each trap line the following environmental variables were estimated: percentages of cover for the layers of trees, shrubs and herbs (each log-transformed by the relation $y' = \log(y + 1)$), height (cm) of herbaceous layer, distances (km) to forest edge, water (river or creek) and nearest village (log-transformed by the relation $y' = \log(y*100 + 1)$), altitude (m) and slope (°). The descriptive statistics of these environment variables in the trap lines are given in Table 1.

Soil moisture, habitat surface and degree of disturbance are considered as ordinal variables with soil moisture being evaluated based on the vegetation structure: 1-xeromesophilous, 2-mesophilous, 3-mesohygrophilous, 4-hygrophilous. Surfaces of the surveyed habitats were coded as: 1-small (less than 0.5 ha), 2-medium (between 0.5 and 1 ha), 3-large (more than 1 ha). Disturbance categories were: 0-none, 1-low, 2-medium, 3-high (mainly overgrazing). Agricultural land use was included in the multivariate analyses as factor variable with seven levels: maize, wheat and alfalfa crops, fallow field, hayfield, pasture and non-agricultural terrains. For univariate analyses we considered the crops together. Season (summer or autumn) was also considered as a factor

Table 1

Descriptive statistics of the quantitative environmental variables in the 103 surveyed habitats. 95% CI Lower and 95% CI Upper are the lower and upper 95% confidence limits of the mean.

	Tree cover (%)	Shrub cover (%)	Herb cover (%)	Herb height (cm)	Distance to forest (km)	Distance to water (km)	Distance to village (km)	Altitude (m)
Minimum	0	0	0	0	0	0	0.2	410
Maximum	95	100	100	150	2.0	2.7	3.5	650
Mean	9.9	9.4	84.9	39.3	0.41	0.61	1.74	475.1
95% CI Lower	5.2	5.9	79.1	32.5	0.32	0.48	1.56	466.3
95% CI Upper	14.6	12.9	90.8	46.0	0.50	0.74	1.91	483.9
Standard Deviation	24.3	18.1	30.3	34.8	0.45	0.68	0.89	45.5

variable. Geographical position (latitude and longitude) of each transect was determined by the position of the centremost trap.

Small mammal trapping

We live-trapped small mammals using artisanal single-catch plastic box-traps ($18 \times 8 \times 6$ cm). Each transect included 30 traps placed at intervals of 10 m. We baited traps with sunflower seeds and apple slices and left them open for three consecutive nights; we checked the traps twice a day, in the morning and at dusk. No prebaiting was done. We conducted the trapping between June and October in 2010 and 2011, and in October 2014. We surveyed 81 sites and because the habitat types were very unequally represented in the studied landscape we had different sample sizes (crop: n = 11, fallow: n = 5, hayfield: n = 16, pasture: n = 23, non-agricultural land: n = 26). The habitats were randomly trapped across the study period. To trace the seasonal changes in the small mammal communities in relation to the changes in the environment, in 2011 we investigated 22 sites (crop: n = 4, fallow: n = 2, hayfield: n = 3, pasture: n = 8, non-agricultural land: n = 5) twice, at a two-month interval. Thus, we set in all 103 trap-lines, resulting in 6060 trap-nights (of which 4400 in agricultural habitats). This trapping effort was calculated as the number of lines (103) multiplied by the number of traps per line (30) and the number of sampling nights (3), excluding the number of non-functional traps (3210). The high number of non-functional traps was due to weather, animal or human disturbance. We identified the captured animals to species based on morphological and biometrical traits, temporarily marked them by fur clipping, and then released each individual at its trapping site. Recaptures were not considered in analyses.

Data analysis

We used abundance and diversity as community metrics. Abundance was expressed as a capture index, i.e. the number of captured animals per 100 functional trap-nights. The sum of the capture indices for all the species in a trap line was the total abundance. We used as measures of assemblage diversity species richness, expressed by the number of species captured per trap line, and heterogeneity, expressed by Shannon index (Magurran, 2004).

The variation of small mammal communities in relation to environmental factors was analysed using Canoco 5 software (ter Braak and Šmilauer, 2012). An indirect gradient analysis, the detrended correspondence analysis (DCA), was first performed to establish the length of the gradients. The length of the longest gradient provides an estimate of the beta diversity in the data set (Šmilauer and Lepš, 2014) and suggests the use of either linear or unimodal ordination methods. For our data set a unimodal method, the canonical correspondence analysis (CCA), was appropriate to investigate the relationships between environmental variables and the capture index of small mammals. Because results based on captures by single-catch traps are biased in favour of common species, especially at high densities (and in several transects trap occupancy reached 100%), the six species with the lowest frequency, captured in less than four transects, were excluded from the multivariate analyses. Species abundance values were log-transformed by the relation $y' = \log(y + 1)$ in order to reduce the range of the data set and transform the multiplicative scale into an additive one. A comparison between constrained and unconstrained analysis was performed in order to compare the overall variation in species composition with the fraction of variation explained by environmental variables. We used the variation partitioning procedure to assess and compare the explanatory importance of the habitat characteristics and the land-use. To test the significance of the effects of environment when partialling out the spatial patterns due to autocorrelation we did variation partitioning of the space (geographical

coordinates) and environment predictors using the principal coordinates of neighbour matrices (PCNM) method (Šmilauer and Lepš, 2014).

Interactive forward selection was applied to choose a parsimonious set of predictors for the CCA. The first variable selected was that with the highest simple term effect (i.e., the independent effect of each environmental factor). Subsequently, the environmental variables were included in order of the magnitude of their conditional term effect (i.e., their contribution to the cumulative effect), having previously estimated their significance, transformed into False discovery rate values to correct for the Type I error inflation. Significance of ordination axes was tested by the Monte-Carlo permutation test with 999 unrestricted permutations per each test. To test the dependence of the temporal changes in species composition on the environmental variables we adopted a linear ordination method, i.e. redundancy analysis (RDA) of repeated observations based on the 22 trap-lines that were doubly surveyed (because several trap-lines were empty in summer, but not in autumn). We used the interactions between time (season) and environmental factors as explanatory variables and the season and transect ID as covariates (Šmilauer and Lepš, 2014).

We assessed habitat specialisation based on species tolerance, i.e. a measure of ecological amplitude (ter Braak and Looman, 1995), to the environmental factors that significantly shaped the species composition. The relationship between specialisation of small mammals and their abundance in agricultural lands was tested by RDA, using land use as a predictor and community-weighted means of tolerances to the environmental factors as response variables.

We explored the relationships between total abundance, species richness and heterogeneity as dependent variables and the habitat factors, as independent variables, through the Generalized Linear Model analysis. We used the Akaike Information Criterion corrected for small samples (AICc) to select the best multiple models. Regression analyses were performed using STATISTICA 13 software trial version (Dell Software, 2015).

We tested for differences of the small mammal community indices (total abundance, species richness, heterogeneity and abundance of dominant species) between summer and autumn using the paired *t*-test. We performed the Shapiro-Wilk normality test for the differences between pairs (McDonald, 2014). The values of capture index for the dominant species were not normally distributed even after the log-transformation, so we used the Wilcoxon matched-pairs signed-rank test. The differences in the small mammal assemblages related to the agricultural land use were tested by one-way ANOVA or the nonparametric Kruskal-Wallis test.

Results

Trapping results

Total captures counted 1393 small mammals belonging to 18 species: 5 shrews (48 individuals: 3.4%) and 13 rodents (1345 specimens: 96.6%): common shrew - *Sorex araneus* Linnaeus, 1758, pygmy shrew - *S. minutus* Linnaeus, 1766, water shrew - *Neomys fodiens* (Pennant, 1771), bicoloured shrew - *Crocidura leucodon* (Hermann, 1780), lesser white-toothed shrew - *C. suaveolens* (Pallas, 1811), hazel dormouse - *Muscardinus avellanarius* (Linnaeus, 1758), edible dormouse - *Glis glis* (Linnaeus, 1766), bank vole - *Myodes glareolus* (Schreber, 1780), montane water vole - *Arvicola scherman* (Shaw, 1801), common vole - *Microtus arvalis* (Pallas, 1778), pine vole - *M. subterraneus* (de Selys-Longchamps, 1836), harvest mouse - *Micromys minutus* (Pallas, 1771), striped field mouse - *Apodemus agrarius* (Pallas, 1771), yellow-necked mouse -

Table 2
Simple and conditional term effects of the environmental variables on small mammal communities computed by the forward-selection in the CCA. P (adj.) is the adjusted probability expressed as False discovery rate values.

| Simple Term Effects:				Conditional Term Effects:			
Variable	Explains%	pseudo-F	P (adj.)	Variable	Explains%	pseudo-F	P (adj.)
% Tree cover	10.4	10	0.001	% Tree cover	10.4	10	0.004
Dist. forest	9.7	9.3	0.001	% Herb cover	4.1	4.1	0.012
Altitude	6.8	6.3	0.001	Herb height	3.9	4	0.004
% Shrub cover	5.4	5	0.001	Dist. forest	3	3.2	0.004
% Herb cover	4.8	4.3	0.001	Moisture	2.3	2.5	0.022
Moisture	4.1	3.7	0.001	Surface	2.2	2.4	0.019
Herb height	3.8	3.4	0.002	Dist. water	1.3	1.5	0.213
Surface	3.7	3.3	0.001	Dist. locality	1.3	1.5	0.213
Disturbance	3.5	3.1	0.001	Disturbance	1	1.1	0.519
Dist. locality	2.9	2.6	0.004	Altitude	0.9	1	0.564
Dist. water	1.8	1.6	0.129	Slope	0.7	0.8	0.666
Slope	1.4	1.2	0.284	% Shrub cover	0.2	0.2	0.988

A. flavicollis (Melchior, 1834), wood mouse - *A. sylvaticus* (Linnaeus, 1758), pygmy field mouse - *A. uralensis* (Pallas, 1811), house mouse - *Mus musculus* Linnaeus, 1758 and brown rat - *Rattus norvegicus* (Berkenhout, 1769). In the agricultural habitats we captured 888 individuals belonging to 14 species. Overall, the prevailing species were *M. arvalis* (representing 45.2%, SE = 1.33 of captures) and *A. agrarius* (26.2%, SE = 1.17). Dominant species varied among habitats: *A. flavicollis* in forests (it was the only species captured in three of the seven forest trap-lines), *A. sylvaticus* in a reed bed (86.6%, SE = 8.95), *S. araneus* in a forest margin with a rich shrubby layer (46.4%, SE = 9.41) and *M. musculus* in the maize crop in the vicinity of a farm (75%, SE = 21.6 in summer, 54.5%, SE = 15.0 in autumn).

Effects of the environmental variables on species composition

The DCA revealed a relatively high species turnover along the environment gradients, the length of the longest axis being 4.03. The environmental variables we selected were good predictors of the species composition; the comparison between constrained and unconstrained analyses showed a high efficiency of the first and third constrained axes. These axes summarized 80.7% and 78.8%, respectively, of the variation explained by the homologous unconstrained axes.

The simple and conditional effects of the habitat characteristics on the small mammal community are summarized in Table 2. All the environment predictors except the distance to the closest water body and slope had significant effects on species composition. Tree cover was the most informative factor, explaining 10.4% of the variability. Surface was not included in the final model because the adjusted percentage of explained variation would have exceeded the threshold based on a model including all predictors.

The selected habitat characteristics explained 23.7% of the total species variation, the adjusted explained variation being 19.1%. The first three constrained axes were significant, having an explanatory power of 12.57% (p = 0.001), 4.77% (p = 0.001) and 3.92% (p = 0.004), respectively. The first canonical axis of the CCA was defined by tree cover and distance to forest edge (Fig. 1). Along this first axis, *M. glareolus* had its optimum in habitats with the highest tree cover, *M. avellanarius*, *A. flavicollis*, *S. araneus* and at a lesser extent *C. leucodon* had similar but more intermediate positions, whereas all the other species were characteristic of open habitats situated farther from forests. The t-value biplot (Appendix 2, Fig. A2a) showed that *M. glareolus, A. flavicollis* and *S. araneus* had significant positive responses to the tree cover, but only *M. arvalis* had a significant negative response. The second ordination axis was correlated with moisture and height of herbaceous vegetation, most species being positively correlated with them. *Microtus subterraneus* showed the strongest positive relationship with these factors, its response being significant, while *C. leucodon, A. flavi-*
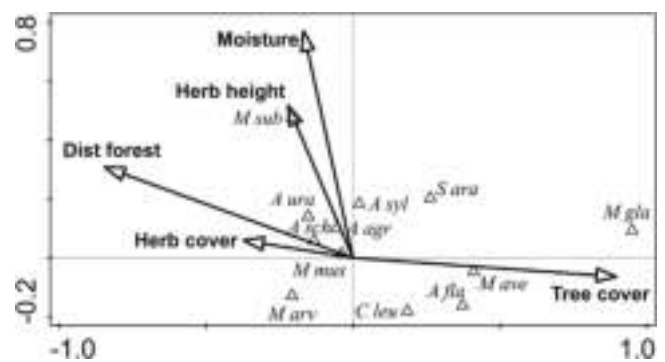
Fig. 1. The species–environment biplot of CCA with the environmental variables selected by the interactive forward selection procedure.

collis and *M. arvalis* were predominant in drier habitats with short vegetation. The characteristics of the herbaceous layer (cover and height) defined the third constrained axis. Along this gradient there was a gradual change in species composition, with *A. scherman, M. subterraneus* and *M. arvalis* reaching their highest abundances in rich herbaceous vegetation and *M. musculus* having its optimum in opposite (poor cover) conditions. *Microtus arvalis* had a significant positive response to the cover of herbaceous layer, while for *M. glareolus* the response was negative (Appendix 2, Fig. A2b).

The habitat characteristics alone had a contribution to all of the adjusted variation in species composition of 11.3% (F ratio = 3.4, p = 0.001). The overlap in the explanatory power (7.8%) between habitat characteristics and land use was higher than the contribution of land use alone (4.1%, F ratio = 1.7, p = 0.014). On a per-variable basis, the habitat characteristics were twice as strong predictors (mean square = 0.081) compared to the land use (mean square = 0.041).

The significant spatial predictors (eigenvectors) were the first three principal coordinates analysis (PCO) axes. Space accounted for only 6% of the adjusted variation (mean square = 0.07, F = 3.3, p = 0.001), but the environmental predictors explained 17.6% (mean square = 0.11, F = 5.1, p = 0.001). The shared proportion of the variation in the small mammal community that could be accounted for by either of them was negligible (1.5%).

Height of herbaceous vegetation and shrub cover were included in all the best multiple linear models for community abundance and diversity (Table 3).

Variation between summer and autumn

In the 22 habitats that we surveyed both during summer and autumn we trapped 519 small mammals (45.6% *M. arvalis* and 22.5% *A. agrarius*). The increase in the abundance from

Table 3
Best multiple linear models ($\Delta_i < 2$) for the synthetic community parameters (total abundance – TA, species richness – S and Shannon index – H) according to Akaike Information Criterion (AIC) corrected for small samples (AICc). Δ_i is the difference between the AIC of the best fitting model and that of model i and w_i is the Akaike weight for model i.

Model	df	AIC	AICc	Δ_i	w_i
Response: TA					
Shrub cover, Herb height	2	940.2	940.6	0	0.375
Shrub cover, Herb height, Dist water	3	940.5	941.1	0.453	0.299
Herb height	1	941.9	942.1	1.534	0.174
Herb height, Dist water	2	942.0	942.4	1.817	0.151
Response: S					
Dist forest, Shrub cover, Herb height, Surface	4	365.3	366.1	0	0.673
Dist forest, Shrub cover, Herb height	3	367.0	367.7	1.518	0.315
Response: H					
Dist forest, Shrub cover, Herb height, Surface	4	125.4	126.3	0	0.648
Dist forest, Shrub cover, Herb height	3	127.7	128.3	1.995	0.239

summer (mean = 11.33 individuals/100 trap-nights, SE = 3.01) to autumn (mean = 20.41 individuals/100 trap-nights, SE = 4.49) was marginally significant (t = 2.026, df = 21, p = 0.056). The number of species was also higher but only with a marginal trend toward significance (t = 1.864, df = 21, p = 0.076), while the increase in H-index was not significant (p = 0.449). The abundance of *A. agrarius* was higher in autumn (Z = 2.135, p = 0.033), while for *M. arvalis* the increase in the capture index was not significant (Z = 0.966, p = 0.334). This resulted in a drop in relative abundance of *M. arvalis*, from 50.9% (SE = 3.8) in summer to 43.2% (SE = 2.6) in autumn, in favour of *A. agrarius,* increasing from 16.8% (SE = 2.8) to 25.3% (SE = 2.3).

The changes in species composition from summer to autumn were significant (pseudo-F = 2.7, p = 0.040). Season accounted for 7.4% of the adjusted explained variation, with the seasonal changes being dependent on the environment variables. Herbaceous cover, tree cover and humidity together had a significant effect on the changes in species composition (test on all axes: pseudo-F = 3.4, p = 0.026) and explained 31.3% of the adjusted partial variation. For most species except *A. scherman* and *P. subterraneus*, but especially for the dominant *M. arvalis* and *A. agrarius*, the population increase during autumn was correlated with high herbaceous cover.

Influence of land use

Abundance and diversity were significantly correlated (species richness r = 0.613, p < 0.001, H-index r = 0.516, p < 0.001); the most favourable habitats supported high numbers of species and also of individuals (Fig. 2). There was a significant difference between the agricultural (total abundance: mean = 20.7, SE = 2.53, species richness: mean = 1.97, SE = 0.15, H-index: mean = 0.4, SE = 0.04) and the non-agricultural (total abundance: mean = 33.1, SE = 2.54, species richness: mean = 3.38, SE = 0.18, H-index: mean = 0.8, SE = 0.05) habitats in respect to all the considered parameters (t = 2.238, df = 101, p < 0.001 for the total capture index, t = 3.933, df = 101, p < 0.001 for the number of species, t = 3.859, df = 101, p = 0.027 for H-index).

For the different agricultural land uses (crop, fallow, hayfield, pasture) the ANOVA also indicated significant differences in the community parameters: total abundance (F = 4.911, df = 3, p = 0.004), number of species (F = 13.008, df = 3, p < 0.001) and Shannon index (F = 7.350, df = 3, p < 0.001). Fallows sheltered significantly more abundant (Fig. 3) and diverse assemblages than crops and grasslands. A similar model was found for *A. agrarius* (H = 20.548, df = 3, p < 0.001), while *M. arvalis* (H = 9.638, df = 3, p = 0.022) had similarly high abundances in fallows and hayfields.

The species composition was also significantly related to the land use (test on all axes: pseudo-F = 3.0, p = 0.001). The first two
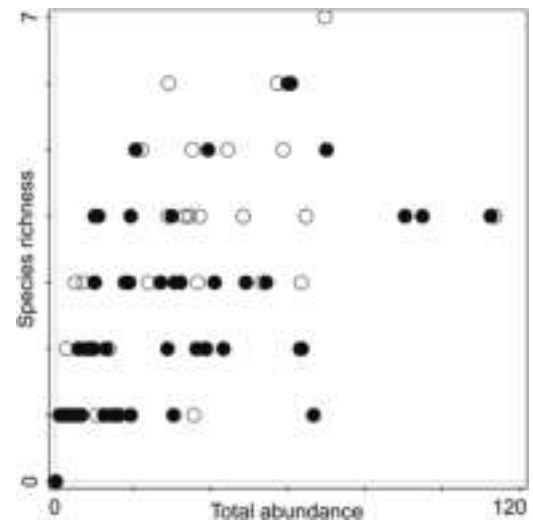

Fig. 2. Total abundance and species richness in the 103 trap-lines. Black dots indicate samples from agricultural habitats while circles represent transects in non-agricultural habitats.
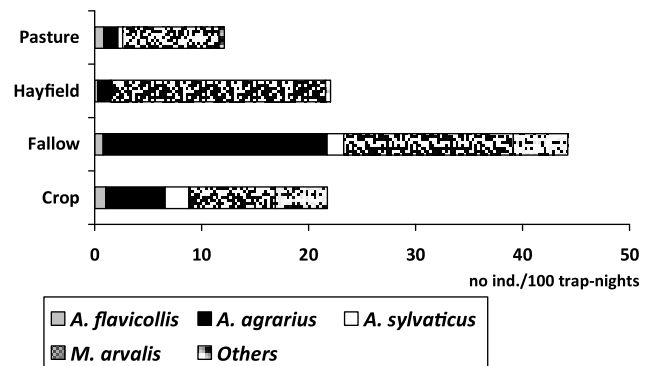
Fig. 3. The abundance (number of individuals per 100 trap-nights) of captured rodent species in the four agricultural habitat types.

constrained axes were significant (p = 0.001 and p = 0.003, respectively). In the ordination space small mammal species formed three groups (Fig. 4). The first group, characteristic for cereal crops,
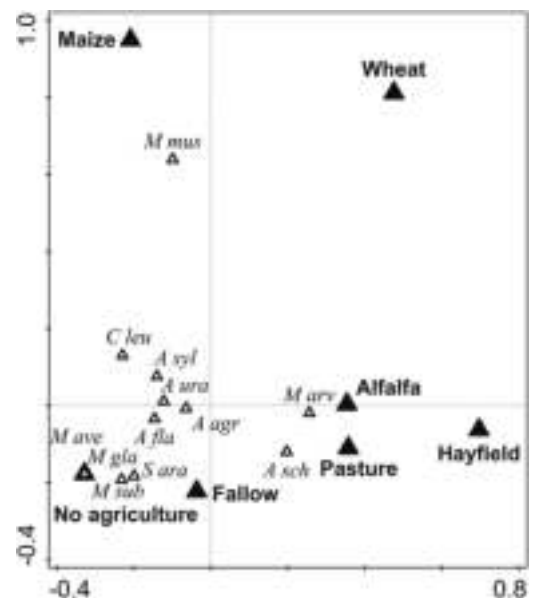
Fig. 4. The species–environment biplot of CCA with the agricultural land uses.

Table 4
Simple term effects of the agrarian land uses on small mammal communities computed by the forward-selection in the CCA. P (adj.) is the adjusted probability expressed as False discovery rate values.

Land use	Explains%	pseudo-F	P (adj.)
Maize	5.2	4.7	0.006
Hayfield	5.1	4.6	0.006
Pasture	2.1	1.8	0.104
Fallow	1.8	1.6	0.225
Wheat	1.3	1.1	0.355
Alfalfa	0.6	0.5	0.704

Table 5
Ecological amplitudes of the small mammal species expressed as tolerances to the environmental gradients. Habitat specialisation is indicated by low values.

Species Tolerance to	Tree cover	Dist forest	Moisture	Herb cover	Herb height
M. glareolus	0.53	0.61	1.09	1.77	1.46
A. flavicollis	1.09	1.34	0.99	1.04	0.92
S. araneus	1.31	1.37	1.22	0.63	0.78
A. agrarius	0.91	0.78	0.98	0.94	1.01
M. avellanarius	0.42	1.42	1.42	2.14	1.96
A. sylvaticus	0.94	1.06	1.14	0.32	0.67
M. subterraneus	0.62	0.47	0.70	0	0.55
M. arvalis	0.70	0.52	0.86	0.46	0.73
A. uralensis	0.85	0.65	1.11	1.65	1.44
C. leucodon	0.69	1.02	1.25	2.38	1.97
M. musculus	1.05	0.68	0.44	1.85	1.55
A. scherman	0.57	0.79	0.55	0	0.62

Fig. 5. Ordination diagram with the first two axes of RDA, using land use as predictors and community-weighted means of tolerances to the environmental gradients as response variables. TolTree: tolerance to tree cover; TolDistf: tolerance to the distance from the forest edge; TolMoist: tolerance to soil moisture; TolHcovr: tolerance to the cover of herbaceous layer; TolHheig: tolerance to the height of herbaceous layer.

included only one species, *M. musculus*, the second group, comprised of *M. arvalis* and *A. scherman*, was characteristic for grassland habitats, whereas the rest of the species were associated with non-agricultural habitats and fallows. *Myodes glareolus* and *M. avellanarius* were found only in habitats with no agrarian land use. Maize crops and hayfields had most distinctive communities (Table 4).

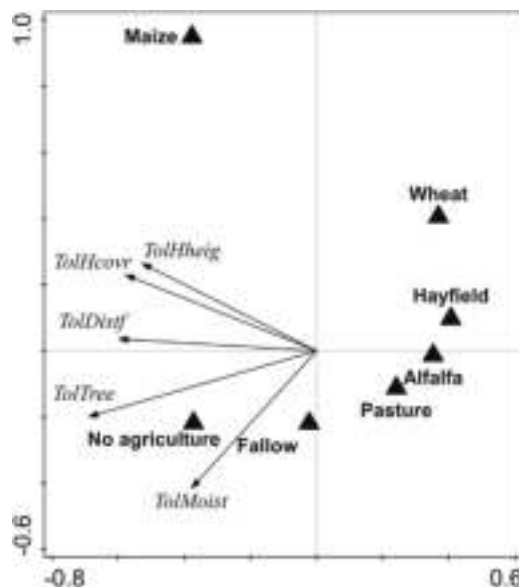*Habitat specialisation of small mammals*

Ecological amplitudes of the small mammal species were expressed as tolerances to the environmental gradients which had significant effects on species composition (Table 5). Tolerance to tree cover and distance from the forest edge were mostly correlated. *Myodes glareolus*, being a forest specialist, had a low tolerance to the distance to forest edge whereas the two open-land specialists, *M. arvalis* and *A. scherman*, had low tolerances for forests and were captured far from them. On the other hand, *M. avellanarius* was captured at different distances from forests, but had a strong preference for tree-rich habitats. Tolerance to height and cover of the herbaceous layer were strongly correlated (Fig. 5). *Microtus subterraneus* and *A. scherman* were highly associated with dense vegetation cover, whereas *M. avellanarius* and *C. leucodon* presented the highest tolerance along these gradients (Table 5).

The relationship between tolerances and land uses was highly significant (pseudo-F = 8.5, p = 0.001), the adjusted explained variation being 34.2%. There was a gradient of tolerances to the environmental factors among the different land use types, placing the non-agricultural lands at one extreme and maize crops at the other, at great distance from the nearest wheat fields (Fig. 5).

Discussion

Factors influencing species composition, community abundance and diversity

Small mammals were surveyed in a matrix of habitats in a rural landscape. To the best of our knowledge, this study is the first to evaluate the effect of environment and land use on small mammals in agricultural mosaic landscapes of Eastern Europe.

The structure of vegetation was the most important predictor for small mammal communities. Both the woody and herbaceous vegetation had strong effects, regardless of the parameter we used. Tree cover segregated forest species from open-land species, strongly shaping the community structure. The response to tree cover effectively predicted the presence and abundance of *M. glareolus*, *A. flavicollis* and *S. araneus* and the absence of *M. arvalis*. Shrubs, on the other hand, do not establish distinct habitats in this landscape (they form a compact layer only in small areas in unmanaged forests, mainly at their edges), but they enhance habitat heterogeneity by increasing the microhabitat diversity and, implicitly, the availability of shelter and food resources, leading to an increase in abundance and diversity of small mammals. Species richness and heterogeneity were influenced by the same variables and showed similar patterns, whereas in landscapes with an increased level of agricultural intensification they present different trends (Gentili et al., 2014; Michel et al., 2006; Millan de la Peña et al., 2003).

The agricultural land use influenced the small mammal community structure mainly through the habitat characteristics. The height of the herbaceous layer had an important effect on habitat selection; forest specialists had the optimum at low vegetation heights, but in case of open habitat species there was a gradient of preference from tall (*M. subterraneus*, *A. scherman*) to short (*M. musculus*, *C. leucodon*) vegetation. Community abundance and diversity were also directly dependent on the height of the herbaceous layer. Tall vegetation reduces prey detectability, thus the preference of small mammals for it is an antipredatory strategy (Michel et al., 2007), especially in case of the less agile voles (Brzeziński et al., 2010). Habitats with tall vegetation also provide more abundant food resources, producing larger amounts of green biomass and seeds. Scott et al. (2008) found similar but more abundant small mammal communities in tall grass compared to short grass habitats. In other studies small mammal diversity was higher in plots with either diverse or high vegetation (Heroldová et al., 2005; Janova and Heroldová, 2016).

Grasslands are dominant in our agricultural landscape and are represented mainly by pastures. Elsewhere an intermediate grazing intensity (approximately 400 kg/ha as maximum livestock biomass) benefits small mammals (Schmidt et al., 2005). The more intensive grazing in our study area had a negative influence, reducing in pastures both community abundance and diversity, but with no significant effect on species composition because habitat selection is not evident in disturbed habitats with low carrying capacity (Luza et al., 2016). In contrast, hayfields sheltered more dense and diverse small mammal communities and significantly shaped species composition. The tall grassy vegetation is favourable for several species but seed-rich dicotyledons are less abundant than grasses, so herbivorous voles were more abundant here than granivorous mice.

Crop fields are seasonally dynamic and continuously modified by farming practices and crop phenology. The patterns of seasonal food availability and changes in vegetation cover differ with the type of crop, so the small mammal assemblages supported by each crop type also differ. Because of their sparse herbaceous vegetation maize fields had a distinctive small mammal assemblage dominated by *M. musculus*, tolerant to low cover. In wheat crops *M. arvalis* was the dominant species, most abundant in summer, before harvest, when height and cover of crop vegetation was maximum. Despite being mown several times per year, alfalfa fields are relatively stable habitats that allow the development of complex burrow systems (Jareño et al., 2015) because they are not ploughed for four or five years. Thus, alfalfa fields have small mammal assemblages more similar to those of grasslands than of annual crops, dominated by *M. arvalis*. For other species however, alfalfa fields are poor habitats, some authors reporting consistently the lowest values of all diversity measures (Heroldová et al., 2007). In our study abundance was lower but diversity (both species richness and heterogeneity) was higher than in wheat fields. Land fallowing did not significantly alter species composition, although it caused the increase in small mammal abundance and diversity to their highest values. Fallows are not exposed to agricultural practices, and hence harbour higher floral diversity and non-crop plant biomass than cropped fields (Heroldová et al., 2007). In the surveyed fallows the herbaceous vegetation cover and height had maximum values, so more species met favourable conditions, thereby developing abundant populations.

Although common species are considered most often as habitat generalists and rare species as habitat specialists (Butet et al., 2006; Gentili et al., 2014; Millan de la Peña et al., 2003), at the local (landscape) scale this may not always be true. In our study relatively rare species, such as *S. minutus* or *C. leucodon,* acted as generalist species, being found in numerous habitat types. The locally common species, *M. arvalis* and *A. agrarius*, on the other hand, showed stricter habitat selection. Ecological specialisation affected the species composition in relation to the land use. Wheat fields were colonised by the most specialised open land small mammals, preferring the driest conditions, whereas maize crop fields produced the most peculiar combination of ecological traits: high tolerance to the herbaceous layer and preference for dry soils, characteristic for *M. musculus*. Land fallowing allowed the presence of species that prefer or at least tolerate moisture. Pastures, alfalfa and hayfields supported habitat specialists that preferred open lands, far from forests, with dense herbaceous cover, especially so for *M. arvalis*. Non-agricultural terrains favoured the presence of generalists. Thus, in contrast with other studies (Gentili et al., 2014), we found that open habitat specialists were more prone to be abundant in agricultural lands, whereas habitat generalists prevailed in non-agricultural lands.

Species responses to environmental variables and land use

Because of its high abundance, the responses of *M. arvalis* to the environment gradients were well expressed. It was the only open habitat specialist with a significant negative response to tree cover. Its optimum was in habitats with highest cover of the herbaceous layer. The response to the herbaceous height was more complex. In short compact grassy vegetation characteristic of pastures and mown hayfields *M. arvalis* was dominant although population densities were low. Densities increased with height of herbaceous layer, which (especially dicotyledons in fallows) favoured also *Apodemus* species, and the relative abundance of *M. arvalis* decreased. Although considered characteristic of intensely grazed pastures (Millan de la Peña et al., 2003), in our area *M. arvalis* had higher abundances in less intensely grazed, shrubby pastures. Janova and Heroldová (2016) captured no common vole in maize fields, probably because of the more intensive field management. By contrast, we found that in maize plots with rich cover of weeds *M. arvalis* was abundant, especially in autumn. However, *M. arvalis* had a strong preference for non-crop grasslands.

Among the four *Apodemus* species *A. flavicollis* stood out for its preference for high tree cover at short distances from forest edge, even if it tolerated also less wooded habitats farther from forests, including crops. In Transylvania, *A. flavicollis* inhabits a wide range of woody habitats at different altitudes (Benedek, 2014), being the only dominant species in closed-canopy forests of hilly areas. *Apodemus sylvaticus* is the dominant species in many agricultural landscapes in Western and Central Europe (Heroldová et al., 2007; Gentili et al., 2014), as it can use intensively the crop matrix (Sozio and Mortelliti, 2016) where it frequently prevails (Janova and Heroldová, 2016; Panzacchi et al., 2010). In our study area *A. sylvaticus* was less abundant, being outnumbered by *M. arvalis* or other *Apodemus* species (usually *A. agrarius*), preferring tall and dense herbaceous vegetation.

The presence and abundance of *M. glareolus* was correlated with the woody vegetation, i.e., the tree and shrub layer covers. *Myodes glareolus* had the strongest positive response to tree cover and negative response to the distance from the forest edge, but no specific requirements for the herbaceous vegetation. Being a forest specialist, its optimum was placed at low values of the herbaceous cover, because the herbaceous layer was frequently sparse in forests. The connectivity of suitable habitats plays an important role for *M. glareolus* (Fischer and Schröder, 2014; Sozio and Mortelliti, 2016). The only habitat where we captured this species beyond the forest edge was the strip of high herbaceous vegetation bordering the riparian forests. This is an indication of the connectivity role fulfilled in our study area, in the absence of hedges, by riparian forests.

The synanthropic *M. musculus* was strictly relegated to agricultural lands, and especially to maize crops. In plots where intensive agricultural works were carried out, leaving behind an extremely neat and tidy maize culture, with no other plants among the corn stems, this species dominated an impoverished small mammal community. The affinity of *M. musculus* for the cereal crops might be the result of competition with the other mice species (*Apodemus* spp.), excluding it from habitats with more favourable conditions. In natural and semi-natural habitats *M. musculus domesticus* was shown to be less competitive than *A. sylvaticus* (Berry and Tricker, 1969). Its high tolerance to sparse herbaceous cover enables *M. musculus* to inhabit these cover-poor habitats avoided by other species (Boitani et al., 1985). In effect, it lived in places avoided by native species.

In our study we captured shrews relatively frequently, although results obtained by using box-traps are often considered biased against shrews because of their small size (Nicolas and Colyn, 2006) and because seed baits are not attractive to them (Shonfield et al., 2013). However, *S. araneus,* the most common shrew in our study

area, had the highest ratio between occurrence (15.53%) and relative abundance (2.44%) of all small mammal species. The presence and abundance of this species was associated with the presence of shrubs. In our area *S. araneus* was a habitat generalist, having the highest tolerance to tree cover and distance to forest edge. It was captured in forests but also in open land habitats distant from them, our results being consistent with those in the literature (Canova and Fasola, 1991; Churchfield et al., 1997). On the other hand, it avoided annual crops, its tolerance to the herbaceous cover being low.

Implications for management

Studies on the distribution of small mammals, and especially of rodents, in farmlands have two major implications: for biodiversity conservation and for pest management. Very often a balance between these two is difficult to achieve. Trade-offs have to be found between biodiversity conservation in combination with related ecosystem functions and sustainable food production (Butler et al., 2007; Fischer and Schröder, 2014). Efficient food production implies intensification of agriculture, which often means increases of field sizes, reduction of field margins, mechanization and extensive use of chemical fertilizers and pesticides. The intensification of agriculture affects small mammals less than other vertebrate or invertebrate communities (Burel et al., 1998). However, intensive agriculture influences the relative abundances of species and tends to favour the most common species (Millan de la Peña et al., 2003). In highly intensified landscapes the crop matrix provides high levels of rodent abundance but low diversity, favouring common generalist species (Gentili et al., 2014) over rare specialists.

In our study area the high heterogeneity of the landscape is the result of low-intensity farming that was practiced for centuries with little change. It was associated with high variability in species composition and species richness, which exceeded that reported in other parts of Europe (Butet et al., 2006; Fischer and Schröder, 2014; Janova and Heroldová, 2016), even when we considered only the agricultural habitats. Our results support the idea that habitat heterogeneity enhances biodiversity in the farmed landscape (Benton et al., 2003; Canova and Fasola, 1991). The landscape scale variability in biodiversity and the historical context of land use should be taken into account in the long term management of agricultural landscapes, when considering spared and shared land use options (von Wehrden, 2014). Our research area is a traditional farmland landscape and the species turnover between habitats is high, supporting thus the land-sharing approach. The continued use of low-intensity practices on existing farmland with high nature value is the most (cost-) effective way to stop the decline of species-rich communities in the short and medium terms (Sutcliffe et al., 2015). The interspersed semi-natural habitats with high vegetation cover enhance not only small mammal diversity but also predator abundances, potentially regulating rodent population densities (Paz et al., 2013). The grasslands between fields with annual crops may act as sink habitats, thereby reducing rodent spillover (Fischer and Schröder, 2014). Land fallowing is believed to increase the risk of pest problems (Firbank et al., 2008), but according to our results, fallow lands are favourable habitats for *S. araneus*, an agent of biological control of invertebrate pests (Luff, 1983).

Because of its wide distribution in agrarian landscapes, its ability to adapt to intensively cultivated areas and its outbreaks, during which it causes important damages to crops, *M. arvalis* is considered a major rodent pest in farmlands across a large part of its range (Jacob et al., 2014; Rodríguez-Pastor et al., 2016), including Romania (Popescu and Murariu, 2001), where this species is the main target for agricultural pest control. *Microtus arvalis* is often blamed for most of crop damage but, at least for cereal fields, the granivorous *Apodemus* mice are very important pests in fields of ripening grains (Heroldova et al., 2008; Heroldová and Tkadlec, 2011). However, for these species the herbaceous vegetation, and especially its height, had great importance, thus managing the herbaceous vegetation by keeping it short in the semi-natural habitats adjacent to the crop matrix, especially from summer to autumn, when tall vegetation enhances population densities, could help reduce crop damage.

The variation partitioning revealed the higher importance of environment gradients compared to geographical position and land use in separation of small mammal species and shaping the community structure. Other authors (Fischer and Schröder, 2014; Michel et al., 2006) have also showed the key role played by landscape, and especially local habitat characteristics, in shaping small mammal communities. The fact that land use has a lesser effect than the vegetation traits and other environmental factors on the targeted communities can be used in land management. Because tree cover strongly segregates rodent species and crop pests are open land specialists, interspersing habitats with woody vegetation in the crop matrix would enhance diversity of small mammals but reduce abundance of pest species.

Conclusions

Although we have found differences concerning the small mammal community structure, abundance and diversity in various habitats and the responses of species to environment and land use, our results share some patterns with other studies in agricultural landscapes of Central and Western Europe. They support the idea that landscape heterogeneity is associated with high species diversity and that environmental factors, and especially vegetation, are most important for small mammals, both on population and community level.

In the context of the intensification of agriculture, not only at European but also at national scale (landscapes in southern, eastern and western Romania are dominated by extensive monocultures), the area we surveyed is a mosaic of farmed and pasture lands with high nature value and representing a valuable landscape for biodiversity and its conservation. We believe that maintaining this complex matrix of small patches of crops arranged within rodent dispersal distances, fallow fields and diverse semi-natural habitats (grasslands and forests) connected by ditches, field margins and especially riparian forests, is crucial for the continued coexistence of habitat specialists and generalists, of common and rare species, and thus of a diverse small mammal community. In addition, preserving this low intensity farming practice would have some benefits in terms of reducing rodent damage, which may not currently be fully taken into account when considering the profitability of farming enterprises.

Acknowledgements

Appendix 1.

Fig. A1. The study area: a. typical rural landscape in southern Transylvania, b. crop matrix with weedy maize field c. fallow land invaded by *Solidago canadensis*, d. shrub encroachment of overgrazed pasture.
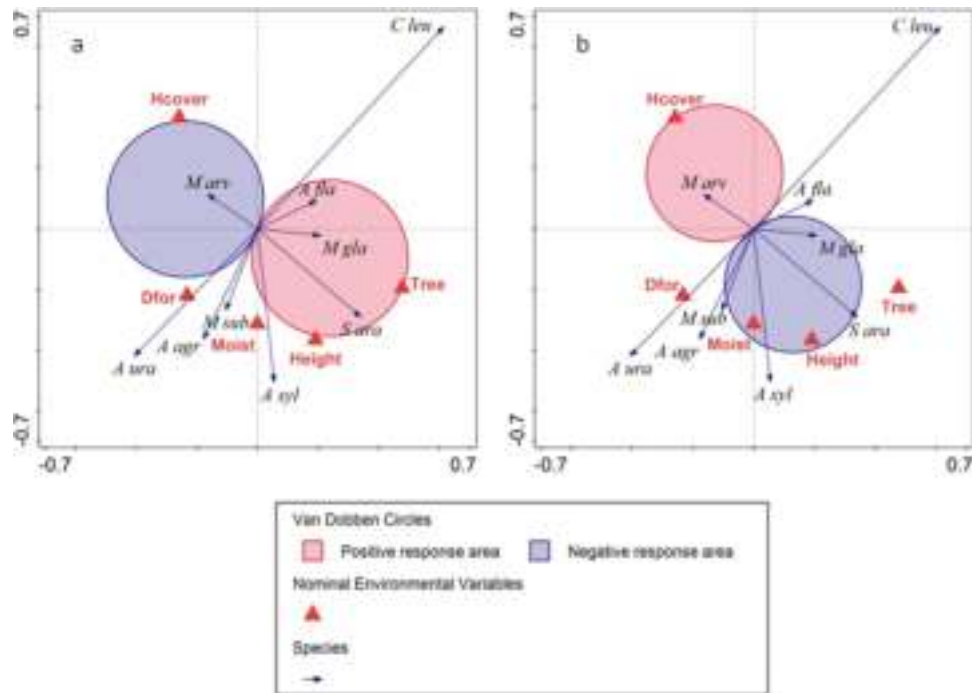
Appendix 2.

Fig. A2. The t-value biplots for the selected environment variables: a. tree cover (Tree), b. cover of herbaceous layer (Hcover).

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