THE INFLUENCE OF PAST LAND-USE AND ENVIRONMENTAL FACTORS ON GRASSLAND SPECIES DIVERSITY

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Abstract. Mountain grasslands are among the most species-rich plant communities in Europe. This is due to the large variability of abiotic conditions and ways of management. However, a significant change in the rural economy has taken place in recent decades. Some grasslands have become forested, while others have been overgrown as a result of succession. Fodder for domestic animals is produced on grasslands created on former arable land. The aim of this study was to estimate the effect of topographic factors (altitude, slope, exposure) and land use (grassland, arable land) in the mid-nineteenth century and the 1930s on the present biodiversity of mountain grasslands. The study was carried out in the basin of the Łomniczanka and Wierchomlanka Rivers in the Beskid Sądecki (Polish Carpathians). A total of 73 phytosociological relevés in an altitude gradient ranging from 660 to 1,060 m a.s.l were made. Past land use was determined on the basis of archival cadastral and topographic maps. The altitude above sea level was the main factor influencing the botanical composition of vegetation. No difference was observed in species composition depending on past land use. The results show the crucial role of altitude in determining the species composition of mountain meadows.
Keywords: *semi-natural grasslands, grasslands management, species diversity, historical land use*

Introduction

Many habitats, such as semi-natural grasslands, are associated with the centuries-long human activity. The long-term effects of mowing, grazing and fertilization has enabled the emergence of plant communities with numerous species occurring exclusively in these habitats. Mountain grasslands used in a traditional, extensive manner are particularly valuable. These are among the most species-diverse plant communities in the world (Wilson et al., 2012; Chytrý et al., 2015). Grassland communities are also associated with invertebrate species, particularly arthropods (Schaffers et al., 2008). Research also shows that an open landscape is essential for numerous bird species (Siramia et al., 2008; Shi et al., 2014).

The existence of such species-rich communities is the result of the interaction of abiotic habitat factors and extensive use. These communities are found in places with low fertility, which prevents dominance by few highly competitive species, as in fertilized grasslands. On the one hand agricultural production is intensified, while on the other hand marginal areas are no longer being used (Strijker, 2005). Both of these factors lead to a decline in biological diversity and the disappearance of many rare species, which usually have a narrow ecological amplitude (Ellenberg, 1985; Cousins et al., 2015).

In the Polish Carpathian Mountains the problem of abandonment of agricultural land is particularly acute. At the start of the 20th century arable land still dominated the landscape up to an altitude of 1,000 m a.s.l. (Bielecka, 1969) and grasslands occupied

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higher areas or other places that were unsuitable as cropland. In recent decades most former grasslands have become afforested or spontaneous forest succession is taking place on them (Bucała, 2014; Kolecka et al., 2015; Morzyniec et al., 2015). At the same time, arable land has been transformed into grassland, although its total area has not decreased (Twardy, 2008). The grassland communities arising in this manner are usually characterized by lower species diversity (Cousins and Eriksson, 2002).

In mountainous areas the current state of grassland communities is influenced by the high degree of variation in topographic factors such as: altitude a.s.l., exposure, inclination, and soil fertility and moisture. These factors usually act together and it is usually difficult to single out the ones with the greatest effect (Janišová et al., 2010; Klimek et al., 2008). Botanical composition is also linked to the process of immigration of species from other grassland areas and their adaptation to habitat conditions and management. Immigration processes of grassland species, in the case of areas isolated from sources of diaspores, may last a long time. This is most likely why 'old' grasslands with a long, uninterrupted history of use are usually richest in species and thus the most ecologically valuable (Reitalu et al., 2010; Pitkänen et al., 2016). The main questions posed in the study were as follows: (i) what is the main factor responsible for the species composition of grassland communities in mountainous areas? (ii) Do grasslands formed on former arable land differ in species composition from those situated in places that were never used to grow crops?

Materials and methods

The study was carried out on clearings located in the Pasmo Jaworzyny mountain range (catchment of the Łomniczanka and Wierchomlanka Rivers), which is part of Beskid Sądecki (Western Carpathians) in the forest zone, in an altitude range of 600–1000 m a.s.l. (*Figure 1*). Bedrock of the Jaworzyna mountain range is composed of flysch sandstones and shales. The soil of all the plots were Haplic Cambisol (Dystric).

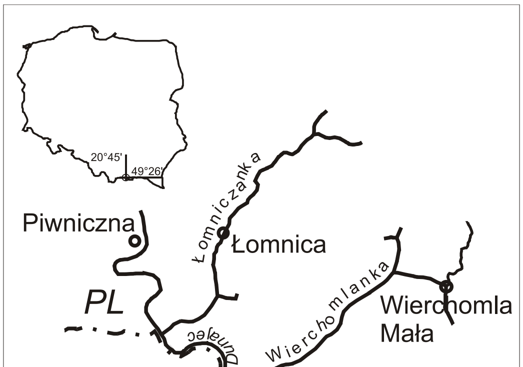

Figure 1. *Localization of research area*

In 2009 73 phytosociological relevés with an area of 100 m^2 were made; a list of plant species was compiled and their coverage were estimated on the five-point scale (Braun-Blanquet, 1964). Species names were taken after Mirek et al. (2002). In each

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place basic topographic parameters were determined: altitude a.s.l., inclination, and exposure. The values for exposure were transformed using trigonometric functions (Roberts, 1986) to create two new variables: northness = cos (exsposure in degrees) and eastness = sin (exsposure in degrees). Cartographic materials were used to determine the type of land use (grassland or arable land) in the mid-nineteenth century, the 1930s and the 1980s. The analysis of past land use was based on Austrian cadastral maps from 1846, a Military Geographical Institute map from 1936 and topographic maps published by the Surveyor General of Poland from 1988. Habitat conditions were evaluated indirectly on the basis of unweighted means of Ellenberg's indicator values (Ellenberg et al., 1992). These were calculated for each relevé for nutrients (N), temperature (T) and soil reaction (R) using JUICE software (Tichý, 2002).

Classification of the phytosociological relevés was based on the similarity of species composition using a modification of TWINSPAN (Roleček et al., 2002). Association of species to vegetation units and statistical significance at $p < 0.05$ (Fisher test) was calculated with JUICE (Tichý, 2002). Syntaxonomic system by Matuszkiewicz (2001) was applied. The ordination analyses were carried out using CANOCO ver. 4.5 software (ter Braak and Smilauer, 2002). In detrended correspondence analysis (DCA) the length of the gradient was 3.6 of the standard deviation and canonical correspondence analysis (CCA) was used to test the effect of topographical factors and use on species composition. Statistical significance was determined by a Monte Carlo permutation test.

Results

Analysis of the phytosociological relevés allowed them to be classified into three main plant communities, forming visible groups with respect to the first DCA axis (*Figure 2A*):

Class: *Vaccinio-Piceetea* Br.-Bl. 1939
Order: *Vaccinio-Piceetalia* Br.-Bl. 1939
Alliance: *Piceion abietis* Pawł. et al.1928

1. Community: *Vaccinium myrtillus*

Class: *Nardo-Callunetea* Prsg 1949
Order: *Nardetalia* Prsg 1949
Alliance: *Eu-Nardion* Br.-Bl. 1926 em. Oberd. 1959

2. Association: *Hieracio-Nardetum* Kornaś 1955 n.n.

Class: *Molinio-Arrhenatheretea* R.Tx. 1937
Order: *Arrhenatheretalia* Pawł. 1928
Alliance: *Arrhenatherion elatioris* (Br.-Bl. 1925) W.Koch 1926

3. Association: *Gladiolo-Agrostietum capillaris* (Br.-Bl. 1931) Pawł. et Wal. 1949

The *Vaccinium myrtillus* community, apart from a large share of this species, was characterized by a substantial share in the area cover of species characteristic of *Hieracio-Nardetum* association: *Nardus stricta*, *Potentilla erecta*, *Deschampsia caespitosa* and herbaceous species: *Hypericum maculatum* and *Luzula luzuloides* (*Table 1*).

This community usually constitutes a stage of overgrowth of unused grasslands and pastures. The number of species in the phytosociological relevé ranged from 7 to 22 (on average 14.1). This community is found in clearings in the upper part of the massif at altitudes from 880 m a.s.l. to at 1060 m a.s.l. (*Table 2*).

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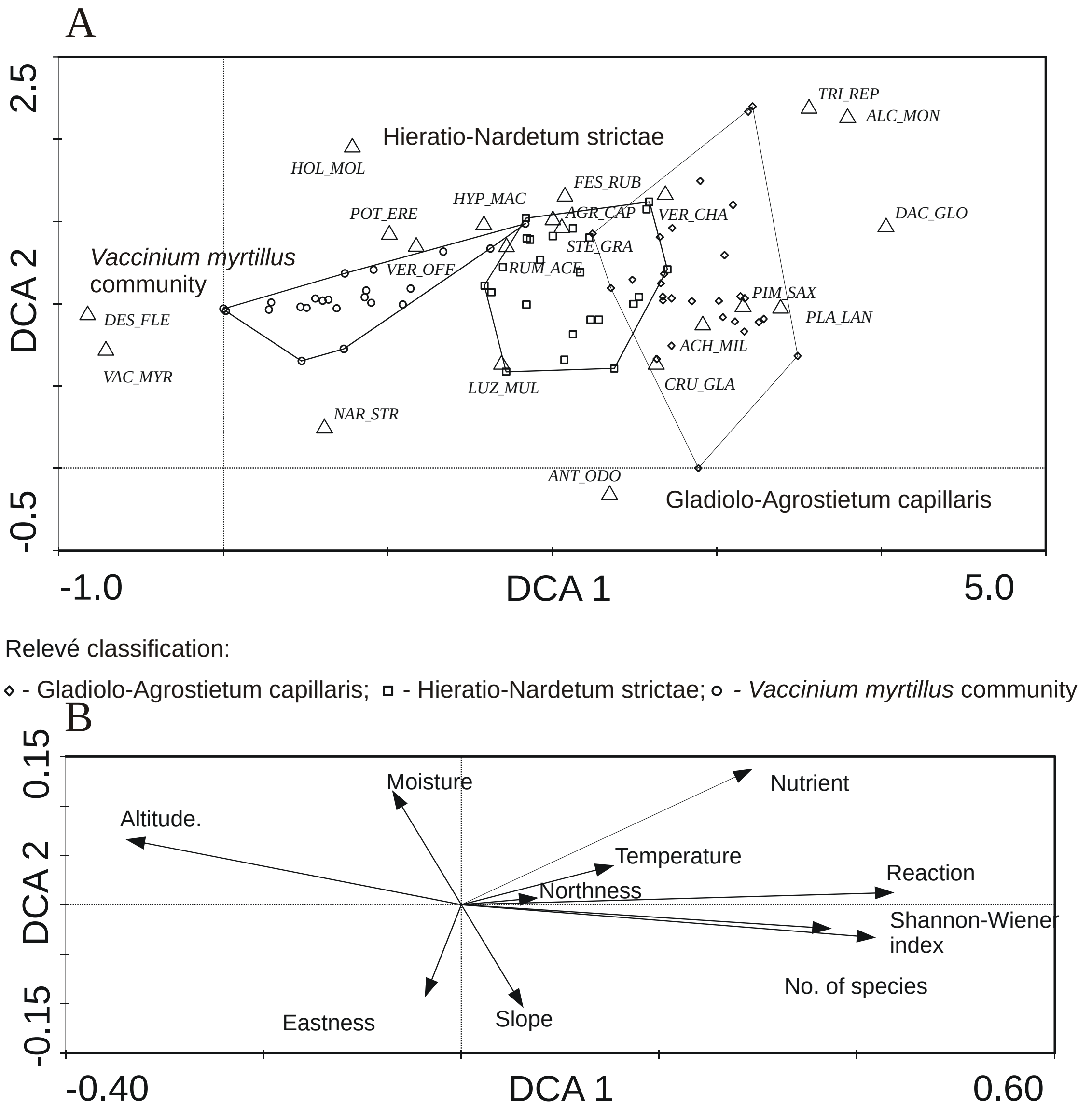

Figure 2. *Ordination diagram (DCA) of the whole data set (eigenvalue of I axis 0.463, II axis 0.127; the length of the main axis gradient is 3.64). A - ordination of phytosociological relevés and species (only species with the highest weight has been presented); B - effect of environmental variables. Species names abbreviation: ACH_MIL - Achillea millefolium, ALC_MON – Alchemilla monticola, ANT_ODO – Antoxanthum odoratum, CRU_GLA – Cruciata glabra, DAC_GLO – Dactylis glomerata, DES_FLE – Deschampsia flexuosa, FES_RUB – Festuca rubra, HOL_MOL – Holcus mollis, HYP_MAC – Hypericum maculatum, LUZ_MUL – Luzula multiflora, NAR_STR – Nardus stricta, PIM_SAX – Pimpinella saxifraga, PLA_LAN – Plantago lanceolata, POT_ERE – Potentilla erecta, RUM_ACE – Rumex acetosa, STE_GRA – Stelaria graminea, TRI_REP – Trifolium repens, VAC_MYR – Vaccinium myrtillus, VER_CHA – Veronica chamaedrys, VER_OFF – Veronica officinalis*

Table 1. *Species associated with vegetation units (phi indicator for species with statistical significance p < 0.05 Fisher test). Only species with constancy > 60% were shown*

Species	Vegetation unit		
	Vaccinium myrtillus community	*Hieracio-Nardetum* association	*Gladiolo-Agrostietum* association
Deschampsia flexuosa	80.0	---	---
Vaccinium myrtillus	62.4	---	---
Nardus stricta	20.9	12.7	---
Holcus mollis	18.6	13.7	---
Veronica officinalis	0.9	28.7	---
Dianthus deltoides	---	34.6	17.9
Stellaria graminea	---	31.6	20.9
Cruciata glabra	---	30.6	31.0
Campanula patula	---	23.4	26.0
Veronica chamaedrys	---	51.0	40.3
Festuca rubra	---	11.4	14.6
Agrostis capilaris	---	4.9	17.9
Achillea millefolium	---	38.6	41.9
Plantago lanceolata	---	21.9	54.9
Pimpinella saxifraga	---	15.3	55.5
Ranunculus acris	---	4.7	58.6
Alchemilla monticola	---	2.6	56.3
Leucantemum vulgare	---	---	49.8
Phleum pratense	---	---	55.9
Lotus corniculatus	---	---	59.4
Prunella vulgaris	---	---	61.7
Trifolium pratense	---	---	67.7
Trifolium repens	---	---	68.4
Cynosurus cristatus	---	---	86.8

Table 2. *General characteristics of plant communities*

Parameter	Vegetation unit		
	V*accinium myrtillus* community	*Hieracio-Nardetum* association	*Gladiolo-Agrostietum* association
Altitude [m a.s.l.] **	881 - 1064	701 - 969	663 – 897
Slope [°]	0 - 25	0 - 35	5 - 30
Ellenberg's indicator values			
Temperature [T] **	4.7	5.3	5.3
Moisture [F]**	5.2	4.9	5.0
Reaction [R]**	3.5	4.5	5.3
Nutrients [N]**	3.1	3.6	4.1
Total number of species **	48	92	128
Mean number of species in relevé **	14.1	28.8	39.0
Shannon-Wiener diversity index **	1.7	2.6	2.9

** - differences between vegetation units significant at $p < 0.01$ (Kruskal-Wallis test)

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Patches of multi-species *Hieracio-Nardetum* association are the remains of once dominant in the Beskid Sądecki type of grassland (Pawłowski, 1925). The sward includes a large share of *Nardus stricta* together with other species characteristic of this association, such as *Carex pilulifera*, *Potentilla erecta* and *Veronica officinalis*. Many species can be found here that are also found in *Gladiolo-Agrostietum* association. These include *Achillea millefolium*, *Veronica chamaedrys*, and *Plantago lanceolata*. Often, however, the dominant species are *Festuca rubra* or *Agrostis capillaris* (*Table 1*). This community is found at lower altitudes (700-970 m a.s.l.). The number of species in the phytosociological relevé ranges from 19 to 41 (on average 28.8) (*Table 2*). The community with the greatest species diversity is *Gladiolo-Agrostietum* association. In the patches of this community 128 plant species were recorded, and in individual relevés from 28 to even 55 species (on average 39). Such meadows are usually found in the lower parts of the massif (600–900 m a.s.l.) (*Table 2*). The sward is often dominated by *Agrostis capillaris,* and the presence of species associated with fertile grassland, such as *Dactylis glomerata, Trifolium pratense* and *Trifolium repens* is typical. Sporadic use as pasture is indicated by the small but frequent share of *Cynosurus cristatus* (*Table 1*). The indicator values show that the communities do not differ significantly in terms of temperature (T) and moisture (F) requirements. However, substantial differences were noted with respect to soil reaction (R) and nutrients (N), which were highest in the case of the *Gladiolo-Agrostietum* association, and lowest in the V*accinium myrtillus* community (*Table 2*). Analysis of the archival maps indicated that most of the 73 phytosociological relevés were situated in sites that had been used as arable land in the mid-nineteenth century and still in the 1930s. Only in the case of one relevé was it found in a location marked as arable land in the 1980s (*Table 3*).

Table 3. *The number of phytosociological relevés on areas with the same type of land use in the past*

Land use	Period of time		
	mid-nineteenth century	1930s	l980s
Arable land	46	51	1
Grassland	27	22	72

The variation in the species composition of communities present in clearings in the Łomniczanka and Wierchomlanka catchment indicate that altitude was a decisive factor. The grasslands analyzed were separated by short distances, but with considerable variation in altitude, up to 400 m. Increasing altitude above sea level was accompanied by a decrease in species variation, expressed both as number of species and the Shannon-Wiener index, and by an increase in the mean indicator value of the plants for nutrients (N) and reaction (R) (*Figure 2B*). Due to an autocorrelation between the way of management in the 1930s and in the mid-19th century, the analysis took into account only the way of management in the 19th century. The selected variables (altitude, exposure, land use in the past, slope) described 17.58% of the total variance in species composition. Altitude above sea level was responsible for the largest part of it - 9.86% and even for 10.29% after eliminating the influence of the remaining variables (pure effect) (*Table 4*).

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Table 4. *Effect of environmental variables (percentage of explained variation), considered individually (marginal effect) and after deducting the impact of other statistically significant variables (pure effect)*

Environmental variables	Marginal effect	p	Pure effect	p
Altitude	9.86	0.002	10.29	0.002
Northness	2.57	0.014	2.14	0.008
Eastness	1.72	0.028	2.14	0.018
Land use mid-nineteenth century	2.14	0.032	1.72	0.028
Slope	1.29	0.164	-	
Total	17.58		16.29	

Discussion

In contrast with our results, many studies on the biodiversity of semi-natural grassland communities have not shown one main factor influencing species composition (Janišová et al., 2010; Pruchniewicz and Żołnierz, 2014). This may be due to differences in the size of the areas studied. The factors determining species composition in a relatively small area may be different than those acting on a larger scale (Vandvik and Birks, 2002). In the catchment of the Łomniczanka and Wierchomlanka Rivers the variation caused by the altitude above sea level was nearly 10%. This is relatively high, considering that in a study on the effect of factors on the formation of grassland communities in Slovakia the total variance explained by all variables together was only 12% (Klimek et al., 2008). The low percentage of explained variance is typical of data containing many zero values (ter Braak and Verdonschot, 1995), as is usually the case with phytosociological data.

As altitude increased climatic determinants change. The mean air temperature falls by 0.72°C/100 m a.s.l., and the length of the growing period in the conditions of Beskidu Sądecki is reduced by 6.2 day per 100 m a.s.l. (Brzeźniak and Czemerda, 1987), while precipitation increases (Brzeźniak et al., 1984). The indicator values for temperature (T) decreased as altitude increased, but this correlation was weak. This may be due to the relatively low variation in plant species in relation to this factor, as manifested by the large number of species for which no T values are given. Changes in altitude are also accompanied by changes in soil conditions (Manojlović, 2011) differences occur in particular between locations on the sides of mountains and on their hilltops (Maciaszek, 2000). The substantial effect of altitude is linked not only to a change in climate and soil conditions, but also to the possibility and profitability of agricultural use (Tasser and Tappeiner, 2002). Thus the change from arable land to grassland, and then to abandonment of agricultural practices , occurs first in areas that are the most difficult to access, usually at higher altitudes (Twardy, 2008; Tasser and Tappeiner, 2002). Influence of altitude on biodiversity is of common nature and concerned different groups of organisms (Sergio and Pedrini, 2007). Grasslands as semi-natural communities arose in the place of forest and are dependent on mowing or grazing to stop the succession process (Szydłowska, 2010; Hejcman et al., 2013; Tälle et al., 2015). For their existence, apart from suitable soil and climate conditions, diaspores of grassland species must appear. This takes place mainly through anemochory (Tackenberg et al., 2003) and zoochory (Cosyns et al., 2006; Purschke et

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al., 2014), but in either case it takes time (Hutchings and Booth, 1996). This time period may vary, depending mainly on the distance from the sources of the diaspores. In a traditional, alternating system of grassland management in the mountains, when at regular intervals the grassland was ploughed and after a few years grassland use was resumed, meadows and arable fields were present in a spatial mosaic. The flow of diaspores from the meadows to the arable fields was easy and the newly formed meadows rapidly regained a rich species composition (Włodarczyk, 1956). Similar fast process of species immigration to old fields from nearby grasslands was observed in case of xerothermic vegetation (Woch, 2011). In the case of forest clearings this process may last a long time (Winsa et al., 2015). One factor that may influence species composition on former arable land is cultivation procedures, particularly fertilizers that alter the chemical and physical properties of the soil (Chmolowska et al., 2016). For this reason many studies have found that the species composition of grasslands depends on how long the land has been used as grassland (Pitkänen et al., 2016, Purschke et al., 2014). In mountain grasslands in Norway, Austrheim and Olsson (1995) found that the most rapid and greatest changes in species composition took place over a period of up to 23 years from the abandonment of ploughing. Cartographical data indicate that during the period between the mid-nineteenth century and the 1930s there were no fundamental changes in land use in the study area. Arable land stretched as far as to altitudes above 1,000 m. a.s.l. (Kubijowicz, 1927). Fundamental changes in land use took place later. The very small percentage of variance (1.72%) explained by the land management in the past shows that the time elapsed from the transformation of the land into grassland was long enough for typical grassland communities to form. The time needed for the formation of typical grassland communities is highly varied and depends on a number of factors. In the case of xerothermic grasslands the effect of arable land use was demonstrated after more than 100 years (Forey and Dutoit, 2012) while in a study by Chýlová and Münzbergová (2008) the presence of xerothermic communities was noted in places that had been managed in different ways 50 years before. In these studies, however, there was no single factor as strong as altitude above sea level determining the species composition of plant communities. Semi-natural grasslands in a forest zone were created by human activities and their existence depends entirely on their current management (Valkó et al., 2012; Pavlů et al., 2016; Kulik, 2014). Hence, abandonment of farming practices is a more important than the way of land use in the past. *Hieracio-Nardetum* association which dominated in the upper parts of Polish Carpathians in the past (Korzeniak, 2016) has been replaced by V*accinium myrtillus* community as a stage of succession of unmanaged grasslands.

Species-rich *Nardus* grasslands (6230 Natura 2000 code) are currently among the most threatened habitats in Poland and Europe (EIONET) and has been considered as a priority habitat in Natura 2000 network (European Commission). The preservation of such high natural value communities requires their mowing or grazing, which is not possible without subsidies under agrienvironmental programs (Jellinek, 2016).

Conclusions

1. The varied species composition of the grassland communities in the study area was mainly due to the effect of their location at different altitudes above sea level.

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2. The highest species diversity was noted for the *Gladiolo-Agrostietum* association, situated at low altitudes, and the lowest for the *Vaccinium myrtillus* community, located in the higher parts of the massif.

3. As the altitude above sea level increased, the fertility and pH of the soils decreased, expressed as the indicator value of the plant species.

4. The influence of the type of land use in the mid-nineteenth century and the 1930s on the species composition was small. All three types of communities were found in both the fields that had been used as arable land and in those used as grassland in the mid-nineteenth century and the 1930s.

5. None of the plots in the study area (except one) had been ploughed for at least 30 years. This period was sufficient for the formation of grassland communities.

6. The abandonment of plant communities management is one of the most important factors that influenced botanical composition of grasslands.

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