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Biodiversity of herbaceous vegetation in abandoned and managed sites under protection regime: a case study in the Central Forest Reserve, NW Russia

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Keywords: abandonment, coenotic groups, Indicator Species Analysis (ISA), mainland meadows, species richness.

Ključne besede: opuščanje, cenotske skupine, analiza indikatorskih vrst (ISA), celinska travišča, vrstna pestrost.

Abstract

The aim of the study is to characterise herbaceous vegetation (meadows and ruderal communities) remaining after several decades of protection and compare it to the vegetation of currently managed local sites in the Central Forest Reserve, Tver Oblast, Russia. Cluster analysis of the communities was based on 209 relevés, while their ecological features were analysed using phytoindication assessment. The analyses revealed four types of herbaceous communities: managed mesic meadows, abandoned mesic meadows, tall-herb meadowsweet communities and ruderal tall-herb communities. These four types differ in management, floristic composition and ecological conditions as well as in coenotic and functional group shares (including forbs, graminoids and woody species). The occurrence of these species groups determines the current state of the herbaceous communities. Our study revealed that mesic meadows have retained all the key meadow features for more than 25 years without any management, although their area has shrunk and shares of coenotic and functional groups have changed. The observed herbaceous communities encompass around 40% of the reserve flora including four red list species and 16 alien species.

Izvleček

V članku smo opisali zeliščno vegetacijo (travišča in ruderalne združbe), ki se je ohranila po nekaj desetletjih zaščite in jo primerjali s sedanjo vegetacijo na gospodarjenih rastiščih v Osrednjem gozdnem rezervatu, Oblast Tver, Rusija. S klastrsko analizo smo klasificirali 209 vegetacijskih popisov, njihove rastiščne značilnosti pa smo analizirali s pomočjo fitoindikacije. Z analizo smo ugotovili 4 tipe zeliščne vegetacije: gojena vlažna travišča, opuščena vlažna travišča, visoka steblikovja brestovolistnega oslada in ruderalna visoka steblikovja. Štiri rastlinske združbe se razlikujejo po načinu gospodarjenja, vrstni sestavi in rastiščnih razmerah kot tudi glede na delež cenotskih in funkcionalnih skupin (delež zelišč, trav in lesnatih vrst). Pojavljanje teh skupin vrst označuje trenutno stanje zeliščnih združb. Z raziskavo smo pokazali, da so vlažna travišča ohranila vse ključne značilnosti travišč tudi po 25. letih brez kakršnega koli gospodarjenja, vendar se je njihova površina zmanjšala, deleži cenotskih in funkcionalnih skupin pa so se spremenili. V obravnavanih združbah smo zabeležili 40% celotne flore rezervata, vključno s štirimi vrstami z rdečega seznama in 16 tujerodnih vrst.

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Introduction

Palaearctic grasslands are known for their high biodiversity in many taxa (Habel et al. 2013, Dengler et al. 2014, Dengler et al. 2016). In particular, European grasslands are among the most diverse ecosystems in the world (Wilson et al. 2012, Dengler et al. 2014). Extensively used mainland meadows are considered to be the most species-rich in small spatial scales (Kull & Zobel 1991). Today many of the grassland ecosystems are threatened by the change of land use towards intensification, abandonment and afforestation. Under these changing conditions, the current state of grasslands is still poorly studied. Hence our research is aimed at filling this knowledge gap. Traditionally, the term "grassland (vegetation)" is understood as formation dominated by grasses (or graminoids), usually with a single-layered structure and sometimes (in case of wooded savannas or savannoid vegetation) with an open woody plant cover (modified after Rutherford et al. 2006, reviewed by Mucina et al. 2016). However, in later studies (Dengler et al. 2014) on palaearctic grasslands, steppes are considered as dry grasslands and meadows as mesic grasslands. According to Mucina et al. (2016), meadow (vegetation) is a plant formation dominated by grasses (or other graminoids) and herbs usually found in humid to mesic habitats. Most European meadows are of anthropogenic origin, dependent on regular management such as mowing (Mucina et al. 2016); therefore, they are considered as semi-natural communities.

Semi-natural grasslands are an essential part of the cultural landscape of Europe and resulted from centuries or millennia of low-intensity land use since the beginning of the Neolithic period (Pott 1995, Poschlod et al. 2009, Ellenberg & Leuschner 2010, Hejcman et al. 2013, reviewed by Dengler et al. 2014). Such grasslands are mainly used for grazing or hay-making, but might also represent successional stages of abandoned arable fields. Moreover, grasslands provide essential ecosystem services (Bruun & Ejrnæs 1998, Gibson 2009, Zavaleta et al. 2010, reviewed by Moeslund et al. 2013) and are important habitats for many light-demanding and nitrophobic red list plant species (Meadows of Nechernozemie 1984, Bulokhov 2001, Semenishchenkov 2009, Dengler et al. 2014). The presence of a wide range of redlist species makes extensively managed meadows biodiversity hot-spots.

Mainland meadows of the East European forest zone are formed and maintained by human activities. In most studies, anthropogenic impact and soil pH have been shown to be the most important determinants of local vegetation patterns in grasslands (Saunders et al. 1991, Hansson & Fogelfors 2000, Stevens et al. 2004, Maskell et al. 2010, Reitalu et al. 2010, reviewed by Moeslund et al. 2013), although some studies also mention the role of other abiotic factors and topography (Moeslund et al. 2013). The impact of abiotic and biotic factors on species assemblage composition (abundance and species richness) is of major interest in conservation ecology (Habel et al. 2013).

Semi-natural grasslands were widespread in Europe at the turn of the XX century. During the last century, due to changes in land use, the area of semi-natural grasslands decreased across whole Europe (van Dijk 1991, Rūsiņa 2006, Zelnik & Čarni 2013, Dengler et al. 2014). Not only has the area declined dramatically, but their condition has also suffered due to factors such as fragmentation, improper management and using synthetic fertilisers and pesticides, increased cutting frequency and lowered cutting height in meadows, higher stocking rates on pastures as well as frequent re-sowing with artificial seed mixtures (van Dijk 1991, Myśliwy & Bosiacka 2009, Dengler et al. 2014). Further sources of threat include eutrophication through airborne nitrogen deposition and, in some cases, biotic invasions (Janišová et al. 2011). Grassland loss through transformation into arable land, quarries or settlements and infrastructure also occurred; however, it is generally of lower importance than the twin threats of intensification and abandonment (Valkó et al. 2012).

This trend leads to a strong decrease in biodiversity. Successional changes in grassland communities, with many red-listed species disappearing from them, is still taking place. Large areas of grasslands become overgrown with shrub and woody vegetation, which has negative consequences for conservation and restoration of meadow communities (Falińska 1999, Korobeynikova 2002, Helm et al. 2006, Gornov & Evstigneev 2011, Evstigneev 2012, Budzhak et al. 2016). Nowadays species-rich semi-natural grasslands, also termed High Nature Value grassland (Veen et al. 2009), are under threat and included in the European Red List of Habitats (2016). Today many of the European grassland ecosystems of high conservation value are threatened by the change of the very land use that formerly created and maintained them, i.e. replacement of traditional management systems with intensification, abandonment, afforestation etc. (Valkó et al. 2012, WallisDeVries et al. 2002, Öckinger et al. 2006, Veen et al. 2009, reviewed by Habel et al. 2013).

According to van Dijk (1991), important efforts have been made for the protection of threatened habitats and species over the past one hundred years of nature conservation. However, grassland and arable land vegetation has been neglected in the development of effective conservation actions (van Dijk 1991). Traditional biodiversity conservation started with nature reserves from which all kinds of human impact (including grazing) were excluded.

In the case of European grasslands, strict exclusion of human land use most often leads to a loss of grassland area due to succession into scrubland and forest (Pärtel et al. 2005). They do not fit the usual protection systems because they are maintained by anthropogenic influence. Therefore, meadows in the territories of reserves are also under threat. However, the actual drivers of local grassland plant diversity patterns are not fully understood, and hence, conserving and managing these semi-natural habitats is challenging (Moeslund et al. 2013, Zelnik & Čarni 2013, Habel et al. 2013).

The aim of our study carried out in NW Russia is to survey grasslands remaining after several decades of protection regime in the Central Forest Nature Reserve. We addressed the following questions: 1) How strong is the variety of grassland vegetation in the reserve and adjacent territories; 2) How variable are different vegetation types in terms of species richness, species diversity, type of management and site conditions; 3) What are the differences in functional and coenotic structure of the floristic composition in different community types.

Materials and methods

Study area

The research was carried out in the territory of the Central Forest State Nature Biosphere Reserve (CFR), Tver Oblast, Russia (Figure 1).The Central Forest Reserve was established in 1931. The core area comprises 21,348 ha, the transition area 46,061 ha (Minyaev & Konechnaya 1976). The reserve is located in the SW part of the Valdai Upland within the main Caspian-Baltic watershed of the Russian plain (Latitude: 56° 26' – 56° 39' N, Longitude: 32° 29' – 33° 01' E). The relief is mostly flat, with only low and generally gentle slopes of riverbanks and streams. The soils are sod-podzolic and gley-podzolic (Minayeva & Shaposhnikov 1999).

The climate is humid continental (Minayeva & Shaposhnikov 1999). The mean annual rainfall for the period 1963–2014 is 760 mm (510 to 1050 mm in different years). The mean January temperature is –8.6 °C (the absolute minimum is –39.4° C), and the mean July temperature is +16.9 °C (the absolute maximum is +36.5 °C). Long-term climatic data were obtained from the meteorological station "Forest reserve" (http://www.clgz.ru/page.php?al=sci_monitor), which is available as database from the archive of the Central Forest Reserve.

The territory of the Central Forest Reserve belongs to the mixed coniferous forest zone. Forests represent the prevailing vegetation type: spruce forests cover 47% of the whole area, mixed secondary forests 40%. Boggy pine forests occupy 9%, oligotrophic and mesotrophic mires 4%. The area of meadows is much smaller and occupies less than 1% of the territory (Kurayeva et al. 1999).

Figure 1: Location of the study area. The red dot indicates the reserve location. The red line is the border of Tver Oblast.

Slika 1: Lokacija preučevanega območja. Rdeča točka prikazuje lokacijo rezervata. Rdeča črta je meja Oblasti Tver.

According to floristic studies of Konechnaya (2012), 43 red-listed species were noted in the territory of the reserve. These species are listed in the IUCN Red List of Threatened Species of Russia (Red Data Book of the Russian Federation) (three species) and the IUCN Red List of Threatened Species of Tver Oblast (Red Data Book of Tver Oblast) (40 species).

Object of research

The object of our research is herbaceous vegetation (meadows and ruderal communities) under protection regime in the CFR and under agricultural use in adjacent territories. All biosphere reserves must contain zones free of human interference (core area), buffer zones commonly used for cooperative activities compatible with sound ecological practices such as educational and research activities and transition areas where restricted agricultural use is allowed (http://www.unesco.org/). Thus, the grasslands of the core area have not been in use due to the protection regime since the early 1960s. In the grasslands of the transition area, agricultural use is allowed, but most of them are abandoned nowadays. In addition to the protected herbaceous vegetation, we explored managed grasslands to identify features associated with management.

In the core area of the CFR, herbaceous vegetation occurs only as small patches in the places of former settlements (villages, farmsteads, forest huts). Most of the grasslands were abandoned 30–60 years ago. After that, the vegetation of hay meadows and pastures began to change. Some communities still look like grass-forb meadows. Others have completely changed into shrub or forest vegetation. Large areas are covered by ruderal tall-herb stands with dominance of forbs (*Urtica dioica*, *Anthriscus sylvestris*, *Chamaenerion angustifolium* etc.). These communities can be found in the places of abandoned houses, backyards and vegetable gardens in former villages. In the transition area and the (one kilometre) buffer zone, meadows occupy large areas around villages. Most of them are abandoned, others are used at present. The managed meadows are comparatively small and characterised by mixed extensive usage (mowing and grazing). They were studied in the vicinities of CFR headquarters and around inhabited villages situated in both buffer zone and transition area of the reserve and in adjacent territories.

Data collection

The data discussed below was collected in 2013 and 2014. The two years were similar in climatic conditions: The annual rainfalls were 715.6 mm and 725.7 mm, respectively. The mean January temperatures were −9.8 °C and −10.0 °C, the mean July temperatures +17.0 °C and +18.3 °C (respectively), which is close to the long-term average.

Our study was based on 209 relevés of herbaceous vegetation. We made 88 relevés in six sites (Ovsyaniki, Mezha, Krasnoye, Starosel'e, Zapovedniy, Fyodorovskoe) in the South of the reserve in 2013 and 111 relevés in nine sites (Moshary, Kruglaya Luka, Trozhkov Lug, Bol'shoe Makarovo, Shlyuz, Gusevka, Osinovka, Pogorelka, Gorbunovka) in the North and 10 relevés (Zapovedniy) in the South of the reserve in 2014 (Figure 2). Thus, we investigated most of the meadows in the core area of the CFR. The plot size of each relevé was 100 m^2, which is considered appropriate for grassland vegetation (Mirkin & Naumova 2012, Baranova et al. 2016, Belonovskaya et al. 2016, Budzhak et al. 2016). Our relevés represent almost all herbaceous communities in the reserve according to physiognomy and land use type. Samples were placed using the method of preferential selection of sites considered typical and homogenous (Gauch 1982). The relevés were compiled in homogenous appearing contours of vegetation along the visible gradients of the relief, as a rule from the edge to the centre of the meadow to cover the entire diversity of plant communities of each site. The distance between the plots depended on the size of the homogeneous plant community contour: the smaller the contours, the smaller the distance between

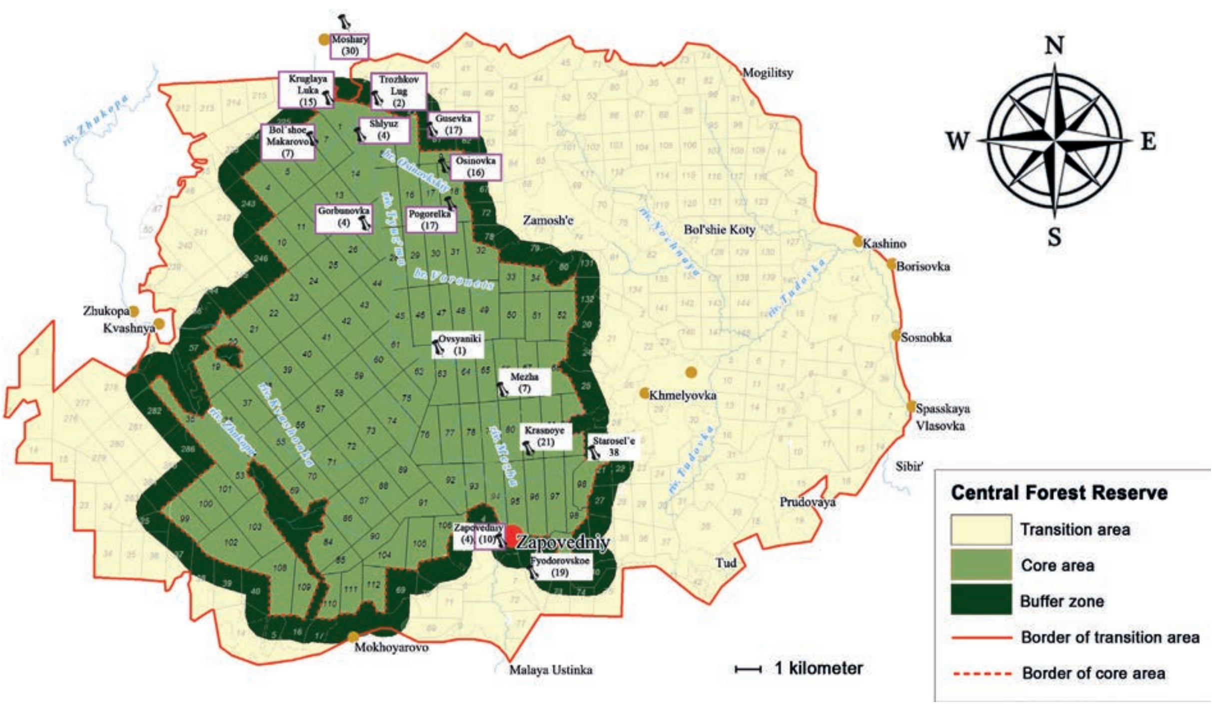

Figure 2: Location of the explored sites in the territory of the reserve (no frame – explored in 2013; purple frame – explored in 2014).
Slika 2: Lokacija preučevanih rastišč na območju rezervata (brez okvirja – preučevano leta 2013; vijoličast okvir – preučevano leta 2014).

the plots. Nevertheless, the minimum distance between neighbouring plots was 10 m, as was the minimum distance to the nearest forest edge. If there were single trees in the meadow, the plots were placed to exclude the influence of tree roots. Shading during the day took place on abandoned sites in some cases due to the small area of these sites.

To identify specific features of herbaceous vegetation under protection regime, we took relevés of abandoned communities in the core area as well as managed meadows in buffer zone, transition area and adjacent territories. Within the sample plots we collected the following data: (1) species composition of vascular plants; (2) species abundance (according to the scale of Braun-Blanquet (1964)); (3) total live vegetation cover (as area percentage); (4) height of the herbage layer, (5) presence and character of disturbance, (6) management pattern, (7) geodata (using a Garmin GPS), (8) micro- and mesorelief features. Species names are given after Cherepanov (1995).

Especially, we put stress on the presence of two particular groups of species as related to the type of community and the management: red list species and alien (including invasive) ones. The list of alien and invasive species follows Vinogradova et al. (2011). The list of red list species follows the Red Data book of the Russian Federation (plants and fungi) (2008) and the Red Data Book of Tver Oblast (2002).

Data analysis

Classification of vegetation was carried out by cluster analysis (flexible beta method using PC-ORD v.6 software, $\beta = -0.25$). To check the significance of the differentiated clusters, we then proceeded with a Multi-Response Permutation Procedure based on Euclidian (Pythagorean) dissimilarity distance measure (Peck 2010, McCune & Mefford 2011). Diagnostic species of the vegetation units (clusters) were identified using Indicator Species Analysis (phi coefficient (Tichý & Chytrý 2006)) with randomisation test realised in the PC-ORD v.6 software (Peck 2010, McCune & Mefford 2011). Species with phi values above 0.25 were considered to be diagnostic and those with values above 0.5 as highly diagnostic (Chytrý 2007).

The site conditions were characterised by calculating cover-weighted averages of Landolt's and Ramensky's ecological indicator values (Ramensky et al. 1956, Landolt et al. 2010) for each plot using EcoScale v.5 software (Grokhlina & Khanina 2015). We choose four Landolt indicators for the analysis (F – soil moisture, N – soil nitrogen pool, L – light, R – soil reaction) and one Ramensky indicator (PD1 – grazing intensity for the forest zone).

The functional composition of community types was studied by calculating shares of forbs and graminoids in the total species number for each relevé. The coenotic composition was analysed according to Ulanova & Zhmylev (2014). Coenotic groups are species assemblages confined to main vegetation types of the region (Yurtzev & Kamelin 1991). We used the system of coenotic groups proposed by Ulanova and Zhmylev for the Moscow region. They reveal coenotic affiliation of 1209 species of vascular plants. As a result, 13 coenotic groups could be distinguished: forest species – grow only or predominantly in forest communities (including floodplain willows); meadow species – only or predominantly in meadow communities (including steppe meadows and large glades); mire species – only or predominantly in mires of different types; aquatic species – only or predominantly in water and riparian communities (including temporary ponds, streams and springs); weed species – only or predominantly in synanthropic communities; forest-meadow – in forests and meadows; forest-mire – in forests and mires; meadow-aquatic – grow in meadows and riparian water communities; meadow-mire – in meadows and mires; aquatic-mire – in riparian water communities and mires; weed-forest – in synanthropic and forest communities; weed-meadow – in synanthropic and meadow communities; weed-mire species – in synanthropic and mire communities. The distribution of species recorded in our study among these groups can be found in Appendix 1.

In this analysis, only the native fraction of the flora (257 species) was included; the alien species became the object of another analysis. In total, the flora of the investigated meadows included species from 12 out of 13 coenotic groups. There were no species of the aquatic species group. In addition, 12 species (four of which belonged to the genus *Pilosella* and two to the genus *Dactylorhiza*) were absent in the species list of Ulanova & Zhmylev (2014). For the analysis we have chosen the coenotic groups that are represented in all types of communities and have more than 25 species. Thus, we used the four coenotic groups of forest, meadow, forest-meadow and weed-meadow species. We did not include weed species in the analysis because they were poorly represented in two types of communities.

Diversity was assessed using Simpson diversity index (1-D) (Magurran 2004), which was calculated in PC-ORD v.6. Species richness was estimated as the total number of vascular plant species per plot (100 m²). We used Kruskal-Wallis tests with post-hoc multiple comparisons of mean ranks in Statistica v.10 to compare numerical parameters of clusters revealed: ecological indicator values, species richness, Simpson diversity index, herbage height, shares of coenotic and functional species groups.

Results

Diversity of herbaceous communities

Cluster analysis revealed four herbaceous community types, which differed by physiognomic, ecological and topological criteria (Table 1). The significance of species composition differences between the groups was found by Multi-Response Permutation procedure: A = 0.14, $p < 0.0001$ (A = chance-corrected within-group agreement). Appendix 2 shows diagnostic species for each type of the herbaceous communities according to the results of the indicator species analysis.

Cluster 1 – managed mesic meadows (MMM) (Figure 3a). All MMMs are located in the buffer zone and in the transition area (Fyodorovskoe site), where they are situated around villages and in adjacent territories (Moshary site). This type comprises shortgrass communities with dominance of grasses and meadow forbs on flat places and upper parts of gentle slopes. Diagnostic species were: *Potentilla anserina*, *Leontodon autumnalis*, *Taraxacum officinale*, *Plantago major*, *Cynosurus cristatus* etc. (Appendix 2). We found a total of 177 species of vascular plants (Table 1) in the type. These meadows are characterised by mixed usage with moderate grazing and irregular mowing. Some sites are currently overgrazed.

Cluster 2 – abandoned mesic meadows (AMM) are mostly located in the core area and in the buffer zone and confined to habitats similar to the previous (Figure 3b). In the past these communities were mown, but this usage was ceased more than 25 years ago (in some cases 50–60 years ago). However, until now these communities still appear as typical meadows with dominance of forbs and grasses. Diagnostic species were: *Viola canina*, *Trollius europaeus*, *Acetosa pratensis*, *Hieracium umbellatum*, *Potentilla erecta* etc. (Appendix 2). In AMM we found 182 species of vascular plants (Table 1).

Cluster 3 – meadowsweet tall-herb communities (MTC) (dominated by *Filipendula ulmaria*) form tiny patches located in the core area and in the buffer zone (Figure 3c). These communities developed on wet and mesic soils in small relief depressions and along temporary streams, probably after abandonment of hayfields. Diagnostic species were: *Filipendula ulmaria*, *Viola palustris*, *Galium palustre*, *Crepis paludosa*, *Cirsium palustre* etc. (Appendix 2). In MTC we found 145 species of vascular plants (Table 1).

Cluster 4 – ruderal tall-herb communities (RTC) are located in the core and in the buffer zone of the reserve and occupy habitats heavily disturbed in the past, such as places of abandoned houses and kitchen gardens. They are currently not in use and totally covered with tall herbs, with ruderal and nitrophilous species like *Anthriscus sylvestris*, *Dactylis glomerata*, *Cirsium arvense*, *Urtica dioica*, *Chamaenerion angustifolium* as the main dominants (Figure 3d). We consider the above species as diagnostic (Appendix 2). In most cases RTCs are associated with natural disturbance caused by wild boars rooting for plant rhizomes. In RTC communities we found 156 species of vascular plants (Table 1).

Table 1: Recognised herbaceous community types.
Tabela 1: Obravnavane zeliščne združbe.

Community type	Number of relevès in cluster	Total number of species	Herbage height, mean ± s.e., cm	Presence and character of disturbance	Current state	Management pattern
Managed mesic meadows	51	177	58±4	Low-disturbed	Managed	Mowing, grazing
Abandoned mesic meadows	79	182	75±2	-	Abandoned	Former hayfields and pastures
Meadowsweet tall-herb communities	24	145	100±8	-	Abandoned	Former hayfields and pastures
Ruderal tall-herb communities	55	156	140±4	Soil disturbance: rooting by wild boars	Abandoned	Former kitchen gardens

Figure 3: Photos of community types: a) Managed mesic meadow mowed with a small tractor; b) Abandoned mesic meadow: a young spruce tree (*Picea abies*) on herbaceous background; c) Meadowsweet tall-herb community; d) Ruderal tall-herb community. Photos: O.V. Cherednichenko.

Slika 3: Fotografije rastlinskih združb: a) gojena vlažna travišča, košena z majhnim traktorjem; b) opuščena vlažna travišča: mlade smreke (*Picea abies*) v ozadju; c) visoko steblikovje z brestovolistnim osladom; d) ruderalno visoko steblikovje. Fotografije: O. V. Cherednichenko.

There are some differences in herbage height between MMM, MTC and RTC. In the first case, herbage is significantly shorter than in the last two cases. The RTC are significantly different from all other types of communities, and the herbage is the tallest here. Abandoned mesic meadows are intermediate between MMM and MTC and not significantly different from these types.Our phytoindication approach revealed ecological features of the community types studied (Table 2). MTCs are characterised by the highest values of soil moisture according to the Landolt scale (from wet to very wet).Values for the other community types are significantly lower (p <0.01) and not very different from each other; they all correspond to moderately wet soils (Landolt et al. 2010). Comparatively high values on the soil nitrogen pool scale are characteristic of the RTCs, which can be considered as moderately rich. The values for the other types range from poor to moderately rich soils, and their mean ranks do not differ significantly between each type, but they do differ significantly from the RTCs (p <0.01).The highest values of the light scale are characteristic of the MMMs. Indeed, managed meadows usually occupy large open spaces. All three types of abandoned communities are characterised by lower light availability because they usually have small areas located in glades etc. In addition, the tall herbage of MTCs and RTCs itself produces shade, which increases the proportion of shade-tolerant species in its near-surface layer. Nevertheless, all medians are between 3 and 4 (semi-shaded and open sunny places), so there are only slight differences, although they are statistically significant (p <0.01). Also, differences in the soil reaction scale were revealed. The lowest value on the soil reaction scale was observed in the MMMs (slightly acid) and the highest in the RTCs (neutral). The AMMs and MTCs occupy an intermediate position: The former showed no differences from MMMs, and the latter none from RTCs. In general, all values range from slightly acid to neutral soils (pH 4.5–7.5) according to the Landolt scale.

Table 2: Ecological indicator values for community types revealed. Landolt scale: F – soil moisture, N – soil nitrogen pool, L – light, R – soil reaction; Ramensky scale: PD1 – grazing intensity. Superscripts refer to significant differences between groups (p < 0.01, Kruskal-Wallis test).

Tabela 2: Ekološke indikatorske vrednosti za posamezne združbe. Landoltove vrednosti: F – vlažnost, N – dušik v tleh, L – svetloba, R – reakcija tal; Vrednosti po Ramenskem: PD1 – intenzivnost paše. Nadpisane vrednosti prikazujejo statistično značilne razlike med skupinami (p < 0.01, Kruskal-Wallis test).

Community type	F	N	L	R	PD1
MMM	2.99^{A}	3.17^{A}	3.60^{A}	2.86^{A}	3.81^{A}
AMM	3.11^{A}	3.08^{B}	3.43^{A}	2.88^{AB}	3.32^{B}
MTC	3.62^{B}	3.19^{C}	3.27^{A}	2.97^{BC}	3.27^{C}
RTC	3.12^{A}	3.63^{C}	3.24^{B}	2.96^{C}	3.02^{BC}

The comparison of the types according to the grazing intensity scale (Ramensky et al. 1956) also revealed significant differences (p<0.01, Table 2). For AMMs moderate influence of grazing was typical. For the other community types, the scale indicated a very weak effect or lack of grazing influence.

Species richness and species diversity of herbaceous communities

The flora of herbaceous communities investigated in the Central Forest Reserve consists of 273 species of vascular plants (from 163 genera and 50 families), that is 46.1% of its whole flora, which consists of 592 species (Konechnaya 2012). Moreover, the flora of the explored herbaceous communities accounts for 17.3% of the Tver Oblast checklist (1579 species) (Notov 2005).

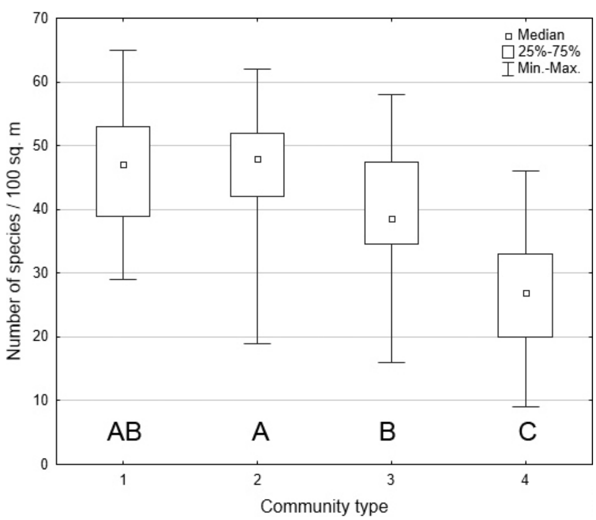

Figure 4: Species richness in four community types: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Capitals refer to significant differences between groups (p<0.05, Kruskal-Wallis test).

Slika 4: Vrstna pestrost v štirih združbah: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Črke kažejo na statistično značilne razlike med skupinami (p<0.05, Kruskal-Wallis test).

The following graph shows no significant differences in species richness (Figure 4) between MMM and AMM (medians are 47 and 48, respectively). The abandoned mesic meadows have the highest values of this parameter, which exceed by far those of MTC and RTC (medians are 39 and 27, respectively). The latter type is significantly poorer in species due to the dominance of tall herbs. The maximum number of species (65) per 100 m^2 was observed in MMM. The minimum number of species (9) per 100 m^2 was noted in RTC. The analysis of species diversity demonstrates that MMM and AMM have higher diversity than MTC and RTC. At the same time there is no significant difference in species diversity between MMM and AMM.

Ratio between graminoids and forbs

The share of graminoid species (with respect to the total number of species per relevé) is significantly higher in MMM than in other types. The smallest fraction of graminoid species is found in RTC. Abandoned mesic meadows and meadowsweet communities are not significantly different by this parameter (Figure 5a). The share of forbs in MMM is significantly lower than in all tall-herb types (MTC and RTC), but not significantly different from the fraction of forbs in AMM (Figure 5b).

Ratio of coenotic groups

For the analysis we selected some coenotic groups well represented in number of species in our dataset, i.e. forest, meadow, forest-meadow and ruderal-meadow species group. As shown in Figure 6, the composition of coenotic groups differs significantly between all community types. Though the largest part of the species totals is always

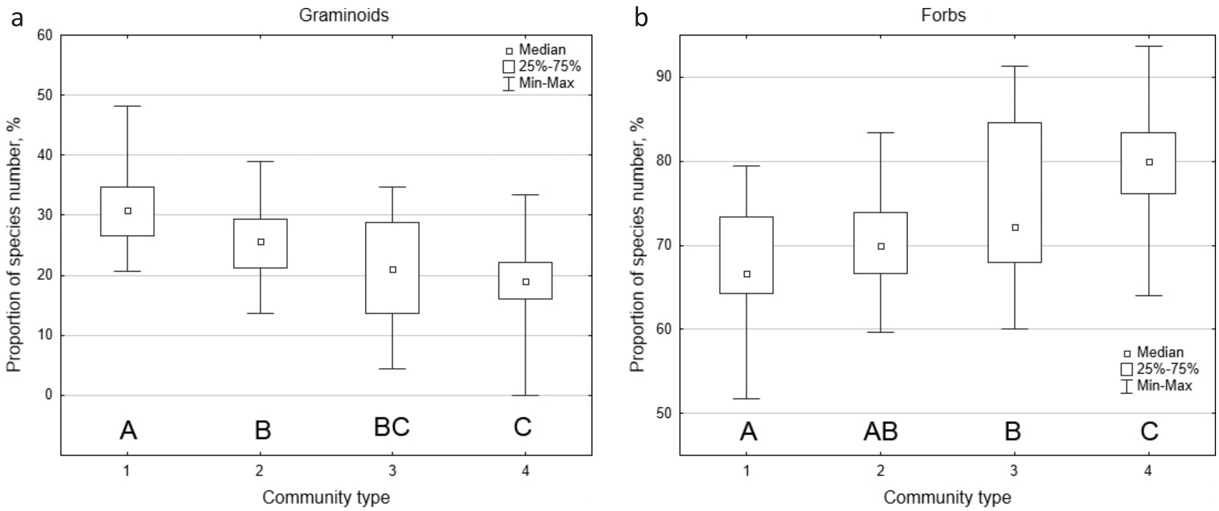

Figure 5: Graminoid (a) and forb (b) diversity in four community types: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Capitals refer to significant differences between groups (p<0.05, Kruskal-Wallis test).

Slika 5: Pestrost trav (a) in zelišč (b) v štirih združbah: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Črke kažejo na statistično značilne razlike med skupinami (p<0.05, Kruskal-Wallis test).

made up of meadow species (median from 30 to 45%), there are significant differences in the share of the group between different community types. Thus we can divide the studied types into two groups by the ratio of meadow species in the herbage: In MMM and AMM, the participation of meadow species is remarkably higher than in RTC and MTC (Figure 6a).

The share of forest species ranges from 2% to 11%, but it is significantly lower in the MMM versus the three other types, which are all abandoned and appear similar by this parameter (Figure 6b). Forest-meadow species (Figure 6c) are best represented in AMM (median 24%), obviously due to the spreading of these species in the absence of agricultural use. Also, a high share of forest-meadow spe-

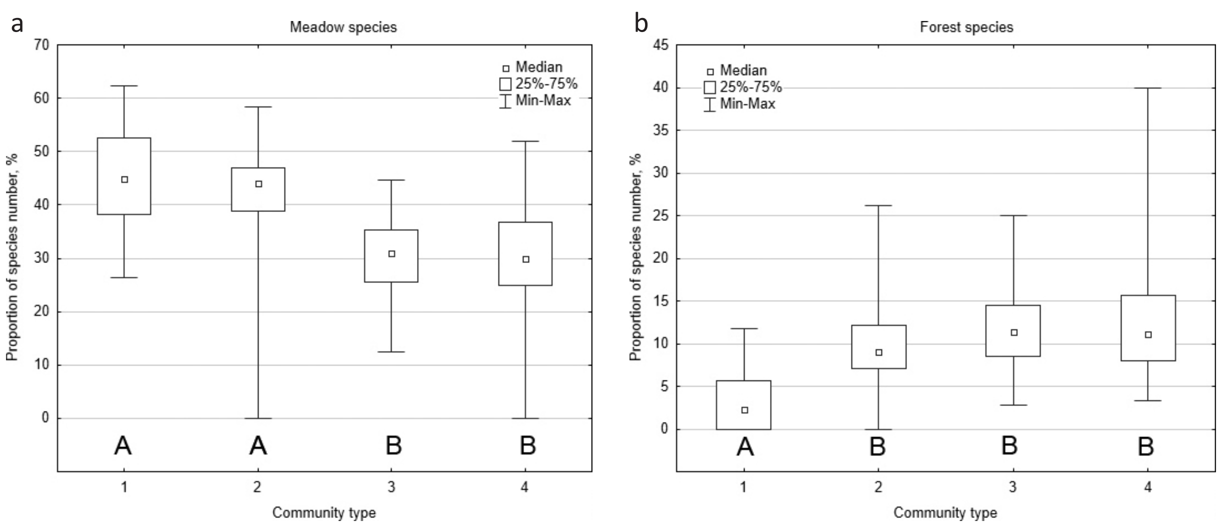

Figure 6: Coenotic groups in four community types: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Capitals refer to significant differences between groups (p<0.05, Kruskal-Wallis test).

Slika 6: Cenotske skupine v štirih združbah: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC. Črke kažejo na statistično značilne razlike med skupinami (p<0.05, Kruskal-Wallis test).

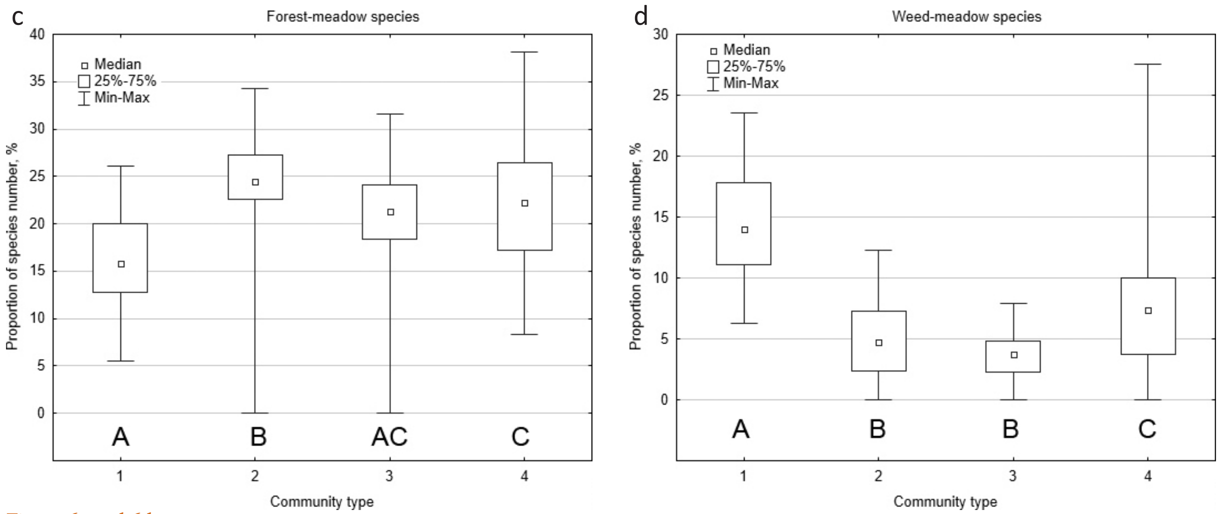

Figure 6c and 6d

cies is characteristic of RTC (but its share is significantly lower than in AMM). The lowest share of these species occurs in MMM (median 16%). The largest participation of weed-meadow species is found in MMM (median 14%) (Figure 6d). This group is comparatively well represented in RTC, too (median 7%), its share being significantly lower than in MMM, but significantly higher than in AMM and MTC (medians 5% and 4%, respectively). Here, the high share of weed-meadow species in managed meadows and ruderal communities suggests a stronger disturbance intensity than in the two other groups. Thus, the spectra of the coenotic groups indicate both the intensity of disturbance and the successional status of the herbaceous communities investigated.

Encroachment of trees

A total of 29 woody species were observed in the four community types. The AMM are the richest in woody species (18 species, 72% frequency). MMM and RTC are similar on the number of woody species and their occurrence: 10 species, 25% frequency in MMM and 10 species, 33% frequency in RTC. MTC occupies an intermediate position by these parameters between the previous two groups and AMM (13 species, 58% frequency). Thus, the frequency of woody species is rather low in disturbed habitats (MMM and RTC).

The most frequently occurring woody species are not the same in different habitats. *Salix caprea* and *Salix myrsinifolia* have the highest frequency (10% each) in MMM; all the other species account for only 2–5%. The AMM are of particular interest for the highest frequency of *Malus domestica* (32%). Two other typical trees here are *Betula pendula* (25%) and *Picea abies* (20%). In MTC the common meadow willow *Salix myrsinifolia* (33%) has the highest frequency, along with some moisture-demanding species: *Alnus incana*, *Betula pubescens*, *Salix aurita* (21% each). In RTC *Malus domestica* is also comparatively frequent (15%), while the occurrence of other species does not exceed 5%.

Alien and invasive species

Sixteen alien species occurred in the community types, including invasive plants (according to the list of Vinogradova et al. (2011)) and cultivated species (Table 3). The number of alien species was highest in AMM, where we found ten species (six invasive and four cultivated). In MMM only seven species (five invasive and two cultivated) were recorded, but here their frequency is the highest among all studied community types. The alien species number in RTC was rather low (three invasive and one cultivated species), while in MTC no alien species were observed at all (Table 3).

Red list species

In the herbaceous community types in the Central Forest Reserve, we found only four red list species recorded by Konechnaya (2012). Of those, *Dactylorhiza baltica* (*D. longifolia*) is listed in the Red Data Book of the Russian Federation. The others (*Salix phylicifolia*, *Coeloglossum viride*, *Gymnadenia conopsea*) are in the Red Data Book of Tver Oblast (2002). All red list species were observed only in abandoned communities. In AMM we found three red list orchids (*Gymnadenia conopsea, Coeloglossum viride, Dactylorhiza baltica*), while one species (*Salix phylicifolia*) is associated with MTC.

Table 3: Frequency (%) of alien species in the four community types. Invasive species are given after Vinogradova et al. (2011). Community types: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC.

Tabela 3: Frekvenca (%) tujerodnih vrst v štirih združbah. Invazivne vrste so podane v skladu z Vinogradova et al. (2011). Združba: 1 – MMM, 2 – AMM, 3 – MTC, 4 – RTC.

Alien species	State	Community type			
		1	2	3	4
Conyza canadensis	Invasive	-	1	-	-
Epilobium adenocaulon	Invasive	14	1	-	2
Festuca arundinacea	Invasive	-	3	-	2
Juncus tenuis	Invasive	35	4	-	-
Lepidotheca suaveolens	Invasive	2	-	-	-
Lolium perenne	Invasive	12	-	-	-
Malus domestica	Invasive	2	32	-	15
Petasites hybridus	Invasive	-	-	-	2
Populus balsamifera	Invasive	-	1	-	-
Cornus alba	Cultivated	2	-	-	-
Dianthus barbatus	Cultivated	-	1	-	-
Lychnis chalcedonica	Cultivated	-	1	-	-
Populus longifolia	Cultivated	-	1	-	-
Rosa rugosa	Cultivated	-	1	-	-
Symphyotrichum sp.	Cultivated	-	-	-	1
Triticum aestivum	Cultivated	4	-	-	-
Number of species		7	10	0	4

Discussion

Our study revealed the coenotic, floristic and functional group diversity of herbaceous vegetation in the Central Forest Reserve to be connected with ecological conditions, productivity and type of management. Until now, the diversity of the reserve's meadows had not been studied. Our results supplement data on species diversity of mainland meadows in the forest zone. Species richness on studied mesic meadows is higher than on mainland meadows in other regions of the forest zone of northern and central Russia (Martynenko 1989, Rabotnov 1984, Marakulina & Degteva 2008).

The results we have obtained indicate a high level of diversity in the studied herbaceous communities and their importance for biodiversity conservation in the CFR because the meadow flora makes up more than 40% of the reserve's whole flora, and the species richness in the studied meadows is comparatively high. Overgrowing of meadows under protection regime is also observed in some other reserves of the forest zone of Russia, for example in the Nizhnesvirsky Nature Reserve (Tikhodeeva et al. 2016) and in the Polistovsky Nature Reserve (Cherednichenko 2014). Thus, meadows in nature reserves of the forest zone require a special protection regime, and an investigation of its features is needed to develop adequate conservation methods.

Nevertheless, our study confirms that mesic meadows are quite stable systems, which retain their characteristics for a long time. In our case, more than 25 years after abandonment, these communities still remain to be meadows. According to Tikhodeeva et al. (2016), woody plants appear and take root on meadows when there is no haymaking for 11–20 years or more; after that, meadows can become overgrown in different ways. If meadows are overgrown by single trees, they retain their structure and species composition for a long time (Tikhodeeva et al. 2016). However, after abandonment the functional composition of meadows changes in course of time.

Factors determining species richness are complicated and often act in opposite directions. An overview by Dengler et al. (2014) discusses the impact of the main leading factors: the availability of mineral nutrients and other soil conditions, topography, climate, intensity of disturbance etc. In spite of the supporting effect of increasing nutrient availability on biomass production and a positive productivity–diversity relationship, negative effects of excess nutrients (especially phosphorus, nitrogen and potassium) on species diversity have been reported for different types of grassland vegetation (Janssens et al. 1998, Austrheim 2002, Hejcman et al. 2010, Merunková & Chytrý 2012 reviewed by Dengler et al. 2014). Our results also prove that ruderal nitrogen-rich communities are poorer in species than mesic meadows.

Apart from site conditions, land use type and intensity can influence species diversity and floristic composition (Wellstein et al. 2007, Dengler et al. 2014). In their investigation of mesic meadows in Germany, Wellstein et al. (2007) have shown that site conditions may have greater influence on species composition than management type. They explained this by the low-intensity usage of these meadows. In our case, too, species richness and diversity and participation of graminoids and forbs in AMM were more similar to MMM than to other abandoned types (moister MTC and RTC on nitrogen-richer soils). However, there remain some differences in species composition between MMM and AMM, reflected in coenotic group spectra and in grazing intensity according to Ramensky's indicator values.

Some features that managed and abandoned mesic meadows have in common can be explained by the fact that the present-day diversity patterns are more affected by former management systems than by present ones (Helm et al. 2006, Reitalu et al. 2014 reviewed by Dengler et al. 2014). We can assume that our abandoned meadows bear some traces of the past management. The former hayfields and pastures also retain some traits of managed meadows, e.g. a significant proportion of graminoids and typical meadow forb species. Ruderal communities are associated with high levels of disturbance in the past and differ greatly from the "real" meadows (grasslands) of the present. Their prevailing disturbance caused by wild boars in essence mimics the specific features of their former use – digging, natural "plowing" and "weeding".

The meadows in and around the Central Forest Reserve are generally under haphazard management. They are mostly used as irregular hayfields and pastures for moderate grazing. However, we have seen a few intensively used sites. In our analysis we did not divide the meadows by the usage intensity, but considered all management types as one group – one reason why we could not find any strong connection between management patterns and either species diversity or richness of meadows. Species numbers and Simpson index of MMM do not significantly differ from those of AMM, though some studies have shown that the highest species diversity is observed at an average level of grazing – something between heavy grazing and abandonment (Dengler et al. 2014). However, the coenotic group composition of the four community types showed significant differences. With a similar share of meadow species in MMM and AMM, there is a greater share of weed-meadow species in MMM, while forest and forest-meadow groups were better represented in AMM.

An increase in the share and diversity of forb species after cessation of agricultural usage has been shown for different types of grasslands in the broad-leaved forest and the forest-steppe zone (Evstigneev 2012, Ronkin & Savchenko 2016). We observed the same trend in case of mesic mainland meadows of the northern forest zone. In abandoned mesic meadows, the share of forb species is significantly greater than in the managed ones, with a higher share of graminoids.

As mentioned above, tree encroachment poses a serious problem in abandoned grasslands. The appearance of woody species (trees and shrubs) favours the further invasion of forest herbs. This process can occur both in dry and wet grasslands and tends to lower biodiversity levels (Helm et al. 2006, Vassilev et al. 2011, Evstigneev 2012, Valkó et al. 2012, Ronkin & Savchenko 2016). The abandoned meadows in the Central Forest Reserve are no exception. We find the highest woody-species diversity (and frequency) in all abandoned types of communities (mesic and moist with meadowsweet) that have experienced the lowest disturbance level. In disturbed communities, encroachment of trees is not going on so fast. Also, abandoned mesic meadows are of particular interest for the highest frequency of *Malus domestica* (32%), which may be caused by the activities of brown bears that feed on apples in abandoned villages and spread the seeds (Zhiryakov 1980, Ogurtsov 2012, 2016). The presence of trees and shrubs in managed meadows is caused by their low-intensity usage in some sites.

It is possible to put the differences in coenotic group composition in connection with some changes in habitats caused by tree encroachment. Our dataset demonstrates an increased role of forest and forest-meadow species in all abandoned (and currently undisturbed) meadows in the study area. Remarkably, the total number of species in abandoned and managed mesic meadows is almost identical (177 and 182 species, respectively), the species richness per 100 m^2 does not differ significantly, and the proportion of meadow species is equally high. This suggests that after abandonment the vascular plant diversity remains at the same level due to a kind of compensation: a significant increase of forest and forest-meadow species on the one hand and a significant decrease of weed-meadow species on the other hand, while the number of meadow species remains at the same level. We could have expected that as the number of tree species has increased, the proportion of meadow species must have declined, and the overall species diversity has decreased in the course of a new forest community formation. In fact, after 25 (in some places even more) years of lack of any management the abandoned meadows still remain to be grasslands and retain a significant proportion of meadow species.

Chytrý et al. (2005) showed that grasslands generally appeared to be quite resistant against vascular plant invasions, with average cover values of neophytes for different grassland types being only 0.1–1.7%. In the studied meadows of the Central Forest Reserve, there is a palpable fraction of alien species (6% of the total number of species), although their average coverage has nowhere exceeded 1% so far.

Over the past 40 years, a number of alien species (*Festuca arundinacea*, *Epilobium adenocaulon*, *Malus domestica*) have naturalised in local plant communities and also increased their presence in the reserve itself. Some species remained in the places of decorative plantings and did not spread farther. But their artificial populations are quite stable and have endured in surrounding grasslands for a long time (more than 40 years), so the threat from their spreading and invasion still remains. One cultivated species, *Cornus alba*, spreads from hedgerows, another, *Triticum aestivum*, was found in a disturbed MMM near an agricultural field. Some species (*Juncus tenuis*, *Lepidoteca suaveolens*) are mainly associated with disturbances. Three species (*Epilobium adenocaulon*, *Juncus tenuis* and *Lepidoteca suaveolens*) have been present in the reserve over decades and already been mentioned by Minyaev & Konechnaya in 1976. *Epilobium adenocaulon* and *Juncus tenuis* used to be rare in the past (Minyaev & Konechnaya 1976), but are nowadays widespread in semi-natural and ruderal communities (Konechnaya 2012). *Lepidoteca suaveolens* has long since been widespread in disturbed habitats (Minyaev & Konechnaya 1976) and remains so these days (Konechnaya 2012). The frequency of *L. suaveolens* in our relevès is low since it prefers heavily disturbed habitats, not meadows. An invasive transformer species, *Festuca arundinacea*, was once cultivated in grass mixtures. Now it occurs in abandoned meadows, but its frequency in the studied communities is extremely low (1%), in contrast to a tendency to spread massively over most of the territory of Tver Oblast (Vinogradova et al. 2011). Thus, regular monitoring is needed as one of the activities to control alien species in the reserve.

Grasslands are habitats of various red list and valuable species (Bruun & Ejrnæs 1998, Gibson 2009, Zavaleta et al. 2010, reviewed by Moeslund et al. 2013). Disappearance of red list species may, as some experts predict (Evstigneev 2012), follow meadow abandonment. The same author believes that red list species persist most successfully in hand-mown herbaceous communities. This might explain the absence of red list species in our RTC because these communities probably emerge in the sites of destroyed houses and abandoned vegetable gardens in former villages. Most likely, many red list species are unable to survive in modern tractor-mown meadows with quite intensive usage (Evstigneev 2012).

Conclusions

We have identified four types of herbaceous communities in the reserve. They are all different in management, productivity (herbage height), floristic composition and ecological conditions. Generally, herbaceous vegetation in the Central Forest Reserve features high ecological, floristic and phytocoenotic diversity. Encompassing around 40% of the reserve flora, the meadows also include four red list species, for which grasslands make the most suitable habitats.

Mesic meadows are relatively stable ecosystems. For more than 25 years without any management, they have retained all the key meadow features, although their area has shrunk and the spread of alien species increased. In the long run, however, meadows under protection regime require special maintenance activities because they can not last on their own, and eventually, the loss of the vegetation will cause a significant loss of biodiversity of the entire protected area. Monitoring of the populations of red list and invasive species is highly required, as well as regular mowing, preferably by hand.

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Appendix 1: Frequency (%) of species in the four community types and coenotic affiliation. Abbreviations: MMM – managed mesic meadows, AMM – abandoned mesic meadows, MTC – meadowsweet tall-herb communities, RTC –ruderal tall-herb communities.* – alien species, [R] – red list species.

Dodatek 1: Frekvenca (%) vrst v štirih združbah in njihova cenotska pripadnost. Okrajšave: MMM – gojena vlažna travišča, AMM – opuščena vlažna travišča, MTC – visoka steblikovja z brestovolistnim osladom, RTC – ruderalna visoka steblikovja.* – tujerodne vrste, [R] –vrste z rdečega seznama.

Species	Coenotic group	MMM	AMM	MTC	RTC
Acetosa pratensis	meadow	47	94	83	13
Acetosella vulgaris	weed	24	-	-	-
Achillea millefolium	meadow	96	94	33	42
Aconitum septentrionale	forest	-	1	-	-
Aegopodium podagraria	forest	2	9	13	22
Agrostis gigantea	meadow	10	3	-	2
Agrostis stolonifera	meadow-mire	8	-	-	-
Agrostis tenuis	forest-meadow	98	97	29	53
Ajuga reptans	forest-meadow	4	18	4	-
Alchemilla vulgaris	forest-meadow	90	91	50	51
Alnus incana	forest-mire	6	15	21	-
Alopecurus geniculatus	meadow-mire	8	-	-	-
Alopecurus pratensis	meadow	-	6	-	4
Angelica sylvestris	forest-meadow	14	82	79	56
Anthemis tinctoria	weed-meadows	1	-	-	-
Anthoxanthum odoratum	meadow	92	89	17	-
Anthriscus sylvestris	forest-meadow	27	41	33	89
Arctium tomentosum	weed	2	-	-	7
Artemisia vulgaris	weed-meadows	8	1	-	18
Asarum europaeum	forest	-	-	4	-
Athyrium filix-femina	forest	2	1	4	4
Barbarea vulgaris	weed	24	-	-	-
Betula pendula	forest	2	25	4	4
Betula pubescens	forest-mire	-	10	21	-
Bistorta major	meadow	10	37	50	11
Botrychium lunaria	forest-meadow	2	-	-	-
Briza media	meadow	45	75	17	5
Bromopsis inermis	weed-meadows	-	-	-	5
Calamagrostis canescens	mire	-	11	42	-
Calamagrostis epigeios	weed-meadows	6	20	54	18
Calamagrostis phragmitoides	indefinite	-	-	4	2
Caltha palustris	mire	2	-	17	-
Campanula glomerata	meadow	16	8	-	-
Campanula latifolia	forest	-	-	-	7
Campanula patula	meadow	55	77	29	24
Campanula rapunculoides	weed-meadows	-	3	-	7
Capsella bursa-pastoris	weed	4	-	-	2
Carduus crispus	weed	6	-	-	7
Carex acuta	aquatic-mire	2	1	4	2
Carex appropinquata	mire	-	-	4	-
Carex brunnescens	forest-mire	-	-	4	-
Carex cespitosa	mire	-	-	-	4
Carex contigua	meadow	63	19	-	4

Species	Coenotic group	MMM	AMM	MTC	RTC
Carex echinata	mire	-	-	8	-
Carex flava	meadow-mire	18	4	21	-
Carex hirta	weed-meadow	27	11	4	5
Carex juncella	indefinite	-	6	8	-
Carex leporina	forest-meadow	90	35	42	4
Carex nigra	meadow-mire	37	28	50	-
Carex pallescens	forest-meadow	67	89	58	7
Carex panicea	meadow-mire	10	3	13	-
Carex vesicaria	aquatic-mire	4	3	25	-
Carum carvi	weed-meadow	59	8	-	-
Centaurea jacea	meadow	80	47	17	7
Centaurea phrygia	meadow	37	97	83	60
Cerastium holosteoides	meadow	92	37	4	-
Chaerophyllum aromaticum	forest	10	15	-	31
Chamaenerion angustifolium	weed-forest	-	15	21	58
Chenopodium album	weed	-	-	-	2
Chrysaspis spadicea	meadow	-	3	-	-
Chrysosplenium alternifolium	forest	-	1	8	5
Cirsium arvense	weed	18	6	4	42
Cirsium heterophyllum	forest-meadow	-	27	54	11
Cirsium oleraceum	forest-mire	2	6	33	13
Cirsium palustre	forest-mire	6	14	67	7
Cirsium vulgare	weed	18	-	-	-
Coccyganthe flos-cuculi	forest-meadow	20	51	67	5
Coeloglossum viride	forest-meadow	-	-	4	-
Comarum palustre	mire	2	-	8	-
Convolvulus arvensis	weed	2	-	4	-
*Conyza canadensis**	weed	-	1	-	-
*Cornus alba**	indefinite	2	-	-	-
Corylus avellana	forest	-	-	-	2
Crepis paludosa	forest	2	29	83	13
Cuscuta europaea	forest-meadow	-	-	-	4
Cynosurus cristatus	meadow	65	9	-	-
Dactylis glomerata	meadow	45	72	38	98
Dactylorhiza baltica[R]	indefinite	-	-	4	-
Dactylorhiza fuchsii	indefinite	2	3	8	2
Dactylorhiza maculata	forest-mire	8	10	17	-
Deschampsia cespitosa	forest-meadow	59	90	58	35
*Dianthus barbatus**	indefinite	-	1	-	-
Dianthus deltoides	meadow	2	-	-	-
Dryopteris carthusiana	forest	-	-	4	2
Dryopteris expansa	forest	-	1	-	-
Dryopteris filix-mas	forest	-	-	-	2
Echium vulgare	weed-meadow	1	-	-	-
Elymus caninus	forest	-	-	-	2
Elytrigia repens	weed-meadow	47	24	8	71
*Epilobium adenocaulon**	weed	16	1	-	2
Epilobium hirsutum	weed-mire	2	-	4	-
Epilobium palustre	mire	2	1	21	-
Equisetum arvense	weed-meadow	51	52	54	29

Species	Coenotic group	MMM	AMM	MTC	RTC
Equisetum fluviatile	aquatic-mire	-	-	8	-
Equisetum palustre	forest-meadow	10	-	29	4
Equisetum pratense	forest-meadow	-	1	-	11
Equisetum sylvaticum	forest	6	18	42	16
Eriophorum polystachyon	mire	2	-	-	-
Erysimum cheiranthoides	weed	-	-	-	2
Euphorbia virgata	weed-meadow	-	-	-	2
Euphrasia brevipila	meadow	24	5	-	-
Fallopia convolvulus	weed	-	-	-	2
*Festuca arundinacea**	weed	-	3	-	2
Festuca pratensis	meadow	100	90	50	51
Festuca rubra	meadow	86	66	21	11
Filipendula ulmaria	meadow-mire	20	48	96	45
Fragaria vesca	forest-meadow	-	4	-	4
Frangula alnus	forest	-	18	-	4
Galeopsis bifida	weed	24	20	8	51
Galeopsis speciosa	weed	39	28	25	69
Galium mollugo	forest-meadow	27	25	8	24
Galium palustre	meadow-mire	-	-	46	-
Galium uliginosum	mire	47	84	75	25
Geranium palustre	forest-mire	22	68	75	76
Geum rivale	meadow-mire	41	46	92	42
Geum urbanum	weed	2	-	-	-
Glechoma hederacea	forest-meadow	-	1	8	4
Gnaphalium uliginosum	weed	2	-	-	-
Gymnadenia conopsea[R]	meadow	-	9	4	-
Heracleum sibiricum	weed-meadow	2	15	-	25
Hieracium umbellatum	forest-meadow	12	44	4	-
Hierochloe odorata	meadow	2	5	21	2
Hylotelephium triphyllum	meadow	-	1	-	-
Hypericum maculatum	forest	65	95	71	58
Juncus articulatus	weed-mire	16	1	-	-
Juncus bufonius	weed-mire	2	-	-	-
Juncus compressus	weed-meadow	-	1	-	-
Juncus conglomeratus	meadow-mire	4	6	4	-
Juncus effusus	meadow-mire	35	24	46	-
Juncus filiformis	meadow-mire	10	27	46	-
*Juncus tenuis**	weed	35	4	-	-
Juniperus communis	forest	-	1	-	-
Knautia arvensis	meadow	29	77	21	38
Lamium maculatum	forest	-	-	4	5
Lathyrus pratensis	meadow	67	54	79	51
Lathyrus sylvestris	forest	-	1	-	5
Leontodon autumnalis	meadow	76	1	-	-
Leontodon hispidus	meadow	24	44	-	-
*Lepidotheca suaveolens**	weed	2	-	-	-
Leucanthemum vulgare	meadow	80	75	4	22
Linaria vulgaris	weed-meadow	-	-	-	2
Linum catharticum	indefinite	2	-	-	-
Listera ovata	forest	2	13	4	-

Species	Coenotic group	MMM	AMM	MTC	RTC
*Lolium perenne**	weed	12	-	-	-
Lonicera xylosteum	forest	-	-	-	1
Luzula multiflora	meadow	51	65	29	-
Luzula pallidula	forest-meadow	2	10	-	-
Luzula pilosa	forest	-	-	-	2
*Lychnis chalcedonica**	indefinite	-	1	-	-
Lysimachia vulgaris	forest-mire	22	15	42	18
Maianthemum bifolium	forest	-	1	-	2
*Malus domestica**	indefinite	2	32	-	15
Matteuccia struthiopteris	forest	-	-	-	2
Melampyrum nemorosum	forest	14	89	54	71
Melandrium album	weed-meadow	2	-	-	-
Melandrium dioicum	forest	-	4	4	16
Mentha arvensis	weed-meadow	27	8	17	2
Mercurialis perennis	forest	-	-	4	-
Milium effusum	forest	-	-	-	2
Myosotis arvensis	weed	12	-	-	4
Myosotis palustris	forest-mire	24	43	25	-
Nardus stricta	meadow	2	6	8	-
Oberna behen	weed-meadow	2	-	-	-
Odontites vulgaris	weed-meadow	-	4	-	4
Omalotheca sylvatica	forest	6	11	-	-
Ophioglossum vulgatum	meadow	-	3	25	4
Padus avium	forest	-	1	-	2
Persicaria amphibia	meadow-aquatic	2	-	-	-
Persicaria minus	weed-meadow	2	-	-	-
*Petasites hybridus**	weed	-	-	-	2
Phalaroides arundinacea	meadow-mire	-	3	8	4
Phleum pratense	meadow	98	91	50	49
Picea abies	forest	-	20	13	5
Pilosella caespitosa	indefinite	4	28	-	2
Pilosella flagellaris	indefinite	4	-	-	-
Pilosella officinarum	forest-meadow	-	11	-	-
Pilosella onegensis	indefinite	12	18	13	2
Pilosella scandinavica	indefinite	2	-	-	-
Pimpinella saxifraga	meadow	41	34	-	9
Pinus sylvestris	forest	-	1	-	-
Plantago lanceolata	meadow	73	49	4	4
Plantago major	weed	71	1	-	2
Plantago media	meadow	18	1	-	2
Platanthera bifolia	forest	18	57	29	5
Poa angustifolia	meadow	76	84	21	35
Poa annua	weed	12	-	-	-
Poa compressa	weed	2	-	-	-
Poa nemoralis	forest	-	1	-	-
Poa palustris	meadow-mire	-	8	4	7
Poa pratensis	meadow	47	8	4	4
Poa trivialis	meadow	33	27	46	18
Polemonium caeruleum	forest-meadow	-	29	54	60
Polygala vulgaris	meadow	6	24	-	-

Species	Coenotic group	MMM	AMM	MTC	RTC
*Populus balsamifera**	indefinite	-	1	-	-
*Populus longifolia**	indefinite	-	1	-	-
Populus tremula	forest	6	5	8	-
Potentilla anserina	weed-meadow	75	-	-	-
Potentilla erecta	forest-meadow	53	95	75	18
Potentilla goldbachii	indefinite	-	1	-	4
Potentilla intermedia	weed	10	-	-	-
Prunella vulgaris	weed	88	47	17	2
Ptarmica vulgaris	meadow	6	-	-	-
Ranunculus acris	meadow	100	85	75	20
Ranunculus auricomus	meadow	20	42	88	9
Ranunculus cassubicus	forest	-	-	17	2
Ranunculus flammula	meadow	10	-	-	-
Ranunculus repens	aquatic-mire	88	20	25	7
Raphanus raphanistrum	weed	8	-	-	-
Rhinanthus minor	meadow	25	13	-	2
Rhinanthus serotinus	weed-meadow	4	-	-	-
Ribes nigrum	forest	-	-	-	1
Rorippa palustris	weed-mire	6	-	-	-
Rosa majalis	forest	-	1	-	2
*Rosa rugosa**	indefinite	-	1	-	-
Rubus idaeus	weed-forest	-	-	4	13
Rumex confertus	weed-meadow	2	1	-	-
Rumex crispus	weed-meadow	31	4	-	2
Rumex longifolius	meadow	2	1	8	2
Rumex obtusifolius	weed-forest	2	4	4	9
Sagina procumbens	weed	14	-	-	-
Salix aurita	mire	2	18	21	-
Salix caprea	forest	10	9	4	-
Salix cinerea	mire	6	1	4	-
Salix myrsinifolia	meadow-mire	10	16	33	2
Salix pentandra	mire	4	-	4	-
Salix phylicifolia[R]	indefinite	-	-	4	-
Salix rosmarinifolia	meadow-mire	-	-	4	-
Salix starkeana	meadow-mire	-	8	4	2
Scirpus sylvaticus	aquatic-mire	6	5	33	9
Scrophularia nodosa	forest	-	-	8	9
Scutellaria galericulata	forest-mire	-	-	25	-
Selinum carvifolia	forest	-	3	-	-
Solanum dulcamara	forest-mire	-	-	13	-
Solidago virgaurea	forest-meadow	2	18	-	2
Sorbus aucuparia	forest	-	1	-	-
Stachys palustris	weed-mire	4	5	-	4
Stachys sylvatica	forest	2	1	-	2
Stellaria graminea	meadow	92	95	54	60
Stellaria holostea	forest	-	11	21	5
Stellaria nemorum	forest	-	3	-	7
Succisa pratensis	forest-meadow	33	73	46	2
Symphyotrichum sp.*	indefinite	-	-	-	1
Taraxacum officinale	weed-meadow	80	6	-	4

Species	Coenotic group	MMM	AMM	MTC	RTC
Thalictrum aquilegifolium	forest	-	8	29	27
Thalictrum flavum	meadow-mire	-	-	4	2
Thalictrum lucidum	forest-meadow	2	9	-	9
Thlaspi arvense	weed	-	-	-	2
Tilia cordata	forest	-	1	-	2
Trientalis europaea	forest	-	-	4	-
Trifolium hybridum	weed-meadow	55	38	-	2
Trifolium medium	forest-meadow	57	82	21	78
Trifolium pratense	weed-meadow	82	25	-	2
Trifolium repens	weed-meadow	82	24	-	7
Tripleurospermum inodorum	weed	18	-	-	-
*Triticum aestivum**	indefinite	4	-	-	-
Trollius europaeus	meadow	12	81	67	29
Urtica dioica	weed-forest	8	1	17	67
Valeriana officinalis	meadow	6	11	54	9
Veronica chamaedrys	forest-meadow	82	99	83	75
Veronica longifolia	meadow	-	8	13	11
Veronica officinalis	forest	-	9	4	-
Veronica scutellata	mire	2	-	4	-
Veronica serpyllifolia	weed-meadow	20	-	-	-
Viburnum opulus	forest	-	1	-	-
Vicia cracca	meadow	94	86	63	80
Vicia sepium	meadow	29	34	46	47
Vicia villosa	weed	2	-	-	-
Viola arvensis	weed	4	-	-	-
Viola canina	forest-meadow	6	42	4	9
Viola epipsila	forest-mire	-	1	4	-
Viola nemoralis	indefinite	-	15	4	-
Viola palustris	forest-mire	-	15	67	2
Viola tricolor	weed	-	-	-	9
Total number of species		177	182	145	156

Appendix 2: Diagnostic species of different community types according to phi coefficient. Only species with phi >0.25 are shown; phi coefficient values for the highly diagnostic species are highlighted in bold. Monte Carlo test of significance of the observed maximum indicator value for each species, with 999 randomisations, including p-values.

Dodatek 2: Diagnostične vrste različnih združb glede na fi koeficient. Prikazane so samo vrste s koeficientom fi >0.25; fi koeficienti za pomembne diagnostične vrste so prikazani krepko. Monte Carlo test statistične značilnosti maksimalne indikatorske vrednosti za posamezno vrsto z 999 slučajenjem vključno z p-vrednostmi.

Herbaceous community type	Phi	Mean	Standard deviation	p-value
Managed mesic meadows (MMM)				
Potentilla anserina	**0.829**	**0.089**	**0.047**	**0.0002**
Leontodon autumnalis	**0.827**	**0.09**	**0.046**	**0.0002**
Taraxacum officinale	**0.777**	**0.089**	**0.046**	**0.0002**
Plantago major	**0.772**	**0.089**	**0.046**	**0.0002**
Cynosurus cristatus	**0.659**	**0.089**	**0.047**	**0.0002**
Cerastium holosteoides	**0.655**	**0.088**	**0.045**	**0.0002**
Ranunculus repens	**0.654**	**0.087**	**0.045**	**0.0002**
Trifolium pratense	**0.649**	**0.088**	**0.045**	**0.0002**
Trifolium repens	**0.632**	**0.087**	**0.046**	**0.0002**
Carum carvi	**0.626**	**0.089**	**0.046**	**0.0002**
Carex leporina	**0.57**	**0.088**	**0.045**	**0.0002**
Prunella vulgaris	**0.541**	**0.088**	**0.045**	**0.0002**
Carex contigua	**0.529**	**0.09**	**0.047**	**0.0002**
Poa pratensis	0.488	0.09	0.047	0.0002
Juncus tenuis	0.477	0.089	0.046	0.0002
Centaurea jacea	0.456	0.088	0.045	0.0002
Barbarea vulgaris	0.433	0.09	0.049	0.0002
Acetosella vulgaris	0.433	0.091	0.049	0.0002
Rumex crispus	0.421	0.09	0.047	0.0002
Plantago lanceolata	0.41	0.088	0.046	0.0002
Festuca rubra	0.402	0.088	0.044	0.0002
Veronica serpyllifolia	0.393	0.091	0.048	0.0002
Ranunculus acris	0.373	0.086	0.044	0.0002
Cirsium vulgare	0.372	0.093	0.049	0.0002
Tripleurospermum inodorum	0.372	0.092	0.048	0.0002
Euphrasia brevipila	0.339	0.09	0.047	0.0004
Trifolium hybridum	0.339	0.088	0.045	0.0004
Sagina procumbens	0.326	0.091	0.051	0.0004
Juncus articulatus	0.318	0.091	0.047	0.0016
Plantago media	0.315	0.091	0.048	0.0004
Festuca pratensis	0.309	0.086	0.043	0.0002
Leucanthemum vulgare	0.303	0.087	0.044	0.0006
Poa annua	0.302	0.09	0.052	0.0022
Lolium perenne	0.302	0.089	0.052	0.0028
Epilobium adenocaulon	0.29	0.092	0.046	0.0022
Phleum pratense	0.287	0.086	0.043	0.0002
Ranunculus flammula	0.275	0.092	0.049	0.001
Potentilla intermedia	0.275	0.092	0.048	0.002
Mentha arvensis	0.272	0.091	0.048	0.0036
Abandoned mesic meadows (AMM)				
Viola canina	**0.519**	**0.089**	**0.046**	**0.0002**
Trollius europaeus	0.469	0.087	0.045	0.0002

Herbaceous community type	Phi	Mean	Standard deviation	p-value
Acetosa pratensis	0.464	0.087	0.045	0.0002
Hieracium umbellatum	0.459	0.088	0.045	0.0002
Potentilla erecta	0.45	0.087	0.044	0.0002
Briza media	0.446	0.088	0.046	0.0002
Succisa pratensis	0.445	0.089	0.046	0.0002
Knautia arvensis	0.415	0.087	0.044	0.0002
Platanthera bifolia	0.407	0.089	0.047	0.0002
Anthoxanthum odoratum	0.404	0.088	0.045	0.0002
Carex pallescens	0.397	0.088	0.045	0.0002
Centaurea phrygia	0.39	0.086	0.044	0.0002
Melampyrum nemorosum	0.387	0.087	0.044	0.0002
Pilosella sp.	0.387	0.09	0.047	0.0002
Leontodon hispidus	0.383	0.089	0.046	0.0002
Galium uliginosum	0.362	0.087	0.044	0.0002
Deschampsia cespitosa	0.356	0.088	0.043	0.0004
Angelica sylvestris	0.345	0.086	0.044	0.0002
Frangula alnus	0.345	0.091	0.048	0.0004
Polygala vulgaris	0.345	0.09	0.047	0.0004
Malus domestica	0.336	0.089	0.046	0.0004
Betula pendula	0.335	0.089	0.047	0.0006
Campanula patula	0.328	0.088	0.045	0.0004
Agrostis tenuis	0.313	0.086	0.043	0.0002
Hypericum maculatum	0.31	0.087	0.043	0.0002
Alchemilla vulgaris	0.308	0.088	0.044	0.0006
Solidago virgaurea	0.299	0.09	0.047	0.0008
Myosotis palustris	0.297	0.09	0.046	0.0012
Poa angustifolia	0.282	0.087	0.044	0.0002
Ajuga reptans	0.271	0.091	0.047	0.0016
Meadowsweet tall-herb communities (MTC)				
Viola palustris	**0.624**	**0.091**	**0.048**	**0.0002**
Galium palustre	**0.623**	**0.09**	**0.047**	**0.0002**
Crepis paludosa	**0.611**	**0.089**	**0.046**	**0.0002**
Cirsium palustre	**0.578**	**0.088**	**0.047**	**0.0002**
Ranunculus auricomus	**0.541**	**0.088**	**0.045**	**0.0002**
Filipendula ulmaria	0.489	0.087	0.045	0.0002
Valeriana officinalis	0.483	0.088	0.046	0.0002
Calamagrostis canescens	0.458	0.09	0.047	0.0002
Scutellaria galericulata	0.447	0.09	0.052	0.0002
Geum rivale	0.422	0.087	0.045	0.0002
Cirsium heterophyllum	0.398	0.089	0.046	0.0002
Calamagrostis epigeios	0.383	0.088	0.046	0.0004
Ophioglossum vulgatum	0.367	0.092	0.047	0.0006
Carex vesicaria	0.367	0.092	0.048	0.0008
Equisetum palustre	0.364	0.091	0.048	0.0004
Epilobium palustre	0.36	0.091	0.05	0.0004
Scirpus sylvaticus	0.343	0.089	0.048	0.0008
Coccyganthe flos-cuculi	0.339	0.088	0.045	0.0006
Caltha palustris	0.334	0.092	0.047	0.0004
Ranunculus cassubicus	0.334	0.093	0.049	0.001
Cirsium oleraceum	0.332	0.089	0.047	0.0004

Herbaceous community type	Phi	Mean	Standard deviation	p-value
Juncus filiformis	0.332	0.089	0.046	0.001
Solanum dulcamara	0.311	0.098	0.047	0.0012
Equisetum sylvaticum	0.294	0.09	0.048	0.0042
Hierochloe odorata	0.287	0.09	0.047	0.003
Bistorta major	0.272	0.089	0.046	0.0044
Carex nigra	0.265	0.089	0.046	0.0054
Betula pubescens	0.257	0.09	0.048	0.0094
Juncus effusus	0.254	0.088	0.046	0.007
Ruderal tall-herb communities (RTC)				
Urtica dioica	**0.645**	**0.09**	**0.047**	**0.0002**
Chamaenerion angustifolium	0.481	0.089	0.047	0.0002
Anthriscus sylvestris	0.457	0.088	0.044	0.0002
Cirsium arvense	0.38	0.089	0.047	0.0002
Elytrigia repens	0.373	0.088	0.045	0.0004
Dactylis glomerata	0.37	0.087	0.044	0.0002
Galeopsis bifida	0.325	0.09	0.046	0.0002
Galeopsis speciosa	0.316	0.087	0.045	0.0004
Polemonium caeruleum	0.315	0.088	0.045	0.0006
Rubus idaeus	0.285	0.092	0.048	0.0016
Viola tricolor	0.269	0.092	0.048	0.0026
Artemisia vulgaris	0.264	0.09	0.047	0.0034