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SUCCESSIONAL STATE OF FORESTS IN THE UPPER PLATEAU OF THE VOLGA UPLAND

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Abstract. *Background.* Long-term and intense anthropogenic impact on the forest-steppe nature of the Russian Plain has led to destruction of vast areas with natural vegetation and significant reduction in their biological diversity. Forests as a component of forest-steppe complexes have undergone the most significant transformation. *Materials and methods.* The biodiversity analysis was based on geobotanical descriptions obtained as a result of route and stationary studies of forest vegetation. The structural diversity of communities was assessed by the ratio of ecological-coenotic groups (ECGs) of species in the vegetation cover. To assess the successional state, we used the following parameters: representativeness of potential flora, rate of participation of R-species (explants) in the tree layer, dominance degree, proportion of demographically full-member and immortal populations. *Results and conclusions.* The modern vegetation cover of the upper plateau of the Volga Upland is represented by four formations (pine, birch, aspen, and black alder forests), one group of formations (broad-leaved forests), 34 groups of associations, and 112 associations. It was revealed that the forest flora includes 423 plant species belonging to 257 genera and 85 families. The maximum species richness is noted in the communities of association groups of all the formations dominated by nemoral species. A distinctive feature of the landscape communities of erosion and denudation plains (EDP) is the high constancy of the nemoral species *Convallaria majalis* in the herbaceous cover. Formation of modern forests is regulated by human. Their transformations are caused by a complex combination of felling of different types and intensity, plowing, grazing, and fires. The existing differences in the succession status of forests of different formations are manifested in changing species composition of stands and floristic diversity of all community synusiae (trees, shrubs, grasses).

Keywords: upper plateau of the Volga Upland, forest vegetation, succession status, floristic diversity, synusia

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СУКЦЕССИОННОЕ СОСТОЯНИЕ ЛЕСОВ ВЕРХНЕГО ПЛАТО ПРИВОЛЖСКОЙ ВОЗВЫШЕННОСТИ

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Аннотация. *Актуальность и цели.* Длительное и интенсивное антропогенное воздействие на природу лесостепи Русской равнины привело к уничтожению огромных площадей естественной растительности, произошло значительное сокращение их биологического разнообразия. Наиболее существенную трансформацию как компонент лесостепных комплексов претерпели леса. *Материалы и методы.* Изучение лесной растительности осуществлялось при маршрутных и стационарных исследованиях. Полученные геоботанические описания послужили материалом для анализа биоразнообразия. Структурное разнообразие сообществ оценивалось по соотношению в составе растительного покрова эколого-ценотических групп (ЭЦГ) видов. Для оценки сукцессионного состояния использовались параметры: представленность потенциальной флоры; доля участия R-видов (эксплерентов) в древесном ярусе; степень доминирования; доля демографически полночленных популяций; доля неморальных. *Результаты и выводы.* Современный растительный покров верхнего плато Приволжской возвышенности представлен 4 формациями (сосновые, березовые, осиновые, черноольховые леса), 1 группой формаций (широколиственные леса), 34 группами ассоциаций и 112 ассоциациями. В составе флоры лесов выявлено 423 вида растений, принадлежащих к 257 родам и 85 семействам.

Максимальное видовое богатство отмечено в сообществах групп ассоциаций всех формаций, где наблюдается доминирование неморальных видов. Отличительной особенностью сообществ ландшафтов эрозионно-денудационных равнин (ЭДР) является высокое постоянство в травяном покрове неморального вида – *Convallaria majalis*. Современные леса формируются под воздействием человека и трансформированы в результате сложного сочетания рубок разных типов и интенсивности, распахек, выпаса и пожаров. Существующие различия сукцессионного статуса лесов разных формаций проявляются в изменении видового состава древостоев, флористического разнообразия всех синузий (деревьев, кустарников, трав) сообществ.

Ключевые слова: верхнее плато Приволжской возвышенности, лесная растительность, сукцессионный статус, флористическое разнообразие, синузия

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Introduction

The study region is located in the central and most developed part of the European Russia and occupies the upper plateau of the Volga Upland (within the boundaries of the Penza region). Large amplitude of heights, readily Paleogene permeable rocks, deep groundwater, widespread loess-like, and solifluction Quaternary deposits contribute to the fact that the main processes of landscape formation in this territory are erosions, suffusions, and, less often, solifluctions. The landscapes of the upper plateau of the Volga Upland are combined into a group of erosion-denudation plain (EDP) landscapes [1–5].

Earlier works [3, 6–10] discussed the species composition, structure, ecological features and confinement of the main types of forests in this area. This work analyzes successional state, dynamics, and development forecast (from a population point of view) of forest communities on the upper plateau of the Volga Upland.

Methods of research

The forest vegetation on the upper plateau of the Volga Upland is represented by formations of pine, birch, aspen, and black alder forests, as well as by a group of formations of deciduous forests.

Route and stationary studies of the composition and structure of forest vegetation were conducted on test plots (TP) with a size of 10 m x 10 m (100 m²). The resulting geobotanical descriptions served as material for the analysis of biodiversity.

The structural diversity of communities was assessed by the ratio of ecological-coenotic groups (ECGs) of species, i.e. species ecologically close in their genesis, associated with different types of communities, in the composition of the vegetation cover. We used the ECG classification proposed by O. V. Smirnova and L. B. Zaugolnova [11–13] and refined by the methods of multidimensional statistics by V. E. Smirnov et al. [14] based on the ecological groups proposed by A. A. Nitsenko [15] and taking into account the historical formations

proposed by G. M. Zozulin [16, 17]. All vascular plant species noted in geobotanical descriptions were divided into nine ECGs: nemoral (Nm), boreal (Br), nitrophilous (Nt), oligotrophic (Og), piny (Pn), steppe (St), meadow-forest edge (Md), wetland (Wt), and adventive (AdCult).

Within the forest vegetation, formations were grouped by dominants of the tree layer, with the exception of the group of formations of deciduous forests, which was considered as a whole: pine forests with *Pinus sylvestris* stand as an edificator, aspen forests dominated by *Populus tremula*, birch forests dominated by *Betula pendula*, alder (black alder) forests dominated by *Alnus glutinosa*, and a group of deciduous forest formations dominated by *Quercus robur*. Groups of associations were identified based on the dominance of ECGs in the grass-dwarf shrub layer.

The biodiversity of the vegetation cover was assessed by species saturation on the TP and species (floristic) richness, i.e. the total number of registered species in communities of a certain type, followed by compiling lists of communities of dominant and constant types. Species, for which the numerical value of coverage-abundance on at least one TP included in the description group was at least 40 %, were considered dominant. The constancy (constancy class) of the species was calculated according to the following scheme: 1st class – the species was present on no more than 20 % of plots in the description group, 2nd class – the species was present on from 20 % to 40 % of plots.

To assess the successional state, we used the following parameters [11, 18–21]: representativeness of potential flora – the ratio of the number of species of real flora to the number of species of potential flora in the ecotope (%); the share of participation of R-species (explants) in the tree layer – the ratio of the coverage of explant species to the total coverage of all types of tree canopy (%); the degree of dominance – the ratio of the coverage of the most abundant species to the total coverage of the species included in the layer (%); the share of demographically full-member populations – the share of species with full-member populations

in the total number of synusia species (the indicator was calculated for tree and shrub synusia); the share of nemoral species – the ratio of the total coverage of species of the nemoral group (taking into account the abundance) to the total abundance of grass cover species (%).

To assess the main ecological parameters, the obtained geobotanical descriptions were processed according to the ecological scales by D. N. Tsyganov [22].

Results and discussion

The modern vegetation cover in the EDP landscapes is represented by four formations, one group of formations, 34 groups of associations, and 112 associations (Table 1). The communities contain clear traces of economic activity: intensive grazing, felling, recreational load, and fires.

Table 1

Ecological-coenotic classification of EDP forest vegetation

Association group	Associations
1	2
Pine stand formation – <i>Pineta sylvestris</i> (P)	
<i>Pineta boreo-herbosa</i> (P-Br)	<i>Pinetum equisetum-moliniosum</i> , <i>Pinetum moliniosum</i> , <i>Pinetum myrtillosum</i> , <i>Pinetum calamagrostidosum arundinacii-myrtillosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta nemoro-boreo-herbosa</i> (P-Nm_Br)	<i>Pinetum calamagrostidosum arundinaceae</i> , <i>Pinetum convallarioso-calamagrostidosum arundinaceae</i> , <i>Pinetum vaccinioso-hylocomiosum</i> , <i>Pinetum ruboso saxatili-hylocomiosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta prato-boreo-herbosa</i> (P-Md_Br)	<i>Pinetum equisetosum sylvaticum</i> , <i>Pinetum tilieto-herbosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta aqua-uligino-boreo-herbosa</i> (P-Wt_Br)	<i>Pinetum poeosum palustris</i>
<i>Pineta nemoro-herbosa</i> (P-Nm)	<i>Pinetum coryloso-stellarioso-caricosum pilosae</i> , <i>Pinetum caricosum pilosae</i> , <i>Pinetum aegopodiosum</i> , <i>Pinetum aceroso-convallariosum</i> , <i>Pinetum caricosum digitatae</i> , <i>Pinetum convallariosum</i> , <i>Pinetum stellariosum</i> , <i>Pinetum brachypodiosum-convallariosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta boreo-nemoro-herbosa</i> (P-Br_Nm)	<i>Pinetum calamagrostidosum-brachypodiosum</i> , <i>Pinetum aceroso-convallariosum</i> , <i>Pinetum euonymoso-convallariosum</i> , <i>Pinetum myrtilloso-convallariosum</i> , <i>Pinetum herboso-convallariosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta pine-herbosa</i> (P-Pn)	<i>Pinetum pteridiosum</i> , <i>Pinetum chamaecytisoso-calamagrostidosum epigeios</i> , <i>Pinetum calamagrostidosum epigeios</i>
<i>Pineta boreo-pine-herbosa</i> (P-Br_Pn)	<i>Pinetum herboso-pteridiosum</i> , <i>Pinetum pteridioso-vacciniosum</i> , <i>Pinetum hylocomiosum</i> , <i>Pinetum herbosum</i>
<i>Pineta boreo-prato-herbosa</i> (P-Br_Md)	<i>Pinetum calamagrostidosum arundinacii-fragariosum</i>
<i>Pineta nemoro-prato-herbosa</i> (P-Nm_Md)	<i>Pinetum fragariosum</i> , <i>Pinetum agrostidosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta nemoro-pine-herbosa</i> (P-Nm_Pn)	<i>Pinetum herboso-calamagrostidosum epigeios</i> , <i>Pinetum cladinosum</i> , <i>Pinetum mixto-herbosum</i>
<i>Pineta steppe-nemoro-herbosa</i> (P-St_Nm)	<i>Pinetum coryloso-graminosum</i> , <i>Pinetum aceroso-herbosum</i>
<i>Pineta steppe-herbosa</i> (P-St)	<i>Pinetum querceto-bromopsiosum ripariae</i> , <i>Pinetum querceto-caricosum supinae</i> , <i>Pinetum fragarioso-poeosum angustifoliae</i>
<i>Pineta nitrophilo-herbosa</i> (P-Nt)	<i>Pinetum urticosum</i> , <i>Pinetum mixto-herbosum</i>
Broad-leaved forest formations – <i>Querceta</i> (Q)	
<i>Querceta nemoro-herbosa</i> (Q-Nm)	<i>Quercetum coryloso-caricosum pilosae</i> , <i>Quercetum caricosum pilosae</i> , <i>Quercetum stellariosum</i> , <i>Quercetum convallariosum</i> , <i>Tilieto-Quercetum coryloso-aegopodiosum</i> , <i>Acereto-Tilietum coryloso-aegopodiosum</i> , <i>Aceretum coryloso-aegopodiosum</i> , <i>Quercetum aegopodiosum</i> , <i>Quercetum brachypodiosum</i> и <i>Quercetum mixto-herbosum</i> .
<i>Querceta boreo-nemoro-herbosa</i> (Q-Br_Nm)	<i>Quercetum convallarioso-calamagrostidosum arundinacii</i> , <i>Quercetum rubosum saxatili</i>
<i>Querceta nemoro-pine-herbosa</i> (Q-Nm_Pn)	<i>Quercetum calamagrostidosum epigeios</i> и <i>Quercetum pteridiosum</i>
<i>Querceta nemoro-nitrophilo-herbosa</i> (Q-Nm_Nt)	<i>Quercetum mixto-herbosum</i> , <i>Quercetum caricosum</i> , <i>Quercetum urticosum</i> , <i>Quercetum filipendulosum</i> , <i>Quercetum herboso-urticosum</i>

End of Table 1

1	2
<i>Querceta nemoro-prato-steppe-herbosa</i> (Q-Nm_Md-St)	<i>Quercetum poeosum angustifoliae</i> , <i>Quercetum bromopsiosum ripariae</i> , <i>Quercetum herboso-bromopsiosum inermiae</i> , <i>Quercetum caricosum supinae</i> , <i>Quercetum poeoso angustifoliae-herbosum</i> , <i>Quercetum fruticoso-herbosum</i> , <i>Quercetum mixto-herbosum</i> .
Aspen stand formation – <i>Tremuleta</i> (Pp)	
<i>Tremuleta nemoro-herbosa</i> (Pp-Nm)	<i>Tremuletum convallariosum</i> , <i>Tremuletum aegopodiosum</i> , <i>Tremuletum mixto-herbosum</i> , <i>Tremuletum coryloso-caricoso-aegopodiosum</i> , <i>Tremuletum caricosum pilosae</i> .
<i>Tremuleta boreo-nemoro-herbosa</i> (Pp-Br_Nm)	<i>Tremuletum calamagrostidosum arundinacae</i> и <i>Tremuletum mixto-herbosum</i>
<i>Tremuleta nemoro-pine-herbosa</i> (Pp-Nm_Pn)	<i>Tremuletum pteridiosum</i>
<i>Tremuleta prato-nemoro-herbosa</i> (Pp-Md_Nm)	<i>Tremuletum bromopsioso-brachypodiosum</i> , <i>Tremuletum brachypodiosum</i> и <i>Tremuletum mixto-herbosum</i>
<i>Tremuleta nitrophilo-nemoro-herbosa</i> (Pp-Nt_Nm)	<i>Tremuletum mixto-herbosum</i>
Birch stand formation – <i>Betuleta</i> (B)	
<i>Betuleta nemoro-herbosa</i> (B-Nm)	<i>Betuletum caricosum pilosae</i> , <i>Betuletum aegopodioso-caricosum pilosae</i> , <i>Betuletum aegopodiosum</i> , <i>Betuletum melampyrosom</i> , <i>Betuletum convallariosum</i> , <i>Betuletum brachypodiosum</i> , <i>Betuletum caricosum digitatae</i> , <i>Betuletum mixto-herbosum</i>
<i>Betuleta nemoro-boreo-herbosa</i> (B- Nm_Br)	<i>Betuletum aegopodioso- calamagrostidosum arundinacae</i> , <i>Betuletum herboso-calamagrostidosum arundinacae</i> и <i>Betuletum mixto-herbosum</i>
<i>Betuleta boreo-herbosa</i> (B-Br)	<i>Betuletum rubosum saxatilis</i> , <i>Betuletum mixto-herbosum</i> , <i>Betuletum pyrolosom rotundifoliae</i> , <i>Betuletum molinioso-myrtillisum</i> , <i>Betuletum myrtillosum</i> и <i>Betuletum moliniosum</i>
<i>Betuleta nemoro-pine-herbosa</i> (B-Nm_Pn)	<i>Betuletum calamagrostidoso-pteridiosum</i> , <i>Betuletum hylocomiosum</i> , <i>Betuletum calamagrostidosum epigeios</i> u <i>Betuletum pteridiosum</i>
<i>Betuleta prato-herbosa</i> (B-Md)	<i>Betuletum poeoso angustifolii-fragariosum</i>
<i>Betuleta nitrophilo-herbosa</i> (B-Nt)	<i>Betuletum urticosum</i> и <i>Betuletum mixto-herbosum</i>
<i>Betuleta boreo-aqua-uligino-herbosa</i> (B-Br_Wt)	<i>Betuletum calamagrostidosum canescens</i>
Black alder stand formation – <i>Alneta glutinosa</i> (A)	
<i>Alneta nitrophilo-herbosa</i> (A-Nt)	<i>Alnetum herboso-aegopodiosum</i> , <i>Alnetum aegopodioso-urticosum</i> , <i>Alnetum herboso-urticosum</i>
<i>Alneta nemoro-nitrophilo-herbosa</i> (A-Nm_Nt)	<i>Alnetum athyriosum</i>
<i>Alneta nitrophilo-aqua-uligino-herbosa</i> (A-Nt_Wt)	<i>Alnetum caricosum riparii</i>

We revealed that the forest flora includes 423 plant species belonging to 257 genera and 85 families, among which dicotyledonous flowering plants predominate.

The maximum species richness was noted in the communities of the groups of associations of

all the formations with the dominance of nemoral species, while the total number of species in deciduous forests with nemoral grasses is two or more times more than in other groups of associations (Table 2).

Table 2

The number of plant species in landscapes of erosion-denudation plains

Formation	Association groups	Average species saturation	Number of species:				
			general	trees	shrubs	grasses	mosses and lichens
1	2	3	4	5	6	7	8
P	P-Br	16,3	99	10	10	74	5
	P-Nm_Br	19,1	138	12	10	110	6
	P-Md_Br	15,5	92	10	7	75	
	P-Wt_Br	16,5	24	2	1	21	
	P-Nm	14,2	126	11	9	104	2
	P-Br_Nm	16,8	161	14	11	130	6
	P-Pn	16,2	92	10	9	69	4

End of Table 2

1	2	3	4	5	6	7	8
P	P-Br_Md	22,1	44	5	3	33	3
	P-Br_Pn	19,4	121	13	9	93	6
	P-St_Nm	13,8	58	10	6	42	
	P-Nm_Md	15,5	104	10	7	85	2
	P-Nm_Pn	17,6	128	9	9	104	6
	P-St	17,5	74	6	5	63	
	P-Nt	12,3	55	12	9	34	
Q	Q-Nm	13,7	216	15	9	191	1
	Q-Br_Nm	14,1	60	9	3	48	
	Q-Nm_Md_St	15,3	198	12	13	173	
	Q-Nm_Nt	12,4	95	13	9	73	
	Q-Nm_Pn	16,6	97	10	3	84	
Pp	Pp-Nm	10,7	133	11	6	113	3
	Pp-Br_Nm	12,4	92	10	9	71	2
	Pp-Nm_Pn	15,8	64	7	3	54	
	Pp-Md_Nm	17,5	86	10	6	70	
	Pp-Nt_Nm	9,1	20	6		14	
B	B-Nm	12,6	186	14	10	159	3
	B-Nm_Br	13,7	75	9	7	56	3
	B-Br	14,8	113	11	6	92	4
	B-Nm_Pn	19,6	148	9	9	124	6
	B-Md	26,7	46	4		42	
	B-Nt	8,8	24	5	3	16	
	B-Br_Wt	22,3	49	3	1	45	1
A	A-Nt_Wt	26,3	50	5	1	42	2
	A-Nt	21,4	41	6	1	32	2
	A-Nm_Nt	24,2	86	9	4	71	2

Nemoral broad-leaved forests are leaders in terms of the number of species and the species richness of tree and grass synusia. In second place are deciduous forests with a predominance of species of nemoral, meadow, and steppe ECGs. These communities are characterized by the highest abundance of shrub synusia. Among the formation of pine forests, the maximum species richness is characteristic of communities with a high participation of boreal and nemoral species. Low values of species richness are typical for black alder forests and forests with a high proportion of nitrophilous and wetland ECG species in the herbaceous layer.

The total species richness in the noted communities varies from 9.1 to 26.7 species per 100 m². The lowest value of the total species saturation is typical for nitrophilous birch forests, which is obviously explained by strong anthropogenic transformation of the vegetation of this group of associations and absolute dominance of *Urtica dioica* in the herbaceous layer that leads to the loss of species diversity.

The communities of most groups of associations are characterized by slightly different values of species saturation (10.7–19.6). The highest rates were recorded in meadow birch forests – 26.7 forests and nitrophytic wetland black alder forests forests and nitrophytic wetland black alder forests 26.3 species per 100 m². They were due to the introduction of a large number of meadow-steppe species to the formers and nitrophilous and wetland species to the latters.

The analysis of the flora of the identified formations showed (Table 3) a high vegetation similarity of pine and birch forests, a medium similarity of aspen forests and birch and pine forests, as well as similarity of broad-leaved forests and birch forests, aspen forests and pine forests, which is obviously explained by the similar participation in their species composition of nemoral, meadow, and boreal ECGs as well as similar highly constant species (Table 4).

Table 3

Floristic similarity of formations in EDP landscapes (Jaccard coefficient)

Formation	B	P	Pp	Q	A
B		0.64	0.51	0.53	0.20
P			0.49	0.56	0.19
Pp				0.49	0.15
Q					0.17

Table 4

High-constant types of association groups (4th and 5th constancy classes)

Formation	P														Q				Pp				B				A							
Species	Association group																																	
	Br	Nm_Br	Md_Br	Wt_Br	Nm	Br_Nm	Pn	Br_Md	Br_Pn	St_Nm	Nm_Md	Nm_Pn	St	Nt	Nm	Br_Nm	Nm_Md_St	Nm_Nt	Nm_Pn	Nm	Br_Nm	Nm_Pn	Md_Nm	Nt_Nm	Nm	Nm_Br	Br	Nm_Pn	Md	Nt	Br_Wt	Nt_Wt	Nt	Nm_Nt
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Convallaria majalis	IV	V	IV	V		V	V	V	V	V	V					V			IV	IV	V	IV		V	IV		IV							
Sorbus aucuparia	IV			V		IV	V	V	V	V	IV										IV					V	IV	V			IV		V	IV
Pinus sylvestris	V	V	V	V	V	V	V	V	V	V	V	V	V																					
Betula pendula	IV							V					IV										V		V	V	V	V		V				
Quercus robur					IV						V		IV		V	V	V	V	V				IV			V	V	V						
Calamagrostis arundinacea	IV	IV				IV		V								IV					IV					V		IV						
Fragaria vesca		V	V					V			IV		IV						IV				IV						V					
Populus tremula																				V	V	V	V	V		V		IV						
Calamagrostis epigeios							V			IV		IV							IV									IV	IV					
Stachys officinalis								IV								IV	IV		IV				IV						IV					
Aegopodium podagraria															IV					IV						IV						IV		V
Brachypodium pinnatum											IV					V			V			IV							IV					
Euonymus verrucosa																V			IV	IV					IV	V								
Padus avium														V				V						V							V		V	
Poa angustifolia										IV			V				IV		IV										V					
Rubus saxatilis	IV							V																		V	V			V				
Glechoma hederacea																	IV															IV	V	V
Alnus glutinosa																															V	V	V	
Filipendula ulmaria																																V	V	IV
Lysimachia vulgaris																													IV	V	V			
Melica nutans		IV								IV																								
Pleurozium schreberi		V						V	IV																									
Pyrethrum corymbosum													IV						IV										V					
Tilia cordata					IV																				V	V								
Dryopteris carthusiana																																IV	V	
Frangula alnus																														V		V		
Geum urbanum														IV										IV										
Hieracium umbellatum							V		IV																									
Maianthemum bifolium				V																											V			
Potentilla erecta				V																											V			
Scirpus sylvaticus		V																												V				
Stellaria holostea										IV																				IV				
Trifolium alpestre													IV					V											V					
Urtica dioica																		V																V
Ulmus glabra																														V		IV		
Acer platanoides																										IV								
Achillea millefolium																													IV

End of Table 4

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>Antennaria dioica</i>								IV																										
<i>Athyrium filix-femina</i>																																	V	
<i>Bromopsis riparia</i>																	IV																	
<i>Chamaecytisus ruthenicus</i>												IV																						
<i>Calamagrostis canescens</i>																																	V	
<i>Carex ericetorum</i>								V																										
<i>Carex riparia</i>																																V		
<i>Carex vaginata</i>				V																														
<i>Dactylis glomerata</i>																													V					
<i>Deschampsia cespitosa</i>																																V		
<i>Dicranum scoparium</i>								V																										
<i>Dryopteris cristata</i>																																IV		
<i>Equisetum sylvaticum</i>				V																														
<i>Hieracium pilosella</i>																													V					
<i>Humulus lupulus</i>																														V				
<i>Lathyrus vernus</i>																													IV					
<i>Leucanthemum vulgare</i>																													V					
<i>Lupinaster pentaphyllus</i>								IV																										
<i>Lycopus europaeus</i>																																V		
<i>Melampyrum pratense</i>		IV																																
<i>Molinia caerulea</i>				V																														
<i>Orthilia secunda</i>		IV																																
<i>Phragmites australis</i>																																	V	
<i>Pimpinella saxifraga</i>																														V				
<i>Poa palustris</i>				V																														
<i>Potentilla alba</i>																														IV				
<i>Potentilla argentea</i>																													IV					
<i>Pteridium aquilinum</i>																						V												
<i>Pulmonaria obscura</i>																										IV								
<i>Pulsatilla patens</i>								V																										
<i>Pyrola rotundifolia</i>																																V		
<i>Ribes nigrum</i>																													IV					
<i>Silene viscosa</i>								IV																										
<i>Solidago virgaurea</i>								V																										
<i>Trientalis europaea</i>																																V		
<i>Ulmus glabra</i>																	IV																	
<i>Vaccinium myrtillus</i>	IV																																	
<i>Vaccinium vitis-idaea</i>		IV																																
<i>Urtica dioica</i>																																V		

Note: The species with the highest occurrence in forests and erosion-denudation plain landscapes are highlighted in bold and color.

The phytocenoses are characterized by 74 highly constant species (see Table 4). A distinctive feature of the EDP communities is the high constancy of the nemoral species in the grass cover – *Convallaria majalis*.

Differences in the composition of communities are also expressed in quantitative relationships between different ECGs (Fig. 1). A high participation of species of nemoral, meadow, and boreal ECGs is quite clearly traced in almost all groups of associations.

Fig. 1. The number of species of different ecological-coenotic groups in the flora of association groups in erosion-denudation plain landscapes

The ecological analysis of geobotanical descriptions showed the greatest correlation of different groups of associations with soil characteristics such as moisture and nitrogen content, generalized salt regime, and acidity (Fig. 2). Communities of different formations with a high participation of meadow-steppe species occupy the driest, the richest in peat, poor in nitrogen, and close to neutral habitats. The best soils for forests dominated by boreal ECG species are the most humid, acidic, but poor in terms of the generalized salt regime and nitrogen.

Communities with a high participation of nitrophilous ECG species occupy well-moisturized and nitrogen-rich habitats with weakly acidic soils. The ecological space of groups of associations with a predominance of species of nemoral ECGs have similar scoring indicators and mutually intersect for most environmental factors, while, according to the generalized salt regime factor, nemoral deciduous forests occupy the richest habitats in terms of this environmental factor. Nemoral pine, birch, and aspen forests are characterized by similar lower soil peat content, but differ from each

other in soil moisture content – birch forests occupy the least moisturized soils, whereas aspen forests occupy the wettest soils

The lightest forests are communities with a predominance of meadow-steppe species; they are also characterized by moderately variable soil moisture content. Nemoral deciduous forests are the most shaded forests. Forests with a high proportion of boreal species are characterized by a medium illumination score, but they occupy habitats with relatively stable moisture content.

The assessment of the successional state of the forest cover of the EDP landscapes showed (Table 5, Fig. 3) that all modern forests are strongly transformed and are at different demutation stages after felling of varying degrees of intensity, grazing, fires, and plowing.

In general, all forests are characterized by low preservation rate of ontogenetic abundance of arboreal synusia and floristic diversity in almost all synusiae (see Fig. 3). Approximately 80 % of the area of EDP landscapes is occupied by phytocenoses, in which the forest stand is formed by R-species, which are explants. The highest onto-

genetic abundance of trees were noted in nemoral birch and nemoral pine forests. This is obviously due to the fact that a significant number of trees

can recover from stumps as shrubs under favorable light conditions that develop in these types of forests.

Fig. 2. Distribution of association groups of different formation communities in the ecological space. Environmental factors: Hd – soil moisture content, Nt – soil nitrogen richness, Rc – soil acidity, Tr – generalized salt regime of the soil, Lc – illumination – shading, fH – variability of soil moisture

In the shrub synusia, the greatest preservation rate of floristic diversity is noted in water-boreal aspen forests. The highest ontogenetic abundance is noted in communities with a high proportion of

nemoral species (nemoral pine forests, broad-leaved forests).

In the grass synusia, a low preservation rate of floristic diversity is noted in all types of forests,

while a low participation of species of nemoral ECG is noted in all communities, except for nitrophilous-nemoral aspen forests.

All synusia of pine forests, which cover the main part of the erosion-denudation plain landscapes, are floristically poor. The arboreal layer of these phytocenoses is often formed only by R-species, i.e. explants – *Pinus sylvestris*, *Betula pendula* и *Populus tremula*. Demographically complete populations of trees and shrubs are either absent in them, or their share is small. In the shrub synusia, the largest number of full-member populations is found in nemoral pine forests and only for shade-tolerant species (*Euonymus verrucosa*,

Corylus avellana). The grass layer is characterized by a low proportion of nemoral species.

Broad-leaved forests are “fragments” of polydominant broad-leaved and coniferous-broad-leaved forests transformed by long-term economic activity. The share of participation of R-species (explants) in their stand is one of the lowest among all forest types in EDP landscapes. The degree of floristic richness is low in arboreal and shrub synusia and very low in grass synusia. Demographically full-member populations are characteristic of a small number of shade-tolerant tree and shrub species (*Acer platanoides*, *Tilia cordata*, *Euonymus verrucosa*, *Corylus avellana*).

Table 5

Assessment of signs of the successional state of forests in EDP landscapes

Formation																																		
P										Q					Pp					B					A									
Association group																																		
P-Br	P-Nm_Br	P-Md_Br	P-Wt_Br	P-Nm	P-Br_Nm	P-Pn	P-Br_Md	P-Br_Pn	P-St_Nm	P-Nm_Md	P-Nm_Pn	P-St	P-Nt	Nm	Br_Nm	Nm_Md_St	Nm_Nt	Nm_Pn	Nm	Br_Nm	Nm_Pn	Md_Nm	Nt_Nm	Nm	Nm_Br	Br	Nm_Pn	Md	Nt	Br_Wt	Nt_Wt	Nt	Nm_Nt	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
tree synusia																																		
Share of demographically full-member populations, %																																		
30	33,3	0	0	36,4	42,9	50	20	23,1	10	20	44,4	16,7	16,7	42,8	22,2	41,7	30,8	44,4	45,5	30	42,9	20	33,3	59,6	22,2	36,4	67,7	0	20	0	22,2	33,3	40	
Share of R-species in the tree layer, %																																		
95,3	100	91,3	100	74,8	93,4	98,1	100	98,7	90,2	84,4	95,9	80,6	93,6	5,7	8,6	3,6	15,6	7,3	93,6	90,8	96	87,5	100	92,4	100	98,6	97,6	100	100	100	10,4	19,4	20,7	
Floristic richness, %																																		
55,6	61,1	44,4	11,1	44,4	41,7	38,9	11,1	55,6	22,2	16,7	33,3	33,3	66,7	38,9	33,3	55,6	11,1	55,6	61,1	44,4	11,1	44,4	41,7	38,9	11,1	55,6	22,2	16,7	33,3	33,3	66,7	38,9	33,3	
Number of species in all descriptions																																		
11	12	11	2	11	14	10	5	13	10	10	9	6	12	14	9	12	13	9	11	10	7	10	6	14	9	11	9	4	5	3	9	6	5	
Dominance in the tree layer, %																																		
72,1	89,6	79,6	54,7	70	84,8	91	95,4	91,1	82,3	78,7	89,5	71,1	70,5	73,6	91,4	95,9	82,9	92,4	90,8	84,5	94,5	85,3	75	76,9	79,6	74,3	86,4	45,9	65,9	40,2	88,6	80,6	80,1	
Average (maximum) number of species in tier A per 100 m ²																																		
1,8 (3)	1,5 (3)	1,6 (2)	1	2,2 (4)	1,6 (3)	1,3 (2)	1,2 (2)	1,3 (3)	1,8 (6)	1,6 (3)	1,4 (3)	2,2 (6)	2,0 (4)	1,8 (5)	1,3 (2)	1,2 (4)	1,7 (3)	1,3 (3)	1,8 (3)	1,6 (4)	1,2 (3)	1,5 (3)	2,3 (4)	2,2 (4)	2,0 (4)	1,7 (3)	1,6 (3)	1	1	1	1,4 (2)	2 (3)	1,6 (2)	
shrub synusia																																		
Floristic richness, %																																		
33,3	60	26,7	6,7	33,3	40	20	20	33,3	20	13,3	20	6,7	13,3	0	20	26,7	0	33,3	60	26,7	6,7	33,3	40	20	20	33,3	20	13,3	20	6,7	13,3	0	20	
Number of species in all descriptions																																		
9	6	7	1	9	1	9	3	9	6	7	9	5	9	1	1	1	9	4	8	9	3	6	0	1	0	7	6	9	0	3	1	4	1	1
Share of demographically full-member populations, %																																		
22,2	33,3	14,3	0	44,4	18,2	0	0	11,1	16,7	28,6	11,1	0	11,1	45,5	33,3	35,7	11,1	11,1	25	11,1	33,3	16,7	0	20	14,3	33,3	22,2	0	33,3	0	25	0	0	

End of Table 5

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Average (maximum) number of species per 100 m ²																																	
0,8 (3)	0,9 (3)	0,8 (2)	0,7 (1)	1,1 (4)	0,7 (3)	0,7 (3)	0,9 (3)	0,7 (3)	1,0 (3)	0,4 (2)	0,3 (2)	0,2 (2)	0,7 (2)	1,1 (4)	1,0 (2)	0,9 (3)	0,3 (2)	1,0 (3)	1,8 (3)	1,1 (3)	0,8 (2)	0,9 (3)	0	1,1 (4)	1,8 (4)	0,6 (2)	1,2 (4)	0	1	0,7 (1)	0,3 (1)	0	0
Degree of dominance of shrubs in synusia, %																																	
53,3	35,2	15,8	57,4	65,8	75,3	45,8	0	2,3	75,2	5,2	0	0	65,8	71,4	63,1	65,3	5	54,5	76,5	68,6	58,3	65,8	0	72,6	68,7	21,3	45,1	0	49,5	35,1	8,3	0	0
<i>grass sinusia</i>																																	
Floristic richness, %																																	
11,3	19,3	9,3	5,3	42,7	17,3	6,7	2,7	18	12,7	7,3	4,7	2,7	11,3	2,7	24,7	28	14	11,3	19,3	9,3	5,3	42,7	17,3	6,7	2,7	18	12,7	7,3	4,7	2,7	11,3	2,7	24,7
Share of nemoral species, %																																	
23	28,6	17,3	9,5	39	25,4	18,8	12,1	28	33,3	25,9	26,9	23,8	41,2	23,8	27,1	21,5	38,4	26,2	32,4	29,6	34	27,1	64,5	28,9	30,4	32,6	27,6	14,3	43,8	26,7	23,9	18,8	33,3
Number of species in all descriptions																																	
74	110	75	21	105	130	69	33	93	42	85	104	63	34	189	48	172	73	84	111	71	53	70	14	159	56	92	123	42	16	45	71	32	42
Average (maximum) number of species per 100 m ²																																	
11,2 (18)	13,0 (25)	11,7 (28)	13,6 (21)	8,2 (30)	11, (29)	10,7 (20)	21,8 (36)	12,6 (24)	8,9 (17)	11,6 (20)	12,6 (23)	14,3 (31)	6,5 (10)	9,7 (34)	10,5 (29)	11,9 (26)	65,5	12,9 (29)	5,4 (27)	7,7 (23)	12,1 (19)	13,2 (26)	6,1 (10)	7,7 (33)	6,9 (23)	10,4 (26)	12,1 (40)	24,4 (29)	5,2 (12)	19,5 (30)	19,3 (33)	15,6 (23)	19,1 (25)
Degree of dominance of grasses in the synusia, %																																	
42,3	37,5	57,1	46,9	62,5	83,5	65,8	43	42,9	46,2	58,3	66,7	62,5	52,3	75,2	52,6	67,4	65,8	58,4	72,6	40,5	82,1	58,6	33,3	75,5	75,5	69,7	62	42,3	66,7	66,7	70,8	46,5	56,6

Fig. 3. Assessment polygrams of the successional state of association groups of forest formations based on diagnostic features of different synusia

In the grass synusia, the share of potential flora is only 10–20 %, which is explained by the unfavorable light situation under the canopy of trees and shrubs, the absence of a gap mosaic, and only in deciduous nemoral and nemoral-meadow forests it is approximately 40 %. The participation share of species of nemoral ECG in the herbaceous cover is small.

Small-leaved forests (birch, aspen) are characterized by low values of floristic richness in all synusiae. In the arboreal layer, the explant species (R-species – *Betula pendula*, *B. pubescens*, *Populus tremula*) account for the greatest share. The largest share of demographically full-member tree populations is characteristic of nemoral and nemoral-upland birch forests, whereas nitrophilous birch forests are characterized by the largest share of shrubs. In the grass cover, the participation rate of nemoral ECG species is highest in nitrophilous-nemoral aspen forests.

The black alder forests are characterized by the minimum scores of the successional state in all synusiae.

Conclusion

The assessment of the successional state showed that all modern forests are formed under the human influence and are transformed as a result of a complex combination of felling of different types and intensity, plowing, grazing, and fires.

The existing differences in the successional status of forests of different formations are manifested in the changing species composition of forest stands and floristic diversity of all community synusiae (trees, shrubs, grasses).

Anthropogenic activity always leads to depletion of the species composition, coequality of tree layers, and violation of the mosaic-layer organization of phytocenoses.

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