Plant component features of forest-bog ecotones of eutrophic paludification in the south of boreal forest zone of West Siberia

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Abstract. Paludified forests formed in transitional forest-bog zone aren’t studied enough, inspite of its high expected diversity and large areas in the south of boreal forest zone of West Siberia. In this article wet birch (Betula pubescens) forests of forest-bog ecotones of eutrophic paludification are investigated on Vasyugan plain with nutrient-rich calcareous clays as soil-forming rocks. Species diversity and ecocoenotic structure of these phytocoenoses are discussed. They correlated with wetness and nutrient-availability of habitats evaluated with indicator values of plants. The participation of hydrophyllous species is increasing as wetness of habitats increasing in the forest-to-bog direction like in mesotrophic paludification series. However the number of species is higher in the phytocoenoses of eutrophic paludification. The share of species required to nutrient availability is also higher, both in number and in abundance. A lot of these species are usual for eutrophic boreal forested swamps with groundwater input and absent in forests of mesotrophic paludification. Accordingly the nutrient-availability of habitats is also higher. All these features we connect with birch to be a forest forming species instead of dark-coniferous and with the influence of nutrient-rich parent rocks, which is evident in forest-bog ecotones of Vasyugan plain gradually decreasing together with peat horizon thickening.

1. Introduction
In recent decades forest-bog ecotones attract attention as an integral part of bog ecosystems important for its functioning [1]. They make a valuable contribution to the water and carbon cycles [2, 3]. Due to the variety of habitats, often specific, they provide the basis for biological diversity, appeared on different levels [4]. Being vulnerable to environmental changes the forest-bog ecotones have a great potential in the evaluation of current climate changes and also their consequences using space-for-time substitution approach [5]. Of special importance is the study of forest-bog ecotones in West Siberia, where a significant portion of forested area is swamped (paludified forests occupy 25% of the territory in the middle of forest boreal zone and 11% – in the south of forest boreal zone [6]). Although the share of shallow peat forests (with a peat thickness less than 30 cm) is not so high on the whole (7% – in the middle, 4% – in the south [6]), but in some places it strongly increases, so on Vasyugan plain – up to 13–30% of the study area [7]. Despite the fact that a lot of studies of paludified forests have been carried out [2, 3, 7-9], the knowledge about its floristic, phytoecenotic and ecotope specificity is still insufficient and that leads to significant differences in estimates of resources and processes occurring...
there [2, 10] and complicates the development of an evidence-based approach to economic use and/or protection of these plant communities. We study paludified forests formed in the forest-bog ecotones on Vasyugan plain. Because of calcareous clays to be parent rocks, the eutrophic paludification develops there in contrast to mesotrophic paludification of forests on loams [11, 12]. Accordingly wet herbaceous forests with low abundance of sphagnum are characteristic for the study area [7, 12, 13]. Most of them have been burned or cut down earlier, therefore birch (\textit{Betula pubescens}) communities, secondary after dark-coniferous forests, are considered. In this article the floristic composition and ecocoenotic structure of these plant communities are discussed to identify the features of plant component of forest-bog ecotone specific for eutrophic paludification.

2. Objects and methods
The study area is east part of Vasyugan plain in Ob-Vasyugan interfluve (figure 1, site 1). It is the south of boreal forest (taiga) zone of West Siberia [14]. The climate is cold and continental. The mean January temperature is –20˚C, the mean July temperature being 18˚C. The duration of the frost-free period is about four months. The annual precipitation is up to 500 mm, it is about 100–200 mm greater than potential evaporation [14]. The soil-forming rocks are calcareous clays [15]. For comparison we use data on mesotrophic paludification of dark-coniferous forests on loams of Chulym plain [16] (figure 1, site 2). We study plant communities in peripheral areas of small oligotrophic bogs on the north-east edge of Great Vasyugan mire. Aspen-birch-mixherbaceous-sedge communities (the most abundant species are \textit{Betula pubescens}, \textit{Populus tremula}, \textit{Carex macroura}, \textit{Aegopodium podagraria}, \textit{Calamagrostis obtusata}, \textit{Equisetum pratense}, \textit{Rubus saxatilis}) – secondary after dark-coniferous forests of southern taiga [17] – are common in uplands [13], inhabiting dark-humus organo-accumulative soils [15].

The pine-dwarf shrubs-sphagnum communities (the most abundant species are \textit{Pinus sylvestris}, \textit{Ledum palustre}, \textit{Chamaedaphne calyculata}, \textit{Sphagnum angustifolium}) occupy bog habitats [13, 18, 19]. We identify two plant associations related to the ecotone parts in transition forest-bog zone given in order to gain influence from the bog: 1) forest part of ecotone with birch-reed grass communities formed on

![Figure 1. Geographical location of the study area. 1 – Vasyugan plain; 2 – Chulym plain.](image-url)
hydromorphic organo-accumulative mucky–dark-humus soils, 2) bog part of ecotone with pine-birch-dwarf shrubs-moss communities formed on periodically flooded peat soils [8]. We investigate 11 bogs. In peripheral area of each of the bogs from 1 to 3–4 study plots (25*25m) were laid out in each part of ecotone and also in adjacent ecosystems for vegetation releves (species list with cover (horizontal projection, %) as abundance measure). On the whole we get 21 vegetation releves in uplands, 25 – in forest part of ecotone, 10 – in bog part of ecotone, 38 – in bogs. Based on this data the floristic diversity of plant associations was analyzed. We use the means of number of species per plot 25 x 25 m as alpha-diversity measure and species richness of a set of vegetation releves as gamma-diversity measure. Interpolated and extrapolated species richness were obtained in EstimateS program [20] using presence/absence data. Jaccard index (Kj) and Morisita index (Km), which both are similarity indices changing from 0 to 1, were calculated to assess beta-diversity according to recommendations [21] using application PAST 1.87b. We analyze ecological and coenotic structure of plant communities with groups of species suggested by E D Lapshina [18]. In addition the wetness and nutrient availability of habitats in forest-bog ecotones were evaluated with indicator values of plants developed by I A Tsatsenkin et al [22]. The calculations of the habitat statuses of these factors were made using the whole floristic species-list of the phytocoenoses and taking into account indicative importance and abundance of each species by recommendations of A A Zverev [23].

3. Results
The species richness of birch-reed grass association (forest part of ecotone) does not differ significantly (p>0.05) from that of aspen-birch-mixherbaceous-sedge association (upland), where the maximum number of species is found (figure 2). The species richness of pine-birch-dwarf shrubs-moss association (bog part of ecotone) is a little less than that of upland forests. The minimum of species is in bog. The mean species numbers per plot 25 x 25 m have the same pattern (figure 2, for a single sample; figure 3, A).

The species composition of upland birch forests and that of bogs have little in common (Kj=0.10, Km=0.05). Pairwise comparison of phytocoenoses across the gradient “forest” – “bog” using presence/absence data (table 1, Kj) shows high rate of species replacement in transition zone (plant communities are less than half-overlapped in species indentity in all pairs). The similarity is higher with species abundance data (table 1, Km). However it is due to shared dominant-species of tree layer in case “forest part of ecotone” – “upland forests” and in lower degree in case “forest and bog parts of ecotone”, because without taking tree species into account the similarity of phytocoenoses is much lower. Such results indicate the higher sensitivity of ground layer species than tree species to the strengthening hydromorphism of habitats under bog influence.

The ecocoenotic structure of upland forests and that of bogs are rather simple. In forests birch and aspen form a tree layer; forest species, which are mostly mesophytic and mesotrophic, dominate in well-developed herb layer both in number and in abundance (cover) (figure 3). In bogs oligotrophic species have the maximum abundance; the sparse tree layer is formed by the bog form of pine (Pinus
sylvestris f. uliginosa, height from 8–10 m to 12–15 m, trunk diameter from 10–15 cm to 20–25 cm). In plant communities of forest part of ecotone tree layer is composed with birch and aspen as in uplands.

Table 1. Comparison of plant communities across the gradient “forest” – “bog”.

| Pairs of phytocoenoses | FOR–FPE | FPE–BPE | BPE–BOG |
|------------------------|---------|---------|---------|
| Jaccard index (Kj)     | 0.45    | 0.43    | 0.36    |
| Morisita index (Km)    | 0.55/0.08 | 0.58/0.26 | 0.74/0.80 |

Note. There is value of index for the communities in a whole (before slash) and without taking into account tree species (after slash). Abbreviations of communities are the same as in figure 2.

Figure 3. Coenotic spectra of plant communities across gradient “forest” – “bog” (abbreviations are the same as in figure 2) in accordance with species number per plot 25 x 25 m (A) and with species cover (B).

However in ground layer species from different coenotic groups co-dominate, all of them are more hydrophilous: meadow-swamp Calamagrostis purpurea s.l. (20 % of cover), forest Equisetum sylvaticum (10 %) and bog meso- oligotrophic Carex globularis (10 %). Besides the occurrence of forest- and meadow-swamp species is higher than in uplands, that is reflected both in larger species number per plot 25 x 25 m and also in greater abundance of this coenotic group. Forest- and meadow-swamp species as well as forest species are mesotrophic. The presence of those and other in ground layer of forest part of ecotone is well coordinated with the comparatively high nutrient-availability of both habitats (table 2, FOR and FPE). In phytocoenoses of bog part of ecotone tree layer is composed with birch and pine. Compared with bog one the pine is better developed – forest form (hight 16–20 m, trunk diameter 25–30 cm). In ground layer oligotrophic species, which bog dominating, have high cover (Ledum palustre (10 %), Chamaedaphne calyculata (5 %) and Sphagnum angustifolium (35 %)). But in contrast to bogs hydromesophytic forest, forest- and meadow-swamp species (as in forest part of ecotone) constantly meet, and also meso- oligotrophic bog species meet, which have lower cover and occurrence in bogs or absent there. Accordingly the nutrient availability of bog part of ecotone habitat is higher than in bog one, while the wetness statuses of both – coinside (table 2).

Table 2. Wetness and nutrient-availability statuses of habitats across gradient “forest” – “bog”.

|                     | Eutrophic paludification (Vasyugan plain) | Mesotrophic paludification (Chuly plain) |
|---------------------|------------------------------------------|----------------------------------------|
|                     | Wetness | Nutrient-availability | Wetness | Nutrient-availability |
| FOR                 | 68,2±1,2 | 9,0±0,3               | 68,8±0,7 | 7,5±0,2               |
| FPE                 | 72,5±1,0 | 8,4±0,4               | 71,6±1,0 | 7,4±0,2               |
| BPE                 | 75,3±2,0 | 7,4±0,3               | 73,6±1,1 | 7,2±0,2               |
| BOG                 | 75,1±1,4 | 7,0±0,2               | 75,2±1,2 | 7,0±0,2               |

Note. There are values of average and standart deviation. Abbreviations are the same as in figure 2.
Therefore, the plant communities of forest-bog ecotones of Vasyugan plain are stand out with its floristic composition. There are species, which are absent in adjacent upland forests and in bogs (or which met there rarely with less abundance). A lot of them are forest- and meadow-swamp and better presented in phytocoenoses of forest part of ecotone, the last are mire mesotrophic and bog mesooligotrophic, growing mostly in bog part of ecotone. On the whole these species put together up to 40% of floristic composition and 20–40% of abundance (cover) of ground layers in plant communities of forest-bog ecotones on Vasyugan plain.

4. Discussion
The wet birch (Betula pubescens) forests of forest-bog ecotones of Vasyugan plain have the features, which differ them from the relative plant communities of another regions of West Siberia. It is difficult to compare the numbers of species because the published estimates concern the taxa of different levels or different area-size. Thus we could admit, that there are far less number of species found in dark-coniferous forests composing mesotrophic paludification series on Chulym plain (113 plant species in 107 samples), however it is situated further to north, on the boundary between middle and southern taiga [16]. In the southern taiga of West Siberia there is also less number of species showed (for comparison: 122 species for well drained herbaceous dark-coniferous forests and 103 species for wet dark-coniferous forests with sphagnum cover [12]). Relatively high plant species richness in birch (Betula pubescens) forests of Vasyugan plain, which are secondary after dark-coniferous, may be connected with more sun light penetrating through tree layer and besides with better soil qualities caused by change of leaf fall and litter, that draw habitats together with habitats in aspen-birch forests, replaced dark-coniferous in the southern boundary of boreal forest (taiga) zone, and lead to settling more southern plant species. Thus, there are more such species in secondary birch forest of southern taiga than in dark-coniferous one [17]. Besides, the nutrient-rich soil-forming rocks of Vasyugan plain seem to influence species number of plant communities in the same way – by drawing habitats together with more southern.

As for ecoenotic structure, wet birch (Betula pubescens) forests of eutrophic paludification investigated and wet dark-coniferous forests of mesotrophic paludification [12, 16] have likeness and difference. In both series the number of forest species decreases and the number of hydrophilous bog species increases together with the degree of paludification from upland to bog. Accordingly wetness statuses of correspondent habitats are similar (table 2), while nutrient-availability statuses differ, and also ecological structure of the plant communities is not the same. In the forest part of ecotones of Vasyugan plain in relation with more nutrient availability of ecotopes the participation of mesotrophic species is much higher. For all that a lot of forest- and meadow-swamp species of studied phytocoenoses are usual for eutrophic boreal forested swamps of West Siberia with groundwater input united in order Calamagrostio purpureae-Piceetalia obovatae of class Alnetea glutinosae of ecologo-floristic classification and described by E D Lapshina [19] – herbs Filipendula ulmaria, Carex canescens, C. disperma, C. vaginata, C. cespitosa, mosses Calliergon cordifolium, Climacium dendroides, Plagiomnium ellipticum, Sphagnum squarrosum and others. These species are not met in forests of mesotrophic paludification series. Its presence in the wet birch (Betula pubescens) communities of forest part of ecotone we connect with high soil nutrient availability caused by meadow type of humus-accumulation in weakly-acid media turned out on calcareous parent rocks [8]. In the bog part of ecotone the status of nutrient availability is lower than in forest part. That is why the listed upper oligotrophic species which grow in ombrotrophic bogs with moisture input (class Oxyccoco-Sphagnetea of ecologo-floristic classification [19]) compose the ground layer of paludified forests together with mesooligotrophic species (Carex globularis, S. russowii) which usually more abundant in the peripheral areas of oligotrophic bogs in plant communities transitional between paludified Pinus sylvestris forests of class Vaccinio-Piceetea on the one hand and forested with Pinus sylvestris f. uliginosa bogs of class Oxyccoco-Sphagnetea on the other hand. The presence of these species draw the pine-birch forests of Vasyugan plain (eutrophic paludification) together with corresponded forests of Chulym plain (mesotrophic paludification), where the same species are
dominating. However the status of nutrient availability of the first is a little higher yet. It is displayed in constant presence of forest- and meadow-swamp species (although they are not so abundant as in phytocoenoses of forest part of ecotone). Such floristic composition and ecocoenotic structure of pine-birch communities of Vasyugan plain we connect with soil nutrient availability, higher than in oligotrophic bogs. The accumulation of eutrophic peat (sedge-tree), turned out there [8], confirm our conclusion.

5. Conclusion
The plant component features of forest-bog ecotones of Vasyugan plain are caused largely by birch to be a forest forming species instead of dark-coniferous and by biogeochemical background of the clayey calcareous parent rocks. It determines eutrophic way of forest paludification on the study area. The influence of high nutrient availability of ecotopes is evident as in upland forests and also in paludified communities across the gradient “forest”–“bog” up to habitats where the process of forming nutrient-rich litter is replaced with the process of peat accumulation. High level of soil nutrient availability cause abnormally high participation (and even dominating) of mesotrophic species in phytocoenoses of forest-bog ecotones. A lot of these species usually grow in eutrophic boreal forested swamps with groundwater input and absent in forests forming mesotrophic paludification series. Besides high nutrient availability cause high species number in the plant communities of uplands and of forest-bog transition zone. That is why the ecotone effect is revealed only from bog.

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