DIVERSITY ASSESSMENT OF BEETLES (INSECTA, COLEOPTERA) OF HERB-SHRUB LAYER IN THE PEAT BOG OF THE STATE HYDROLOGICAL SANCTUARY«BOLOTO MOKH» (BELARUS)

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Peat bogs of Eastern Europe are tundra patches in the temperate zone. Their highly specific environmental conditions foster the formation of unique biodiversity, with a high proportion of cold-adapted species and postglacial relicts. Due to the peat extraction in the XX century, their area has sharply decreased. Currently, peatlands are considered among the most vulnerable ecosystems in the world. Hence peat bogs preserved in an intact state play an important role in the maintaining of biodiversity in the light of current climate changes and anthropogenic disturbance. They provide appropriate environmental conditions, such as a high water table and acidity, low mineral nutrient content, and specific microclimate characteristics, for cold-adapted plants. Such highly specific plant communities may contribute to the formation of specialised insect assemblages. Coleoptera (hereinafter – beetles) are among the most numerous inhabitants of terrestrial ecosystems. They are among the suitable object for assessing of the diversity patterns. Many beetle species are phytophagous, capable of forming stable trophic relationships with plants in the herb-shrub layer of peat bogs. It has been suggested that the largest peatland in Belarus, within the state hydrological sanctuary «Boloto Mokh», reflects the main patterns of insect species richness and diversity in herb-shrub layer due to a low disturbance. Using sweep-netting in six of the most typical peat bog habitats 84 beetle species belonging to 11 families were recorded. The Shannon (H' = 1.97–2.54) and Pielou (J' = 0.42–0.79) index values showed relatively low diversity and evenness in beetle assemblages. The significantly ($p < 0.05$) highest diversity was in open bog and lagg, whereas the lowest diversity was in hummocks and dome. The NMDS ordination showed the separation between assemblages of habitats covered mainly by herbs (lagg and hummocks) and assemblages of habitats with shrub predominance in the plant communities. Twelve recorded beetle species were peat bog specialists. This is only 14.28% of the species richness. However, the abundance of specialised species is more than twice higher that of all other species in all habitats except the hollows. Overall, *Lochmaea suturalis* was the most abundant species in all habitats with a well-developed shrub layer. *Contacyphon kongsbergensis*, *Actenicerus sjaelandicus*, *Cantharis figurata*, and *Plateumaris discolor* predominated in sites with a high proportion of herbs in the cover. Other peat bog specialists, such as *Altica longicollis*, *Aphthona erichsoni*, and *Cryptocephalus labiatus* were regularly presented in most habitats, but their abundance was low. These studies demonstrated that one of the largest peat bogs in Belarus, located within the state hydrological sanctuary «Boloto Mokh», harbours a specific complex of highly specialised beetle species associated with the herb-shrub layer. Consequently, this intact peatland may be a valuable object for comparative assessment of the insect biodiversity of such ecosystems in Europe.

Key words: abundance, beetle assemblages, peatland, Protected Area, species composition, species richness

Introduction

Peat bog ecosystems of Eastern Europe play an important role in biodiversity conservation. They provide appropriate environmental conditions, such as specific temperature and water regime, high water acidity, and plant communities characteristic of the tundra, for cold-adapted animals in the temperate zone. Most of them have persisted in peat bogs since the early Holocene (Spitzer & Danks, 2006; Dedyukhin, 2016). Consequently, these ecosystems support very specific animal communities and preserve a unique gene pool of postglacial biota. Currently, many boreal and subarctic species in such tundra patches inhabit near the southern borders of their range. In addition, many peat bog specialist species are found only in these habitats (Spitzer & Danks, 2006; Sushko, 2017a). High specialisation of plant and animal communities is a very noticeable feature of the peat bogs (Zeliankevich et al., 2016). Under natural conditions, they are highly resilient and capable of preserving their unique biota for several millennia (Spitzer & Danks, 2006). However, climate change and anthropogenic transformation are leading to a reduction in the area of natural peatlands and a loss of their biodiversity. Nowadays, peat bogs of Europe are heavily degraded due to drainage, afforestation, fragmentation of habitats, peat cutting, and agricultural activities. Only few countries in Europe, including Belarus, have maintained more than 50% of their peatlands in a relatively natural condition (Bragg & Lindsay, 2003).

Protected Areas play the most important role in preserving peatland biodiversity. In Belarus 2396 km^2 of peat bogs are preserved within Protected Areas. Of particular interest to scientists is the Sanctuary «Boloto Mokh», located in the Vitebsk Region in northern Belarus. It is almost intact and one of the largest peat bogs in Belarus. Here the most typical peat bog habitats are located, including hummock-hollow complexes and mineral islands covered by forest (Kozulin, 2005; Zeliankevich et al., 2016). The high importance of the Sanctuary «Boloto Mokh» for the biological diversity conservation is confirmed by its international conservation status: Important Bird Area. Rare and protected bird species such as *Ciconia nigra* (Linnaeus, 1758), *Pandion haliaetus* (Linnaeus, 1758), *Circaetus gallicus* (Gmelin, 1788), *Grus grus* (Linnaeus, 1758), *Asio flammeus* (Pontoppidan, 1763), and *Larus canus* Linnaeus, 1758 were recorded here (Kozulin, 2005). Thus, the Sanctuary «Boloto Mokh» is a very suitable model object for studying the biodiversity and ecological properties of peat bogs in their natural state.

Among peatland inhabitants, insects are one of the most abundant and species-rich taxa. Furthermore, they include many specialised species compared to other taxa. In particular, among the vertebrate animals in Belarus, excluding birds, no species is known to occur only in peat bogs, even though certain species are found mostly on peatlands. The sanctuary «Boloto Mokh» provides a habitat for many threatened insects, including peat bog specialists listed in the Red Data Book of the Republic of Belarus (2025). *Sympecma paedisca* (Brauer, 1877) (Odonata), *Carabus clathratus* Linnaeus, 1761, *C. menetriesi* Hummel, 1827, *C. nitens* Linnaeus, 1758, *Chlaenius costulatus* (Motschulsky, 1859) (Coleoptera), *Bombus muscorum* Fabricius, 1775, *B. schrenckii* Morawitz, 1881 (Hymenoptera), *Colias palaeno* (Linnaeus, 1761), and *Oeneis jutta* Hübner, 1806 (Lepidoptera) are among them. Furthermore, arcto-boreal and boreal insect species rare and sporadic for Eastern Europe were identified within the Sanctuary «Boloto Mokh», like *Aeschna subarctica* Walker, 1908, *Somatochlora arctica* Zetterstedt, 1840 (Odonata), *Ophiola russeola* (Fallén, 1826), *Cymatia bonsdorffii* (C.R. Sahlberg 1819) (Hemiptera), *Agonum ericeti* (Panzer, 1809) (Coleoptera), *Formica forsslundi* Lohmander, 1949, *F. uralensis* Ruzsky, 1895 (Hymenoptera), *Argyroploce lediana* (Linnaeus, 1758), *Eupithecia gelidata* Moschler, 1860, *Coranarta cordigera* (Thunberg, 1788), and *Vacciniina optilete* (Knoch, 1781) (Lepidoptera), which inhabit in Belarus only peat bogs (Sushko & Zeliankevich, 2025). Therefore, the Sanctuary «Boloto Mokh» is an important object for the conservation and investigation of unique biodiversity of postglacial genesis. This is especially important in the light of climate changes.

Most studies of peat bog insect diversity have focused on ground beetles and other epigeic taxa, because mosses of the genus *Sphagnum* are the main ecosystem edificators that directly or indirectly shape the habitat conditions (Spitzer et al., 1999; Främbs et al., 2002; Buchholz et al., 2009; Lehmitz et al., 2020; Sushko, 2025). At the same time, the herb-shrub layer also plays an important role as a habitat for several insects, providing shelter and food for phytophages. However, research on the insect biodiversity of this important ecological niche in peat bogs is limited. Most of the previous studies are mainly faunistic and provide insight into the species composition in a limited number of habitats (Mossakowski, 1977; Philippov & Pestov, 2014; Sazhnev & Prokin, 2021; Alekseev et al., 2024). In the Republic of Belarus, studies of insects in the herb-shrub layer in peat bogs are mainly confined to «Yelnya» peat bog (Sushko, 2012, 2017b).

As can be seen, detailed studies of peat bog beetle assemblages of herb-shrub layer that covers the entire range of habitats and characterise alpha and beta diversity patterns are currently limited. Therefore are needed studies of diversity parameters in a reference, intact peat bog for comparative analysis of variability of beetle assemblages in both pristine and degraded peat bogs. The aim of the presented study is to assess the diversity and species composition of beetles inhabiting the herb-shrub layer of a large intact peat bog on the territory of the State Hydrological Sanctuary «Boloto Mokh» in Belarus.

Material and Methods

The core of the State Hydrological Sanctuary «Boloto Mokh» is one of the largest in Belarus ancient peat bog. The studied peatland (55.622587° N, 22.478365° E) is located in the postglacial region: Belarusian Lake District (Fig. 1). The study area is characterised by a temperate continental humidity climate, favourable for peat accumulation. The peat layer of the studied peat bog can be as deep as 4 m. The area of the peat bog is 43 km^2. (Yakushko, 1971; Zeliankevich et al., 2016). As a result, the peat bog has a dome-shaped structure, including a slope, a peak (dome), a slope, and lagg located at the border zone. The studies were conducted in 2019–2023 in six of the most characteristic peat bog habitats, namely in the lagg zone (Lag), pine bog (PB), open bog (OB), hummock (HM), hollow (HL) and dome (DM).

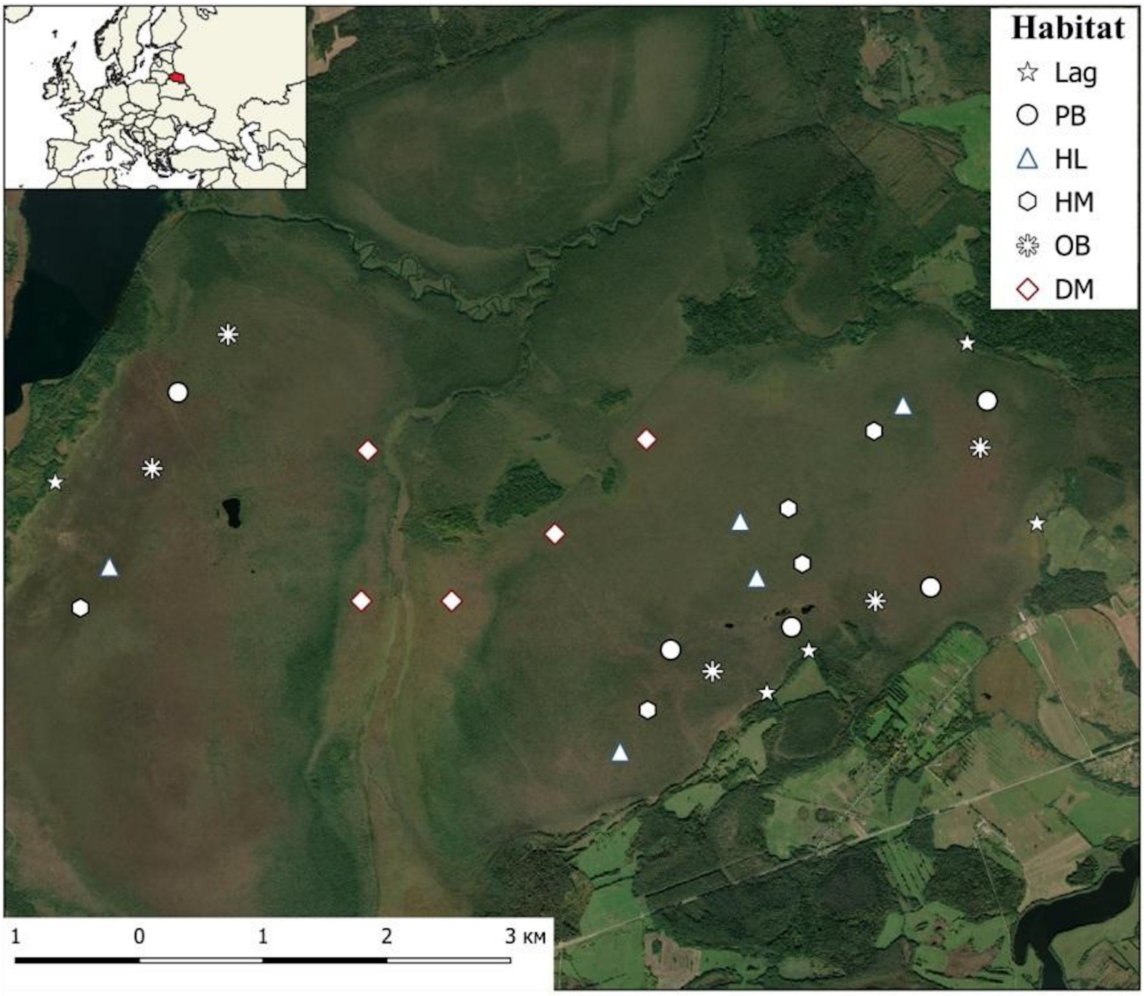

Fig. 1. The location of the State Hydrological Sanctuary«Boloto Mokh», Belarus. Designations: Lag – lagg zone, PB – pine bog, HL – hollow, HM – hummock, OB – open bog, DM – dome.

The lagg zone at the bog margin is characterised by a sparse herb-shrub layer with a predominance of *Eriophorum vaginatum* L. The plant community also includes several species of *Carex* and a few dwarf shrubs, such as *Vaccinium oxycoccos* L. and *Andromeda polifolia* L. (Fig. 2a).

The pine bog is widespread on the slope of the peat bog and forms the so-called «forest ring». Such sites are covered with short sparse pine (*Pinus sylvestris* L.) trees. The herb-shrub layer is well developed, in which plants such as *Eriophorum vaginatum*, *Rhododendron tomentosum* Harmaja, *Chamaedaphne calyculata* (L.) Moench, *Empetrum nigrum* L., and *Calluna vulgaris* L. Hull are most common (Fig. 2b).

Hollows are a structural component of the hollow-hummock complexes, which are presented by a mosaic of elevated, relatively dry hummocks of various sizes (diameter: 20–100 cm; height: 15–50 cm) and they are permanently wet depressions. The edges of the hollows are covered with hygrophilous herb species, predominantly *Rhynchospora alba* (L.) Vahl.; *Scheuchzeria palustris* L. has also been identified here (Fig. 2c).

Hummocks of the hollow-hummock complexes are covered mainly with *Eriophorum vaginatum*, *Andromeda polifolia*, *Rhododendron tomentosum*, *Chamaedaphne calyculata* and *Vaccinium oxycoccos* (Fig. 2d). The hollow-hummock complexes are located mainly on the peat bog slope.

Open bog sites on the slope are represented by a more uniform surface compared to the previous habitats. The herb-shrub layer here is relatively homogeneous and well developed. *Eriophorum vaginatum*, *Andromeda polifolia*, *Rhododendron tomentosum*, *Chamaedaphne calyculata* and *Vaccinium oxycoccos* occur here most often (Fig. 2e).

Dome is the driest ombrotrophic (water comes mainly from precipitation) area of a peat bog. The most common plants of the dome are *Calluna vulgaris*, *Rhododendron tomentosum*, *Chamaedaphne calyculata*, and *Eriophorum vaginatum* (Fig. 2f).

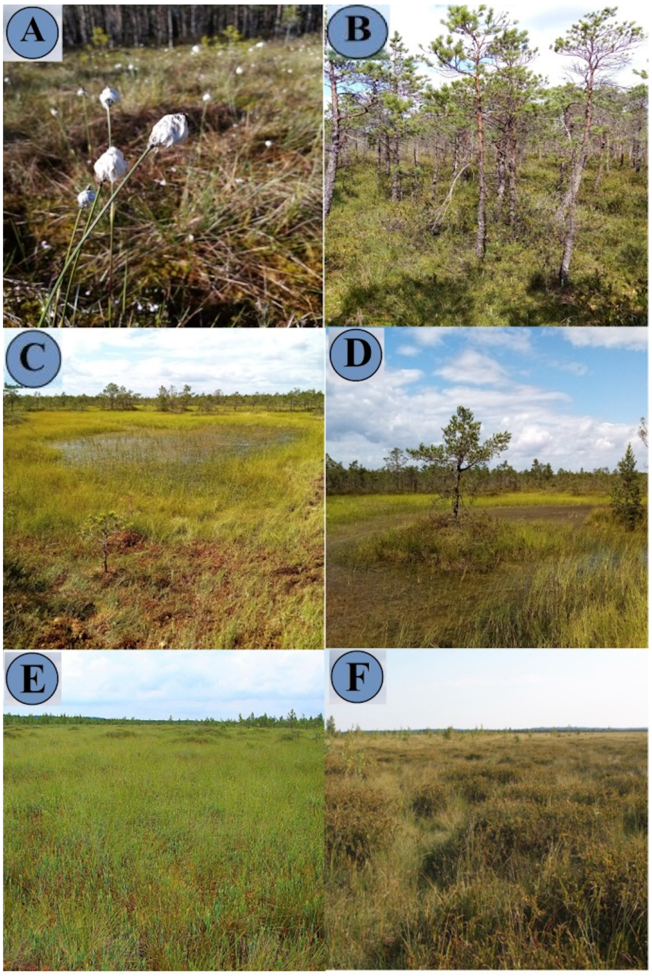

Fig. 2. Studied habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus. Designations: lagg zone (A), pine bog (B), hollow (C), hummock (D), open bog (E) and dome (F).

Beetles were sampled using an entomological sweep-net (diameter: 30 cm). In each habitat type five sites were selected. Each year, research was carried out in different parts of each habitat. Exactly 50 net sweeps in five-fold repetition were done along the linear transects twice a month. For statistical analysis, all data from each site were summed to obtain a single value per habitat. Accordingly, a total of five replications in each of the habitat types were used.

The order of taxa of beetles is given in accordance with Aleksandrowicz et al. (2023). The collected material was deposited in the Biological Museum of the Vitebsk State University named after P.M. Masherov (Belarus).

To reduce the spatial autocorrelation probability, sampling sites were selected randomly at a distance of at least 50 m from each other. Surveys were conducted during the main activity period of imago beetles between late April and early November. Beetles were identified to species level according to Bei-Bienko (1965), Ler (1996), Lopatin & Nesterova (2005). The habitat and diet preferences of beetles follow Peus (1928), Bei-Bienko (1965), Ioannisiani (1972), Mossakowski (1977), Klausnitzer (1996), Lopatin & Nesterova (2005), Spitzer & Danks (2006), and the Database of Insects and their Food Plants (DBIF, 2026). The effect of habitat type and year of investigation on abundance, species richness and diversity were tested using two-way ANOVA in order to analyse the potential spatial autocorrelation. The differences among the alpha-diversity metrics, such as species richness, abundances (number of individuals in samples), Shannon and Pielou indexes, were tested using Kruskal-Wallis test with Dunn's post hoc test (Magurran, 2004). Prior to analyses, the data were tested using Shapiro-Wilk's test and normality distribution was not detected. To estimate true beetle species richness in the studied peat bog habitats the estimator Chao 2 was applied. The calculations were performed using PAST 4.16c (Hammer et al., 2001).

Permutational Analysis of Variance (PERMANOVA) was applied for estimating of differences in beetle species composition in all the studied habitats (beta-diversity). Analysis was conducted using the Bray-Curtis dissimilarity measure with 999 permutations in the «vegan» R package (Oksanen et al., 2019). For visualisation of differences in species composition, non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance was applied. The abundance of species (number of individuals in samples) were $\log(x + 1)$ transformed, prior to multivariate ordination analysis (Legendre & Gallagher, 2001). The most characteristic species for the studied habitat types were identified using the indicator value procedure (IndVal) with «indicspecies» R package (De Cáceres & Legendre, 2009). Indicator values range from 0 (no indication) to 1 (perfect indicator value), with statistical significance $p < 0.05$. Calculations were performed using the R ver. 4.1.0 programming environment (R Core Team, 2020).

Results

A total of 6423 beetle specimens belonging to 11 families and 84 species were recorded. Chrysomelidae were presented by 31 species, Curculionidae by 15 species, Coccinellidae by 12 species, Cantharidae by nine species, Elateridae by five species, while other families, including Brentidae, Dasytidae, Oedemeridae, Scarabaeidae, Scirtidae and Tenebrionidae, were represented by lesser than five species. In most habitats, the families Chrysomelidae and Coccinellidae had the highest number of species. Additionally, Curculionidae prevailed in the species number in lagg, pine bogs, and dome.

Chrysomelidae abundance, as well as species richness, was the highest in most habitats. The families Scirtidae and Cantharidae also had high relative abundance, while Curculionidae species were not abundant (Table S1).

The observed number of species varied from 25 to 62 in the studied habitats (Table 1). The non-parametric species richness estimator Chao 2 showed expected species richness that is close to the actual number of observed species. The estimated species richness in the studied habitat types varied from 34 to 73 species, suggesting that the observed number of species represented 73.52% to 94.84% of the estimated species richness. The mean species richness differed significantly ($\chi^2 = 45.11$, $p < 0.001$) among study sites. The highest average number of species was found in pine bogs. In open habitats with a well-developed shrub layer, such as hummocks, open bogs, and dome, as showed the post-hoc test, species richness did not differ significantly ($p > 0.05$). The significantly ($p < 0.05$) lowest species richness of beetle assemblages was in hollows (Fig. 3).

The mean abundance of beetles of herb-shrub layer differed significantly ($\chi^2 = 52.61$, $p < 0.001$) (Table 2). The abundance showed a similar trend to species richness. Specifically, in open habitats with a well-developed shrub layer, no significant ($p > 0.05$) differences in the number of individuals in the samples were found. Furthermore, lagg and hollows were characterised by a significantly ($p < 0.05$) lower abundance (Fig. 4). The abundance distribution models according to pine bogs, hummocks, open bogs and dome reflect a rapid decrease in species abundance by rank, which corresponds to uneven assemblages with relatively low diversity and the dominance of a few of the most adapted species (Fig. S1).

The Shannon diversity index differed significantly ($\chi^2 = 25.51$, $p < 0.001$) and was the highest ($p < 0.05$) in open bog and lagg (Table 1). The lowest mean Shannon index value was in the beetle assemblages of hummocks and dome (Fig. 5). The beetle assemblages of lagg and hollows were characterised by the highest Pielou index value (Table 1). The lowest evenness was detected for pine forest and dome beetle assemblages due to the dominance mainly of *Lochmaea suturalis* (Thomson, 1866) (46.05–47.78% of all collected individuals).

Table 1. The diversity metrics of beetle (Insecta, Coleoptera) assemblages of herb-shrub layer in different peat bog habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus

Diversity metrics	Habitats					
	Lagg	Pine bogs	Hollows	Hummocks	Open bogs	Dome
Total number of observed species	55	62	25	39	40	37
Estimated number of species (Chao 2)	72	73	34	44	44	39
Mean number of species in samples	17 ± 1.95	22 ± 1.16	10 ± 0.60	19 ± 0.76	20 ± 0.95	20 ± 0.55
Mean number of individuals in samples	53 ± 5.22	135 ± 9.29	23 ± 3.25	104 ± 6.47	103 ± 7.32	140 ± 10.10
Mean Shannon diversity index values (H’)	2.53 ± 0.11	2.20 ± 0.09	1.97 ± 0.09	2.39 ± 0.07	2.54 ± 0.08	2.04 ± 0.07
Mean Pielou evenness index values (J’)	0.79 ± 0.02	0.42 ± 0.02	0.76 ± 0.05	0.58 ± 0.03	0.54 ± 0.02	0.44 ± 0.03

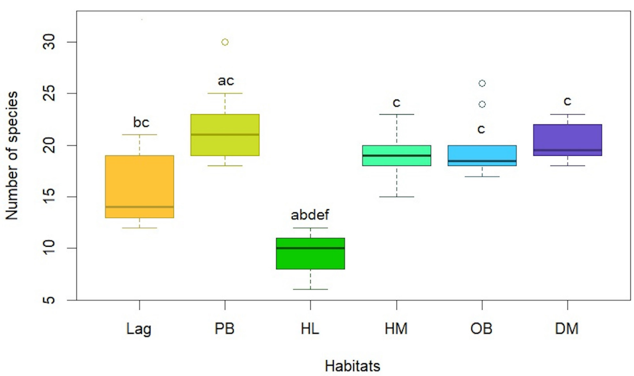

Fig. 3. Mean values (±SE) of species richness of beetle (Insecta, Coleoptera) assemblages of herb-shrub layer in the peat bog habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus. Designations: lagg zone (Lag), pine bogs (PB), hollows (HL), hummocks (HM), open bogs (OB), dome (DM). Pairwise comparisons based on Kruskal-Wallis test with Dunn’s post hoc test; different letters corresponding to sites denote significant pairwise differences among studied sites of $p < 0.05$.

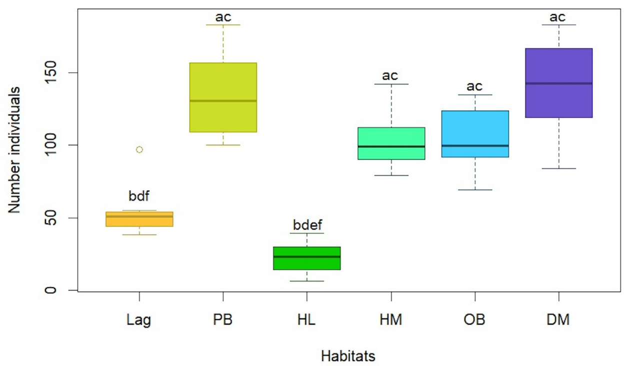

Fig. 4. Mean values (±SE) of abundance of beetle (Insecta, Coleoptera) assemblages of herb-shrub layer in the peat bog habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus. Designations: lagg zone (Lag), pine bogs (PB), hollows (HL), hummocks (HM), open bogs (OB), dome (DM). Pairwise comparisons based on Kruskal-Wallis test with Dunn’s post hoc test; different letters corresponding to sites denote significant pairwise differences among studied sites of $p < 0.05$.

In the lagg zone, *Contacyphon padi* (Linnaeus, 1758) (18.90%), *Cantharis figurata* Mannerheim, 1843 (17.96%), *Plateumaris discolor* (Herbst, 1795) (7.37%), and *Lochmaea suturalis* (7.18%) were dominant species. *Contacyphon padi* (Linnaeus, 1758) (23.28%) and *Plateumaris discolor* (Herbst, 1795) (21.55%) prevailed in herb-shrub layer of hollows (Table S2), while *Lochmaea suturalis* (36.02%), *Podistra schoenherri* (Dejean, 1837) (7.11%), *Cantharis figurata* (8.17%), and *Cryptocephalus labiatus* (Linnaeus, 1761) (7.78%) were the most abundant species in hummocks. *Lochmaea suturalis* (47.78%), *Coccinella hieroglyphica* Linnaeus, 1758 (7.08%), and *Podistra schoenherri* (7.58%) were dominant species in dome. *Lochmaea suturalis* (46.05%), *Podistra schoenherri* (6.20%), and *Contacyphon padi* (7.90%) prevailed in herb-shrub layer of pine bogs. *Lochmaea suturalis* (40.76%), *Podistra schoenherri* (7.39%), and *Coccinella hieroglyphica* (7.20%) were the most abundant species in open bog.

The results of two-way ANOVA showed that habitat type significantly ($p < 0.05$) influenced the diversity parameters of beetle assemblages of herb-shrub layer, whereas the year of investigation did not have a significant ($p > 0.05$) effect on these metrics (Table S3). Therefore, spatial autocorrelation was not detected.

PERMANOVA tests showed that the species composition of beetles in the herb-shrub layer differed significantly ($F = 42.29$, $p = 0.001$) among the habitat types of the studied peat bog. The NMDS ordination (Fig. 6) showed a clear separation of species composition between assemblages of habitats covered mainly by herbs (lagg and hummocks) and assemblages of habitats with shrub predominance in the plant communities. At the same time, in the second habitat cluster pine bog and dome were the most separated in terms of beetle species composition.

Twelve species that provide the highest differentiation in beetle assemblages of the studied habitats were identified (IndVal = 0.26–0.56, $p < 0.05$) (Table S4). *Oxythyrea funesta* (Poda von Neuhaus, 1761), *Contacyphon ochraceus* Stephens, 1830, and *Cantharis figurata* were more associated with lagg habitats in the border of peat bog. *Sericus brunneus* (Linnaeus, 1758) was associated with pine bog habitats. *Anisosticta novemdecimpunctata* (Linnaeus, 1758) and *Cryptocephalus labiatus* preferred hummocks. *Hippodamia tredecimpunctata* (Linnaeus, 1758) was associated with open bogs. *Micrelus ericae* (Gyllenhal, 1813), *Strophosoma capitatum* (De Geer, 1775), *Lochmaea suturalis* and *Coccinella hieroglyphica* were most associated with dome. Other species were characterised by a low indicator significance.

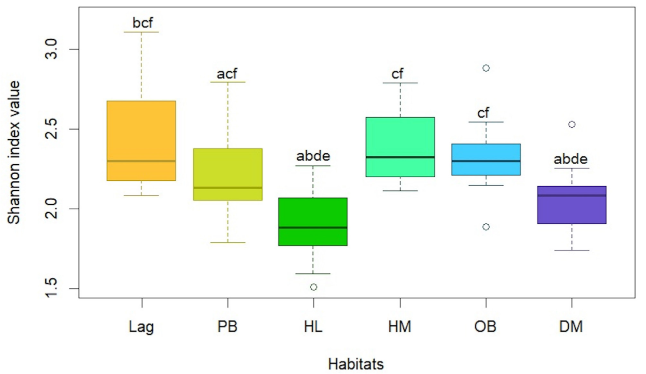

Fig. 5. Mean values (±SE) of Shannon diversity index of beetle (Insecta, Coleoptera) assemblages of herb-shrub layer in the peat bog habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus. Designations: lagg zone (Lag), pine bogs (PB), hollows (HL), hummocks (HM), open bogs (OB), dome (DM). Pairwise comparisons based on Kruskal-Wallis test with Dunn's post hoc test; different letters corresponding to sites denote significant pairwise differences among studied sites of $p < 0.05$.

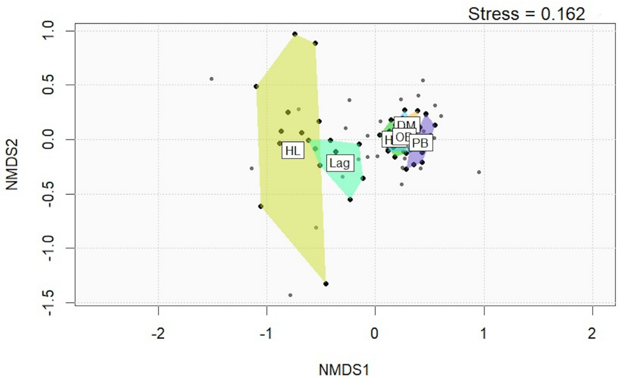

Fig. 6. Non-metric multidimensional scaling (NMDS) of beetle (Insecta, Coleoptera) assemblages of herb-shrub layer in the peat bog habitats in the State Hydrological Sanctuary «Boloto Mokh», Belarus. Designations: lagg zone (Lag), pine bogs (PB), hollows (HL), hummocks (HM), open bogs (OB), dome (DM).

All peat bog dwellers are characterised with respect to the «tyrpho-classification» of tyrphobionts (strongly associated with peat bog), tyrphophiles (bog affiliates, but are not exclusively confined to them) and tyrphoneutrals (Spitzer & Danks, 2006). Peat bog specialists belong to the first two groups. Of the 84 recorded beetle species, 12 were peat bog specialists. This is only 14.28% of all identified species. However, the abundance of specialised species is more than twice as high as in all habitats, except the hollows. The highest abundance of specialists was found in the peat bog dome (Fig. S2). This is due to the high abundance of tyrphophilous species such as *Lochmaea suturalis* and *Coccinella hieroglyphica* (54.86% of all caught individuals). Overall, *Lochmaea suturalis* was the most abundant species in all habitats with a well-developed shrub layer. *Podistra schoenherri* and *Coccinella hieroglyphica* also had a high relative abundance on such sites. *Contacyphon kongsbergensis* Munster, 1924, *Actenicerus sjaelandicus* (Müller, 1764), *Cantharis figurata*, and *Plateumaris discolor* predominated on sites with a high proportion of herbs in the cover. Other peat bog specialists, such as *Altica longicollis* (Allard, 1860), *Aphthona erichsoni* (Zetterstedt, 1838), *Chaetocnema sahlbergii* (Gyllenhal,1827), and *Cryptocephalus labiatus* were regularly presented in most habitats, but their abundance was low.

Most of the beetle species (21 species, 75% of all recorded species) in the herb-shrub layer are phytophagous. The beetle abundance showed a similar trend (Fig. S3). In particular, the pine bogs and dome had the highest abundance of phytophagous species. On the other hand, dome habitats were characterised by a high abundance of zoophages, due to the dominance of *Coccinella hieroglyphica*. The most abundant zoophagous species were *Cantharis figurata*, *Podistra schoenherri*, *Chilocorus bipustulatus* (Linnaeus, 1758), and *Coccinella hieroglyphica*, which occurred in all studied habitat types.

Discussion

The presented studies demonstrated that the beetle assemblages of the herb-shrub layer of a large intact peat bog within the State Hydrological Sanctuary «Boloto Mokh» were characterised by low diversity and evenness. Compared to previously studied, ground beetles, which form the core of the beetle assemblages of the moss layer (Sushko, 2025), the α-diversity parameters of beetles in the herb-shrub layer were higher.

The Shannon index values analysis showed that the sites covered by scrubs support a similar diversity. Whereas, in sites covered predominantly by herbs, the diversity was more variable. The higher diversity in beetle assemblages of lagg zone can be explained by the occurrence of migrant species. On the other hand, the low diversity in the hollows is due to a low plant species richness, which can be food for phytophagous beetles (Sushko, 2017a). The herbaceous layer here is presented by mainly two plants. The most abundant was *Rhynchospora alba*, with which mainly the specialised peat bog species *Aphthona erichsoni* is trophically associated (Dedyukhin, 2017). Many studies of European peat bogs showed low species richness, diversity and evenness of different insect assemblages (Spitzer & Danks, 2006; Dapkus & Tamutis, 2008; Brigić et al., 2017; Philippov et al., 2021) and species composition (Maavara, 1957; Mossakowski, 1977; Klausnitzer, 1996; Philippov & Pestov, 2014; Sazhnev et al., 2019; Sazhnev & Prokin, 2021). Our presented results correspond with these observations.

Beta diversity analysis revealed a separation between the beetle assemblages of habitats covered by herbs and habitats covered by shrubs. Such beetle spatial heterogeneity reflects the prevalence of species trophically associated with *Carex* spp. (*Limnobaris t-album* (Linnaeus, 1758), *Plateumaris discolor*), and ericaceous dwarf scrubs (*Cryptocephalus labiatus*, *Lochmaea suturalis*, *Altica longicollis*, *Micrelus ericae*) (Ioannisiani, 1972; Lopatin & Nesterova, 2005; Sazhnev et al., 2019). Despite the high similarity of the beetle assemblages of habitats with a well-developed shrub layer, the dome stands out in this cluster. Ombrotrophic plant communities of the peat bog dome contain a high proportion of *Calluna vulgaris*. Consequently, the abundance of species topically (*Coccinella hieroglyphica*) and trophically (*Lochmaea suturalis*, *Micrelus ericae*) associated with this plant species (DBIF, 2026) increases here. Similar diversity trends in beetle assemblages were identified in another large protected peat bog in Belarus, the State Landscape Sanctuary «Yelnya» (Sushko, 2006, 2012, 2017b), confined as well as for other insect taxa in the herb-shrub layer (Spitzer & Danks, 2006; Sushko, 2016, 2017a).

Previous studies have shown that 142 insect species identified in the peat bogs of the Belarusian Lake District were specialists, of which 43 were tyrphobionts and 99 were tyrphophiles. The largest number of such species was recorded in the herb-shrub layer. Among specialised phytophages, oligophages are the most numerous (42 species). Most herbivorous species are trophically associated with ericaceous shrubs (Sushko & Zeliankevich, 2025). In Northern Europe, particularly Lapland, many cryophilic insect species inhabit not only raised bogs but also tundra, subarctic birch and pine forests, heathers, and meadows. In the temperate climate of Central Europe, most of these species inhabit exclusively raised bogs (Mikkola & Spitzer, 1983). This is particularly true in the Czech Republic, Slovakia, and Austria, where the southernmost peat bogs in temperate Europe are located. It should be noted that the meso- and microclimate of peat bogs, with their sharp temperature gradients, is not the only ecological key factor determining the high proportion of specialised species. Another, equally important factor is the highly specific plant communities of peat bogs. They include, on the one hand, floristic elements of periglacial flora (currently widespread in the subarctic tundra) and, on the other hand, elements of the European Atlantic flora (Rydin & Jeglum, 2006).

Beetles revealed in the herb-shrub layer demonstrated a higher specialisation for peat bogs compared to moss-layer inhabitants. Specifically, among beetles in the *Sphagnum* carpet, two or three specialised species were recorded in different habitats (Främbs et al., 2002; Lehmitz et al., 2020; Sushko, 2025). Twelve such species were identified in the herb-shrub layer of the studied peat bog. However, tyrphobionts, which are strongly associated with peat bogs in a specific region, were not abundant (e.g. *Aphthona erichsoni* and *Altica longicollis*). Moss-layer tyrphobionts, are represented in previous studies by zoophagous boreal species such as *Agonum ericeti*, *Formica forsslundi*, and *F. uralensis* (Sushko, 2025). These species belong to the most abundant *Sphagnum* mat dwellers (Maavara, 1957; Spitzer & Danks, 2006). Herb-shrub layer beetle assemblages also included arcto-boreal and boreo-montane species such as *Lochmaea suturalis*, *Altica longicollis*, and *Micrelus ericae*, occurring in the peat bogs of Eastern Europe (Maavara, 1957; Lopatin & Nesterova, 2005; Dedyukhin, 2016).

It is also worth noting that some species, not belonging to peat bog specialists, were found in all studied habitats. These species have been reported in peat bogs in other studies (Maavara, 1957; Mossakowski, 1977; Klausnitzer, 1996; Philippov & Pestov, 2014; Sazhnev & Prokin, 2021). *Contacyphon pubescens*, *C. padi*, *Sericus brunneus*, *Rhagonycha elongata* (Fallen, 1807), *Chilocorus bipustulatus*, *Aphthona euphorbiae*, and *Protapion fulvipes* are among them. These species are considered tyrphoneutral. They are likely adapted to the extreme conditions of peat bogs and find here their food and shelter. Some of them, such as *Rhagonycha elongata*, *Chilocorus bipustulatus*, *Contacyphon padi*, and *Aphthona euphorbiae* (Schrank, 1781), were characterised by a relatively high abundance. Among such tyrphoneutral beetles with a high abundance inhabiting *Sphagnum* cover, was mainly *Drusilla canaliculata* (Fabricius, 1787) (Sushko, 2006).

As previous studies have shown, carnivorous beetles dominated the moss layer of peatlands, while in the herb-shrub layer herbivorous beetles were most numerous (Maavara, 1957; Mossakowski, 1977). The presented studies, using a large peatland in northern Belarus as an example, demonstrated a similar trend. The core of the zoophagous complex consisted of beetles belonging to families of Cantharidae and Coccinellidae. They were most abundant in habitats dominated by dwarf shrubs in the plant cover. This can likely be explained by the fact that dwarf shrubs, due to their higher species richness, serve as host plants for a larger number of phytophagous insect species, which can become prey for predatory beetles.

The higher diversity and specialisation of beetles in the herb-shrub layer are likely due to a wider range of ecological niches. This layer provides trophic resources, shelter, and more favourable microclimatic conditions for its inhabitants compared to the moss layer. Previous studies have shown that the main drivers of insect diversity in the herb-shrub layer were herb cover and shrub cover proportions, as well as the number of plant species (Sushko, 2016, 2017a,b). Consequently, beetle diversity is largely determined by the persistence of the herb-shrub layer. Conservation of large pristine peat bogs is a basic priority for plant and animal diversity preservation. Specialised peat bog beetles and many other insect taxa are very sensitive to environmental changes. Therefore, it is necessary to reduce the human impact on peat bog ecosystems and maintain the hydrological regime of surrounding areas. Currently, peat bogs provide isolated habitats for many cold-adapted tyrphobiont and tyrphophilous species from the Early Holocene or Middle Holocene (Sushko, 2019). Therefore, protecting large ancient peatlands in temperate Europe is essential for the future survival of subarctic, boreal, and boreoalpine insects in a warming climate.

Conclusions

The large peat bog of the State Hydrological Sanctuary «Boloto Mokh» includes all main habitats typical for intact East European peatlands. In the herb-shrub layer beetle species composition was typical for peat bogs in the temperate zone of Europe. Beetle assemblages showed low diversity and evenness. This is due to the predominance of several highly abundant species, including peat bog specialists, in each of the studied habitats. Our research identified key species strongly associated with peat bogs of Eastern Europe, such as *Altica longicollis*, *Aphthona erichsoni*, *Chaetocnema sahlbergii*, and *Cryptocephalus labiatus*. The species composition of beetles dwelling in herb-shrub layer differed significantly between habitats with a well-developed shrub layer and habitats dominated by herbs. The beetle assemblages were distinguished by a predominance of phytophages and demonstrated a higher specialisation for peat bogs compared to moss-layer inhabitants. Since in many European countries pristine peat bogs are extremely rare, the studied territory is very important for assessing the current state of biodiversity of such tundra patches in temperate zone, as well as for long-term monitoring and comparative analysis of their changes due to anthropogenic transformation.

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Supporting Information

Additional data for the paper by Sushko (2026) may be found in the **Supporting Information**.

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ОЦЕНКА РАЗНООБРАЗИЯ ЖЕСТОКРЫЛЫХ (INSECTA, COLEOPTERA) ВЕРХОВОГО БОЛОТА ГОСУДАРСТВЕННОГО ГИДРОЛОГИЧЕСКОГО ЗАКАЗНИКА «БОЛОТО МОХ» (БЕЛАРУСЬ)

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Верховые болота Восточной Европы представляют собой участки тундры в умеренной зоне. Их весьма специфичные экологические условия способствуют формированию уникального биоразнообразия с высокой долей холодолюбивых видов и постгляциальных реликтов. Из-за добычи торфа в XX в. их площадь резко сократилась. В настоящее время торфяники считаются одними из самых уязвимых экосистем в мире. Поэтому верховые болота, сохранившиеся в малонарушенном состоянии, играют важную роль в поддержании биоразнообразия в свете современных климатических изменений и антропогенного воздействия. Они обеспечивают подходящие условия окружающей среды, такие как высокий уровень грунтовых вод и кислотность, низкое содержание минеральных питательных веществ и специфические микроклиматические характеристики, для холодолюбивых растений. Такие специфичные сообщества растений верховых болот могут способствовать формированию высоко специализированных сообществ насекомых. Coleoptera (далее – жуки), являющиеся одними из самых многочисленных обитателей наземных экосистем, представляют собой подходящий объект для оценки закономерностей биоразнообразия. Многие виды жуков являются фитофагами, способными формировать стабильные трофические связи с растениями в травяно-кустарниковом ярусе верховых болот. Мы предположили, что крупнейшее в Беларуси верховое болото, расположенное в пределах гидрологического заказника «Болото Мох», отражает основные закономерности биоразнообразия насекомых травяно-кустарникового яруса мало нарушенных торфяников. С помощью энтомологического кошения в шести наиболее типичных местообитаниях было зарегистрировано 84 вида жуков, принадлежащих к 11 семействам. Значения индексов Шеннона (H’ = 1.97–2.54) и Пиелу (J’ = 0.42–0.79) показали относительно низкое разнообразие и выравненность в ассамблеях жуков. Наибольшее разнообразие ($p < 0.05$) было отмечено на открытых участках болот и окрайках, а наименьшее – на кочках грядово-мочажинного комплекса и на вершине болота. Ординация NMDS продемонстрировала отчетливые различия между ассамблеями жесткокрылых местообитаний, покрытых преимущественно травами (окрайки и мочажины), и ассамблеями, приуроченными к местообитаниям с преобладанием кустарничков. С помощью процедуры IndVal были выявлены двенадцать видов, обеспечивающих наибольшую дифференциацию ассамблей жуков в изученных местообитаниях. Из всех зарегистрированных видов жуков 12 были специализированными видами верховых болот. Это составляет всего 14.28% видового богатства. Однако их обилие более чем в два раза превышает таковое всех других видов во всех местообитаниях, за исключением мочажин. В целом, вид *Lochmaea suturalis* был наиболее многочисленным во всех местообитаниях с хорошо развитым кустарничковым ярусом. *Contacyphon kongsbergensis*, *Actenicerus sjaelandicus*, *Cantharis figurata* и *Plateumaris discolor* преобладали на участках с высокой долей травянистых растений в ярусе. Другие специализированные обитатели верховых болот, такие как *Altica longicollis*, *Aphthona erichsoni* и *Cryptocephalus labiatus*, регулярно встречались в большинстве местообитаний, но их численность была низкой. Представленное исследование показало, что одно из крупнейших верховых болот Беларуси, расположенное в пределах гидрологического заказника «Болото Мох», является местообитанием специфического комплекса высокоспециализированных видов жуков, ассоциированных с травяно-кустарниковым ярусом. Следовательно, это нетронутое верховое болото может стать ценным объектом для сравнительной оценки биоразнообразия насекомых данных экосистем в Европе.

Ключевые слова: ассамблеи жуков, видовое богатство, видовой состав, обилие, особо охраняемая природная территория, торфяник