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ABSTRACT

Elements of the ancient periglacial flora such as peat bog shrubs provide a paleorefugium in Central Europe for survival of glacial biota and other cold-adapted species during recent climate change. This study provides evidence that diversity of one of the most numerous consumers in peat bogs, beetles, was higher in mid-successional stages characterized by the highest degree of shrub encroachment, compared with early and old stages. The main autogenic factor driving successional changes of herb-shrub layer coleopteran assemblages were shrub cover and bog water level. Younger successional stages contained the highest abundance of herb dwellers (chortobionts) and polyphagous species, whereas middle and old stages contained shrub inhabitants (chamebionts), which are oligophagous species specializing on ericaceous dwarf shrubs. Species richness and abundance of cold-adapted inhabitants of peat bogs (tyrphobiontic and tyrphophilous) increased from young to old successional stages along with increased shrub cover. Herb dwellers and polyphagous species are among the first primary consumers to colonize peat bogs. With changes in late-successional habitats, in particular the invasion of ericaceous dwarf shrubs, chamebiontic and oligophagous species start colonizing.

RÉSUMÉ

Des éléments de la flore périglaciaire ancienne comme les arbustes des tourbières ombrotrophes fournissent des paléorefuges pour la survie des espèces glaciaires et adaptées au froid durant le changement climatique récent en Europe centrale. Cette étude montre que la diversité d'un des plus importants consommateurs des tourbières ombrotrophes, les coléoptères, était plus élevée dans les stades de milieu de succession caractérisés par le plus haut degré d'envahissement par les arbustes, comparativement aux stades de début et de fin de succession. Le principal facteur autogène causant les changements successionnels des assemblages de coléoptères du niveau herbacées-arbustes étaient le recouvrement arbustif et le niveau d'eau de la tourbière. Les stades de début de succession montraient l'abondance la plus élevée en espèces vivant dans les herbacées (chortobiontes) et d'espèces polyphages, tandis que les stades de milieu et de fin de succession avaient des espèces vivant dans les arbustes (chamebiontes), qui sont des oligophages spécialistes des éricacées de petite taille. La richesse spécifique et l'abondance d'espèces adaptées au froid (tyrphobiontes et tyrphophiles) augmentait du début à la fin du gradient successionnel, en phase avec le recouvrement arbustif. Les espèces vivant dans les herbacées et polyphages sont parmi les premiers consommateurs primaires à coloniser les tourbières ombrotrophes. La colonisation par les espèces chamebiontes et oligophages est amorcée par les changements des habitats de fin de succession, particulièrement l'invasion par les éricacées de petite taille.

Introduction

Peatlands are a widely distributed in landscapes south of the tree line between latitudes 50° and 70° N, which include boreal and subarctic plants and animals (Spitzer and Danks 2006). Peat bogs develop by accumulation of *Sphagnum* peat over long periods. Some peat bogs are ancient and have persisted since the early Holocene, about 12,000 to 13,000 years ago (Pidoplichko 1961; Geltman 1982; Spitzer and Danks 2006; Yelovicheva et al. 2008). Nowadays, peat bogs of Central Europe are heavily degraded due to peat cutting, agricultural activities and drainage. Only five countries of Central Europe, including Belarus, have maintained more than 50% of their peatlands in a relatively natural condition (Bragg et al. 2003). Large, ancient and almost intact Belarusian peat bogs are valuable for the study of

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autogenic succession, something not possible in most other countries.

A better understanding of the ecological mechanisms of natural succession is a key challenge of contemporary ecology. One of the most suitable objects for such investigation is Coleoptera. About 75% of beetle species are phytophagous in both the larval and adult stages, living in or on plants, wood, fungi, and playing an important role in ecosystems (Gillott 2005). Beetles are important members of food webs in most terrestrial ecosystems, and are among the most abundant animal groups in peatlands (Maavara 1955; Spitzer and Danks 2006; Sushko 2012). Peat bogs have high conservation value for subarctic and boreal insects, including beetles, in Central Europe (Spitzer and Danks 2006; Sushko 2014).

Succession is a fundamental dimension in ecosystems, and can be studied better in peatlands than in most other ecosystems because changes are preserved in the peat laid down beneath successive vegetation communities (Rydin and Jeglum 2006). The effects of autogenic succession on peat bog plant communities in Belarus have been well studied (Geltman 1982; Belenki and Kurzo 1988; Yelovicheva et al. 2008). While studies have been done on successional influence on bog consumers, studies on herbivores or organisms that occupy other trophic levels are rare (Spitzer et al. 1999; Dapkus 2004).

Peat bogs contain a record of the various stages of vegetation succession over time. Vegetation composition of the peat has revealed that cotton grass and pine trees dominated among vascular plants in the early succession stages (Boreal period), whereas ericaceous dwarf shrubs colonized peat bogs in later stages (Atlantic period). In the Subatlantic period, ombrotrophic subclimax heather communities appeared in the convex central part of the peat bog (Belenki and Kurzo 1988; Yelovicheva et al. 2008). Such open plant communities persist for a very long time on large Belarusian bogs due to the lack of pine seeds in the convex central bog area (Pidoplichko 1961). The ombrotrophic peat of a bog dome is isolated from the influence of groundwater and surface water and receives all of its moisture from precipitation, so it is especially sensitive to climate change and can serve as a valuable archive to reconstruct past environments (Blackford 2000). The *Sphagnum* carpet and shrub layer form a specific peat bog environment. *Sphagnum* mosses and peat layers maintain strong acidity, insulate the habitat, and high water tables prevent warming of the soil surface. The herb-shrub cover is more heterogeneous and provides different microclimate conditions. Average temperature within a peat bog can be 5 to 8° C lower than temperatures outside the bog (Spitzer and Danks 2006). Moreover, shrubs are the main food resource for peat bog phytophagous consumers (Rydin

and Jeglum 2006, Spitzer and Danks 2006). Relative to pioneer succession stages, which support rarefied herb cover including cotton-grass, the middle-stage shrub layer gets less solar radiation and reduced air temperature, modifying the microclimate and possibly moderating peat bog environmental conditions (Belenki and Kurzo 1988; Yelovicheva et al. 2008). Due to the microclimate and boreal dwarf shrub cover, peat bog ecosystems are important environments for the survival of cold-adapted insects, including beetles, as the climate warms. On the other hand, various food resources and microclimatic conditions of the shrub layer along the succession gradient can host different beetle assemblages.

Among peatland dwellers are specialized species (tyrophobionts and tyrphophils) strongly associated with abiotic factors and plants of these ecosystems. Most of these species are insects, including beetles (Rabeler 1931; Maavara 1957; Spitzer and Danks 2006). Specialized species are sensitive to changes in peat bog environmental conditions and react to decreased humidity and acidity, degradation of plant cover (Främbs et al. 2002; Spitzer and Danks 2006; Dapkus and Tamutis 2008; Brigić et al. 2017). It should be noted that for ecological condition assessment, species richness is the indicator most often used in practice (Spitzer et al. 1999; Främbs et al. 2002; Dapkus 2004; Spitzer and Danks 2006; Dapkus and Tamutis 2008; Brigić et al. 2017). However, parameters such as species' habitat preferences, trophic relationships and diet range of consumers can also be used to assess habitat change.

In this study, I addressed the following hypotheses: (1) there are significant differences in species richness, abundance, and diversity of coleopteran assemblages between various peat bog primary successional stages; (2) ericaceous dwarf shrubs can be considered one of the main drivers of the difference in species richness and abundance of herb-shrub layer beetles in the different habitats of a successional series; (3) beetle habitat preferences, trophic relationships and diet range vary significantly in the different habitats of successional stages of a pristine peat bog; (4) the environmental sensitivity of beetles may make them valuable bioindicators of successional stages.

Material and methods

Study site

This research was carried out during 2014–2016 in the 'Moch' peat bog (55°37′ N 28°06′ E), which is one of the largest in Central Europe (4602 ha). This peatland is currently protected as a hydrological reserve and is

the least anthropogenically modified in Belarus. The 'Moch' peat bog is also one of the oldest in Belarus; it began to form in the Younger Dryas (about 11,000 years ago) (Belenki and Kurzo 1988).

The following successional stage sequence is described according to Razumovsky (1981). Study sites corresponding to three successional stages were selected: pioneer young (lagg zone – LZ); middle (pine bog – PB and open bog – OBS on the bog slope); and subclimax old (dome – D). The middle stage was characterized by both open bog and closed stands with rarefied pines on the slope of the peat bog; hence, the middle stage was split into two different sites. Five replicates (50 m × 5 m transects) in the central part of each of these four sites were randomly selected (20 transects in total). The sites were spaced at least 300 m apart along a gradient from the edge to the dome across the sampling area.

Vegetation surveys were conducted by the method of Brown (1954) in June 2015. In each transect, three randomly placed plots (1 × 1 m^2) were sampled and four vegetation parameters were recorded: total vascular plant cover (%), shrub cover (%), herb cover (%), and number of vascular plants species. The average tree cover (%) in sites with *Pinus sylvestris* was also measured (Table 1). Plots were ≥100 m from each other.

Coleoptera sampling

Coleoptera were sampled along the transects described above using an entomological sweep-net (diameter: 30 cm). Exactly 50 net sweeps were done on each transect twice a month. For statistical analysis, all data from each site type in the three successional stages were summed to obtain a single value per habitat. Surveys were conducted during the main activity period of imago beetles between May and October. Voucher specimens were deposited at the Zoological Museum of Vitebsk State University.

The following ecological terminology is from Spitzer and Danks (2006): tyrphobionts are associated with peat bogs; tyrphophilous species are more abundant on peat bogs than in other ecosystems; and tyrphoneutral taxa are eurytopic and occur in many other ecosystems. The four main life forms of beetle species

identified by Lopatin and Nesterova (2005) were recorded: chortobionts (herb dwellers); chamebionts (dwarf shrub dwellers); tamnobionts (bush dwellers); and dendrobionts (trees dwellers).

The ecological preferences, host plants and diet range of Coleoptera follow Iosiniani (1972), Lopatin and Nesterova (2005), Information System about Beetles of Poland (Coleoptera Poloniae http://www.coleoptera.ksib.pl), and the Database of Insects and their Food Plants (https://www.brc.ac.uk/DBIF/).

Data analysis

The α-diversity values of the Coleoptera assemblages of various successional stages were compared using the Shannon index (H'). To examine the β-diversity and to compare differences in beetle assemblages, hierarchical cluster analysis (single link method) was employed.

Differences in environmental parameters, Shannon diversity, species richness, abundance and ecological group composition of the Coleoptera assemblages among the four vegetation types of the successional stages were examined using the Kruskal–Wallis H test with Dunn's post hoc test (Siegel and Castellan 1988).

To assess the environmental variables that explain the Coleoptera species richness and abundance (all, habitat generalists, habitat specialists), generalized linear models (GLM) with a Poisson distribution were used. For percentage data of environmental variables, arcsine transformations were used. Prior to conducting GLM analysis, possible intercorrelations of all environmental variables (total plant cover, shrub cover, herb cover, number of vascular plant species, tree cover, and bog water level) were examined with Spearman rank-correlation (r_s). Several variables were correlated ($r_s > 0.6$). Collinearity in the explanatory variables was assessed by calculating variation inflation factors (VIF) (command 'vif' in the R package car), which indicated highly correlated variables (VIF > 5) (Zuur et al. 2009). Bog water level and shrub cover were included in the GLM analysis. Non-significant predictors were excluded by stepwise backward selection (step function) using the Akaike Information Criterion (AIC) values

Table 1. Environmental variables (mean ± SE) in the habitats of various successional stages.

Environmental variable	Lagg zone (LZ)	Pine bog (PB)	Open bog (OBS)	Dome (D)	p
Tree cover (%)	–	33.7 ± 10 [c]	5.1 ± 3[b]	–	*
Dwarf shrub cover (%)	7.8 ± 2[bc]	57.9 ± 11[acd]	59.4 ± 9[abd]	56.1 ± 7[bc]	***
Herb cover (%)	68.8 ± 6[bcd]	12.1 ± 4[acd]	28.5 ± 8[abd]	24.7 ± 2[abc]	*
Total vascular plant cover (%)	68.8 ± 6[bcd]	85.7 ± 16[ad]	77.7 ± 13[abd]	81.1 ± 19[abc]	*
Number of vascular plant species	3 ± 1[bcd]	10 ± 2[acd]	9 ± 0.5[abd]	7 ± 1[abc]	**
Bog water table	4.8 ± 0.5[bcd]	38.5 ± 1[ad]	40.5 ± 2[ad]	35.5 ± 2[abc]	

Note: Significance (Kruskal–Wallis): ***p ≤ 0.0001, **p ≤ 0.001, *p ≤ 0.05; [a,b,c] Letters indicate significance in this model

from the final model. The variables entered in the final GLM were dwarf shrub cover and bog water table.

Because overdispersion was detected, I used a quasi-Poisson GLM. To evaluate the goodness of fit of each model, the pseudo R^2 ((null deviance – residual deviance)/null deviance) was used (Zuur et al. 2009).

To determine which species were indicators of the stages of primary peat bog succession, the IndVal procedure was used in the R library 'labdsv'. This procedure combines relative species abundance and occurrence in the various habitats. Species' indicator values ranged from 0 (no indicator value) to 1 (perfect indicator value) with statistical significance P < 0.01 (Dufrêne and Legendre 1997).

Species distribution among sites along the successional gradient was studied using principal component analysis (PCA) based on a correlation matrix. The Hellinger transformation for PCA and species data were applied. Rare species, which occurred as singletons, were excluded from the ordination (Jongman et al. 1995).

Statistical analyses were performed using Past (Hammer et al. 2001), MVSP (MVSP 2002), and R 3.4.2 (R Development Core Team 2011) softwares.

Results

Vegetation

Vegetation parameters differed significantly among successional stages (Table 1). The young successional stages had a higher percentage of herb cover and low plant species richness (Table 1). The most common plant species of these successional stages were *Eriophorum vaginatum* Linnaeus, 1753, *Carex* spp., and *Andromeda polifolia* Linnaeus, 1753.

In pioneer successional stages, herb cover reached 68.8%, while in later successional stages there was a higher plant species richness and dwarf-shrub cover (56.1–59.4%). The most common plants of the middle successional stages were *Ledum palustre* (Linnaeus, 1753), *Chamaedaphne calyculata* Moench, 1794, *Empetrum nigrum* Linnaeus, 1753, *Vaccinium uliginosum* Linnaeus, 1753 and *Calluna vulgaris* Hull, 1808. *C. vulgaris* prevailed among shrubs in old successional stages (86%). Trees occurred predominantly in the pine bog habitat and were sparse.

Coleoptera species richness, abundance and diversity

Beetle species richness differed significantly among successional stages (Kruskal–Wallis test H = 28.55, p = 0.0002; Table S1). No significant difference was recorded in mean number of beetle species among the three study seasons in each habitat (Kruskal–Wallis test H = 33.45, p = 0.785). On the other hand, mean number of beetle species in pine bogs and open bog spaces (middle succession stages) did not differ significantly (Tables S1, S2). The highest species richness was in the young stages, whereas the lowest number of species was captured in the subclimax stages (Figure 1(a); Table S2).

Coleoptera abundance varied significantly among successional stages (Kruskal–Wallis test H = 27.55, p = 0.0001; Table S1) and was highest in old stages. Beetle abundance did not differ among the three study seasons in each habitat (Kruskal–Wallis test H = 21.96, p = 0.473). The lowest abundance was in the early stages (Figure 1(b)). However, mean number of individuals in pine bogs and open bog spaces (middle succession stages) did not differ significantly (Tables S1, S2).

In the habitats of different successional stages, species composition was also different. In the early stages, *Cyphon padi* (Linnaeus, 1758) and *Plateumaris discolor* (Herbst, 1795) were most abundant. In the middle successional stages, *Absidia schoenherri* (Dejean, 1837), *Lochmaea suturalis* (Thomson, 1866), *Altica longicollis* (Allard 1860) and *Cryptocephalus labiatus* (Linnaeus, 1761) were recorded in high abundance. In old stages, species such as *Cyphon kongsbergensis* Munster, 1924, *Micrelus ericae* (Gyllenhal, 1813) and *Lochmaea suturalis* prevailed (Table S3).

Shannon diversity differed significantly among successional stages (Kruskal–Wallis test H = 25.26, p = 0.003; Table S1). No significant difference in mean values of the Shannon index was recorded among three study seasons in each habitat (Kruskal–Wallis test H = 14.78, p = 0.644). The highest diversity (H' = 2.664–2.801) was in the middle successional stages, whereas the lowest Shannon index value was in the oldest sites (H' = 2.364; Figure 1(c)). On the other hand, mean values of the Shannon index in beetle assemblages of pine bogs and open bog spaces (middle succession stages) did not differ significantly (Table S1).

Analysis of the β-diversity showed highest differences between Coleoptera assemblages of early and later successional stages such as pine bog, open bogs on the slope and on the dome (PB, OBS and D), which were similar to each other (Figure 2). On the other hand, a higher similarity was found between open bog space coleopteran assemblages and subclimax assemblages.

Coleoptera response to successional stages and environmental variables

The PCA showed the relations between beetle species and successional stages. The first two axes explained
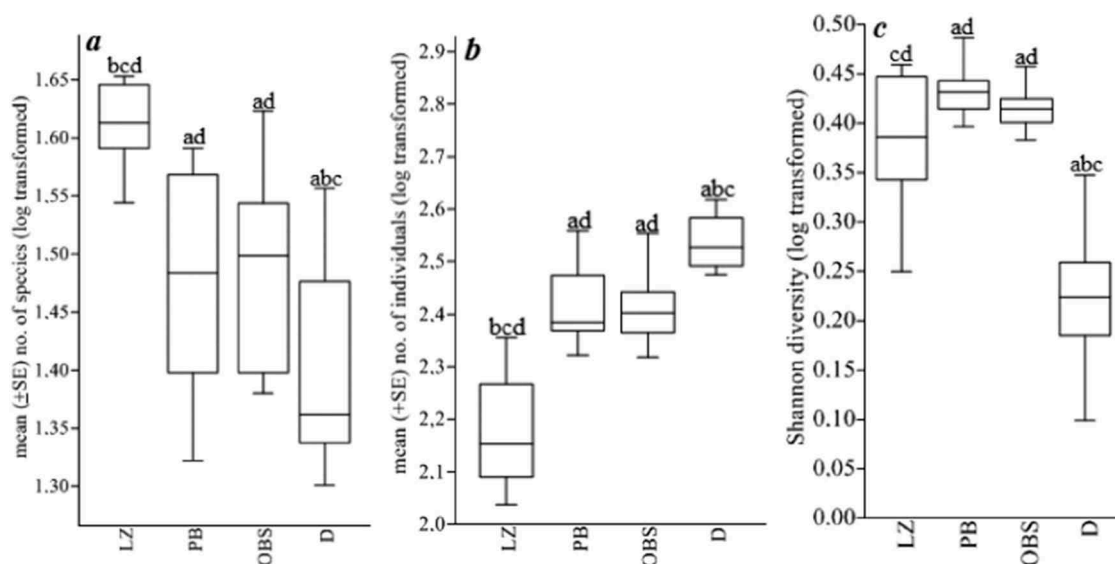
Figure 1. Mean values (± SE) of (a) species richness, (b) abundance and (c) Shannon diversity of beetles in three peat bog successional stages.

Notes: LZ (a) – early stages; PB (b) and OBS (c) – middle stages; D (d) – subclimax. Differences among successional stages were tested using the Kruskal–Wallis test. Different letters (a, b, c, d) indicate significant differences (post hoc Dunn's test; $P < 0.05$) among successional stages.
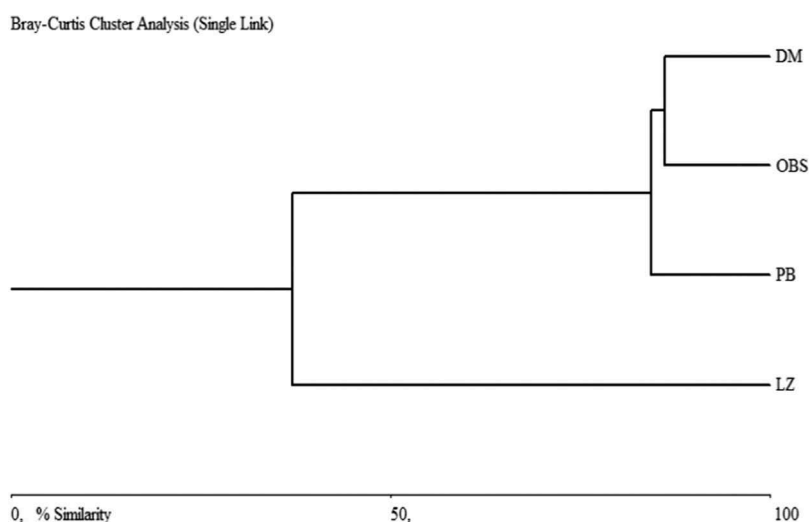
Figure 2. Hierarchical cluster diagram of similarity/difference in beetle assemblages of different stages of peat bog succession.

Notes: Successional stage abbreviations: LZ – early stages; PB and OBS – middle stages; DM – subclimax.

88.55% and 9.13% of the total variance (cumulative percentage: 97.68%). In the ordination diagram, habitats ranged from young to old successional stages (Figure 3).

The PCA ordination diagram showed that *P. discolor*, *A. erichsoni* and *A. sjaelandicus* (Müller, 1764) correlated with early successional stages. *C. labiatus, L. suturalis* and *A. longicollis* correlated with later stages, whereas *M. ericae* and *Coccinella hieroglyphica* Linnaeus, 1758 were most affiliated with subclimax habitats. Thus, three clusters of species represented the different successional stages and showed a similar response to the habitats (Figure 4). On

the other hand, I identified nine indicator beetle species of young (four species), middle (four species) and old (one species) peat bog successional stages (Table 2).

The significant predictor variables in the GLM for beetle abundance and species richness were dwarf shrub cover and bog water table. Moreover, species richness showed significant negative relations with water level (Table 3).
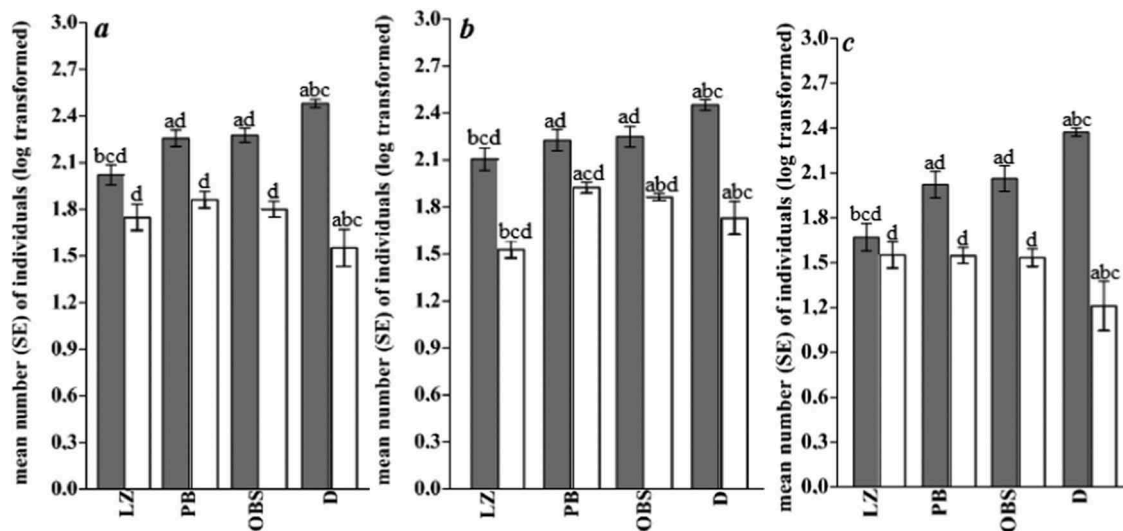
Differences in beetle ecological groups

Thirteen tyrphobionts and tyrphophilous species (habitat specialists) were recorded (Table S3). Habitat
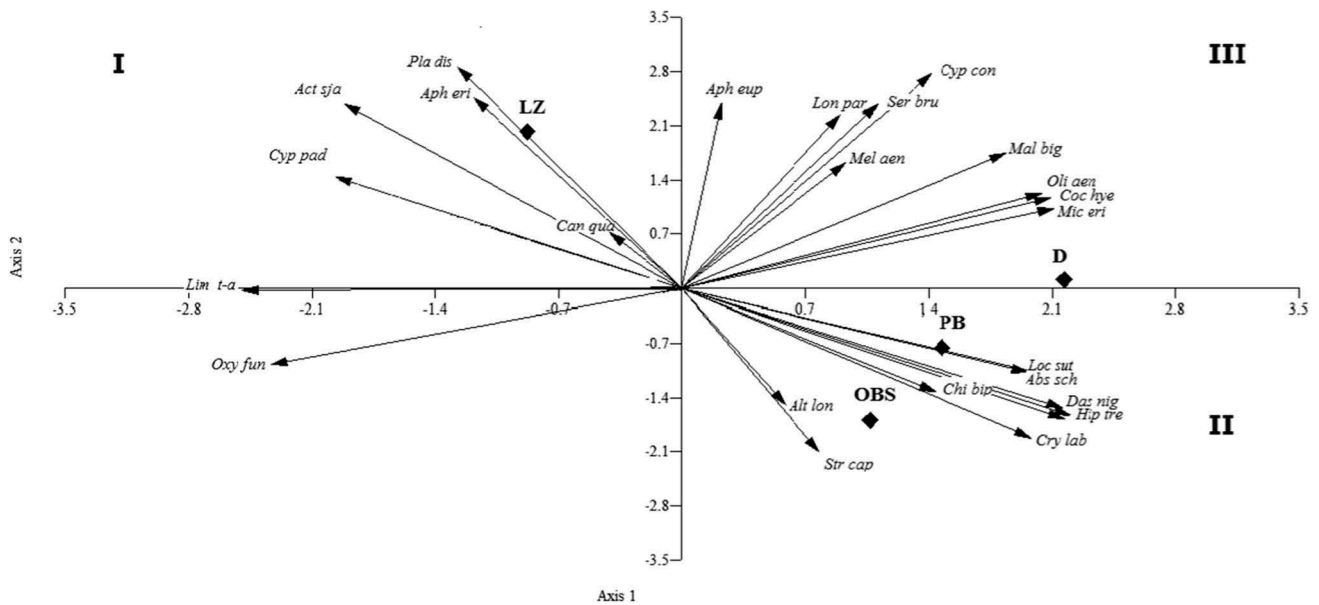
Figure 3. Ordination diagram of principal component analysis for species and for the habitats of the different successional stages: LZ – early stages; PB and OBS – middle stages; D – subclimax.

Notes: Aph eri = Aphthona erichsoni, Aph eup = A. euphorbiae, Abs sch = Absidia schoenherri, Act sja = Actenicerus sjaelandicus, Alt lon = Altica longicollis, Cry lab = Cryptocephalus labiatus, Can qua = Cantharis quadripunctata, Chi bip = Chilocorus bipustulatus, Coc hie = Coccinella hieroglyphica, Cyp kon = Cyphon kongsbergensis, Cyp pad = Cyphon padi, Lim t-a = Limnobaris t-album, Loc sut = Lochmaea suturalis, Lon par = Longitarsus parvulus, Mal big = Malthinus biguttatus, Mel aen = Meligethes aeneus, Mic eri = Micrelus ericae, Olibrus aeneus = Olibrus aeneus, Oxy fun = Oxythyrea funesta, Pla dis = Plateumaris discolor, Ser bru = Sericus brunneus, Str cap = Strophosoma capitatum.

Figure 4. Differences (mean ± SE) in beetle abundance in (a) ecological types (habitat specialists – gray columns; habitat generalists – white columns), (b) trophic groups (phytophagous species – gray columns; zoophagous species – white columns), and (**c**) groups by diet range (oligophagous species – gray columns; polyphagous species – white columns) in three peat bog successional stages. LZ (a) – early stages; PB (b) and OBS (c) – middle stages; D (d) – subclimax.

Notes: Differences among successional stages were tested using the Kruskal–Wallis test. Different letters (a, b, c, d) indicate significant differences (post-hoc Dunn's test; P < 0.05) among successional stages.

specialist abundance differed significantly among successional stages (Kruskal–Wallis test H = 32.06, p = 0.002; Table S1). On the other hand, mean numbers of specialized species in pine bogs and open bog spaces (middle succession stages) did not differ significantly (Tables S1, S2). The abundance of highly

Table 2. Indicator values of specialized peat bog beetle species.

Species	Successional stages	IndVal	p	Frequency
Plateumaris discolor *	E	0.989	0.001	38
Actenicerus sjaelandicus **	E	0.854	0.003	21
Aphthona erichsoni *	E	0.773	0.014	33
Cantharis quadripunctata *	E	0.518	0.001	24
Cryptocephalus labiatus *	M	0.994	0.001	33
Altica longicollis *	M	0.987	0.002	37
Lochmaea suturalis **	M	0.761	0.011	39
Absidia schoenherri **	M	0.557	0.004	39
Micrelus ericae **	O	0.757	0.006	26

Note: E – early stages, M – middle stages, O – old stages. *tyrphobiontic, **tyrphophilous species.

Table 3. Results of multiple regression analysis (GLM) on beetle diversity and abundance to environmental variables.

Variables	Estimate	SE	t	p
Abundance of all species (pseudo R^2 = 0.655)				
Intercept	4.994	0.068	72.457	***
Shrub cover	0.168	0.030	5.542	***
Bog water table	0.053	0.015	3.418	**
Species richness (pseudo R^2 = 0.787)				
Intercept	3.568	0.127	27.925	***
Shrub cover	0.401	0.013	1.391	***
Bog water table	−0.017	0.003	−5.642	***
Abundance of habitat generalists (pseudo R^2 = 0.430)				
Intercept	3.838	0.191	20.029	***
Shrub cover	0.008	0.002	4.422	***
Bog water table	−0.021	0.004	4.812	***
Abundance of habitat specialists (pseudo R^2 = 0.641)				
Intercept	4.492	0.176	25.423	***
Shrub cover	0.201	0.003	5.695	***
Bog water table	0.005	0.002	2.813	**

Note: Significance codes: ***$p \leq 0.0001$, **$p \leq 0.001$, *$p \leq 0.05$

specialized peat bog species increased from young to old successional stages. Conversely, habitat generalists were least abundant in old stages (Figure 4(a)).

Among the recorded beetles, phytophagous species prevailed (Figure 4(b)). Herbivorous beetle abundance differed significantly among successional stages (Kruskal–Wallis test H = 23.02, p = 0.0003; Table S1) and increased from young to old successional stages. However, the mean number of phytophagous species in habitats of middle successional stages (pine bogs and open bog spaces) did not differ significantly (Table S1, S2). The abundance of zoophagous species was highest in these stages (Figure 4(b)).

Oligophagous species were abundant among the phytophagous beetles in all successional stages (Figure 4(c)). Their abundance differed significantly among successional stages (Kruskal–Wallis test H = 31.55, p = 0.0001; Table S1). Mean number of oligophagous species in pine bogs and open bog spaces (middle succession stages) did not differ significantly (Tables S1, S2). On the contrary, the highest abundance of polyphagous species was in young stages (Figure 4(c)). Oligophagous species such as *P. discolor, C. labiatus, L. suturalis, A. erichsoni, A. longicollis*, and *Limnobaris t-album* (Fabricius, 1777),

which are trophically associated with specialized peat bog plants, were most abundant (Table S3). It should be noted that numbers of oligophagous beetles were the highest in subclimax habitats (Figure 4(c)).

Herb dweller abundance was significantly higher in early successional stages (Kruskal–Wallis test H = 24.49, p = 0.002; Table S1), while in middle and old stages the mean abundance of shrub inhabitants increased (Kruskal–Wallis test H = 32.95, p = 0.0001; Table S1; Figure 5(a)). The mean numbers of beetles feeding on sedges (Kruskal–Wallis test H = 25.13, p = 0.0001; Table S1) and on shrubs (Kruskal–Wallis test H = 32.99, p = 0.003; Table S1) differed significantly among successional stages. Beetles feeding on *Eriophorum vaginatum* and other sedges dominated in early successional stages (Figure 5(b)). These are species such as *P. discolor, A. erichsoni, A. sjaelandicus, Limnobaris t-album*. The highest numbers of shrub feeders were recorded in subclimax habitats (Figure 5(b)). Among them were *C. labiatus, L. suturalis*, and *A. longicollis*. The heath feeder *L. suturalis* was most abundant in old successional stages (Table S3).

Discussion

The results of this study showed that autogenic peat bog succession influenced beetle diversity, abundance, and species composition. Coleoptera species richness was highest in pioneer stages. The high number of beetle species of these stages can be explained by the fact that the majority of the beetles are migrants; their abundance was not high, except for a few specialized species. The highest beetle abundance was recorded in old successional stages, which probably have suitable environmental conditions mainly for specialized inhabitants of peat bogs, since the mean numbers of such species increased from young to old successional stages. The same was observed for Lepidoptera and Carabidae in peat bogs in the Czech Republic (Spitzer et al. 1999). However, the total number of species in this range decreased.

The response of species assemblages to the environmental conditions of different successional stages was also reflected through diversity. Diversity was higher in middle successional stages which are characterized by the highest degree of shrub encroachment and the highest vascular plant species richness, in comparison to early and old stages. On the other hand, subclimax Coleoptera assemblages and early stage assemblages were the least similar, which demonstrates large differences in environmental conditions between these stages of the successional series. The diversity, abundance and species richness of beetles in mid-successional stages
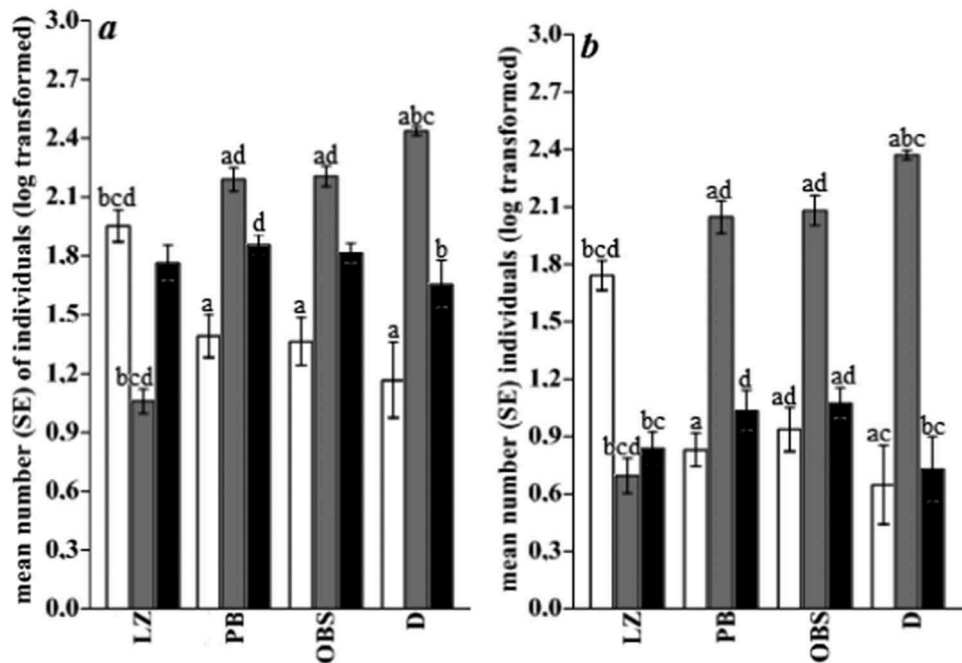
Figure 5. Differences (mean ± SE) in beetle abundance in (a) life forms (chortobionts – white columns; chamebionts – gray columns; other – black columns) and (b) trophic preferences (feeding on sedges – white columns; feeding on shrubs – gray columns; other – black columns) in three peat bog successional stages.

Notes: LZ (a) – early stages; PB (b) and OBS (c) – middle stages; D (d) – subclimax. Differences among successional stages were tested using the Kruskal–Wallis test. Different letters (a, b, c, d) indicate significant differences (post-hoc Dunn's test; P < 0.05) among successional stages.

did not differ significantly. However, cluster analysis showed a higher similarity of open bog space coleopteran assemblages with subclimax assemblages. This indicates some differentiation of the middle successional stages.

For butterflies, it has been shown that population density reflects differences in quality of adult and larval resources between the sites (Dennis et al. 2003, 2006). It can be assumed that fluctuations of plant communities along the peat bog successional gradient (from hygrophilous herbs to heathland shrubs) will be key factors in the distribution of herb-shrub layer beetles, most of which are primary consumers. In this study, among the variables included in the GLM, shrub cover had a positive effect on both the mean total abundance of beetles and the abundance of specialized species, as well as on species richness. The moisture regime was the second explanatory variable. Ericaceous dwarf shrubs were the main element of the periglacial flora and they migrated to peat bogs due to climate warming in the Atlantic period of the Holocene, where they found suitable ecological conditions (Geltman 1982). On the other hand, ericaceous dwarf shrubs together with peat bog pioneers such as Sphagnum mosses and cotton grass, created

unique environmental conditions that were preserved in natural bogs.

It is possible that many of the phytophagous beetles migrated to peat bogs after these plants. Therefore, periglacial species have survived in cold 'microclimatic peat bog traps' (Turlure et al. 2009, 2010) during warm periods of the Holocene. Nowadays, Central European peat bogs seem to be an important link to the historical postglacial environment, providing a paleorefugium for survival of postglacial biota and highly specialized forest-tundra plants and animals during recent climate change (Spitzer and Danks 2006; Sushko 2014).

Tyrphobiontic and tyrphophilous beetle species showed preferences for certain sites along the successional range, such that they can be considered indicators of different successional stages. Therefore, beetles are suitable model taxa to analyze the effects of environmental change of the peat bog successional gradient. These findings have important implications for diversity monitoring programs being implemented in Central European peat bogs. Tyrphophilous species *P. discolor*, *A. erichsoni* and *A. sjaelandicus* were more associated with early successional stages. On the other hand, later stages offered favorable conditions to other specialized peat bog Coleoptera species such as *A.longicollis*, *C. labiatus*, and *L. suturalis*.
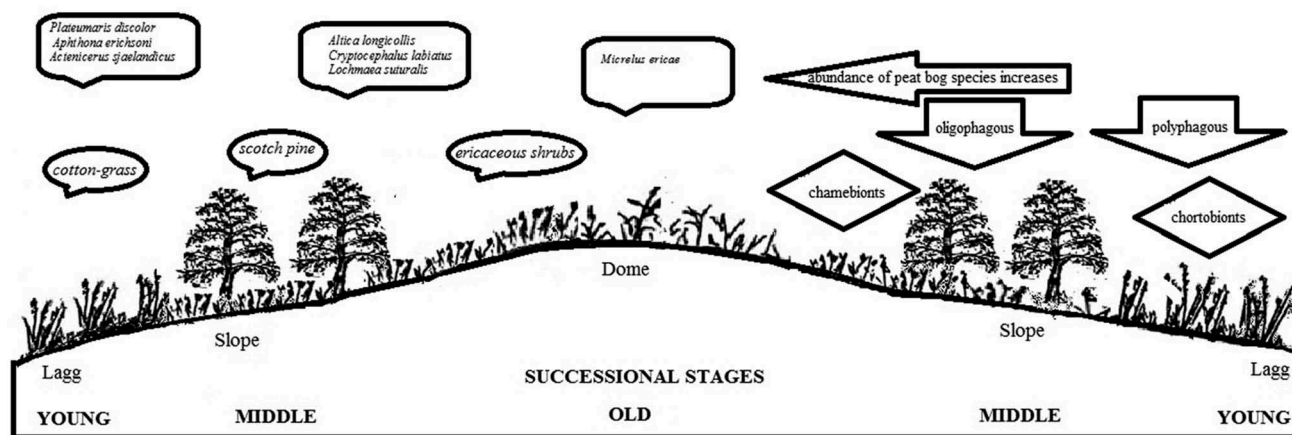
Figure 6. Change in various beetle assemblages along the successional range of habitats in a peat bog.

Composition of beetle ecological groups can help interpret successional dynamics of consumers of pristine peat bogs. Previous studies have focused on changes in insect species richness (Spitzer et al. 1999; Dapkus 2004) and very little is known about ecological group composition during primary succession. This study revealed differences in habitat and trophic preferences, in a diet range of phytophagous and life forms of coleopteran species, that correspond to different successional stages. Younger successional stages were characterized by poor food resources for phytophagous beetles and showed highest abundance of several chortobiontic (herb dwellers) and polyphagous beetles. In sites of middle successional stages, species number and shrub cover were higher, which lead to higher food resources. These stages showed a higher cover of ericaceous dwarf shrubs such as *L. palustre, C. calyculata* Moench, 1794, *C. vulgaris, O. palustris* (Persoon, 1805), and *V. uliginosum* and highest plant species richness; these species were the main larval and imaginal host plants of phytophagous beetles in the middle successional stages. *C. vulgaris* was one of the main host plants of Coleoptera in old successional stages. Ericaceous dwarf shrubs offer a poor food supply for oligophagous species that specialize on *E. vaginatum* and *Carex* spp., which might explain the low abundance of chortobionts at that stage. The dome habitat corresponding to the old successional stages showed a higher percentage of heath in dwarf shrub cover and a high abundance of oligophagous beetles, which feed on this shrub. It should be noted that species richness and abundance of specialized, cold-adapted inhabitants of peat bogs (tyrphobiontic and tyrphophilous species) increases from young to old successional stages along with the increase in shrub cover. This once again characterizes ericaceous dwarf shrubs as a key

factor for the survival of cryophilous species in peat bogs. Pristine Belarusian peat bogs offer favorable conditions to many cold-adapted boreal beetles such as *C. kongsbergensis, C. labiatus, A. longicollis* and others (Sushko 2012, 2014). Specialized peat bog beetles are strongly associated with plant cover and bog water level. They are more abundant than other Coleoptera primarily responding to changes in habitat conditions, both in autogenic successional gradient, and in case of anthropogenic disturbance (Främbs et al. 2002; Brigić et al. 2017). Therefore, they are sensitive indicators that could be used for peatland conservation purposes. A general recommendation for the conservation of peat bog cold-adapted beetles is to preserve plant communities, for example, by avoiding disturbances to the regional water table and limiting the pesticide use nearby (Spitzer and Danks 2006; Sushko 2014).

The historical development of individual bogs is reflected by differences among the ecological group composition of insect assemblages. Among the first insects to colonize peat bogs are herb dwellers (chortobiontic) and polyphagous beetles. These constitute the pioneers of natural peat bog succession. With habitat changes in mid-successional stages, in particular the invasion of ericaceous dwarf shrubs, many shrub dwellers (chamebiontic) and oligophagous species start colonizing. When heath and other dwarf shrubs completely colonize the dome of the bog, chamebiontic and oligophagous predominantly specialized species invade the subclimax habitats (Figure 6).

Conclusion

The results of this study provide evidence that diversity of one of the most numerous consumers in peat bogs, beetles, was highest in middle successional stages characterized by the highest degree of shrub encroachment and the highest

vascular plant species richness. General linear modeling results indicated that main autogenic factors are driving successional changes of herb-shrub layer coleopteran assemblages caused by the interactions of ericaceous dwarf shrub cover. Younger successional stages had the highest abundance of chortobiontic and polyphagous species, whereas middle and old stages contained chamebiontic and oligophagous species specializing on ericaceous dwarf shrubs. Species richness and abundance of cold-adapted inhabitants of peat bogs (tyrphobiontic and tyrphophilous) increased from young to old successional stages along with the increase in shrub cover. Among the first primary consumers to colonize peat bogs are chortobiontic and polyphagous species. With habitat change in later successional stages, in particular the invasion of ericaceous dwarf shrubs, chamebiontic and oligophagous species start colonizing. Nowadays, elements of the ancient periglacial flora such as peat bog ericaceous dwarf shrubs provide a paleorefugium in Central Europe for survival of postglacial biota and other cold-adapted species during recent climate change. Specialized coleopteran species can be indicators of different successional stages.

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