

## Diversity patterns of carabid beetle (Coleoptera, Carabidae) assemblages in the pine forests of Northern Belarus

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Scotch pine *Pinus sylvestris* is the dominant tree species in the Northern Belarus, which formed characteristic boreal forest stands of different types on the border between Eurasian coniferous forest zone and European broad-leaved zone. The knowledge of ground beetle diversity in a range of various pine forest types is sparse.

We investigated the carabid beetle diversity and species composition structure patterns in 60 sites across the main five pine forest types. We conducted pitfall trapping between April and November of 2018. In total, 3,290 individuals belonging to 62 species were collected. In general, the ground beetle diversity was not high. The Shannon-Wiener index ranged from 1.383 to 2.131. Pine forest type with prevailing *Calluna vulgaris* in understory vegetation showed the highest Shannon-Wiener index, whereas the lowest values were recorded from *Cladoniosum* type. NMDS showed differences of species composition of carabid assemblages corresponding pine forest types. The driest *Cladoniosum* forest type was the most different. The IndVal analysis detected several species which were characteristic for one of the forest types. However, many dominant species preferred two or more pine forest types. A significant difference in carabid species composition was detected, but in pairwise comparisons several types of pine forests revealed no significant differences between each other. In this study ground beetles protected in Belarus such as *Carabus coriaceus* (NT), and *Carabus violaceus* (NT) were collected. Among them in pine forests of North Belarus only *Carabus violaceus* is a relatively common species.

Key words: Carabids, Diversity, Pine forests, Belarus

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### INTRODUCTION

Among the forest inhabitants, ground beetles play an important role as predators in the food webs. Carabids are abundant and species rich in forests all over the world (Lövei and Sunderland

1996). Ground beetles are efficient bioindicators because of their quick response to environmental changes and adaptability. At the same time, knowledge about their diversity in natural or most intact pine forests in Central Eastern Europe is rather poor (Selyavko 1991; Solodovnikov 2008;

Aleksandrowicz 2014). As a whole, most of studies in recent decades focus on carabid responses to changing environmental conditions caused by logging, tornadoes, fires, etc. (Rainio & Niemelä 2003). Some studies in Belarus reported about ground beetle assemblage composition, species richness and abundance in different forests, including pine forests (Solodovnikov 2008; Aleksandrowicz 2014). However, many aspects of ground beetle  $\alpha$ -diversity patterns are still unknown and almost no detailed studies on their spatial distribution in main types of pine forests in the Northern Belarus exist. It should also be noted that this region belongs to the southern taiga. In contrast to Central and Southern Belarus, the fauna of the northern part of the country is younger as it has a postglacial genesis (Yakushko 1971).

Thirteen vegetation types of pine forests in Belarus were described (Geltman 1982). These forest types differ widely in environmental conditions; in particular, pine forests can be located both on dry sand soils and on extremely wet peat soils. Their vegetation cover can be represented only by lichens and mosses on the one hand, heather shrubs and various herbs on the other hand. In addition, the number of pine forest vegetation types varies across Belarus in a longitude gradient according to climate change. In particular, the most common for the north region of Belarus are 5 vegetation types such as *Pinetum cladoniosum*, *Pinetum pleuroziosum*, *Pinetum callunosum*, *Pinetum vaccinosum* and *Pinetum myrtillosum*. Comparisons of carabid assemblages of different pine forest types from dry to wet are needed to reveal more accurately species requirements in the habitat gradient.

This study aimed to investigate the ground beetle diversity patterns in a range of different Scots pine forest types on the territory of Northern Belarus. More specifically we aimed to: (1) compare the carabid beetle diversity of the most typical for the north of Belarus pine forest types, (2) find species composition differences and possible characteristic species for the sampled forest types, (3) study the contribution of the different

pine forests to the maintenance and conservation of local biodiversity.

## MATERIALS AND METHODS

The study was conducted in the Vitebsk region in Northern Belarus (Table 1). The mean summer air temperature is 17 °C, the vegetation growth period lasts from 185 to 195 days, and the annual rainfall is approximately 600–700 mm. Forests occupy about 40% of the region. *Pinus sylvestris* prevails, proportion of which reaches 58%. The forest type was determined in accordance with prevailing understory vegetation. We selected for study five pine forest types, which occur in the north of Belarus: *Pinetum cladoniosum* (PCL), *Pinetum pleuroziosum* (PP), *Pinetum callunosum* (PC), *Pinetum vaccinosum* (PV), *Pinetum myrtillosum* (PM) (Table 1). These forest types are homogenous stands within large (2 ha) pine woodland blocks and were at least 100 m apart. The height of the trees was recorded within 10 m×10 m plots of each study site using the optical rangefinder RGK D 1500 (Table 1). According to the measured mean average of the tree height, the pine stands of the studied sites can be attributed to the III class of the stand age (middle-aged stands) (Lazareva & Klimovich 2009). The following stand types were distinguished: one-storied pine stands (*Pinetum cladoniosum*, *Pinetum pleuroziosum*), one-storied pine stands with understory (*Pinetum callunosum*, *Pinetum vaccinosum*), and pine stands with a second story composed of sporadic deciduous trees (*Pinetum myrtillosum*).

The study was conducted in 2018. Carabids were sampled using pitfall traps in the form of plastic cups (250 cm<sup>3</sup>) with a preservative liquid (100 ml of 11% vinegar solution and 10 g of NaCl). Each treatment was repeated 6 times in each of the 5 forest type. In total 6 research sites were set up per forest type. On each site 5 traps were placed 5 m apart (i.e. 5 traps per site, 30 traps per forest type, and 150 traps in total). Sites were at least 100 m apart and 20 m from forest type edge (Fig. 1).

The beetles were collected at 10–14 day intervals. That involved replacing the jar and its contents with a new, empty one. Pitfall trapping was started in the first half of April and all traps were removed at the beginning of November. Ground beetle species were identified according to Freude et al. (2004).

All data from the 5 traps set in each of the 6 sites in each of the five forest types were summed to obtain individual samples for the statistical analyses. Accordingly, we used a total of 30 samples in our analyses. To estimate the potential number of species, the estimators Chao 1 and ACE were used (Magurran 2004; Chao et al. 2009). To examine the carabid alpha-diversity, Shannon–Wiener ( $H'$ ) and Pielou's evenness ( $J'$ ) indexes were calculated. Differences of ground beetle species richness, abundances and Shannon–Wiener diversity were examined using Kruskal–Wallis H test with Dunn's post hoc test and with analysis of variance (one way ANOVA) using Tukey HSD permutation tests (the level of significance  $P < 0.05$ , tests with Bonferroni correction). Prior to the analyses, the data were tested for normality using Shapiro–Wilk normality test.

Non-metric multidimensional scaling (NMDS) based on the Bray–Curtis similarity index using

the R package 'vegan' (Oksanen et al. 2007) and analysis of similarity test (ANOSIM) were applied to assess assemblage composition at the different forest types. The characteristic species for the various forest types were identified using the IndVal (indicator value) procedure (Dufrene & Legendre 1997) with 'indicspecies' R package (De Caceres & Legendre 2009). Species' indicator values ranged from 0 (no indicator value) to 1 (perfect indicator value) with statistical significance  $P < 0.01$ . Analyses were performed in R software (R Development Core Team 2011); Past (Hammer et al. 2001) and EstimateS (Colwell 2013).

## RESULTS

During the study a total of 3,290 individuals belonging to 62 species were collected. The mean species richness (ANOVA,  $df=4$ ,  $F=9.19$ ,  $p<0.001$ ) differed significantly among the carabid assemblages of the five forest types. (Fig. 2a).

The mean number of carabid species was greater in the PC ( $15.21 \pm 0.75$ ), whereas the lowest mean number of species in PCL ( $6.40 \pm 0.21$ ) were recorded. In the PP ( $10.60 \pm 0.99$ ) and in PV ( $10.25 \pm 0.86$ ) the number of species was almost similar. In PM the mean number of species was

Table 1. Summary of the characteristics of the sampling sites in the pine forests (PCL – *Pinetum cladoniosum*, PC – *Pinetum callunosum*, PV – *Pinetum vaccinosum*, PP – *Pinetum pleuroziosum*, PM – *Pinetum myrtillosum*)

Sampling site/Forest type	The main plants in the herb-shrub and moss layers	Soil type	The mean ( $\pm$ SE) height of the pine trees
PCL	<i>Festuca ovina</i> , <i>Hieracium umbellatum</i> , <i>Dicranum polysetum</i> , <i>Pleurozium schreberi</i> , <i>Polytrichum juniperinum</i>	Sand	$18.35 \pm 0.85$
PC	<i>Calluna vulgaris</i> , <i>Vaccinium vitis-idaea</i> , <i>Festuca ovina</i> , <i>Dicranum polysetum</i> , <i>Pleurozium schreberi</i>	Sand	$19.7 \pm 0.74$
PV	<i>Vaccinium vitis-idaea</i> , <i>V. myrtillus</i> , <i>Calluna vulgaris</i> , <i>Melampyrum pratense</i> , <i>Convallaria majalis</i> , <i>Dicranum polysetum</i> , <i>Hylocomium splendens</i> , <i>Pleurozium schreberi</i> , <i>Ptilium crista-castrensis</i>	Sand/Podzol	$21.47 \pm 0.76$
PP	<i>Calamagrostis epigeios</i> , <i>Dicranum polysetum</i> , <i>Hylocomium splendens</i> , <i>Pleurozium schreberi</i>	Sand/Podzol	$22.41 \pm 0.87$
PM	<i>Vaccinium myrtillus</i> , <i>V. vitis-idaea</i> , <i>Festuca ovina</i> , <i>Calamagrostis epigeios</i> , <i>Melampyrum pratense</i> , <i>Dicranum polysetum</i> , <i>D. scoparium</i> , <i>Pleurozium schreberi</i>	Podzol	$20.36 \pm 1.09$

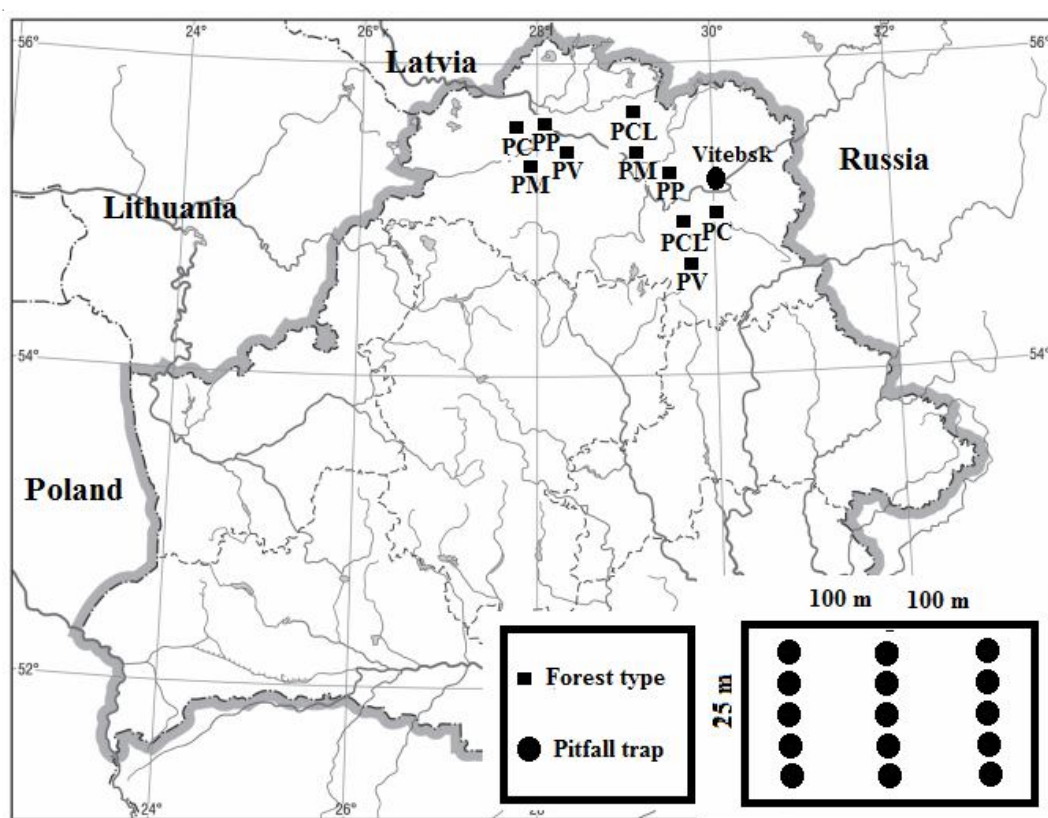


Fig. 1. Map showing the location of the pine forests of the different types (PCL – *Pinetum cladoniosum*, PC – *Pinetum callunosum*, PV – *Pinetum vacciniosum*, PP – *Pinetum pleuroziosum*, PM – *Pinetum myrtillosum*)

Table 2. The main diversity parameters of carabid beetle assemblages of pine forests (PCL – *Pinetum cladoniosum*, PC – *Pinetum callunosum*, PV – *Pinetum vacciniosum*, PP – *Pinetum pleuroziosum*, PM – *Pinetum myrtillosum*)

Parameters	Habitats				
	PCL	PC	PV	PP	PM
Number of observed species	19	44	37	34	38
Chao1	22.46	68.97	42.99	37.36	44.87
Estimate standard deviation	3.63	7.40	7.61	7.51	6.23
ACE	29.27	52.68	46.98	37.78	49.76
Estimate standard deviation	3.51	2.74	2.91	1.90	5.31
Singletons	4	15	16	11	8
Doubletons	2	4	6	3	6
Percentage share of singletons and doubletons (%)	31.57	43.18	59.45	31.81	36.84
Shannon-Wiener diversity index (H')	1.383	2.131	1.610	1.651	1.631
Standard error	0.15	0.08	0.09	0.14	0.07
Pielou evenness index (J')	0.861	0.514	0.521	0.573	0.512
Standard error	0.04	0.03	0.02	0.03	0.01

9.15±0.42. The total ground beetle species richness in each treatment was higher compared to the mean values and ranged from 19 in PCL to 44 in PC (Table 2).

The non-parametric species richness estimators Chao 1 and ACE provided average expected species richness that are close to the actual number of species recorded in the study forest types (Table 1). The estimators showed that the mean number of carabid species in the different forest types was 22.46–68.97 species suggesting that the observed total of 19–44 species represented 64.91% to 94.05% of the overall richness recorded in the study area (Table 2).

The mean abundance (Kruskal-Wallis test,  $\chi^2 = 5.89$ ,  $p = 0.003$ ) differed significantly among the carabid assemblages of the five forest types and was the highest in PM, while the lowest abundance was detected in the PCL (Fig. 2b).

The ground beetle *Carabus arvensis* (6.14%–67.47%) was the most abundant species in all forest types, except PCL. The species *Calathus erratus* (29.54%), *Carabus arvensis* (26.13%), *Poecilus lepidus* (15.0%) and *Harpalus rufipes* (7.95%) were the dominants in the PCL, whereas *Calathus micropterus* (5.8%–22.19%) was among

abundant species in all forest types, except PCL. The ground beetles *Calathus erratus* (21.8%), *Pterostichus oblongopunctatus* (9.55%), *Pterostichus niger* (8.35%), *Carabus violaceus* (7.57%) and *Poecilus lepidus* (5.31%) were among the most numerous species in PC. The species *Pterostichus niger* (11.64%), *Pterostichus oblongopunctatus* (7.91%) and *Carabus hortensis* (6.64%) also prevailed in PV. Among abundant species in PM were *Carabus hortensis* (13.21%), *Pterostichus niger* (12.41%) and *Pterostichus oblongopunctatus* (6.57%) (Table 3). A high proportion (31.57%–59.45%) of carabid species in the assemblages is represented by singletons or doubletons (Table 2).

The pine forest type with prevailing *Calluna vulgaris* in the understory vegetation showed the highest Shannon-Wiener index mean value ( $H_2 = 2.131$ ), whereas the lowest value was recorded from the *Cladoniosum* type ( $H_2 = 1.383$ ). In other carabid assemblages the diversity index values were slightly lower ( $H_2 = 1.610$ – $1.651$ ). The Pielou index peaked only in *Cladoniosum* type ( $J' = 0.861$ ); in other carabid assemblages the evenness was lower ( $J' = 0.512$ – $0.573$ ).

Table 3. Relative abundance (%) of the most numerous (>5%) carabid beetle species of pine forests (PCL – *Pinetum cladoniosum*, PC – *Pinetum callunosum*, PV – *Pinetum vaccinosum*, PP – *Pinetum pleuroziosum*, PM – *Pinetum myrtillosum*)

Species	Habitats				
	PCL	PC	PV	PP	PM
<i>Carabus violaceus</i> Linnaeus, 1758	0	7.57	0	0	0
<i>Carabus hortensis</i> Linnaeus, 1758	0	0	6.64	0	13.21
<i>Carabus arvensis</i> Herbst, 1784	26.13	20.38	29.63	67.46	27.52
<i>Poecilus lepidus</i> Leske, 1785	15.00	5.31	0	0	0
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	0	9.55	7.91	0	6.57
<i>Pterostichus niger</i> (Schaller, 1783)	0	8.35	11.64	0	12.41
<i>Pterostichus rhaeticus</i> Heer, 1837	0	0	0	0	0
<i>Pterostichus diligens</i> (Sturm, 1824)	0	0	0	0	0
<i>Calathus micropterus</i> (Duftschmid, 1812)	0	5.80	19.85	8.96	22.19
<i>Calathus erratus</i> (Sahlberg, 1827)	29.54	21.80	0	0	0
<i>Agonum ericeti</i> (Panzer, 1809)	0	0	0	0	0
<i>Harpalus rufipes</i> (Degeer, 1774)	7.95	0	0	0	0

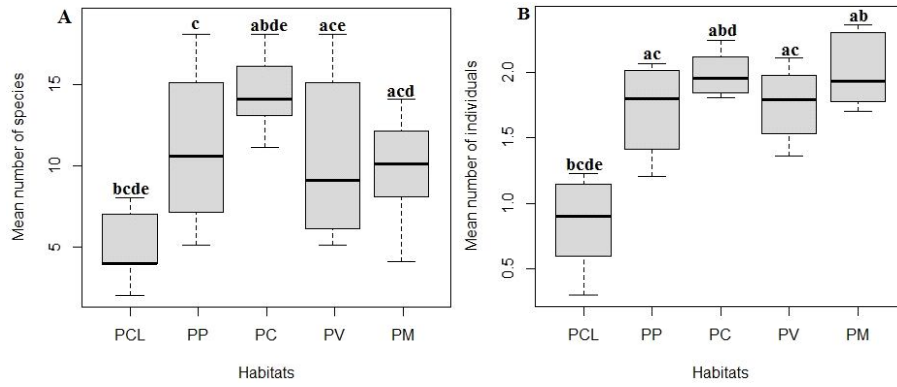


Fig. 2. Box-whisker plots with median, 25% and 75% percentiles (box) and minimum and maximum values (whiskers) for (A) changes of species richness and (B) abundance (log transformed) in carabid beetle assemblages of pine forests: (a) PCL – *Pinetum cladoniosum*, (b) PP – *Pinetum pleuroziosum*, (c) PC – *Pinetum callunosum*, (d) PV – *Pinetum vaccinosum*, (e) PM – *Pinetum myrtillosum*. Differences among forest types were tested using the ANOVA and Kruskal-Wallis test. Letters (a, b, c, d, e) indicate significant differences (Tukey's and Dunn's post-hoc tests;  $P < 0.05$ )

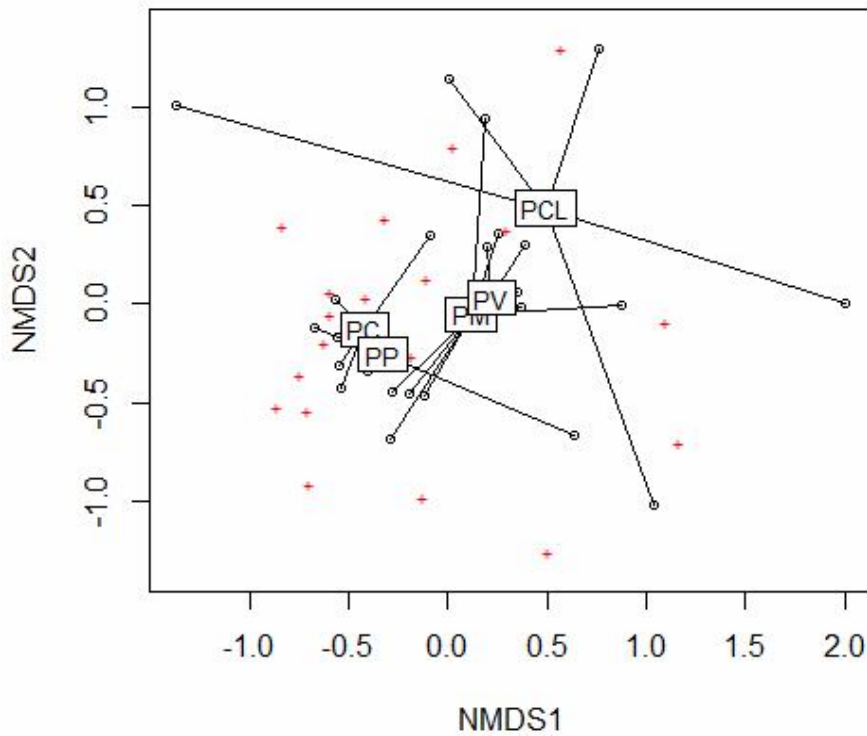


Fig. 3. NMDS-ordination diagram of the carabid beetle assemblages of pine forests: PCL – *Pinetum cladoniosum*, PP – *Pinetum pleuroziosum*, PC – *Pinetum callunosum*, PV – *Pinetum vaccinosum*, PM – *Pinetum myrtillosum*

Table 4. Indicator values of carabid beetle assemblages of pine forests: PCL – *Pinetum cladoniosum*, PP – *Pinetum pleuroziosum*, PC – *Pinetum callunosum*, PV – *Pinetum vaccinosum*, PM – *Pinetum myrtillosum*

Species	Habitats	IndVal	p
<i>Calathus erratus</i> (Sahlberg, 1827)	PC	0.776	0.001
<i>Poecilus lepidus</i> Leske, 1785	PC	0.695	0.001
<i>Poecilus versicolor</i> (Sturm, 1824)	PC	0.581	0.003
<i>Carabus hortensis</i> Linnaeus, 1758	PM	0.764	0.001
<i>Carabus glabratus</i> (Paykull, 1790)	PM	0.633	0.001
<i>Pterostichus niger</i> (Schaller, 1783)	PM	0.579	0.006
<i>Amara brunnea</i> (Gyllenhal, 1810)	PP	0.653	0.004
<i>Synuchus vivalis</i> (Illiger, 1798)	PC+PV	0.622	0.003
<i>Calathus micropterus</i> (Duftschmid, 1812)	PM+PV	0.793	0.001
<i>Cychris caraboides</i> (Linnaeus, 1758)	PM+PV	0.599	0.006
<i>Carabus arvensis</i> Herbst, 1784	PC+PM+PP	0.749	0.001
<i>Pterostichus aethiops</i> (Panzer, 1797)	PC+PM+PP	0.576	0.004
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	PC+PM+PP+PV	0.585	0.003
<i>Carabus violaceus</i> Linnaeus, 1758	PC+PM+PP+PV	0.500	0.028

The IndVal analysis detected species which were characteristic for the various forest types. The species *Calathus erratus*, *Poecilus lepidus* and *Poecilus versicolor* preferred the *Callunosum* pine forest type. The species *Carabus hortensis*, *Carabus glabratus* and *Pterostichus niger* were more associated with the *Myrtillosum* type. The species *Amara brunnea* preferred the *Pleuroziosum* type. On the other hand, many dominant species preferred two or more pine forest types. The species *Calathus micropterus*, *Carabus arvensis* and *Pterostichus oblongopunctatus* were among them (Table 4).

The ANOSIM was performed to test the significance of forest type in forming the ground beetle species composition. A significant difference in carabid species composition was detected (ANOSIM,  $R=0.459$ ,  $p<0.001$ ), but in this case several types of pine forests revealed no significant differences between each other. Pairwise comparisons revealed that species composition was not significantly different between PV and PM and between PC and PP. NMDS showed that PCL was widely dispersed, indicating higher ground beetle assemblage heterogeneity. On the other hand, PV and PM and also PC and PP were less different (Fig. 3).

## DISCUSSION

In the present study, we determined the spatial distribution and diversity patterns of ground beetles in five main Scots pine forest types in Northern Belarus differing in ecological condition represented by hydrology, plant community composition, soil chemistry and other habitat characteristics (Geltman 1982).

Several studies in Belarus reported about ground beetle assemblage composition, species richness and abundance in different forests, including pine forests (Solodovnikov 2008; Aleksandrowicz 2014). However, not many detailed studies about ground beetle diversity in all pine forest types of the postglacial northern part of Belarus have been carried out. Moreover these findings are based on last century studies which were conducted more than 30-40 years ago.

The number of carabid species in the Northern and Southern Belarus was different. In particular, Aleksandrowicz (2014) reported 89 species and noted the higher species richness (72.7% of all species recorded in forests) of ground beetles in pine forests than in mixed and deciduous forests. In the north of Belarus, we recorded 62 species. On the other hand, there are differences in the diversity parameters of the ground beetle assemblages of some habitat types. In the

*Pinetum cladoniosum* type in the south of Belarus, a higher species number and Shannon index value compared to our studies were recorded, whereas the species richness of the ground beetles of the *Pinetum callunosum* and *Pinetum myrtillosum* types in the northern part of Belarus was higher.

Solodovnikov (2008) reported 93 carabid species in pine forests including mixed types (*Piceeto-Pineta*) in the Belarus Lake District (Northern and North-Western Belarus). However, in various pine forests, except mixed types, only 10-18 carabid species were recorded. Our results showed that the observed recent ground beetle species richness in pine forests of the Northern part of the country is almost two times higher.

The mean abundance of ground beetles and species richness revealed clear assemblage patterns in different forest types. The lowest species richness and abundance were recorded in the driest type, such as *Pinetum cladoniosum*. Diversity showed the same trends, whereas evenness was higher in well insolated and warmed sites covered only by lichens and mosses. Besides, in these sites without shrub layer, the open habitat species *Harpalus rufipes*, *Poecilus cupreus*, and *Harpalus autumnalis* were more frequent compared to other forest types.

As predators, ground beetles are not strictly associated with plants. However, high biological productivity and specific habitat condition may increase numbers of invertebrate herbivores, i.e. carabid prey, and thus indirectly affect their abundance (Halme & Niemelä 1993). Moreover, on the soil surface of pine stands the numbers of other invertebrates caught varied in the same way as the carabids (Butterfield 1992; Butterfield et al. 1995). As shown by our study, pine forest types with shrubs (PC, PV, PM) supported higher carabid species richness than habitats without shrubs (PCL, PP). It should be noted, that among the variables influencing carabid species richness and abundance in the pine bogs was also vascular plant cover (Sushko 2019). On the other hand, changes to the microclimate and soil prop-

erties following the understory plant cover in various forest types can also affect diversity of ground surface inhabitants and promote the appearance of species characteristic for other ecosystems (Heinrichs & Schmidt 2009).

The most abundant species in all studied pine forests were the typical forest species *Carabus arvensis*, *Carabus hortensis*, *Pterostichus oblongopunctatus*, *Pterostichus niger*, and *Calathus micropterus*. However, they did not show strong preferences for certain of the studied forest types. These results are consistent with other studies (Szyszko 1983; Aleksandrowicz 2014; Skłodowski 2014; Skłodowski 2017). Among all recorded carabids only seven species preferred one of the pine forest type and had relatively high indicator value ( $>0.5$ ). However, among them are not only specialized forest species, but also generalists who prefer open habitats, such as *Harpalus rufipes* and *Poecilus versicolor*. It probably resulted from the carabid response to the greater access to the light in pine stands (Skłodowski et al. 2018). Nevertheless, some species could have the potential to become bioindicators of various pine forest types. In particular, less abundant species were more sensitive and showed more specific habitat requirements. According to Aleksandrowicz (1991, 2014), *Notiophilus germinyi*, *Miscodera arctica*, *Bradycellus caucasicus*, and *Amara infima* are known as inhabitants of dry *Pinetum cladoniosum* and *Pinetum callunosum* pine forest types in the western part of the European Forest zone. We collected these species, except *Amara infima*, in the same habitats and *Notiophilus germinyi* in *Pinetum myrtillosum* forest type as well.

NMDS revealed a separation of the carabid assemblages corresponding to the studied pine forest types and supported diversity differences between the driest and other forest types. Besides, multivariate analysis described very high similarity in species composition between *Pinetum vaccinosum* and *Pinetum myrtillosum* types. Similarity in the composition of carabid assemblages of these forest types may be ex-



plained by structure of the vegetation layer and accordingly microclimatic conditions, which were formed by shrubs represented by blueberries and lingonberries. Despite differences in species richness and diversity, and plant community structure there was high similarity between the ground beetle species composition of *Pinetum pleuroziosum* and *Pinetum callunosum* forest types. In this case, habitat heterogeneity between these sites reflected carabid diversity, which was higher in the *Pinetum callunosum* forest type.

Our study indicates that various, relatively large and homogeneous pine forest types are habitats for rare and protected species. In this study ground beetles protected in Belarus such as *Carabus coriaceus* (NT), and *Carabus violaceus* (NT) were collected. Of these only *Carabus violaceus* is a relatively common species in pine forests of North Belarus. Therefore, the cutting of mature pine forests must be done very carefully and selectively. In addition, it is necessary to reduce the recreational load in the habitats of these protected species.

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## REFERENCES

Alexandrovich O.R. 1991. The carabid fauna (Coleoptera, Carabidae) of Belarus. In: Fauna and Ecology of Beetles of Belarus. Minsk. pp. 37-78. (In Russian; abstract in English).

Aleksandrowicz O.R. 2014. Ground beetles (Coleoptera, Carabidae) of the West Part of Russian Plane. Fauna, zoogeography, ecology. Pub-

lisher: Lambert Academic Publishing, Saarbrücken. 456 p. (In Russian; abstract in English).

Butterfield J. 1992. The effect of conifer plantations on the invertebrate communities of peat moorland. In: Bragg O.M., Robertson P.D. and Ingram H.A.P. (eds.), Peatland ecosystems and man: an impact assessment. International Peat Society, Cambridge University Press, Cambridge. pp. 309–315.

Butterfield J., Luff M.L., Baines M., Eyre M.D. 1995. Carabid beetle communities as indicators of conservation potential in upland forests. Forest Ecology and Management 79: 63-77.

Chao A., Colwell R.K., Lin C., Gotelli N.J. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90: 1125-1133.

Colwell R.K. 2013. EstimateS and user's guide: statistical estimation of species richness and shared species from samples. Version 9.1. <http://purl.oclc.org/estimates>.

De Caceres M, Legendre P. 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90 (12): 66–74.

Dufrene M., Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Freude H., Harde K., Lohse G.A. 2004. Die Käfer Mitteleuropas. Band 2. Adepaga 1. Carabidae (Laufkäfer). Spektrum-Verlag, Heidelberg-Berlin. Akad. Verl. 302 pp.

Geltman V.S. 1982. Geographic and typological analysis of forest vegetation in Belarus. Minsk: Science and technology. 326 pp. (In Russian; abstract in English)

Lazareva M.S., Klimovich L.K. 2009. Forestry: a practical guide. Gomel: Gomel State University named after F. Skaryna. 125 pp. (In Russian)

Halme E., Niemelä J. 1993. Carabid beetles in fragments of coniferous forest. Annales Zoologici Fennici 30: 17-30.

- Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1-9.
- Heinrichs S., Schmidt W. 2009. Short-term effects of selection and clear cutting on the shrub and herb layer vegetation during the conversion of even-aged Norway spruce stands into mixed stands. *Forest Ecology and Management* 258: 667-678.
- Lövei G.L., Sunderland, K.D. 1996. Ecology and Behavior of Ground Beetles (Coleoptera: Carabidae). *Annual Review of Entomology* 41: 231-256.
- Magurran A. E. 2004. *Measuring Biological Diversity*. Oxford: Blackwell Publishing. 256 öö.
- Oksanen J.R., Kindt P., Legendre B., O'Hara R.B., Simpson G. L., Stevens M.H. 2007. *Vegan: Community Ecology Package*. <http://r-project.org>.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org>.
- Rainio J., Niemelä J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* 12: 487-506.
- Red Book of the Republic of Belarus. 2015. *Animals: rare and endangered species of wild animals* / ed. I.M. Kachanovsky. Minsk: BelEn. 320 pp.
- Selyavko T.M. 1991. Coleoptera complexes of the ecological range of pine forests of the Berezinsky reserve. In: *Fauna and Ecology of Beetles of Belarus*. Minsk. pp. 226-234. (In Russian; abstract in English).
- Skłodowski J. 2014. Consequence of the transformation of a primeval forest into a managed forest for carabid beetles (Coleoptera: Carabidae) – a case study from Białowieża (Poland). *European Journal of Entomology* 111 (5): 639-648.
- Skłodowski J. 2017. Three phases of changes in carabid assemblages during secondary succession in a pine forest disturbed by windthrow – results from the first 10 years of observations. *Insect Conservation and Diversity* 10: 449-461.
- Skłodowski J., Bajor P., Trynkos M. 2018. Carabids benefit more from pine stands with added understory or second story of broad-leaved trees favored by climate change than from one-storied pine stands. *European Journal of Forest Research* 137: 745-757.
- Solodovnikov I.A. 2008. *Ground beetles (Coleoptera, Carabidae) of the Belarusian Lake District. With a catalog of species of ground beetles in Belarus and neighboring countries: monograph*. Vitebsk: UO "VSUP.M. Masherov". 325 pp. (In Russian; abstract in English).
- Sushko G. 2019. Key factors affecting the diversity of sphagnum cover inhabitants with the focus on ground beetle assemblages in Central-Eastern European peat bogs. *Community Ecology* 20 (1): 45-52.
- Szyszkowski J. 1983. State of Carabidae (Col.) fauna in fresh pine forest and tentative valorisation of this environment. *Treatises and Monographs. SGGW-AR*. Warszawa. 28: 1-80.
- Yakushko O.F. 1971. *Belarusian Lake District*. Minsk. 336 pp. (In Russian; abstract in English).

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