Comparison of the diversity of ground beetle (Coleoptera: Carabidae) assemblages in small and large temperate peat bogs

Gennadi G. Sushko[1], Sergey V. Buga[2], Yulia I. Novikova[1]

[1] Department of Ecology and Geography, Vitebsk State University named after P.M. Masherov, Vitebsk, Belarus
[2] Department of Zoology, Belarusian State University, Minsk, Belarus

SUMMARY

We present a study comparing assemblages of ground beetles between small and large pristine peat bogs in Central-Eastern Europe, to better understand biodiversity variability in peatland ecosystems in tundra patches in the temperate zone. We found that Shannon diversity and Pielou evenness indices and species composition for carabid assemblages of small peat bogs were significantly higher compared to large peat bogs. However, NMDS ordination revealed a high similarity between the assemblages of open habitats in peat bogs of different sizes. Regardless of peat bog size, assemblages included mostly specialised, medium-sized and flightless species. The predominance of habitat specialists with poor dispersal ability indicates that the habitat conditions in both small and large peat bogs are stable in the region. Small peat bogs were represented by a higher number of open habitat and forest dweller species, but their abundances were not high. When comparing ground beetle assemblages of small peatlands and adjacent pine forests on mineral soils, clear differences in diversity, species composition, imago body size and flight ability were revealed. Only some forest dwellers were recorded in peat bog habitats, while peat bog specialists were not found in the pine forests. Consequently, even small peat bogs can support highly specialised species assemblages and represent an environmental filter (probably due to the high humidity and acidity of *Sphagnum* mosses), which can exclude most generalist species and species from adjacent habitats.

KEY WORDS: body size, carabid diversity, habitat preferences, flight ability, peatlands, pine forest

INTRODUCTION

Peat bog ecosystems provide many important ecosystem services including regulation of climate conditions, long-term carbon and greenhouse gas sequestration, and hosting biodiversity (Minayeva *et al.* 2008). The specific environmental conditions of peat bogs such as high water table and acidity, low mineral nutrient availability, and microclimate characteristics determine their highly specialised flora and fauna, included many cold adapted subarctic and boreal species (Spitzer & Danks 2006). Peat bogs can be viewed as habitat islands and tundra patches in temperate zones. They were once typical habitats in western and central Europe but nowadays, as a result of peat extraction, drainage and farm land management, the degradation of peat bogs has become pronounced (Joosten & Clarke 2002, Wieder & Vitt 2006). Moreover, the unique peat bog biodiversity is globally affected by climate warming (Keddy 2010). Understanding diversity patterns of pristine ecosystems including peat bogs and the processes driving them are important interests in ecology in terms of current climate change and conservation of unique post-glacial biota.

The current biodiversity of European peat bogs formed during the Holocene (Spitzer *et al* 1999, Sushko 2019a). Many of these peat bogs are ancient and have been preserved since the early Holocene, about 9,000 to 11,000 years ago, while some of the peat bogs began to form later, in particular by formation of swamps from lakes in the middle Holocene (Geltman 1982). This is indicated by the thickness and composition of their peat deposits (Pidoplichko 1961, Geltman 1982). Studying peat bog biota in relation to bog age and size can show how such different habitats contribute towards biodiversity conservation. One of the most appropriate taxa for such research is ground beetles. Predatory carabid beetles are one of the most abundant insect groups living in the moss cover of temperate peatlands and are consequently important members of peat bog food webs (Krogerus 1960, Främbs *et al.* 2002, Mossakowski *et al.* 2003, Dapkus

& Tamutis 2008). On the other hand, predominantly non-flying ground beetles can be quite sensitive to environmental change and are suitable bioindicators of habitat conditions (Rainio & Niemelä 2003). The proportion and abundance of specialised carabid species with particular habitat preferences are thus of interest due to their sensitivity to habitat condition changes (Lövei & Sunderland 1996, Aleksandrowicz 2014). Carabid beetle wing state and body size are particular characteristics that influence species' ability to adapt to different habitat conditions and to disperse (Darlington 1943, Lövei & Sunderland 1996, Rainio & Niemelä 2003). Consequently, study of ground beetle assemblage composition, habitat preferences and dispersion ability could provide important information about the biodiversity in peat bogs of different size and age.

Within Europe, pristine peat bogs are located primarily in the north and east, because land use and degradation of peatlands in western Europe has been much more intensive. In Central-Eastern Europe, only five countries, including Belarus, have maintained more than 50 % of their peatlands (25,605 km^2) in an almost intact condition (Bragg & Lindsay 2003, Joosten *et al*. 2017). In the northern postglacial region of the country (Belarusian Lake District), peat bogs are one of the most typical landscape elements and cover 185,000 ha. Plenty of large, ancient and small, relatively young, natural peat bogs remain in this region (Grumo *et al.* 2010).

The insect diversity of large ancient Belarusian peat bogs is relatively well known (Sushko 2012, 2021, 2022). Such peatlands are stable ecosystems if natural conditions are not disturbed by human activity (Pidoplichko 1961, Grumo *et al.* 2010). The most stable areas are the central parts of large peat bogs. Their insect assemblages include mainly cold-adapted specialised (tyrphobiontic and tyrphophilic) species (Spitzer *et al* 1999, Spitzer & Danks 2006). Previous studies showed that the carabid assemblages of large peat bogs include very few generalists and species associated with other habitats due to the extreme conditions in *Sphagnum* mats, such as permanent humidity and high acidity (Mossakowski *et al*. 2003, Aleksandrowicz 2014, Sushko 2019b). On the other hand, large convex peat bogs are characterised by a long transition zone, where in spring and early summer water that flows from the dome is retained. This may be a barrier to the migration of flightless insect species from adjacent habitats, imagoes of which are active during this period, including ground beetles (Aleksandrowicz 2014). At the same time, we have much less information on the diversity patterns of small peat bogs adjacent to dystrophic lakes. Their relatively small peat deposits suggest that such peat bogs are probably much younger than the large peatlands that are widespread in Belarus. They do not have a convex structure or an extended wet transit zone and are surrounded mainly by pine forests on mineral soils. Therefore, *Sphagnum* mat insect assemblages of small and large peat bogs may differ.

The primary aim of this study was to assess the diversity patterns and species composition of carabid beetles of small temperate peat bogs compared to large peatlands. In addition, we characterised carabids of small and large peat bogs by habitat preferences, as well as wing morphology and body size. This links to dispersal ability, because carabid assemblage composition and diversity may be related to these important ecological characteristics. We also compare diversity, species composition, habitat preferences, wing morphology and body size of carabid beetles between small peat bogs and adjacent pine forests on mineral soils. We predicted that, due to increased migration of individuals from adjacent habitats in small peat bog areas: (1) small peat bogs would have a higher carabid beetle species diversity compared to large bogs; (2) small peat bogs would have a higher proportion of generalists and forest species compared to large bogs; and (3) small peat bogs would exhibit a higher proportion of flying species, and large-bodied species with high dispersal ability from adjacent pine forests.

METHODS

Study site

The study area is the Lake District in the north of the Republic of Belarus (55° 34' – 55° 37' N; 27° 55' – 28° 06' E). The habitats of this region, where the Eurasian coniferous forest zone closely approaches the European broad-leaved zone, was formed after the last glacial period (Pidoplichko 1961). The study was conducted in two large, ancient peat bogs (Yelnia: 19,984 ha., coordinates 55° 59' N, 27° 82' E; and Mokh: 4,602 ha., 55° 62' N, 27° 54' E) and two small peat bogs adjacent to dystrophic lakes (area of 3–3.5 ha., 55° 17' N, 29° 94' E and 54° 88' N, 30° 35' E) (Grumo *et al.* 2010). We collected carabids in habitats with the same general plant community composition in these peat bogs of different sizes, including open bogs and pine bogs, as well as pine forests adjacent to small peat bogs (Figure 1).

We established 50 sampling sites: 10 sites in open bogs of small peat bogs (obe), 10 sites in open bogs of large peat bogs (obo), 10 sites in pine bogs of small peat bogs (pbe), 10 sites in pine bogs of large peat bogs (pbo) and 10 sites in pine forests adjacent to

Figure 1. Habitat types: (a) open small peat bog, (b) open large peat bog, (c) pine small peat bog, (b) pine large peat bog (d), pine forest on mineral soil (e, f).

small peat bogs (pf). At each pitfall trap location (see below), environment variables were recorded in a 1 × 1 m plot at 10–14 day intervals between 30 April and 01 November 2021. Electrical Conductivity and pH in the *Sphagnum* mat water were measured using a multiparameter portable meter (model HI 9813-51). The coverage (%) of vascular plants, number of plant species and plant height in the herb-shrub layer were surveyed in June and August 2021 (Table 1).

The study sites were selected to represent the two main peat bog habitats in the area: open bogs on the peat bog margin and pine bogs on the slopes. The open bog sites were located at least 20–30 m from the bog margin. Their vegetation was mainly composed

Table 1. Mean values (±SE) of environmental variables in the study sites of peat bogs and adjacent pine forests. Significant differences (ANOVA or, where listed in parentheses, Kruskal-Wallis test): *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Pairwise comparisons were conducted using the post hoc (Tukey's or Dunn') tests and different superscript letters indicate significant differences between groups at $p < 0.05$.

Environmental variables	F / (χ^2)	p	Habitats				
			open bogs (small)^{a}	open bogs (large)^{b}	pine bogs (small)^{c}	pine bogs (large)^{d}	pine forests^{e}
total vascular plant cover (%)	(12.31)	**	29.8±4.3^{c,d,e}	27.2±8.7^{c,d,e}	73.3±8.5^{a,b,e}	75.7±0.4^{a,b,e}	37.5±3.6^{a,b,c,d}
shrub cover (%)	(26.52)	***	7.4±1.3^{c,d,e}	6.9±0.9^{c,d,e}	67.3±5.4^{a,b,e}	68.6±6.8^{a,b,e}	27.9±3.5^{a,b,c,d}
herb cover (%)	(31.74)	***	26.5±1.6^{c,d,e}	28.7± 2.3^{c,d,e}	10.3± 2.6^{a,b,e}	11.1± 2.4^{a,b,e}	3.95±0.94^{a,b,c,d}
number of vascular plant species	14.59	**	3^{c,d,e}	3^{c,d,e}	7^{a,b,e}	8^{a,b,e}	10^{a,b,c,d}
plant height (cm)	8.78	*	35.8±1.8^{c,d,e}	39.1±0.8^{d,e}	44.6±2.4^{a,e}	46.2±1.4^{a,b,e}	11.84±3.4^{a,b,c,d}
pH	(12.41)	**	3.54±0.03^{e}	3.35±0.01^{e}	3.21±0.01^{e}	3.41±0.04^{e}	5.74±0.02^{a,b,c,d}
Conductivity (µS cm^{-1})	(18.26)	**	78.3±4.5^{c,d,e}	82.1±2.8^{c,d,e}	39.3±0.5^{a,b,e}	42.1±1.8^{a,b,e}	119.8±12.1^{a,b,c,d}
bog water level (cm)	4.38	*	6.3±0.94^{c,d}	5.9±1.2^{c,d}	22.6±2.7^{a,b}	19.8±0.95^{a,b}	n/a
peat deposit thickness (m)	9.32	*	2.6±0.2^{c,d}	2.9±0.5^{c,d}	3.1±0.7^{a,b}	3.4±0.2^{a,b}	n/a

of *Sphagnum angustifolium*, *Eriophorum vaginatum*, *Andromeda polifolia* and *Oxycoccus palustris*. The pine bog sites were located at least 50 m from the peat bog edge and 30 m from the open bogs. These were covered predominantly by *Sphagnum magellanicum*, *Ledum palustre*, *Chamaedaphne calyculata*, *Calluna vulgaris*, *Vaccinium oxycoccus*, *V. uliginosum* and sparse short pines (*Pinus sylvestris*). The cover of ericaceous dwarf shrubs was low in open bogs and high in pine bogs. On the other hand in open bogs, the cover of grasses, represented predominantly by cottongrass, was higher than in pine bogs (Table 1).

On large peatlands, similar habitats can be found at much greater distances from their edge. However, this may represent different succession stages. To account for this, we measured the thickness of the peat deposit. As it turned out, peat thickness in the study habitats on small peat bogs was similar compared to large peatlands (Table 1). Consequently, an assessment of the ground beetle assemblage composition in similar environmental conditions of peat bogs of various sizes was carried out. This is confirmed by both the similar plant community composition and the thickness of the peat deposit.

The plant communities of pine forests on sandy soil adjacent to the small peat bogs included mainly *Vaccinium vitis-idaea*, *V. myrtillus*, *Calamagrostis epigeios, Melampyrum pratense* and *Pleurozium schreberi*. The height of the trees here ranged from 20 m to 35 m.

Ground beetle survey

At each of the 50 sampling sites, we placed three pitfall traps to survey ground beetles. The data from these sets of three traps were summed to obtain individual samples for the statistical analyses. Accordingly, we used a total of ten replications in each of the five studied habitat types in our analyses. To reduce the probability of spatial autocorrelation, sampling sites were located randomly and at least 20 m apart. The traps were plastic cups (250 cm^3) filled with a 4 % formaldehyde solution, to which we added a few drops of detergent. The pitfall traps were set on 30 April 2021 and removed on 01 November

2021. The traps were checked at 14-day intervals. Carabid beetles were identified to species according to Freude *et al.* (2004).

The collected ground beetles were assigned to groups according to their habitat preferences: peat bog specialists, forest species, open habitat species, and generalists. Imago body sizes for the carabid species analysed were classified into following categories: small (< 6 mm), medium (6−10 mm), large (10.1−15 mm) and largest (> 15 mm). According to the degree of hind wing development, ground beetles were also classified into the following categories: brachypterous (hind wings reduced), dimorphic (short-winged and long-winged forms), macropterous (hind wings fully developed). These classifications were based on the literature (Freude *et al.* 2004, Aleksandrowicz 2014) and according to the Information System about Beetles of Poland (Coleoptera Poloniae 2015).

Data analysis

We tested the differences among ground beetle species richness, total abundances, Shannon diversity and Pielou evenness indexes, species traits and environmental parameters using analysis of variance (ANOVA) and Tukey post hoc tests or, where parametric test assumptions were not met, using Kruskal-Wallis tests with Dunn's post hocs, with a Bonferroni correction applied (level of significance $p < 0.05$). Prior to analyses, Shapiro-Wilk's and Levene's tests were used to check for normality and homogeneity of variance.

To examine differences in the carabid species richness and diversity, sample-size-based rarefaction and extrapolation curves based on Hill numbers were computed, using the iNEXT.4steps package (Chao 2020). The first three Hill numbers (q 0 = species richness, q 1 = the exponential term of the Shannon index, q 2 = the inverse of the Simpson index) and Pielou evenness index based on the abundance data matrix (Chao *et al.* 2014) were applied for each ground beetle assemblage within each habitat type and bog size combination.

To test whether peat bog size and habitat type had a significant effect on carabid beetle species composition, a Permutational Analysis of Variance (PERMANOVA) was applied using the Bray-Curtis dissimilarity measure with 999 permutations in the "vegan" R package (Oksanen *et al*. 2019). Differences in composition of ground beetle assemblages were tested by non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance using the Past 4.08 software (Hammer *et al*. 2001). Carabid abundance data were $\log(x + 1)$ transformed prior to multivariate analysis (Legendre & Gallagher 2001). The characteristic carabid species for the various habitat types were identified using the indicator value procedure (IndVal) with the "indicspecies" R package (De Caceres & Legendre 2009). Indicator values range from 0 (no indication) to 1 (perfect indicator value) with the statistical significance level set at $p < 0.05$.

RESULTS

Most of the measured environmental variables differed significantly among the two peat bog habitat types and adjacent pine forests on the mineral soils (Table 1). Only pH values did not differ significantly among peat bog habitats. Pairwise comparisons showed no significant differences in total herb-shrub layer cover, shrub cover, herb cover, number of vascular plant species and plant height of the herb-shrub layer, or in conductivity and bog water level between open bogs and between pine bogs, regardless of the peat bog size (Table 1).

A total of 3,592 carabid beetle specimens belonging to 36 species were recorded (Table A1 in the Appendix). The abundance of ground beetles differed significantly among the assemblages of the five studied habitat types (Figure 2a). However, carabid abundance did not differ significantly between open habitats ($p = 0.081$) and between pine bogs ($p = 0.255$) of small and large bogs. On the other hand, the abundance of ground beetles in pine bogs was significantly higher ($p = 0.003$) than in adjacent pine forests (Figure 2a).

Species richness in open bog habitats did not differ significantly between small and large peatlands ($p = 0.352$), and was significantly lower than in pine bogs ($p = 0.001$). The species richness in pine bogs was significantly higher in small peat bogs than in large bogs ($p = 0.022$), but was significantly lower than in non-bog pine forests ($p = 0.003$) (Figure 2b). The overall accumulation of carabid species was more saturated (Hill number q 0) across open peat bog sites and pine bogs of large peatlands (Figure 3).

The Shannon diversity index was significantly higher in the small peat bog compared to large peat bog sites ($p = 0.002$). Significant differences were found between bog sites and pine forests (Figure 2c). The same trend was detected for evenness based on Pielou index values (Figure 2d). Diversity metrics such as exponential Shannon's index (Hill number q 1) and inverse Simpson index (Hill number q 2) were similar (Figure 3).

Based on PERMANOVA tests (Table 2), the

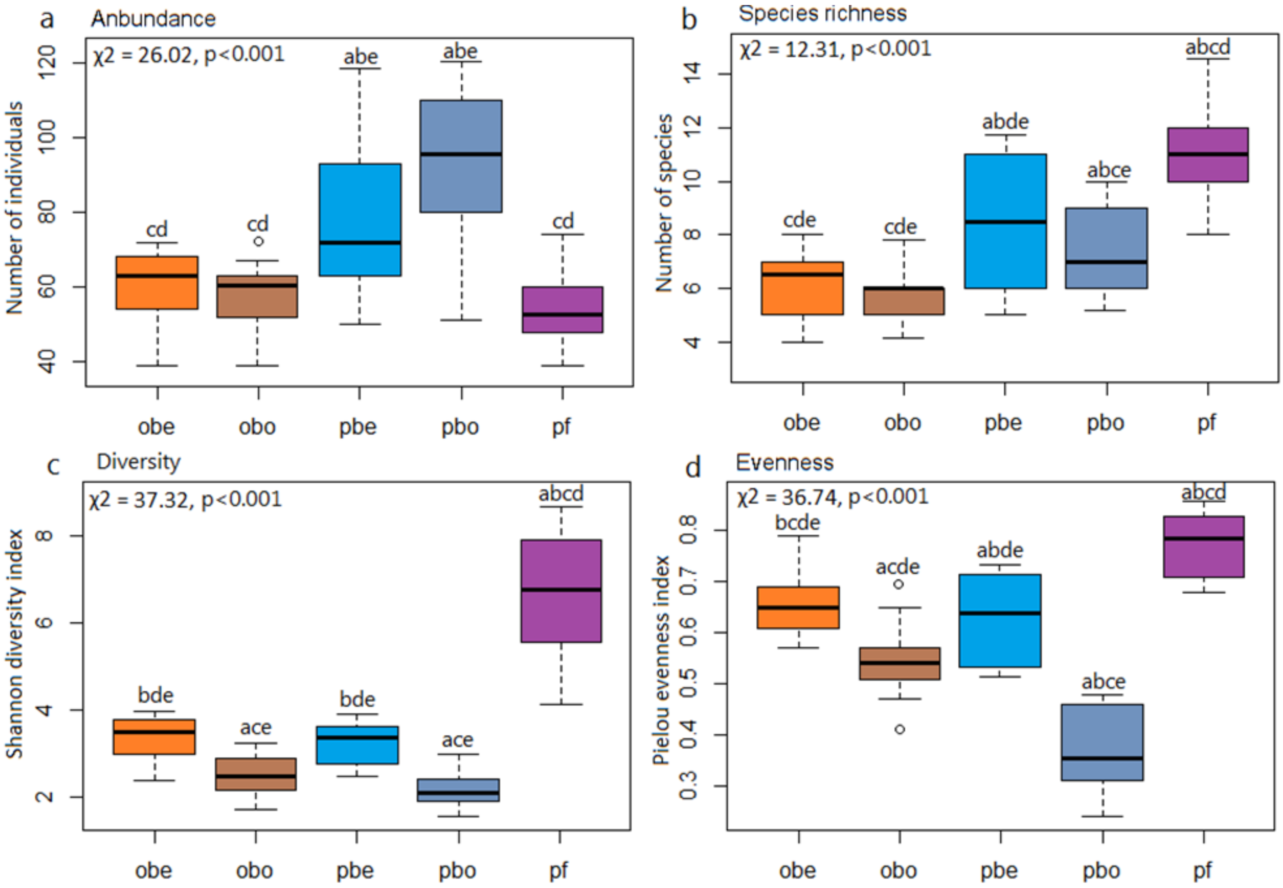

Figure 2. Mean values (±SE) of ground beetle abundance, species richness, diversity and evenness in assemblages of peat bogs and adjacent pine forests: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo) and pine forests (pf). Pairwise comparisons based on Kruskal-Wallis test with Dunn's post hoc test (different letters denote significant differences; the level of significance $p < 0.05$).

species composition of ground beetle assemblages varied significantly ($p = 0.001$) among both habitat types and size of peat bogs. However, no significant interaction between habitat and size of peat bogs could be detected. In the NMDS ordination (Figure 4), a clear separation of species composition between the open bogs and pine bogs was observed. On the other hand, higher similarity was found between the assemblages of open habitats.

We identified five significant indicator species in peat bog habitats of different sizes, but their indicator value was not high (IndVal range 0.37–0.41) (Table 3). *Poecilus cupreus* and *Poecilus versicolor* were more associated with open sites of small peat bogs. These two species are generalists of open habitats. *Pterostichus diligens* was associated predominantly with pine bogs in small peat bogs. The specialised species *Pterostichus rhaeticus* and *Agonum ericeti* preferred pine bogs of large peatlands. Among indicator species in peat bogs, forest specialists such as *Carabus hortensis*, *C. arvensis* and *Pterostichus oblongopunctatus* were not recorded, but these species were characterised by high indicator significance in adjacent pine forests.

Peat bog carabid assemblages included predominantly specialised species (tyrphobiontic and tyrphophilic) regardless of peatland size (Figure 5). Large peat bogs were characterised by significantly higher abundance of such species ($p < 0.001$), whereas small peat bogs were represented by the higher abundance of open habitat dwellers (Table A2). On the contrary, the carabid assemblage of adjacent pine forests mainly consisted of forest specialists and generalists (Figure 5), and the peat bog inhabitants were not collected here.

In both small and large bogs, carabid assemblages were mainly characterised by medium-sized and flightless species (Figures 6 and 7). In contrast to the peat bogs, pine forest ground beetle assemblages were represented by higher numbers of individuals belonging to the large and largest body size ranges, and dimorphic species (Table A2).

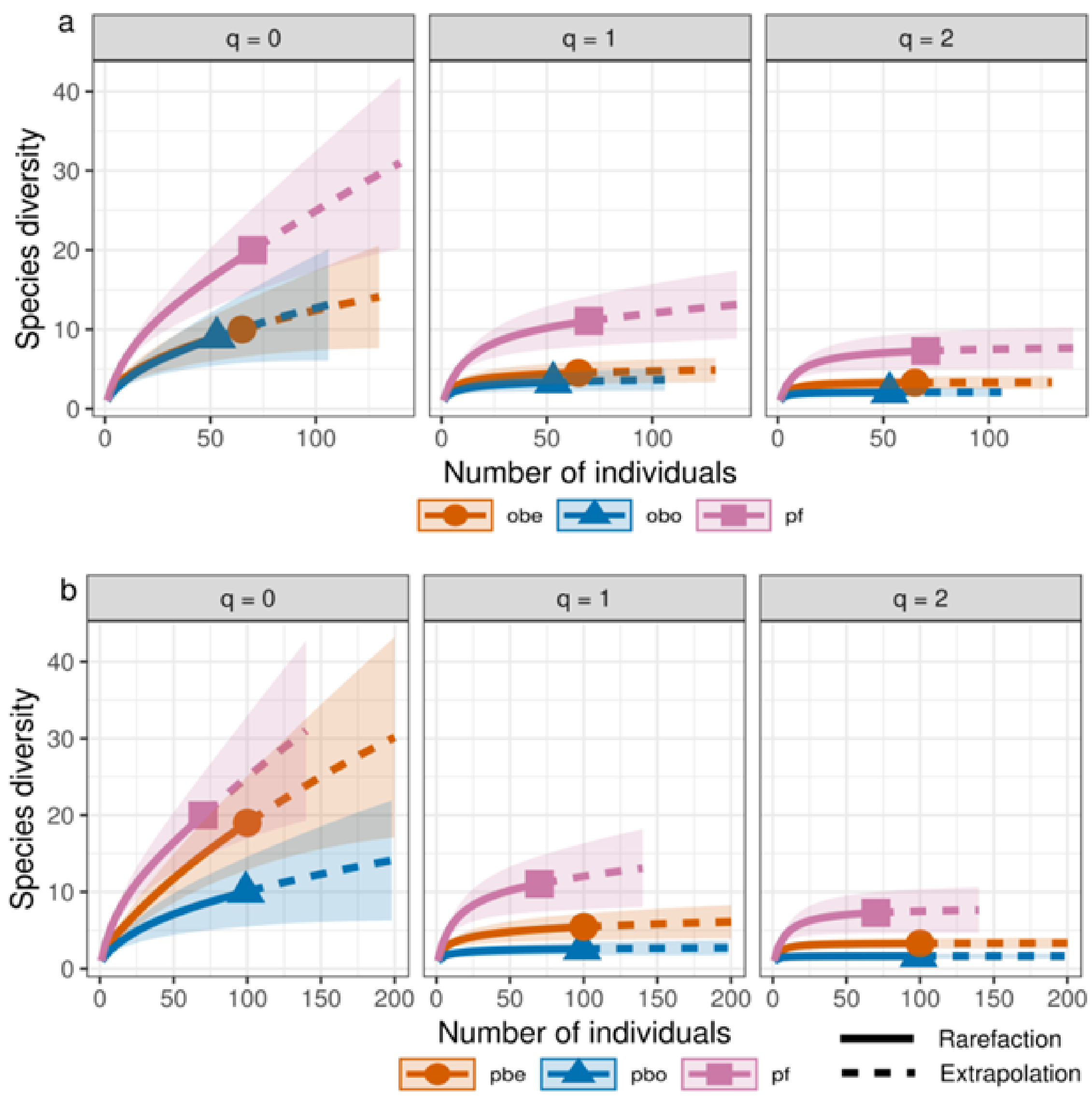

Figure 3. Diversity of ground beetle assemblages in peat bogs and adjacent pine forests: (a) open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine forests (pf); (b) pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf). Curves based on observed individuals show species richness (Hill number q=0) and diversity (Hill numbers q=1 and q=2). Curves were constructed with 95 % confidence intervals (shaded regions), which were obtained by a bootstrap method based on 100 replications.

Table 2. Results of a PERMANOVA on ground beetle species composition in relation to habitat type and peat bog size (based on Bray-Curtis dissimilarities and 999 permutations).

Variables	Sum of squares	df	Mean squares	F	p
Habitat type	1.742	3	0.580	18.28	0.001
Peat bog size	1.168	1	1.168	36.78	0.001
Habitat type × Peat bog size	1.168	3	0.389	12.26	0.910
Residual	1.080	34	0.031		
Total	2.822	41			

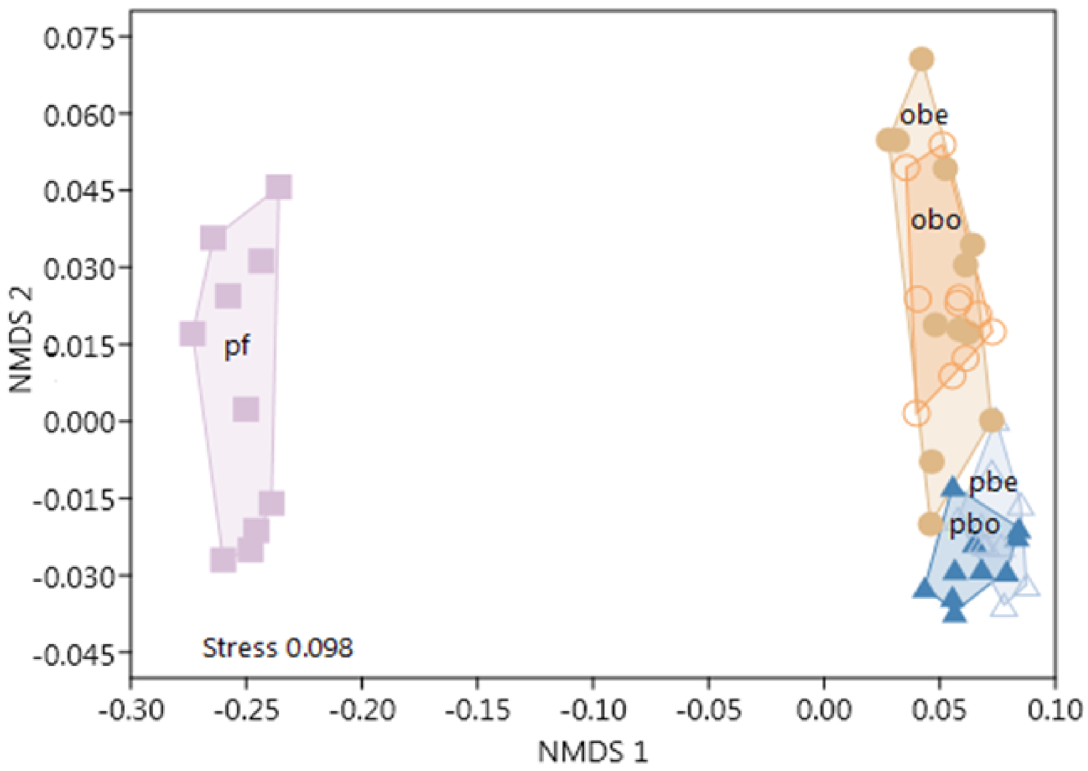

Figure 4. Non-metric multidimensional scaling (NMDS) of ground beetle assemblage composition in peat bogs and adjacent pine forests. Acronyms: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf).

Table 3. Indicator values (IndVal) of ground beetle species in assemblages of peat bogs and adjacent pine forests.

Species	Habitats	IndVal	p
Poecilus cupreus (Linnaeus, 1758)	open bogs (small)	0.38	0.045
Poecilus versicolor (Sturm, 1824)	open bogs (small)	0.41	0.018
Pterostichus diligens (Sturm, 1824)	pine bogs (small)	0.46	0.009
Pterostichus rhaeticus Heer, 1837	pine bogs (large)	0.37	0.018
Agonum ericeti (Panzer, 1809)	pine bogs (large)	0.41	0.009
Carabus glabratus Paykull, 1790	pine forests	0.41	0.009
Carabus hortensis Linnaeus, 1758	pine forests	0.97	0.009
Carabus arvensis Herbst, 1784	pine forests	0.94	0.009
Pterostichus oblongopunctatus (Fabricius, 1787)	pine forests	0.98	0.009
Pterostichus niger (Schaller, 1783)	pine forests	0.67	0.009
Calathus micropterus (Duftschmid, 1812)	pine forests	0.98	0.009

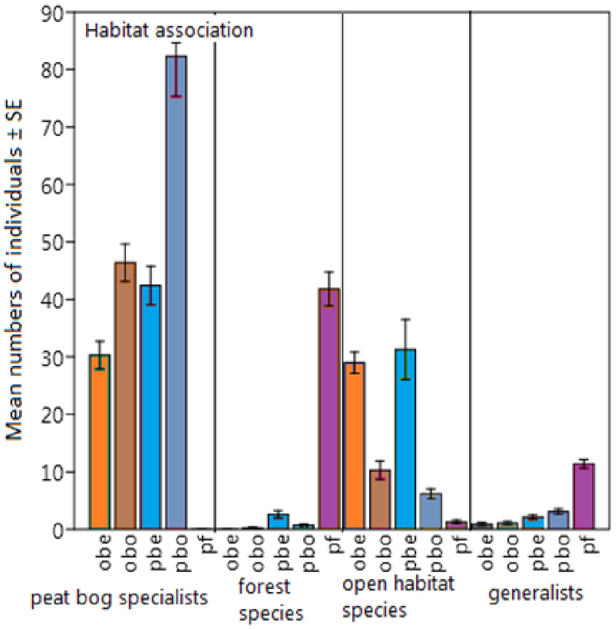

Figure 5. Relationships (mean values ± SE) among ground beetle habitat associations in assemblages of peat bogs and adjacent pine forests. Acronyms: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf). Whiskers indicate standard error.

DISCUSSSION

Our comparison of small and large peat bogs revealed patterns in ground beetle diversity between these habitats. Species richness and abundance of ground beetles were higher in the pine bogs regardless of peat bog size. This can be explained by the structural complexity of these habitats. Previous studies indicated the importance of plant cover and especially dwarf shrub cover in supporting insect biodiversity, with bog plant community structure and moisture being important environmental factors in determining the spatial distribution of invertebrate taxa (Urák *et al*. 2023; Sushko 2016, 2019b, 2019c, 2022; Gallé *et al*. 2021). Canopy closure of pines and dwarf shrubs in pine bogs may influence the microclimatic conditions of the *Sphagnum* mat, thereby affecting ground beetle distribution (Spitzer *et al*. 1999, Sushko 2019b). On the other hand, we found the environmental variables affecting peat bog ground beetle diversity were found to be abiotic factors such as bog water level, pH and the conductivity (reflects salinity) of the *Sphagnum* mat water, as has also been demonstrated elsewhere (Sushko 2019b).

Species diversity and evenness were higher in small compared to large peat bogs. Our comparison

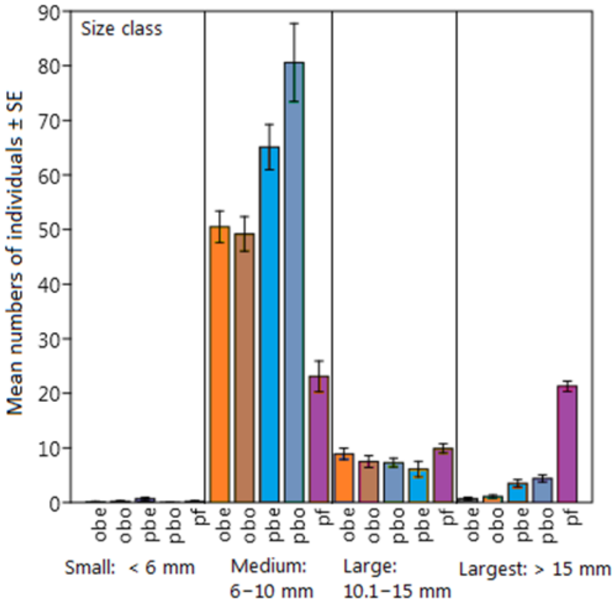

Figure 6. Relationships (mean values ± SE) among ground beetle body sizes in assemblages of peat bogs and adjacent pine forests. Acronyms: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf). Whiskers indicate standard error.

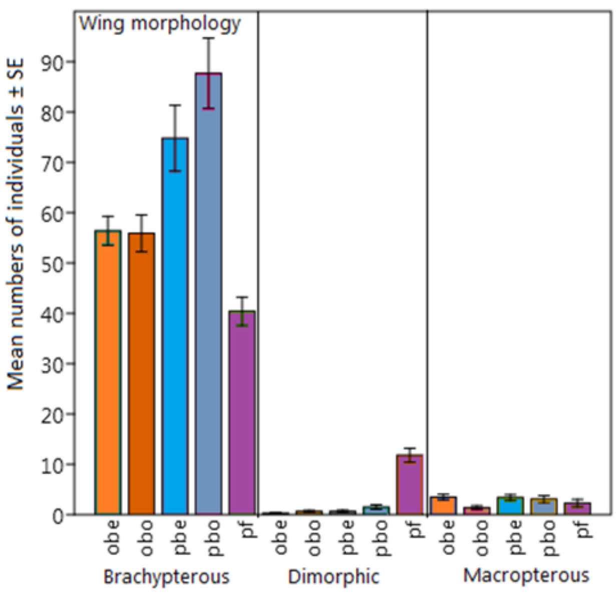

Figure 7. Relationships (mean values ± SE) among ground beetle wing morphologies in assemblages of peat bogs and adjacent pine forests. Acronyms: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf). Whiskers indicate standard error.

of ground beetle species composition showed that the assemblages of both small and large sized peatlands included many of the same species. Consequently, differences in ground beetle diversity of small and large peat bogs were due to variations in the abundance of some species. In particular, the proportion of *Pterostichus diligens* was higher in small peatlands, whereas proportions of *Pterostichus rhaeticus* and *Agonum ericeti* were higher in large peatlands. As a result, the ground beetle assemblages of small peat bogs are characterised by higher evenness and diversity. Among recorded specialised ground beetles, *Agonum ericeti* showed a strong association with peat bogs in Europe, and *Pterostichus diligens* and *P. rhaeticus* often occurred in peat bogs, however, they are also recorded in moorland, damp woodland and grassland habitat types (Spitzer & Danks 2006, Aleksandrowicz 2014). When comparing ground beetle assemblages of small peatlands and adjacent pine forests on mineral soils, clear differences in both diversity and species composition were revealed.

An analysis of the habitat preferences of the recorded ground beetles showed a predominance of specialised species in both small and large peat bogs. Studies of spider fauna of peat bogs in Romania, in which tyrphophilic species were recorded even in the smallest bogs, showed similar results (Gallé *et al.* 2019). Hence, there appears to be a strong association between invertebrate assemblage structure and habitat features in such bog habitats. In peat bogs, very specific habitat conditions are likely to represent an environmental filter, which can exclude most of the generalist invertebrate species. Peat bog habitats are known to be cool relative to the surrounding terrain (Spitzer & Danks 2006) and *Sphagnum* mosses form extreme conditions for many soil inhabitants, such as high humidity and acidity (Krogerus 1960, Mossakowski *et al.* 2003, Spitzer & Danks 2006). In our study, only a few open habitat dwellers (*Poecilus cupreus*, *P. versicolor*) and forest specialists (*Cychris caraboides*, *Pterostichus niger*, *P. oblongopunctatus*) found suitable niches in the studied peat bogs, but their abundance was not high. These species have been reported in other studies from peat bog habitats as well (Främbs *et al* 2002, Mossakowski *et al.* 2003, Dapkus & Tamutis 2008, Aleksandrowicz 2014, Sushko 2019b).

In addition, among the key factors affecting the occurrence of carnivorous ground beetle species from surrounding habitats in the very specific environment of peat bogs may be abundance and quality of prey. The high humidity and acidity of *Sphagnum* mosses may hinder development and reduce diversity for many soil inhabitants including springtails, on which the most abundant ground beetles of pine forests feed (*Calathus micropterus*, *Oxypselaphus obscurus*, *Pterostichus oblongopunctatus* and others) (Aleksandrowicz 2014). The low structural complexity of peat bogs causes simplification of trophic networks, leading to a decrease in diversity of other carabid prey items such as isopods, caterpillars, earthworms, wireworms and slugs. These prey items are food for abundant inhabitants of open habitats and forests including *Poecilus cupreus*, *P. versicolor*, *Cychrus caraboides*, *Carabus violaceus* and *C. arvensis* (Freude *et al.* 2004, Aleksandrowicz 2014). The peat bogs studied herein were characterised by low abundance of phytophagous and omnivorous carabids (*Harpalus* spp., *Amara* spp.). This may be due to low vascular plant species richness compared to meadows, resulting in impoverished potential food sources, such as seeds (Freude *et al* 2004, Aleksandrowicz 2014).

On the other hand, small peat bogs were characterised by lower abundance of specialised species compared to large peat bogs. This may be explained by the younger ages of these habitats. Previous studies have revealed that abundance of tyrphobiontic and tyrphophilous insects increased from young to old successional stages (Sushko 2016, 2019c). The small peat bogs were represented by a higher abundance of open habitat dwellers and forest species. However, only some open habitat species were found in these small bogs, such as *Poecilus cupreus, P. versicolor, Amara communis*. The abundance of these species in peat bog habitats is lower than in meadows and fields (Aleksandrowicz 2014). Forest species recorded in small pine bogs were predominantly large-bodied carabid beetles such as *Carabus arvensis, C. glabratus, C. hortensis* and *Cychris caraboides*. Most of these were not captured in large peat bogs. It is likely that these ground beetles migrated from adjacent pine forests. The ground beetle assemblages of small peat bogs, as well as large peatlands, consisted of medium-sized flightless species. The predominance of habitat specialists with poor dispersal ability indicates that the habitat condition in small peat bogs is as stable as in large peat bogs and the studied sites are appropriate for the long-term persistence of ground beetle populations (Niemelä 2001).

On the other hand, adjacent pine forests have more species with better dispersal abilities, including both dimorphic and large-bodied species that are more effective migrators compared to medium-sized non-flying carabids (Lövei & Sunderland 1996). For example, recorded large-sized wingless carabids such as *Carabus arvensis, C. glabratus, C. hortensis* and *C. arvensis* may occupy a relatively large area due to their higher running speed, compared to medium-sized or small-sized species. However, such species were rare in peatlands including small peat bogs. This may be due to the higher density of shrub and herb cover in the peat bogs compared to pine forests, which hinder the migration of large-bodied running species.

In addition, it should be noted that small peat bogs may serve as refugia for cold-adapted ground beetles in the temperate zone of Europe, such as the Sibero-European species *Pterostichus rhaeticus*, *Bembidion humerale* and *Agonum ericeti* (Aleksandrowicz 2014). Previous studies have reported that the large ancient Belarusian peat bogs could be suitable habitats for some boreal insect species since the early Holocene (Spitzer & Danks 2006, Sushko 2019a).

AUTHOR CONTRIBUTIONS

GGS: conceptualisation, experimental planning, field sampling, writing original draft, review and editing of subsequent versions. GGS, SVG, YIN: field sampling and environmental measurements, review and editing previous versions of the manuscript.

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Author for correspondence: Dr Gennadi Sushko, Department of Ecology and Geography, Vitebsk State University named after P.M. Masherov, Moskovskij Avenue 33, Vitebsk, Belarus 210038.
Tel: +375 33 3804442; E-mail: gennadisu@tut.by

Appendix

Table A1. Relative abundance (%) of ground beetle species assemblages in peat bog habitats and adjacent pine forests.

Species	Habitat				
	open bogs (small)	open bogs (large)	pine bogs (small)	pine bogs (large)	pine forests
Carabus arvensis Herbst, 1784	0	0	0.42	0	2.57
Carabus cancellatus Illiger, 1798	0	0.34	0	0	2.02
Carabus glabratus Paykull, 1790	0	0	0.21	0	1.28
Carabus granulatus Linnaeus, 1758	0.33	0.86	0.21	1.38	0
Carabus hortensis Linnaeus, 1758	0	0	0.42	0	13.76
Carabus menetriesi Hummel, 1827	0	0	0.11	0.25	0
Carabus nemoralis Muller, 1764	0	0	0	0	3.30
Cychris caraboides Linnaeus, 1758	0	0	1.80	0.75	1.28
Leistus ferrugineus Linnaeus, 1758	0	0	0	0	5.50
Notiophilus aquaticus Linnaeus, 1758	0	0	0	0	0.18
Notiophilus palustris (Duftschmid, 1812)	0	0.34	0.21	0	0.18
Poecilus cupreus Linnaeus, 1758	5.15	1.38	2.76	1.63	0.73
Poecilus versicolor (Sturm, 1824)	5.48	1.90	2.44	0.13	1.28
Pterostichus aethiops (Panzer, 1797)	0	0	0	0	0.18
Pterostichus diligens (Sturm, 1824)	37.21	13.45	36.52	2.88	0
Pterostichus melanarius (Illiger, 1798)	0	0	0.11	0	0.92
Pterostichus niger (Schaller, 1783)	0.83	0.69	1.06	2.25	14.86
Pterostichus oblongopunctatus (Fabricius, 1787)	0	0	0	0.13	14.86
Pterostichus rhaeticus Heer, 1837	3.82	8.97	2.34	5.88	0
Calathus micropterus (Duftschmid, 1812)	0	0	0	0	33.58
Amara bifrons (Gyllenhal, 1810)	0	0	0	0	0.18
Amara communis (Panzer, 1797)	0.33	0.34	0.42	1.00	2.20
Amara eurynota (Panzer, 1797)	0	0	0	0.50	0
Amara ovata (Fabricius, 1792)	0	0.17	0	0	0
Amara plebeja (Gyllenhal, 1810)	0	0	0.21	0	0
Amara similata (Gyllenhal, 1810)	0	0	0	0.25	0
Anisodactylus signatus (Panzer, 1796)	0	0	0	0	0.92
Bembidion humerale Sturm, 1825	0.17	0	0.21	0	0
Agonum ericeti (Panzer, 1809)	46.35	71.03	49.47	83.00	0
Oxypselaphus obscurus (Herbst, 1784)	0	0	0.21	0	0
Epaphius secalis (Paykull, 1790)	0	0	0.32	0	0
Stomis pumicatus (Panzer, 1796)	0	0	0.11	0	0
Harpalus affinis (Schrank, 1781)	0	0.17	0	0	0
Harpalus laevipes Zetterstedt, 1828	0	0	0	0	0.18
Harpalus latus (Linnaeus, 1758)	0	0	0.11	0	0
Harpalus rufipes (Degeer, 1774)	0.33	0.34	0.32	0	0

Table A2. Kruskal–Wallis (χ2; p) and Dunn’s post-hoc test results for differences in the proportions of individuals according to their habitat association, body size and wing morphology among ground beetle assemblages of peat bogs and adjacent pine forests. Acronyms: open bogs of small peat bogs (obe), open bogs of large peat bogs (obo), pine bogs of small peat bogs (pbe), pine bogs of large peat bogs (pbo), pine forests (pf).

Species trait	Group	Total catch	Number of species	χ2	p	Dunn’s post-hoc test
Habitat association	Peat bog specialist	2014	4	24.43	<0.001	pbo>(obe<(obo=pbe))
	Forest specialist	453	13	31.10	<0.001	pf>(pbe>(obo=obe=pbo))
	Open habitat species	781	8	41.75	<0.001	(obe=pbe)>(obo=pbo)>pf
	Generalist	186	11	33.79	<0.001	pf>(pbo>(obo=obe=pbe))
Size class	Small: < 6 mm	12	4	12.30	n.s.	
	Medium: 6−10mm	2715	13	32.38	<0.001	pbo>pbe>(obe=obo)>pf
	Large: 10.1−15mm	397	10	8.31	n.s.	pf>(pbe=obo=obe=pbo)
	Largest: > 15mm	310	9	40.98	<0.001	pf>(pbe=pbo)>(obo=obe)
Wing morphology	Brachypterous	3152	17	27.25	<0.001	pbo>pbe>(obe=obo)>pf
	Dimorphic	150	7	26.82	<0.001	pf>(pbe=obo=obe=pbo)
	Macropterous	137	12	8.33	n.s.	