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RESEARCH ARTICLE

Dispersal and colonization success of ground beetles (Coleoptera, Carabidae) on the Solovetsky Islands (the largest archipelago of the White Sea)

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Abstract

In this study, we analyzed the patterns of dispersal and colonization of ground beetles on the Solovetsky Islands. Our goals were to: (1) revise the Carabidae fauna and its structure, including that of the nearby mainland Onega Peninsula; (2) explore the migration flow of species from the mainland; and (3) reveal the spatial and temporal structures of carabid communities on the Solovetsky Islands. We collected specimens of ground beetles during the summer months from 2008 to 2010 and in 2024 on the Solovetsky Archipelago and the Onega Peninsula (in the suburbs of Onega town) in 2011 and 2012. Using pitfall traps and hand-capture methods, we gathered 19,925 Carabidae specimens identified as 80 species on the Solovetsky Islands, while the Onega Peninsula yielded 1,696 specimens representing 85 species. Cluster analysis supported the biogeographic theory that the primary migration flow of Carabidae to the archipelago was from nearby mainland territories, particularly the Onega Peninsula. Both local faunas exhibited a high proportion (over 70%) of macropterous species; however, brachypterous species were more abundant on the islands. We did not find significant interannual changes in the species composition of the carabid fauna on the archipelago. Cluster analysis and non-metric multidimensional scaling (MDS) revealed that the carabid communities maintained stable spatial and temporal structures among studied sites. Carabid assemblages of natural vegetation types, such as forests and seaside meadows, were more stable than those of anthropogenic meadows. Carabid communities of forests showed the highest stability year-to-year (up to 74% according to the partial Mantel test).

Keywords
Ground beetles, Solovetsky Islands, fauna, communities

Introduction

The Solovetsky Islands are the biggest archipelago of the White Sea (65°10'N, 35°32'E), which includes 6 relatively large islands (with a total area of 295.23 km^2) and more than 110 small islands (Iglovsky 2007). The major island of the archipelago is Bolshoy Solovetsky, which has an area of 225.3 km^2 and a 181 km length of coastal line (Iglovsky 2007). Most islands have a plain relief with an average altitude of 40 m. However, the northern part of the Bolshoy Solovetsky Island is occupied by moraine hills and ridges (the highest hills are Podnebesnaya – 80.7 m and Sekirnaya – 71.0 m). Over 70 % of the archipelago territory is covered by taiga forests with spruce and pine as dominant species (Kiseleva et al. 2005; Shmidt 2005). Bogs cover 10% of the archipelago area and meadows occupy less than 10% of it (on the seaside with natural origin, hayfield and grassland as a consequence of anthropogenic activity) (Kiseleva et al. 2005; Shmidt 2005). The unique floristic associations of the Solovetsky Islands are wastelands with *Empetrum nigrum* and «crooked» birch forests with *Betula tortuosa* occupying coastal areas (Kiseleva et al. 2005).

According to paleogeographic reconstructions, the last ice sheet covered the Solovetsky Archipelago up to the Early Holocene, and after glacier digression, the islands were connected with the Onega Peninsula via drained areas of the sea shelf of Onega Bay (Sherbakov and Govberg 2002, Bolotov 2014). The connection between the archipelago and the peninsula existed before the boreal period and 9-8 ka BP the territories were finally separated by the quick rise of sea level (Bolotov 2014). The coastal lines of islands obtained contemporary outlines later on, 6.3 ka BP (Ludikova et al. 2023). So, the main migration flow of flora and fauna from the mainland to the archipelago was approximately 10–9 ka BP in a period of sea level decline (Bolotov 2014).

Flora of the Solovetsky Islands was included in the Onega floristic region of north taiga by vast floristic analysis (Shmidt 2005). High continuity between plant associations of the archipelago and the Onega Peninsula was detected (Shmidt 2005). Analysis of insular fauna showed an extremely reduced variant of mainland northern boreal species complex with rare elements of Arctic and nemoral biota (Bolotov 2014). Migration flows of fauna and ecological patterns of species adaptation to insular conditions have been studied in detail for invertebrate taxa, including insects (Lepidoptera and Hymenoptera) and freshwater mussels of the Solovetsky Islands. Due to different migration potential among studied taxa, the most convincing conclusion about fauna distribution through the Onega Peninsula to the archipelago was detected for freshwater mussels (Bespalaya et al. 2009, 2011). Butterflies (Lepidoptera, Papilionoidea and Hesperoidea) fauna demonstrated division into resident species and temporary invaders with interannual changes of species migration between the archipelago and the mainland (Bolotov 2014). Bumblebee (Hymenoptera, Apidae) species were constant in fauna on the archipelago but in some years vagrant species were registered (Bolotov 2014). The abundance changes between two dominant species of bumblebees between years in the archipelago were explained by patterns of environmental conditions (Bolotov 2014). Also, based on regular field studies (from 2001 to 2011) on archipelago the 'compensation' of low species richness by high abundance of one or two species in communities was detected for bumblebees, butterflies, and freshwater mussels (Bolotov 2014). For other insects' taxa with relatively high species diversity on the Solovetsky Islands such as ground beetles (Coleoptera, Carabidae) and leaf beetles (Coleoptera, Chrysomelidae), the fauna was studied and the most abundant species of prevailing plant associations (forests, meadows, and peat bogs) were detected (Bolotov et al. 2011, Bolotov 2014).

Our regular studies of ground beetles during a few years on the Solovetsky Islands provide an opportunity for a more detailed analysis of their biogeographical history and contemporary migration flow of species including spatial and temporal structures of communities. Ground beetles are sensitive to soil and plant environmental conditions and have relatively stable communities in different plant associations on the mainland in northern taiga (Sharova and Filippov 2004). Also, carabid species have different dispersal potential (group exhibits wing and wing-muscle polymorphism) in contrast with insects that demonstrated a high dispersal power such as pollinators (bumblebees and butterflies). So, ground beetles can show other patterns in colonization under the insular conditions of the Solovetsky Archipelago.

Our goals were to revise (1) Carabidae fauna and its structure (including nearby mainland fauna of the Onega Peninsula) to explore (2) the migration flow of species from the mainland and to revile (3) spatial and temporal carabid community structures on the Solovetsky Islands.

Materials and methods

Material sampling and study sites. The study was based on data analysis about ground beetles (1) fauna, (2) communities, and (3) biology of the Solovetsky Islands and nearby mainland territories. We adhered to the biogeography theory about the main migration flow of fauna from the Onega Peninsula to the archipelago before the boreal period (Bolotov 2014). Therefore, the Carabidae fauna of the Onega Peninsula was also studied.

Specimens of ground beetles were collected on the Solovetsky Islands (Bolshoy Solovetskiy, Bolshoy Zayatsky, Bolshaya Muksalma, and Anzer islands) in 2008–2010, and in 2024, as well as on the Onega Peninsula (suburbs of Onega town) in 2011 and 2012 (Table 1). The Carabidae specimens were sampled from May to September (throughout the warm season) on the archipelago only in 2009-2010 years and on the Onega Peninsula in 2011. The beetles were sampled using pitfall traps (Heydemann 1956), i.e., 500 ml plastic cups with a trap hole diameter of 93 mm, and using hand collection with an exhauster. Specimens were fixed by 4% formaldehyde and 98 % ethanol. The 10–20 traps were installed for each site in one or two parallel lines (10 traps per line) with a distance of 10 m between traps and lines. The material was sampled from the traps once every ten days. According to the local fauna method, we explored sites within the main types of plant associations on the archipelago and the mainland: pine and spruce forests, alder and birch forests, gramineous-herb meadows, upland peat moss, sedge, and woody (pine) bogs. Also, wastelands with *Empetrum nigrum* and «crooked» forests with *Betula tortuosa* as unique plant associations in the Solovetsky Archipelago were studied.

As a result, 19925 specimens of imago were sampled on the Solovetsky Islands and 1696 specimens of imago were sampled on the Onega Peninsula (Table 1).

Table 1. Data of ground beetles sampling on the Solovetsky Islands and Onega Peninsula

Territory, year	Number of sites (trap)	Number of traps	Trap-days	Number of specimens (N), (by traps)	Number of specimens (N), (by exhauster)
Solovetsky Islands, 2008, 2009, 2010, 2024	42	848	70 982	19 333	592
Onega Peninsula, 2011, 2012	12	260	22 160	1380	316

Fauna analysis. Specimens were examined using a stereomicroscope (Leica M165C, Germany). Checklists of Lindroth (1985, 1986), Fedorenko (1996), and Goulet (1983) were used for species identifications. The Catalogue of Palaearctic ground beetles (Löbl and Löbl 2017) was used for taxonomic classification and nomenclature. The dried specimens of ground beetles are deposited in the Russian Museum of Biodiversity Hotspots (RMBH) insect collection, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences (Arkhangelsk), Russian Federation.

For each species, the known ranges for Russia and adjacent territories as well as for North America were determined with checklists and databases (Lindroht 1992; Kryzhanovskij et al. 1995; Bousquet et al. 2013; Makarov et al. 2020; Global Biodiversity Information Facility 2024). Trophic species groups were detected according to the life forms classification of Sharova (1981). Also, ground beetles were grouped by the potential of flight into three groups: macropterous, brachypterous, and dimorphic species according to Lindroth (1985, 1986, 1992).

Similarities between faunas of ground beetles of the Solovetsky Archipelago and nearby mainland and islands of White Sea were analyzed by a hierarchical clustering approach based on binary data (presence/absence data in species lists) using unweighted pair-group average algorithm (UPGMA) and Jaccard similarity index in the software PAST v. 4.14 (Hammer 2023). For this analysis, we used information about ground beetles of Fennoscandia (Finland: Ok – Ostrobottnia kajanensis, Ks – Kuusamo, Karelia: Kr – Karelia rossica and Murmansk Region: Lr – Lapponia rossica) (Lindroht, 1986). Also, we used species lists of the Carabidae for local faunas: Onega Peninsula; suburbs of Arkhangelsk (Sharova and Filippov 2004; Filippov and Zezin 2006); Kindo Peninsula (Benkovsky and Nikitsky 2008); and reserved islands of the Kandalaksha Bay (Byzova et al. 1986).

Community analysis. The Carabidae communities were analyzed for eight model sites of the Bolshoy Solovetskiy Island studied in the second decade of July in 2009, 2010, and 2024 (see supplementary file 1). The sites were chosen among the most common forest and meadow plant associations on the island from north to south within the Savvatyevo and Isakovo settlements, Botanical Garden, and the Pechak Cape (see Suppl. material 1: Table S1).

We used 'dynamic' abundance of species or catchability, i.e., the number of specimens in 10 traps per day (specimens/10 traps-day), in samples for data analyses. We used a one-way ANOVA test to compare the number of species and their relative abundance on model sites between three years of the July study period on the Box-Cox transformed abundance data in PAST v. 4.14 (Hammer 2023).

Similarities between the abundance of ground beetles of the model sites were analyzed by hierarchical clustering procedure using an unweighted pair-group average algorithm (UPGMA) and Bray-Curtis similarity index on the Box-Cox transformed abundance data in the software PAST v. 4.14 (Hammer 2023). The similarity percentage method (SIMPER) was used to assess the species contributing most to similarities within groups defined by cluster analysis. Non-metric multidimensional scaling (non-metric MDS) with Bray-Curtis similarity index was used for better visualization of correspondence between sites within groups of cluster analysis and allowed plotting of species together with samples (sites).

The correspondence of carabid communities from model sites between three years of the study was tested using simple and partial Mantel tests that were implemented between Euclidean distance matrices in the software PAST v. 4.14 (Hammer 2023). A partial Mantel test was performed to test for the correlation between three distance matrices to estimate their influence (Fortin and Gurevitch 2001). It investigates the correlation between two matrices while controlling the effect of a third one, and thus tries to remove spurious correlations. We computed (1) the correlation between the abundance of species distances of all study sites for two years while controlling for the effect of the third year, (2) repeated the analysis for forest sites, and (3) meadow sites separately. The significance of correlations between distance matrices was assessed using 10,000 permutations of the data to test the null hypothesis that the matrices are independent in the software PAST v. 4.14 (Hammer 2023).

Results

Fauna

The 80 species of ground beetles from 31 genera were recorded on the Solovetsky Archipelago (see Supplementary file 2). The largest number of species was discovered within three genera: *Amara* (15 species), *Bembidion* (11 species), and *Pterostichus* (6 species). The rarest species of the archipelago fauna and that of the Archangelsk Region, i.e., *Calosoma maderae* (Fabricius, 1775), *Bembidion chaudoiri* Chaudoir 1850 and *Dicheirotrichus gustavii* Crotch, 1871, were detected for seaside and coastal sites (meadows and sand beaches). Also, the Red List species of Archangelsk Region (Zubrii and Filippov 2020) – *Carabus nitens* Linnaeus, 1758 – was sampled in peat bogs with *Pinus sylvestris* on the Bolshoy Solovetskiy Island.

For the Onega Peninsula (suburbs of Onega town), 85 species of ground beetles from 31 genera were recorded (See supplementary file 2). The most numerous genera were as follows: *Bembidion* (20 species), *Amara* (11 species), and *Pterostichus* (9 species). A similar result was obtained for the Carabidae fauna of the Solovetsky Archipelago. Three species were sampled for the first time on the Onega Peninsula and Arkhangelsk Region: *Notiophilus aestuans* Dejean, 1826, *Agonum carbonarium* Dejean, 1828, and *Chlaenius quadrisulcatus* Paykull, 1790.

The dendrogram from the cluster analysis of species lists indicated that the carabid faunas of the White Sea islands were closely related to those of nearby mainland territories (Fig. 1). The carabid species lists showed a 45% similarity between the Solovetsky Archipelago and the suburbs of Onega town and Arkhangelsk city. Additionally, the carabid species list from the Kandalaksha Bay islands was most similar to the list of ground beetles from the Kindo Peninsula. In contrast, the other analyzed mainland faunas from Karelia, Finland, and the Murmansk Region formed a distinct group.

The Carabidae species from both the Solovetsky Archipelago and the Onega Peninsula have been recorded across all geographical regions of Russia and its adjacent territories, as categorized by Kryzhanovskij et al. (1995), as well as in North America (Bousquet et al. 2013; Global Biodiversity Information Facility 2024). The highest number of species from both local faunas was found in Europe and the Ural Region, where nearly 100% of the same species have been identified. Furthermore, a significant species proportion of both faunas was noted in the middle and southern parts of Western Siberia, with up to 84% for the archipelago and 80% for the Onega Peninsula. Similarly, species with ranges in the Altai-Sayan and middle Siberian regions show up to 84% for both faunas (see Supplementary file 2). Approximately 40% of species from both local faunas have also been recorded in North America (see Supplementary file 2). Among the trophic groups of ground beetles (imago), zoophages dominate, representing 67.5% for the Solovetsky Islands and 72.1% for the Onega Peninsula and outnumbering mixophytophages.

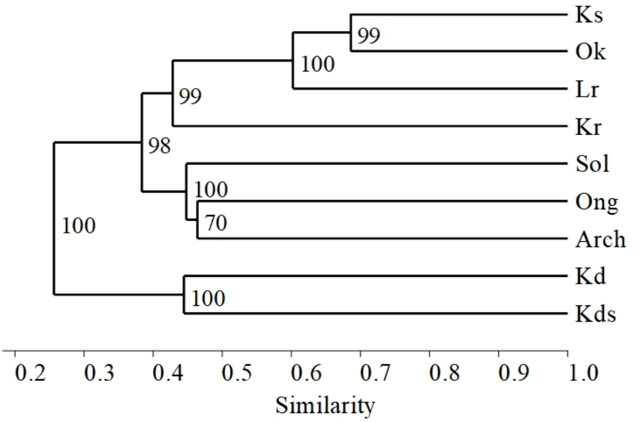

Figure 1. Hierarchical classification of the White Sea islands and nearby mainland territories, grouped by lists of carabid species (Jaccard similarity index, UPGMA). Numbers in nodes indicate the percentage of probabilities by bootstrapping. Note: Ok – Ostrobottnia kajanensis, Ks – Kuusamo, Kr – Karelia rossica, Lr – Lapponia rossica, Arch – suburbs of Archangelsk city, Sol – Solovetskiy Archipelago, Ong – Onega Peninsula (suburbs of Onega town), Kd – Kindo Peninsula, Kds – reserved islands of Kandalaksha bay.

A significant proportion of macropterous species was found among the ground beetles on the Solovetsky Islands (71%) and the Onega Peninsula (74%). In contrast, brachypterous species were the least common, making up only 8% of the fauna in the archipelago and 10% on the Onega Peninsula. Species with dimorphic wing types represented 21% of the archipelago's fauna and 16% of that on the Onega Peninsula (see Suppl. material 2: Table 2).

Community

In July of 2009, 2010, and 2024, the model sites revealed between 20 and 25 species of ground beetles, with the highest species richness observed in 2009. The mean relative abundance (± standard error) of ground beetles at these sites in July ranged from 3.50 ± 0.73 specimens per 10 trap-days in 2024 to 4.52 ± 1.13 specimens per 10 trap-days in 2010. The differences in the number of species and the relative abundances of ground beetles across the different years were not statistically significant (number of species: $F_{2,19} = 2.07$, $p = 0.16$, and relative abundance: $F_{2,19} = 0.41$, $p = 0.67$).

Cluster analysis based on the carabid abundance matrix of the studied sites revealed three distinct groups (Fig. 2). These groups correspond to carabid communities of forests (1), natural seaside meadows (2), and anthropogenic meadows (3), as shown in the dendrogram. Notably, the carabid community of the Botanical Garden meadow studied in 2024 did not group with the anthropogenic meadows and hayfields, as it did in 2009 (Fig. 2). Additionally, the carabid community of the meadow (previously a hayfield) at Savvatevo Settlement consistently grouped with the nearby aspen forest community across both study years (2009 and 2024) (Fig. 2).

The analysis of species contribution to the spatial structure of the sites (with a cut-off of approximately 95%) identified one or two key species in each group (Table 2). For the sites in the first group of forest associations, the highest contribution had two species: *Carabus glabratus* Paykull, 1790 and *Calathus micropterus* (Duftschmid, 1812). For the seaside meadows in the second group, the key species was *Calathus melanocephalus* (Linnaeus, 1758). Finally, in the third group of anthropogenic meadows, the most abundant species was *Pterostichus niger* (Schaller, 1783).

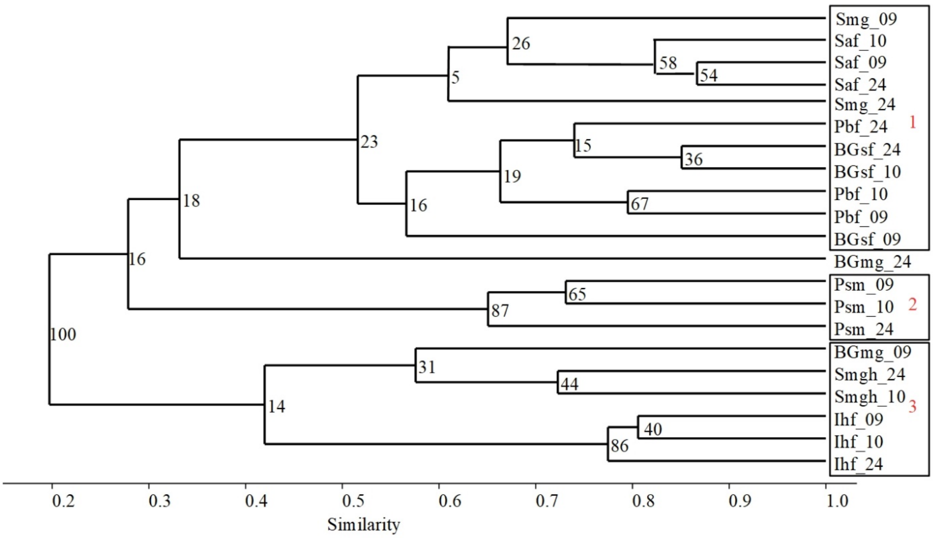

Figure 2. Hierarchical classification of eight sites studied on the Bolshoy Solovetskiy Island, based on the abundance of ground beetles and grouped by three years as follows: 09 – 2009, 10 – 2010, and 24 – 2024 (Bray-Curtis similarity index, UPGMA). Numbers in nodes indicate the percentage of probabilities by bootstrapping. Note: S – Savvatyevo Settlement, I – Isakovo Settlement, BG – Botanical Garden, P – Pechak Cape; af – aspen forest, bf – birch forest, sf – spruce forest, mg –meadow grass, sm – seaside meadow grass, hf – hayfield meadow.

The non-metric MDS analysis of three groups of Carabidae communities indicated their strong spatial aggregation on the plot (Fig. 3). This analysis also highlighted the species preferences of different plant associations on the Bolshoy Solovetskiy Island (Fig. 3). The positions of key or grouping species in communities on the plot corresponded with the results obtained from the SIMPER analysis (Table 2).

Table 2. The average similarities percentage (SIMPER) for the groups defined by cluster analysis. Note: n/a – not available

Species	Groups		
	1	2	3
Leistus terminatus (Hellwig in Panzer, 1793)	n/a	6.60	n/a
Carabus glabratus Paykull, 1790	39.33	3.35	2.91
Cychrus caraboides (Linnaeus, 1758)	2.01	8.18	0.19
Loricera pilicornis (Fabricius, 1775)	n/a	n/a	9.59
Bembidion lampros (Herbst, 1784)	n/a	n/a	2.91
Patrobus assimilis Chaudoir, 1844	0.48	5.73	n/a
Pterostichus niger (Schaller, 1783)	7.51	n/a	73.10
Calathus melanocephalus (Linnaeus, 1758)	2.33	67.81	0.43
Calathus micropterus (Duftschmid, 1812)	44.60	2.20	0.97
Agonum fuliginosum (Panzer, 1809)	n/a	n/a	4.62

The simple Mantel test supported a correspondence of carabid community structures at the model sites of the Bolshoy Solovetskiy Island between three years of study (Table 3). The partial Mantel tests showed the same pattern. The correlations of carabid communities across the three years ranged from 37% to 56% and were higher for forest associations (45–74%) compared to meadows (43–63%).

Table 3. Summary of simple (r) and partial (r) Mantel tests for correspondence between carabid communities of study sites (all together (community) and for forests (forest) and meadows (meadow) associations separately) in 2009, 2010, and 2024 on the Bolshoy Solovetskiy Island

Simple Mantel Tests		
	r	p
community 2009 × community 2010	0.90	0.0001
community 2009 × community 2024	0.89	0.0001
community 2010 × community 2024	0.88	0.0001
forest 2009 × forest 2010	0.88	0.0002
forest 2009 × forest 2024	0.91	0.0002
forest 2010 × forest 2024	0.92	0.0004
meadow 2009 × meadow 2010	0.79	0.0002
meadow 2009 × meadow 2024	0.58	0.0003
meadow 2010 × meadow 2024	0.63	0.0001

Partial Mantel Tests		
	r'	p'
community 2009 × community 2010 (2024)	0.56	0.0003
community 2009 × community 2024 (2010)	0.48	0.0004
community 2010 × community 2024 (2009)	0.37	0.003
forest 2009 × forest 2010 (2024)	0.45	0.1
forest 2009 × forest 2024 (2010)	0.50	0.002
forest 2010 × forest 2024 (2009)	0.74	0.003
meadow 2009 × meadow 2010 (2024)	0.63	0.0003
meadow 2009 × meadow 2024 (2010)	0.43	0.006
meadow 2010 × meadow 2024 (2009)	0.45	0.0001

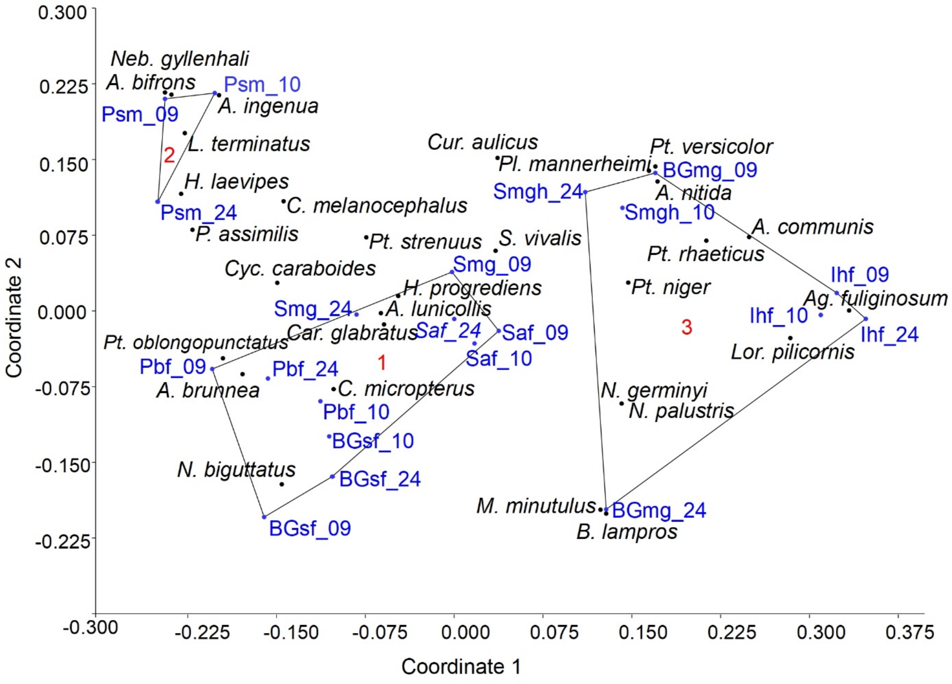

Figure 3. Non-metric multidimensional scaling (non-metric MDS) of sampling sites on the Bolshoy Solovetskiy Island according to an abundance of carabid species and grouped by results of cluster analysis (see Fig. 2) in a two-dimensional coordinate system (stress: 0,145). Note: black color – species: *A.* – *Amara*, *Ag.* – *Agonum*, *B.* – *Bembidion*, *C.* – *Calathus*, *Car.* – *Carabus*, *Cyc.* – *Cychrus*, *H.* – *Harpalus*, *L.* – *Leistus*, *Lor.* – *Loricera*, *M.* – *Microlestes*, *N.* – *Notiophilus*, *Neb.* – *Nebria*, *P.* – *Patrobus*, *Pl.* – *Platynus*, *Pt.* – *Pterostichus*; blue color – sites (ID of sites see Supplementary file 1); polygons and red numbers – groups in cluster analysis (see Fig. 2).

Discussion

Our revision of the Carabidae fauna of the Solovetsky Islands has expanded the species list to 80 species compared with 68 species observed in previous studies (Bolotov et al. 2011, Bolotov 2014). Species richness of ground beetles of the Solovetsky Archipelago is close to that on the Onega Peninsula (85 species) but lower by approximately 30-50% in comparison with other nearby mainland localities (Bolotov et al. 2011, Bolotov 2014). Despite the overall reduction in the species list of ground beetles on the archipelago, it is close to the nearby mainland of the northern taiga of Archangelsk Region (Sharova and Filippov 2004; Filippov and Zezin 2006; Mokhnatkin et al. 2011). Widespread Palearctic and Holarctic carabid species prevailed in the fauna of the Solovetskiy Archipelago. Results of cluster analysis of species similarities showed the closest relation between faunas of the Solovetsky Islands and the nearby mainland suburbs of Onega and Archangelsk. Therefore, this confirms a biogeography theory that the primary migration flow of the Carabidae to the archipelago was from nearby mainland territories such as the Onega Peninsula before the boreal period.

The main pool of Carabidae species on the Solovetsky Islands was sampled in 2009. The species list was not expanded after 2010. Ground beetles of the Solovetsky Islands have no significant interannual change of species in fauna as it was revealed for Lepidoptera (Bolotov, 2014). So, either the Carabidae fauna of the archipelago is quite sustainable to contemporary migration flow from the mainland or such flow is absent. The carabid species have different flight capabilities (brachypterous, macropterous, or wing polymorphic species), and their dispersal probabilities are expressed by an index of potential migrants (Imp) (Matalin 2003). Although it was detected that macropterous species had the highest dispersal power and Imp (Matalin 2003), the contradictory results about colonization success via species flight capabilities were obtained for the sea islands of Northern Europe (Kotze 2008). The proportion of brachypterous species in the fauna of the Baltic Sea islands was increased from Finland mainland (0.12) via the main island of Aland (0.30) to small islands (0.33) (Kotze 2008). Also, brachypterous species had the highest abundance on the Baltic Sea islands and were accordingly recognized as more successful colonizers (Kotze and Niemela 2002; Kotze 2008). For the Solovetsky Islands, the opposite effect has been detected, when the observed proportion of brachypterous species in fauna slightly decreased from the archipelago (0.08) to the mainland of the Onega Peninsula (0.1) (Suppl. material 2: Table 2S). However, the most abundant species on the archipelago (43 % of sampled specimens) were the brachypterous *C. glabratus* Paykull, 1790, *C. caraboides* (Linnaeus, 1758), and *C. micropterus* (Duftschmid, 1812) (Suppl. material 2: Table 2S). A similarly high proportion of macropterous species on the Solovetsky Islands (0.71) and nearby mainland of the Onega Peninsula (0.74) are usually characteristic for territories with young and unstable habitats (Kotze 2008). For Øygarden islands (Norway) and Zuidelijke polder (Netherlands) of the North Sea, another result of ground beetles colonization was detected, with the lowest proportion of brachypterous species in fauna and the highest abundance of macropterous species on different islands (Hatteland et al. 2008; Ranta and As 1982). The authors concluded that macropterous species with smaller body sizes are more successful in island colonization (Ranta and As 1982).

Some species that were abundantly collected on the nearby mainland of the White Sea, such as *Pterostichus melanarius* (Illiger, 1798) and *Carabus granulatus* Linnaeus, 1758, were not registered on the Solovetsky Islands (Bolotov et al. 2011; Bolotov 2014). One of the assumptions on the lack of *P. melanarius* on small and remote islands of the Baltic Sea is that it has a reduced dispersal power (Imp=0.06±0.02) compared to a more frequently collected species, *P. niger*, having an Imp of 0.25±0.09 (Kotze 2008). The Imp is a complex index that requires additional anatomical examinations of all sampled specimens for the species within a population. Such a study has been conducted for the Moldavian population of *P. melanarius* (Matalin 2003) but not for populations on the Baltic Sea islands or the Solovetsky Islands. So, we cannot use the results of Imp indexes obtained for forest-steppe populations of both species and conclude that the dispersal power of *P. melanarius* may have a significant effect on its absence on the Solovetsky Islands of north taiga. Furthermore, we cannot use the Imp index to explain the absence of the wing-polymorphic *C. granulatus* on the archipelago since another species from the same genus, *C. glabratus* (which is brachypterous), is abundantly occurred on the islands.

Results of previous studies showed that ground beetles of Northern Europe were non-randomly distributed on islands and obtained patterns of their distribution were mainly focused on the species' biology (life cycles and reproductive rates) and their niche breadths (Niemelä et al. 1985, 1987, 1988, 2007; Kotze and Niemela 2002; Kotze 2008, Kotze et al. 2000; Hatteland et al. 2005, 2008). It was detected on the Baltic Sea and North Sea islands that generalist species with wide niche breadths are highly eurytopic and occur in various vegetation types (Kotze 2008). There are three to five species, which are the most abundant on these islands (Kotze 2008). This pattern, defined as a compensation for low species richness by high abundance of several species was previously described by Chernov (2005) under extreme environmental conditions. For the Solovetsky Islands, this pattern has been observed for insect communities (butterflies and bumblebees), as well as for freshwater mussel communities (Bolotov 2014). In our study five abundantly collected species were discovered (approximately 62% of sampled specimens) as follows: *C. glabratus*, *C. caraboides*, *P. niger*, *C. melanocephalus*, and *C. micropterus*. These species were found in most plant associations on the Solovetsky Islands but with the highest abundance recorded in one particular association.

Results on species-area relations (SAR) models for islands in the Baltic and North Seas have revealed that the size of the island area is less important than habitat size when it comes to species diversity and the stability of assemblages (Hatteland et al. 2008, Kotze 2008). It has been shown that inland forests are more stable plant communities than shore vegetation and that the first ones support the stability of Carabidae assemblages on the island (Ranta and As 1982; Kotze 2008). However, even for large islands the structure of carabid assemblages can change significantly over time, as it was shown for the main island of Aland between 1982 and 1999 (Kotze and Niemela 2002). On the Bolshoy Solovetsky Island, which is the main island of the Solovetsky Archipelago, the carabid assemblages had shown not only aggregation in spatial structures but their temporal stability between 2009, 2010, and 2024. Both carabid communities of forests and seaside meadows showed temporal and spatial stability. The woodland carabid assemblages exhibited the highest temporal stability, up to 74% between 2010 and 2024. In contrast, the spatial and temporal instability was registered for several assemblages of inland agricultural meadows on the island. Although the SAR model was not tested, these habitat patches had the smallest area among studied sites and we supposed that their size influences the stability of the carabid communities. Additionally, forest sites showed the highest abundance of brachypterous species (*C. glabratus* and *C. micropterus*), as it was observed on North Sea islands (Ranta and As 1982). According to Ranta and As (1982), this is an indicator of the most stable habitats which favor an allocation to efficiency in resource utilization rather than migration.

Conclusions

Overall, 80 Carabidae species were recorded on the Solovetsky Islands, and 85 species were sampled on the nearby mainland of the Onega Peninsula. Despite the reduction of species in the carabid fauna of the archipelago, it was close to nearby mainland territories with the highest similarities with the Onega Peninsula. This confirms a biogeography theory that the main migration flow of Carabidae to the archipelago was from nearby mainland territories such as the Onega Peninsula before the boreal period. Most Carabidae species on the Solovetskiy Archipelago are predators and widespread in the Palearctic and Holarctic regions as observed for the Onega Peninsula. Both faunas had a high proportion (more than 70 %) of macropterous species which indicates relatively recent colonization of studied territories. The proportion of brachypterous species is decreasing from the mainland to the Solovetsky Archipelago, but brachypterous species are the most abundant on the island. However, the flight potential of ground beetles cannot explain the absence of some wing polymorphic species on the archipelago which are abundantly distributed on mainland of the Archangelsk Region. The significant interannual changes of species in the Carabidae fauna of the archipelago were not revealed.

The carabid communities had stable spatial and temporal structures for the studied sites on the Bolshoy Solovetsky Island. The carabid assemblages of natural vegetation types (forests and seaside meadows) were more stable than anthropogenic meadows. The Carabidae communities of forests were the most stable year-to-year with abundantly collected brachypterous species.

So, dispersal power and successful adaptation are two complementary factors important for carabid species during the stochastic process of island colonization. Sometimes the contradictory results of such process are observed even for relatively young island biota with common biogeography history as in Northern Europe. The species-environmental models can potentially reveal more patterns for better insight into the carabid colonization of the Solovetsky Islands.

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Supplementary material 1

Table S1. Model sites and ground beetles materials sampled in second decade of June in 2009, 2010 and 2024 on the Bolshoy Solovetsky Island

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Data type: table

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Supplementary material 2

Table S2. List of ground beetles species (Coleoptera, Carabidae) of the Solovetsky Islands and Onega Peninsula (suburbs of Onega town)

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Data type: table

Link: http://journal.asu.ru/biol/article/view/16562/14208