



Original article

Lost and found: Short-term dynamics of the flora on 100 small islands in the White Sea

Alexey Shipunov^{a,*}, Polina Volkova^b, Liudmila Abramova^b, Polina Borisova^c^a Department of Biology, Minot State University, 500 University Ave W, Minot, ND 58701, USA^b Moscow South-West High School (No. 1543), 26 Bakinskikh komissarov str. 3-5, RU-119571 Moscow, Russia^c Biological Department, Moscow State University, Vorob'evy Gory, RU-119899 Moscow, Russia

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ABSTRACT

The aim was to uncover factors that influence short-term (decade) flora dynamics and species richness of northern marine islets characterized by poor flora and weak anthropogenic pressure. The study used presence–absence data of vascular plant species on 100 small uprising islets of the Kandalaksha Gulf of White Sea (Northern Karelia, Russia). We investigated the influence of islands' attributes on species richness and rates of flora dynamics. Two island types were analyzed separately: younger, stone-like and older, islet-like (which generally are larger and have higher diversity of habitats). Sampled islands were studied via classical biogeographical *per island* approach and metapopulation *per species* approach. Stone-like islands had noticeably poorer flora with higher rates of immigration and extinction when compared to those of islet-like islands. The species number for islet-like islands correlated positively with number of habitats, abundance of different habitat types and island area. Species richness of stone-like islands correlated positively only with number of habitat types. Plant species associated with birds, crowberry thickets and coastal rocks were the most stable, and the species of disturbed habitats were significantly less stable. Floristic changes that have occurred have been caused by the massive establishment of new species rather than the extinction of pre-existing taxa. Thus, most of these islands are still in the colonization (assortative) stage. While we found no relationship between island area and species number for stone-like islands, this relationship was seen on islet-like islands.

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1. Introduction

The quantitative study of species dynamics in natural communities has received a lot of attention from ecologists, and was stimulated by the establishment of the dynamic equilibrium theory (MacArthur and Wilson, 1967). Small islands are considered to be “natural experiments”, since they are well-defined and, at the same time, abundant in nature (Panitsa et al., 2006). Studies have focused on revealing of the key factors that influence species richness.

Island isolation (distance from the mainland: MacArthur and Wilson, 1967) and available energy (Wright, 1983) may play an important role in shaping species richness on the global scale, as was demonstrated recently for birds (Kalmar and Currie, 2006). Nevertheless, knowing available energy and degree of island isolation is not enough for determining species richness (Vidal et al., 2000; Snogerup and Snogerup, 2004; Burns, 2005). The

habitat diversity and the area of an island are thought to be more important determinants of the species richness on the local scale. At the same time, habitat diversity and island area are not independent variables (Rydin and Borgegård, 1988; Burns, 2005; Panitsa et al., 2006). Finally, in addition to physical environment insular flora is affected substantially by stochastic processes, such as plant dispersal and persistence (Connor and Simberloff, 1978; Cody, 2006).

Even though species numbers on islands are viewed as temporal scores in a continuing interplay of extinction and immigration (MacArthur and Wilson, 1967), studies of biotic changes (species turnover) are scarce, especially for plants (Vidal et al., 2000). Most investigations of flora dynamics on sea islands have dealt with colonization of one or a few islands and discussed floristic changes on each island separately (e.g. Snogerup and Snogerup, 1987; Partomihardjo et al., 1992; Robinson et al., 1994; Harrison et al., 2001; Backus et al., 2002; Snogerup and Snogerup, 2004).

Few studies of quantitative flora dynamics exist for large samples of sea islands. Most of these analyses were focused on tropical (Abbott and Black, 1980: western Australia; Morrison,

* Corresponding author. Tel.: +1 701 858 3116.

E-mail address: dactylorhiza@gmail.com (A. Shipunov).

2003: Bahamian islands), subtropical (Panitsa et al., 2008: Aegean sea) and Mediterranean (Vidal et al., 1998, 2000) islands with rich floras, for which exhaustive plant species inventories are difficult to perform (Vidal et al., 2000). The available studies in more northern climates were conducted either in the Baltic Sea (Vartiainen, 1967; Glazkova, 2001; Herloff, 2003) or in the western Canadian province of British Columbia (Cody, 2006), where the islands are under high anthropogenic pressure (this is partly true and for the above-mentioned tropical and subtropical islands).

Furthermore, it is known that “it is easy to overlook [plant] species on an island even if it was searched thoroughly” (Nilsson and Nilsson, 1982). In studies of flora dynamics, comparison of incomplete results of successive plant inventories causes so-called “pseudoturnover” of species (Nilsson and Nilsson, 1982; Vidal et al., 2000). Consequently, it is important to determine the proportion of missed species (i.e., sensitivity of survey methods) in each case prior to analysis of flora dynamics (Vittoz et al., 2010). As the species are missed in a nearly-random fashion, a large sample of islands would provide a way to correct the species sampling biases (Nilsson and Nilsson, 1982; Vittoz et al., 2010).

The aim of our work was to uncover factors influencing short-term (decade) flora dynamics of northern marine islets characterized by species-poor native flora under weak or non-existing anthropogenic pressure. Our results based on quantitative analysis of three floristic surveys of 100 islands (with correction for unobserved species) give the comprehensive picture of changes in northern marine island habitats.

2. Materials and methods

2.1. Study area and island variables

The study was conducted in the Kandalaksha Gulf of the White Sea (Northern Karelia, Russia, approximately N 66° 25' E 33° 45'). All the studied islands appeared after the last glacial maximum recession (ca. 12,000 BP; Svendsen et al., 2004) due to permanent uplift which has risen to 4.5 mm × year⁻¹ (Koshechkin, 1979; see also Serebryanaya and Shipunov, 2009). As a rule, the larger is the island, the older it is.

Winds have a strong effect on insular vegetation: islands that are protected from the wind are mostly covered with northern taiga (pine, birch and spruce forests), and more open islands of the same size are dominated by tundra-like vegetation, mostly crowberry (*Empetrum hermaphroditum* Hager.) thickets. Tides with height about 2 m have an impact on the seashore vegetation. The studied islands usually serve as resting and nesting places for seabirds, which also affect the vegetation in many ways, as some plant species are strongly associated with them (Breslina, 1987). Human pressure on these islands is low: the only visitors are a few wilderness campers in the summer time. Moreover, one of the studied archipelagos (Kem-Ludskij) is strictly protected as part of State Natural Reserve “Kandalakshskij.”

Length and width of the smaller islands were measured manually by walking steps, and corrected using available maps. Sizes of larger islands and their distance to the continent and to the nearest island were measured on the detailed 1:50,000 map. The area of an island was estimated by making two perpendicular measurements of length and width of the island, which approximated the major and minor axes of an ellipse, whose area was calculated. It varied between 600 and 180,000 m², and the total area of 100 islands was 2,090,000 m². The distance to the continent varied from 40 to 9050 m.

For each island we estimated the abundance of different habitat types: boulders, stone placers, bogs, crowberry thickets, forests and seashore biotopes (driftwood, littoral, sand and gravel beaches,

meadows, and rocks). We also estimated the intensity of anthropogenic pressure by counting fire pits, places of soil damage and constructions (mainly remains of tourist camps: tables, shelters etc.).

Island type was determined in accordance with the classification of Breslina (1987) which is based on habitat diversity, age and geomorphology. In general, older islands have greater area and habitat diversity, but these relations are not straightforward as the relief and location of the island vary (Breslina, 1987). Prior to the data analysis, we divided islands into younger, stone-like and older, islet-like islands (see Table 1 for the detailed explanation).

2.2. Survey techniques

We surveyed the majority of islands at least twice. All the information about the islands (including maps, photos, descriptions and floristic lists) can be found on the Web site of the White Sea expedition of Moscow South-West high school: <http://ashipunov.info/belomor/english/islands.htm>. The first survey was conducted between 2000 and 2005. The last floristic inventory was performed in 2011. Additionally, 64 of these islands were studied again in 2007. While the majority of analysis has been based on the 64 islands that were investigated three times, we occasionally used data of all 100 islands in order to obtain more stable results (it was always indicated in the text). In all, there were 27 stone-like islands (16 investigated three times) and 73 islet-type islands (48 investigated three times).

Table 1

Classification of island types, based on habitat diversity, age and geomorphology of the islands (Breslina, 1987) and groups of island types.

Island group	Island type ^a	Description
Stone-type	Korga	The earliest stage of island formation. Part of sea bottom (usually rocky) which is located above the water only in the low-tide. Main habitat types: littoral, sometimes there is also low coastal meadow (in case of presence of loose sediments). Birds rest, but not nest here.
	Kamen ^b	Next stage of island formation (after korga). Small rocky islet; it is above the water even in high-tide. Main habitat type: coastal rocks; higher plants are almost absent. Birds rest, but not nest here.
	Baklysh	Next stage of island formation (after kamen). This is small rocky high islet. Main habitat types: narrow littoral and coastal rocks, sometimes there are also patches of crowberry thicket. Herring gulls are the birds that mainly nest here.
Islet-type	Ludka	Later stage of island formation (after baklysh), is open to winds. Islet with not-indented coastline, built of rocks and loose sediments. Main habitat types: crowberry thicket on the plateau on the top, also littoral, rocks and meadow. Eider duck, herring gulls and common gulls nest in crowberry thicket and on rocks.
	Ostrovok ^c	Later stage of island formation (after baklysh). Islet with not-indented coastline, built mainly of loose sediments. Main habitat type: forest, narrow coastal meadow and littoral. Eider duck normally nests here.
	Luda	Island with indented coastline, originated due to merging of several growing islets of “ludka” type. The main difference from the latter is a more complex relief.
	Ostrov	Island with indented coastline, originated due to merging of several growing islets of “ostrovok” type. The main difference from the latter is a more complex relief.

^a Traditional terms of White Sea coast-dwellers.

^b “Stone” in Russian.

^c “Islet” in Russian.

All islands were surveyed with a unified sampling protocol (see below) by research teams of several persons, led by the same senior researchers. This should minimize several common biases, such as differences in sampling intensity (Connor and Simberloff, 1978), species determination (Scott and Hallam, 2002) and personnel qualifications (Vittoz et al., 2010). Additionally, floristic surveys made by more than one person are much less prone to species overlooking (Scott and Hallam, 2002; Vittoz et al., 2010).

During each of the three surveys every island was visited once in the last half of July or first half of August. In the Kandalaksha Gulf, this is a peak of summer. The islands were examined thoroughly, even in the least accessible areas. Participants of the second and the third inventories did not use floristic lists from previous surveys, thus each of the three surveys were similar in their approach but can be viewed as independent sampling.

In every survey, we noted presence of all vascular plant species. Plants of several genera poorly distinguished in the field (*Euphrasia*, *Puccinellia*, *Hieracium*) were not determined to the species level, and thus these taxa were excluded from the analyses. We accepted species *sensu lato*: *Betula pubescens* s.l., including *Betula czerepanovii* Orlova, *Betula kusmisscheffii* (Regel) Sukacz. and *Betula subarctica* N.I. Orlova; *Carex viridula* s.l., including *Carex scandinavica* E.W. Davis, we also treated *Carex recta* aggr. (including *C. recta* Boot, *Carex salina* Wahlenb., *Carex subspatheacea* Wormsk. ex Hornem.) as one biological species, according to recent molecular data (Volkova et al., 2008). Such broad species treatment and exclusion of several genera from the species list will lead to some underestimation of the turnover rates but, more importantly, will prevent “taxonomical turnover” (*sensu* Panitsa et al., 2008).

2.3. Quantification of flora dynamics

We analyzed flora dynamics using both classical biogeographical (*per island*) and metapopulation approaches (Vidal et al., 2000). The latter is the *per species* equivalent of the insular approach, where emphasis is on the extinction-colonization dynamics of individual species, rather than on individual islands. Grouping species by functional similarity may substantially help to understand and predict plant community dynamics (Vidal et al., 2000).

To describe the dynamics of insular floras, we used three measures: immigration rate (S_{imm}/S in the *per island* approach and I_{imm}/I in the *per species* approach), extinction rate (S_{ext}/S and I_{ext}/I respectively) and stability (S_{all}/S and I_{all}/I respectively). In the *per island* approach, S was the total number of species on an island (found at least in one survey), S_{imm} was the number of species that appeared on an island (found only in the last survey), S_{ext} was the number of disappeared species (found only in the first survey) and S_{all} was the number of species that were registered on an island in all three surveys.

In the *per species* approach, I was the number of islands at which a species was registered at least once, I_{imm} was the number of islands on which a species was present only in the last survey, I_{ext} the number of islands on which a species was present only in the first survey, and I_{all} was the number of islands on which a species was registered in all three surveys.

Only first and third surveys were used for the calculation of rates discussed below. In addition, the data on one of the studied Kem-Ludskij archipelago were compared with our previous results for earlier long-term (1962–2001) study (Shipunov and Abramova, 2006).

Relative species turnover was calculated using method explained in details elsewhere (Vidal et al., 2000; Panitsa et al., 2008).

2.4. Assessment of the method sensitivity

We have previously estimated the proportion of missed species in our research on four islands of the Kandalaksha Gulf. Two islands (Utichij and Chernyshov) are located in the Chupa Bay within the area of current investigation and two islands are outside this area (Volkova et al., 2007). Recently, in 2011, we conducted a similar simultaneous floristic survey on an additional island (“Srednyaya Odinskaya Luda”). Each island was investigated by two independent research groups in the same day. Simultaneous floristic descriptions of the island were treated as descriptions made in the different years. For example, the species was treated as “disappeared” if it was overlooked by one of the groups. Thus, for each pair of floristic lists we calculated three measures of flora dynamics that were used in this paper (we could call them “pseudo-rates”). Pseudo-extinction and pseudo-immigration rates were equal to 0.05–0.15 and pseudo-stability rate was equal to 0.74–0.90 (Volkova et al., 2007). In the current work, we used these values as baselines, setting the rates of extinction and immigration lower than 0.15 to 0, and rate of stability higher than 0.7 to 1 prior to the main analysis.

We calculated Cohen’s kappa statistic (Petrie and Sabin, 2000) to estimate the degree of agreement between pairs of simultaneous floristic descriptions made by different research subgroups for the three islands (Utichij, Chernyshov and “Srednyaya Odinskaya Luda”) in our research area. We also tested for randomness of overlooked plant species on different islands by Pearson’s chi-squared test.

2.5. Plant biological traits

Each plant species was characterized by three biological traits: dispersal mode, growth form and habitat preferences. Seed dispersal modes were separated into four main categories according to our personal observations and all available literature: anemochory, autochory, hydrochory and zoochory. Five growth form categories were considered based on Raunkiaer (1934): phanerophytes, chamaephytes, hemicyptophytes, cryptophytes and therophytes. We empirically determined the following specific habitat preferences (each species could be associated with more than one habitat): littoral, meadows, coastal rocks, bogs, crowberry thicket, forest, stone places, fresh water species, species of disturbed habitats and also species associated with bird nests (in accordance with Breslina, 1987). To evaluate the relationships between measures of insular flora dynamics, species number and island variables, we used a Spearman correlation test and ANCOVA. Parameters of linear relationship between species number and island area were estimated with linear regression. Pairs of samples were compared by different modifications of the Wilcoxon rank sum test as appropriate (i.e., paired or not, two- and one sided, with Bonferroni correction for multiple comparisons). Comparisons of more than two samples were performed by the Kruskal–Wallis rank sum test. For all calculations we used statistical environment R 2.15.2 (R Development Core Team., 2012).

3. Results

3.1. Methodology

There was no significant correlation (Spearman correlation tests, all absolute $r_s < 0.19$, all $p > 0.05$) of the time span between the first and the last investigations and the three rates which were used for quantitative investigation of floristic changes.

Cohen’s kappa statistic for simultaneous floristic surveys made by different research subgroups on each of the three islands was

equal to 0.9. This value indicates “excellent agreement” (Petrie and Sabin, 2000). Plant species on different islands appeared to be missed in essentially random fashion (chi-squared test: Chi-square = 86.39, $p = 0.47$), i.e., chance of overlooking the given species on one island did not correlate to such chance on another island.

3.2. Per island approach

Flora of most islands (81%) was moderately stable (rate of stability between 0.4 and 0.7), flora of about 10% of the islands was less stable (rate of stability < 0.4) and about 10% was extremely stable (rate of stability = 1). Stability rate correlated negatively with the extinction (Spearman correlation test: $r_s = -0.39$, $p < 0.05$) and immigration ($r_s = -0.74$, $p < 0.05$) rates.

For most (81%) of the islands, species extinction rate was equal to 0, for 14% of the islands, extinction rates varied from 0.15 to 0.23, and for the remaining three stone-like islands, it was 0.3–0.6. On 27% of islands, the immigration rate was equal to 0. On the rest, it varied from 0.15 to 0.4, reaching 0.55 for one stone-like island. Species relative turnover per year varied 2.0–4.1% for stone-like islands and 1.5–2.0% for islet-like islands. This difference was significant (Wilcoxon test $p < 0.001$).

The number of species per island during the third floristic survey was significantly higher than during the first (paired one-sided Wilcoxon test: $p < 0.001$).

Different island types were characterized by different rates of flora dynamics (Wilcoxon test $p < 0.001$, Fig. 1). Immigration and extinction rates were significantly higher for stone-like islands than for islet-like. In contrast, stability rate was significantly higher for the latter.

Island area was not associated with the rates of immigration and stability on the 64 islands that were surveyed three times (Spearman correlations: all $p > 0.05$). However, if all 100 investigated islands were taken into account, the rate of stability was positively correlated with island area (Spearman correlation:

$r_s = 0.40$, $p < 0.001$), and extinction rate was negatively correlated with it (Spearman correlation: $r_s = -0.41$, $p < 0.001$). Neither distance to the mainland nor distance to the nearest island were associated with the three rates of flora dynamics.

ANCOVA showed that both area and island type (stone-like vs. islet-like) had significant impact on species number on the island ($p < 0.01$), suggesting a different species–area relationship for each island type. A species area model for islet-type islands was statistically significant: $\log(\text{species number}) = 0.28 \times \log(\text{area}) + 0.72$ ($p < 0.001$, $R^2 = 0.75$). In contrast, relationship for stone-like islands was statistically not significant ($p = 0.12$, $R^2 = 0.17$, Fig. 2). There were no significant correlations between abundance of different habitat types and rates of flora dynamics for both stone- and islet-like islands when analyzed separately. Species richness of stone-like islands correlated positively ($p < 0.05$, $r_s = 0.7$) only with the number of habitat types. The species number for islet-like islands correlated positively ($p < 0.05$, $r_s = 0.3–0.7$) with number of habitats and with island area. Species richness on these islands was also correlated ($p < 0.05$, $r_s = 0.3–0.6$) with the abundance of driftwood, gravel, forest, stones and bogs, which were in turn positively influenced by island area ($p < 0.05$, $r_s = 0.4–0.5$).

We did not find significant correlations between the rates of flora dynamics and the measures of anthropogenic pressure (number of fire pits, places of soil damage and constructions); all stone-like islands and about one half of islet-like islands had no signs of disturbance.

We compared our data for the flora dynamics on 24 islands of the Kem-Ludskij archipelago with an earlier study of the long-term dynamic of their flora (Shipunov and Abramova, 2006). Stability and immigration rates for earlier and recent time spans were correlated positively (Spearman correlation: $p < 0.05$, $r_s = 0.78$ and $r_s = 0.42$ respectively). At the same time, stability rate in 2001–2011 was significantly higher than in 1962–2001 (Wilcoxon paired test: $p < 0.001$, mean \pm SD: 0.73 ± 0.227 and 0.45 ± 0.237 respectively). This was caused mainly by a decrease of immigration rate (Wilcoxon paired test: $p = 0.017$, mean \pm SD: 0.38 ± 0.328 and 0.21 ± 0.169 respectively), as difference between extinction rates for the two time spans was not significant.

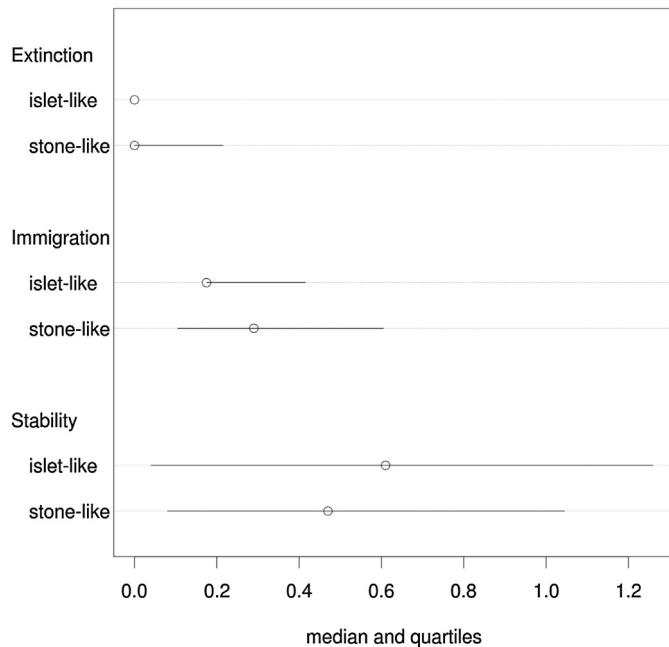


Fig. 1. Median and upper and lower quartile values for immigration, extinction and stability rates in stone-like and islet-like islands (described in Table 1).

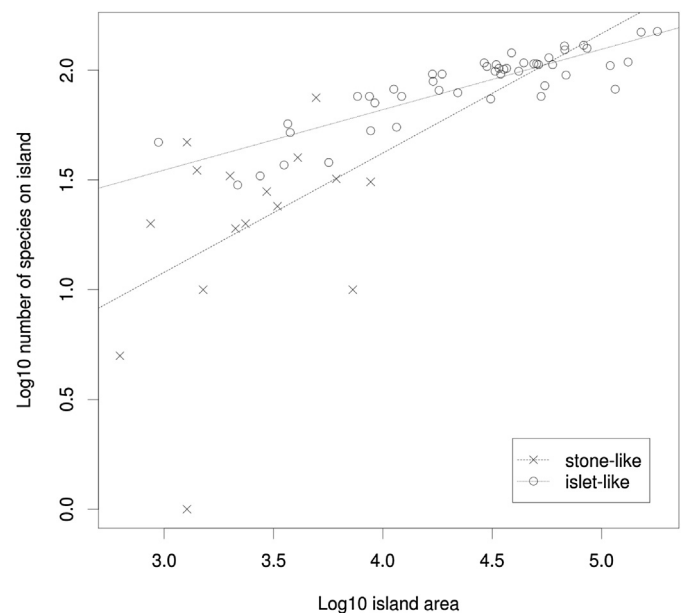


Fig. 2. Log–log species-area curves for stone-like and islet-like islands (described in Table 1). Area was measured in m².

3.3. Per species approach

We recorded 210 plant species during the first survey and 227 species during the third (243 species in total).

By the mode of dispersal, 26% of species were recorded as anemochorous, 15% – zoochorous and 4% were hydrochorous. There were no significant differences in dynamics for species with different modes of dispersal (Kruskal–Wallis rank sum test for all the three rates: $p > 0.1$).

Most plant species grew on coastal meadows (30%), in forests (32%), in crowberry thickets (27%), on coastal rocks (22%), on bogs (21%), or were ornithophilous (36%) (The sum of percents here is greater than 100 as one species could be associated with more than one habitat). Less species were associated with fresh water (10%), littoral (9%), stone placers (3%) or disturbed habitats (14%). Plant species associated with birds had significantly higher stability rates and significantly lower immigration rates. Species associated with crowberry thickets and coastal rocks were more stable whereas species of disturbed habitats were significantly less stable (Fig. 3) (All of the above were supported by Wilcoxon tests: $p < 0.001$).

Among the growth forms, cryptophytes and hemicryptophytes were the most abundant (35% and 38% of all species respectively). Therophytes accounted for 12% of insular flora, phanerophytes 10% and chamaephytes the remaining 5%. Chamaephytes and phanerophytes had significantly lower extinction rates (Kruskal–Wallis rank sum test: $p < 0.001$) than other growth forms taken together (therophytes, cryptophytes and hemicryptophytes) (Fig. 4).

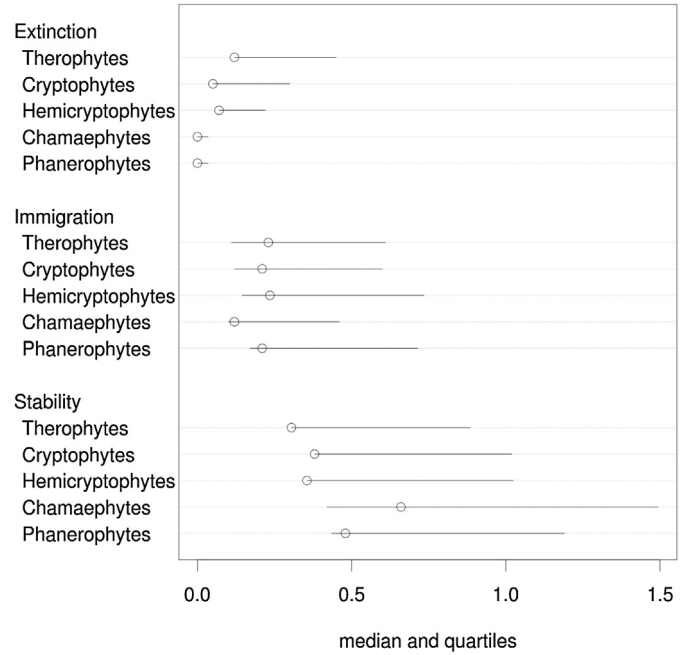


Fig. 4. Median and upper and lower quartile values for immigration, extinction and stability rates for groups of plant species defined according to Raunkiaer's (1934) life forms classification.

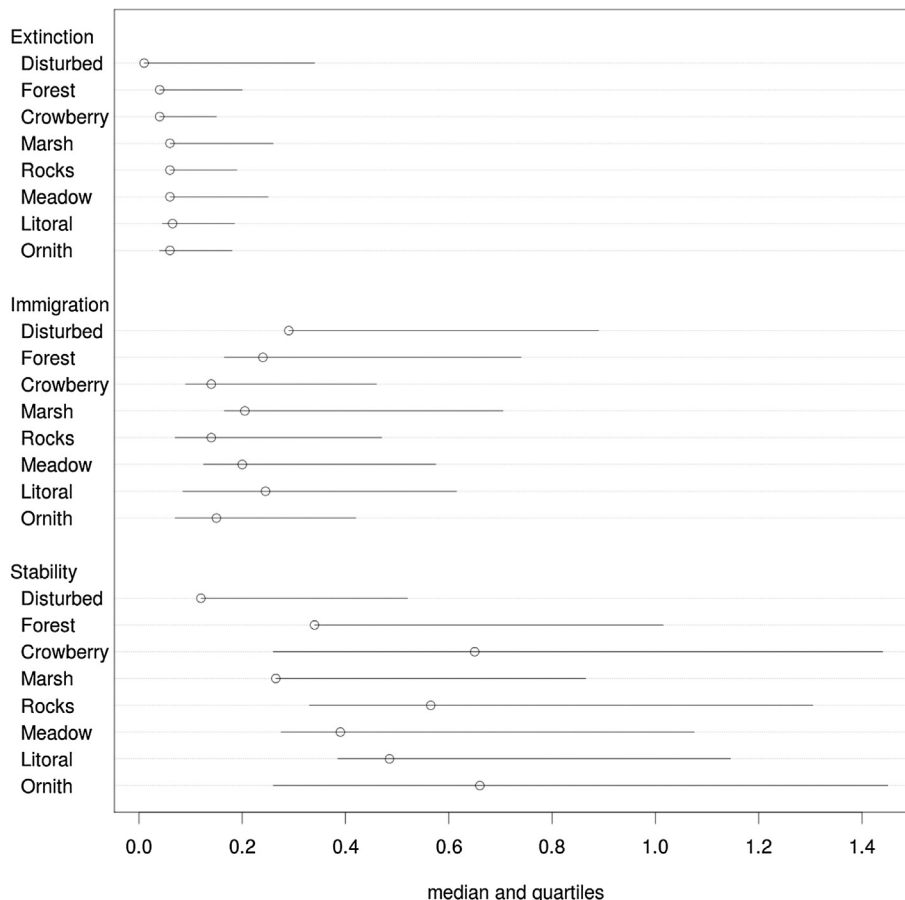


Fig. 3. Median and upper and lower quartile values for immigration, extinction and stability rates for plant species groupings reflecting different habitat preferences.

4. Discussion

4.1. Per species approach

The prominent role of sea birds in shaping insular floras of the White and Barents seas was pointed out by Breslina (1987). Low immigration rate and high stability of ornithophilous species suggest that birds do not increase the diversity of island flora (as it was shown e.g. by Dean et al., 1994) but rather maintain its stability, probably by improving habitat conditions with enrichment of soil nutrients and organic matter. In addition, it is believed that birds use only restricted numbers of plant species for their purposes (Karpovich, 1989). This result agrees with our earlier results on the long-term dynamic of flora (Shipunov and Abramova, 2006). The modest role of birds in island colonization is consistent with the low fraction of zoochorous species in insular floras, as was also shown for Mediterranean islands (Vidal et al., 2000).

Low stability of the species associated with disturbed habitats is not surprising because of ephemerality of this habitat type. Species of coastal rocks and crowberry thickets were more stable probably because sea birds frequently inhabit and “maintain” these habitats (Breslina, 1987). The higher stability of species associated with crowberry thickets may be also explained by resistance of these habitats to scraping which comes from the winter ice. Woody species (chamaephytes and phanerophytes) are more resistant to extinction, possibly because of their deeper root systems, longer average lifespan and better physical robustness (Vidal et al., 2000).

4.2. Per island approach

The fact that stability rate was shown to be much more strongly correlated with immigration than with extinction, suggested that the floristic changes that have occurred owe much more to the massive establishment of new species rather than to the extinction of pre-existing taxa. This was supported by low extinction rates compared with immigration rates and by a constant increase in species number. The short-term (2001–2011) dynamics of the insular flora of Kem-Ludskij archipelago is consistent with the earlier long-term dynamics in 1962–2001 (Shipunov and Abramova, 2006). This is true for both stability and immigration rates, and means that studied islands are still at the stage of colonization associated with the increase of species richness (MacArthur and Wilson, 1967). A similar non-equilibrium situation (i.e., growth in species number caused by enlarging island area due to land elevation) has been described on a more limited sample for the islands in the Gulf of Bothnia (Vartiainen, 1967) and also for a large sample of Canadian Barkley Sound islands (Cody, 2006).

High turnover rates on our islands are in agreement with values obtained from very small islands of Aegean Sea (Panitsa et al., 2008). Our stone-like islands have extremely small surface, and high rates of species turnover that conform to the predictions of the dynamic equilibrium theory (MacArthur and Wilson, 1967).

The floras of our islands have not yet reached the equilibrium, yet extinction rates decline and stability grows with the increase of island area. This contradicts with data for small Bahamian islands (Morrison, 2003) and, at the same time, is consistent with the dynamic equilibrium theory (MacArthur and Wilson, 1967) and with the data on lake islands in Ireland (Roden, 1998), in China (Yu et al., 2012) and also on Canadian continental islands (Cody, 2006). At the same time, immigration rate does not decline for more isolated islands as is postulated by the dynamic equilibrium model. This could be explained by accessibility of even the most isolated islands in our region from avian dispersals (Breslina, 1987), which is also seen for Canadian land-bridge islands (Burns, 2005), for Russian Far

East (Khoreva, 2003) and for small Bahamian islands (Morrison, 2003). Hence, characteristics of islands other than physical distance from the mainland could be important for the insular flora dynamics (Snogerup and Snogerup, 2004), especially for continental islands (as in our case).

Our analysis supports the idea of increasing stability and richness of flora with age on the uprising islands (Vartiainen, 1967; Breslina, 1987). Younger, smaller, stone-like islands have noticeably poorer flora with higher rates of immigration and extinction, compared with older, larger, islet-like islands. Interestingly, our finding of positive relationship between insular flora stability and area was not supported by data on islets in the Aegean Sea (Panitsa et al., 2008). The authors explained the absence of such a relation by small size of the studied islands, but the areas (5000–350,000 m²) were similar to the areas of the islands studied by us. However, the dependence of dynamics and richness of island flora on island characteristics is not uniform (see below).

Recently, special attention has been paid to the diversity-size dependencies on the islands, such as species–area relationship, which is best approximated with a log–log linear model (log-transformed area and species number: Triantis et al., 2012). Though species–area relationship was crucial for the development of major theories in ecology and biogeography (reviewed by Lomolino and Weiser, 2001), there is still no agreement about the right end of the species–area curve (i.e., whether it is asymptotic or not, see Williamson et al., 2001) or about its left end (whether it starts with a constant interval, see the references in Whittaker and Triantis, 2012). The debate about the left end of the curve is in fact equivalent to the questioning of the “Small Islands Effect” (MacArthur and Wilson, 1967), i.e., the absence of any significant effect of area on species richness below a certain island size, which is still disputed (Tjørve and Tjørve, 2011) despite a growing number of supporting examples (e.g. Lomolino and Weiser, 2001; Gentile and Argano, 2005).

Our data provide some evidence compatible with the Small Island Effect (Lomolino and Weiser, 2001). Although our species–area curve does not flatten on the left (below some threshold value of island area), there was no significant linear relationship between logarithms of area and species number for stone-like islands as opposed to the strong linear species–area relationship for islet-like islands.

The richness of unstable floras of our stone-like islands is substantially shaped by stochastic processes of dispersal and persistence. This is consistent with the important role of stochasticity that was also shown for floras of the Galapagos Islands (Connor and Simberloff, 1978), of islands in the Mediterranean Sea (Vidal et al., 1998), in the Aegean Sea (Panitsa et al., 2008) and of the Bahamian islands (Morrison, 2003). The only island variable that influenced species richness of stone-like islands was the number of available habitats.

In contrast to stone islands, the richness of islet-like islands' flora is determined to a much larger extent by the islands' area, but also influenced by habitat diversity. It is difficult to disentangle the roles of these two factors because habitat diversity is determined heavily by the island area (Rydin and Borgegård, 1988; Burns, 2005; Panitsa et al., 2006), which in our case is explained mainly by the island age (Breslina, 1987).

Interestingly, the dynamics of insular floras at our study sites appears to be insensitive to the degree of anthropogenic pressure. However, this should not be interpreted as robustness of insular floras against anthropogenic transformation. On the contrary, islands are “fragile”, prone to disturbance (Vidal et al., 2000; Panitsa et al., 2006). This is especially true in the Arctic (Breslina, 1987), and our results confirm only the initial conception of very low levels of anthropogenic pressure on the studied islands.

To conclude, the influence of island characteristics on short-term flora dynamics of northern marine islands is not uniform. Younger, smaller, stone-like islands have noticeably poorer flora with higher rates of immigration and extinction, compared with older, larger, islet-like islands. The species number for islet-like islands correlate positively with number of habitats, abundance of different habitat types and island area. Species richness of stone-like islands is influenced only by number of habitat types. Flora of our stone-like islands was substantially shaped by stochastic processes and therefore unique.

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References

- Abbott, J., Black, R., 1980. Changes in species composition in floras on islets near Perth, Western Australia. *J. Biogeogr.* 7, 399–410.
- Backus, R.H., Polloni, P.T., Reid, B.L., Somers, P., Hendrickson, T.O., 2002. The flora of Penikese island, Massachusetts: the fifth survey (1998–1999) with emphasis on the woody vegetation. *Rhodora* 104, 219–252.
- Breslina, I.P., 1987. Plants and Water Birds of Marine Islands of Kola Subarctic. Nauka, Leningrad (in Russian).
- Burns, K.C., 2005. Abundance-age-area relationships in an insular plant community. *Folia Geobot.* 40, 331–340.
- Cody, M.L., 2006. Plants on Islands: Diversity and Dynamics on a Continental Archipelago. University of California Press, Berkeley.
- Connor, E.F., Simberloff, D., 1978. Species number and compositional similarity of the Galapagos flora and avifauna. *Ecol. Monogr.* 48, 219–248.
- Dean, W.R.J., Milton, S.J., Ryan, P.G., Moloney, C.L., 1994. The role of disturbance in the establishment of indigenous and alien plants at inaccessible and Nightingale Islands in South Atlantic Ocean. *Vegetatio* 113, 3–23.
- Gentile, G., Argano, R., 2005. Island biogeography of the Mediterranean sea: the species relationship for terrestrial isopods. *J. Biogeogr.* 32, 1715–1726.
- Glazkova, E.A., 2001. Vascular Flora of the Islands of the Eastern Gulf of Finland: Structure and Analysis. St. Petersburg University Press, St. Petersburg (in Russian).
- Harrison, R.D., Banka, R., Thornton, I.W.B., Shanahan, M., Yamuna, R., 2001. Colonization of an island volcano. Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. II. The vascular flora. *J. Biogeogr.* 28, 1311–1337.
- Herloff, B., 2003. Floristic changes during the twentieth century in the southern archipelago of Goeteborg, SW Sweden. *Sven. Bot. Tidskr.* 97, 3–14 (in Swedish).
- Kalmar, A., Currie, D.J., 2006. A global model of island biogeography. *Glob. Ecol. Biogeogr.* 15, 72–81.
- Karpovich, V.N. (Ed.), 1989. Ecology of Birds from the Islands and the Coast of Northern Kola Peninsula. Murmansk book publisher, Murmansk (in Russian).
- Khoreva, M.G., 2003. Island Flora of the Northern Okhotia. IBPN FEB RAS, Magadan (in Russian).
- Koshechkin, B.I., 1979. Holocene Tectonic of the Eastern Part of Baltic Shield. Nauka, Leningrad (in Russian).
- Lomolino, M.V., Weiser, M.D., 2001. Towards a more general species–area relationship: diversity on all islands, great and small. *J. Biogeogr.* 28, 431–445.
- MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.
- Morrison, L.W., 2003. Plant species persistence and turnover on small Bahamian islands. *Oecologia* 136, 51–62.
- Nilsson, I.N., Nilsson, S.G., 1982. Turnover of vascular plant species on small islands in lake Mockeln, South Sweden 1976–1980. *Oecologia* 53, 128–133.
- Panitsa, M., Tzanoudakis, D., Triantis, K.A., Sfenthourakis, S., 2006. Patterns of species richness on very small islands: the plants of the Aegean archipelago. *J. Biogeogr.* 33, 1223–1234.
- Panitsa, M., Tzanoudakis, D., Sfenthourakis, S., 2008. Turnover of plants on small islets of the eastern Aegean Sea within two decades. *J. Biogeogr.* 35, 1049–1061.
- Partomihardjo, T., Mirmanto, E., Whittaker, R.J., 1992. Anak Krakatau's vegetation and flora circa 1991, with observations on a decade of development and change. *Geof.* 28, 233–248.
- Petrie, A., Sabin, C., 2000. Medical Statistics at a Glance. Blackwell science, London.
- R Development Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Raunkiaer, C., 1934. The Life-forms of Plants and Statistical Plant Geography. Clarendon, Oxford.
- Robinson, G.R., Yurlina, M.E., Handel, S.N., 1994. A century of change in the Staten island flora: ecological correlates of species, losses and invasions. *B. Torrey Bot. Club* 121, 119–129.
- Roden, C., 1998. Persistence, extinction and different species pools within the flora of lake islands in western Ireland. *J. Biogeogr.* 25, 301–310.
- Rydin, H., Borgegård, S.-O., 1988. Plant species richness on islands over a century of primary succession: lake Hjälmaren. *Ecology* 69, 916–927.
- Scott, W.A., Hallam, C.J., 2002. Assessing species misidentification rates through quality assurance of vegetation monitoring. *Plant Ecol.* 165, 101–115.
- Serebryanaya, A., Shipunov, A., 2009. Morphological variation of plants on the uprising islands of northern Russia. *Ann. Bot. Fenn.* 46, 81–89.
- Shipunov, A.B., Abramova, L.A., 2006. Floristic changes on islands of Kem-Ludskij archipelago (1962–2004). *Bull. MOIP, Ser. Biol.* 111, 45–56 (in Russian).
- Snogerup, S., Snogerup, B., 1987. Repeated floristical observations on islets in the Aegean. *Plant Syst. Evol.* 155, 143–164.
- Snogerup, S., Snogerup, B., 2004. Changes in the flora of some Aegean islets 1968–2000. *Plant Syst. Evol.* 245, 169–213.
- Svendsen, J.L., et al., 2004. Late Quaternary ice sheet history of northern Eurasia. *Quaternary Sci. Rev.* 23, 1229–1271.
- Tjørve, E., Tjørve, K.M.C., 2011. Subjecting the theory of the small-island effect to Ockham's razor. *J. Biogeogr.* 38, 1836–1839.
- Triantis, K.A., Guilhaumon, F., Whittaker, R.J., 2012. The island species–area relationship: biology and statistics. *J. Biogeogr.* 39, 215–231.
- Vartiainen, T., 1967. Observations on the plant succession of the islands of Krunit, in the Gulf of Bothnia. *Aquila Ser. Botanica* 6, 158–171.
- Vidal, E., Madail, F., Taton, T., Vidal, P., Roche, P., 1998. Functional analysis of the newly established plants introduced by nesting gulls in Riou archipelago (Marseille, France). *Acta Oecol.* 19, 241–250.
- Vidal, E., Médail, F., Taton, T., Bonnet, V., 2000. Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. *Oecologia* 122, 427–434.
- Vittoz, P., Bayfield, N., Brooker, R., Elston, D.A., Duff, E.I., Theurillat, J.-P., Guisan, A., 2010. Reproducibility of species lists, visual cover estimates and frequency methods for recording high-mountain vegetation. *J. Veg. Sci.* 21, 1035–1047.
- Volkova, P.A., Altshuler, E.P., Shipunov, A.B., 2007. Complete Flora of Islands and Lakes as a Statistical Hypothesis. In: The Materials of the White Sea Expedition of Moscow South-west High School, vol. 7 [Electronic resource]. URL: <http://ashipunov.info/belomor/english/2007/noise.htm>.
- Volkova, P.A., Shipunov, A.B., Elven, R., Brochmann, C., 2008. The seashore sedges of the Russian Kola Peninsula: how many species? *Flora* 203, 523–533.
- Whittaker, R.J., Triantis, K.A., 2012. The species–area relationship: an exploration of that ‘most general, yet protean pattern’. *J. Biogeogr.* 39, 623–626.
- Williamson, M., Gaston, K.J., Lonsdale, W.M., 2001. The species–area relationship does not have an asymptote. *J. Biogeogr.* 28, 827–830.
- Wright, D.H., 1983. Species–energy theory: an extension of species–area theory. *Oikos* 41, 496–506.
- Yu, M., Hu, G., Feeley, K.J., Wu, J., Ding, P., 2012. Richness and composition of plants and birds on land-bridge islands: effects of island attributes and differential responses of species groups. *J. Biogeogr.* 39, 1124–1133.