

Morphological variation of plants on the uprising islands of northern Russia

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Received 20 May 2008, revised version received 16 Feb. 2009, accepted 24 Feb. 2009

Serebryanaya, A. & Shipunov, A. 2009: Morphological variation of plants on the uprising islands of northern Russia. — *Ann. Bot. Fennici* 46: 81–89.

The purpose of our study was to test whether any significant morphological differences exist between island and mainland plant populations of the north European White Sea. Six polymorphic species were studied: *Atriplex nudicaulis* (Chenopodiaceae), *Euphrasia wettsteinii* (Orobanchaceae), *Achillea millefolium* (Asteraceae), *Parnassia palustris* (Parnassiaceae), *Potentilla egedii* (Rosaceae) and *Rhodiola rosea* (Crassulaceae). Based on the multivariate analyses of our data, we found 10 cases where differences between island and mainland populations are best explained by the existence of short-scale evolutionary processes. These results suggest that plant populations on islands of recent origin may display local morphological divergence in a short evolutionary time frame.

Key words: evolution, islands, plant morphology, variation, White Sea

Introduction

Islands have been considered natural laboratories for exploring the evolutionary processes from the times when Charles Darwin discovered finch diversity on the Galapagos Islands, which lead him to the idea of geographical speciation (Darwin 1839, Grant 1996, Emerson 2002, Whittaker & Fernandez-Palacios 2007). There are multiple examples of recent evolutionary studies on islands, and in numerous cases plants are the main objects of research (Soejima *et al.* 1994, Barrett *et al.* 1996, Ito *et al.* 1998, Baldwin & Sanderson 1998, Stuessy 1998, Ballard 2000, Stuessy *et al.* 2006).

It is known that small-scale morphological differentiation is often subject to natural selection (Gurevitch 1992, Linhart & Grant 1996) and microevolution rates are sometimes surprisingly high (Cody & Overton 1996, Van Vuren & Bowen 1999, Bone & Farris 2001). Of particular importance to our study is that there is a significant geographical variation in certain morphological characteristics of plants (Andersson 1991, Andersson 1995, Widen 2003, Barrera & Walter 2006). Moreover, many aspects of islands' flora are greatly influenced by island surface area and its remoteness from the mainland (McMaster 2005, Kalmar & Currie 2006). In general, morphological differences could happen due to

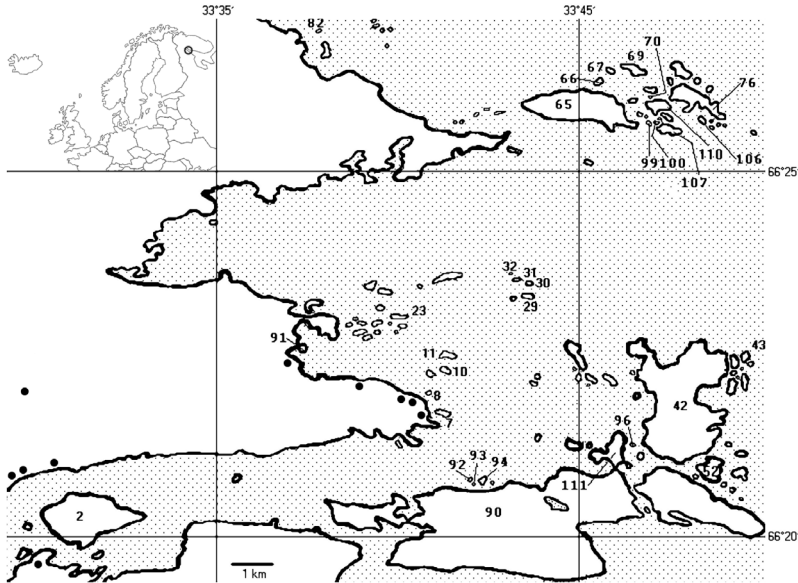


Fig. 1. Map of the region, with designations of all investigated islands. Names of islands with “contrasts” are set in boldface; dots indicate locations of mainland samples. Inset in the upper left corner shows the part of Europe enlarged in the main map. Islands of the *Odinokie Ludi* archipelago: 29 = **Boljshaya Odinokaya Luda**, 30 = **Malaya Odinokaya Luda**, 31 = *Srednyaya Odinokaya Luda*, 32 = **Ochenj Odinokaya Luda**. Islands of the *Kem’-Ludy* archipelago: 65 = **Kemludskij**, 66 = *Perejma*, 67 = *Korablik*, 69 = *Korzhnichiha*, 70 = *Sinopchiha*, 76 = **Bol’shoj Asaf’ev**, 99 = *Zhguchij*, 100 = *Matrasik*. Other islands: 2 = *Olenij*, 7 = *Ivanjkov*, 8 = *Rihzhenjkiyj*, 10 = *Skeletov*, 11 = *Drakonchik*, 23 = *Izbyanaya Luda*, 42 = **Sidorov**, 43 = *Cherepakha*, 49 = *Vihsokaya Luda*, 52 = *Vichennaya Luda*, 82 = *Morschovec*, 90 = *Keret’*, 91 = *Pryaostrov*, 92 = *Pizhmyak*, 93 = *Kivsyak*, 94 = *Lahtak*, 96 = *Zvezdov*, 106 = **Gusinyj**, 107 = **Zelenyj**, 110 = **Izbyanoj**, 111 = *Bolshoj Andronin*.

selection and/or genetic drift (Abdelkrim 2005, Stuessy *et al.* 2006), and should correlate with the remoteness of the island as a measure of isolation (Mayr 1942, Grant 1996). They could also be caused by phenotypic variation but that can be excluded (at least partly) by using properly selected species and parameters, multiple observations, and investigations of local variability.

To investigate the geographic impact on plant morphology, we chose to study the uprising islands and islets of Chupa and Kiv gulfs and *Kem’-Ludy* archipelago of the big *Kandalaksha* gulf of the north Russian White Sea (Fig. 1). The history of these islands is unique. During the last ice age (12–15 000 years ago) the entire northern Europe was covered with ice, which was around 3 km deep and caused enormous pressure on the Earth’s crust. As a result, the whole region of the future White Sea sank to form a depression of 0.2–0.3 km deep (Hattestrand & Clark 2007). Later, when the climate became warmer, the ice melted, forming the sea and its islands. As a con-

sequence of the former depression, many islands are still rising today with a speed of approximately 5–8 mm per year, and new islands are constantly appearing (Koshechkin 1979, Shipunov & Abramova 2006).

The flora of these islands is relatively poor (Shipunov & Abramova 2006) since the majority of plants belong to the northern taiga. Distant islands are covered with tundra-like flora mainly due to strong winds (Breslina 1987). A variety of plants that occur both on the mainland and the islands of the White Sea were noted to be taxonomically diverse (Sokoloff & Filin 1996). We chose six herbaceous (two annual and four perennial) species that are common to the studied area and have the reliable taxonomic diversity under the species level: *Atriplex nudicaulis* (Chenopodiaceae), *Euphrasia wettsteinii* (Orobanchaceae), *Achillea millefolium* (Asteraceae), *Parnassia palustris* (Parnassiaceae), *Potentilla egedii* (Rosaceae) and *Rhodiola rosea* (Crassulaceae). For example, *Atriplex* species are extremely

variable, both morphologically and genetically, and some of their characters can be affected by the environment conditions (Ortiz-Dorda *et al.* 2005, Bouda 2006). *Euphrasia* is also known for its high morphological variability, especially in northern regions (Swann 1973, Yeo 1978, Gussarova 2005). Many of *Achillea* species are taxonomically problematic, with bottleneck effects having a large impact on variation in several species, especially among those in isolated habitats (Saukel & Langer 1990, Guo *et al.* 2004, 2005, 2008). *Parnassia palustris* can be diploid and tetraploid (the last form occurs specifically in the northern Europe and alpine habitats), both types show morphological variation, and are often confused with other species (Borgen & Hultgard 2003). Similar situations exist in *Potentilla egedii* (Kamelin 2001) and *Rhodiola rosea* (Uhl 1952, Sokoloff & Filin 1996).

Thus, the high variability of the chosen plant species set makes them a reliable tool to study plant variability on islands. Consequently, the goal of our research was to check if plants evolve differently on the mainland as compared with the islands, and if the geographical characteristics of the islands (such as height and surface area) influence these changes.

Materials and methods

Typically at least one population from each island was studied. Each sample consisted of approximately 20–25 plants from every population (topographically isolated group of plants). On each plant 7–10 morphological characteristics were measured, and in most cases we used parameters that were already known as variable and/or helpful for distinguishing plants on the intra-species level (Swann 1973, Yeo 1978, Saukel & Langer 1990, Sokoloff & Filin 1996, Kamelin 2001, Gussarova 2005).

In addition to the classical morphological characteristics, in two cases (*Atriplex* and *Rhodiola*) we used leaf contours of the largest leaf for geometric morphometry, namely, thin plate spline (TPS) analysis of the leaf shape diversity between populations (Adams *et al.* 2004, Shipunov & Bateman 2005). The leaf shapes of *Atriplex* and *Rhodiola* were described by 8 or

6 landmarks, respectively, situated on the bend points of the leaf contour. The coordinates of landmarks were written to a data file with the help of a screen digitizer tpsDig (Rohlf 2006). The relative warps, characterizing the degree of differences between the specimen and consensus configuration, were calculated with tpsRelw (Rohlf 2007) and then used in the overlap analysis (*see below*). Original coordinates were normalized using the Procrustes fit method ($\alpha = 0$).

To explore the variation of plant species within one island we performed a thorough sampling on some islands for *Achillea* and *Rhodiola*. We tried to choose multiple sites that belonged to different habitats and were most distant from each other. This was done to eliminate the possibility of small-scale impacts of local conditions on the sample populations. The same overlap analysis (*see below*) was used with this kind of data.

The analytical part of our study started with the comparison of overlaps derived from principal components analysis (PCA) for scaled data (we used scaled data to eliminate the effects of the different nature of parameters used). For each species, extreme points on the PCA graph(s) of most informative principal components (usually PC1 and PC2, sometimes also PC3) were used for plotting convex hulls, which depicted different populations (*see Fig. 2*). In most cases, polygons were intersected and therefore let us calculate the percentage of overlap between each pair of polygons. Since we used polygons instead of original points, we were able to take into account the whole norm of reaction and identify the sampling effect. Thus, overlap coefficients were calculated for all pairs of populations, along with the mean overlap for each population as a measure of morphological remoteness. We used 20%–25% of mean overlap as a boundary value for initiating further investigations with the population. In several cases, the overlap was adjusted by removing obvious outliers from the PCA. In addition to the PCA, we used multi-dimensional scaling (MDS) and linear discriminant analysis (LDA), but the results of these attempts were not significantly different. In the cases of *Rhodiola* and *Atriplex*, two different PCA (with classical and geometric morphometry parameters) were performed, and two separate series of overlap were calculated.

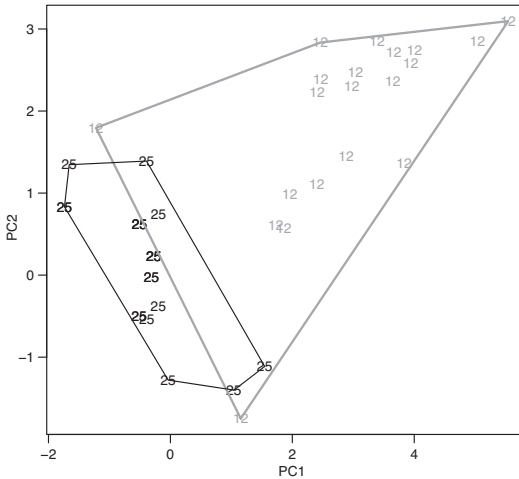


Fig. 2. An example of the overlap analysis for a PCA plot. Two populations of *Achillea millefolium* are represented: no. 12 is from island contrast whereas no. 25 is the population from mainland. Since the overlap is an asymmetric measure (calculated as $\text{Overlap}_{a,b} = \text{Area}_{a \cap b} / \text{Area}_a$), overlap values in this case are 12.64% and 40.71%, respectively. The mean overlap of all cases is 26.68%.

To obtain statistical support for the differences between mainland and island populations and to find characters with significant variation, we performed multivariate and partial ANOVA analyses for selected data (all mainland and contrasting island populations were selected) with “mainland vs. island” as an independent variable.

To find out if the differences between island and mainland populations correlated with an island’s parameters (altitude, area, and distance from mainland) we used Gower distances calculated between island and mainland populations

on the base of median character values. Next, the Spearman rank correlation tests were used to obtain values and statistical significance of correlations between distances and island parameters. We employed this analysis twice: for all characters measured, and for characters selected from MANOVA results.

For all statistical calculations, R statistical environment and language (R Development Core Team 2007) was used.

Results

In total, over 2800 plants were measured from 145 populations (topographically isolated groups of plants), taken from 33 islands and 32 locations on mainland (Fig. 1 and Table 1). In total, 51 morphological characteristics were measured (see Table 2). Several plants from each location were put into a herbarium.

Among the populations with a low overlap percentage, we searched for cases in which the difference in morphology from mainland populations correlated with the geographic position of the studied island. We refer to those as “island contrasts” and hereafter use the following abbreviations for the three different cases:

- A: when population(s) from one island differed from mainland populations;
- B: when the difference existed between populations of neighboring islands (i.e., parts of one archipelago) and mainland; and
- C: when we observed differences between main-

Table 1. Numbers of investigated units for each species.

Species	Number of investigated plants	Number of investigated populations	Number of investigated islands	Islands investigated in each case (see Fig. 1 for island names and locations)
<i>Achillea millefolium</i>	573	32	16	2, 7, 10, 11, 29, 31, 32, 42, 67, 69, 76, 91, 99, 106, 107, 110
<i>Atriplex nudicaulis</i>	488	25	21	2, 7, 8, 29, 30, 31, 42, 43, 49, 52, 65, 66, 76, 90, 91, 92, 93, 94, 96, 110, 111
<i>Euphrasia wettsteinii</i>	608	31	18	7, 8, 10, 23, 29, 31, 32, 42, 43, 67, 69, 70, 91, 99, 100, 106, 107, 110
<i>Parnassia palustris</i>	295	15	10	8, 31, 42, 49, 65, 66, 76, 82, 90, 110
<i>Potentilla egedii</i>	147	8	1	76
<i>Rhodiola rosea</i>	691	34	16	7, 8, 29, 30, 31, 43, 49, 52, 66, 70, 76, 82, 94, 96, 106, 110

land populations and groups of populations from distant islands.

The most reliable types are A and B, where population(s) from one island or densely located group of islands have a small overlap with all the studied mainland populations of a certain species. This is a putative evidence of evolutionary divergence. Type C may be the results of parallel evolution and/or colonization.

In most cases, the average overlap values for the entire species ranged between 30% and 40%. The only exception were the results of geometric morphometry, in which these values were 49.29% and 51.02% (for *Atriplex* and *Rhodiola* leaf contours, respectively). Therefore, in both cases of geometric morphometry there was not enough of an overlap to select populations, because all the values were well above 25%.

The thorough sampling (multiple sites on each island, data from different years pooled together) resulted in high overlap values for all investigated populations from one island: 44.15% for six *Achillea* populations from one island, and 39%–73% for eighteen *Rhodiola* populations from three different islands.

Based on the analysis of individual populations, 19 populations of interest with the lowest overlap values were chosen. In two cases (both with *Euphrasia*) the construction of reliable contrasts was impossible, because other populations from the same island had a significantly higher overlap. As a result, only 17 populations were used in island contrasts (Table 3). Most of the contrasts were of type A, but in the case of *Parnassia* only type C was found. The most distinct populations were located on the Kem'-Ludy and Odnokie Ludy archipelagos, but not on all studied islands. All islands with contrasts (with the exception of Ochen' Odnokaya Luda, no. 32, see Fig. 1) were different from the other studied islands because of their relatively large size (median area 167 000 m² vs. 34 574 m², Wilcoxon rank test = 58, $p = 0.05833$) and greater distance from mainland (4616 m vs. 2200 m, Wilcoxon rank test = 54, $p = 0.0527$), whereas the altitudes were not significantly different (12.6 m vs. 7.93 m, Wilcoxon rank test = 77, $p = 0.2754$). The largest number of island contrasts (4) belong to Bol'shoj Asaf'ev island (no. 76,

Table 2. Morphological characteristics measured for each plant species. Characters with significant differences (with $p < 0.01$) in all partial ANOVA analyses for island contrasts are set in boldface.

Species and characters measured	
<i>Achillea millefolium</i>	Number of stem leaves Length of first stem leaf (mm) Number of first order lobes on the first stem leaf Length of maximal first order lobe (mm) Width of maximal first order lobe (mm) Relative position of maximal first order lobe (mm) Length of central flowering head (mm) Length of maximal ligule (mm) Width of maximal ligule (mm)
<i>Atriplex nudicaulis</i>	Length of petiole of the largest leaf (mm) Length of maximal leaf (mm) Width of maximal leaf (mm) Relative position of maximal leaf width (mm) Length of largest bract (mm) The level of accretion of bract pair (points) Abundance of bract teeth (points)
<i>Euphrasia wettsteinii</i>	Length of main stem (mm) Number of first order branches Number of main nodes Length of internode under lower bract (mm) Length of lower bract (mm) Width of lower bract (mm) Number of teeth on lower bract Length of corolla of flower adjacent to lower bract (mm)
<i>Parnassia palustris</i>	Height of flower stalk (mm) Position of upper bract leaf (mm) Length of upper bract leaf (mm) Width of upper bract leaf (mm) Position of width of upper bract leaf (mm) Length of sepal (mm) Width of sepal (mm) Form of sepal apex (points) Length of petal (mm) Number of lobes on staminode
<i>Potentilla egedii</i>	Length of maximal leaf (mm) Relative position of maximal leaflet (mm) Length of maximal leaflet (mm) Width of maximal leaflet (mm) Amount of hairs on maximal leaflet (points) Type of hairs on maximal leaflet (points) Length of maximal tooth on the leaflet (mm) Distance from tooth base to midrib of the leaflet (mm) Type of sepal, points Diameter of flower (mm)
<i>Rhodiola rosea</i>	Length of maximal leaf (mm) Width of maximal leaf (mm) Relative position of maximal leaf width (mm) Width of leaf base of maximal leaf (mm) Number of bracts Length of sepal (mm) Position (bend level) of bracts (points)

see Fig. 1), and among plants — to *Achillea* and *Atriplex* (4 in each case).

From 51 characters measured, 19 were significantly different in all partial ANOVA analyses for island contrasts (Table 2). All MANOVA analyses for contrasts were significant (Table 3), whereas Wilks' λ showed that ~50% or more of variation was explained by the island vs. mainland factor in 8 of 10 cases, with notable exception for contrasts from *Euphrasia* and *Potentilla* (Table 3).

In most cases, coefficients of correlation were not high, and correlations for the selected characters were higher than for all characters (Table 4). Coefficients for *Euphrasia* were negative in all cases (and significant for altitudes and distances), whereas all other significant coefficients were positive. In the case of *Achillea*, no significant correlations were found. The highest and most stable correlations (with both area and altitude of islands) were in the case of *Atriplex*.

Discussion

From 113 island populations studied, we found 17 that were morphologically different from all the other studied populations of the same species. According to the geographical distribution, these 17 populations were grouped into 10 island contrasts. Most of these contrasts belong to two groups of relatively big and remote islands. Some of these islands host more than one (in some cases up to 4) contrasts. Moreover, some positive correlations were found between an island age (represented by surface area and altitude) and its remoteness from the mainland, on the one hand, and morphological distances in island and mainland populations, on the other hand. Between populations of *A. millefolium* and *R. rosea* collected on the same island, no significant differences were found by the thorough sampling. We believe that the observed island contrasts represent early stages of local geo-

Table 3. Results of the MANOVA analyses for selected island contrasts. For the numbers of islands, see Fig. 1. All differences significant at $p < 0.001$.

Species	Islands in the contrast	Type of contrast	Wilks' λ
<i>Achillea millefolium</i>	29, 32	close islands vs. mainland	0.3874
<i>Achillea millefolium</i>	76, 107, 110	close islands vs. mainland	0.533
<i>Atriplex nudicaulis</i>	29	island vs. mainland	0.5219
<i>Atriplex nudicaulis</i>	65	island vs. mainland	0.237
<i>Atriplex nudicaulis</i>	76, 110	close islands vs. mainland	0.289
<i>Euphrasia wettsteinii</i>	106	island vs. mainland	0.6649
<i>Parnassia palustris</i>	42, 76	distant islands vs. mainland	0.278
<i>Potentilla egedii</i>	76	island vs. mainland	0.6642
<i>Rhodiola rosea</i>	30	island vs. mainland	0.0051
<i>Rhodiola rosea</i>	110	island vs. mainland	0.2988

Table 4. Spearman rank correlations between morphological distances between island and mainland populations, and characteristics of islands. Significant correlations (at $p < 0.05$) are set in boldface.

Species	Correlation with island altitude	Correlation with island area	Correlation with distance from island to mainland
<i>Achillea millefolium</i> (all characters)	-0.164	-0.283	0.316
<i>Achillea millefolium</i> (selected characters)	0.137	0.014	-0.122
<i>Atriplex nudicaulis</i> (all characters)	0.383	0.451	0.276
<i>Atriplex nudicaulis</i> (selected characters)	0.422	0.510	0.211
<i>Euphrasia wettsteinii</i> (all characters)	-0.372	-0.264	-0.385
<i>Euphrasia wettsteinii</i> (selected characters)	-0.365	-0.326	-0.005
<i>Parnassia palustris</i> (all characters)	0.103	0.224	0.552
<i>Parnassia palustris</i> (selected characters)	0.304	0.438	0.809
<i>Rhodiola rosea</i> (all characters)	-0.336	-0.186	0.279
<i>Rhodiola rosea</i> (selected characters)	0.455	0.632	0.196

graphic speciation, resulting from initial colonization and subsequent selection and/or from accumulation of neutral mutations. This agrees well with the results of known studies on the morphological diversity of island and mainland plant populations (Kawakubo 1986, Andersson 1995, Cody & Overton 1996), where the largest differences were usually observed on oldest and most remote islands (Andersson 1995, Barrett *et al.* 1996) and comparably fast evolutionary rates were found (Cody & Overton 1996, Van Vuren & Bowen 1999, Bone & Farres 2001).

However, since plants usually have high phenotypic plasticity, we cannot exclude the possibility of observed differences being caused directly by environmental conditions. Still, we have some indirect evidence against the latter explanation. To begin with, similarity between populations within one island was high and did not significantly change across the years despite of our attempts to measure populations from most diverse environmental conditions. In addition, several studies of plant phenotypic plasticity led other authors to the conclusion that morphological diversity of size parameters coincides well with genetic diversity (Gurevitch 1988, 1992, Linhart & Grant 1996, Housman *et al.* 2002, Widen & Schiemann 2003). Even in the case of “pure” phenotypic plasticity, observed differences may be a good sign of evolutionary process (Pigliucci *et al.* 2006). Moreover, the recent AFLP investigations of some of our *Achillea* populations already revealed that plants from the most remote islands (*see* the “Ra1” and “Ra13” samples in Guo 2008) have the highest level of genetic divergence, and the overall genetic diversity between our samples is high (Y. Guo pers. comm.). Nevertheless, thorough molecular genetic studies along with common garden experiments are needed to provide better support for differences found.

Among ten island contrasts found, three belonged to type B (where populations from a group of neighboring islands collectively differ from the mainland populations). This is most likely due to either a relatively high level of interchange between neighboring islands or to one colonization event. Only one island contrast of type C was found, and the best explanation is that this is a result of parallel selection,

especially if we take into account that contrasting characters of *P. palustris* are clearly correlated with pollination (shorter flowering stalk but larger sepals, petals, and staminodes). However, the existence of multiple colonization routes for *P. palustris* (Borgen & Hultgard 2003) increase the possibility of observing different “waves of colonization,” where “oldest” plants occupy the most remote islands. The high correlation (Spearman $\rho = 0.809$, $p = 0.005$) between geographical and morphological distances provides additional support for the latter explanation.

It should be noted that the studied species are unequal. *Achillea millefolium*, *Atriplex nudicaulis* and *Rhodiola rosea* demonstrated most of the evidence of possible evolutionary processes. These species have the maximal numbers of island contrasts and the highest age/diversity correlations. Among them, the diversity of *A. millefolium* is best studied (Guo *et al.* 2004, 2005, 2008). Since *A. millefolium* aggregate includes different phases of speciation (Guo *et al.* 2005, 2008) it should be easy to find the traces of very recent evolutionary events. *Atriplex nudicaulis* and *R. rosea* are much less studied. Nevertheless, complex taxonomic situations in both cases (Uhl 1952, Sokoloff & Filin 1996, Ortiz-Dorda *et al.* 2005, Bouda 2006) could be the results of similar complexity.

Among the studied species four (*A. nudicaulis*, *E. wettsteinii*, *P. palustris* and *R. rosea*) belong to the bird-dependent, “ornithophilous” (in terms of Breslina 1987) plants, because their distribution correlates well with the distribution of sea birds, especially gulls. In addition, first two species are annuals, and *A. nudicaulis* is a wind-pollinated plant and also the only hydrochorous plant (fruits dispersed by sea currents). However, we cannot prove any relation between these features and patterns of distribution of our island contrasts.

Euphrasia wettsteinii seems to be the least reliable species for a study like ours. We found only one contrast, and two other potential contrasts were spoiled by the presence of much less divergent populations from the same islands. Moreover, correlations between diversity and age were negative, supporting the view that in the case of *E. wettsteinii* the observed differences were accidental. Unfortunately, the prelim-

inary AFLP analysis of our *Euphrasia* samples was unsuccessful because of DNA extraction problems (G. Gussarova pers. comm.). Similarly, in our geometric morphometry approach, leaf shape of *A. nudicaulis* and *R. rosea* did not provide valuable information. It is hard to say whether *P. egedii* was a good candidate for plant diversity research, since only one island population was studied, and this one was morphologically different from all the 7 mainland populations that were investigated.

Overall, we believe that changes in plant morphology we observe for the uprising islands as compared with the mainland represent early stages of small-scale evolutionary processes. These changes have likely been caused by a colonization effect, followed by selection on the islands. The future of island contrasts remains unclear. In theory, some of the island populations can evolve further and become separate species. However, geological processes in the region are running fast and in the future many of our islands will merge (many of Kem'-Ludy islands are already connecting during low tides: Shipunov & Abramova 2006) and finally connect with the mainland. This will result in the fading and mutual disappearance of isolation barriers, and then probably with the elimination of existing morphological differences. Nevertheless, the rising islands of the White Sea will remain a natural laboratory for studying short-scale evolutionary processes as long as they exist.

Acknowledgements

We are cordially grateful to all members of the White Sea Expedition of Moscow South-West High School (headed by S. Glagolev), who collected all the material in the field; to specialists who helped us in plant identification: D. Sokoloff, G. Gussarova, A. Sukhorukov and N. Tzvelev; to E. Altschuler, O. Kudina, M. Lyovina and D. Vasyukov who assisted on the initial stages of statistical processing; and to P. Volkova and P. Petrov for their valuable comments on the manuscript.

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