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Vascular plants on the islands and peninsulas of Maloe More (Lake Baikal): patterns of diversity and species turnover

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Unique biota of the Lake Baikal region face many threats due to increasing human activities. We documented spatial patterns in diversity of vascular plants, explored effects of natural (bird colonies) and human-induced (tourism) disturbances on species richness of semi-desert and steppe-desert plant communities of 12 islands and 4 peninsulas, and estimated species turnover within a 30-year period. Floras of surveyed islands/peninsulas contained 9 to 143 species; species–area relationship followed the power law model. Species richness did not change between 1979 and 2009, but the proportion of ruderal species doubled during this period. Mean relative turnover rate was 1.17% of species per year. The islands with large bird colonies had lower species richness than the islands with small or no colonies. Imposing restrictions on tourist visitation to at least three islands (Zamogoj, Khubyn and Khunuk) is a feasible way to conserve substantial part of regional biodiversity.

Introduction

Lake Baikal is unique in many characteristics, including its size, location, quality of water, and geological history (Moore *et al*. 2009). When it was included in the World Heritage list, the need for the research and monitoring activities of the lake was specifically stressed by the International Union for Conservation of Nature (UNEP 2006). Still, we were unable to locate any recent study exploring spatial patterns and temporal changes in plant communities near the Baikal shoreline, although regional diversity of vascular plants is reasonably well documented (Zarubin *et al*. 2005, Chepinoga *et al*. 2008).

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Island ecosystems are favourite objects of ecological research due to their unique biological features (Whittaker 2007). First data on vegetation of Olkhon Island, the largest of Lake Baikal islands, were collected in 18th century (Galazii and Molozhnikov 1982). Ushkanji Islands were first explored by botanists in 1914 (Sukachev and Poplavskaya 1914), and several of Maloe More islands — only in 1978 (Petrochenko 1987). To our knowledge, flora of the remaining islands (different sources list 6 to 47 islands in Lake Baikal; Gusev 1974) have not been explored.

Pollution is generally seen as the largest threat to biodiversity of Lake Baikal and its

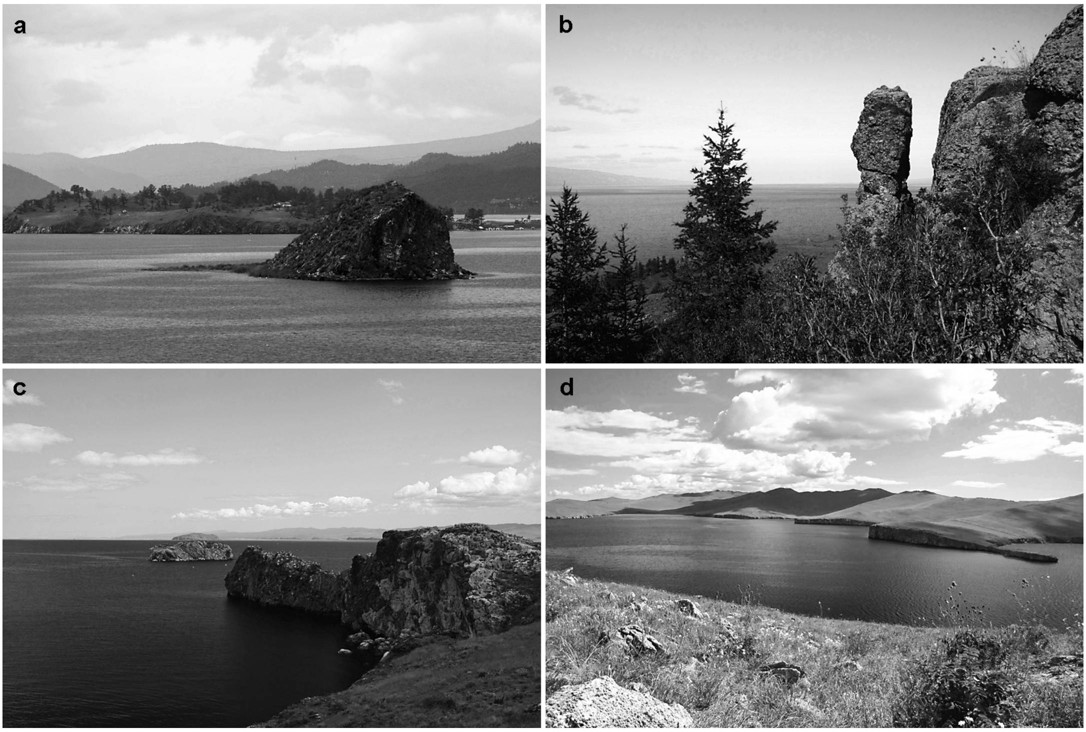

Fig. 1. Landscapes of Lake Baikal islands: (**a**) Malyi Tojnak Island, (**b**) northern part of Zamogoj Island, (**c**) gull colony on the eastern part of Oltrek Island and view on Borga-Dagan Island, and (**d**) semi-arid plant community on the southern part of Zamogoj Island.

watershed (Sansom 2004, Moore *et al*. 2009). The most acute problems are associated with the pulp and paper mill in Baikalsk (Tretyakova and Bazhina 2000, Voinikov *et al*. 2008) and with contamination of the Selenga river flowing into Baikal (Khazheeva *et al*. 2008). However, rapidly increasing tourism (from nearly 50 000 visitors in 2000 to nearly 250 000 in 2004; Rosabal and Debonnet 2005) has been imposing substantial pressure on terrestrial ecosystems. This in particular concerns the shores of the Maloe More area, a shallow part of Lake Baikal between its northwestern shore and Olkhon Island, which hosts the largest number of natural objects determining the recreational value of the region.

Untouched and pristine nature is the principal tourist attraction of Lake Baikal. Islands of the Maloe More area (Figs. 1 and 2) are located close to the mainland, and are perceived by the visitors as natural beauties. However at present, tourism activities are implemented in a disorganised and uncontrolled way, thus creating problems of disturbance and pollution and often damaging important natural areas (Rosabal and Debonnet 2005, Markova *et al*. 2008). In 2005–2006 more than 70 localities were used for tourism, totalling about 700 ha impacted by housing and beach activities (Romanova 2007). Vegetation along several dozens of kilometres of the shoreline is severely disturbed (Markova *et al*. 2008, and pers. obs.).

The primary goals of our study were to document spatial patterns in diversity of vascular plants, explore effects of natural (bird colonies) and human-induced (tourism) disturbances on richness of semi-desert and steppe-desert plant communities of 12 islands and 4 peninsulas, and estimate species turnover on a subset of five islands within a 30-year period. We use our results to assess the conservation value of Maloe More islands and to develop recommendations for protection of regional biodiversity.

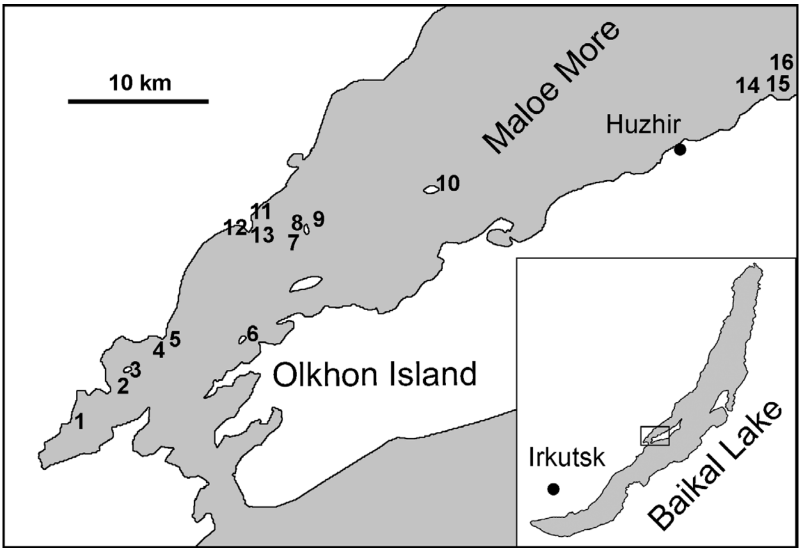

Fig. 2. The map of the study area. 1 = Tojnak Island, 2 = Malyi Tojnak Island, 3 = Bolshoi Tojnak Island, 4 = Khunuk Island, 5 = Sarminskaya Peninsula, 6 = Khubyn Island, 7 = Shara-Dagan Island, 8 = Oltrek Island, 9 = Borga-Dagan Island, 10 = Zamogoj Island, 11 = Ujuga Peninsula, 12 = Nameless Peninsula, 13 = Nameless Peninsula, 14 = Kharantsy Island, 15 = Modoto Island, 16 = Edor Island. Insert: position of the study area within Lake Baikal.

Material and methods

Study area

Lake Baikal is located in southern Siberia. The study region (Fig. 2), situated within an area of approximately 53°02´–53°15´N and 106°45´–107°27´E, belongs to the Irkutsk Oblast of Russia. Maloe More is about 70 km in length and covers about 800 km^2 between the mainland and Olkhon Island (the largest island of Lake Baikal). This area includes 13 rocky islands and two alluvial islands. In this paper, we use transliterations of Russian geographical names from the most detailed map available to us (East Siberian Aerial Land-Surveying Enterprise 2007).

Climate of the Maloe More region is arid, with annual precipitation of 230 mm or less. Annual temperature is –1.2 °C; frost-free period lasts 110–127 days. This climate is typical for dry steppe regions. Additionally, small islands are exposed to strong winds, up to 40 m s^{-1} in autumn (Ladeishchikov 1977). Consistently with low level of precipitation and strong wind impact, islands of Maloe More area are treeless (except for Zamogoj Island; Fig. 1b); dominant plant communities (Fig. 1d) are classified as various kinds of steppes (Petrochenko 1987). Both 1979 (the year when Yu. N. Petrochenko conducted his surveys) and 2009 (when we surveyed the islands) were slightly warmer than average.

Plant sampling

We visited the study area on 31 July–3 August 2009. Surveys of vascular plants were conducted simultaneously by all of us (four persons). On small islands and on all peninsulas sampling was discontinued individually by each collector when she/he decided that the chances of locating previously unrecorded species were minor. In practice, we attempted to stop searching when no new species were recorded during the last 5 minutes. However, practical constrains forced us to allocate fixed time for surveying the largest islands (Khubyn, Oltrek, and Zamogoj); for sampling effort (person-hours of work) *see* Table 1.

One of us (VVC, the expert in regional flora) recorded common species using pre-printed forms, and collected only those specimens, identification of which required laboratory investigation. Three other collectors sampled aboveground parts of each species seen on their way; these samples were identified by VVC on the day of collection. Species found by each collector were recorded separately. Materials collected in the course of this work are deposited in the Herbarium of the Irkutsk State University (IRKU). Plant nomenclature follows Chepinoga *et al*. (2008); plant attribution to endangered or ruderal species follows Zarubin (2001) and Chepinoga *et al*. (2008), respectively.

Table 1. Characteristics of study areas, sampling efforts, and observed and estimated species richness of vascular plants.

Characteristics of study areas								Impact scores[f]		Sampling effort (person-hours)	No. of samples	Sample characteristics[g]				Estimated species richness[h]	
No.	Name	Type[a]	Lat. N[b]	Long. E[b]	Max. elevation (m)[c]	Area (m²)	Distance (km)[e]	Recreation	Birds			T	S_{obs}	Q_1	Q_2	S_{jack}	S_{chao}
1	Tojnak	Is	53°02´02´´	106°46´02´´	[20]	6120	0.30	0.50	0	3.0	4	165	64	19	9	85	79
2	Malyi Tojnak	Is	53°04´24´´	106°49´38´´	[15]	6575	0.86	0.25	0.25	3.0	4	160	53	8	5	61	58
3	Bolshoi Tojnak	Is	53°04´40´´	106°50´05´´	12	65150	1.45	0.50	0.50	4.0	4	198	80	24	18	104	92
4	Khunuk	Is	53°05´11´´	106°51´39´´	1.2	6110	1.00	0.50	0.25	2.0	4	181	70	16	17	84	76
5	Sarminskaya Kosa	Pns	53°05´39´´	106°52´04´´	0.7	5260	0	0.25	0.25	2.0	4	157	55	13	7	69	64
6	Khubyn	Is	53°05´48´´	106°56´31´´	33	87110	0.34	0	0.25	4.0	4	240	89	21	18	109	98
7	Shara-Dagan	Is	53°09´07´´	106°58´09´´	[15]	4255/100[d]	0.67	0	1.75	0.2	1	9	9	9	0	–	–
8	Oltrek	Is	53°09´37´´	106°59´21´´	35	134500	1.35	0.75	0.25	5.7	4	335	141	45	25	189	171
9	Borga-Dagan	Is	53°09´46´´	106°59´59´´	[15]	5020	1.49	0	2	0.5	3	29	13	3	4	15	14
10	Zamogoj	Is	53°10´38´´	107°06´26´´	77	490100	2.63	0.25	0.25	8.0	4	385	143	37	26	181	163
11	Mys Ujuga	Pns	53°09´11´´	106°57´32´´	[20]	14455	0	2	0.25	2.0	4	226	98	33	24	131	115
12	Nameless	Pns	53°09´24´´	106°56´57´´	1.5	20	0	0	0	0.1	1	20	20	20	0	–	–
13	Nameless	Pns	53°08´59´´	106°56´24´´	[5]	2095	0	1.75	0	2.0	4	173	70	17	23	84	75
14	Kharantsy	Is	53°14´04´´	107°24´31´´	12	42800	0.17	0.75	1	3.0	4	205	83	27	16	111	100
15	Modoto	Is	53°14´09´´	107°26´26´´	5	1655	0.27	0	0.75	1.0	4	71	28	9	5	38	34
16	Edor	Is	53°14´41´´	107°26´39´´	[20]	3240/2000[d]	0.96	0	2	1.0	4	37	12	3	0	16	15

[a] Types of sampled areas: Is = island; Pns = peninsula. [b] Geographical co-ordinates refer to central parts of the sampled areas. [c] Height data in brackets are based on visual estimation. [d] total area of an island/surveyed part of an island. [e] The shortest distance between the island and mainland shorelines. [f] Means of four observations (consult the text). [g] T = total number of incidences (i.e., sums of species' records across all samples), S_{obs} = observed species richness (all samples pooled), Q_1 = the number of species found in one sample only, Q_2 = the number of species found in two samples only. [h] S_{jack} = calculated by jackknife method, S_{chao} = calculated by Chao2 method.

Collection of additional information

Areas of islands and of the investigated parts of peninsulas (Table 1) were determined either from space photographs (available at GoogleEarth) or from measurements conducted during fieldwork (small islands and peninsulas: nos. 4, 5, 11, 12 and 13 in Table 1). Impacts of tourism and colonies of herring gull (*Larus argentatus* Pontoppidan) on sampling areas were estimated by averaging scores given individually by each of four observers. Tourism and recreational activities: 0 = no visible traces of visitation; 1 = rubbish or other signs of visitation were occasionally seen; 2 = trampled vegetation, paths, scrap-heaps and bonfire places frequent across the island/peninsula. Bird colonies: 0 = absent; 1 = present but affecting minor part of island/peninsula; 2 = affecting more than a half of island/peninsula.

Data analyses

Both species numbers and the sampled areas were log-transformed prior the regression analysis. Effects of isolation (islands *vs*. peninsula), recreation (low *vs*. high), and colonial birds (low *vs*. high) on floristic diversity were tested by ANCOVA using sampled area as a covariate (SAS Institute 2009). Breakpoint regression was calculated using Excel macros developed by Lomolino and Weiser (2001).

Species lists were analysed with Integrated Botanical Information System (Zverev 2007); indicatory values for soil fertility and moisture characteristics were calculated using ecological scales of south-Siberian plant species (after Korolyuk 2006). Similarities in species composition between study areas were described using the Jaccard index, i.e., the number of common species divided by the total number of species recorded at both sites. A dendrogramm was constructed using Statistica for Windows with WPGMA algorithm (Weighted Pair Group using Arithmetic Averages).

Changes in overall species richness and species turnover during the past 30 years were explored for five islands by comparing our species lists with the lists based on surveys of 1979 (Klimina 1980, Petrochenko 1987). Absolute (TA) and relative (TR) turnover rates were calculated using the following formulae (Panitsa *et al*. 2008):

$$TA = (I + E)/2t,$$
$$TR = [(I + E)/t(S_{1979} + S_{2009})] \times 100,$$

where t is the period between censuses (i.e., 30 years in our case), E is the number of species observed only in 1979 (i.e., extinct between 1979 and 2009), I is the number of species observed only in 2009, S_{1979} and S_{2009} are the total numbers of species recorded in 1979 and 2009, respectively. Numbers of species recorded in 1979 and 2009 were compared using a paired *t*-test (SAS Institute 2009).

Overall (i.e., expected) species richness was calculated from the numbers of species recorded by one of four observers only (‘singletons’, Q1 in Table 1), and by two of four observers (‘doubletons’, Q2). To estimate the numbers of yet undiscovered species we employed the Chao2 and jackknife methods, which showed the best performance in several comparative studies (Walther and Morand 1998, King and Porter 2005).

Variables whose distributions did not fulfill the normality assumption were analysed by nonparametric tests, including Spearman’s rank correlation (r_S) and a Kruskal-Wallis test (SAS corr and npar1way procedures, respectively; SAS Institute 2009).

Results

Diversity of vascular plants

We recorded 269 species of vascular plants (*see* Appendix). Species richness adjusted for sampling areas did not differ between islands and peninsulas (Table 2).

Numbers of recorded species (Table 1) ranged from 9 (Shara-Dagan Island) to 143 (Zamogoj Island). *Elymus sibiricus* was found in all 16 study areas; 76 species were each recorded a the single study area. The highest proportions of these ‘unique’ species were found on Khunuk Island (15.7% of the entire species list) and Zamogoj Island (12.6%).

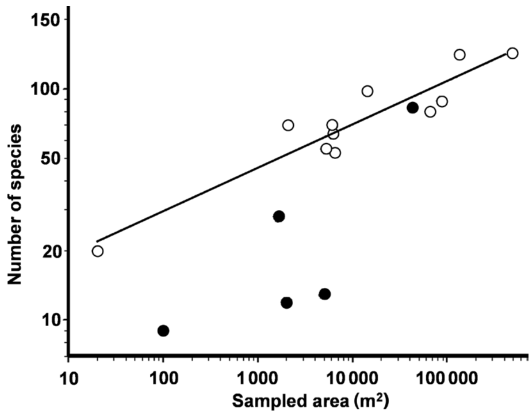

Fig. 3. Relationship between the observed number of species (*S*) and area (*A*) of the surveyed territory. Filled circles = islands with high impacts of colonial birds; empty circles = islands/peninsulas with low or no impacts of colonial birds. Regression is based on data from islands/peninsulas with low or no impacts of colonial birds: $\log S = 2.52\ (\pm 0.22) + 0.188\ (\pm 0.023) \times \log A$; $r^2 = 0.88$, $p < 0.0001$.

Areas with large bird colonies had significantly smaller species richness than areas with small or no colonies (Table 2; least square means adjusted for island areas: 28 and 65 species, respectively). The current impact of tourism and recreational activities did not cause detectable changes in plant diversity (Table 2).

The breakpoint model fitted the entire data set (Fig. 3) slightly better than the log-log linear model ($r^2 = 0.654$ and 0.609, respectively). However, when islands heavily affected by colonial birds were excluded from the analysis, the species-area relationship was better described by the log-log model (Fig. 3). Accounting for the distance to the mainland did not improve the model (data not shown).

The jackknife estimation method generally predicted higher values of species richness (127% of the observed species number) than the Chao2 method (116%). The ratio between the predicted and observed numbers of species did not differ between islands where we allocated a fixed time for the surveys and where surveys were continued until discoveries of new species became very infrequent (ANOVA, jackknife: $F_{1,12} = 0.03$, $p = 0.87$; Chao2: $F_{1,12} = 0.01$, $p = 0.91$). This ratio also did not depend on the sampled area (jackknife: $r = 0.14$, $n = 14$, $p = 0.62$; Chao2: $r = -0.01$, $n = 14$, $p = 0.97$). Consistently, the slopes of the log-log species-area regressions did not differ between the observed species richness and the two estimates of the expected numbers of species (ANCOVA: $F_{2,38} = 0.14$, $p = 0.87$).

Similarities between sampled areas

WPGMA dendrogramm revealed an isolated position of Shara-Dagan and Modoto Islands, and identified (at the similarity level 0.25) three main clusters (Fig. 4). The first cluster included small rocky islands (Borga-Dagan and Edor) and a nameless stony peninsula. Species-poor (9 to 28 species) floras of these rocky habitats, two of which are heavily affected by colonial birds, have high indicator values for soil fertility and

Table 2. Effects of isolation, tourism, and bird colonies on diversity of vascular plants (ANCOVA, log-transformed values, type III sums of squares). For characteristics of the sampled areas *see* Table 1.

Classificatory variable	Source	df	Mean square	*F*	*p*
Isolation	Isolation (islands *vs*. peninsulas)	1	0.533	1.72	0.21
	Area (= covariate)	1	5.370	17.33	0.0013
	Isolation × Area	1	0.262	0.84	0.38
	Error	14	0.310	–	–
Birds colonies	Birds (high *vs*. low impact)	1	0.931	7.44	0.02
	Area (= covariate)	1	4.037	32.25	0.0001
	Birds × Area	1	0.301	2.41	0.15
	Error	14	0.125	–	–
Tourism	Tourism (high *vs*. low impact)	1	0.020	1.74	0.23
	Area (= covariate)	1	0.948	81.01	< 0.0001
	Tourism × Area	1	0.002	0.17	0.69
	Error	9	0.012	–	–

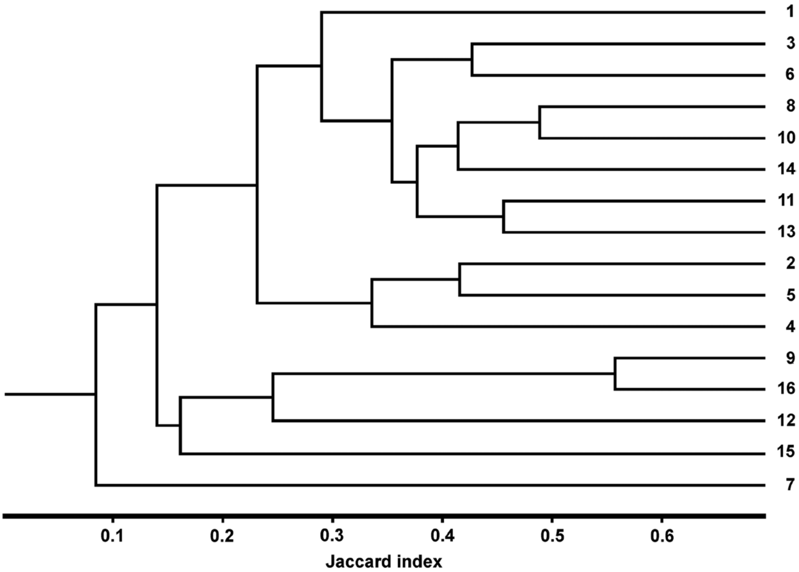

Fig. 4. Floristic similarities between sampled areas. For names of islands and peninsulas, *see* Fig. 2.

low indicator values for moisture (Fig. 5).

The largest cluster included six islands and two peninsulas with high diversity of habitats and high (64–143) numbers of recorded species (Fig. 4). In terms of ecological requirements, these floras are very similar to each other, demonstrating moderate indicator values for both soil fertility and moisture (Fig. 5).

The final cluster, consisting of two small islands (Toinak and Khunuk) and one peninsula (Sarminskaya Kosa) (Fig. 4), combines floras with moderate numbers of species (53–70) which have the lowest requirements for soil fertility combined with the highest indicator values for moisture (Fig. 5).

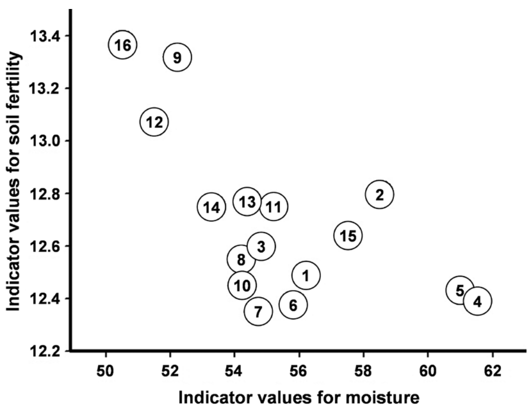

Fig. 5. Ordination of sampled areas by indicator values for soil fertility and moisture. For names of islands and peninsulas, *see* Fig. 2.

Species turnover

A total of 284 species were recorded on a subset of five islands that were surveyed in both 1979 and 2009 (Table 3). Among these, 228 were found in 1979 (Petrochenko 1987), 237 in 2009 (Appendix), and 181 were common for both surveys. We found no differences in species richness between the surveys (paired *t*-test: $t_4 = 1.81$, $p = 0.15$).

Mean absolute turnover rate was 1.06 species per year, and mean relative turnover rate was 1.17% of species per year, i.e., 35% mean species change between the subsequent observations. Absolute turnover was independent of islands area ($r_S = -0.10$, $n = 5$ islands, $p = 0.87$), whereas relative turnover decreased with increase in island size ($r_S = -1.00$, $n = 5$ islands, $p < 0.0001$). Comparisons of species' lists from 1979 and 2009 did not reveal any differences in indicator values for soil fertility and moisture ($p > 0.10$).

Protected and ruderal species

We recorded five locally protected species: *Stipa* *glareosa* (in 3 study areas), *Oxytropis popoviana* (in 3 areas), *O. tragacanthoides* (in 2 areas), *Deschampsia turczaninowii* (in 12 areas), and *Lilium pumilum* (in 2 areas). All these species were present on Zamogoj Island; none was found on Tojnak, Khunuk, Shara-Dagan and Modoto Islands; all other areas included 1–3 species. Incidences of these species (i.e., the numbers of areas in which they were recorded) did not differ from incidences of all other (non-protected) species (Kruskal-Wallis test: $\chi^2_1 = 0.24$, $p = 0.63$). The median proportion of protected species (6%) among plants that have disappeared from island floras between 1979 and 2009 was higher than among immigrants (0%), but the differences were far from the significance level ($\chi^2_1 = 0.65$, $p = 0.42$).

We recorded 37 species classified as ruderal. Proportions of ruderal species varied from 4% (Kharantsy Island) to 31% (Sarminskaya Peninsula); they peaked in medium-sized study areas and showed no relationships with either recreational loads ($r_S = -0.33$, $n = 16$, $p = 0.21$) or impacts imposed by bird colonies ($r_S = 0.23$, $n = 16$, $p = 0.39$), or distance to the nearest shore ($r_S = -0.07$, $n = 16$, $p = 0.81$). Incidences of ruderal species did not differ from incidences of all other (non-ruderal) species (Kruskal-Wallis test: $\chi^2_1 = 0.15$, $p = 0.70$). Proportion of ruderal species among immigrants was twice higher than among species that disappeared from island floras between 1979 and 2009 (13%–26% and 0%–15%, respectively; Kruskal-Wallis test: $\chi^2_1 = 5.34$, $p = 0.02$).

Discussion

Observed and estimated species richness

It is only rarely possible to enumerate all the species present in the study area, even for vascular plants (Connor and Simberloff 1978, Gilbert and Lee 1980, Herwitz *et al*. 1996). Along with low occurrence of some species, constrained sampling effort unavoidably leads to the incompleteness of species' lists. Since the number of recorded species increases with both sampling effort and the sampled area, uneven sampling efforts may distort conclusions concerning species–area relationships (Preston 1979, Cam *et al*. 2002b).

Ecological studies commonly use three types of methods to estimate total species richness: fitting of species-abundance distributions, extrapolation of species accumulation curves, and non-parametric estimators (Walther and Morand 1998). The use of the first method for plants is hampered by practical impossibility to accurately quantify abundances of individual species. The second method requires an objective measurement of sampling effort. While the number of collected specimens is commonly used for animals (Kozlov 1997, Willott 2001, Mauffrey *et al*. 2007), this measure is hardly applicable to field surveys of vascular plants. The use of collecting time is also questionable, because of both collector's personality and unavoidable uncontrolled variation in working efficiency. Therefore the only practical choice is to use non-parametric estimation methods.

Table 3. Species turnover between 1979 and 2009.

Island		Species richness			Turnover			
No.	Name	S_{1979}	S_{2009}	S_{pool}	*I*	*E*	TA	TR
3	Bolshoi Tojnak	89	80	120	31	40	1.183	1.400
4	Khunuk	59	70	97	38	27	1.083	1.679
6	Khubyn	63	89	102	39	13	0.867	1.141
8	Oltrek	123	141	169	46	28	1.233	0.934
10	Zamogoj	136	143	168	32	25	0.950	0.681

Species richness: S_{1979} = in 1979 (Petrochenko 1987), S_{2009} = in 2009 (this study), S_{pool} = both censuses pooled. Turnover: *E* = number of extinct species (i.e., species observed only in 1979), *I* = number of immigrants (i.e., species observed only in 2009), TA = absolute turnover, TR = relative turnover (see text for the formulae).

The jackknife method (in agreement with conclusions by Walther and Morand 1998) predicted on average 10% higher values of species richness than the Chao2 method; these two estimates can be seen as the boundaries between which the actual value of species richness lies (Chiarucci *et al*. 2003). Therefore, we conclude that the completeness of our inventories ranged from 77% to 89% of the potential species richness, which is very close to published estimates for ants collected by pitfall traps (71%–90%; King and Porter 2005) and for point counts of birds (79%–100%; Cam *et al*. 2002a).

Chiarucci *et al*. (2003) concluded that at least 15%–30% of the total area needed to be sampled to obtain reasonable estimates of total species richness. During our surveys, we walked with an average speed 2 km h^{-1} and recorded plants within an approximately 4-m-wide area. With the applied effort (Table 1) we surveyed 13% to 100% of the areas designed for sampling. Allocation of the fixed time to three largest islands and, consequently, relatively low coverage of these islands by the surveying routes (13%–37%) did not decrease completeness of our surveys. Therefore, we conclude that when sampling is not random but driven by 'botanist's internal algorithm' (intuition) this coverage was still sufficient to avoid underestimation which is seen as the basic problem of field surveys that cover only minor part of the total study area (Chiarucci *et al*. 2003).

Impacts of colonial birds on local floras

Herring gull is the most common bird nesting on the Maloe More islands. Island colonies of this species totaled about 500 nests in the early 1970s (Litvinov 1979); surveys of 1977–1984 revealed 2850–3825 gulls (Skryabin and Pyzh'yanov 1987), and since then the number of nesting gulls has steadily increased (Pyzh'yanov 1997). However, since no recent data are available, we chose to use a subjective rank of bird impact on our study areas. Importantly, our estimates were generally consistent ($r_S = 0.59$, $n = 11$ islands, $p = 0.06$) with bird numbers recorded in 1977–1984 (after Skryabin and Pyzh'yanov 1987), confirming stability of bird colonies over a long period of time.

Impacts of colonial birds on vegetation are documented for maritime islands of different regions. Large bird colonies are usually surrounded by specific plant communities, which consist of a few species that are able not only to sustain heavy nitrogen and phosphorous loading, but even benefit from it (Luther 1961, Sobey and Kenworthy 1979, Glazkova 2009, and references therein). Vegatation of small islands hosting large bird colonies is extremely degraded (Gillham 1953, Zelenskaya and Khoreva 2006).

Consistently with these observations, we found more than two-fold decrease in overall species richness on islands with large gull colonies. However, no plant species was found exclusively on these islands, although their floras consisted of plants with low-moisture and high soil-fertility requirements (Fig. 5). An isolated position of Shara-Dagan Island on the dendrogramm (Fig. 4) is explained by the absence of information on plants growing on the upper part of this rock, which was impossible to reach without alpinist skills. Vegetation of the surveyed stony parts at the bottom of this rock was less nitrofilous than on Borga-Dagan, Edor, and Modoto Islands (Fig. 5), in spite of the presence of large gull colony on Shara-Dagan Island (Table 1).

Species–area relationships

Although hundreds of studies fitted the relationship between the number of species and the area of an island (or island-like fragment) with the power-law function (reviewed by Drakare *et al*. 2006), its generality has frequently been questioned. In particular, it has been suggested that the power law adequately describes species accumulation only in medium-sized to large islands and fragments, while on small islands richness may vary independently of island area (a phenomenon called the Small Island Effect). This hypothesis dates back to the 1960s and was extensively debated in the past (Woodroffe 1986); the recent review by Lomolino and Weiser (2001) renewed interest in it.

Lomolino (2000) explained the low number of data sets that demonstrated small island effect by low frequency of studies involving smallest islands and fragments, and called for collecting additional data. Since our study also covered very small and isolated habitats (Table 1), we fitted our data with both linear and breakpoint regression models. In agreement with many earlier studies (e.g., Woodroffe 1986, Heatwole 1991, Fridley *et al.* 2005, Panitsa *et al.* 2006), we failed to detect the small island effect in our data set.

The slope of the power-law function fitting our data (z = 0.188) lies within the 95% confidence limits (0.13–0.23) calculated from several dozens of studies that used independent (i.e., not nested) sampling scheme in non-forested terrestrial habitats (Drakare *et al.* 2006).

Species turnover

The dynamics of the insular floras and faunas forms the core of the equilibrium theory of island biogeography (MacArthur and Wilson 1967). Many researchers attempted to estimate turnover rates (reviewed by Panitsa *et al.* 2008); however, the measured values were always approximations of real values due to unavoidable confounding effects of cryptoturnover (undetected turnover, when both extinction and colonisation by the same species occurred between the observations) and pseudoturnover (when species present on the island have not been detected during one of two censuses). Under these circumstances, accumulation of data on turnover rates in different biomes during different periods of time is critically needed to allow identification of both general patterns and sources of variation in the balance between local extinction and colonisation processes.

Yu. N. Petrochenko (pers. comm.) informed us that his team visited each island several times, and that surveys of larger islands lasted for several days. This clearly exceeded our own sampling effort and, therefore, we have the reasons to believe that the completeness of the first floristic inventory (in 1979) was at least not worse than the completeness of the second one (in 2009). This conclusion is indirectly supported by an overall similarity in the numbers of species recorded during these two surveys. At the same time, species lists of 1979 and 2009 demonstrated substantial differences: an average overlap was only 49% of the pooled lists (Table 3).

If we hypothesise that the larger part of differences between the surveys was due to incompleteness of the data collected in 2009, then the highest differences should be associated with the largest islands. However, our data yielded the opposite pattern: the highest turnover was found on the smallest island, flora of which was obviously revealed more completely than floras of the largest islands. This result agrees with the pattern observed in Kem-Lud archipelago (Shipunov and Abramova 2006) and fits the predictions of the equilibrium theory, according to which maximum turnover rates are expected in small islands (MacArthur and Wilson 1967). Thus, we conclude that species' lists of 1979 and 2009 are of about the same completeness, and that the differences between these lists are likely to result from species turnover rather than from methodological shortcomings.

The relative turnover rates found for our islands (0.681% to 1.679% of species per year) fit well the ranges reported for other islands (Panitsa *et al.* 2008, and references therein). However, in contrast to observations by Panitsa *et al.* (2008), we detected an obvious trend in species' composition. Although changes were random in terms of ecological requirements of plant species, proportions of ruderal species in local floras doubled (from 6.9% to 11.2%) during the past 30 years. Ruderalisation can be seen as the first indication of the increasing disturbance of island vegetation, in particular due to creation of paths crossing steppe communities. These paths enhance the spread of the opportunistic species and might be a threat for conserving native flora (Godefroid and Koedam 2004). On the other hand, climate warming in the study region (Moore *et al.* 2006) may increase the risk of establishment of ruderal species.

Conservation of local floras

Baikal region in Russia is now experiencing an increasing environmental pressure from mass tourism, which is an important socioeconomic factor of regional development. Visitors to Baikal mostly enjoy camping, fishing, beach activities, walking and viewing picturesque scenery. Eco-tourism is rare, possibly due to absence of a charismatic flagship species, and ecologically ignorant tourists seeking seclusion and relaxation contribute to degradation of landscapes and floristic impoverishment (Kovtonyuk *et al*. 2003, Kas'yanova 2007, Vin'kovskaya 2007). These processes increase the importance of conservation of the Lake Baikal islands, which have so far experienced much lower human pressure than the mainland habitats near the shoreline.

Semi-desert and steppe-desert plant communities of the Maloe More islands include a number of relicts (e.g., *Stipa glareosa* and *Oxytropis tragacanthoides*), steppe species at the northern borders of their distribution limits (e.g., *Filifolium sibiricum* and *Allium burjaticum*), and other endangered and locally protected species (Appendix). The islands remain one of few habitats which secure persistence of regional endemics, such as *Deschampsia turczaninowii*, *Festuca rubra* subsp. *baicalensis*, *Oxytropis popoviana*, and *Artemisia ledebouriana*, and of locally rare species (e.g., *Thymus pavlovii* and *Asplenium altajense*), generally suffering from an increase of recreational impact on the shoreline habitats of Baikal. Imposing restrictions on tourist visitation to at least three islands (in the order of decreasing importance: Zamogoj, Khubyn and Khunuk) is a feasible way to conserve substantial part of local biodiversity and to allow long-term monitoring of climatic effects on structure and dynamics of steppe plant communities at the northern limit of the semi-arid landscapes in northern Asia.

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Appendix. Presence of vascular plants in sampled areas in 2009.

Plant species	Species category	Islands/peninsulas*															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Achnatherum sibiricum		+					+		+		+			+			
Aconogonon alpinum					+	+	+		+		+	+		+	+		
A. angustifolium		+	+	+	+	+	+		+		+	+	+	+	+		
A. ochreatum											+						
Agropyron cristatum		+	+	+			+	+	+	+	+	+		+	+		+
Agrostis trinii		+		+			+					+		+			
Aizopsis aizoon		+	+	+	+	+	+		+		+						
Aleuritopteris argentea											+						
Allium burjaticum					+						+				+		
A. ramosum									+						+		
A. senescens									+		+						
A. splendens		+		+					+		+	+			+		
A. stellerianum				+							+				+		
A. tenuissimum							+		+		+	+		+	+		
Alyssum lenense							+		+		+						
Amblynotus rupestris									+		+						
Amethystea caerulea											+						
Androsace incana				+					+		+				+		
A. lactiflora						+			+			+					
Anemone dichotoma		+	+														
Arabis pendula						+											
Arctopoa subfastigiata	ruderal								+			+					
Artemisia commutata		+	+	+			+	+	+	+	+	+	+	+	+		
A. dolosa											+	+	+	+	+		+
A. dracunculus			+		+		+		+		+						
A. frigida		+	+	+					+		+	+	+	+	+		
A. gmelinii		+	+				+				+						
A. laciniata				+			+		+						+		
A. ledebouriana											+		+	+			
A. leucophylla				+		+	+	+	+								
A. mongolica			+	+	+	+	+	+	+	+	+	+		+	+	+	

Continued

Appendix. Continued.

Plant species	Species category	Islands/peninsulas															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A. monostachya		+					+										
A. pubescens								+	+	+							
A. sericea				+							+						
A. vulgaris	ruderal		+	+	+	+	+		+	+		+		+	+	+	+
Asplenium altajense									+								
Aster alpinus s.l.					+		+		+		+	+			+		
Astragalus chorinensis									+								
A. inopinatus				+			+		+		+	+			+		
A. lupulinus									+		+	+					
A. suffruticosus											+				+		
A. versicolor				+			+		+		+	+		+	+		
Atragene speciosa											+						
Axyris amaranthoides	ruderal								+								
A. hybrida	ruderal			+								+					
Barbarea sp.	ruderal	+															
Betula pendula									+			+					
B. platyphylla									+		+	+		+		+	
Bistorta attenuata				+					+		+	+		+	+		
B. vivipara									+		+						
Bromopsis inermis									+		+	+					
B. korotkiji											+				+		
B. sibirica									+						+		
Bupleurum bicaule				+			+		+		+	+		+	+		
B. scorzonerifolium				+			+		+		+				+		
Calamagrostis epigeios							+				+						
C. langsdorffii		+	+	+	+	+	+										
Callitriche palustris					+												
Campanula rotundifolia				+					+								
Carduus crispus	ruderal	+	+		+												
Carex appendiculata		+	+			+	+				+						
C. argunensis							+		+		+	+		+	+		
C. duriuscula															+		
C. korshinskyi				+			+		+		+						
C. nigra			+	+													
C. pediformis									+		+				+		
C. pseudocuraica					+												
C. rhynchophysa					+												
C. rostrata					+												
C. sajanensis			+						+								
Chamaenerion angustifolium	ruderal	+	+	+		+	+				+			+		+	
Chamaerhodos altaica							+		+		+	+		+			
C. erecta				+	+												
C. grandiflora		+							+		+	+		+			
Chenopodium album	ruderal	+	+	+	+	+	+		+	+	+	+	+	+		+	+
C. aristatum	ruderal										+						
C. hybridum				+													
C. novopokrovskianum	ruderal							+									
Chryzanthemum zawadskii				+					+		+	+		+	+		
Cirsium setosum	ruderal	+				+											
Clausia aprica									+								
Cleistogenes squarrosa				+													
Comarum palustre									+								
Corydalis impatiens					+	+			+								

Continued

Appendix. Continued.

Plant species	Species category	Islands/peninsulas															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cotoneaster melanocarpus				+					+		+						
Critesion brevisubulatum												+			+		
Cystopteris fragilis											+						
Dasiphora fruticosa						+					+						
Dasystephana decumbens											+	+					
Delphinium grandiflorum									+		+				+		
Deschampsia turczaninowii	protected		+	+		+	+		+	+	+	+	+	+	+		+
Dianthus versicolor				+			+				+						
Dontostemon integrifolius											+	+					
D. pinnatifidus					+							+					
Dracocephalum nutans	ruderal										+						
D. olchonense											+						
D. pinnatum									+			+	+				
Duschekia fruticosa							+										
Elymus sibiricus		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Elytrigia repens			+		+				+	+	+	+			+	+	+
Ephedra monosperma		+	+				+		+		+	+		+			+
Epilobium palustre												+					
Equisetum arvense		+				+					+						
Eremogone meyeri		+		+	+		+		+		+	+		+	+		
Erysimum cheiranthoides	ruderal	+	+		+	+						+					
E. hieracifolium	ruderal				+												
Euphrasia pectinata									+			+					
Fallopia convolvulus	ruderal			+	+	+											
Ferulopsis hystrix							+		+		+			+			
Festuca lenensis		+		+			+		+		+	+	+	+	+		
F. ovina											+				+		
F. rubra ssp. *rubra*									+								
F. rubra ssp. *baicalensis*									+						+		
F. sibirica							+		+		+						
Filifolium sibiricum											+						
Fornicium uniflorum							+		+		+						
Galeopsis bifida	ruderal	+	+		+	+			+			+					
Galium aparine	ruderal		+			+											
G. uliginosum					+												
G. verum		+	+	+		+	+		+		+	+	+	+	+		
Geranium pratense									+							+	
G. sibiricum	ruderal		+		+	+			+		+	+				+	
Goniolimon speciosum									+								
Gypsophila patrinii									+		+						
Hedysarum gmelinii ssp. *setigerum*									+								
Helictotrichon altaicum											+						
H. hookeri ssp. *schellianum*									+		+						
Heteropappus altaicus		+							+						+		
H. biennis							+				+	+			+		
Hierochloe glabra							+										
Hylotelephium triphyllum				+	+	+				+							
Hypericum gebleri			+														
Iris humilis							+		+		+	+		+	+		
Isatis oblongata	ruderal	+	+	+	+	+					+	+		+			
Kitagawia baicalensis									+		+				+		
Kochia prostrata							+				+						
Koeleria cristata ssp. *cristata*				+					+		+				+		

Continued

Appendix. Continued.

Plant species	Species category	Islands/peninsulas															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
K. cristata ssp. *hirsutiflora*									+		+	+					
Lamium album		+			+				+								
Lappula redowskii					+											+	
Larix × *czekanowskii*				+					+		+						
Lathyrus pilosus		+															
Leontopodium leontopodioides											+						
Leonurus deminutus		+	+	+	+	+	+		+								
Lepidium apetalum	ruderal		+	+												+	
Leymus chinensis			+	+			+		+	+	+	+	+		+	+	+
Lilium pumilum	protected						+				+						
Linaria acutiloba					+	+									+		
L. buriatica		+			+						+				+		
Lupinaster pentaphyllus				+	+	+	+				+						
Lychnis sibirica											+				+		
Lycopodioides sanguinolenta		+							+		+	+		+			
L. siberica		+		+			+		+		+	+		+	+		
Minuartia stricta														+			
M. verna												+					
Mulgedium sibiricim		+	+	+	+	+	+										
Odontites vulgaris												+		+			
Orobanche caesia		+					+		+		+				+		
Orostachys spinosa		+	+	+	+		+		+	+	+	+	+	+	+		+
Oxytropis coerulea				+			+		+		+	+		+	+		
O. popoviana	protected								+		+	+					
O. tragacanthoides	protected								+		+						
O. turczaninovii									+		+	+		+	+		
Papaver nudicaule		+			+	+			+			+			+		
Parnassia palustris							+										
Patrinia rupestris				+			+				+				+		
P. sibirica				+					+		+	+					
Pedicularis rubens				+			+		+		+			+			
Persicaria amphibia		+	+		+	+			+								
P. hydropiper					+												
P. lapathifolia	ruderal		+	+	+	+								+			
Peucedanum puberulum												+					
Phalaroides arundinacea		+	+	+	+	+											
Phlojodicarpus sibiricus		+		+	+		+		+		+	+		+	+		
P. villosus							+										
Phlomis tuberosa									+			+					
Pinus sylvestris ssp. *kulundensis*											+						
Plantago depressa	ruderal											+	+				
P. media	ruderal											+		+			
Poa angustifolia			+	+	+	+	+		+		+	+	+		+	+	
P. attenuata		+	+	+	+		+	+	+		+	+	+	+	+	+	
P. palustris					+				+								
P. pratensis			+						+							+	
Polygala tenuifolia											+			+	+		
Polygonatum odoratum							+		+		+						
Polygonum aviculare s.l.	ruderal					+											
Populus tremula							+		+					+			
Potentilla acaulis									+			+					
P. acervata				+			+				+						
P. anserina	ruderal	+				+	+		+		+	+		+			

Continued

Appendix. Continued.

Plant species	Species category	Islands/peninsulas															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
P. arenosa									+								
P. bifurca		+	+	+		+			+		+	+		+	+	+	
P. conferta												+					
P. longifolia		+	+	+			+		+		+	+			+		
P. sericea		+		+	+		+		+		+	+		+	+		
P. tanacetifolia				+	+												
P. tergemina							+		+			+		+		+	
Ptilotrichum tenuifolium		+							+		+	+		+			
Puccinellia hauptiana	ruderal							+									
Pulsatilla patens s.l.											+						
P. tenuiloba									+		+			+			
P. turczaninovii		+		+	+		+		+		+	+		+	+		
Ranunculus propinquus						+			+			+					
Rheum rhabarbarum															+		
Rhinanthus serotinus			+			+											
Rhododendron dauricum											+						
Ribes nigrum												+					
Rorippa palustris					+	+											
Rosa acicularis	ruderal	+					+				+						
R. majalis		+															
Rumex acetosella	ruderal											+					
R. aquaticus					+												
R. thyrsiflorus						+			+			+					
Salix bebbiana																+	
S. dasyclados									+								
S. jenisseensis							+							+		+	
S. rhamnifolia									+								
S. rorida					+		+										
S. taraikensis				+	+		+		+		+		+	+	+	+	
S. viminalis							+										
Salsola collina	ruderal		+											+			
Sanguisorba officinalis				+	+	+	+		+		+	+		+	+	+	
Saussurea salicifolia									+								
S. schanginiana									+								
Saxifraga cernua															+		
S. spinulosa				+			+		+		+	+		+	+		
Scabiosa comosa				+										+			
Schizonepeta multifida		+		+							+						
Scorzonera austriaca									+		+						
S. glabra				+			+		+		+						
Scrophularia incisa					+	+			+			+		+			
Scutellaria scordiifolia		+	+		+	+	+		+		+	+			+		
Serratula centauroides							+		+		+				+		
Silene jeniseensis		+		+			+		+		+			+	+		
S. repens				+	+		+		+		+	+		+	+		
Sisymbrium heteromallum	ruderal										+						
Sium suave			+	+	+	+											
Smelowskia alba		+					+		+		+				+		
Sonchus arvensis	ruderal		+			+											
Sorbus sibirica												+					
Sphallerocarpus gracilis	ruderal				+												
Spiraea media		+		+			+		+		+						
Stachys aspera			+		+	+						+					

Continued

Appendix. Continued.

Plant species	Species category	Islands/peninsulas															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Stellaria cherleriae									+								
S. dichotoma		+	+	+		+	+		+		+	+	+	+	+		+
S. longifolia						+											
Stipa baicalensis		+							+		+	+		+	+		
S. glareosa	protected										+	+		+			
S. krylovii											+						
Taraxacum ceratophorum	ruderal		+		+	+			+					+		+	
T. dissectum					+											+	
T. mongolicum	ruderal		+	+	+	+	+		+		+	+		+	+	+	
Tephroseris integrifolia											+	+			+		
Thalictrum appendiculatum											+						
T. foetidum		+		+			+		+		+	+			+	+	
Thermopsis lanceolata ssp. *sibirica*															+		
Thlaspi arvense	ruderal				+												
Thymus baicalensis		+		+	+		+		+		+	+	+	+	+		
Urtica cannabina	ruderal	+	+	+					+	+	+	+			+	+	+
U. dioica	ruderal				+	+			+			+		+			
Utricularia intermedia					+												
Valeriana officinalis															+		
Veronica longifolia		+			+		+										
Vicia cracca			+		+	+	+		+		+			+	+	+	
V. nervata					+	+			+		+					+	
Vincetoxicum sibiricum											+						
Viola rupestris												+					
Youngia tenuifolia		+	+	+			+		+		+	+	+	+	+		

* Islands/peninsulas: 1 = Tojnak Island, 2 = Malyi Tojnak Island, 3 = Bolshoi Tojnak Island, 4 = Khunuk Island, 5 = Sarminskaya Peninsula, 6 = Khubyn Island, 7 = Shara-Dagan Island, 8 = Oltrek Island, 9 = Borga-Dagan Island, 10 = Zamogoj Island, 11 = Ujuga Peninsula, 12 = Nameless Peninsula, 13 = Nameless Peninsula, 14 = Kharantsy Island, 15 = Modoto Island, 16 = Edor Island. For coordinates and other characteristics, *see* Table 1.