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Biodiversity and biogeography of the islands of the Kuril Archipelago

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Abstract

Aim Based on seven consecutive seasons of biotic survey and inventory of the terrestrial and freshwater plants and animals of the 30 major islands of the Kuril Archipelago, a description of the biodiversity and an analysis of the biogeography of this previously little known part of the world are provided.

Location The Kuril Archipelago, a natural laboratory for investigations into the origin, subsequent evolution, and long-term maintenance of insular populations, forms the eastern boundary of the Okhotsk Sea, extending 1200 km between Hokkaido, Japan, and the Kamchatka Peninsula of Russia. A chain of more than 56 islands, the system is only slightly smaller than the Hawaiian Islands, covering an area of 15,600 km^2 and providing 2409 km of coastline.

Methods Collections of whole specimens of plants and animals, as well as tissue samples for future molecular studies, were made by teams of scientists from Russia, Japan, and the USA, averaging 34 people for each of the seven annual summer expeditions (1994–2000). Floral and faunal similarities between islands were evaluated by using Sorensen's coefficient of similarity. The similarity matrix resulting from pair-wise calculations was then subjected to UPGMA cluster analysis.

Results Despite the relatively small geographical area of all islands combined, the Kuril Island biota is characterized by unusually high taxonomic diversity, yet endemism is very low. An example of a non-relict biota, it originated from two primary sources: a southern source, the Asian mainland by way of Sakhalin and Hokkaido, and a northern source by way of Kamchatka. The contribution of the southern source biota to the species diversity of the Kurils was considerably greater than the northern one.

Main conclusion The Bussol Strait, lying between Urup and Simushir in the central Kurils, is the most significant biogeographical boundary within the Archipelago. Of lesser importance are two transitional zones, the De Vries Strait or 'Miyabe Line', which passes between Iturup and Urup in the southern Kurils, and the fourth Kuril Strait, between Onekotan and Paramushir in the northern Kurils.

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INTRODUCTION

The Kuril Archipelago is a chain of more than 56 islands, only slightly smaller than the Hawaiian Islands, covering an area of 15,600 km^2 and providing 2409 km of coastline (Fig. 1). Stretching 1200 km between Hokkaido, Japan, and the Kamchatka Peninsula of Russia (from 43° to 51°N latitude), the Kurils divide the Sea of Okhotsk from the Pacific Ocean and form the northern extension of an insular arc that originates in the Ryukyu and Mariana archipelagos to the south and continues as the Aleutian Islands to the north and east. It is composed of two main ridges: the Lesser Kuril Ridge and the Greater Kuril Ridge. The Lesser Kuril Ridge includes the Nemuro Peninsula of eastern Hokkaido, the Habomai Island group, and Shikotan, and continues to the northeast as the submarine Vityaz Ridge. The Greater Kuril Ridge includes the Shiretoko Peninsula of eastern Hokkaido, all of the remaining Kuril Islands, from Kunashir north to Shumshu, and the southern tip of the Kamchatka Peninsula.

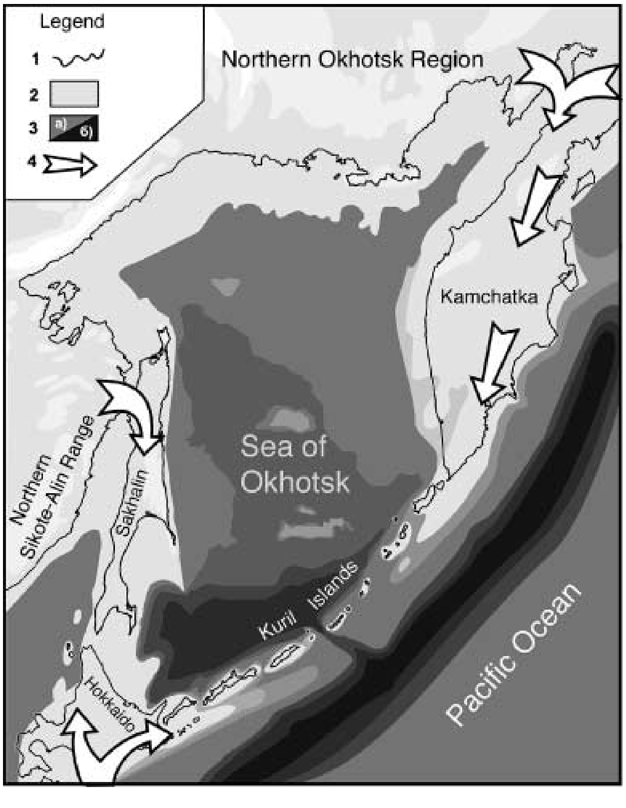

Figure 1 The sea of Okhotsk region in the Late Würm, *c.* 18,000–15,000 yr BP (after Bezverkhniy *et al.*, 2002). 1, recent coastline; 2, the Late Würm coastline; 3, sea regions [(a) shallow, (b) deepwater]; 4, pathways of biotic immigration from southern and northern source areas.

All of the Kurils are volcanic in origin, ranging in age from Upper Cretaceous to Late Pleistocene. About 160 volcanoes can be counted today, 40 of them currently active. The largest are Alaid (maximum elevation 2339 m) on Atlasova Island at the northern end of the chain and Tyatya (1819 m) on Kunashir Island at the southern end. Available habitat is highly variable ranging from sea-level sand, rocky-beach, and grassland to high-mountain stream/conifer forest; from deep, slow-moving lowland rivers to fast-flowing gravelly streams; and from sphagnum bogs to high mountain lakes. Each island has a unique geological and biological history. Substantial opportunities for *in situ* diversification are provided by great distances between the islands and mainland source biotas, and by significant barriers to plant and animal dispersal, such as deep channels between islands, associated with strong ocean currents.

The island chain is bounded on each side by very deep water. On the Pacific side, the 8000-m isobath is situated *c.* 145 km southeast of Simushir Island, while on the west in the Sea of Okhotsk the isobath of 3500 m lies *c.* 130 km northwest of Simushir. In contrast, depths between adjacent islands are relatively shallow, most not exceeding 100 m. The only exception is the Bussol Strait, lying near the centre of the Archipelago between Urup and Simushir, which has a maximum depth of 2659 m.

Although the general outlines of the flora and fauna of the Kurils can be summarized, more detailed information has been non-existent or unpublished; what little is available is confined to the Russian and, to a lesser extent, the Japanese scientific literature. Prior to the work described here, little systematic collecting had ever been carried out, and since the close of World War II, only a few Russian biologists had done any work of significance in this region. With the exception of a few Russian collections (e.g. those of the various institutes of the Russian Academy of Sciences at Vladivostok, Magadan, St Petersburg, Moscow, Novosibirsk and Yuzhno-Sakhalinsk), museum samples of plants and animals originating from the Kurils have been unavailable and frozen tissues completely non-existent. The biota is a mix of Japanese, Kamchatkan, and endemic species, but the biodiversity of the islands, relative to each other and to the mainland, has remained unknown. Limited coastal regions of several of the larger, more strategically positioned islands have been heavily impacted since the close of World War II by the construction of Russian military installations, but otherwise the islands remain undisturbed (although most likely perturbated extensively in the recent past by indigenous peoples, i.e. maritime hunters and gatherers; Fitzhugh *et al.*, 2002). Only six islands are currently inhabited.

Despite the lack of comprehensive work, limited greatly in the recent past by political, climatic, and logistical difficulties, a few biogeographical studies of the flora and fauna of some of the Kuril Islands have been conducted by Japanese and Russian investigators. The results of some of this work provide evidence for a number of significant faunal and floral boundaries within the Archipelago that divide the chain into a number of biotic regions. For example, Tatewaki (1947, 1957) presented evidence for a floral break between Iturup and Urup. He named this boundary the 'Miyabe Line' after the famous Japanese botanist Kingo Miyabe (1860–1951) who was one of the very first scientists to study Kuril Island plants. Tatewaki's conclusion was quickly accepted and is now almost universally recognized among Japanese botanists (e.g. see Takahashi, 2001). Similarly, Takhtajan (1978, 1986), in his well-known *Floristic Regions of the World*, drew the boundary between the Eastern Asiatic and Circumboreal regions through the Kuril Archipelago, between the islands of Iturup and Urup (i.e. the De Vries Strait). Considering animal distributions on the Kurils, Semenov Tian-Shanskij (1935) recognized the boundary between Palearchearctic and Eurosiberian subregions of the Palearctic Region at the southern end of the Archipelago between Hokkaido and Kunashir (see also Kuwayama, 1967; Kryvolutskaja, 1973). In agreement with Berg (1949), Takhtajan (1978, 1986), based on an analysis of fresh-water ecosystems, drew the boundary between the Palearctic Region and an Amur-Manchurian Transitional Region between Iturup and Urup. Finally, Starobogatov (1970) considered a transition zone between the Palearctic Region and a Chino-Indian Region to coincide with some indefinite specific site in the central Kuril Islands. In the light of these several competing hypotheses, a primary goal of this paper is to clarify the major patterns of biodiversity and biogeography of the Kuril Archipelago.

The work described here is based on a long-term programme designed to survey and inventory the biota of the islands of the Kuril Archipelago: the International Kuril Island Project (IKIP), focusing primarily on plants, aquatic and terrestrial insects, spiders, freshwater and terrestrial mollusks, freshwater fishes, amphibians, and reptiles. Having now completed seven field seasons of collecting (1994–2000), on all 30 major islands, it is now possible to provide some general distributional and zoogeographical information. Here is a report specifically on the vascular plants, insects, freshwater and terrestrial mollusks, and freshwater fishes.

MATERIALS AND METHODS

Collections of whole specimens of plants and animals, as well as tissue samples for future molecular studies, were made by teams of scientists from Japan, Russia, and the USA, averaging 34 people for each of the seven annual summer expeditions (1994–2000). For all 7 years combined, a total of 164 students and professionals (97 Russians, 50 Americans, and 17 Japanese) helped to collect some 500,000 specimens that are now archived in various institutions of all three nations. Taxa of major emphasis included vascular plants, aquatic and terrestrial insects, spiders and harvestmen, freshwater and terrestrial mollusks, freshwater fishes, amphibians, and reptiles, but significant collections of lichens, mosses, liverworts, fungi, diatoms, platyhelminths, oligochaetes, amphipods, pseudoscorpions, mites, decapods, water fleas, centipedes, millipedes, and marine fishes were also made. A research vessel provided by the Russian Academy of Sciences, Far East Branch (the 68.5-m *Professor Bogorov* in 1994, 1995, and 1997; the 75.5 m *Academic Oparin* in 1996, 1998, and 1999; and the 100-m *Okean* in 2000), served as a means of transportation to and from the islands, as sleeping quarters, the source of all meals, and as a floating research laboratory while at sea and when on-site. Large rubber inflatables, equipped with 40-horsepower engines, were used to transport equipment and personnel between ship and shore. On some of the larger inhabited islands (Paramushir, Urup, Iturup, and Kunashir), Russian military vehicles were used to move between distant collecting sites. Specific collection sites, totaling *c.* 6700, were selected to maximize geographical and habitat diversity. To the extent possible, collections were sorted and identified aboard ship, and field data entered into a computer data base. Following each expedition, the data were downloaded to an IKIP website (available via *http://www.okhotskia.ws*), maintained at the University of Washington, Seattle, to provide easy access to project results and data bases. The website provides a full-text search interface to access both locality and taxonomic data bases. In addition, the locality data base can be accessed via maps that show survey and inventory sites. This map-based browser allows the user to click on maps to select an island, then to click on major collection areas to get a list of all collection sites for that area, and finally to view the full locality record.

Indicator taxa used for a quantitative assessment of Kuril biodiversity and patterns of distribution were selected on the basis of the following five criteria: (1) those taxa with a well-known and stable taxonomy; (2) those having a number of contained species sufficient for mathematical analysis; (3) those containing at least some species that are broadly distributed geographically, over a breadth of habitat types, with limited dispersal capabilities; (4) those containing at least some subtaxa sensitive to habitat change and represented by endemic species and subspecies within the study area; and (5) those that occupy the majority of the terrestrial and/or freshwater ecosystems available on the Archipelago. For example, such well-known taxa as birds and marine mammals were not considered in this study based on criteria 3 and 4. Lists of species of indicator taxa identified in preliminary analyses of Kuril Island distribution patterns are provided by Kholin (1993); Kerzhner & Marusik (1996); Mutin & Barkalov (1997); Nilsson *et al.* (1997); Belokobylskij & Tobias (1998); Mutin & Barkalov (1999); Nilsson *et al.* (1999); Barkalov (2000); Belokobylskij & Tobias (2000); Kupianskaya *et al.* (2000); Lelej & Kupianskaya

(2000); Lelej (2001); Marusik & Crawford (2001); Pietsch *et al.* (2001); Barkalov (2002); Kostenko (2002); Lafer (2002); Lelej *et al.* (2002); Marusik (2002); Prozorova *et al.* (2002); Prozorova (2002); Shedko (2002); Storozhenko (2002) and Teslenko (2002).

Floral and faunal similarities between islands were evaluated, without regard to differences in island area or degree of isolation from source biotas at either end of the island chain, by using Sorensen's coefficient of similarity: $S = 2a/(2a + b + c)$, where a is the number of species common to both islands and b and c are the number of species occurring on each of the islands (see Legendre & Legendre, 1998). The similarity matrix resulting from pair-wise calculations was then subjected to single and complete linkage clustering as well as unweighted arithmetic average clustering (UPGMA; NTSYS program, version 1.70, Net Technology Systems, Ecully, France). The results obtained by these approaches being all very similar, we constructed dendrograms using UPGMA. Cluster analysis was performed on the following groups: vascular plants (1194 species), terrestrial mollusks (45), freshwater mollusks (90), true bugs (230), diving beetles (36), and syrphid flies (207). The accuracy of each cluster was estimated by bootstrap analysis using the statistical program CMS3 2.0 (developed by Y. Kuwahara of the Hokkaido Abashiri Fisheries Experimental Station, Abashiri, Japan). A dendrogram was deduced from 10,000 bootstrap samples.

The general biotic similarity of the islands was analysed using principal coordinate analysis (Legendre & Legendre, 1998). This method allows objects (in this case species found on islands) to be plotted in a space of reduced dimensionality that preserves as much as possible the distance relationships between them. The principal coordinate analysis for 16 selected islands was based on distributions of 2425 species of the follow taxa: vascular plants (1194 species), terrestrial mollusks (45), freshwater mollusks (90), freshwater fishes (28), terrestrial mammals (24), and the following insect taxa: the order Heteroptera (230 species), the coleopteran families Carabidae (181) and Dytiscidae (36), the dipteran family Syrphidae (207), and the hymenopteran families Braconidae (341), Formicidae (30), and the apid subfamily Bombinae (16).

PALEOGEOGRAPHY OF THE KURIL ARCHIPELAGO

The formation of the Kuril Archipelago (Fig. 1) apparently began in the Late Cretaceous, *c.* 90 Myr BP, when the Okhotsk Terrane of the Kula Plate collided with the Siberian continent, thereby creating a subduction zone along the southeastern margin of the Okhotsk Terrane (Kimura & Tamaki, 1985). This subduction zone initiated the formation of the Kuril Kamchatka Trench and the subsequent volcanism that created the Academy of Sciences Rise (now located in the central Sea of Okhotsk) and the Lesser Kuril Ridge. Volcanic activity and uplift in the region of the Lesser Kuril Ridge intensified during the Paleocene and Eocene, as the Kula–Pacific Ridge was subducted into the Kuril–Kamchatka Trench. It was probably during this period that the Lesser Kuril Ridge emerged from the sea. After the subduction of the Kula–Pacific Ridge, a volcanic hiatus ensued, and there is no evidence of subsequent volcanic activity in the Lesser Kuril Ridge. During the hiatus of the Late Eocene and Oligocene, the Okhotsk Plate was subsiding, and there is evidence that the Lesser Kuril Ridge may have been submerged during part of this period (Kimura & Tamaki, 1985; Pietsch *et al.*, 2001).

Late in the Oligocene (*c.* 30 Myr BP) the Okhotsk Terrane began to rotate clockwise and the backarc basin that now forms the southern Sea of Okhotsk began to open to the west of the Kuril Arc. During this period, volcanic activity resumed near the Kuril–Kamchatka Trench, but was concentrated in the location of what is now the Greater Kuril Ridge. Consequently, the oldest rocks in the main arc of the Kuril Islands are of Late Oligocene and Early Miocene age (Markhinin, 1968; Markov & Khotin, 1973). The backarc basin was fully formed by Mid-Miocene. Although this period marks the beginning of the formation of the primary chain of the present-day Kuril Islands, sediment records indicate that they probably did not emerge above the sea surface until the Early Pliocene (Kimura & Tamaki, 1985). During the past 10 Myr, the Greater Kuril Ridge has experienced intense volcanic activity and crustal uplift (Markhinin, 1968; Yakushko & Nikonov, 1983; Gnibidenko, 1985). Although most of the islands along this ridge have not been studied closely, there is good evidence that the southern Kuril Islands of Kunashir and Iturup emerged from the sea during the Pliocene or Early Pleistocene and have been above sea level ever since (Bulgakov, 1996).

The coastline of the Sea of Okhotsk in the Early Pleistocene (1.8 Myr BP) was very similar to the present configuration, indicating that the subsequent evolution of the Okhotsk basin relates primarily to global climate changes (Bezverkhniy *et al.*, 2002). During the Late Pleistocene there were at least two major sea-level regressions associated with glacio-eustatic changes in this region (Briggs, 1974; Korotkii, 1985). Sea level fluctuations varied between a low of −140 m and a high of +10 m relative to present-day level (Morley *et al.*, 1986; Keigwin & Gorbarenko, 1992; Bezverkhniy *et al.*, 2002). The present biotic features of the Kuril Island ecosystem were evidently laid down primarily during the large-scale regression of the Late Würm (the fourth of the four great glacial stages of the Pleistocene of Europe) and the subsequent rise of sea level.

The lowest sea level of the Late Würm (*c.* 18,000–15,000 yr BP) is estimated to have been −130 m (Chappell & Shackleton, 1986; Bezverkhniy *et al.*, 2002). During that period, Sakhalin, Hokkaido, Habomai, Shikotan, Kunashir, and probably Iturup were united into a single mountainous region that was connected as well to the mainland Sikhote-Alin Mountains that presently stretch along the east coast of Primorski Krai (Fig. 1). At the same time, Paramushir and Shumshu in the north were connected to Kamchatka, and the southern Kuril islands of Urup, Chirpoi, Brat Chirpoev, and Broutona were probably united as a single island, as were the central islands of Ekarma, Shiashkotan, Kharimkotan, and Onekotan. Glaciers covered the northern and central islands during the glacial maxima of the Late Würm, but probably did not extend any farther south than central Iturup (there are no traces of glaciation on Kunashir or in the Lesser Kuril Islands; Kryvolutskaja, 1973). Throughout the year, most of the surface of the Okhotsk Sea was covered with ice, which blocked the shallow straits between most of the islands. The deep Bussol Strait, however, even in the most extreme glacial epochs, was never covered by ice because of strong current exchange between the Sea of Okhotsk and the Pacific Ocean (Bezverkhniy *et al.*, 2002). All things considered, the Bussol Strait was and is an important limiting factor for the distribution of the Kuril biota.

At the end of the Late Würm (*c.* 15,000–13,000 yr BP) the climate became warmer as the post-glacial transgression period began. Climatic warming during this time was rapid; for example, during a period of only 750 years (13,150–12,400 yr BP) the average air temperature in East China increased by 7 °C (Yang & Xie, 1983). At *c.* 12,500 yr BP, very rapid hydrological changes also occurred in the near-bottom layers of the Okhotsk Sea (Khusid & Basov, 1999). Probably the most intensive introduction of warm-adapted elements of the Kuril biota took place during this time, when the climate was warm but the sea-level low.

Subsequent warming and continued sea-level rise resulted in a sequence of isolation of the islands. Between 15,000 and 14,000 yr BP, Iturup was separated from Kunashir, Shikotan, and Habomai in the south, and from Chirpoi, Brat Chirpoev, and Broutona in the north (Bezverkhniy *et al.*, 2002). Sakhalin was separated from Hokkaido *c.* 12,000–11,000 yr BP, Paramushir and Shumshu from Kamchatka *c.* 10,000 yr BP, Kunashir from Hokkaido, 7500 yr BP, and Sakhalin from the Asiatic Mainland *c.* 7000 yr BP. Full isolation of the Kurils as we see them today was thus complete by mid-Holocene.

RESULTS AND DISCUSSION

Biodiversity of the Kuril Archipelago

The Kuril Archipelago supports an unusually high taxonomic diversity, despite its relatively small total area (Zhuravlev, 2001; Zhuravlev & Sazonova, 2002). This can be illustrated by comparing the Kurils with Sakhalin Island. The area encompassed by Sakhalin is 76,400 km^2 while the Kurils total only *c.* 15,600 km^2. Sakhalin and the Kurils are nearly equal in length, extending over a distance of 948 and 1200 km, respectively, at almost the same range of longitude. The overall vegetation types, the general landscape, and the average elevation above sea level are also similar. Only the largest volcanos of the Kurils, Alaid on Atlasova (maximum elevation 2339 m) and Tyatya on Kunashir (1819 m), are higher than Mount Lopatina, the highest point on Sakhalin (1609 m). The climate of Sakhalin and the Kurils is predominantly oceanic temperate, with relatively abundant precipitation and a low annual mean temperature.

The floras of Sakhalin and the Kurils contain virtually the same number of vascular plant species, although the area of Sakhalin is nearly five times greater than that of the Kurils: excluding introduced forms, there are 1196 species, 462 genera, and 122 families of vascular plants on Sakhalin compared with 1194 species, 550 genera, and 135 families on the Kurils. This difference strongly contradicts the almost universally accepted ideas about island biogeography as demonstrated by MacArthur & Wilson (1967). (MacArthur and Wilson hypothesized that the number of species on one large island should be larger than that found on two or more smaller islands having the same combined area; but clearly, in this case, the numbers are nearly the same despite the huge discrepancy in area.) The flora of Kamchatka includes *c.* 890 species, while that of Hokkaido contains *c.* 1700 species. It should be pointed out that the species richness of the southern Kuril flora is more than two times greater than that of the northern Kurils and about three times greater than that of the central Kurils (Fig. 2).

The insect fauna of the Kuril Archipelago is also rich compared with outlying regions. Although Kuwayama (1967) reported only 1917 species and Kryvolutskaja (1973), 2884 species, the current estimated number of Kuril insects is *c.* 8000 in 441 families and 25 orders. Only five insect orders, which are otherwise widely distributed in the Russian Far East (RFE) and in Japan, are absent on the Kuril Islands: Mantoptera, Isoptera, Grylloblattida, Phasmoptera, and Raphidioptera (Lelej *et al.*, 2002; Storozhenko *et al.*, 2002). In general, the number of the insect species found on the Kurils comprises a full 25% of the total number of species known from the RFE, despite a total area that is only 0.5% of that of the RFE (Table 1). In another example, the number of species of carabid beetles (Carabidae and Cicindelidae) on Hokkaido is 373 species, whereas Kunashir Island at the southern end of the Archipelago supports 140 species (37.5% of the fauna of Hokkaido), although the area encompassed by Kunashir is less than 2% of that of Hokkaido (1490 vs. 78,500 km^2; Lafer, 2002).

As with vascular plants, the number of insect species of the Kuril Archipelago is almost the same as that of Sakhalin, but larger than that of Kamchatka and smaller than that of Hokkaido (Table 1). The insect diversity of the large continental regions in the temperate zone of the Northern Hemisphere generally depends on latitude rather than area (Storozhenko *et al.*, 2002). For example, the total number of insect species found in the RFE (with a total area of 3,016,000 km^2) is almost equal (*c.* 30,000 species) to that of Canada (total area 9,976,000 km^2); moreover the percentages of the insect faunas contained by large orders such as the Lepidoptera (16%) and Diptera (24–25%) are the same. The southernmost boundaries of these vast regions have the same latitude (42° N), resulting in similar climates and vegetation belts, which in turn strongly influence the distributions and diversity of organisms.

Our data on the insect faunas of the Kurils and Sakhalin (Table 1) show that the number of species in these temperate-zone island systems, which stretch over long north–south distances (much like large mainland regions), correlates primarily with latitude (especially southern borders) rather than with area. Moreover, such regularity of species

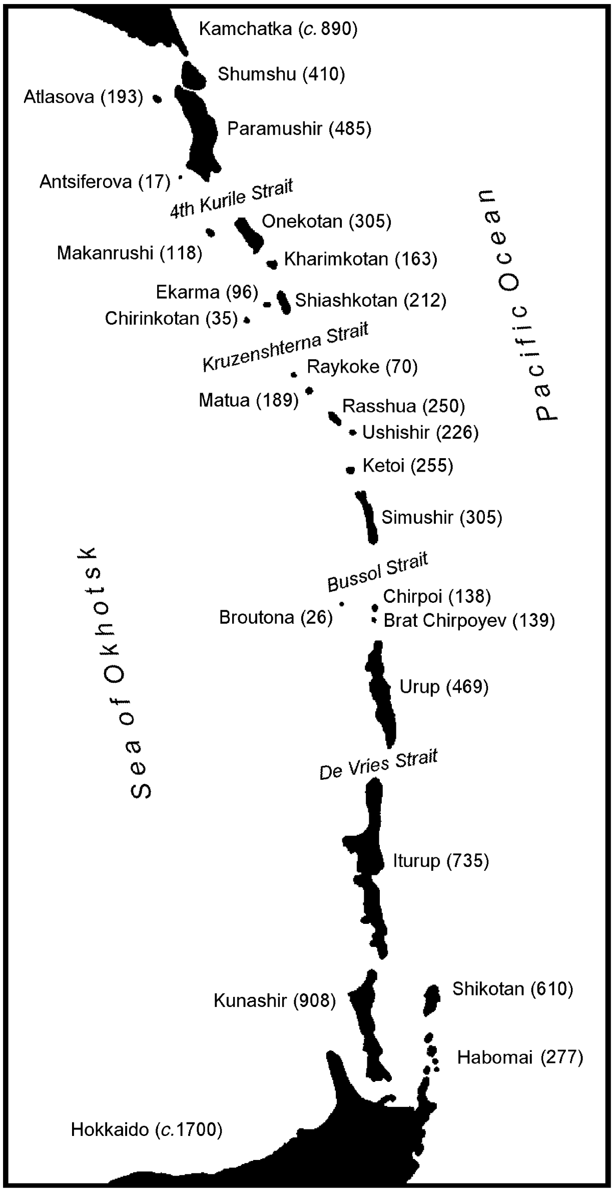

Figure 2 The Kuril Archipelago showing (in parentheses) the number of species of vascular plants on each island.

diversity is supported by our data on vascular plants as well, and is probably characteristic of all taxa of the two parallel island systems, the Kurils and Sakhalin. Obviously, there are other factors that contribute to the nearly equal numbers of species on both Sakhalin and the Kurils. The biodiversity of both island systems is influenced by paleogeographical factors, by the more intensive warm-water currents (Kuroshio) near the southern Kurils, as well as by the presence of numerous refugia for warm-adapted species near active volcanoes (hot springs, etc.) in the Kurils, which are completely absent on Sakhalin.

Similarly, the numbers of terrestrial and freshwater mollusks found on the Kurils are similar to those found on Sakhalin, Hokkaido, and Kamchatka (Table 2). However, the number of freshwater fishes known to inhabit the Archipelago (28 species) is about half that of Sakhalin (64) and Hokkaido (64), and slightly less than that of Kamchatka (33).

Endemic species

The proportion of endemic species found in island ecosystems is determined by the duration and degree of island isolation, keeping in mind that taxa containing slowly moving organisms more often display endemism than highly mobile ones. The Kuril Archipelago has a very low number of endemic species. For example, there are 25 endemic species of vascular plants, which account for only 2% of the 1367 species found on the Kurils (Barkalov, 2000). Of some 300 species of birds either inhabiting or migrating through the Kurils, there is only one known endemic subspecies, *Cepphus columba snowi* (Zhuravlev & Sazonova, 2002). There are no endemic species or subspecies of fishes on the Kurils (Pietsch *et al.*, 2001). As for mammals, there is only one endemic species (*Sorex leucogaster*; see Kostenko, 2002) although the percentage of endemic mammal species in nearby Japan is 40% (Millien-Parra & Jaeger, 1999). While no endemic mammal species are found on Hokkaido (61% of the mammal fauna is continental in origin while the remaining 39% appears to have originated from Honshu), there are numerous examples distributed in the southern parts of Japan. Of *c.* 425 species of spiders found on the Kurils, there are no known species restricted to the archipelago (Marusik & Crawford, 2001; Marusik, 2002). Neverthless, there are endemic species of insects and freshwater mollusks, but even these numbers are low. For example, of 27 species of Orthoptera known from the Kuril Islands, only two species (*Podisma tyatiensis* and *Podismopsis konakovi*) and four subspecies (*Diestrammena japanica kurilensis*, *Podisma sapporensis kurilensis*, *Chorthippus fallax saltator*, and *Ch. fallax kurilensis*) are found only there (Storozhenko, 2002). There are six known endemic species of freshwater mollusks: *Lymnaea zarenkovi*, *Cincinna chishimana*, *C. iturupensis*, *Kunashiria sinanodontoides*, *Beringiana compressa*, and *Lacustrina etorohuensis* (Prozorova *et al.*, 2002), which account for only 6.7% of the 90 species known to inhabit the Archipelago. In summary, the vast majority of Kuril Island species have distributions that extend well beyond the Archipelago, and those few forms that are endemic are closely related to species distributed in nearby Japan, Sakhalin, and the Asian mainland.

Patterns of distribution

Most botanists recognize the 'Miyabe Line' coinciding with the De Vries Strait between the islands of Iturup and Urup as a significant biogeographical boundary for plants (Tatewaki, 1933, 1947, 1957; Vorobev, 1963; Takhtajan, 1986). However, based on a detailed analysis of the northernmost limits of Kuril plant taxa, Barkalov (2000, 2002) recognized a distinct but more northern transition zone through the

Table 1 Numbers of species of selected insect orders found in various regions of the Far East

Order	Sakhalin	Hokkaido	Kuril Islands	Kamchatka	RFE	Japan
Hymenoptera	2210	1785	2280	1070	9000	4297
Diptera	1970	1872	2020	950	8000	5215
Coleoptera	1480	2302	1410	560	5500	9125
Lepidoptera	1230	2375	1260	600	5000	5132
Other orders	910	1544	1030	520	4000	5068
Totals	7800	9878	8000	3700	31,500	28,837

Data for Russian localities are numbers of estimated species, following Storozhenko *et al.* (2002); those for Japanese localities are actual numbers of recorded species, following Hirashima (1989, 1990) and Nakatani (1999). Values given for Japan and the Russian Far East (RFE) are totals for those regions .

Table 2 Numbers of species of terrestrial and freshwater mollusks found in selected regions of the Far East

Habitat	Sakhalin	Hokkaido	Kuril Islands	Kamchatka
Terrestrial	40	72	45	23
Freshwater	75	80	90	73
Totals	115	152	135	96

Bussol Strait between Urup and Simushir. He designated this zone as the boundary between the Circumboreal and East Asiatic regions. Similarly, a UPGMA cluster analysis of vascular-plant similarities among the islands shows two major assemblages that divide the chain into northern and southern parts, the gap between again coinciding with the Bussol Strait (index of similarity 0.33; see Fig. 3). This same analysis shows the 'Miyabe Line' to form a significant floral boundary, but with a much higher index of similarity (*c.* 0.65). Cluster analyses of terrestrial (45 species) and freshwater (90 species) mollusk distributions show the same thing, the latter group especially supporting the argument for the importance of the Bussol Strait, with a similarity index very close to zero (Figs 4 & 5).

Most insect species are restricted in distribution to the southern Kurils (Lelej *et al.*, 2002); for example, the spider wasps (Hymenoptera: Pompilidae) extend only as far north as Urup (Fig. 6). In contrast, true bugs (Heteroptera) and braconid wasps (Hymenoptera: Braconidae) are found throughout the Archipelago but *c.* 95% of the species are southern; by far most are found on Kunashir Island (Figs 7 & 8). Hover-flies (Diptera: Syrphidae), diving beetles (Coleoptera: Dytiscidae), ground beetles (Coleoptera: Carabidae), ants (Hymenoptera: Formicidae), and bumble bees (Hymenoptera: Apidae) are more evenly distributed throughout the Archipelago (Figs 9–11). Cluster analyses of faunal similarities among the Kurils for the most well-studied of these insect taxa (Heteroptera, Dytiscidae, Syrphidae; Figs 8, 10 and 11) all produce two major clusters: Kunashir, Iturup, Shikotan, and Habomai forming a stable cluster in the south; and the central and northern Kurils forming the branches of a northern cluster. The insect fauna of Urup more often clusters with that of the

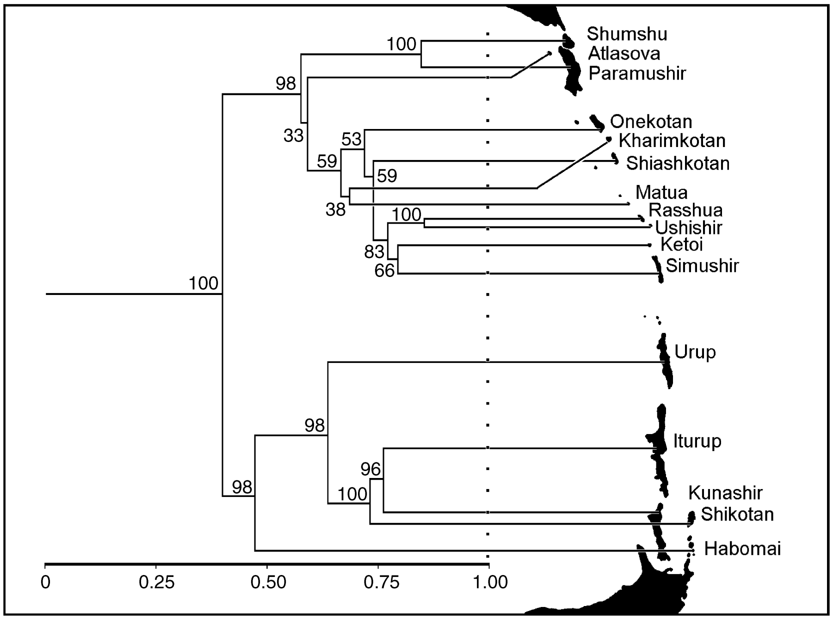

Figure 3 Similarity of 1994 species of vascular plants among 16 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

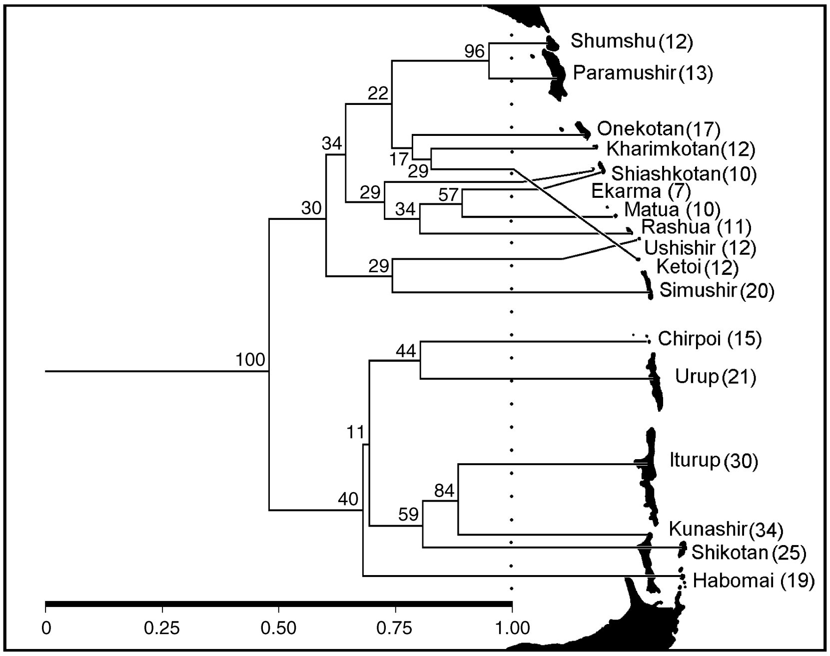

Figure 4 Similarity of 45 species of terrestrial mollusks among 17 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

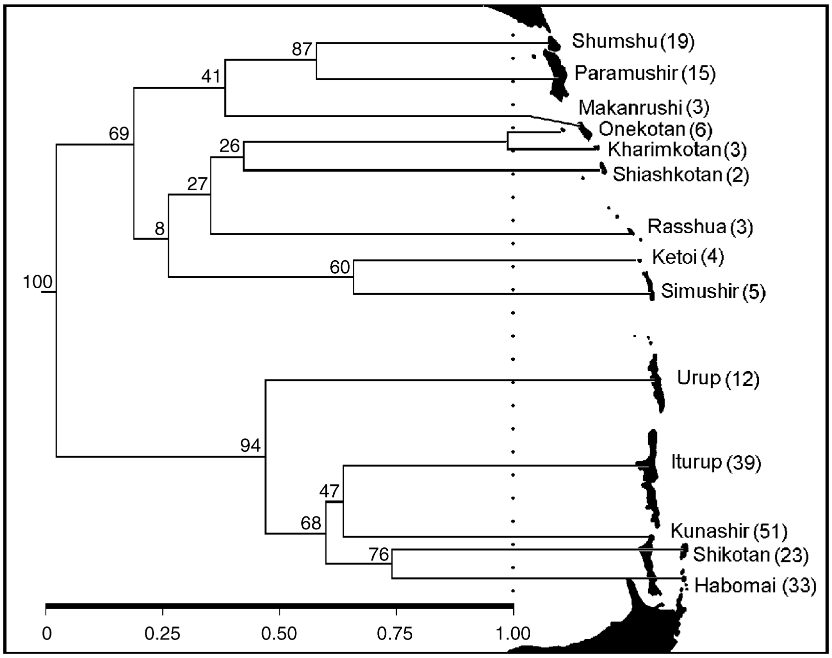

Figure 5 Similarity of 90 species of freshwater mollusks among 14 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

southern Kurils (Figs 8, 10), but for some groups (e.g. Syrphidae), Urup clusters with the northern assemblage (Fig. 11). In some cases (e.g. Heteroptera), Simushir clusters with the southern assemblage (Fig. 8). Admittedly, the faunas of Urup and Simushir appear to be somewhat intermediate (and not studied as well as that of Kunashir), but certainly the bulk of the evidence obtained from Kuril insects agrees well with that for vascular plants and mollusks, supporting the Bussol Strait as the single most important biogeographical boundary in the Archipelago.

Biogeography

The patterns of distribution displayed by Kuril Island plants and animals correlate well with the geological history of the Archipelago. Despite the relatively ancient origin of the Greater Kuril Ridge (Late Oligocene, *c.* 25–30 Myr BP) and still older Lesser Kuril Ridge, the recent biota of the Kurils has probably been forming since Early Pleistocene (around 1 Myr BP). During that glaciation there were land connections between the islands and with the mainland. The

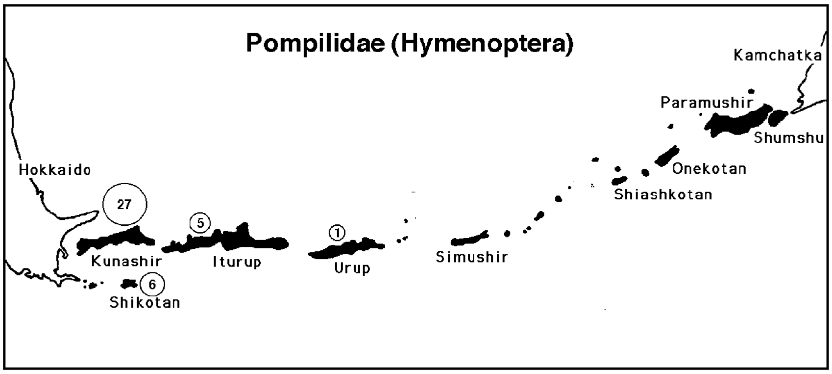

Figure 6 Numbers of species of wasps of the family Pompilidae (Hymenoptera) on islands of the Kuril Archipelago.

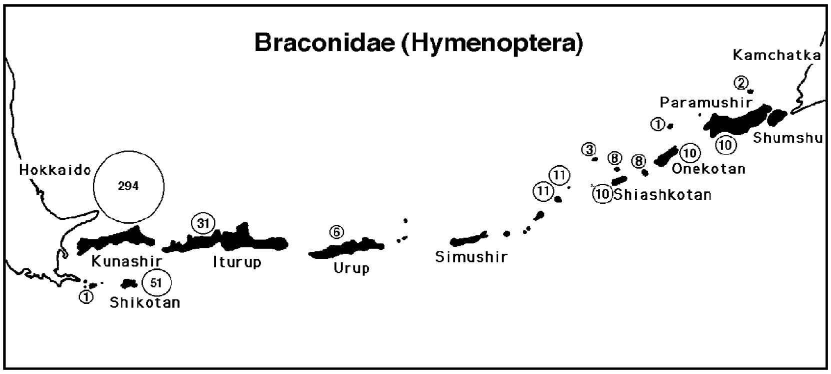

Figure 7 Numbers of species of wasps of the family Braconidae (Hymenoptera) on islands of the Kuril Archipelago.

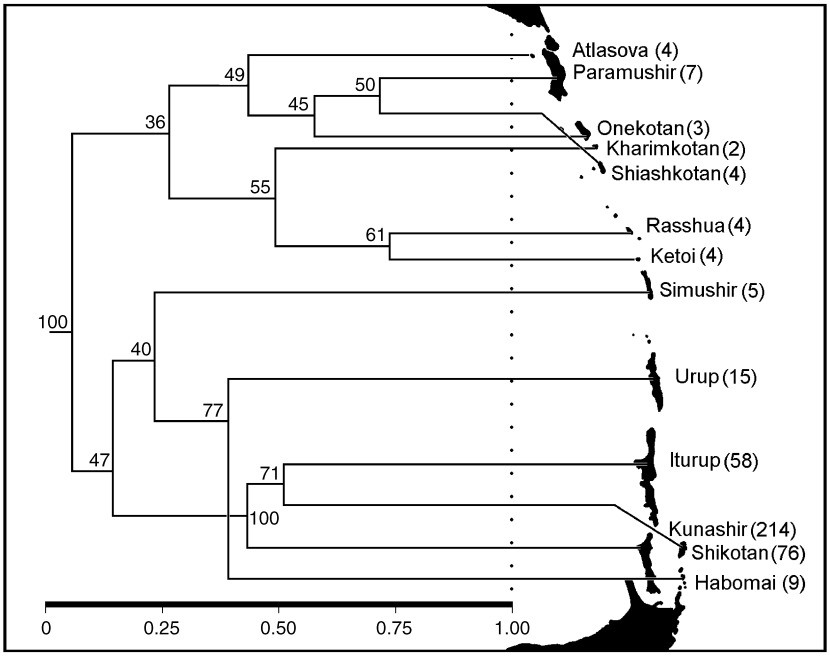

Figure 8 Similarity of 230 species of true bugs (Heteroptera) among 13 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

alternation of glacial and interglacial epochs resulted in a broad range of sea-level fluctuations from a low of −140 m to a high of +10 m. During sea-level regression, mainland species spread to the Kurils. During subsequent transgression some of the islands were covered by the sea, or at least divided into several small islands, no doubt resulting in local extinction of many species.

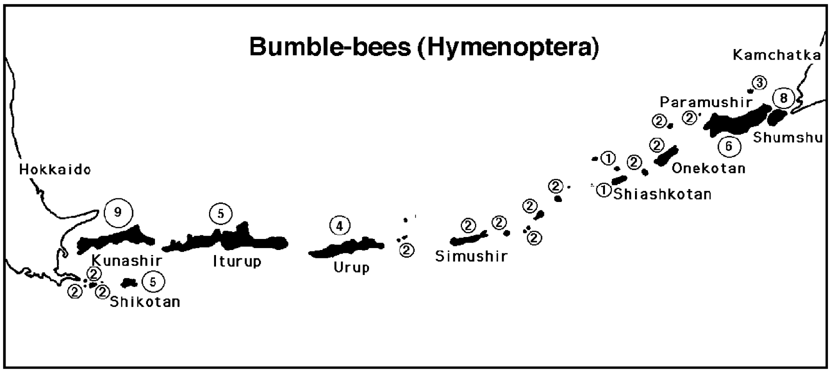

Figure 9 Numbers of species of bumble bees (Hymenoptera, Apidae, Bombinae) on islands of the Kuril Archipelago.

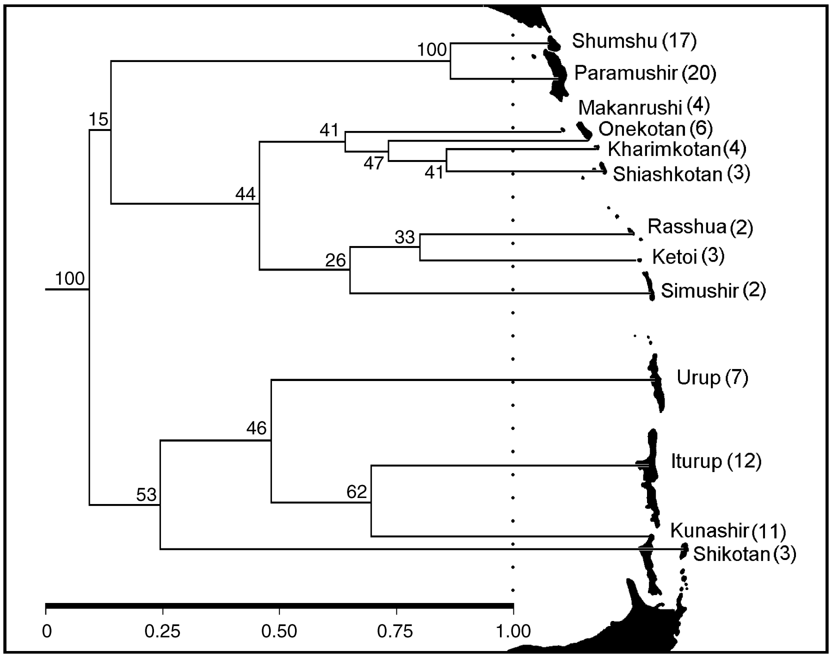

Figure 10 Similarity of 36 species of diving beetles (Dytiscidae, Coleoptera) among 13 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

The most important time for the formation of the present Kuril biota was the period from Late Würm to Holocene, when Sakhalin, Hokkaido, Habomai, Shikotan, Kunashir, and probably Iturup were united into a single landmass that was connected as well with the mainland Sikhote–Alin Mountains. During this time many warm-adapted species probably spread from southern source areas to the southern Kurils. The northern extent of distribution of most of these East Asian (Manchurian–Japanese) species of plants, insects, non-marine mollusks, and terrestrial vertebrates on the Kurils has been limited by the deep Bussol Strait (Barkalov, 2002; Bogatov, 2002; Kostenko, 2002; Lelej *et al.*, 2002; Prozorova, 2002; Prozorova *et al.*, 2002; Teslenko, 2002). At the same time, many cool-adapted species have spread from Sakhalin to Hokkaido and the southern Kurils. Similarly, during the Late Würm to the mid-Holocene, Paramushir and Shumshu were connected to Kamchatka allowing boreal and arctic-alpine species to spread southward from northern sources areas, including high-mountain regions. Thus the Archipelago was colonized from two adjacent source biotas: a southern source, the Asian mainland by way of Sakhalin and Hokkaido, and a northern source by way of Kamchatka. The contribution of the southern source biota to the present-day species diversity of the Kuril Archipelago was considerably greater than the northern source.

A principal coordinate analysis of biotic similarity of the Kurils, based on the known distributions of 2425 species of terrestrial and freshwater plants and animals, again indicates the importance of the Bussol Strait (Fig. 12). These results agree remarkably well with the pattern of distribution of the littoral zone biota of the Archipelago as described by Sukhanov (1982).

Besides the Bussol Strait there are two additional, but less obvious, biogeographical boundaries: the De Vries Strait in the south and the so-called fourth Kuril Strait in the north (Fig. 12). These two straits divide the chain into continental and oceanic islands (see Fig. 1). The De Vries Strait effectively limits the northward dispersal of freshwater fishes

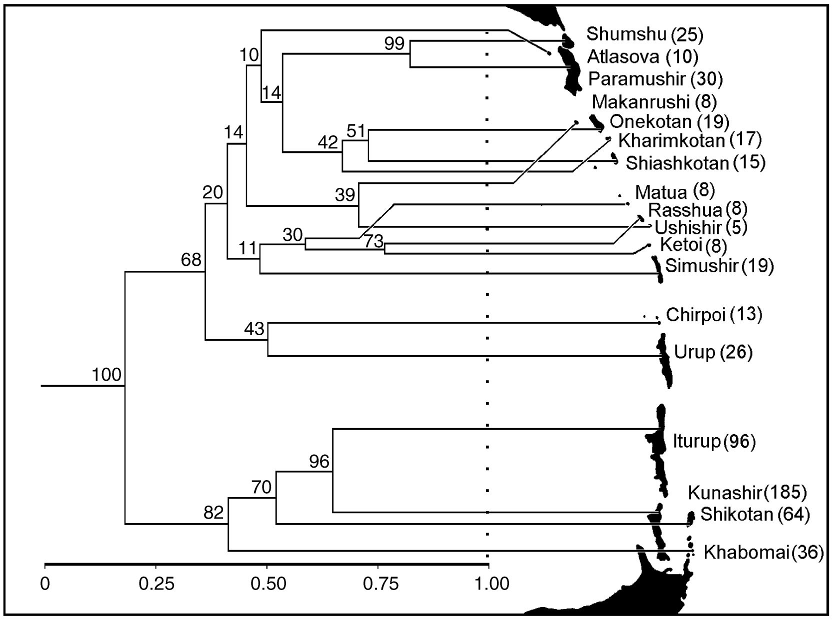

Figure 11 Similarity of 207 species of hover flies (Syrphidae, Diptera) among 18 islands of the Kuril Archipelago. Bootstrap probabilities (expressed in percentage) are indicated at the node of each cluster.

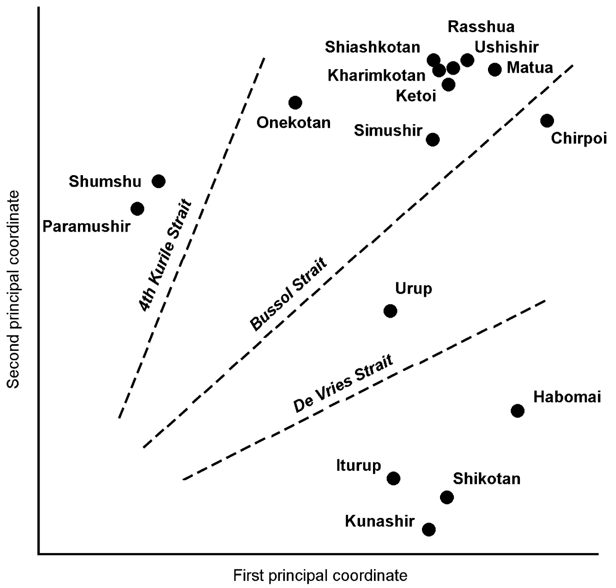

Figure 12 Ordination of the islands of the Kuril Archipelago in the reduced space of the first two principal coordinates. Dashed lines indicate major biogeographical boundaries between the island groups.

and terrestrial mammals (Kholin, 1993; Pietsch *et al.*, 2001; Kostenko, 2002; Shedko, 2002), while the fourth Kuril Strait limits the southward movement of freshwater mollusks (Prozorova *et al.*, 2002) as well as freshwater fishes (Pietsch *et al.*, 2001; Shedko, 2002). For all practical purposes, these straits delimit a central transitional zone characterized by extremely low species diversity, the absence of terrestrial vertebrates (except for birds and introduced mammals), and overlapping ranges of East Asian and boreal species (Bogatov, 2002). Similar attributes have been described for transitional zones within other archipelagos, for example, the Lesser Sunda Islands of the Malay Archipelago (Darlington, 1966).

CONCLUSION

The present-day Kuril Island terrestrial and freshwater biota is characterized by high species diversity and a low degree of endemism at the species level. It is thus an example of a non-relict biota formed from two source pools: a northern source by way of Kamchatka and a southern source, the Asian mainland by way of Sakhalin and Hokkaido. The contribution of the southern pool to present-day species diversity was considerably larger than the northern one. The current biodiversity of each island of the Archipelago is thus the result of a combination of factors including geological history, area, distance from adjacent source biotas, climate, warm and cold oceanic currents, and the presence of warm-water refugia.

The UPGMA cluster analyses of several well-known selected plant and animal taxa, as well as principal coordinate analysis of the full Kuril biota as presently known, clearly demonstrate that the Bussol Strait is the most important boundary between two large biogeographical regions. Current climatic conditions increase the importance of the Bussol Strait as a boundary between the relatively warm southern Kurils and the cold northern Kurils. In addition to the Bussol Strait there are two less obvious biogeographical boundaries, which are perhaps better described as transitional zones: one in the south that coincides with the De Vries Strait or 'Miyabe Line,' between Iturup and Urup; and another in the north, the so-called fourth Kuril Strait between Onekotan and Paramushir (Fig. 13).

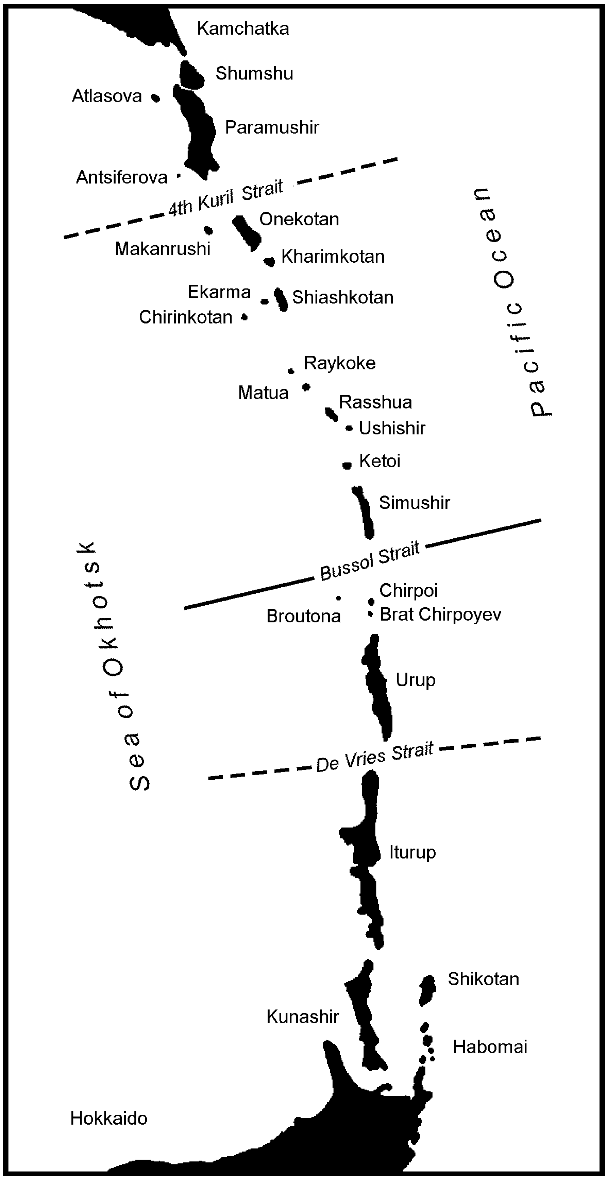

Figure 13 Biogeographical boundaries of the Kuril Archipelago, the Bussol Strait, with secondary boundaries, the De Vries Strait and the fourth Kuril Strait, encompassing a central transitional zone.

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BIOSKETCHES

The authors of this paper are a subset of some 90 students and professionals who have participated in a decade-long effort to document the biodiversity and explain the present-day patterns of distributions of plants and animals on the islands of the Russian Kuril Archipelago and nearby Sakhalin Island. We are of diverse interests and backgrounds but we all share a deep interest in biodiversity. **Theodore W. Pietsch** is an ichthyologist, interested primarily in marine benthic and deep-sea fishes; **Victor V. Bogatov** is a hydrobiologist, with expertise in freshwater molluscan taxonomy; **Kunio Amaoka** is a marine ichthyology and world authority on pleuronectiform fishes; **Yuri N. Zhuravlev** is a population geneticist specializing in rare and endangered species, including the plant genera *Panax, Aralia*, and *Iris*; **Vyacheslav Y. Barkalov** is a botanist interested primarily in the floras of cold-temperate regions of the Northern Hemisphere; **Sarah Gage**, again a botanist and Collections Manager of the University of Washington Herbarium; **Hideki Takahashi**, a botanist and world authority on the vascular plants of Japan and the Pacific Rim; **Arkady S. Lelej** is an entomologist specializing in Hymenoptera; **Sergey Y. Storozhenko** is also an entomologist specializing in Orthoptera; **Norobu Minakawa** is an aquatic entomologist and authority on the biology of mosquitoes as malaria vectors; **Daniel J. Bennett** is a graduate student studying wasp systematics; **Trevor R. Anderson** is a highly talented undergraduate at the University of Washington currently searching for a graduate school to study systematic entomology; **Masahiro Ôhara** is an entomologist specializing in ground beetle systematics; **Larisa A. Prozorova** is a malacologist and authority on the terrestrial gastropods of the Russian Far East; **Yasuhiro Kuwahara** is also a malacologist specializing in Far East freshwater bivalves; **Sergey K. Kholin** is an entomologist specializing in insect ecology; **Mamoru Yabe** is a marine ichthyologist and world authority on cottid fishes; **Duane E. Stevenson** is also an ichthyologist with expertise in the marine fauna of the North Pacific Ocean and Bering Sea; and **Erin L. MacDonald** is a graduate student at the University of Washington working toward a doctorate in larval fish taxonomy.