Botanica Pacifica. A journal of plant science and conservation. 2024.
DOI: 10.17581/bp.2024.13101

RESEARCH PAPER

Variations of plant communities in diversity and composition along the western coast of Lake Khanka caused by high water level

Elena A. Marchuk[1]*, Anastasiya K. Kvitchenko[1,2], Dmitry E. Kislov[1], Vyacheslav Yu. Barkalov[3], Valentina A. Kalinkina[1,2], Lyubov A. Kameneva[1] & Svetlana V. Nesterova[1]

Elena A. Marchuk [1]*
e-mail: pimenova@botsad.ru

Anastasiya K. Kvitchenko [1,2]
e-mail: kvitchenkoanastasia@yandex.ru

Dmitry E. Kislov [1]
e-mail: kislov@easydan.com

Vyacheslav Yu. Barkalov [3]
e-mail: barkalov@biosoil.ru

Valentina A. Kalinkina [1,2]
e-mail: conf-lf@yandex.ru

Lyubov A. Kameneva [1]
e-mail: lubavar1188@mail.ru

Svetlana V. Nesterova [1]
e-mail: svnesterova@rambler.ru

[1] Botanical Garden-Institute FEB RAS, Vladivostok, Russia

[2] Far Eastern Federal University, Vladivostok, Russia

[3] Federal Scientific Center of the East Asia Terrestrial Biodiversity FEB RAS, Vladivostok, Russia

* corresponding author

Manuscript received: 02.10.2023
Review completed: 26.10.2023
Accepted for publication: 01.11.2023
Published online: 03.11.2023

ABSTRACT

Lake Khanka is the largest freshwater body of water in northeast Asia, with a basin of about 25 000 km^2. The hydrological regime of the lake is cyclical in nature due to various factors affecting water inflow and outflow. The last increase of water level in the lake began in the 2000s and by 2015 reached the maximum value of 416 cm (with the average annual level of 293 cm). A steady decline in water level has been observed since 2021. To assess the diversity and structure of coastal plant communities on the sandy-pebbly substrate along the western shore of Lake Khanka and their dynamics under the influence of flooding, we laid 20 transects and performed descriptions at seven sites, including two sites in the protected area of the Cluster Sosnovy of the Khanka Nature Reserve. Using the diversity and similarity/difference indices, plant communities were compared across the sites. It was shown that their heterogeneity is due to the diversity of both aboriginal and adventive species. In protected areas, the role of adventive species is significantly lower than in recreational areas. The five dominant species in the communities account for 50 % or more of the total abundance. Vegetation groupings in the three identified zones, which have been inundated for different periods of time, have a similar diversity, with differences due only to the native fraction of species. The second zone, characterized by the greatest influx of species of different ecological and cenotic groups during water recession, differs in species richness. The obtained data show for the first time the diversity and structure of coastal plant communities of the sandy-pebble beech of the western coast of Lake Khanka and reflect some processes of its dynamics in connection with the long-term standing water. For more successful coverage of the issues raised, long-term monitoring on the laid transects, at least covering one 20–30-year cycle of the dynamics of the hydrological regime of Lake Khanka, is necessary.

Keywords: flora, aboriginal species, adventive species, diversity, similarity, differences, floods, Lake Khanka, Primorye Territory

РЕЗЮМЕ

Марчук Е.А., Квитченко А.К., Кислов Д.Е., Баркалов В.Ю., Калинкина В.А., Каменева Л.А., Нестерова С.В. Различия в разнообразии и составе растительных сообществ вдоль западного побережья озера Ханка, вызванные высоким уровнем воды. Озеро Ханка – самый крупный пресноводный водоем на северо-востоке Азии, бассейн которого занимает около 25 тыс. км^2. Гидрологический режим озера носит циклический характер, обусловленный различными факторами, влияющими на приток и сток воды. Последнее повышение уровня воды в озере началось с 2000-х г. и к 2015 г. достигло максимального значения 416 см (при среднемноголетнем уровне 293 см). С 2021 г. наблюдается стабильный спад уровня воды. Для оценки разнообразия и структуры прибрежных растительных сообществ на песчано-гелечном субстрате вдоль западного берега озера Ханка и их динамики под влиянием затопления, нами были заложены 20 трансект и выполнены описания на семи участках, в том числе на двух участках охраняемой территории кластера «Сосновый» заповедника «Ханкайский». Используя индексы разнообразия и сходства-различия было проведено сравнение растительных сообществ по участкам. Показано, что их разнородность обусловлена разнообразием как аборигенных, так и адвентивных видов. На охраняемых территориях роль адвентивных видов значимо ниже, чем на рекреационных. На пять доминирующих видов в сообществах приходится 50% и более от общего обилия. Растительные группировки на трех выделенных зонах, разное время находящихся в затоплении, имеют сходное разнообразие, различия обусловлены только аборигенной фракцией видов. По богатству видов отличается вторая зона, характеризующаяся наибольшим притоком видов разных эколого-ценотических групп при отступлении воды. Полученные данные впервые показывают разнообразие и структуру прибрежных растительных сообществ песчано-галечного побережья западного берега озера Ханка и отражают некоторые процессы ее динамики в связи с длительным стоянием воды. Для более успешного освещения поставленных вопросов необходим долгосрочный мониторинг на заложенных трансектах, по крайней мере охватывающий хотя бы один 20-30-летний цикл динамики гидрологического режима озера Ханка.

Ключевые слова: флора, аборигенные виды, адвентивные виды, разнообразие сосудистых растений, коэффициенты сходства, коэффициенты различия, затопление, озеро Ханка, Приморский край

Electronic Appendix:
http://www.geobotanica.ru/bp/2024_13_01/BP_2024_13_1_marchuk_e_suppl.pdf

Lake Khanka (興凱湖 [*Xingkǎi Hú*] in Chinese), part of the Amur River watershed, is a transboundary water body between the Russian Federation (RF) and the People's Republic of China (PRC). The Russian part of the lake is located in Primorye Territory, while the Chinese part is located in Heilongjiang Province. Lake Khanka, as well as the Khanka Lowland, has a large natural resource potential and determines the socio-economic structure of the population living in this territory with a total area of about 25 000 km^2 (Bazarov et al. 2021). The resources of the lake are actively exploited by both countries. The main economic activity in the lake basin is agriculture, mainly crop production. On the Chinese side, the development of agriculture began in 1945 (Jin & Jiang 2007); on the Russian side, the history of active land use in the lake basin goes back about 140 years. In Primorye Territory, land use was most intensive during the Soviet period until the 1980s. The economic downturn of the 1990s also led to a decrease in anthropogenic pressure on the lands around Khanka.

In the last two decades, the Russian part of the basin has seen an increase in economic activity and the recovery of arable land. As of 2021, the total cultivated area in Primorye Territory is 476 000 ha (Baukova 2022), of which more than 50 % is in the Khanka Lowland. The most pronounced changes in the coastal part of the lake that occurred in the 20th century were associated with the construction of an irrigation system including distribution canals, reservoirs, and hydraulic structures covering nearly 900 km^2 in the PRC and 500 km^2 in the RF. In PRC, these facilities are still in active operation, while in Russia most of the irrigation system is not used. Rice crops currently occupy an area 25 times smaller than that under soybeans, for example (Baukova 2022).

Another actively exploited resource of Lake Khanka is its recreational component. Over the past 10 years, the number of tourist attractions and, consequently, the number of vacationers has increased significantly in the western coastal areas of the lake. From May to July, when the sea is still not warm enough, most tourists prefer to go to the shores of Khanka, where average monthly temperatures are 1–2°C higher than, for example, on the coast in the Khasan District. Mass tourism is also developing in the Chinese part of the lake basin. According to the Biang news site (https://biang.ru/) on July 27, 2023, the number of tourists is estimated at 16 000 on weekends and up to 10 000 on weekdays.

To preserve the unique biodiversity of the lake, protected areas have been organized on both sides of the lake. In 1976, the Lake Khanka basin was granted the status of wetlands of international importance in accordance with the Ramsar Convention on Wetlands (Director 1971). In 1986, the Xingkai Hu Nature Reserve was established in China (since 2007 it has the status of a biosphere reserve), and on the neighboring Russian side the Khanka State Nature Reserve was established in 1990 (since 2005 it has the status of a biosphere reserve). In 1996, an intergovernmental Russian-Chinese agreement was signed on the establishment of the International Reserve Lake Khanka on the basis of the existing reserves (Kozhenkova et al. 2022).

Lake Khanka is characterized by cyclic fluctuations of water level, which is calculated as the difference between the inflow and outflow parts of the water balance. However, it is rather difficult to take into account the totality of natural and climatic factors causing water level fluctuations. The last cycle of water level rise in Lake Khanka began in the 2000s. In 2015, it reached its historical maximum (Georgievsky et al. 2017, Zuenko et al. 2020). According to other data, the water level in the lake increased until the end of 2017, and since 2021 there has been a steady decrease in the level (Kolomiets et al. 2022). Thus, by 2023, high water levels have been observed at different sites for three to seven years, with part of the area still in the flood zone.

Due to the rising water level in the lake, agricultural land, infrastructure facilities and residential houses of rural settlements in the coastal areas were submerged. The high water level led to flooding of low-lying areas along the entire coastline, including protected areas of the Khanka Nature Reserve. The following sites of the Reserve were flooded on the western side of the lake: Sosnovy Island, Cape Przhevalsky and Cape Arsenyev. The total area of flooding and waterlogging within the Russian part of the lake basin reached 812 km^2 (Bortin & Gorchakov 2016). The phenomenon of high lake level has attracted much attention of the public, authorities and scientific community, but has not yet received an unambiguous explanation. The literature offers different points of view on the causes of the water level rise, provides forecast estimates of further dynamics, and formulates measures to regulate the lake level (Bortin & Gorchakov 2016, Georgievsky et al. 2017, Bolgov & Arefieva 2019, Zuenko et al. 2020, Bolgov & Korobkina 2022, Kolomiets et al. 2022). Scientific discussions organized to address the whole set of geo-ecological problems in the Lake Khanka basin (Zhuravlev & Klyshevskaya 2016, Zhuravlev et al. 2018, Baklanov et al. 2019) emphasize the need for integrated research and international monitoring to ensure sustainable environmental management. The importance of long-term monitoring of the high level of Lake Khanka was pointed out in a recent publication on the Khanka Reserve (Kozhenkova et al. 2022). Unfortunately, no comprehensive monitoring has been conducted so far. In available publications, we found only information on the impact of lake level on the condition of the Amur soft-shelled turtle (*Pelodiscus maackii* (Brandt, 1857)) (Maslova 2016, 2021, Bazarova et al. 2022, Maslova et al. 2023) and on commercial fish stocks (Zuenko et al. 2020). Data on the impact of flooding and waterlogging on vegetation cover and flora composition, including the state of populations of *Oxytropis chankaensis* Jurtzev, a rare psammophyte species, are extremely scarce, fragmentary and largely incomparable (Bazarova et al. 2022, Kozhevnikova & Maslova 2022).

Concern about the situation caused by the catastrophic rise in water levels in Lake Khanka and the lack of long-term monitoring of the state of the biota necessitated our study and determined its scope.

The aim of the study was to determine the composition and structure of coastal plant communities, the role of adventive and aboriginal species in their functioning, and the distribution of species affected by high water levels in Lake Khanka. This paper presents the results of the survey conducted in the western part of the lake in July 2023.

Study area

The area of our research is the western shore of Lake Khanka, stretching approximately 70 km from the village of Astrakhanka in the south to the village of Tury Rog in the north (Fig. 1). The western shore of the lake is higher compared to the eastern shore and is characterized by a rugged coastline with capes and bays, hilly relief, and forests on coastal ledges. The largest rivers in the western catchment area of the lake are the Komissarovka, Bolshiye Usachi and Turga rivers.

Geomorphologically, the western shore of Lake Khanka is an abrasion ledge 30 to 70 m high with an intermittent strip of sand and pebble beach several meters to 60 m wide. In the estuaries of the rivers the coast is gentle, with waterlogged depressions, oxbow lakes and channels. Geological studies of the coastal outcrops have shown that three types of sediments predominate in the profiles: pebbles, gravel and rocks composed of siltstone (Bazarova et al. 2008, Bazarova et al. 2022).

According to the physiographic zoning proposed by Ivashinnikov (1999, 2010), the territory of the Khanka Lake basin belongs to the Far Eastern monsoon sector, the Priamurye-Primorye country and the Khanka province. The climate of the Khanka lowland is formed mainly due to the circulation of air masses, the redistribution of which is determined by orographic barriers in the form of Sikhote-Alin and East Manchurian mountain ranges. The average temperature in January is -19°C, in July – +20°C. The annual precipitation is 650 mm, of which 90 % falls in the warm season. The range of annual precipitation at some stations is 384–852 mm (Tury Rog) and 323–837 mm (Astrakhanka). The day degree temperatures (above 10°C) in the Khanka Lowland is the highest in Primorye Territory and varies from 2 600 to 2 664°C in different areas. The duration of the growing period ranges from 211 to 217 days. The strongest and most frequent winds are observed in spring, in April and May.

According to the Köppen-Geiger scale, the climate in most parts of Primorye Territory is classified as Dwb, which corresponds to a continental humid climate with dry winters and warm humid summers (Peel et al. 2007).

Causes of water level rise in Lake Khanka

The average area of Lake Khanka is 4 070 km^2 and the average volume is 18.3 km^3. Due to water level fluctuations, these parameters vary from 3 940 to 5 010 km^2 and from 12.7 to 22.6 km^3, respectively (Bortin & Gorchakov 2016). The lake volume fluctuations are cyclic in nature and have approximately 30-year periodicity since the beginning of the 20th century, and since the 1980s the periods have become shorter – 20 years (Zhuravlev et al. 2018). The lake is fed mainly by 24 rivers flowing into it and atmospheric precipitation. The major rivers with the largest catchments are the Komissarovka, Melgunovka and Ilistaya. The main outflow of water is provided by the only transboundary river Sungacha, which, flowing out of the lake, has a confluence with the Ussuri River, as well as by water evaporation. After the construction of the irrigation system, artificial regulation of water withdrawal from the lake, discharge from rice fields and regulation of the flow of the Muling River in China began to have a pronounced impact on the redistribution of the lake's water balance. Since the 2000s, another cycle of increasing Lake Khanka level began, which in 2015 reached 416 cm (with a mean annual level of 293 cm) or 69.78 m in the 1977 Baltic Normal Elevation System (with a mean annual level of 68.54 m) (Georgievsky et al. 2017, Zuenko et al. 2020). Up to the end of 2017, the lake level was increasing; further, until 2021, lake level fluctuations occurred with an amplitude of 0.5 m (Kolomiets et al. 2022). The values of Lake Khanka level obtained from satellite altimetry data presented in the Appendix S1 are on average lower than the observations of the Astrakhanka gauging station, with the correlation coefficient of these series estimated at r = 0.96 (Bortin & Gorchakov 2016), which gives reason to consider

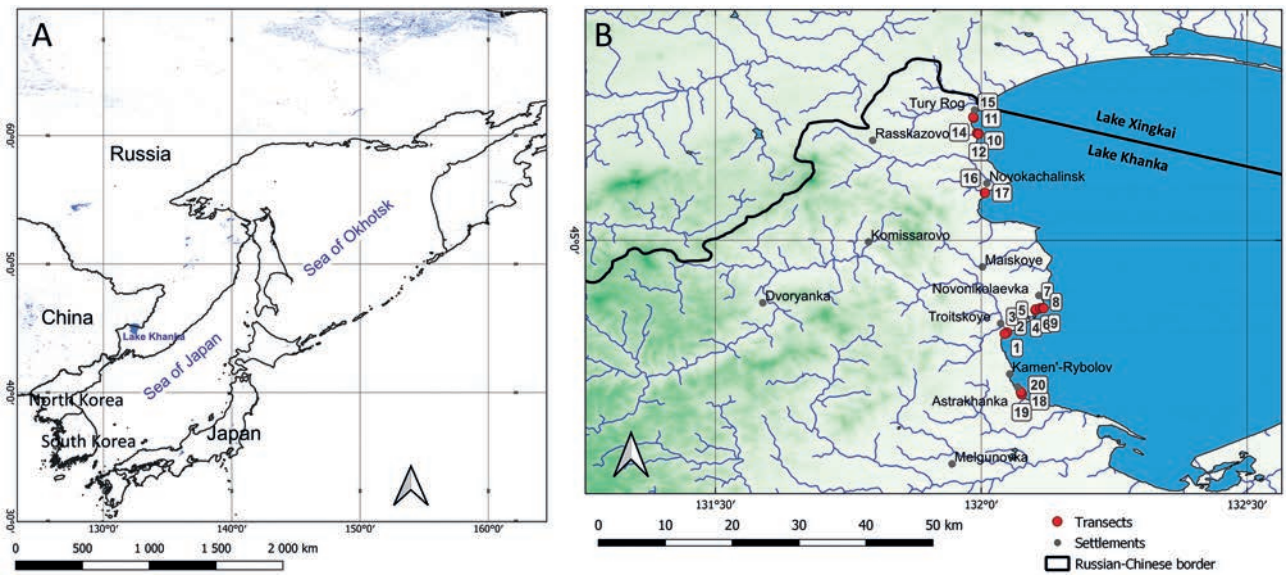

Figure 1 Study area: A – geographic position in northeast Asia, where Lake Khanka is the largest lake in the region; – sampling localities along the western coast of Lake Khanka (here and below, the transect numbers correspond to those in Table 1). Source for the lake polygons (in shapefile): Messager et al. 2016, https://www.hydrosheds.org

the results of altimetric measurements to be sufficiently representative. According to the altimetric data, after 2021 the lake level began to steadily decrease.

The current shape of the Lake Khanka shore is closely related to the history of the lake formation in the periods of climatic shifts, changes in river channels and the nature of accumulation. On a historical time scale, it becomes evident that water levels rise during periods of lake transgression and fall during periods of regression, which in turn were associated with climate warming and cooling, respectively (Baklanov et al. 2019, Bazarova et al. 2022). The description of sedimentary rock layers composing the coastal formations suggests that the lake in its present form began to form in the second half of the middle Holocene (Pavlyutkin & Hanchuk 2002, Bazarova et al. 2018, 2022). The last regression of the lake dates back to the Little Ice Age (1,369 ± 46 – 1,577 ± 63 AD), and the last transgression began in the first half of the 19th century (Bazarova et al. 2022).

Seismic processes may also be responsible for changes in the shoreline and water level of the lake (Baklanov et al. 2019). In 1967, an earthquake occurred near the lake, with ground shaking in Spassk-Dalniy reaching magnitude 6 on the MSK-64 scale (Kolomiets et al. 2022). The last earthquake with magnitude 3.3 was recorded in January 2017 in the southwestern part of the lake. Earthquakes up to magnitude 8 are potentially possible in this area (Kulakov & Myasnikov 2008).

In the Khanka Lake basin, as well as throughout the entire Northwest Pacific Ocean, an increase in precipitation has been observed over the last 20 years, which is associated with an increase in cyclonic activity, including tropical cyclones, which cause various damage to those areas that previously did not fall within the zone of their impact (Altman et al. 2018, Studholme et al. 2022). In 2012–2016, according to data from the Astrakhanka weather station, an abnormally high amount of precipitation fell during the warm seasons (Weather and Climate Reference Portal: http://www.pogodaiklimat.ru/). During this period, the intervals between such anomalies were too short and, consequently, the lake did not have time to discharge excess water. Regression and transgression of the lake basin, seismic phenomena, and increased cyclonic activity are the processes responsible for the long-term fluctuations of the lake water level. However, fluctuations in the lake water level also occur throughout the year, which is related to the amount of precipitation in different seasons, evaporation of moisture from the lake surface, and as a result of wind denivelations. Wind tides, similar to seiches caused by atmospheric pressure fluctuations in different parts of the lake, reach 0.5–0.6 m, and even 1.5–1.6 m at wind speeds of more than 30 m/s (Vas'kovsky 1978, Bortin & Gorchakov 2016, Georgievsky et al. 2017, Baklanov et al. 2019).

In addition to these main causes, whose influence on the lake level is estimated to be high, there are also less obvious factors that may increase with time, such as input of material with surface runoff and siltation of the lake (Bortin & Gorchakov 2016) or poorly studied groundwater flow (Vas'kovsky 1978, Bortin & Gorchakov 2016, Kolomiets et al. 2022).

Vegetation

The most complete information on the vegetation of the Khanka lowland, including the western shore of Lake Khanka, was published by Kurentsova (1962). No further generalizing studies on the plants of the Khanka Lake basin have been conducted. Information on individual communities and plant groups can be found in the works of different authors. Meadow cenoses were additionally considered by Yaroshenko (1962), pine forests by Urusov (1999), and rare plant communities by Krestov & Verkholat (2000). Information on aquatic and semi-aquatic plants was published by Pshennikova (2005). The populations of the rare species *Oxytropis chankaensis* have been studied in the most detail (Nesterova & Bezdeleva 2003, Kholina & Kholin 2008, Kholina et al. 2009). The last list of the flora of the Khanka Lowland was published by Kozhevnikov et al. (2007), but without specifying habitats and species occurrence. Data on the composition of the flora of the Khanka Nature Reserve are given in the publication of Barkalov & Kharkevich (1996), where 150 species of vascular plants are listed for the Cluster Sosnovy on the western side of the lake. Basic information on the composition and occurrence of plants in the coastal communities of Lake Khanka is contained in numerous herbarium collections from the first ones made by R.K. Maak in 1859, F.B. Schmidt in 1859–1862 and N.M. Przhevalsky in 1867–1869 to the present time, i.e. more than 160 years. Most specimens are stored in LE, VLA, VBGI collections (according to Index Herbariorum, Thiers 2022), some material is available in the Global Biodiversity Information Facility (GBIF 2023: https://www.gbif.org/).

In the current survey, the vegetation of the western shore of Lake Khanka is represented by forest communities interspersed with shrublands and meadows, damaged almost annually by fires, sometimes repeatedly. The main oak-birch forests are formed by *Quercus mongolica* Fisch. ex Ledeb. and *Betula davurica* Pall. with other deciduous species such as *Tilia amurensis* Rupr., *Maackia amurensis* Rupr. & Maxim., *Acer mono* Maxim. ex Rupr., and major shrubs such as *Corylus heterophylla* Fisch. ex Trautv., *Lespedeza bicolor* Turcz. and *Rhododendron dauricum* L. (Fig. 2A). In the forests on the territory from Novokachalinsk settlement to Tury Rog village, the proportion of *Tilia amurensis*, *T. mandshurica* Rupr. (Fig. 2B) and *Armeniaca mandshurica* (Maxim.) Skvortsov on open stony slopes is rather significant in the stand composition (Fig. 2C). Coniferous species on the west coast are represented only by *Pinus* × *funebris* Kom. (*Pinus sylvestris* L. in the broad sense). Small patches of pine forests, and more often individual groups of trees are preserved along the coastal sandy clay hills in the vicinity of Tury Rog and along the crests of steep rocky watersheds (Fig. 2D), where fires do not reach. In these areas, the rare species *Juniperus rigida* Siebold & Zucc. occurs in pine forests, with individuals reaching 7–8 m in height. Forest communities are interspersed with meadows of different types: steppe meadows are located on dry slopes and terraces, mesophytic meadows – on gentle slopes and high river terraces, and wet and marshy meadows – in river mouths and lowlands. The

Figure 2 Plant communities of the western coast of Lake Khanka. A – Plant community with *Quercus mongolica* Fisch. ex Ledeb., *Betula davurica* Pall., *Lespedeza bicolor* Turcz. on the abrasive shore of the western coast of Lake Khanka (photo by V.A. Kalinkina – VK); B – Plant community with *Tilia mandshurica* Rupr. and *Quercus mongolica* on the slope facing Lake Khanka, near the village of Tury Rog (photo by VK); C – *Armeniaca mandshurica* (Maxim.) Skvortsov on a steep slope of Lake Khanka near the village of Novokachalinsk (photo by VK); D – Plant community with *Pinus* × *funebris* Kom., *Quercus mongolica*, *Juniperus rigida* Siebold & Zucc. on a clay/sand ledge near the village of Tury Rog (photo by E.A. Marchuk – EM); E – Plant community with *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla, *Nymphoides peltata* (S.G. Gmel.) Kuntze, *Trapa natans* L. near the mouth of the Kamyshovaya River (Cluster Sosnovy of the Khanka Nature Reserve) (photo by V.Y. Barkalov – VB); F – Plant community with *Zizania latifolia* (Griseb.) Hance ex F. Muell., *Carex cespitosa* L., *Butomus umbellatus* L. (adventive species) near the mouth of the Malye Usachi River (village of Novokachalinsk) (photo by EM); G – Plant community with *Ulmus pumila* L., *Artemisia rubripes* Nakai, *Festuca pratensis* Huds. (adventive species) on the shore near the village of Tury Rog (photo by EM); H – Plant community with *Ambrosia artemisifolia* L., *Xanthium orientale* L., *Conyza canadensis* (L.) Cronquist (adventive species) on the Przhevalsky Spit (Cluster Sosnovy of the Khanka Nature Reserve) (photo by VB); I – Plant community with *Salix pierotii* Miq., *Artemisia macilenta* (Maxim.) Krasch., *Corispermum stauntonii* Moq. on the sandy shore near the mouth of the Vtoraya Rechka River (photo by VB); J – Plant community with *Oxytropis chankaensis* Jurtzev, *Potentilla supina* L., *Hierohloe glabra* Trin. on the Przhevalsky Spit (Cluster Sosnovy of the Khanka Nature Reserve) (photo by VB)

estuaries of large rivers (Komissarovka, Bolshiye Usachi, Vtoraya Rechka) are characterized by a large number of channels and small lakes with quite diverse communities of aquatic and semi-aquatic plants (Figs 2E, F). Along the coast near settlements, anthropogenically modified meadow plant communities occupy significant areas (Fig. 2G) with domination of adventive species and weeds such as *Festuca pratensis* Huds., *Bromopsis inermis* (Leyss.) Holub, *Trifolium repens* L., *T. pratense* L., *Artemisia rubripes* Nakai, *A. sieversiana* Willd. On gentle slopes, interhilly depressions and riverside terraces extensive areas are used for arable land, hayfields and pastures. The immediate (flooded) strip of the lake shore is characterized by an unstable set of species, including groups of coastal psammophytes, hygrophytes, anthropophytes, and groups of weedy plants (Fig. 2H). Among tree and shrub species on the coast are *Salix pierotii* Miq. (Fig. 2I), *S. miyabeana* Seemen and *Spiraea salicifolia* L. On the sandy shores of the lake there are communities of the Khanka endemics: *Thymus przewalskii* (Kom.) Nakai and *Oxytropis chankaensis* (Fig. 2J). In places of destruction of high banks with oak communities, some species from these forests reach the coast, where they form temporary groups, generally not characteristic of the coast.

MATERIAL AND METHODS

Sampling

A field expedition was conducted on the western coast of Lake Khanka from July 6 to 11, 2023. Seven sites were selected and 20 transects were laid along a 70-km stretch of the coast from Astrakhanka village to Tury Rog village, six of which (Nos. 4-9) were located within the Cluster Sosnovy of the Khanka Reserve (Fig. 1, Table 1). The Vtoraya Rechka site was also assumed to be a protected site because, being in a difficultly accessible location, it was inaccessible for automobile travel. The remaining four sites had recreational status as they are currently used for recreation and fishing, and three of them (Troitskoye, Novokachalinsk, Tury Rog) have recreation centers and associated facilities along the shoreline. Transect sites were selected based on the location of populations of the rare species *Oxytropis chankaensis*. Information about them was obtained from herbarium specimens stored at the VBGI, VLA, LE and specialized literature (Nesterova & Bezdeleva 2003, Kholina & Kholin 2008, Kholina et al. 2009). The transects were evenly spaced across the selected sites and covered the coastline, which was inundated between 2000 and 2021 and freed from water by July 2023. Figure 3 shows a fragment of the map of the Cluster Sosnovy of the Khanka Reserve with a layer of water surface fluctuation data from 1984 to 2021 provided by Global Surface Water (Pekel et al. 2016; https://global-surface-water.appspot.com/). As can be seen, the transect points are located on the continuous water presence layer through 2021. The pixel size of the publicly available data is equivalent to a 30 × 30 m square, so this information cannot be used for more accurate monitoring. However, it is acceptable for a rough estimate of the extent of flooding. Transects ranging in length from 12 to 58 m were laid perpendicular to the shore in a direction from the water's edge inland along the width of the sand and pebble inundation strip. On the western coast, this inundation strip is bounded from land by a high abrasive bank, either by wetlands or oxbow lakes at the mouths of rivers, and therefore its boundaries are clearly visible. The coordinates of the start and end points of the transects were entered into Android All-in-one OfflineMaps 3.11d software. Along each transect (to the left of the water's edge), 2 × 2 m sample plots were laid out with the distance from the water's edge measured. The size of plots was selected based on the size of natural species communities. A total of 326 plots were identified. All plant species were recorded in each plot, with their abundance expressed as a percentage (projection of above-ground plant parts onto the plot; the sum of the abundance of each plant in this case does not equal the total abundance). For ease of calculation, the lowest abundance value was taken as 1 %. For each plant species, the status of aboriginal or adventive was indicated. All transects were also divided into zones (numbered from the water's edge) corresponding to periods of water retreat, which can be clearly seen by the density of plant clusters repeating wave-like spray lines (Table 2). Two zones were distinguished on the banks of some sites with a narrow strip, such as Vtoraya Rechka, Tury Rog, Sosnovy, and Astrakhanka, and three zones were distinguished in the rest of the sites.

Plant names are given according to Plants of the World Online (POWO, 2023; https://powo.science.kew.org/). In some cases, species names in the narrow sense have been adopted, e.g. *Chenopodium vachellii* Hook. & Arn., *Oxytropis chankaensis*, *Thymus przewalskii*, *Pinus* × *funebris*, used in Russian publications on floras and keys (Kharkevich 1985–1996, Kozhevnikov at al. 2019). The authors give species names according to the International Plant Name Index (IPNI, 2023; https://www.ipni.org/). Species whose identification required further confirmation were collected in herbarium and subsequently deposited in the VBGI. Information on the collected specimens is available in the electronic herbarium of the Botanical Garden-Institute of the

Table 1. Characteristics of the survey sites along the western coast of Lake Khanka

Site No.	Site name	Status	Latitude, ° N	Longitude, ° E	Numbers of transects	Length of transect, m	Number of plots	Number of all species	Number of adventive species
1	Troitskoye	recreation	44°49'37.4"	132°2'54.7"	1, 2, 3	32/ 54/ 36	61	42	12
2	Sosnovy	protected	44°52'7.7"	132°6'6"	4, 5, 6	22/ 24/ 26	36	63	9
3	Sosnovy2	protected	44°52'21.9"	132°6'54.7"	7, 8, 9	32/ 32/ 36	50	59	11
4	Vtoraya Rechka	protected	45°12'3.1"	131°59'32.9"	10, 11, 12	16/ 12/ 14	21	32	6
5	Tury Rog	recreation	45°13'50.4"	131°59'8"	13, 14, 15	42/ 36/ 22	50	44	11
6	Novokachalinsk	recreation	45°5'20"	131°0'24.3"	16, 17	58/ 46	52	42	9
7	Astrakhanka	recreation	44°42'37.9"	132°4'33"	18, 19, 20	44/ 44/ 24	56	76	25

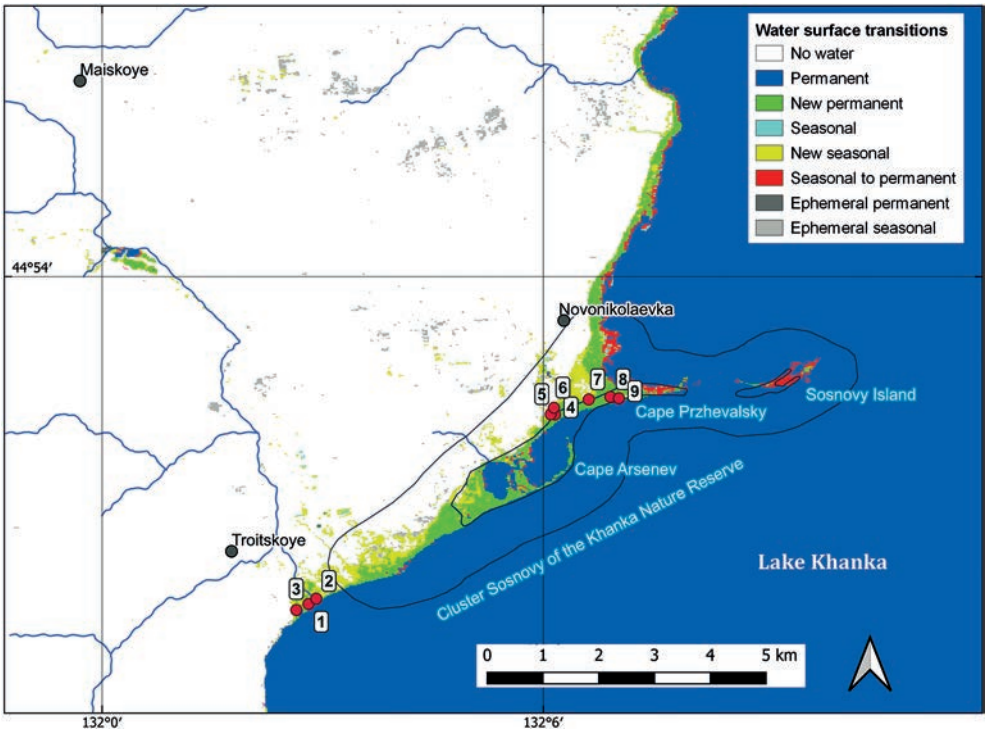

Figure 3 Map of water surface transitions in 1984–2021 for the Cluster Sosnovy of the Khanka Nature Reserve (source for the water surface transitions layer: EC JRC/Google (Pekel et al. 2016; https://global-surface-water.appspot.com/)

FEB RAS (e-Herbarium VBGI; Kislov et al. 2017). The decision on the belonging of the plant to the adventive group was made taking into account the information on the species published in works on the flora of Primorye Territory (Kozhevnikov & Kozhevnikova 2012, 2014, Kozhevnikov et al. 2019) and in the Black Book of the Flora of the Far East (Vinogradova et al. 2021). Maps were produced in QGIS 3.28 (QGIS Development Team 2023).

Diversity analysis

To identify the characteristic features of plant community structure on the western shore of Lake Khanka, we compared the composition and abundance of species at seven sites (Fig. 1; Table 1). For this purpose, we calculated the total number of species (total species richness), the number of aboriginal and adventive species, and their average abundance on the identified transects (alpha-diversity). The Shannon-Wiener (H) and Simpson's (D) diversity indices and the Pielou's evenness index (E) for species abundance were calculated for each site. The resulting index values were then tested for normality of distribution using the Shapiro-Wilk normality test. Analysis of variance (ANOVA) or Kruskal-Wallis test (nonparametric analog of ANOVA) was used to test the significance of differences between indices for transects and sites, depending on the results of the Shapiro-Wilk normality test. Species dominance curves were constructed, and the most abundant species for each site and their proportions relative to the remaining species were determined. Species diversity of aboriginal and adventive species was compared for protected and unprotected recreational sites and the significance of the differences obtained was assessed. The Jaccard similarity coefficient (JAC) was used to assess the significance of differences of sites in terms of species composition (beta diversity) of all species, aboriginal and adventive species separately, and Bray-Curtis dissimilarity (BC) was used to assess the significance of differences of sites in terms of species composition (beta diversity) of all species, aboriginal and adventive species separately. Permutational multivariate analysis of variance (PERMANOVA) based on the Bray-Curtis distance matrix (BC), implemented using the "adonis2" function in the R package "vegan", was applied to assess the significance of differences. PERMANOVA indicates whether group species have similar centroids or not, and assumes equal beta dispersion between groups rather than normality. The "betadisper" function from the R package "vegan" was used to test for beta dispersion. Metric multidimensional scaling – principal coordinates analysis (PCoA) for Bray-Curtis and Jaccard dissimilarity matrices – was used to visualize pairwise comparisons of community structures.

Averaged data from plots laid out along transects at different distances from the shoreline were compared to identify patterns of plant species composition and abundance depending on distance from the water's edge, i.e. for areas that were free of flooding at different times. All sections of the shoreline were included in the analysis, except for the Przhevalsky Spit (Sosnovy2 site), one transect of the Astrakhanka section and one transect of the Sosnovy site, where banded patches of *Phragmites australis* (Cav.) Trin. ex Steud were located between open water and the beginning of the sandy shore. Depending on the wind and tide direction, the spit is subject to multidirectional wave processes and wave rollovers across the sandy spit, which is why, unlike the main shore, there is no clearly defined band of vegetation here. To date, there is no reliable information

Table 2. Characteristics of the zones, corresponding to periods of water retreat, of the coast of Lake Khanka

Zone	Number of plots	Mean width of zone, m	No. of all species	No. of aboriginal species	No. of adventive species
I	89	11.1	72	58	14
II	94	11.1	94	74	20
III	93	17.2	71	56	15

on when this or that strip became flood-free. The available satellite images and the results of their processing have a resolution of 30 m^2, and the observations of the only gauging station in Astrakhanka village cannot be extrapolated to all sites with sufficient accuracy. Information on water recession obtained from local residents and eyewitnesses also varies greatly, even for the same sites. Therefore, zone delineation was conducted visually based on wave splash pattern and plant location. Species diversity was assessed for the three overgrown zones, and Shannon-Wiener (H) and Simpson's (D) indices and Pielou's evenness index (E) of species abundance were calculated. Pairwise comparisons of selected bands were made using Jaccard's similarity coefficient (JAC) and Bray-Curtis dissimilarity (BC). Significance of results was assessed in the same way as in the analysis for sites. Calculations and visualization of results were performed using Microsoft Excel 2013 and the packages "vegan" (Oksanen et al. 2022) and "ggplot2" (Wickham 2016), available in R v. 4.3.0 (R Core Team 2023).

RESULTS

A total of 139 species of vascular plants from 100 genera and 42 families were recorded at all study sites. Of these, 30 species (21.6 %) were alien, including 23 species listed in the Black Book of the Flora of the Far East (Vinogradova et al. 2021). The largest number of species was represented by the following families: Asteraceae (27 species), Poaceae (20), Fabaceae (15), Polygonaceae (12) and Cyperaceae (9). The group of adventive species was also dominated by the family Asteraceae (13). The highest number of species (76) was recorded at the Astrakhanka site, of which one third (25) were adventive species, which is also the highest for all compared sites (Fig. 4). The Shannon-Wiener diversity index for this site also had the highest value of 3.32. The Simpson index, which is sensitive to the presence of abundant species and independent of species richness, had a high value of 0.93, indicating an even distribution of abundance of dominant species. In contrast, the lowest Simpson index value (0.90) was recorded at the Vtoraya Rechka site, where a single species *Phragmites japonicus* Steud was dominant with high abundance. The Astrakhanka, Sosnovy, Novokachalinsk and Troitskoye sites were similar in terms of evenness of species abundance (Fig. 4A). The highest diversity in the proportion of aboriginal species was observed at the Sosnovyy site – 54, with a Shannon-Wiener index of 2.97 and the evenness of abundance of 0.74, which is almost the same as at the Astrakhanka site (Fig. 4B). The lowest number of species was recorded at the Vtoraya Rechka site – 32, the lowest Shannon-Wiener index was 2.77, and the evenness had a value of 0.80. Evenness had the highest values at this site and at the Tury Rog site. The diversity of adventive species at the five sites had approximately the same values (9 to 12 species), but differed in evenness of abundance (Fig. 4C). The same pattern was evident at all sites, with the top five species in abundance accounting for 50 % or more, and the remaining 27 to 71 species accounting for 50 % or less across sites (Appendix S2, S3). Of the 23 species most frequently occurring at different sites, seven were adventive. The invasive species *Ambrosia artemisiifolia* was recorded at six of the seven sites and was most abundant at the Troitskoye and Novokachalinsk sites. The adventive species *Artemisia sieversiana* was recorded only at the Tury Rog and Novokachalinsk sites, where it was among the five most abundant. The Tury Rog site with the dominant species *Xanthium orientale* was the only site with the highest abundance of adventive species. All of the most abundant adventive species were concentrated in areas subject to high recreational or management pressure. Evaluation of Shannon-Wiener diversity index values for adventive species showed significant differences ($F = 9.8$, $p < 0.01$) between protected and recreational sites (Fig. 5). For total species and separately for the aboriginal fraction, the significance of differences was not confirmed ($p = 0.4$ and 0.9, respectively).

Pairwise comparison of descriptions for all species revealed the greatest differences between the Tury Rog and Sosnovy2 sites (BC = 0.89) and the greatest similarity between the Novokachalinsk and Sosnovy2 sites (JK = 0.80). In terms of adventive species, the greatest differences in terms of species abundance were also found between sites Tury Rog and Sosnovy2 (BC = 0.91); sites Vtoraya Rechka and Troitskoye (JK = 0.81) were the most similar in terms of the presence of common species. PERMANOVA based on Bray-Curtis dissimilarity showed significant differences between sites for all species ($F = 3.25$, $p < 0.001$) and separately for aboriginal ($F = 3.15$, $p < 0.001$) and adventive species ($F = 3.12$, $p < 0.001$), indicating that the centroids of these groups were different; however, beta dispersions were not significantly different only for the adventive species groups. This means that the PERMANOVA result may have been due to differences in group variance visualized with PCoA (Fig. 6).

The following zones were conditionally accepted according to the distance from the water's edge: I zone, freed from standing water 1 year ago; II zone – 2–3 years ago; III zone – 3 and more years ago. We compared the composition of all plant species and, separately, of aboriginal and adventive species, Shannon-Wiener and Simpson diversity indices, and the evenness of species abundance in the three selected zones for six sites and in general for the entire coast. It appeared that total species diversity and separately aboriginal and adventive species did not differ among all three zones by sites ($p = 0.3–0.6$) (Fig. 7). When comparing the three zones for all six sites, the highest total diversity (94) and the highest diversity of aboriginal (74) and adventive species (20) was in the second zone from the water's edge (Table 2). Total diversity was similar in the first and third zones with 72 and 71 species, respectively. However, the Shannon-Wiener index, which takes into account the proportion of species in the community, was highest for zone one (3.65) and lowest for zone three (3.40). The distribution of dominant species was similar in zones one and two, with the top five species accounting for 30 and 35 %, respectively; in zone three, 43 % (Appendix S4, S5). The dominant species composition in all zones was represented by both aboriginal and adventive species. The first zone was dominated by the perennial long-rhizomatous *Trifolium repens*, which was not

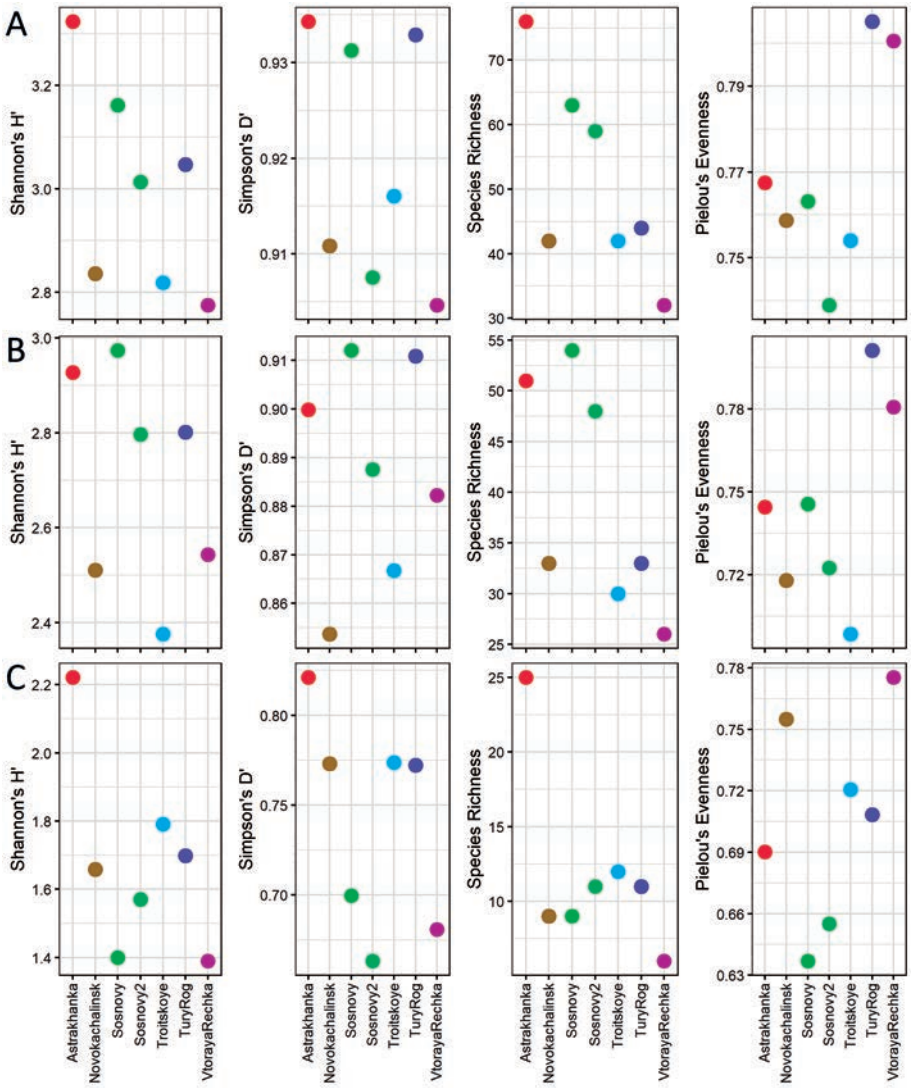

Figure 4 Species diversity indices, abundance, and evenness of plant communities at the survey sites on the western coast of Lake Khanka: A – all species; B – aboriginal species; C – adventive species

expected for this most dynamic strip. However, this species is known for its ability to survive prolonged flooding. The presence of this and a number of other perennials near the water's edge is explained by their biological peculiarities. Individuals washed out of communities away from the shore were thrown as individual ramets (fragments of rhizomes or parts of turf) onto the shore. As the water recedes, the ramets readily become rooted in the loose sandy soil. In addition to this species, the first zone was dominated by juveniles of the aboriginal perennials *Carex capricornis* Meinsh. ex Maxim. and *Artemisia macilenta* (Maxim.) Krasch., the annual *Chenopodium vachellii*, and the invasive annual *Ambrosia artemisiifolia*. In the second zone, *Salix pierotii* was the dominant species. Habitat conditions in this zone (light substrate and periodic moistening) favor the growth throughout the zone of not only this but also other species of the genus *Salix* spp. that remain alive and actively growing after periodic flooding and in the absence of erosion that weakens the root system.

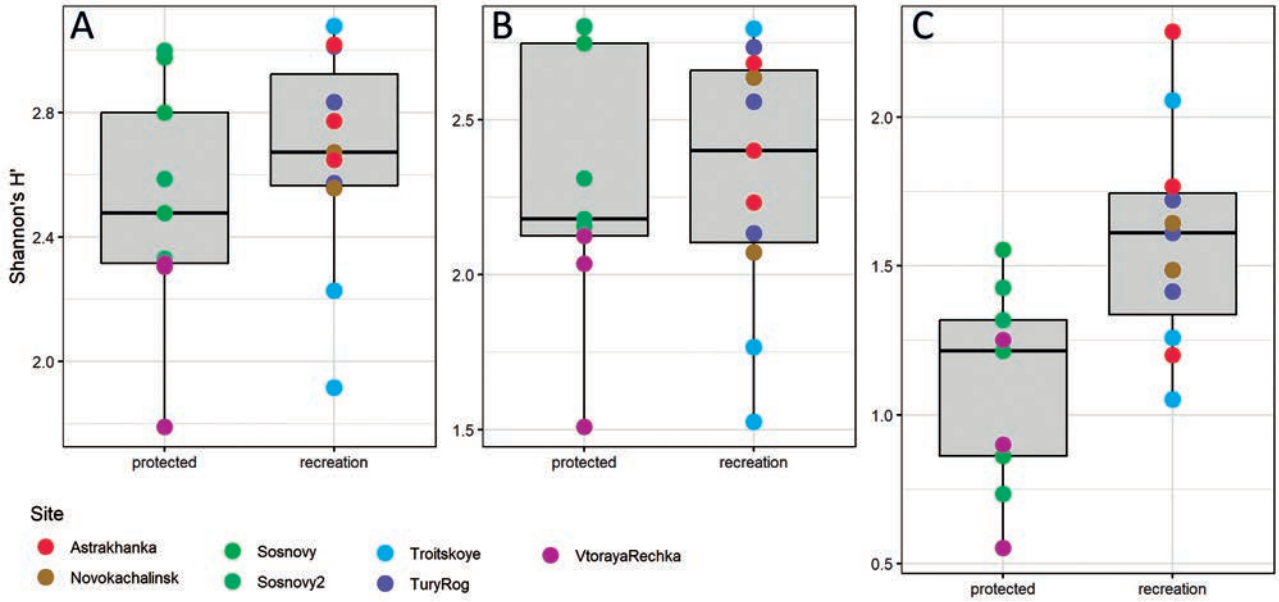

Figure 5 Shannon's diversity index for the protected and recreational sites on the western coast of Lake Khanka: A – all species; B – aboriginal species; C – adventive species ($F = 9.8$, $p < 0.01$)

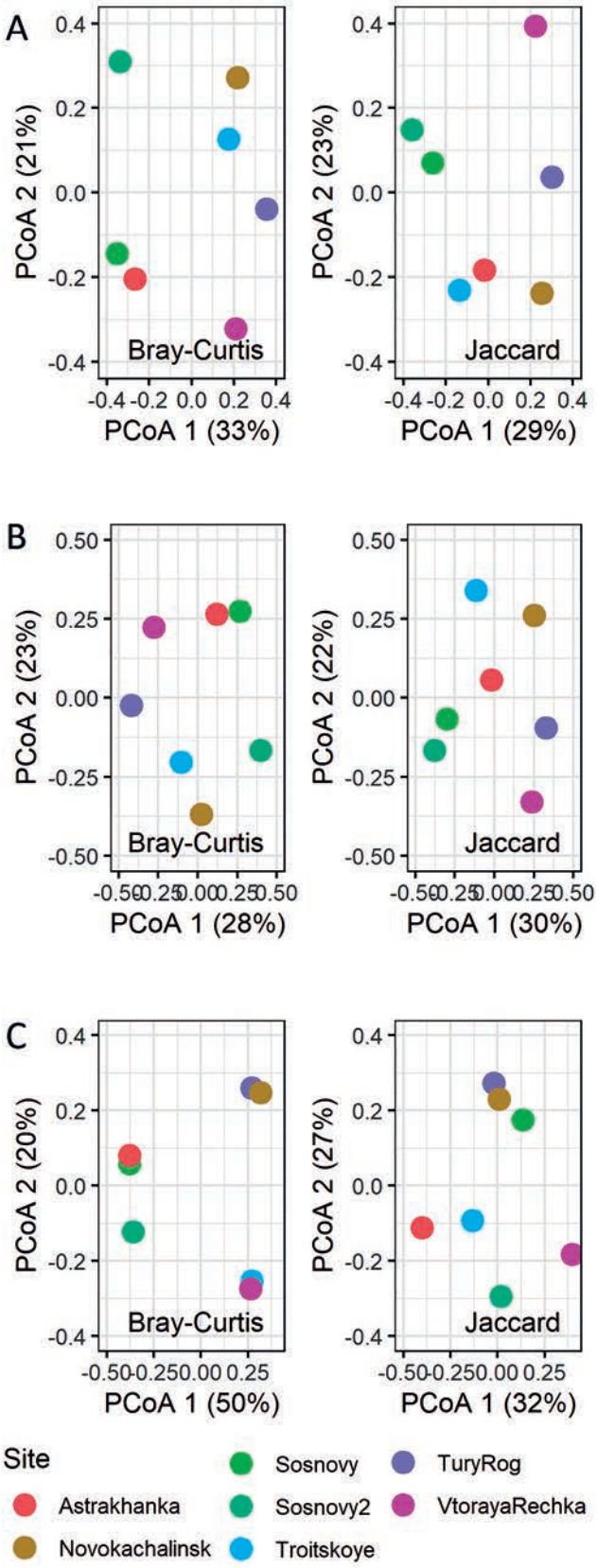

Figure 6 Ordination plots of principal coordinates analysis for Bray-Curtis and Jaccard dissimilarity matrices of community structure across the survey sites on the western coast of Lake Khanka: A – all species; B – aboriginal species; C – adventive species

In the same zone, residual small water bodies or wetlands characterized by moisture-loving species were often observed. Therefore, the second dominant species here was *Phragmites japonicus*. The group of the most abundant species in the second zone already included the endemic *Oxytropis chankaensis*. Among the adventive species, *Trifolium repens* and *Ambrosia artemisiifolia* were the most frequent. In the third zone the main dominants were aboriginal species *Setaria pumila* (Poir.) Roem. & Schult., *Oxytropis chankaensis*, *Potentilla supina* L., and the adventive species *Ambrosia artemisiifolia* and *Oenothera biennis* L.

Pairwise comparisons of descriptions for all species revealed that significant differences existed only between aboriginal species ($F = 1.35$, $p < 0.05$), although beta dispersions for all groups compared were not significantly different. Adventive species were more evenly distributed across the overgrown zones. When comparing the three zones as a whole across all sites, they were found to be different from each other, but the greatest differences were between the first and third zones (BC = 0.62) and the greatest similarity was between the first and second zones (JAC = 0.58). When these three groups were ordinated by the matrices of the calculated Bray-Curtis dissimilarity and Jaccard similarity indices, they separated along the two PCoA axes, which explained 100 % of the variance differences (Fig. 8).

DISCUSSION

Visual assessment of species diversity of the coastal strip of Lake Khanka revealed that abundant adventive species such as *Ambrosia artemisiifolia*, *Xanthium orientale*, *Artemisia* spp. were dominant at all sites, while aboriginal species were few in number. Thus, for the described communities of the western shore of the lake, the share of adventive species amounted to 21.6 %. This is quite a high value compared to the total adventitization of the flora of Primorye Territory, which is 23.3 % (Kozhevnikov et al. 2019). The adventitization index of the flora of the Khanka Nature Reserve, part of the territory of which was included in our study, is 12.1 % (Kozhevnikov & Kozhevnikova 2012). Thus, the ratio of aboriginal and adventive species for the described plant communities of the western coast was two times lower than for the entire Khanka Nature Reserve. According to Barkalov & Kharkevich (1996), 14 adventive species (or 9.3 % of the floristic composition of this cluster) were recorded in the Cluster Sosnovy. According to our data, 14 adventive species were recorded at the same site, of which 11 species appeared to be common since 1996. However, our data reflect the composition of plant communities on transects only; this value will be higher for the flora of the Cluster Sosnovy as a whole. Comparison of species diversity at transects located in the protected area of the Reserve and at unprotected recreational sites showed that the contribution of adventive species is much lower in the former case. However, the visual assessment of the structure of the coastal strip communities did not correspond to the real one. Diversity analysis showed rather high values of the Shannon-Wiener index for individual sites, and for the Astrakhanka site this index was greater than 3 (Fig. 4). Aboriginal dominant species at the Vtoraya

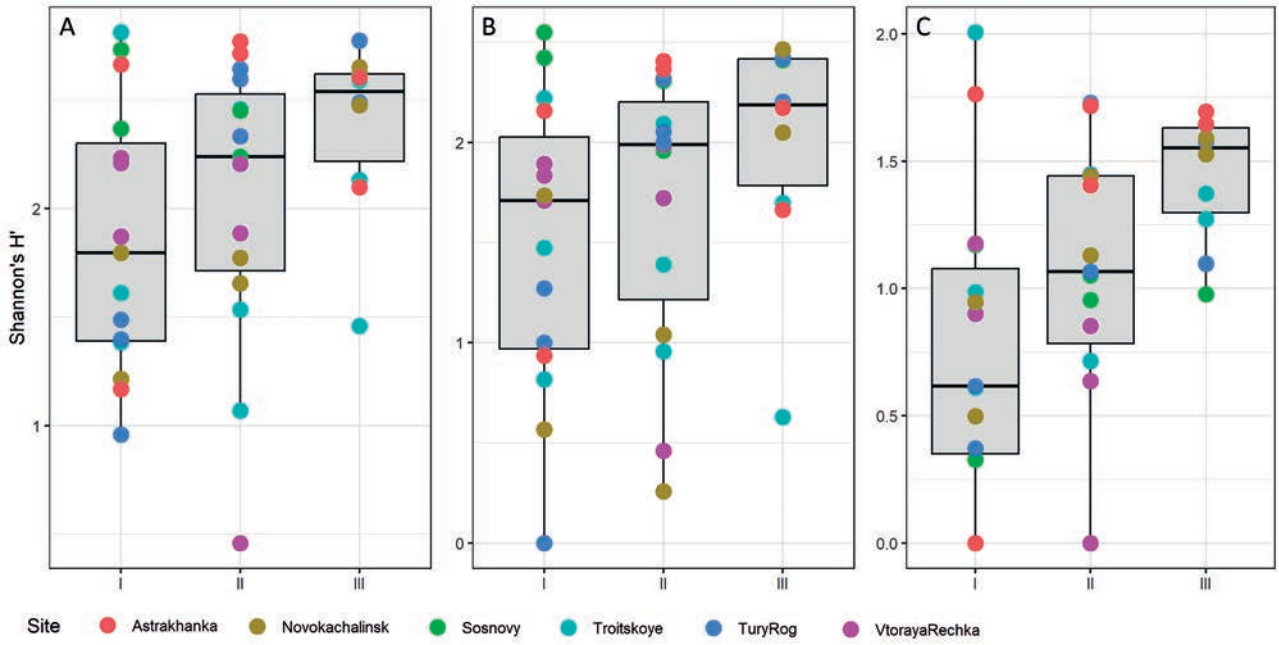

Figure 7 Shannon's diversity index for three flooded zones on the western coast of Lake Khanka: A – all species; B – aboriginal species; C – adventive species

Rechka site were *Artemisia macilenta* and *Corispermum stauntonii* Moq., which formed communities resembling sand dunes or steppes. At the Troitskoye site, the most abundant of the aboriginal species was *Potentilla supina*, which sometimes formed monodominant continuous beds. The evenness of abundance of aboriginal species also had high values, indicating a significant diversity of species in the community (Fig. 4). Five out of six species were typically dominant, 10–12 species had medium abundance, and the highest diversity was observed for species with low abundance (Appendix S2). Species dominance curves in a community that have a long right-hand side indicate a large number of rare species and are considered characteristic of communities developing under favorable conditions where

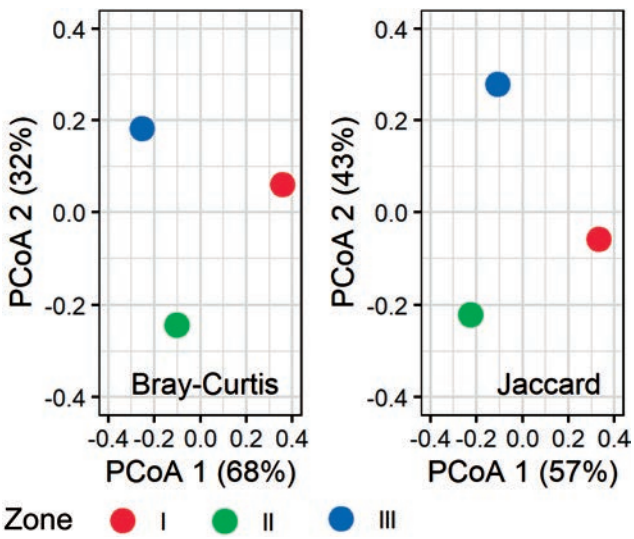

Figure 8 Ordination plots of principal coordinates analysis for Bray-Curtis and Jaccard dissimilarity matrices of community structure with all species across the flooded zones on the western coast of Lake Khanka

competition determines structure (Mirkin & Naumova 2012). However, our study area is subject to periodic floods of varying duration. The flooding factor acts as a stressor. For stressed communities, abiotic factors are the main factors determining their structure, and species diversity usually decreases. In the studied communities, the proportion of species in total abundance was low, not more than 50 %, and hence competition for habitat was low in the communities. Therefore, the main factor responsible for the presence and dominance of species was most likely the rate of their immigration (Akatov et al. 2019). Seed availability played a significant role in this process. Thus, a study of the influence of seed bank in different periods of short-term floods on the formation of coastal communities on the example of water bodies in Australia showed that this factor has a significant effect on the composition and abundance of species under frequent water level fluctuations (Casanova & Brock 2000). In general, the structure of coastal flooded communities on the shores of Lake Khanka is determined by many factors, such as the availability of propagules, competition, plant development cycles, animal pressure, plant resistance to flooding and others, which we did not consider in our study. The results obtained showed the composition and structure of communities only for a certain period of time and under certain conditions, which when changed will also change the pattern of diversity and structure of plant communities.

Assessment of the vegetation cover of the western shore of Lake Khanka revealed well-defined undulating zones differing in species composition and structure in the direction from the water's edge to the island's interior. When laying transects and plots, we immediately marked the boundaries of these visually distinguishable zones. Subsequently, because we were unable to accurately determine standing water periods for some sections of the shoreline, we decided to use these visible zones to estimate the con-

ventionally accepted three periods of water rise and retreat. A similar analysis on vegetation zones was conducted for 20 years in Lake Michigan (Wisconsin, USA) (Rutherford et al. 2022). It showed vegetation dynamics by year between submerged and emergent zones. Our analysis of the diversity of selected overgrowth zones for the six compared sites showed no differences, i.e., for all sites, both the third, earliest emergent zone and the first, recently open drained zone showed a small range of Shannon-Wiener diversity index values (Fig. 7). The lack of significant differences can be explained by the fact that when water receded from the third zone (or even from the wetland meadow), ramets of both individual perennial species and groups of species were transferred to the second and first zones. This equalized the differences in species composition of the overgrowth zones. Generalization of data across zones for all sites showed the highest species richness in the second zone, again due to the introduction of parts of perennials with outgoing water and the presence of residual shallows or wetlands with hydrophytes. Significant differences between overgrowth zones were only shown for aboriginal species, which are more selective to habitat conditions. Regarding the recovery of the endemic *Oxytropis chankaensis*, this species ranked fifth on the dominance diagram for the second zone and second for the third overgrowth zone (Appendix S5), indicating that it had already reached co-dominant status on the coast a few years after the water receded and was recovering its abundance. Thus, the visual assessment of overgrowth after water retreat did not coincide with the calculated one. However, in our opinion, with observations over several years and taking into account the data on plant immigration, it is possible to find a relationship between the overgrowth of the coastal strip and the duration of flooding.

CONCLUSIONS

In general, the data obtained showed for the first time the diversity and structure of coastal plant communities on the sandy-gravel shore of the western shore of Lake Khanka and revealed some processes in their dynamics associated with prolonged water standing. It should be noted that the presented results relate only to temporary plant communities formed on loose sandy-pebble substrates under certain conditions of high water standing. We include the following as major accomplishments of the study: (1) laid relief transects that can be used for further monitoring of vegetation subject to lake level changes, both in unprotected areas subject to recreational pressure and in protected areas of the Khanka Reserve; (2) special attention in the analysis was paid to the diversity of separate fractions of aboriginal and adventive plant species, whose abundance has been shown to be related to various factors such as, firstly, lake level fluctuations and, secondly, anthropogenic load; and (3) these are the first studies that, with further development, will allow estimating the duration of floods based on the composition and structure of plant communities. To address these issues more successfully, long-term monitoring along transects covering at least one 20-30-year cycle of changes in the hydrological regime of Lake Khanka is needed.

ACKNOWLEDGEMENTS

We are grateful to Yu.P. Sushitsky, A.Yu. Baranets, and V.M. Kozyrev for their invaluable support of the field study in the Khanka Nature Biosphere Reserve.

Funding

This research was financially supported by the Russian Science Foundation, grant No. 23-24-00341, https://rscf.ru/project/23-24-00341/.

LITERATURE CITED

Akatov, V.V., T.V. Akatova & S.G. Chefranov 2019. Plant communities of harsh and favorable environments: peculiarities of the organization, dominant structure and its relation to species richness. *Zhurnal Obshchei Biologii* 80(2):145–160 (in Russian with English summary). [Акатов В.В., Акатова Т.В., Чефранов С.Г. 2019. Растительные сообщества суровых и благоприятных местообитаний: особенности организации, структура доминирования и ее связь с видовым богатством // Журнал общей биологии. Т. 80, № 2. С. 145–160].

Altman, J., O.N. Ukhvatkina, A.M. Omelko, M. Macek, T. Plener, V. Pejcha, T. Cerny, P Petrik, M. Srutek, J.-S. Song, A.A. Zhmerenetsky, A.S. Vozmishcheva, P.V. Krestov, T.Y. Petrenko, K. Treydte & J. Dolezal 2018. Poleward migration of the destructive effects of tropical cyclones during the 20th century. *PNAS* 115:11543–11548.

Baklanov, P.Ya., A.N. Kachur, V.V. Ermoshin, S.I. Kozhenkova, A.N. Makhinov, A.N. Bugaets, V.B. Bazarova, V.I. Kim & V.V. Shamov 2019. Current geo-ecological problems within the Lake Khanka drainage basin. *Geography and Natural Resources* 40(4):325–334.

Barkalov, V.Yu. & S.S. Kharkevich 1996. Vascular plants of the Khanka State Reserve. *Botanicheskii Zhurnal* 84(11):104–116 (in Russian). [Баркалов В.Ю., Харкевич С.С. 1996. Сосудистые растения Ханкайского государственного заповедника // Ботанический журнал. Т. 84, №11. С. 104–116].

Baukova, N.G. (ed.) 2022. *Primorsky Krai in numbers: Brief statistical collection*. Primorskstat, 66 pp. (in Russian) [Приморский край в цифрах: Краткий статистический сборник / под ред. Н.Г. Бауковой. Приморскстат, 2022. 66 с.].

Bazarov, K.Yu, E.G. Egidarev & N.V. Mishina 2021. Land use analysis of Lake Khanka basin using remote sensing data. *IOP Conf. Series: Earth and Environmental Science* 895:012007.

Bazarova, V.B., M.S. Lyashchevskaya, T.R. Makarova, R.A. Makarevich & L.A. Orlova 2018. Holocene overbank deposition in the drainage basin of Lake Khanka. *Geologiya I Geofizika* 59(11):1765–1776 (in Russian with English summary). [Базарова В.Б., Ляшевская М.С., Макарова Т.Р., Макаревич Р.А., Орлова Л.А. 2018. Обстановки голоценового осадконакопления в поймах рек бассейна озера Ханка // Геология и геофизика. Т. 59, № 11. С. 1765–1776].

Bazarova, V.B., R.A. Makarevich, E.P. Kudryavtseva, K.Yu. Bazarov, P.F. Brovko & E.G. Egidarev 2022. Development and modern condition of the Western coast of Khanka Lake. *Tikhookeanskaya Geografiya* 3:14–26 (in Russian with English summary). [Базарова В.Б., Макаревич Р.А., Кудрявцева Е.П., Базаров К.Ю., Бровко П.Ф., Егидарев Е.Г. 2022. Развитие и современное состояние западного побережья озера Ханка // Тихоокеанская география. № 3. С. 14–26].

Bazarova, V.B., L.M. Mokhova, L.A. Orlova & P.S. Belyanin 2008. Variation of the Lake Khanka Level in the Late Holocene, Primorye. *Russian Journal of Pacific Geology* 2(3):272–276.

Biang. Available from: https://biang.ru/ Last accessed 28.07.2023.

Bolgov, M.B. & E.B. Arefyeva 2019. Risk assessment of flooding of coastal territories of Lake Khanka with the purpose of developing measures to prevent transboundary emergency situations. *Nauchnye I Obrazovatel'nye Problemy Grazhdanskoi Zashchity* 1(40):57–65 (in Russian with English summary). [Болгов М.В., Арефьева Е.В. 2019. Оценка риска затопления прибрежных территорий озера Ханка с целью выработки мероприятий по предупреждению трансграничных чрезвычайных ситуаций // Научные и образовательные проблемы гражданской защиты. № 1 (40). С. 57–65].

Bolgov, M.V. & Korobkina E.A. 2022 Assessment of the water level of the transboundary Lake Khanka resulted from implementation of the design solutions on cleaning of the Sungacha riverbed from sediments. *Vodnoe Khozyaistvo Rossii: Problemy, Tekhnologii, Upravlenie* 2:53–67. (In Russian with English summary). [Болгов М.В., Коробкина Е.А. 2022. Оценка характеристик уровенного режима трансграничного озера Ханка в результате реализации проектных решений по расчистке истока реки Сунгача // Водное хозяйство России: проблемы, технологии, управление. № 2. С. 53–67].

Bortin, N.N. & A.M. Gorchakov 2016. Causes of the transboundary Lake Khanka extreme high water level. *Vodnoe Khozyaistvo Rossii: Problemy, Tekhnologii, Upravlenie* 4:62–84 (in Russian) [Бортин Н.Н., Горчаков А.М. 2016. Причины экстремально высокого уровня воды трансграничного озера Ханка // Водное хозяйство России: проблемы, технологии, управление. №4. С. 62–84].

Casanova, M.T. & M.A. Brock 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? *Plant Ecology* 147:237–250.

Director, Office of International Standards and Legal Affairs United Nations Educational, Scientific and Cultural Organization (UNESCO) 1971. *Convention on Wetlands of International Importance especially as Waterfowl Habitat*. Ramsar, Iran.

Foreign Agricultural Service. *Lake Khanka (000224) Height Variations from TOPEX/POSEIDON and Jason series Altimetry*. Available from: https://ipad.fas.usda.gov/cropexplorer/global_reservoir/gr_regional_chart_jason1.aspx?regionid=rs&reservoir_name=Khanka&lakeid=000224 Last accessed 28.07.2023.

GBIF 2023. *Global Biodiversity Information Facility*. Copenhagen, Denmark. Available from: https://www.gbif.org/ Last accessed 02.07.2023.

Georgiyevskii, V.Y., A.L. Shalygin, M.V. Bolgov & Y.A. Korobkina 2017. Long-term changes in the level of Lake Khanka and problems of its regulation. *Vodnoe Khozyaistvo Rossii: Problemy, Tekhnologii, Upravlenie* 3:69–88 (in Russian). [Георгиевский В.Ю., Шалыгин А.Л., Болгов М.В., Коробкина Е.А. 2017. Многолетние изменения уровня озера Ханка и проблемы его регулирования // Водное хозяйство России: проблемы, технологии, управление. №3. С. 69–88].

Global Surface Water. Available from: https://global-surface-water.appspot.com/ Last accessed 02.07.2023.

International Plant Names Index (IPNI) 2023. Available from: https://www.ipni.org/ Last accessed 02.07.2023.

Ivashinnikov, Yu.K. 1999. *Physical geography of the Russian Far East*. Far Eastern State University Publishing House, Vladivostok. 324 pp. (in Russian). [Ивашинников Ю.К. 1999. Физическая география Дальнего Востока России. Владивосток: Изд-во Дальневосточного гос. университета, 324 с.].

Ivashinnikov, Yu.K. 2010. *Physical geography and natural resources of the Russian Far East*. Far Eastern State University Publishing House, Vladivostok. 340 pp. (in Russian). [Ивашинников Ю.К. 2010. Физическая география и природные ресурсы Дальнего Востока России. Владивосток: Изд-во Дальневосточного государственного университета. 340 с.]

Jin, X. & X. Jiang 2007. Experience and lessons learned brief for Lake Xingkai/Khanka. In: *Status and prospects of the Russian-Chinese Cooperation in Environment Conservation and Water Management: Materials of the international conference*, pp. 81–108. MNR of Russia, Moscow. http://www.ecoinfo.ru/amur/documents/conference2007.pdf

Kharkevich, S.S. (ed.) 1985–1996. *Vascular plants of the Soviet Far East. Vol. 1–8*. Nauka, Leningrad, Saint Petersburg (in Russian). [Сосудистые растения советского Дальнего Востока / отв. ред. С.С. Харкевич. Ленинград; Санкт Петербург: Наука. 1985–1996. Т. 1–8].

Kholina, A.B. & S.K. Kholin 2008. Intraspecific variation of *Oxytropis chankaensis*, a Far Eastern endemic. *Russian Journal of Ecology* 39(1):14–20.

Kholina, A.B., O.G. Koren & Yu.N. Zhuravlev 2009. Genetic structure and differentiation of populations of the tetraploid species *Oxytropis chankaensis* (Fabaceae). *Russian Journal of Genetics* 45(1):70–80.

Kislov, D.E., V.A. Bakalin, E.A. Pimenova, V.P. Verkholat & P.V. Krestov 2017. An electronic management system for a digital herbarium: development and future prospects. *Botanica Pacifica* 6(2):59–68.

Kolomiets, A.G., M.D. Gerasimenko, N.V. Shestakov & G.N. Gerasimov 2022. Geodynamic research in the area of Lake Khanka. In: *Current problems of geodesy, cartography, cadastre, geographic information technologies, rational land and environmental management. Electronic collection of materials from the International Scientific and Technical Conference*, pp. 59–65. Novopolotsk (in Russian with English summary). [Коломиец А.Г., Герасименко М.Д., Шестаков Н.В., Герасимов Г.Н. 2022. Геодинамические исследования в районе озера Ханка. В сборнике: Актуальные проблемы геодезии, картографии, кадастра, геоинформационных технологий, рационального земле- и природопользования. Электронный сборник материалов Международной научно-технической конференции. Новополоцк. С. 59–65].

Kozhenkova, S.I., Yu.P. Sushitsky, I.M. Tiunov & A.N. Kachur 2021. State Natural Biosphere Reserve "Khankaisky": history and current state In: *Man and the Biosphere. The ever-relevant topic is the interaction of man with nature*, pp. 379–402. Media-PRESS, Moscow (in Russian). [Коженкова С.И., Сушицкий Ю.П., Тиунов И.М., Качур А.Н. 2021. Государственный природный биосферный заповедник «Ханкайский»: история и современное состояние // Человек и биосфера. Вечно актуальная тема взаимодействия человека с природой. М.: Медиа-ПРЕСС. С. 379–402].

Kozhevnikov, A.E. & Z.V. Kozhevnikova 2012. Taxonomical composition and features of the flora of state nature reserves of Primorsky Territory. *V.L. Komarov Memorial Lectures* 59:76–126 (in Russian with English summary). [Кожевников А.Е., Кожевникова З.В. 2012. Таксономический состав и особенности флоры государственных природных заповедников Приморского края // Комаровские чтения. Вып. 59. С. 76–126].

Kozhevnikov, A.E. & Z.V. Kozhevnikova 2014. Taxonomic composition and special features of the natural flora in the Primorsky Territory. *V.L. Komarov Memorial Lectures* 62:7–61 (in Russian with English summary) [Кожевников А.Е., Кожевникова З.В. 2014. Таксономический состав и особенности природной флоры Приморского края // Комаровские чтения. Вып. 62. С. 7–61].

Kozhevnikov, A.E., Z.V. Kozhevnikova, M. Kwak & B.Y. Lee 2019. *Illustrated flora of the Primorsky Territory (Russian Far East)*. National Institute of Biological Resources, Incheon, 1124 pp.

Kozhevnikov, A.E., Z.V. Kozhevnikova & M.V. Legchenko 2007. Plant resources of the Prikhankovye (Primorsky Territory): biodiversity of vascular plants and recent evaluation of anthropogenic changes of the natural flora. In: *Biological resources of the Russian Far East: a comprehensive regional project of the Far Eastern Branch of the Russian Academy of Sciences* (Yu.N. Zhuravlev, ed.), pp. 8–44. KMK Scientific Press, Moscow (in Russian with English summary). [Кожевников А.Е., Кожевникова З.В., Легченко М.В. 2007. Растительные ресурсы Приханковья (Приморский край): биологическое разнообразие сосудистых растений и современная оценка антропогенных изменений природной флоры // Биологические ресурсы Дальнего Востока России: комплексный региональный проект ДВО РАН / под ред. Ю.Н. Журавлева. Москва: Товарищество научных изданий КМК. С. 8–44.]

Kozhevnikova, Z.V. & I.V. Maslova 2022. *Oxytropis chankaensis* Jurtz. is endemic to the shores of Lake Khanka. *Khankaiskii Almanakh* 2:19–24 (in Russian). [Кожевникова З.В., Маслова И.В. 2022. Остролодочник ханкайский (*Oxytropis chankaensis* Jurtz.) – эндемик побережий оз. Ханка // Ханкайский альманах. №2. С. 19–24].

Krestov, P.V. & V.P. Verkholat 2003. *Rare plant communities of the Amur Region*. Vladivostok, 200 pp. (in Russian). [Крестов П.В., Верхолат В.П. 2003. Редкие растительные сообщества Приморья и Приамурья. Владивосток. 200 с.]

Kulakov, A.P. & E.A. Myasnikov 2008. Lake Khanka: new ideas about morphostructure and seismic hazard. *Vestnik FEB RAS* 4:51–57 (in Russian). [Кулаков А.П., Мясников Е.А. 2008. Бассейн озера Ханка: новые представления о морфоструктуре и сейсмической опасности // Вестник ДВО РАН. № 4. С. 51–57].

Kurentsova, G.E. 1962. *Vegetation of the Prikhankaisky plain and surrounding foothills*. Academy of Sciences of the USSR, Moscow; Leningrad, 137 pp. (in Russian). [Куренцова Г.Э. 1962. Растительность приханкайской равнины и окружающих предгорий. М; Л.: Академия наук СССР. 137 с.].

Maslova, I.V. 2016. The influence of Lake Khanka's rising water level on the local population of the Amur softshell turtle. In: *Transboundary Lake Khanka: causes of water level rise and environmental threats* (Yu.N. Zhuravlev & S.V. Klyshevskaya, eds), pp. 198–204, Dalnauka, Vladivostok (In Russian). [Маслова И.В. 2016. Влияние подъёма уровня воды в озере Ханка на состояние местной популяции дальневосточной черепахи // Трансграничное озеро Ханка: причины повышения уровня воды и экологические угрозы / под ред. Ю.Н. Журавлева и С.В. Клышевской. Владивосток: Дальнаука. С. 198–204].

Maslova, I.V. 2021. Preliminary assessment of the current state of the Amur softshell turtle *Pelodiscus maackii* (Brandt, 1857) population and its breeding places in Lake Khanka. In: *Transboundary Lake Khanka: current state and prospects of development of the region* (S.V. Klyshevskaya & T.V. Nikulina, eds), pp. 198–215, Dalnauka, Vladivostok (in Russian). [Маслова И.В. 2021. Предварительная оценка современного состояния популяции дальневосточной черепахи *Pelodiscus maackii* (Brandt, 1857) и мест её размножения на оз. Ханка // Трансграничное озеро Ханка: современное состояние и перспективы развития / под ред. С.В. Клышевской и Т.В. Никулиной. Владивосток: Дальнаука. С. 198–215].

Maslova, I.V., V.Yu. Barkalov & I.P. Polyakov 2023. Big value of a small natural monument of regional significance Mys Devich'y Peski (Primorsky Krai, Russia). *Biota and Environment of Natural Areas* 2:44–61 (in Russian with English summary). [Маслова И.В., Баркалов В.Ю., Поляков И.П. 2023. Большая ценность маленького памятника природы регионального значения «Мыс Девичьи Пески» (Приморский край) // Биота и среда природных территорий. № 2. С. 44–61].

Messager, M.L., B. Lehner, G. Grill, I. Nedeva & O. Schmitt 2016. Estimating the volume and age of water stored in global lakes using a geo-statistical approach. *Nature Communications* 7:13603.

Mirkin, B.M. & L.G. Naumova 2012. *Current state of basic concepts in plant science*. Gilem, Ufa, 488 pp. (in Russian). [Миркин Б.М., Наумова Л.Г. 2012. Современное состояние основных концепций науки о растительности. Уфа: Гилем. 488 с.].

Nesterova, S.V. & T.A. Bezdeleva 2003. Morphological structure variability in *Oxytropis chankaensis* Jurtz. depending on recreational pressure. In: *Plants in monsoon climate. III: Proceedings of III Intarnational conference "Plants in monsoon climate" (Vladivostok, 22-25 October)* (S.B. Gontcharova, ed.), pp. 273–278, BGI FEB RAS, Vladivostok (in Russian). [Нестерова С.В., Безделева Т.А. 2003. Изменение морфологической структуры *Oxytropis chankaensis* Jurtz. в зависимости от степеней рекреационной нагрузки // Растения в муссонном климате. III: Материалы III международной конференции «Растения в муссонном климате» (Владивосток, 22-25 октября 2003 г.) / под ред. С.Б. Гончаровой. Владивосток: БСИ ДВО РАН. С. 273–278].

Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, ... & J. Weedon 2022. *vegan: Community Ecology Package. R package version 2.6-4*. https://CRAN.R-project.org/package=vegan

Pavlyutkin, B.I. & A.I. Khanchuk 2002. New data on the age of Lake Khanka, The Russian Far East. *Doklady Earth Sciences* 383(2):187–189.

Peel, M.C., B.L. Finlayson & T.A. McMahon 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences* 11:1633–1644.

Pekel, J.-F., A. Cottam, N. Gorelick & A.S. Belward 2016. High-resolution mapping of global surface water and its long-term changes. *Nature* 540: 418–422.

Plants of the World Online (POWO) 2023. Available from: https://powo.science.kew.org/ Last accessed 20.08.2023.

Pshennikova, L.M. 2005. *Aquatic plants of Russian Far East*. Dalnauka, Vladivostok, 106 pp.

QGIS Development Team 2023. *QGIS Geographic Information System*. Open Source Geospatial Foundation Project. Available from: http://qgis.osgeo.org Last accessed 30.08.2023.

R Core Team 2023. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: http://www.R-project.org/ Last accessed 10.09.2023.

Rutherford, R., J.A. Hartsock & N.P. Danz 2022. Physical and plant community changes at a Lake Michigan coastal marsh related to a two-meter increase in lake level. *Wetlands Ecology and Management* 30:547–560.

Studholme, J., A. Fedorov, S. Gulev, K. Emanuel & K. Hodges 2022. Poleward expansion of tropical cyclone latitudes in warming climates. *Nature Geoscience* 15:14–28.

Thiers, B.M. 2022. *Index Herbariorum*. https://sweetgum.nybg.org/science/ih/

Urusov, V.M. 1999. *Pines and pine forests of the Far East*. Vladivostok State University of Economics and Service, Vladivostok, 385 pp. [Урусов В.М. 1999. Сосны и сосняки Дальнего Востока. Владивосток: Изд-во ВГУЭС, 385 с.].

Vas'kovsky, M.G. 1978. *Hydrological regime of Lake Khanka*. Gidrometeoizdat, Leningrad, 175 pp. (in Russian). [Васьковский М.Г. 1978. Гидрологический режим озера Ханка. Ленинград: Гидрометеоиздат, 175 с.].

Vinogradova, Yu.K., L.A. Antonova, G.F. Darman, E.A. Devyatova, O.B. Kotenko, E.P. Kudryavtseva, E.B. Lesik (Aistova), E.A. Marchuk, E.G. Nikolin, S.V. Prokopenko, ... & P.V. Krestov 2021. *Black Book of Flora of the Far East: invasive plant species in ecosystems of the Far Eastern Federal District*. KMK Scientific Press, Moscow, 510 pp. (in Russian). [Виноградова Ю.К., Антонова Л.А., Дарман Г.Ф., Девятова Е.А., Котенко О.В., Кудрявцева Е.П., Лесик (Листова) Е.В., Марчук Е.А., Николин Е.Г., Прокопенко С.В., Рубцова Т.А., Хорева М.Г., Чернягина О.А., Чубарь Е.А., Шейко В.В., Крестов П.В. 2021. Черная книга флоры Дальнего Востока: инвазионные виды растений в экосистемах Дальневосточного Федерального Округа. М.: Товарищество научных изданий КМК, 510 с.]

Weather and Climate Reference Portal. Available from: http://www.pogodaiklimat.ru/ Last accessed 28.07.2023.

Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York. https://ggplot2.tidyverse.org.

Yaroshenko, P.D. 1962. *Hayfields and pastures of the Primorsky Krai*. USSR Academy of Sciences, Leningrad, 190 pp. [Ярошенко П.Д. 1962. Сенокосы и пастбища Приморского края. Ленинград: Издательство АН СССР. 190 с.].

Zhuravlev, Yu.N, S.V. Klyshevskaya, P.A. Novikova, M.A. Guzev, E.Yu. Nikitina & Ya.O. Timofeeva 2018. Study of the Khanka Lake fluctuations. *Vestnik FEB RAS* 2:88–94 (in Russian with English summary). [Журавлев Ю.Н., Клышевская С.В., Новикова П.А., Гузев М.А., Никитина Е.Ю., Тимофеева Я.О. 2018. К вопросу о колебаниях уровня озера Ханка // Вестник ДВО РАН. № 2. С. 88–94].

Zhuravlev, Yu.N. & S.V. Klyshevskaya (eds.) 2016. *Transboundary Lake Khanka: causes of rising water levels and environmental threats*. Dalnauka, Vladivostok, 284 pp. (in Russian). [Журавлев Ю.Н., Клышевская С.В. (отв. ред.) 2016. Трансграничное озеро Ханка: причины повышения уровня воды и экологические угрозы. Владивосток: Дальнаука. 284 с.].

Zuenko, Y.I., M.E. Shapovalov & A.S. Kurnosova 2020. Recent changes of water level in Lake Khanka and their consequences for its fisheries resources. *Izvestiya TINRO* 200(4):935–950 (in Russian with English summary). [Зуенко Ю.И, Шаповалов М.Е., Курносова А.С. 2020. Современные изменения уровня озера Ханка и их последствия для промысловых ресурсов // Известия ТИНРО. Т. 200, № 4. С. 935–950].