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RESEARCH PAPER

Estimation of population divergence time and potential distribution of the protected evergreen *Rhododendron brachycarpum* in Russia

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ABSTRACT

Rhododendron brachycarpum is a highly ornamental and pharmacologically valuable species with small populations in Russia. In this study, we used previously obtained data on the variability of nuclear SSR markers to analyze the divergence history of two *R. brachycarpum* populations existing in Russia. Approximate Bayesian computation (ABC) analysis revealed that the divergence between the identified "Korean" and "Japanese" large genetic clusters occurred approximately 436 thousand years ago. The separation of the *R. brachycarpum* populations from Primorsky Krai and Iturup Island from the "Korean" and "Japanese" clusters, respectively, occurred approximately 164 thousand years ago. Using the MaxEnt program, we reconstructed the potential distribution of the species during the LIG, the LGM, and future periods (2061–2080). It was shown that the species contracted its range during periods of warming and expanded its range during periods of cooling. Reduced variability and small numbers of populations in the territory of the Russian Federation require special attention to the conservation of the species, including biological methods of combating pathogenic organisms and the possible enrichment of the genetic variability of natural populations through *in situ* introduction of genotypes from the species' main range.

Keywords: Ericaceae, *Rhododendron brachycarpum* subsp. *fauriei*, the Kuril Islands, Sikhote-Alin, protected species, genetic divergence, ecological modeling

РЕЗЮМЕ

Полежаева М.А., Шуваев Д.Н., Бондарчук С.Н. Оценка времени расхождения популяций и потенциальное распространение охраняемого вечнозеленого вида *Rhododendron brachycarpum* в России. *Rhododendron brachycarpum* – высокодекоративный и фармакологически ценный вид с малочисленными популяциями на территории РФ. В настоящем исследовании для анализа истории дивергенции двух существующих на территории России популяций *R. brachycarpum* были использованы данные изменчивости ядерных SSR маркеров, полученные нами ранее. Анализ DIYABC показал, что дивергенция между выявленными "Корейским" и "Японским" крупными генетическими кластерами произошла примерно 436 тыс. лет назад. Отделение популяции *R. brachycarpum* из Приморского края от "Корейского" кластера и популяции с о-ва Итуруп от "Японского" кластера, соответственно, произошло около 164 тыс. л.н. С помощью программы MaxEnt реконструировано потенциальное распространение вида в период LIG, LGM, а также в будущем в 2061–2080 гг. Показано, что в периоды потепления вид сокращал, а в периоды похолодания расширял свой ареал. Сниженная изменчивость и малочисленность популяций на территории РФ требует особого внимания к охране вида, включая биологические методы борьбы с патогенными организмами и возможного обогащения генетической изменчивости природных популяций за счет интродукции *in-situ* генотипов вида из основных частей ареала.

Ключевые слова: Ericaceae, *Rhododendron brachycarpum* subsp. *fauriei*, Курильские острова, Сихотэ-Алинь, охраняемый вид, генетическая дивергенция, экологическое моделирование

Electronic Appendices
http://www.geobotanica.ru/bp/2026_15_02/BP_2026_15_2_polezhaeva_e_suppl_1.pdf
http://www.geobotanica.ru/bp/2026_15_02/BP_2026_15_2_polezhaeva_e_suppl_2.xlsx
http://www.geobotanica.ru/bp/2026_15_02/BP_2026_15_2_polezhaeva_e_suppl_3.pdf

Rhododendrons (*Rhododendron* L.) constitute a large genus of woody plants that are widespread across the Northern Hemisphere (Chamberlain et al. 1996). Recently, this genus has been the subject of active research using population genetic methods, especially in Asia, where the center of its species diversity is located (Milne et al. 2010, Shrestha et al. 2018, Xia et al. 2022). Besides their high ornamental and pharmacological value, wild rhododendron species serve as convenient model organisms for studying various fundamental biological processes, including the history of regional flora formation (Milne et al. 2004, Yu et al. 2019). The genus comprises more than 1 000 species, with only about 20 species occurring in Russia (Aleksandrova 1975, Harmaja 1991), some of which are at the northern limit of their range. Species with restricted or fragmented distributions warrant special attention, since geographically

isolated populations are more vulnerable to anthropogenic impacts and climate change, leading to loss of genetic diversity and decreased adaptive capacity (Lesica & Allendorf 1995, Hampe & Petit 2005, Vranckx et al. 2012).

Rhododendron brachycarpum D. Don ex G. Don. (subgenus *Hemenanthes*) (Fig. 1A,B) is one of the rhododendron species with marginal, small populations in Russia, which has its main range in the southern part of north-east Asia, around the Sea of Japan. The largest populations of this subalpine species are distributed along the mountain range on the eastern edge of the Korean Peninsula and in the central mountain range of Japan (Ohwi 1965, Naganuma et al. 2006, Lee & Shim 2011). It is typical of the upper treeline zone at altitudes of approximately 1000 m above sea level, where it appears as a multi-stemmed shrub 3–5 m tall. At higher altitudes, it assumes a prostrate form up to 1 m in height, leaving the forest zone. Like many rhododendrons, *R. brachycarpum* is a valuable species used in traditional medicine across Asia (Park et al. 2025). Its small populations within its main range are protected (Lee et al. 2002, Lee 2009).

In Russia, *R. brachycarpum* is known from only a few localities in the southern part of the Far East. Populations in the Terneysky District of Primorsky Krai, within the Sikhote-Alin State Nature Biosphere Reserve, were first found in 1968 and described by Shemetova (1970). These plants grow at altitudes of 650–850 m above sea level, in the undergrowth of spruce-fir forests and old, decaying Korean pine forests (Shemetova 1970, Mazurenko 1980, Flyagina 1985, Bondarchuk 2014). Initially, these populations were classified as *Rhododendron fauriei* Franch., but later as *R. brachycarpum* subsp. *fauriei* (Franch.) D.F. Chamb. Although both of these name are still used, it has been considered incorrect under current botanical nomenclature rules. Recent studies employing molecular genetic markers and electron microscopy have shown that *R. fauriei* is not a separate species, and the populations from Primorsky Krai are now classified as *R. brachycarpum* (Polezhaeva et al. 2021a, Terentieva et al. 2025). Additional populations are found in the Kuril Islands: two on Kunashir Island with a small number of individuals, and a more numerous population on Iturup Island (Mazurenko 1980, Barkalov 2009, Linnik et al. 2020, Terentieva et al. 2025). In Russia, this species is listed in the Red Data Books at both federal and regional levels (Geltman 2024, Kozhevnikov 2008, Eremin & Taran 2019).

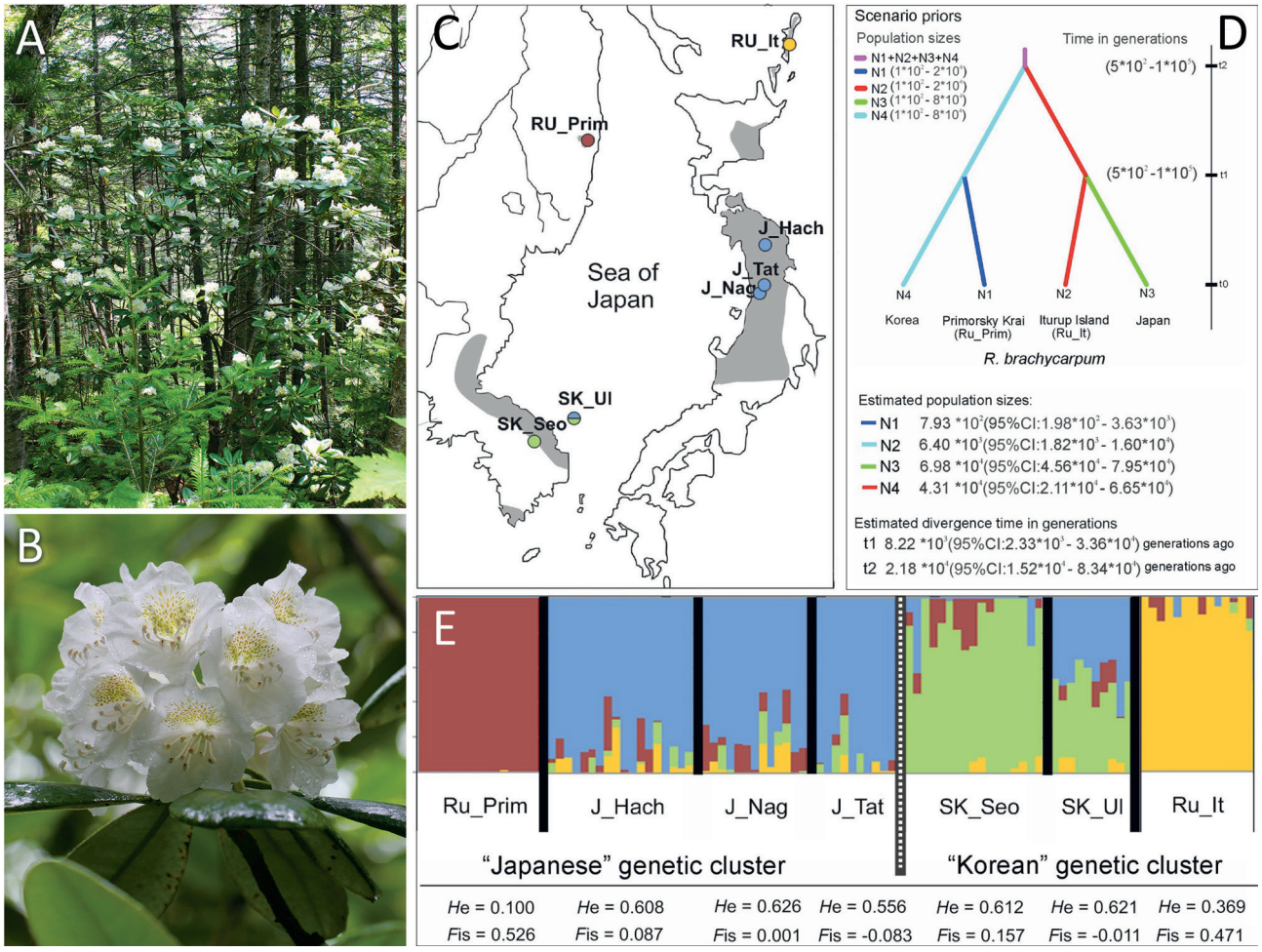

Figure 1 *Rhododendron brachycarpum* D. Don ex G. Don (syn. – *Rhododendron fauriei* Franch.). A – general view and B – inflorescence from Sikhote-Alin State Nature Biosphere Reserve, Primorsky Krai, Russia. Foto by S.N. Bondarchuk; C – geographical localities of the sampling sites of *R. brachycarpum* in North-East Asia; D – DIYABC scenario and estimations of population sizes and divergence time for the two and four genetic clusters within *R. brachycarpum*, respectively; E – STRUCTURE assignment of 97 individuals to ancestral groups (K = 2 – dotted line and K = 4 – solid lines); parameters of genetic diversity (*He*) and coefficient of inbreeding (*Fis*) for marked for each population, corresponding to Polezhaeva at al. 2021a

Recently, there has been considerable discussion regarding threats to the conservation of rhododendron habitats due to anthropogenic pressures, outbreaks of diseases and pests, natural habitat degradation, and competitive displacement by other species driven by climate change (Yu et al. 2019). Projections suggest that many rhododendron species will alter their distribution in the future (Li et al. 2023, Ao et al. 2025), either contracting or shifting their ranges northward, which may predominantly impact marginal populations. Therefore, studying the demographic history of *R. brachycarpum*, including its disjunctive populations in Russia, as well as reconstructing and predicting changes in its range under climate change scenarios, is crucial for developing effective conservation strategies.

Previously, we investigated the genetic variability of 14 nuclear microsatellite loci (SSR, simple sequence repeats) in *R. brachycarpum*, including samples from Primorsky Krai and Iturup Island. We identified the main intraspecific genetic clusters and characterized population variability parameters (Polezhaeva et al. 2021a). However, the divergence time among these genetic clusters was not determined.

In this study, we aim to utilize the existing dataset on the variability of 14 nSSR loci (Polezhaeva et al. 2021a) to estimate the divergence time between genetic clusters, with particular focus on the disjunctive populations of *R. brachycarpum* in Russia. Additionally, we attempt to evaluate how past climatic fluctuations have affected the species' distribution using MaxEnt modeling (Phillips et al. 2006). Projecting into the future under climate change scenarios for 2080 will enable us to assess the potential threat of range reduction for *R. brachycarpum* across Northeast Asia, especially within Russia, where it is listed as VU D2 and requires prioritized monitoring (Geltman 2024).

MATERIAL AND METHODS

Divergence time estimations

For calculations, we used variability data at 14 nSSR loci for 97 individuals from seven *R. brachycarpum* populations from a previous study (Polezhaeva et al. 2021a). The locations of the samples are shown in Fig. 1C. To estimate the time of historical divergence (td) and the historical effective population size (Ne), we employed an Approximate Bayesian Computation (ABC) approach implemented in DIYABC version 2.1.0 (Cornuet et al. 2014). The following scenario (Fig. 2D) was used to estimate the divergence time between previously revealed four genetic clusters within *R. brachycarpum* (Fig. 2E). We estimated the divergence time between the "Japanese" and "Korean" genetic clusters at time t2, as well as the divergence time between the population from Iturup Island and other "Japanese" populations, and between the relict populations from Primorsky Krai and other "Korean" populations at time t1 (Fig. 1D).

The set of priors for the historical parameters was as follows: the effective population sizes for N1 (Primorsky Krai) and N2 (Iturup Island), ranging from 100 to 20 000; and for N3 (Japan) and N4 (Korea), ranging from 100 to 80 000. According to ontogenetic studies (Mazurenko 1980, Vrishch & Rodnova 2004), *R. brachycarpum* (syn. *R. fauriei* Franch.) first flowers in the wild at age 20–30 years, depending on environmental conditions, and individuals can live up to 100 years or longer. Assuming a mean generation time of 20 years, the divergence time t2 (split between the "Japanese" and "Korean" groups) ranged from 500 to 100 000 generations, and the divergence time t1 (differentiation of the population from Primorsky Krai from Korea, and the population from Iturup Island from Japan) also ranged from 500 to 100 000 generations. Since microsatellite variability data were used, a Generalized Stepwise Mutation (GSM) model was applied, with a mutation rate of 10^{-5} to 10^{-3} substitutions per locus per gen-eration (Li et al. 2002). A total of 100 000 simulations were run for the scenario. The DIYABC option 'pre-assessment of a priori combinations of scenarios' was used to initially test the scenario, prior values, and determine the optimal set of summary statistics. The final summary statistics included: the mean number of alleles, mean genic diversity, mean size variance, F_{ST}, and again the mean number of alleles and mean size variance. Subsequently, the 'model checking' option was used for analysis. The estimates in generations were calibrated assuming a mean generation time of 20 years.

Species Distribution Modeling (SDM)

Bioclimatic variables

The all modern bioclimatic layers (from bio1 to bio19) were retrieved from CHELSA Current Bioclimates, Version 1.2. We checked these layers for collinearity using SDM Toolbox v2.5 (Brown et al., 2017), implemented in ArcGIS Desktop 10.8.2 (ESRI, USA). We set $|r| < 0.8$ (the Pearson coefficient) as the threshold for correlation on standardized variables. Bioclimatic layers from correlated pairs were selected based on the jackknife test, using AUC (Area Under Curve) on test data. The future bioclimatic layers (CMIP6 climate projections) were retrieved from WorldClim (Fick & Hijmans 2017) to test SSP126, SSP370, and SSP585 (Shared Socio-economic Pathways) scenarios for the period 2061–2080. These scenarios reflect the lowest various values in terms of anthropogenic radiative forcing, ranging from the optimistic SSP126 to the most pessimistic SSP585 (CMIP6 Model Description 2021).

Occurrence data

Distribution data for *R. brachycarpum* were retrieved from the GBIF database (GBIF 2026). The first dataset included 893 records from the natural distribution range. Subsequently, we performed spatial filtering of records in R 4.0.3 (R Core Team 2013) with the 'spThin' 0.2.0 package (Aiello-Lammens et al. 2015). Thus, we removed obvious outliers and points located at a distance of less than 10 km from each other. The total number of occurrence records for *R. brachycarpum* after data filtering was 289 (Supporting information 2).

MaxEnt modeling

The potential distribution was modeled in MaxEnt v3.4.1 (Phillips et al. 2006). MaxEnt settings were applied using the following options: regularization multiplier values (0.1, 0.5, 1.0, 2.0, 3.0, 4.0); five feature class combinations (linear, quadratic, product, hinge, and threshold features); 500 iterations; 10 replicates; output format (cloglog). The final models were selected based on AUC_{TEST} criteria.

RESULTS

Divergence history

The 'pre-evaluate scenario and priors' option clearly showed that the observed data set was placed within the 1 000 (1 %) simulated data sets (Supporting information 1). Therefore, the chosen statistics are suitable for the priors and fit the model. The analysis revealed the following historical effective population sizes for genetic clusters within *R. brachycarpum*: for the population from Primorsky Krai (RU_Prim, N1) is 793 (95 % CI: 198–3 630); for the population from Iturup Island (RU_It, N2) is 6 400 (95 % CI: 1 820–16 000); for the "Japanese" genetic cluster (J_Hach, J_Nag, J_Tat, N3) is 69 800 (95 % CI: 45 600–79 500); and for the "Korean" genetic cluster (SK_Seo, SK_Ul, N4) is 43 100 (95 % CI: 21 100–66 500). The divergence time estimate (t2) within *R. brachycarpum* was inferred at 2.18×10^4 (95 % CI: 1.52×10^4 - 8.34×10^4) generations ago for the "Japanese" and "Korean" genetic clusters, which, assuming an average generation time of 20 years, corresponds to 436 thousand years ago (95 % CI: 304 Ka – 1.6 Ma). The time estimate (t1) for separating populations from Iturup Island and Primorsky Krai from the "Japanese" and "Korean" genetic clusters, respectively, was inferred 8.22×10^3 (95 % CI: 2.33×10^3 - 3.36×10^4) generations ago, which corresponds 164.4 Ka (95 % CI: 46.6 Ka – 672 Ka) years ago.

Species Distribution modeling

Bioclimatic variables

Three variables showed a correlation threshold below |0.8|: bio7, bio12, and bio13 (Supporting Information 3, Table S1). However, we rejected the bio13 variable, which had the smallest contribution in AUC, to reduce the complexity of the model. Variables bio4, bio6, bio17, bio18, and bio19 were selected from correlated pairs based on the jackknife test, using AUC on test data (Supporting Information 3, Fig. S1). We retained bio1 (annual mean temperature) because it provides greater realism in the current range model. Moreover, the variables bio1 (annual mean temperature) and bio12 (annual precipitation) have the highest gain when used in isolation from other variables. Thus, we used the eight variables: bio1 (annual mean temperature), bio4 (temperature seasonality), bio6 (minimum temperature of the coldest month), bio7 (temperature annual range), bio12 (annual precipitation), bio17 (precipitation of the driest quarter), bio18 (precipitation of the warmest quarter), and bio19 (precipitation of the coldest quarter).

Model accuracy

Values of AUCTEST for different regularization multiplier values are presented in Supporting Information 3 (Table S2, Fig. S2). Based on a comparison of the map outputs, we chose the model for future and past projections with a regularization factor of 1.0, which resulted in the smallest deviation of the predicted range areas from the documented range.

Response curves

For easier interpretation, response curves represent the correlation between each selected variable and other variables (Fig. 2). The optimal range (>0.75 probability) of mean annual temperature (bio1) for *R. brachycarpum* was 5–10°C. The corresponding annual temperature amplitude (bio7) was 30°C. The standard deviation of the mean monthly temperatures × 100 (bio4), or temperature seasonality, ranged from 7000 to 8000. The temperature of the coldest month (bio6) was between -10 and -5°C. The distribution of precipitation data (bio12, bio17, bio18, bio19) was as follows: for average annual precipitation (bio12), 1500–2000 mm; for precipitation of the driest quarter (bio17), 200–600 mm; for precipitation of the warmest quarter (bio18), 500–1200 mm; and for precipitation of the coldest quarter (bio19), 200 mm and more.

Current, past, and future distribution maps

The current distribution prediction for *R. brachycarpum* appeared plausible at a probability threshold of suitable conditions above 0.75 (Fig. 3A). When projecting the model to the Last Glacial Maximum (Fig. 3B), an expansion of suitable areas potentially occupied by *R. brachycarpum* was observed. In contrast, during the Last Interglacial (Fig. 3C), the prediction suggests a reduction in suitable habitats. A stronger reduction in suitable habitats is predicted for future climate change scenarios (Fig. 3D–F).

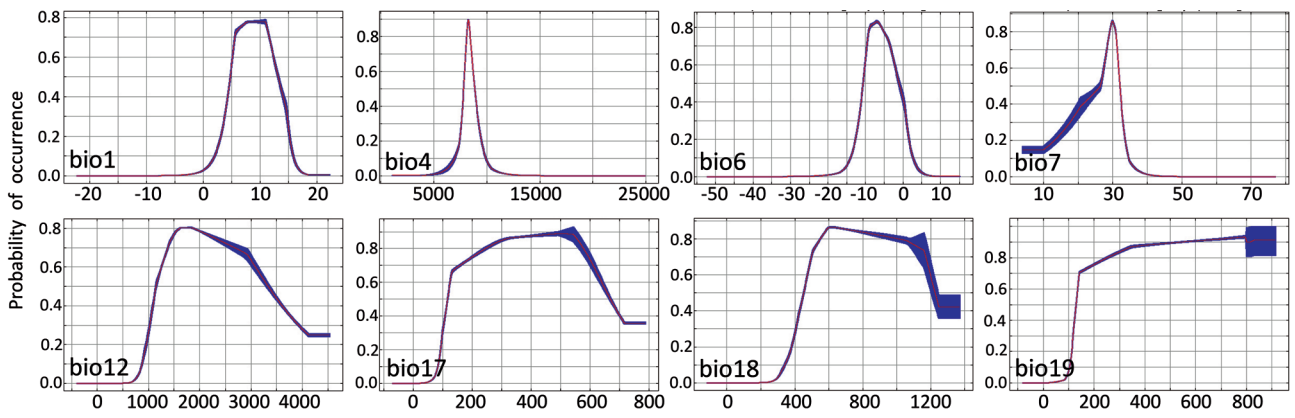

Figure 2 Response curves for probability of presence of *Rhododendron brachycarpum*; mean value (red) and 95 % envelope (blue), n_{rep} = 10

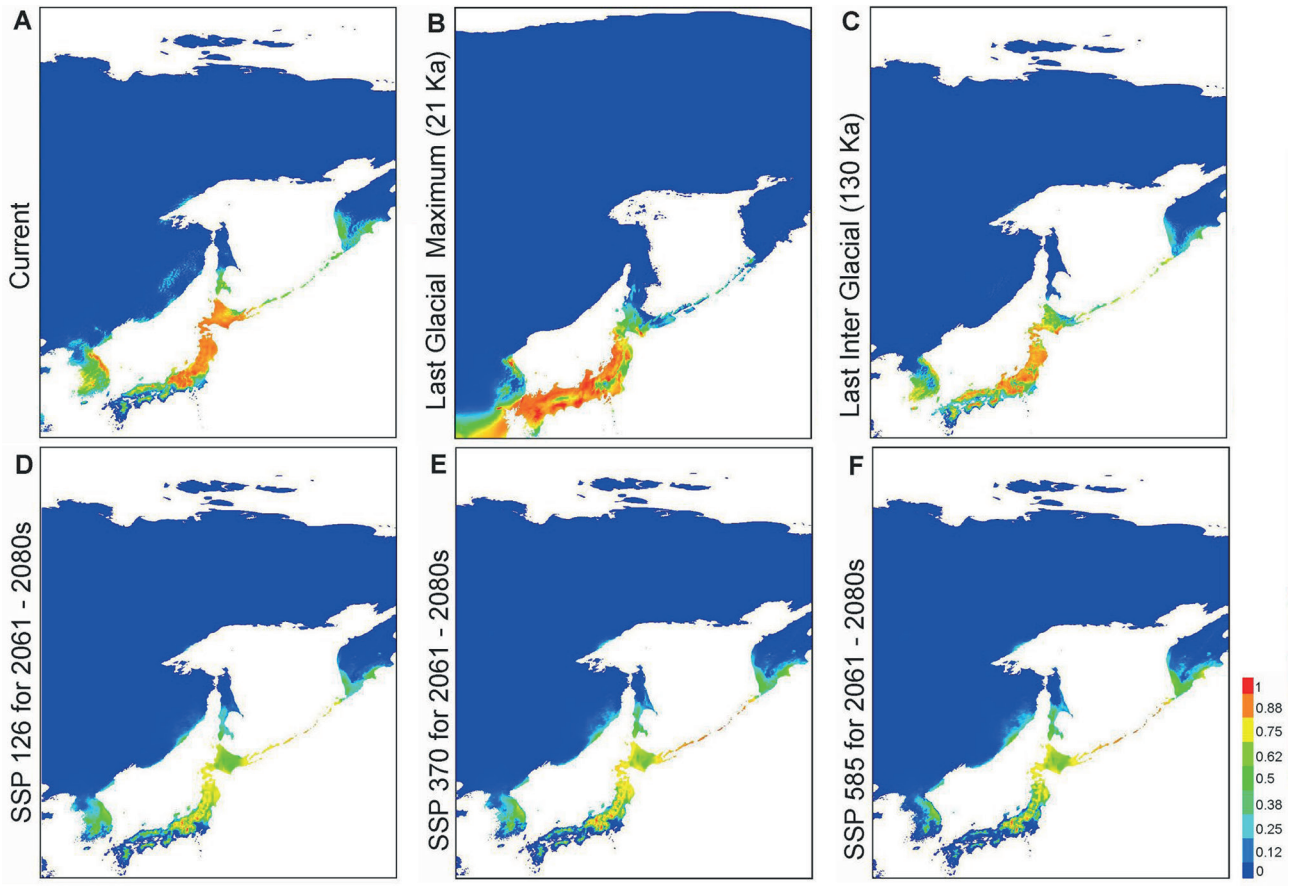

Figure 3 Climatic suitability for *Rhododendron brachycarpum* for the present (A), the Last Glacial Maximum (21000 years BP) (B), the interglacial period (120,000 years BP) (C) and for the 2061–2080 (D–F). Colors from green to red indicate the most suitable habitats

DISCUSSION

Genetic structure and effective population sizes

Previously, we revealed highly structured genetic variation within *R. brachycarpum* (Polezhaeva et al. 2021a). This pattern is consistent with the concept of highly differentiated species with a narrow geographic range and internal migration barriers due to complex topography (Hamrick 2004, Chung et al. 2014). We identified four genetic clusters within the distribution range of *R. brachycarpum* (Fig. 1E): two clusters with populations from Korea and Japan, respectively, and separate clusters with samples from marginal populations of Primorsky Krai (RU_Prim) and Iturup Island (RU_It), respectively. It was shown that the populations of *R. brachycarpum* from Iturup Island were closely related to the Japanese populations, and the populations from Primorsky Krai were closely related to the Korean populations (at K=2, Fig. 1E), which corresponded to their relationship, geographical proximity, and similarity of some morphological characteristics (Polezhaeva et al. 2021a). Moreover, for isolated populations of *R. brachycarpum* from Primorsky Krai on the north-eastern slope of the Sikhote-Alin mountain range and Iturup Island, the lowest degree of genetic diversity (*He*=0.100 and *Ne*=0.369, respectively) and the highest inbreeding coefficient (*Fis*=0.526 and *Fis*=0.471, respectively) were revealed (Fig. 1E). The low genetic variability values are consistent with the DIYABC analysis results obtained in this study, which model a low historical effective population size for the regional populations – only 793 individuals for the population from Primorsky Krai and 6 400 individuals for Iturup Island. Historical effective population sizes from the main parts of the range in Japan and Korea are much higher – 69 800 and 34 000, respectively. The effective population size (*Ne*) reflects the number of individuals required to maintain current genetic diversity and is usually smaller than the actual population size. According to the latest monitoring data from the Sikhote-Alin State Nature Biosphere Reserve (S.N. Bondarchuk, personal observations), the population size in Primorsky Krai is estimated at approximately 0.18 individuals per square meter, with the planting area of the species being approximately 35 hectares. Despite the total number of individuals in the Sikhote-Alin State Nature Biosphere Reserve being estimated at about 4 000 individuals, low genetic variability is observed. Our study involved samples from three monitoring populations, and among 31 individuals, only 15 different genotypes were identified, with only three of the 14 nSSR loci being polymorphic (Polezhaeva et al. 2021a, in Supporting Information). The decrease in genetic variability may be due to the prevalence of clonal reproduction in rhododendrons; however, monitoring data indicate that seeds are the only mode of reproduction in populations of Primorsky Krai (Bondarchuk 2014, Eremin & Taran 2008). It should also be noted that, despite the

large number of individuals, only a small part reach a height of more than 1.5 m and ensure reproduction; numerous seedlings and young plants may not survive to reproductive age at all (Bondarchuk, personal observations; Vrishch et al. 2010). Thus, the significant genetic depletion of these populations can be explained by long-term isolation and the bottleneck effect. On Iturup Island, the actual population size is approximately 1 000 individuals (Geltman 2024), but levels of genetic diversity are higher here, with 10 of 14 nSSR loci found to be polymorphic. DIYABC estimates that the effective population size required for the current genetic diversity on Iturup Island is several times larger than the actual population size, which may indicate less genetic drift in this population and a stable historical size with a recent decline event.

Estimates of divergence time

During the late Pleistocene, the southern Far East was free of glaciation. This created a unique environment where northern and southern biota survived and mixed (Korotky et al. 1999). Many species with a wide range in the southern part of northeast Asia have their northern boundaries or isolated populations in the Russian Far East. Recent studies have extensively addressed the biogeography of mountain flora species common in this region. These include assessments of divergence between closely related species or disjunctive populations within a species based on molecular genetic marker variability (Ikeda 2023). It is generally accepted for European biota that the patterns of genetic variation observed today are primarily due to events during the Last Glacial Maximum (LGM), which occurred approximately 21 000 years ago (Taberlet et al. 1998). However, recent studies of cold-resistant species in northeast Asia show that earlier warming events preceding the LGM had a greater impact on the formation of their genetic structure. For most alpine species in the family Ericaceae, divergence dates to the last interglacial (LIG) period or earlier: for *Cassiope lycopodioides* Pall. about 106.9 Ka (Ikeda et al. 2014), for *Phyllodoce nipponica* Makino – 249.0–180.2 Ka (Ikeda & Setoguchi 2013), for *Phyllodoce aleutica* Spreng. – 82.0–56.4 Ka (Ikeda et al. 2018), for *Therorhodion camtschaticum* Pall. about 228 Ka (Polezhaeva et al. 2025), for *Rhododendron aureum* Georg. 113.4–165.2 Ka (Polezhaeva et al. 2021b). The divergence between *Abies nephrolepis* Maxim. and *A. sachalinensis* Mast., two Far Eastern firs, phytocoenotically associated with *R. brachycarpum*, was approximately 588 Ka. Divergence within *A. sachalinensis* was about 118 Ka, which also aligns with the LIG (Semerikov & Semerikova 2023).

In this study, DIYABC analysis revealed that the divergence time between the main "Japanese" and "Korean" genetic clusters of *R. brachycarpum* is approximately 436 Ka. Taking the confidence interval into account, this estimate corresponds to the middle Pleistocene, specifically within the climate cooling-warming cycle of stages MIS11–MIS12 (the marine isotope stages). The separation of the Iturup Island population from the "Japanese" cluster, and the relict Primorsky Krai population from the "Korean" cluster, dates back to approximately 164.4 Ka. This period nearly coincides with the range of the last interglacial (LIG). Thus, intraspecific divergence aligns with the sensitivity of this cold-resistant species to global temperature increases and climate aridity. These factors are reflected in the contraction of their range during warm climate periods.

It is important to note that divergence estimates depend on many factors. These include wide variations in generation times for herbaceous versus woody species, assumptions about mutation rates of genetic markers, and sometimes broad confidence intervals that can span several climate cycles. Nevertheless, the results, along with data on genetic variability and morphology (Polezhaeva et al. 2021a, Terenteva et al. 2025), enhance our understanding of the origin of marginal populations of *R. brachycarpum* in the Russia. These relict populations probably formed part of a continuously distributed population in the past. They were fragmented by climate changes that favored the species' shift to higher latitudes in southern regions with sufficient moisture. Divergence estimates for these populations emphasize their genetic uniqueness and long-term persistence in their natural habitats. Paleontological data support this scenario, indicating that boreal plant complexes persisted for a long time in the Kuril Islands and Primorsky Krai (on the eastern macroslope of the Sikhote-Alin Mountains) (Korotky et al. 1999, Bogatov 2002, Barkalov 2009, Krestov et al. 2009). This contradicts the theory of a recent migration of *R. brachycarpum* from southern refugia in Korea or Japan.

Ecological modelling

The most plausible current distribution model showed that the key variables for *R. brachycarpum* are: bio1 (mean annual temperature), bio4 (temperature seasonality), bio6 (minimum temperature of the cold month), bio7 (annual temperature range), bio12 (annual precipitation), bio17 (precipitation of the dry quarter), bio18 (precipitation of the warm quarter), and bio19 (precipitation of the cold quarter). The range of bio1 was within the temperate climate zone. This zone is characterized by a clear division of the year into cold and warm seasons (bio7) with pronounced temperature differences (bio4). These estimates are consistent with the annual temperature range in inland mountainous regions of Hokkaido Island and the central mountains of Honshu Island (Japan Alps) (Japan Meteorological Agency, 2025). The high seasonal temperature variations (bio4) are explained by significant microclimate variability in the mountains, near large bodies of water, and in agreement with the narrow latitudinal gradient of the species. *Rhododendron brachycarpum* grows in both coastal and mountainous areas at various altitudes with well-drained soil. Bio6 corresponds to mild winter temperatures. However, cultivation experience indicates that *R. brachycarpum* can withstand short-term cold temperatures down to -35°C (Aleksandrova 1975). Precipitation data (bio12) align with the species' preference for moist, non-wetting soil. In the mountains, rainwater does not linger long on slopes. Optimal precipitation levels for the warm (bio18) and dry (bio17) quarters suggest that *R. brachycarpum* is a typical mesophyte. Its preference for abundant precipitation in the cold quarter (snow, bio19) indicates the importance of this

factor for winter survival. Thus, *R. brachycarpum* is a species tolerant of cold and seasonal temperature fluctuations. It prefers moderately warm or cool summers with sufficient precipitation – up to 2000 mm per year.

The climatic preferences of *R. brachycarpum* define specific distribution patterns when extrapolating the range to the periods of the Last Glacial Maximum (LGM) and Last Interglacial (LIG). These patterns are consistent with those observed for other cold-resistant species from Northeast Asia, such as *Juniperus* (Hantemirova et al. 2017), *Rhododendron aureum* (Polezhaeva et al. 2021b), and *Therorhodion* (Polezhaeva et al. 2025). These species expanded during periods of cooling and contracted during warming. For example, extrapolating the model to the LGM indicates a wide expansion of suitable habitats. These included the southern half of Honshu Island, the southern islands of Shikoku and Kyushu, the Korean Peninsula, and northeastern China (Fig. 3B). During different geological periods, these habitats served as refugia for various vegetation types and ecosystems. In central and southern Honshu during the LGM, refugia existed for evergreen broadleaf forests. These areas were not affected by the overall trend towards climate aridization (Krestov et al. 2009; Takahara et al. 2023). Additionally, the northeastern and southwestern parts of Honshu differed in their dominant species during the LGM. Temperate conifers characterized the southwest, while boreal conifers dominated the northeast (Takahara et al. 2023). Hokkaido Island was also covered by forests of boreal *Larix*, *Pinus*, and *Picea* species (Igarashi 2010). Today, most of Hokkaido is occupied by mixed and broadleaf forests, where *R. brachycarpum* also occurs. In our LGM range extrapolation, the species' preferred conditions primarily corresponded to the southern and northwestern parts of Honshu, but not the northeastern parts or Hokkaido Island. These areas had milder climates. This further emphasizes the relict and isolated status of *R. brachycarpum* populations in Primorsky Krai and the Kuril Islands. They are likely remnants of a once more widespread distribution.

Extrapolations to the LIG indicate a reduction in the species' range during this late Pleistocene thermal maximum. According to literature data (Lee & Shim 2011) and our analysis of preferred bioclimatic variables (Fig. 2), *R. brachycarpum* belongs to the group of montane mesophytes of the coastal-aquatic complex. These species often have ranges limited by specific habitat conditions with narrow tolerances. They are confined to particular mountainous regions that combine moderate moisture, proximity to water bodies, and rocky or pebbly substrates. Therefore, *R. brachycarpum* can grow both near the upper coniferous tree line and within mixed and broadleaf forests (Naganuma et al. 2006, Lee & Shim 2011). Interestingly, our modeling results align with the distribution of vegetation types on Honshu Island based on palynological data. During the MIS5e period (LIG), communities of temperate deciduous broadleaf forests were described for northeastern and central Honshu. The southwestern part of Honshu, on both the Sea of Japan and Pacific Ocean sides, was characterized by heat-loving evergreen broadleaf forests (Takahara et al. 2023). These growing conditions in the southwestern Japanese islands likely were not suitable for *R. brachycarpum*, given its adaptation to moderately cold environments. Our LIG extrapolation suggests that *R. brachycarpum* may have persisted in the Southern Japanese Alps and in the mountain ranges of Shikoku and Kyushu. During both glaciation and warming periods, altitudinal zonation in mountain regions would have allowed populations to survive (Tzedakis et al. 2002).

Our analysis suggests that *R. brachycarpum*, a pacific subalpine species, expanded during the cooling period and contracted during the warming. Extrapolating these findings to future climate models appears pessimistic under three scenarios for 2061–2080 (Fig. 3D–F). All projections show a sharp decline in suitable habitat across all Japanese islands. The greatest decline is expected in southern Honshu and Hokkaido, as well as the Korean Peninsula. Favorable conditions may persist in the central Japanese Alps, possibly in the coastal mountains of northern Honshu and Hokkaido. The central islands of the Kuril chain will also become favorable for the species, although *R. brachycarpum* is currently only recorded on the southern islands and is unlikely to migrate to the central islands by 2061–2080. Interestingly, the most severe scenario, SSP585, shows a weak but significant potential for suitable habitat in the Russian coastal region, where relict populations of *R. brachycarpum* are currently located.

Conservation issues

Past climate change has been a major factor in shifting plant communities. It has also caused localized or even complete extinctions of entire taxa. Species with restricted ranges, adapted to a limited set of environmental factors, are particularly vulnerable. Our prediction for the future range contraction of *R. brachycarpum* is quite pessimistic. This contraction could become even more severe if anthropogenic factors are added to climate-related ones. Currently, continuous monitoring of the species in Russia is conducted only in Primorsky Krai, within the Sikhote-Alin State Nature Biosphere Reserve. Despite the stable numbers of these populations, they deserve special attention. Given the low genetic diversity and small modeled effective population size, most individuals in the population are likely closely related. A study on *R. brachycarpum* in Korea found that parental inbreeding reduces offspring fitness in natural populations. This mainly occurs through decreased survival of inbred seedlings at various developmental stages (Hirao 2010). Furthermore, reduced variability makes these populations vulnerable to rapidly changing biotic and abiotic environmental factors. For example, the development of transport infrastructure and climate change both facilitate the spread of dangerous invasive pathogens into new territories. Recently, new parasitic fungal infestations have been identified in populations of *R. brachycarpum* in the Sikhote-Alin State Nature Biosphere Reserve. Isolated lesions first noted in 2005 and appeared as dried, blackened generative buds on rhododendron plants. Since 2010, when a tourist route was opened in this area, lesions on generative buds and leaf blades have been observed in all three visited sites.

Over the past four years, unfavorable weather conditions, such as short periods of abnormal heat, have caused irreversible damage to the plants. The rhododendron bushes

have suffered from reduced foliage. As a result, the plants are unable to grow normally and enter winter in a weakened state. In the past two years, there have been cases of death among adult generative specimens after hibernation, which is particularly alarming. Mycological studies conducted from 2024 to 2026 identified two species of aggressive parasitic fungi: *Synnemapestaloides rhododendri* and *Seifertia sikhotensis*. The first was a new species for Russia, and the second was new to science (Malysheva et al. 2026).

Therefore, to improve the resistance of these relict populations in the face of biotic and abiotic influences, it is advisable to use biological pathogen control methods. It is also recommended to increase genetic diversity by *in situ* introduction of genotypes from other parts of the range, such as Iturup Island, Korea, and Japan. Enrichment with new genotypes will make populations more stable. At the same time, locally adapted genotypes should be preserved in botanical garden collections and *in vitro* collections.

CONCLUSION

Rhododendron brachycarpum is a unique species with marginal populations in Russia. It requires special conservation attention. Our study showed that the divergence between the main genetic clusters within species occurred approximately 436 000 years ago. The separation of marginal populations in Primorsky Krai and Iturup Island took place around 164 000 years ago. Species distribution modeling indicated that *R. brachycarpum* expanded its range during cooling periods and contracted during warming periods. Future projections for 2061–2080 suggest a significant reduction in suitable habitat. This underlines the need to develop conservation measures, including biological control of pathogens and the increase of genetic diversity of populations in Russia.

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