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Biogeography of *Therorhodion* in Northeast Asia and Western North America Emphasising Their Past and Future Expansion

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ABSTRACT

Aim: To assess the origin, biogeographic history of three *Therorhodion* species in the Pacific region; to reveal the differentiation within *T. camtschaticum* across its range from Beringia to Japan; and to discuss the role of Beringia as a refugium in the past and the future.

Location: Northeast Asia and Western North America.

Methods: We analysed 122 original specimens of three species (*T. redowskianum*, *T. glandulosum* and *T. camtschaticum*) from Russia, China, the United States and 43 GenBank accessions from Japan, using seven nuclear loci. We use different approaches to infer genetic structure, divergence time estimations, ancestral area reconstructions and species distribution modelling to better understand the history of the mountain flora in the Pacific region.

Results: Three genetic clusters with an origin in northeast Asia corresponding to the three species were distinguished. The divergence time between *T. redowskianum* and the other two species was estimated at 19.2 Mya and between *T. glandulosum* and *T. camtschaticum* was estimated at 2.13 Mya. Within *T. glandulosum* and *T. camtschaticum*, no Western or Eastern Beringian clades were recovered. At the same time, two subclusters were inferred within *T. camtschaticum*, one including populations from Kamchatka, the Aleutian Isl., the Kuril Isl. and partly Japan, and a second one including other populations from Japan, Sakhalin and Khabarovsk, which were identified with a divergence time estimation at 228 Ka BP. Species distribution modelling revealed that the global distribution area during the LGM remained relatively stable for all three taxa, although we observed some local geographical contractions. In contrast, global range contractions for the three species were predicted for the LIG and future climatic changes in 2061–2080.

Main Conclusions: We show that *Therorhodion* originated in northeast Asia and diverged during the cooling of the late Miocene, with further diversification and dispersal across the Bering land bridge during the late Pliocene-Pleistocene. Although previous studies found no obvious signs of hybridisation between species in their range overlaps, we revealed traces of some genetic contribution of *T. glandulosum* in *T. camtschaticum* populations in Khabarovsk Krai. This study highlights the significance of the including samples from entire range of a species and using different types of markers for adequate biogeographic inferences. It also supports the role of Beringia as a refugium for arctic flora not only in the past, but also into the future.

1 | Introduction

Beringia is a vast land area between northeastern Asia and western North America periodically exposed due to falling sea levels that was unglaciated during the peaks of the Ice age (Hultén 1937). This land bridge is recognised as both the origin and a refugium of many modern alpine plant species (Hultén 1937; Brubaker et al. 2005; Lozhkin et al. 2007; Ickert-Bond et al. 2009), and it also served as a vital corridor for intercontinental migrations (Wen et al. 2016; Graham 2018; Jiang et al. 2019). Range dynamics of arcto-alpine plants in the Beringian region, depending on climatic oscillations, lead to the expansion of species to the south, the formation or disruption of their ranges, and repeated interactions between disrupted populations during the Pleistocene (Ikeda et al. 2018, 2020). *Therorhodion*, a genus with an only a few species, some of which with a specific distribution on both sides of Beringia in Northeast Asia (Western Beringia) and Western North America (Eastern Beringia) is a good model for the study of diversification and phylogeography in this region.

Therorhodion (Maxim.) Small is a small genus of three species within the Ericaceae, which were formerly placed in *Rhododendron* L. and finally classified as a separate genus after a series of phylogenetic (morphological and molecular) analyses (Gillespie and Kron 2010; Goetsch et al. 2005; Kron 1997; Sarwar and Takahashi 2013; Wang et al. 2007a, 2007b). The genus includes three small alpine deciduous subshrubs with bright pink flowers. *Therorhodion redowskianum* (Maxim.) Hutch. is a diminutive subshrub (5–15 cm tall), found scattered across northeast Asia in small thickets in tundra communities, mainly on rocky ledges. The range covers most of the Siberian territory of Russia including territories around Lake Baikal to the northeast margins of Asia but not reaching Chukotka and with rare occurrence on Sakhalin Island (Aleksandrova 1975; Chepinoga et al. 2024) (Figure 1A). Outside of Russia there are several locations of *T. redowskianum* in North Korea (e.g., Jeju-do Island) and North East China, Jilin (Chang et al. 2014; Fang et al. 2005; Malyschev 2006). *Therorhodion camtschaticum* (Pall.) Small and *T. glandulosum* Standl. ex Small, both known under the common name 'Kamchatka rhododendron', are small shrubs about 30 cm tall with similar morphology. These species are distributed in alpine and subalpine zones, in tundra communities and in the upper forest belt of the Pacific region, both in East Asia and western North America (Figure 1A). Although *T. glandulosum* is often referred to as a variety of *T. camtschaticum* s.l., especially in the Russian-language literature (Aleksandrova 1975; Yurtsev et al. 2010), it is treated as a separate species in western North America (Kron and Judd 2009; Viereck and Little 1972). Several recent studies using molecular markers have substantiated the reciprocal monophyly of these two species (Hata et al. 2017; Oliver 2017; Polezhaeva et al. 2020, 2025). The migration history and distributional boundaries of these species in Beringia have been established using three plastid DNA markers and 10 nuclear microsatellites (Polezhaeva et al. 2025). Two migration paths were determined, the first being a northern route for *T. glandulosum* from northeast Asia (Okhotsk coast, Kolyma region, Chukotka, central and northern Kamchatka) to the Seward Peninsula in northern Alaska. A southern pathway for *T. camtschaticum* extends from the southern part of western Beringia (the Sikhote-Alin, Sakhalin, the Kuril Islands and southern Kamchatka) to the Aleutian Islands and the coast of southeast Alaska. According to demographic analysis using nSSR data, the divergence time between *T. camtschaticum* and *T. glandulosum* is estimated to be in the Pleistocene (Polezhaeva et al. 2025).

Therorhodion is the sister clade to *Rhododendron* in all phylogenies to date, recognised by many as subgenus *Therorhodion* (Khan et al. 2021; Milne 2004; Mo et al. 2022; Shen et al. 2024; Xia et al. 2022), it is the earliest diverging lineage inferred to have diverged in the Palaeocene, ~56 Mya (Mo et al. 2022; Xia et al. 2022). All rhododendron lineages have undergone significant divergence from their Paleogene ancestors, the *Therorhodion* lineage has remained sparse, containing only three species (Xia et al. 2022). Although hybridisation is quite common in rhododendrons (Yan et al. 2017; Zhang et al. 2020; Zheng et al. 2021), there is lack of evidence that *Therorhodion* species share the same habitat or hybridise. In some cases, all three species are mentioned to coexist in the same geographical area. For example, all three of them are identified near the western border of the Sea of Okhotsk in northern Khabarovsk Krai and two species, *T. camtschaticum* and *T. glandulosum*, occur in the Kamchatka Peninsula, (Aleksandrova 1975; Hohryakov 1991; Yakubov and Chernyagina 2004). The divergence between these species maybe attributed to both their distinct, narrow ecological niches and historical range dynamics. Climatic fluctuations such as Pleistocene glacial cycles and ecological specialisation are well-documented drivers of species divergence and range evolution in the Northern Hemisphere (Hewitt 2000; Ikeda 2022).

Species distribution modelling (SDM) can provide insights into species ranges (Gavin et al. 2014) and additional information for phylogeographic conclusions (Alvarado-Serrano and Knowles 2014). SDM methods utilise spatially referenced target species observations and environmental data to predict the relative likelihood of past and future species distributions. Combined with genetics, SDM can shed light on both the past species ranges and their future response to climate change through habitat preferences. The question of future changes in species ranges is of particular interest for *Therorhodion* species as they represent northern communities whose biodiversity is dramatically affected by global warming (Pepin et al. 2015; Rantanen et al. 2022). Predictions have been made for rhododendrons, closely related to *Therorhodion*, indicating that they will shift their ranges northwards or even become extinct under global climate warming (Li et al. 2023, 2024). Although *Therorhodion* species are evaluated as taxa of Least-Concern (Gibbs et al. 2011), they are quite rare and are listed on the regional protected species lists in some territories of Russia (Plantarium 2025). Therefore, it seems necessary to predict future range changes in accordance with the developed climate scenarios. These species, growing at high altitudes, may occupy narrow niches due to the distinct local characteristics of high-mountain ecosystems, which should be taken into account when developing conservation programs. Unfortunately, the ecology of these species remains understudied, but future prospects for changes in their range are of significant interest,

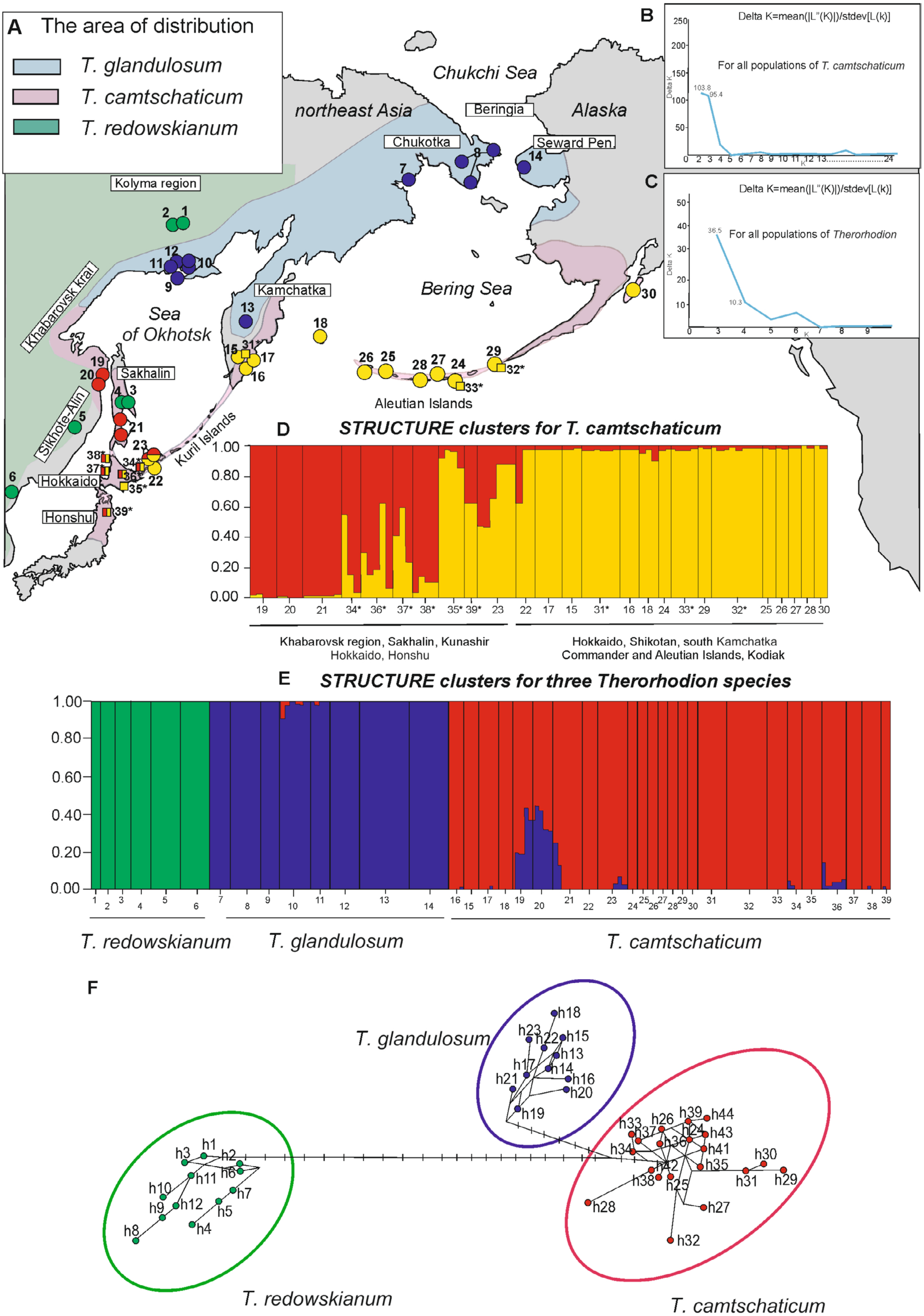

FIGURE 1 | Legend on next page.

FIGURE 1 | Genetic structure of *Therorhodion* species. (A) Distribution range of the three species and sampling sites. Population numbers are defined in Table S1. Colours of circles and squares correspond to STRUCTURE genetic groups: Green for *T. redowskianum*, blue for *T. glandulosum*, yellow and red for *T. camtschaticum*. Circles represent original data, squares represent data from Hata et al. (2017). (B, C) Plots for detecting the number of K groups in STRUCTURE harvester and CLUMPAK that best fit the data. (D) STRUCTURE assignment of 89 individuals of *T. camtschaticum*, including 39 individuals from Hata et al. (2017) to ancestral groups ($K=2$). (E) STRUCTURE assignment of 161 individuals three species of *Therorhodion* to ancestral groups ($K=3$). (F) NETWORK inferred phylogenetic relationships among haplotypes: H1–h12 for *T. redowskianum*; h13–h23 for *T. glandulosum*, h23–h44 for *T. camtschaticum*. Cross-strokes between species groups of haplotypes correspond to mutational events. Within species groups, haplotypes differ by 1 to 3 mutations (not shown).

particularly whether the amphiberingian species *T. camtaschaticum* and *T. glandulosum* differ from the continental species *T. redowskianum*.

Previous studies (Polezhaeva et al. 2020, 2025) have clarified the biogeography of *Therorhodion* and confirmed the independence of the three genetic lineages corresponding to the three species. In this study, we applied seven nuclear markers (EST markers and phytochrome genes) to further understand the origin and divergence times within *Therorhodion*. To enhance our understanding of the genetic diversity of *T. camtschaticum* we added GenBank accessions from northern Japan obtained by Hata et al. (2017), thus covering the entire range of this species. By comparing the genetic structure and divergence time estimates obtained from multiple nuclear loci and SDM analysis we aim to: (1) reveal intraspecific differentiation between populations of *T. camtschaticum* and *T. glandulosum* in Western and Eastern Beringia and northern Japan; (2) find traces of admixture, if any, in the areas of range overlap of the three species; (3) draw conclusions about the historical and future distributions of the three *Therorhodion* species inferred from spatial distribution modelling analyses.

2 | Materials and Methods

2.1 | Genetic Analyses

2.1.1 | Population Sampling

Samples of *T. redowskianum*, *T. camtschaticum* and *T. glandulosum* were collected in the wild. For *T. camtschaticum* and *T. glandulosum*, we sampled from an area covering most of the species' ranges in northeast Asia and North America (Alaska). For *T. redowskianum*, we sampled from six populations at the eastern edge of the species' range in a south-to-north latitudinal gradient. We used the same populations for all three species as in previous studies (Polezhaeva et al. 2020, 2025), with 2–10 individuals for each population, considering each locality as separate population due to significant geographic separation. The sample set consists of 146 individuals from 30 populations; accessions with missing data at any loci were further excluded from the phylogenetic analyses. The final dataset included 122 individuals: 24 specimens of *T. redowskianum*; 48 of *T. glandulosum* and 50 of *T. camtschaticum*. We also added 39 GenBank accessions of *T. camtschaticum* from northern Japan and Beringia according to Hata et al. (2017) for STRUCTURE and DIYABC analyses. For phylogenetic analyses, we used only 28 individuals from Hata et al. (2017) for which sequences were available for all loci examined (see Table S1). The approximate locations of the populations sampled are marked on Figure 1, while coordinates and accession numbers in GenBank for each individual and locus from both our study and Hata et al. (2017) are provided in Table S1 (Appendix S1).

2.1.2 | DNA Extraction and Sequencing of Nuclear Loci

Total genomic DNA was extracted from silica gel-dried or air-dried leaves using the CTAB method according to Devey et al. (1996).

Following Hata et al. (2017), we use seven nuclear loci with primers given by the authors. These seven loci are three phytochrome genes (*PHYA*, *PHYB* and *PHYE*) (Ikeda 2012; Ikeda and Setoguchi 2010) and four EST markers (B1, B7, C16 and C18) (Wei et al. 2005). PCR amplification was optimised for all loci as follow: 96°C for 5 min, followed by 40 cycles of 96°C for 30 s, 56°C for 45 s and 72°C for 1 min, plus a final extension of 72°C for 7 min. PCR products were checked on 1.0% agarose gels, purified with ExPure Kit (NimaGen, the Netherlands) and then used as templates for Sanger sequencing using a Brilliant Dye v. 3.1 kit (NimaGen, Netherlands). The sequences of these fragments for all individuals were obtained using NANOFOR 05 genetic analyser (Syntol, Russia) at the Center for Collective Use 'Modern Technologies for Ecological Research' of the IPAE, Ural Branch of RAS. All sequences were deposited in GenBank with the accession numbers listed in Table S1 (Appendix S1).

2.1.3 | Analyses of Genetic Diversity, Structure and Phylogeny

Parameters of genetic diversity, such as number of segregating sites (S), number of phased haplotypes (N_h), index of haplotype diversity (H_d), nucleotide diversity (π) (Nei 1987), Tajima's D neutrality test (Tajima 1989) were calculated for each locus of each species using the DnaSP 5.0 software (Librado and Rozas 2009).

Genetic differentiation between populations, species and geographic groups within species was assessed by AMOVA using Arlequin 3.5.1.2 (Excoffier and Lischer 2010). The significance of differentiation was estimated based on 10,000 permutations.

Bayesian clustering analysis was conducted using STRUCTURE 2.3.4 (Pritchard et al. 2000; Falush et al. 2003) was used to determine the genetic structure of all populations of the three species, including samples from Hata et al. (2017). Since the STRUCTURE software requires input in a specific numerical format, we converted the nucleotide sequence information from letter codes to numeric values: $A=1$; $T=2$; $C=3$; $G=4$; deletion = 5; insertion = 6. To reflect heterozygotes, each individual was coded with two columns corresponding to the allele combination at each locus. The algorithm was run with 20 repetitions for each of the K values from 1 to 25 (based on the number of populations) using an admixture model (accounting for the probable mixed origin of the samples assuming independence of allele frequencies between clusters) with 10^5 annealing iterations and 10^6 subsequent iterations. The optimal number of groups was selected in STRUCTURE Harvester program (Earl and vonHoldt 2012) and CLUMPAK (Jakobsson and Rosenberg 2007) based on ΔK (Evanno et al. 2005).

The relationships between haplotypes and individuals were evaluated using phylogenetic approaches. A haplotype tree was constructed in NETWORK v. 4.6.1.2 (Bandelt et al. 1999) using the Median Joining (MJ) method.

2.1.4 | Divergence Time Estimations and Ancestral Area Reconstruction

Biogeographic scenarios for representatives of *Therorhodion* were developed based on the results of the phylogenetic analysis. To estimate the time of historical divergence between the three species *T. camtschaticum*, *T. glandulosum* and *T. redowskianum*, we used two approaches. The first approach was the Approximate Bayesian Computation (ABC) approach implemented in DIYABC 2.1.0 (Cornuet et al. 2014). Four scenarios were tested: (1) *T. redowskianum* diverged first, then *T. camtschaticum* and *T. glandulosum* diverged last, (2) *T. redowskianum* diverged from *T. camtschaticum*, (3) *T. redowskianum* diverged from *T. glandulosum* (these two hypothesis were based on the assumption of Yurtsev (1968) on the origin of the continental species *T. redowskianum* as a derivative of the oceanic highland species *T. camtschaticum* s.l.) and (4) the fourth scenario assumed simultaneous divergence of three lineages from a common ancestor. We then estimated the divergence time between groups within *T. camtschaticum*, determined in STRUCTURE and confirmed by AMOVA with a significant F_{CT} value. A set of five historical parameters was used for a priori analysis settings. The effective population sizes of N1 '*T. glandulosum*', N2 '*T. camtschaticum*' and N3 '*T. redowskianum*' ranged from 500 to 100,000 with a log-uniform distribution. A study on the ontogeny of *T. camtschaticum* found that, in the wild, it can flower for the first time between 10 and 40 years of age, with individuals living up to 100–150 years (Mazurenko 1980). Based on these assumptions, we used a conservative generation time of 10 years and the divergence time t1 was set to be a minimum of 10^3 generations and a maximum of 2×10^6 generations and t2 was set to be a minimum of 10^3 generations and a maximum of 3×10^6 generations. A mutation rate of 5.3×10^{-9} substitution per site was used for sequence data from seven nuclear loci, according to Hata et al. (2017). The 'preliminary evaluation of a priori scenario combinations' option in DIYABC was used to initially test scenarios, a priori values and determine the optimal set of summary statistics. A total of 1×10^6 data sets were simulated. The program options with 'model validation' and 'scenario comparison' analyses were then used.

The second approach for divergence time estimation of genotypes is a Yule Bayesian model method implemented in BEAST v.2.7.6 (Drummond and Rambaut 2007). Based on the inferences from the AIC in MrModeltest v.2.2 (Nylander 2004) the HKY model with invariant sites and gamma distribution substitution model was selected. A relaxed molecular clock with uncorrelated lognormal distributed substitution rate was applied. Priors for the most recent common ancestor (MRCA) were set to lognormal distributions with logmean = 1, lognormal SD = 0.5 and offset = 60 Mya as the minimum age for *Rhododendron* following Milne (2004) and using a fossil calibration of *Rhododendron* dated from the upper Palaeocene (Collinson 1978). The MCMC simulation was run for 10^7 generations, with trees sampled every 1000 generations and the first 10% of generations were discarded as burnin. The effective sample size (ESS) assessed in Tracer v.1.7.2 (Rambaut et al. 2018) was > 200 as a quality-measure of the resulting sample sequence. TreeAnnotator 1.6.1 (Drummond and Rambaut 2007) was used to summarise the trees with a criterion of the maximum clade reliability using the mean heights option. The final consensus tree was drawn in FigTree 1.4.3 (Rambaut and Drummond 2009).

To reconstruct the geographic diversification of *Therorhodion*, we performed Bayesian Binary modelling (BBM) as implemented in RASP v. 4.4 (Reconstruct Ancestral State in Phylogenies) (Yu et al. 2015). Three geographical regions were assigned for examined species of *Therorhodion* based on their distribution: (A) northeast Asia; (B) the southern islands of northeast Asia and (C) northern North America. The ultrametric tree generated in BEAST was employed in the BBM analysis. The MCMC chains of the BBM analysis were run simultaneously for 1 million cycles, with a sampling frequency of every 100 generations and a 10% burn-in. The fixed model JC + G (Jukes-Cantor + Gamma) was selected as the best fit among the four models according to MrModeltest v.2.2 (Nylander 2004).

2.2 | Species Distribution Modelling

2.2.1 | Occurrence Data

Global distribution records of the three *Therorhodion* species were collected from the Global Biodiversity Information Facility (GBIF 2025a, 2025b, 2025c). There were 1075, 95 and 493 raw occurrence records of *T. camtschaticum*, *T. glandulosum* and *T. redowskianum* identified. Due to possible identification errors, particularly challenging between *T. camtschaticum* and *T. glandulosum*, we considered some records originally assigned to *T. camtschaticum* as closely related to *T. glandulosum* based on previous phylogenetic results (Polezhaeva et al. 2025) and distribution maps (Hultén 1968). We divided the observations of *T. camtschaticum* and *T. glandulosum* according to their current distribution. Ultimately, a total of 609 *T. camtschaticum* and 416 *T. glandulosum* occurrence records were retained.

We manually deleted records with outlier coordinates or those that are based on cultivated specimens in botanical gardens, arboreta and parks after checking in Google Earth Pro 7.3.6

(Google LLC, USA). A group of records of *T. camtschaticum* and *T. glandulosum* located near the Shantar Islands and the adjacent mainland of Khabarovsk Krai was removed (145 records), since this area may be a hybrid zone and reliable species identification of hybrids seems impossible based on GBIF records. Spatial filtering of records located at a distance of less than 10 km from each other was performed in the R 4.0.3 package (R Core Team 2013) 'spThin' 0.2.0 package (Aiello-Lammens et al. 2015). The total number of occurrence records after data filtering was 249 *T. camtschaticum*, 244 *T. glandulosum*, 299 *T. redowskianum* (Appendix S1, Table S2).

2.2.2 | Bioclimate Data

All 19 bioclimatic variables (except FUTURE) were obtained from PaleoClim v1.0 (Brown et al. 2018). The time series of bioclimatic variables were as follows: contemporary climate (1979–2013), the Last Glacial Maximum (ca. 21 Kya, Karger et al. 2017) and the Last Interglacial (ca. 130 Kya, Otto-Bliesner et al. 2006). Future climate change projections (2061–2080) were based on CMIP6 climate projections. All bioclimatic layers were obtained with a spatial resolution of 2.5 min. We used environmental variables from the MIROC6 climate model downloaded from WorldClim (Fick and Hijmans 2017) to first test scenario SSP126, followed by SSP245, SSP370 and SSP585 (Shared Socio-economic Pathway). These scenarios reflect various values in terms of anthropogenic radiative forcing, starting from optimistic SSP126 (it assumes climate protection measures) to most pessimistic SSP585 (this scenario represents the upper boundary of the range of anthropogenic radiative forcing) (CMIP6 Model Description 2021). We performed Pearson's correlation analysis on the standardised predictors and retained a subset of predictors with correlation coefficients $|r| < 0.8$. This work was performed in SDM Toolbox v2.5 (Brown et al. 2017) implemented with ArcGIS Desktop 10.8.2 (ESRI, USA). Temperature annual range (bio7), annual precipitation (bio12) and precipitation of warmest quarter (bio18) did not show a correlation coefficients higher than |0.8| with any of the other predictors. Therefore, we included them in the model for all three species. Other predictors were selected in the model from correlated pairs based on the criteria of the highest model contribution and training gain using the jackknife test in MaxEnt v3.4.1 (Phillips et al. 2006). Thus, we selected additional predictors: precipitation of driest month (bio 14) and precipitation seasonality (bio 15) for *T. camtschaticum*; annual mean temperature (bio 1) and max temperature of warmest month (bio 5) for *T. glandulosum*; mean temperature of driest quarter (bio 9) for *T. redowskianum*. We performed separate modelling in MaxEnt v3.4.1 for each species.

2.3 | MaxEnt Modelling

The potential distribution of the three *Therorhodion* species was modelled in MaxEnt v3.4.1. MaxEnt settings were performed using the following options: regularisation 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; output format (cloglog); 25% of the locations were randomly selected for testing and 75% of the locations were used for model training. The final models were selected based on AUC_{TEST} criteria (the area under the receiver operating characteristic curve).

3 | Results

3.1 | Genetic Diversity and Differentiation

All loci do not significantly deviate from the expectation of neutrality according to Tajima's test ($p > 0.05$ in 1000 coalescent simulations) in all species, indicating that there is no single locus under selection and therefore all of them can be used for phylogenetic inference. The number of segregating sites and the number of haplotypes for the markers *PHYA*, *PHYB*, *PHYE* and B1, B7 are expectedly lower ($S = 5$–8, $N_h = 5$–10) than for markers C16 and C18 ($S = 10$–13, $N_h = 15$–31), since the former loci are located in more conservative exons, and the latter in more variable introns. Nucleotide diversity and haplotype diversity index were comparable in all three species and slightly higher in *T. camtschaticum* (mean $\pi = 0.0025$, mean $H_d = 0.538$, Table 1).

The optimal number of clusters for the STRUCTURE analysis was $K = 3$ (Figure 1B). Individuals of each species (*T. redowskianum*, *T. glandulosum* and *T. camtschaticum*) were assigned to a separate cluster, with the exception of populations 19, 20 of *T. camtschaticum*, which had a mixed ancestry of both *T. camtschaticum and T. glandulosum* clusters (Figure 1E). According to the AMOVA analysis (Table 2), genetic differentiation considering haplotype relatedness was high between all studied populations ($F_{ST} = 0.887$, $p < 0.001$), as well as between the three species ($F_{CT} = 0.7723$, $p < 0.001$) and within populations for each species (*T. redowskianum* $F_{ST} = 0.618$, *T. glandulosum* $F_{ST} = 0.484$ and *T. camtschaticum* $F_{ST} = 0.721$) (Table 2).

We also conducted a STRUCTURE analysis to identify population structure within *T. camtschaticum* (50 individuals from the original data and 39 from Japan and Kamchatka from Hata et al. 2017). The optimal number of groups was two (Figure 1C,D) with ΔK estimates of 103.8 according to the CLUMPAK algorithm and 411.9 according to STRUCTURE Harvester. The coefficient of differentiation between them was significant $F_{CT} = 0.369$, $p < 0.001$ (Table 2). The first group (Cluster 1) consisted of populations from Khabarovsk Krai (pops. 19, 20), Sakhalin (pop.21), most of the populations from Hokkaido (pops. 34, 36–38); the second group (Cluster 2) consisted of populations from eastern Hokkaido and Honshu (pops. 35, 39), Shikotan (pop.22), Kunashir (pop.23), south-eastern Kamchatka (pops. 15–17, 31), the Commander Islands (pop. 18), the Aleutian Islands (pops.24–30, 32*, 33*) and Kodiak Island (pop. 30). The detailed STRUCTURE plot for *T. camtschaticum* is given in Figure 1D.

Phylogenetic relationships among haplotypes revealed that all three species are highly divergent, with T. *redowskianum* being more distant from *T. camtschaticum* and *T. glandulosum* (Figure 1F).

TABLE 1 | Summary statistics of all loci for molecular analyses of three *Therorhodion* species.

Locus	Species	*n*	pb	*S*	H_d	π	D[a]
B1	All species	122	186	5	0.792	0.0073	0.7391
	T. redowskianum	24	186	1	0.422	0.0023	1.1852
	T. glandulosum	48	186	2	0.524	0.0037	0.3154
	T. camtschaticum	50	186	1	0.453	0.0024	1.5445
B7	All species	122	245	8	0.781	0.0099	1.4042
	T. redowskianum	24	245	3	0.699	0.0053	1.9189
	T. glandulosum	48	245	1	0.081	0.0003	−0.6769
	T. camtschaticum	50	245	2	0.601	0.0029	1.2565
C16	All species	122	452	10	0.827	0.0045	0.4879
	T. redowskianum	24	452	1	0.422	0.0009	1.1852
	T. glandulosum	48	452	4	0.717	0.0023	0.6944
	T. camtschaticum	50	452	4	0.642	0.0027	1.1177
C18	All species	122	355	13	0.908	0.0086	1.0288
	T. redowskianum	24	355	4	0.734	0.0040	1.3473
	T. glandulosum	48	355	5	0.869	0.0047	1.5008
	T. camtschaticum	50	355	7	0.691	0.0045	0.4404
*PHY*A	All species	122	353	6	0.671	0.0043	1.0888
	T. redowskianum	24	353	0	0.000	0.0000	n/a
	T. glandulosum	48	353	0	0.000	0.0000	n/a
	T. camtschaticum	50	353	3	0.335	0.0010	−0.6839
*PHY*B	All species	122	479	8	0.817	0.0048	1.6373
	T. redowskianum	24	479	1	0.120	0.0002	−0.6367
	T. glandulosum	48	479	3	0.720	0.0027	2.2043
	T. camtschaticum	50	479	1	0.505	0.0011	1.8504
*PHY*E	All species	122	341	8	0.737	0.0067	1.5982
	T. redowskianum	24	341	1	0.156	0.0005	−0.4177
	T. glandulosum	48	341	0	0.000	0.0000	n/a
	T. camtschaticum	50	341	3	0.537	0.0030	1.4206
Means	All species	122	344.4	8.2	0.790	0.0066	1.1410
	T. redowskianum	24	344.4	1.6	0.365	0.0019	0.6546
	T. glandulosum	48	344.4	2.1	0.416	0.0020	0.5769
	T. camtschaticum	50	344.4	3	0.538	0.0025	0.9923

Abbreviations: bp, length of sequences for analyses; *D*, Tajima's D; H_d, index of haplotype diversity; *n*, number of sequences for analysis; *S*, number of segregating sites; π, average number of pairwise nucleotide differences per site.
[a]All Tajima's D were not significantly deviated from zero ($D = 0$) based on 1000 coalescent simulations.

3.2 | Phylogenetic Relationships and Divergence Time Estimation Within *Therorhodion* Species

BEAST clustered haplotypes derived from the seven nuclear loci into three lineages corresponding to the three *Therorhodion* species, the STRUCTURE results, and their geographic distribution. Molecular dating with *Phyllodoce nipponica* Makino as the outgroup revealed that *T. redowskianum* was the first to diverge in the Mid Miocene about 8.87 Mya (95% HPD: 0.75–24.2 Mya; Figure 2C). The split between the other two species *T. camtschaticum* and *T. glandulosum* was estimated during the late Miocene at about 4.96 Mya (95% HPD: 1.58–12.1 Mya; Figure 2C). Further divergence within each clade began at the Pliocene–Pleistocene boundary.

TABLE 2 | Hierarchical analysis of molecular variation (AMOVA) for populations of *Therorhodion* species.

Source of variation	Fixation indices	p
Among tree species	F_{CT} 0.772	< 0.001
Among all populations	F_{ST} 0.877	< 0.001
Within all populations	F_{SC} 0.504	< 0.001
Among two clusters within the *T. camtschaticum*	F_{CT} 0.402	0.017
Among populations	F_{ST} 0.721	< 0.001
Within populations	F_{SC} 0.533	< 0.001
Among three clusters within the *T. glandulosum*	F_{CT} 0.380	0.180
Among populations	F_{ST} 0.484	< 0.001
Within populations	F_{SC} 0.167	< 0.001
Among tree clusters within the *T. redowskianum*	F_{CT} 0.407	0.153
Among populations	F_{ST} 0.618	0.003
Within populations	F_{SC} 0.356	< 0.001

Of the four divergence scenarios between *Therorhodion* species (Appendix S2), scenario 1, in which *T. redowskianum* diverged earlier than the others, exhibited a higher posterior probability ($PP_{(\text{direct approach})} = 0.614$; $PP_{(\text{logistic approach})} = 0.981$ with a bias of $0.05_{(\text{direct approach})}$; $0.03_{(\text{logistic approach})}$) (Appendix S2). Comparison of the combination of a priori and posteriori datasets for the model with the observed dataset using the 'Model Checking' function showed that they matched Scenario 1 well (Appendix S2). The analysis revealed a lower effective population size for N3 *T. redowskianum* 198.000 (95% CI: 73.4×10^3–415×10^3) than for N2 *T. camtschaticum*—349.000 (95% CI: 184×10^3–480×10^3) and N1 *T. glandulosum*—376.000 (95% CI: 196.7×10^3–491×10^3) individuals. The recent divergence of *T. redowskianum* was inferred to be 19.2×10^5 generations ago (95% CI: 7.3×10^5–30.4×10^5), and the divergence between *T. camtschaticum* and *T. glandulosum* was inferred to be 2.13×10^5 generations ago (95% CI: 0.876×10^5–8.97×10^5). Assuming an average generation time of 10 years for *Therorhodion*, the divergence time of the clade of *T. camtschaticum* and *T. glandulosum* from *T. redowskianum* was inferred to be 19.2 Mya (95% CI: 7.3–30.4 Mya), and the divergence time between *T. glandulosum* and *T. camtschaticum* was inferred to be 2.13 Mya (95% CI: 0.8–8.97 Mya) (Figure 2A).

In addition, we performed the same analysis for the two clusters within *T. camtschaticum* identified in the STRUCTURE with significant support from those in the AMOVA analysis. Three main scenarios were tested: (1) constant population size after differentiation (t1), (2) decreasing size after differentiation and (3) increasing size after differentiation. Scenario 1 with constant population size was considered the most likely scenario based on the results of the preliminary testing. The estimated effective population sizes were: for cluster1 (N1) – 146.000 individuals (95% CI: 49.7×10^3–196×10^3), for cluster 2 (N2)—71.600 (20.6×10^3–184×10^3). The age of the divergence time of the two clusters was inferred to be about 228 Kya (95% CI: 73.3–889 Kya) (Figure 2B).

3.3 | Ancestral Area Reconstructions

BBM analysis suggests an origin of all *Therorhodion* species in northeast Asia (A, marginal probability 100%). The pie charts at the nodes indicate the relative frequencies of ancestral area optimisation across the entire ancestral area reconstruction tree shown in Figure 3. Northeast Asia is resolved as the most likely ancestral area for *T. glandulosum* populations from Asia and North America. The most likely ancestral areas for *T. camtschaticum* populations include mainly islands on the southern periphery of northeast Asia (marginal probability 94%) and northern North America (marginal probability 47%).

3.4 | Ecological Niche Modelling

The modern range of *Therorhodion* species was predicted with good accuracy (the area under the curve $AUC_{TEST} = 0.942$–0.984) (Swets 1988). We tested all six values of the regularisation multiplier parameter (0.1, 0.5, 1.0, 2.0, 3.0 and 4.0) when building current habitat models. Maximum AUC_{TEST} values were obtained with a regularisation multiplier of 1.0 for each species for four feature class combinations: linear, quadratic, product and hinge features (threshold features were excluded). For all three species, the modelled geographical ranges closely matched their current distributions (Figure 4G–I). The Last Glacial Maximum (LGM) extrapolations for *T. camtschaticum* and *T. glandulosum* predicted range contractions in Kamchatka, Sakhalin Island, the Kuril Islands and Japan (Figure 4D–F). At the same time, extrapolations indicate more suitable conditions in southwestern Alaska, including significant areas of exposed continental shelf. Thus, the SDM analysis indicates that the LGM areas of these species' ranges have changed little compared to the present day, but have undergone significant expansion in western Beringia. The LGM extrapolations for *T. redowskianum* demonstrate a significant shift in the species' range from central mainland Siberia to the Okhotsk coast and the Korean Peninsula. The predicted area in Kamchatka is doubtful, as otherwise there would be a high probability that the species is still present there today, but this species is not currently observed in Kamchatka. Thus, the size of the potential habitat of *T. redowskianum* also remained essentially unchanged compared to the current range. Overall, no general trend of decreasing total area of ranges for all *Therorhodion* species was observed in the LGM. In contrast, model projections for the Last Interglacial (LIG) period indicate widespread range contractions for all *Therorhodion* species (Figure 4A–C), a pattern also observed under future climate change projections for 2061–2080 from the 'soft' scenario of SSP126 (Figure 4J–L). It should be noted that the studied species respond differently when the severity of climate change increases in other scenarios. For example, *T. redowskianum* shows a significant reduction in suitable habitat already starting from the most optimistic scenario SSP126, while the projection with increasing anthropogenic radiative

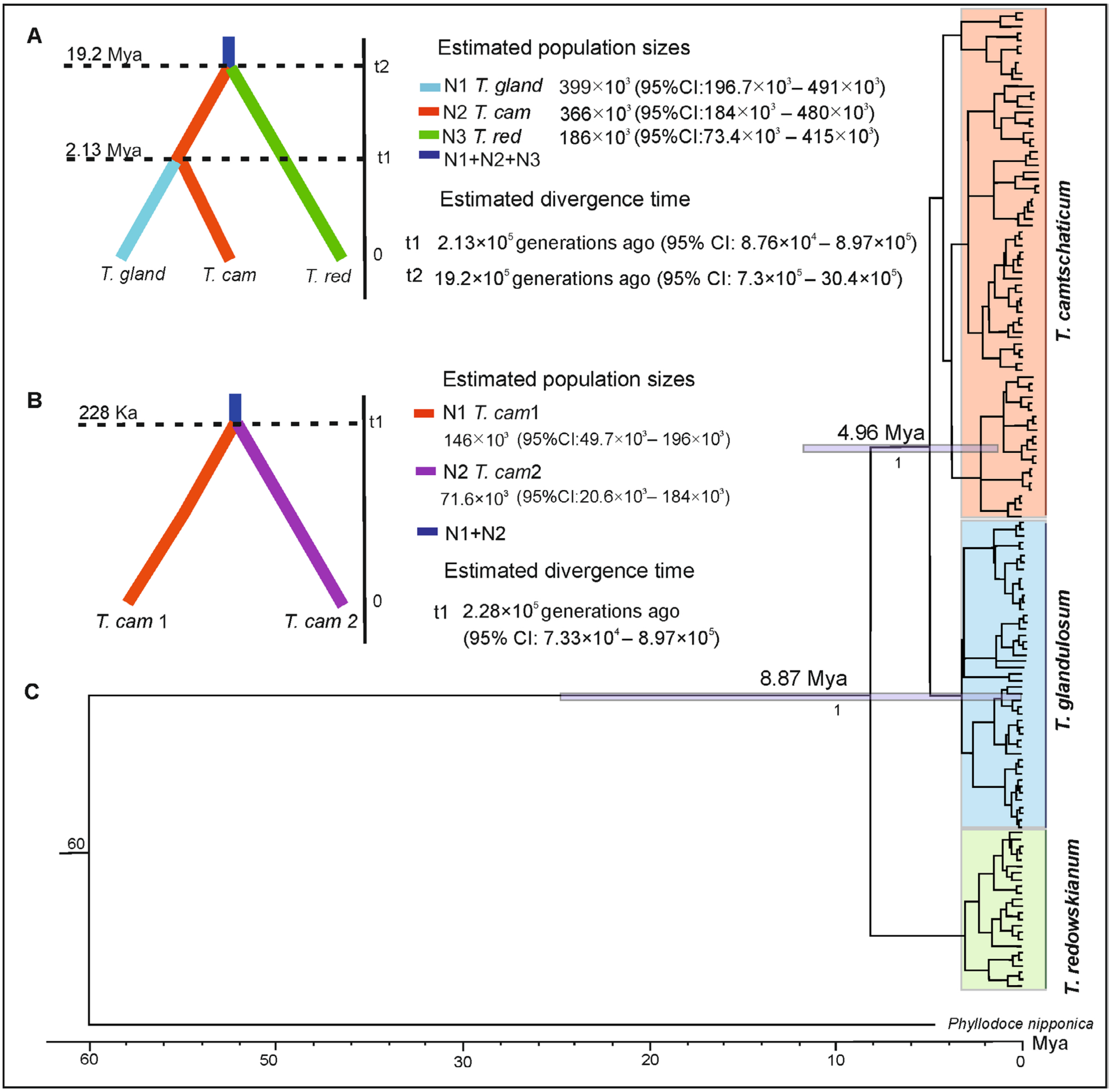

FIGURE 2 | The divergence time estimation of *Therorhodion* species. *T. cam, T. camtschaticum*; *T. gland, T. glandulosum*; *T. red, T. redowskianum*. (A, B) The most likely DIYABC scenario and estimations of population sizes and divergence time for the three species and for two clusters within *T. camtschaticum*, respectively. (C) Time-calibrated estimation according to Bayesian inference obtained in BEAST, posterior probabilities greater than 0.5 shown below the branches. Estimates of the divergence times obtained in BEAST. Shaded bars at tree nodes represent 95% credible intervals for the time estimates relative to the scale below.

forcing from scenario SSP245 to SSP585 shows range impacts already to a much lesser extent (Appendix S3, Figure S1). In contrast, *T. glandulosum* shows progressive range contraction and movement to restricted areas in northern Chukotka and Alaska with increasing pessimistic climate projections for 2061–2080 (Appendix S3, Figure S1). *Therorhodion camtschaticum* shows a slight shift in projected range to northern Sakhalin, Kamchatka and Alaska, but a shift in suitable distribution areas from the central Kuril Islands to their coasts. The Aleutian Islands do not show a similar trend in the shift in the range of *T. camtschaticum* (Appendix S3, Figure S1).

Future predicted ranges of *Therorhodion* species are determined by the degree of importance of bioclimatic variables for every *Therorhodion* species. For *T. redowskianum*, the most significant variables were the mean temperature of driest quarter (bio9) and the precipitation of warmest quarter (bio18). The response curve for bio9 peaked at −30°C, while bio 18 showed an optimal range between 300 and 500 mm. The distribution of *T. glandulosum* was most strongly influenced by the maximum temperature of the warmest month (bio5) and annual precipitation (bio12), with lesser contributions from annual mean temperature (bio1) and temperature annual range (bio7). In contrast, the key predictors

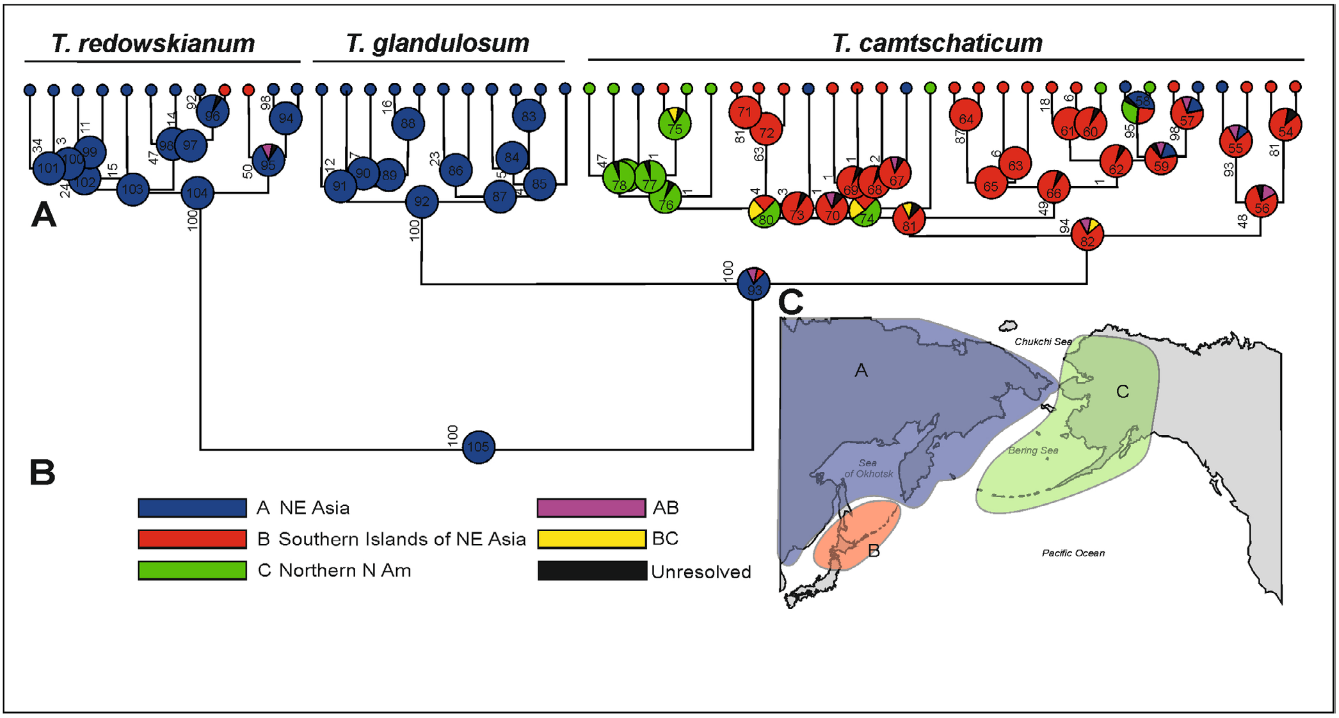

FIGURE 3 | Tree obtained from BBM analysis implemented in RASP. (A) Graphical results of ancestral distributions at the nodes of interest. (B) Colour keys to possible ancestral ranges at nodes. (C) biogeographical regions based on the distribution of the three *Therorhodion* distributions.

for *T. camtschaticum*, were the precipitation of the driest month (bio14) and he precipitation of the warmest quarter (bio18) (Appendix S3, Figure S2).

4 | Discussion

4.1 | Population Genetic Structure

Our phylogeographic study identified three well-defined lineages within *Therorhodion* (Figures 1 and 2), corresponding to three recognised species: *T. camtschaticum* and *T. glandulosum*, which are morphologically similar and have occasionally been treated as subspecies (Aleksandrova 1975; Yurtsev et al. 2010) and *T. redowskianum*, which is morphologically distinct from the other two (Chang et al. 2014; Malyschev 2006). These results, based on seven nuclear loci, are consistent with previously obtained data from plastid DNA and nuclear microsatellites (Polezhaeva et al. 2025). We also discovered high genetic similarity between populations from the North American and northeast Asian parts of Beringia for both *T. camtschaticum* and *T. glandulosum*. These data indicate that the ranges of these species are unlikely to have been divided into separate refugia on either side of Beringia over a long period and support the hypothesis that the dispersal of *Therorhodion* populations from northeast Asia to North America probably occurred relatively recently, before or during the LGM, when the Bering land bridge last existed (Sanmartín et al. 2001; Wen et al. 2016). A similar pattern of limited genetic differentiation across Beringia has been observed in other amphiberingian species such as *Diapensia obovata* (Schmidt) Nakai (Hou et al. 2016), *Phyllodoce aleutica* (Spreng.) A. Heller (Ikeda et al. 2018), *Geranium erianthum* DC. (Kurata et al. 2022) and others (Abbott et al. 2000; Carlsen et al. 2010; DeChaine 2008; Holder et al. 2000; Ickert-Bond et al. 2009).

The amphiberingian species *T. glandulosum* and *T. camtschaticum* have an allopatric distribution in Alaska, with overlapping ranges in the Russian Far East (including Kamchatka and the western Okhotsk coast). However, there is no documented evidence in the literature of their coexistence in the same locality or hybridisation between them. While previous analyses using plastid DNA and nuclear microsatellites failed to detect any genetic admixture between these populations (Polezhaeva et al. 2025), the use of the markers employed in the current study has revealed, for the first time, evidence for genetic admixture. Specifically, *T. glandulosum* genetic clusters were detected within *T. camtschaticum* clusters in two populations at two sites from Khabarovsk krai (pops. 19, 20, Figure 1E), located near the expected species distribution boundary. This admixture of the clusters was caused by several common mutations between *T. glandulosum* and these two *T. camtschaticum* populations in B7 (nucleotide position, np. 117), C16 (np. 225), C18 (np. 120, 282 and 313) and *PHYA* (np. 66) loci (the sequences are available from GenBank, see Appendix S1, Table S1). Individuals from these populations exhibited traits typical of *T. camtschaticum*, including simple foliar trichomes, a pubescent corolla and an average plant height of 30 cm. In contrast, *T. glandulosum* is distinguished by glandular foliar trichomes, a glabrous corolla and a shorter stature, typically ranging from 15 to 20 cm. No individuals from these localities were identified as *T. glandulosum* during field studies. Nevertheless, we cautiously suggest that the observed recombination of independent nuclear markers may reflect historical hybridisation in a previously existing sympatric zone between the two species, even though they currently do not

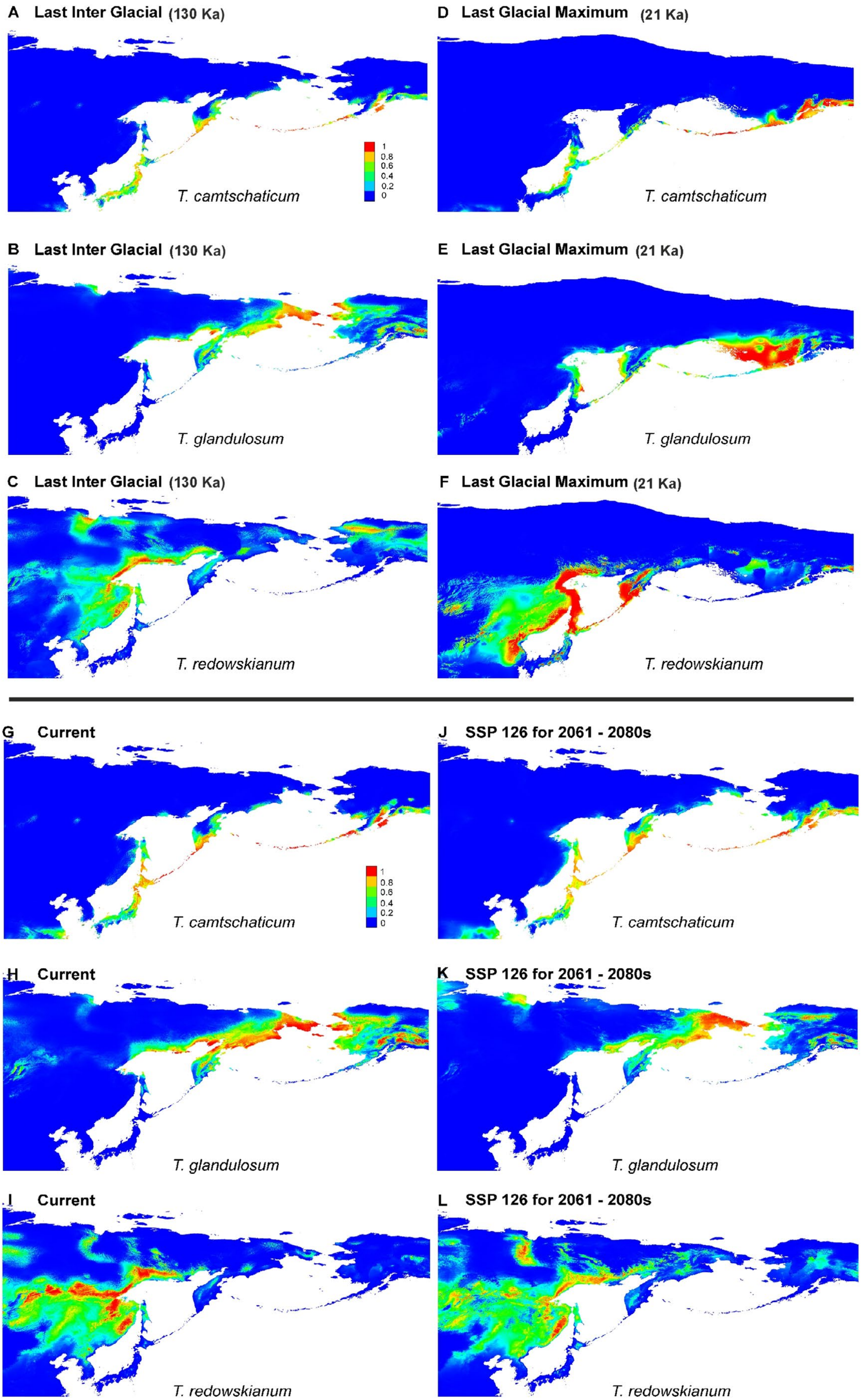

FIGURE 4 | Legend on next page.

FIGURE 4 | Species distribution models showing climatic suitability for *Therorhodion* species in northeast Asia and North America. (A–C) the Last Inter Glacial (LIG; 130 Kya); (D–F) the Last Glacial Maximum (LGM; 21 Kya); (G–I) current conditions and (J–L) 2061–2080. Climatic suitability increases with colour from blue to red. The resolution of the potential distribution map is 2.5 arcminutes.

coexist in the same habitat. The same traces of genetic admixture plausibly arising during the sympatric coexistence in the LGM were shown for *Phyllodoce cerulea* (L.) Bab. and *P. aleutica*, using similar nuclear loci (Ikeda et al. 2016). In our case, more precise sampling in the putative overlap zone and additional genetic markers are needed for more accurate conclusions. Previously, strong differentiation between populations of *T. camtschaticum* from northern Japan and Beringia (Kamchatka and the Aleutian Islands) was revealed by Hata et al. (2017). Our study with a broader sampling, including Hata's GenBank accessions, indicated another cluster within the *T. camtschaticum* lineage. All the populations were divided between the western and eastern parts of the species range, whereas the Japanese populations were split between those two groups. The first one consisted of populations from the western part of the *T. camtschaticum* range (pops. 19–21), and most populations from Hokkaido (pops. 34, 36–38); the second included populations from eastern Hokkaido and Honshu (pops. 35, 39) and the eastern part of the species range, including Beringia (pop. 15–18, 22–33). In our previous study, nSSR markers were not able to capture differentiation between these groups (F_{ST} was non-significant), suggesting that the lack of internal structure may be a sign of recent population expansion (Polezhaeva et al. 2025). Although Hata et al. (2017) also detected genetic differentiation between eastern Hokkaido and Honshu populations (defined as Por and Aki in their paper) and other Hokkaido populations (defined as Rau, Ris, Sho and Dai) in their STRUCTURE analysis, their study primarily focused on the genetic distinctiveness between the Japanese and Beringian populations. The genetic affinity between populations from Rishiri Island (Ris) and certain populations from Hokkaido Island with the Beringia group (from Kamchatka and Alaska) has also been observed in *Geranium erianthum* (Kurata et al. 2022) and *Phyllodoce aleutica* (Ikeda et al. 2018). Thus, the larger sample size allowed more variation to be captured and more accurate genetic relationships to be reconstructed.

4.2 | Biogeographic History

Both Bayesian Evolutionary Analysis, calibrated with fossils, and the ABC method, considering population history, supported the same phylogenetic tree topology for *Therorhodion* but different divergence time estimations. BEAST estimated that the *T. redowskianum* lineage diverged early in the Late Miocene–Early Pliocene at 8.87 Mya (95% HPD: 0.75–24.2 Mya), which is close to our previously inferred dates at 9.70 Mya, based on nuclear microsatellites (Polezhaeva et al. 2025) and 7.49 Mya, based on several plastid and nuclear fragments (Oliver 2017). The split between *T. glandulosum* and *T. camtschaticum* is dated at 4.96 Mya (95% HPD: 1.58–12.1 Mya) corresponding well with the estimates at 5.37 Mya according to Oliver (2017), although older than 1.52 Mya based on nuclear microsatellites according to Polezhaeva et al. (2025). The divergence time estimates from DIYABC are older for the *T. redowskianum* lineage dating back to the Early Miocene at 19.2 Mya (95% CI: 7.3–30.4 Mya) and younger for the split between *T. glandulosum* and *T. camtschaticum* inferred at about 2.13 Mya (95% CI: 0.8–8.97 Mya). The discrepancy in estimates may stem from differences in the analytical software used and specified tree priors, as well as from uncertainty surrounding the average mutation rate of the molecular markers used (containing both substitutions and deletions). This lack of precise mutation rate calibration can lead to an overestimation of divergence times, particularly for ancient events according to DIYABC (Cornuet et al. 2010). The difference in divergence time estimates using DIYABC may be due to the use of a simplified model assuming constant population size, while it does not account for the likely demographic fluctuations associated with historical range shifts. In addition, the relatively small sample size of *T. redowskianum*, nearly half that of the other two species, and the limited number of loci (only seven) used in the analysis may have introduced greater uncertainty in the divergence estimates. Although the values of both analyses fall within their respective 95% HDP confidence intervals, we recognise that relying on a limited number of loci may introduce considerable uncertainty. Therefore, future studies should incorporate larger datasets for producing more robust and accurate estimates of divergence times.

Two groups within *T. camtschaticum* are estimated to have diverged 228 Kya (95% CI: 73.3 Kya–889 Kya), preceding the LGM. This is consistent with the divergence estimate for another Arctic Japanese-Beringian species, *Phyllodoce aleutica*, of 76.9–111.7 Kya (95% HPDs: 46.5–195.1 Kya) (Ikeda et al. 2018). These two species share a similar biogeographic pattern with a boundary running through Hokkaido, where eastern populations are clustered with Beringian populations. However, Hata et al. (2017) inferred that the divergence within *T. camtschaticum* occurred during or after the LGM about 10.6–15.5 Kya (95% HPDs: 1.7–43.5 Kya), using the same EST and phytochrome nuclear loci, but fewer samples. Considerable uncertainty remains regarding the mutation rates of different molecular markers, as well as differences in study design, availability of samples, and analytical approaches, all of which can influence divergence time estimates and demographic reconstructions. Despite these limitations, the general trends remain reliable. The second half of the Pleistocene was a very complex period of dramatic climatic fluctuations that profoundly shaped the modern genetic structure of species, likely obscuring earlier genetic signals associated with initial dispersal events.

Many molecular phylogenetic studies, for example for *Artemisia* L., *Ranunculus* L., *Cassiope* D., indicate that the ancestors of some Arctic lineages originated in the mid- to late Miocene with further diversification later (Hoffmann et al. 2010; Hou et al. 2016; Tkach et al. 2008), which is also true for *Therorhodion*. The oldest lineage of *T. redowskianum* diverged long before the formation of the modern Arctic biome, which is considered to have arisen about 2–3 Mya (e.g., Hedberg 1992; Hultén 1937; Matthews and Ovenden 1990; Murray 1995). The early Late Miocene–Early Pliocene diversification of *T.*

redowskianum coincides with a temperature drop about 8 Mya (Balcerak 2014; Nagalingum et al. 2011; Westerhold et al. 2020; Zachos et al. 2008), while the formation of the other two species *T. glandulosum* and *T. camtschaticum* coincides with the formation of cold-tolerant biomes at the late Pliocene–Pleistocene boundary. Migration across the Bering Land Bridge likely lasted from 1.5 Mya to the end of the LGM caused by marine regression (Clark et al. 2006; Sanmartín et al. 2001), explaining the lack of clear differentiation within *T. glandulosum* and *T. camtschaticum* between Asia and North America. SDM modelling of the LGM ranges of *T. glandulosum* and *T. camtschaticum* supports this assumption, showing no widespread and dramatic range contractions for these species. At the same time, a series of ancient marine regressions exposed significant areas of the ancient Beringian continental shelf that could have potentially been inhabited and repeatedly served as migration corridors between Eurasia and North America (Clark et al. 2006; Sanmartín et al. 2001). Together, these are good prerequisites for an ancient genetic relationship within *T. glandulosum* and *T. camtschaticum* between Asia and North America.

Ancestral area reconstruction revealed that *Therorhodion* is of Asian origin, corroborated by the analysis of the paleoflora (Strong 2021), supporting the theory of an 'out-of-Asia' origin for some other arctic species in North America (Abbott et al. 2000; Carlsen et al. 2010; DeChaine 2008; Ickert-Bond et al. 2009; Wen et al. 2016; Ikeda et al. 2018). The exact place of origin in Asia is difficult to determine, whether it was the adjacent areas south of Beringia with subsequent migration to northern Asia and eastward to North America, or, more likely, it arose in the high latitudes of northern Asia with a southward migration of *T. redowskianum* to Siberia and China and *T. camtschaticum* to the Japanese archipelago. A similar biogeographic pattern has been found for another Arctic genus *Diapensia* L., whose crown age is estimated at about 8 Mya, with a common ancestor originating in high latitudes of East Asia with further southward migration (Hou et al. 2016). An opposite case is the northward migration from Korea and Japan to the southern Russian Far East and the Kuril Islands, respectively, proposed for *Rhododendron brachycarpum* D. Don ex G. Don (Polezhaeva et al. 2021, 2022).

4.3 | Conservation Concerns

Beringia as an ice-free high-latitude land bridge between northeast Asia and western North America that serves as a refugium for Arctic flora was first postulated by Hultén (1937). According to our data, *T. glandulosum* and *T. camtschaticum* experienced a range shift to the Pacific coast that can be explained by the extremely continental climate of Siberia during the LGM. Therefore, these two species may indeed have had more extensive ranges in Beringia during the LGM, which would have favoured their growing conditions (Figure 4D–F), supporting Hultén's suggestion of an Arctic flora refugium in Beringia. Paleofloral analyses combined with recent molecular evidence indicate that the source of many subarctic plant taxa for eastern Beringia (western North America, NAm) is the western Beringia region (northeast Asia, NE Asia) (Abbott et al. 2000; Alsos et al. 2005; Anderson et al. 2010; Ikeda et al. 2018, 2020; Strong 2021). The closest plant refugium in northeast Asia has been reconstructed for the Sea of Okhotsk Coast, the Upper Kolyma region and the Kamchatka Peninsula (Anderson et al. 2010; Shilo et al. 2007). Indeed, the Okhotsk Sea coast had suitable growing conditions for *T. redowskianum* in both the LIG and the LGM according to our modelling results (Figure 4C,F). The potential distribution of *T. redowskianum* in the LGM is almost as large as its current distribution. Overall, it can be said that the harsh conditions of the LGM could have affected the ranges of all three species only locally, and conditions for the preservation of populations were created in other locations (e.g., Alaska, the Okhotsk coast) where populations of these species exist today, but could have expanded during the LGM. In contrast, model projections for the LIG period indicate a contraction of suitable habitat ranges for *T. glandulosum* and *T. redowskianum* (Figure 4B,C). A similar pattern was observed for *T. camtschaticum* when considering a detection probability threshold of $>0.7–0.8$ (Figure 4A). This pattern is expected because *Therorhodion* species are cold-adapted shrubs that may have experienced range suppression during the LIG, a period characterised by generally warm and humid climate marking the onset of the Eemian Interglacial (MIS 5e) (NEEM community members 2013). Notably, a similar contraction in prediction in suitable habitat is projected under future climate change scenarios, including the 'soft' scenario of SSP126 model for 2061–2080 (Figure 4J–L) and even more pronounced under 'harsher' scenarios (Appendix S3, Figure S1). These projections are significant concerns for the long-term conservation of all three *Therorhodion* species in the face of ongoing and future climate change. As we have already noted, with increasing severity of climate change (from SSP126 to SSP585), the future predicted ranges of *Therorhodion* species show different responses. This is undoubtedly due to the degree of importance of bioclimatic variables for each *Therorhodion* species. In Eastern Siberia, as a rule, precipitation is low (450–500 mm), and winters are snowy and very severe, which corresponds to the sharply continental climate of Eastern Siberia and the adaptation of *T. redowskianum* to it. The increasing summer dryness of the climate of Eastern Siberia will contribute to the shift of the *T. redowskianum* boundary to the Pacific coast in the future. The strong influence of the temperature on *T. glandulosum* can be easily observed, and likely explains the projected northward shift in its future distribution range. In contrast, precipitation emerged as the most critical factor for *T. camtschaticum*, which aligns with its ecological preference as a near ocean species. Consequently, future climate projections suggest a shift of its suitable habitat from the interior regions of the islands towards the coasts.

Identifying areas with stable niches and understanding their importance in determining the current distribution of species represent a pivotal task for biodiversity conservation (Marta et al. 2016). Although all three species of the genus *Therorhodion* are abundant in their optimal habitats, they are listed as protected species in some regions of Russia (Plantarium 2025). Climate change is reducing the optimal habitat for both cold-tolerant species and, in particular, for *Rhododendron* species, to which *Therorhodion* is closely related and sometimes referred to as a subgenus (Aleksandrova 1975; Fang et al. 2005; Mo et al. 2022; Shen et al. 2024; Xia et al. 2022). A recent study predicted that the distribution of wide-ranging *Rhododendron* species will decrease with future climate and land use changes, while narrow-ranging species may experience either range expansion or contraction (Yu et al. 2019). Given the general trend of cold-tolerant species shifting northwest over time, northern peripheral populations of *Therorhodion* may play a key role in the species' future conservation.

The predicted areas of high climatic suitability of the three *Therorhodion* species in 2061–2080s are more restricted than that at present and show strong northward shifting (Figure 4J–L). Moreover, global mean annual temperatures are likely to increase by an additional 1°C–4°C by 2100 (Stocker et al. 2013). This is a major challenge for the survival of many organisms, especially cold-adapted taxa inhabiting high mountains such as *Therorhodion*, which may face local extinction at the southern margin of their range and whose suitable habitat will be as limited or more limited in the near future as compared to the LIG (Beever et al. 2011; Wiens 2016). In addition, in the past, processes of population dynamics were extended over many generations, which ensured the stability of gene flow between populations and the preservation of the species' gene pool; while in modern conditions of short-term climate changes, plant species have lost this opportunity. Some of the peripheral populations appear to be better adapted to extreme environmental conditions, which should be taken into account in the context of long-term conservation (Lesica and Allendorf 1995). Thus, Beringia, which was considered a refugium in the past, will retain its role as a refugium for cold-tolerant biota. However, without taking actions, we cannot hope for the full validity of this status in light of rapid climate change in the future.

5 | Conclusion

We examined the divergence of *Therorhodion* species and the influence of climate on this sensitive, cold-adapted genus of small shrubs. Ancestral area reconstruction revealed that *Therorhodion* originated in Asia and diverged during the cooling in the late Miocene, with further diversification and dispersal across the Bering land bridge during the late Pliocene–Pleistocene. All three species differ in their geographic distribution: *T. redowskianum* mainly inhabits continental northeast Asia, while the two other species are widespread in the Pacific regions, with *T. glandulosum* restricted to northern Beringia, while *T. camtschaticum* occurs in southern Beringia and adjacent areas. Despite the overlap of the modelled distribution ranges of the three species in some parts of their past and present ranges, we found no obvious signs of hybridisation between them, except for a trace of some genetic contribution of *T. glandulosum* in *T. camtschaticum* populations in Khabarovsk Krai. Therefore, the biogeography of these species should be considered in light of the factors limiting the geographic distribution of *Therorhodion* species, with a future focus on the ecological specialisation of these species, affecting their distribution, coexistence in the same natural habitats and genetic exchange.

Author Contributions

Maria A. Polezhaeva: conceptualization, funding acquisition, data curation, formal analysis, supervision, validation, laboratory work, visualisation, writing – original draft, writing – review and editing. **Diana R. Iunusova:** formal analysis, software, writing – review and editing. **Denis N. Shuvaev:** formal analysis, software, writing – original draft. **Elena A. Marchuk:** resources, field support, validation, writing – original draft. **Stefanie M. Ickert-Bond:** resources, validation, writing – review and editing. All authors read and approved the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The sequences for each locus for each sample are available in the NCBI database; NCBI numbers are given in Table S1; data occurrence for SDM analyses are given in Table S2. Both tables are in Appendix S1. Files with DIYABC analyses data are all available in Appendix S2. Figure S1. SDM results with scenarios SSP 245, SSP 370 and SSP 585; Figure S2. Plots with response curves of selected climatic variables for each *Therorhodion* species are given in Appendix S3.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jbi70024-sup-0001-AppendixS1.xlsx. **Appendix S2:** jbi70024-sup-0002-AppendixS2.pdf. **Appendix S3:** jbi70024-sup-0003-AppendixS3.pdf.