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RESEARCH ARTICLE

Biogeography of a Global Plant Invader: From the Evolutionary History to Future Distributions

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ABSTRACT

Biological invasions pose a global challenge, affecting ecosystems worldwide and human societies. Knowledge of the evolutionary history of invasive species is critical to understanding their current invasion success and projecting their future spread. However, to date, few studies have addressed the evolutionary history and potential future spread of invaders simultaneously. In this study, we explored both evolutionary history and spatiotemporal dynamic patterns of the distribution of *Reynoutria japonica*, known as one of the world's worst plant invaders. We analysed 265 *R. japonica* samples from its current geographical ranges across three continents, using seven chloroplast DNA (cpDNA) markers to establish the phylogenetic relationships among extant populations. We combined these with ecological niche modelling to infer historical and more recent migration patterns and predict potential future distribution changes under climate change. Our results indicate that climate fluctuations and sea level changes likely facilitated the expansion of *R. japonica* from southern Japan to continental East Asia in the Pliocene, followed by a contraction in East Asian populations. In the recent Holocene, human activities have then enabled a linage of this species to spread from Japan to Europe and North America, resulting in three major global clades. Future climate scenarios suggest a northward expansion of *R. japonica* in Europe and North America, but shrinking habitat in China. Our study, thus, demonstrates the complex influences of historical climate-driven migrations, human activities and future climate changes on the global distribution of an invasive species.

Bo Li and Rui-Ting Ju should be considered joint corresponding author.

1 | Introduction

Human activities have altered the global distributions of many species, both intentionally (e.g., for food, gardening, construction or erosion control) and unintentionally (Elton 1958; Pysek and Richardson 2006). These introductions have resulted in a subset of species becoming invasive and posing major threats to global biodiversity by outcompeting native species for resources (Shea and Chesson 2002). Successful plant invasions have caused significant damage and economic losses in the invaded ranges (Pimentel, Zuniga, and Morrison 2005; Diagne et al. 2021). To prioritise the most critical species and geographical regions for management requires knowledge about the geographical origins and past colonisation history of invaders (Saltonstall 2002; Verlaque et al. 2011) and prediction of their potential future spread (Hickling et al. 2006; Chen et al. 2011).

Investigating the geographical origins and colonisation histories of species can yield valuable insights into evolutionary processes, especially with respect to potential adaptation and the role of population bottlenecks in evolution (Bock et al. 2015). For example, invasion success depends on levels and sources of genetic diversity in introduced populations (Bock et al. 2015). A species' geographic origin may determine its adaptation to specific climatic conditions, and thus likely influences which climatic areas are more suitable for successful invasion (Haider et al. 2010; Wesselmann et al. 2024). So far, such historical biogeographic studies have usually used phylogenetic analyses and ancestral state reconstruction based on molecular data. However, a combination of such population genetic analyses and ecological niche modelling allows for a comprehensive spatiotemporal representation of population migration dynamics, thereby providing deeper insights into speciation and the spatiotemporal distribution of subsequent populations. Despite its potential, such combined approaches have rarely been employed to study the evolution and population dynamics of individual invasive species.

Ecological niche modelling also allows us to predict future distributions, particularly in changing climates. Many introduced species have the potential for further geographic spread under future climatic conditions (Guan et al. 2020), while native communities often struggle with reduced resistance to invasion (Thuiller, Richardson, and Midgley 2007; Parmesan and Hanley 2015; Parmesan and Singer 2022). Previous studies suggest that global climate change will lead to thermophilisation of many ecosystems and a reduced exposure to freezing temperatures, potentially facilitating the poleward and/or elevational spread of many invasive species (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006; Chen et al. 2011; Christina, Limbada, and Atlan 2020). Despite the potential for climate change to exacerbate the spread of invasive species (Dukes and Mooney 1999; Weltzin, Belote, and Sanders 2003; Moore 2004; Thuiller, Richardson, and Midgley 2007), quantitative analyses of the species' responses to future climate scenarios remain rare (but see Chefaoui et al. 2019; Lee et al. 2021; Adhikari et al. 2022).

In our study, we focused on *Reynoutria japonica* (Houtt.) (Polygonaceae), which has been identified as one of the world's worst plant invaders (Lowe et al. 2000). The species is native to eastern China, the Korean Peninsula and the Japanese Archipelago, and was introduced to Europe and North America as an ornamental in the mid-19th century (Bailey and Conolly 2000; Del Tredici 2017). Historical documents suggest that the original sources of the introduction were Japanese populations. In its introduced range, invasive knotweed often grows along riverbanks and roads, and in wetlands and disturbed areas. The species is particularly known for creating dense monocultures in riparian habitats (Mandák, Pysek, and Bímová 2004; Richards et al. 2008; Walls 2010), and reducing native plant diversity (Gerber et al. 2008; Murrell et al. 2011).

Little is known about the levels of genetic diversity in the native range of *R. japonica*, which spans most of the eastern Sino-Japanese Floristic Region (SJFR), a centre of temperate plant diversity and endemism in the Northern Hemisphere (Wu and Wu 1996; Qian and Ricklefs 2000; Qiu, Fu, and Comes 2011). Several previous studies have found that in introduced ranges in both Europe and North America *R. japonica* harbours very low genetic diversity (Richards, Schrey, and Pigliucci 2012; Zhang et al. 2016). Historical data indicate that the introduced populations of *R. japonica* likely originated from southern Japan (Grimsby et al. 2007; Tippery, Olson, and Wendtlandt 2021). Yet, the genetic structure and evolutionary relationships among Japanese, Chinese and Korean populations have not been studied. Given that most plant species in the SJFR originated from mainland China, and many have undergone a bottleneck when migrating to Japan during the last glacial maximum, a large-scale analysis of Eastern Asian populations is important for understanding the evolutionary history of *R. japonica*.

Here, we present a comprehensive, large-scale analysis of the genetic structure and evolutionary history of *R. japonica* across its native (Eastern China, the Korean Peninsula and the Japanese Archipelago) and introduced (European and U.S.) ranges, based on seven chloroplast DNA markers. To further support the evolutionary history, we employed ecological niche modelling to predict the distribution of suitable habitats in East Asia during different geological periods since the emergence of this species. In addition, we projected its global distribution under future climate change scenarios, aiming to fully illustrate the spatiotemporal dynamic patterns of *R. japonica* from the past to the future. Our study aimed to answer three key questions. (1) Where was the biogeographic origin of *R. japonica*? (2) What was the global phylogeographic structure of *R. japonica*? (3) How did past climate changes influence the distribution of *R. japonica*, and what will be the impacts of future climate changes? In doing so, we systematically present the evolutionary history, and spatiotemporal dynamic patterns of the distribution of *R. japonica*, a globally invasive plant, through chloroplast DNA analysis combined with ecological niche modelling.

2 | Methods

2.1 | Plant Materials

The core of our study was 238 samples from 51 Chinese populations, 6 Japanese populations, 21 European populations and 30 North American populations collected across most of the latitudinal extent in each range (Irimia et al. 2023). We collected the plants in 2019 and 2020 and subsequently cultivated them on the campus of Fudan University in Shanghai, China. We also incorporated published cpDNA data on 27 individuals obtained from the NCBI database (https://www.ncbi.nlm.nih.gov) (Tables S1 and S2). Altogether, we worked on 265 samples in our analyses. Detailed information on all plant origins is provided in Table S3.

2.2 | DNA Extraction, PCR Amplification and Sequencing

We extracted genomic DNA from all samples using a Plant Genomic DNA Kit (Tiangen, Beijing, China). We then amplified the gene sequences of seven chloroplast regions (*rbcL*, *matK*, *rbcL-accD*, *accD-psaI*, *ndhF*, *accD*, *trnL-intron*) using seven previously published primers and two specifically designed primers for *ndhF* and *accD* (Table S4). We ran 30-μL PCR reactions consisting of 3-μL genomic DNA, 15-μL Premix Taq (Takara, Dalian, China), 1 μL of each primer and 10-μL dd H_2O. To amplify the fragments, we used an ABI thermal cycler with the following conditions: One cycle at 94°C for 2 min, 35 cycles at 94°C for 1 min, primer annealing (50°C for *rbcL*, *matK*, *rbcL-accD*, *accD-psaI*, *ndhF1* and 54°C for *accd1*, *accD2*, *ndhF2*, *trnL-intron*) for 1 min, 72°C for 2 min and a final extension at 72°C for 5 min. We sent our PCR products to Sheng Gong Company (Shanghai, China) for purification and Sanger sequencing using an ABI-3730XL DNA sequencer. To increase coverage, forward and reserve sequencing reactions were performed for each sequenced fragment. We assembled sequences in SnapGene (https://www.snapgene.com) and aligned them in MEGA X (Kumar et al. 2018). We obtained cpDNA sequences from all 238 new samples and included them in our subsequent analysis.

2.3 | Phylogeography and Phylogeny

For our analyses, we concatenated the sequences from all seven plastid regions into one contiguous sequence per sample. To analyse cpDNA diversity in *R. japonica*, we identified haplotypes using variable sites (single nucleotide polymorphisms and insertions/deletions) and then calculated the numbers of haplotypes, haplotype diversity (h), nucleotide diversity (p) and genetic differentiation coefficient (N_{ST} and G_{ST}) using DnaSP (version 5.0; Librado and Rozas 2009). For visualising genealogical relationships among haplotypes, we employed a median-joining method, optimised by maximum parsimony, using Network 4.5, which constructs and displays genealogical relationships as networks (Polzin and Daneshmand 2003).

For the phylogenetic analysis, we used a maximum likelihood (ML) approach on a total of 46 concatenated haplotypes (H1–H46), along with nine outgroups in MEGA X. This included 1000 rapid bootstrap replicates and a search for the best-scoring maximum likelihood tree (Kumar et al. 2018). To better understand the phylogenetic history of Polygonaceae and differentiation times of *R. japonica*, we included nine outgroups in our analysis: *R. sachalinensis* (two individuals) and *R. multiflora* (two individuals) as closer relatives of *R. japonica*, *Muehlenbeckia platyclada* and *Knorringia sibirica* from the larger Polygonaceae family and then more distantly related *Limonium tenellum* (Plumbaginaceae), *Rhabdodendron amazonicum* (Rhabdodendraceae) and *Simmondsia chinensis* (Simmondsiaceae).

2.4 | Divergence Times and Ancestral Areas

We estimated the divergence times among 46 concatenated haplotypes (H1–H46) of *R. japonica* in two steps. First, we constructed an evolutionary tree to investigate the divergence times between *R. japonica* and related species (Figure S1), using a Bayesian approach implemented in BEAST. For this tree, we selected four *R. japonica* haplotypes (H1, H2, H43 and H44) and nine outgroup individuals from the ML phylogenetic tree, including *R. sachalinensis* (Polygonaceae, two individuals), *R. multiflora* (Polygonaceae, two individuals), *Muehlenbeckia platyclada* (Polygonaceae), *Knorringia sibirica* (Polygonaceae), *Limonium tenellum* (Plumbaginaceae), *Rhabdodendron amazonicum* (Rhabdodendraceae) and *Simmondsia chinensis* (Simmondsiaceae). To accurately date divergence events within *Polygonaceae*, we applied two calibration points. The first calibration constrained the divergence time of Caryophyllales using fossils of *Simmondsia chinensis* and *Rhabdodendron amazonicum* (Bell, Soltis, and Soltis 2010). The second calibration constrained the divergence time between the Plumbaginaceae and Polygonaceae to around 42 Ma (Wilkstrom, Savolainen, and Chase 2001; Wikstrom, Savolainen, and Chase 2003; Fan et al. 2013). We adopted these time points as our best age estimates within Polygonaceae under the relaxed clock log-normal model. The second step was to explore the divergence times among *R. japonica* haplotypes through a new evolutionary tree where the split between *R. sachalinensis* and *R. multiflora* was assumed at 10.16 Ma (Figure S1), similar to a previous study (Fan et al. 2013). We used 46 concatenated haplotypes (H1–H46) of *R. japonica* plus two *R. sachalinensis* and two *R. multiflora* individuals as outgroups. We assumed a mutation rate within *Polygonaceae* of 1.25×10^{-8}, based on the lowest and highest mutation rates recorded for plants (1×10^{-8} and 1.5×10^{-8}) (Ossowski et al. 2010; Holliday et al. 2016).

We conducted Bayesian searches for tree topologies and node ages of the chloroplast data in BEAST using a GTR + G substitution model selected by ModelFinder (http://iqtree.cibiv.univie.ac.at) with a Yule process specified as the tree prior. We ran MCMC runs for 100,000,000 generations where parameters were sampled every 1000 generations. Using the program Tracer 1.7.2 (http://tree.bio.ed.ac.uk/software/tracer/), we confirmed the stabilisation of model parameters and convergence between runs (all ESS values > 200). The first 10% of sampled trees from all runs were discarded as burn-in based on visual inspection in Tracer. We summarised the maximum clade credibility tree using TreeAnnotator (Drummond and Rambaut 2007) and visualised the tree with FigTree 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). We then determined the divergence times with the mean node heights and the 95% highest posterior density (HPD) intervals in millions of years (Ma).

To trace the geographical diversification of *R. japonica*, we conducted RASP analyses (Yu et al. 2015) using the calibrated tree derived from our BEAST analysis. We excluded outgroups due to the uncertainty of their distribution and their significant phylogenetic distance from *R. japonica*. We identified the following five global regions according to the physical geographical regionalisation (Buerki et al. 2011; Wang, Wang, and Su 2014): A, China; B, South Korea; C, Japan; D, North America; and E, Europe.

2.5 | Past and Future Distributions

To assess the potential impacts of past climatic changes on the distribution of *R. japonica*, we constructed an ecological niche modelling (Guisan and Zimmermann 2000) based on species occurrence data from a search for all synonyms of Japanese knotweed (Table S5) in the GBIF database (GBIF.org [21 April 2023] GBIF Download https://doi.org/10.15468/dl.knv9vd). To reduce spatial clustering, we then restricted ourselves to human observations or preserved specimens only. To avoid records with low spatial accuracy and potential erroneous taxonomy, we further limited the data to post-1945 observations. We also removed all observations with aberrant locality data. Our data set included occurrence data from a high-resolution field survey in 2021 (Table S3). This comprehensive dataset included a total of 180,000 coordinates worldwide, with 3396 observations from East Asia. The first ecological model was based on occurrence records from the native range (China, South Korea and Japan) only, and the second model considered the current global distribution of *R. japonica* to be able to project future global distribution changes by 2070. We employed the maximum entropy algorithm (Maxent) to estimate potential geographical distributions using Wallace version 1.9.3–5 (Kass et al. 2018) (the code for analysis is in Zhang, van Riemsdijk, et al. 2024). Maxent uses a machine-learning algorithm which estimates the potential geographical range by comparing the environmental conditions at species-occupied locations against background conditions (Phillips et al. 2017).

To determine whether Japanese knotweed could have survived in mainland Asia during the period when a land bridge existed, we used bioclimatic variables from PaleoClim (paleoclim.org; Hill 2015; Fordham et al. 2017; Karger et al. 2017; Brown et al. 2018) at 2.5-arcmin resolution as predictors. We projected our models using both contemporary (1979–2013) climate conditions and those associated with three past periods: the late Pliocene warm period (3.205 Ma), the Pleistocene MIS19 (*c.* 787 ka) and the Pleistocene in the Last Interglacial period (*c.* 130 ka). Our ancestral area reconstructions indicated that knotweed populations in China and Japan began diverging between 1.42–2.58 Ma. To avoid multicollinearity, we calculated pair-wise Pearson correlation analysis for the 14 bioclimatic variables available for all periods (for MIS19, monthly maximum and minimum temperatures were not available) and randomly removed one variable for each pair with a correlation >0.75 (Dormann et al. 2013). This left us with a subset of five key variables for the Maxent model: annual mean temperature (bio1), temperature seasonality (bio4), mean temperature of wettest quarter (bio8), annual precipitation (bio12) and precipitation seasonality (bio15). We fit the Maxent model with 10,000 background samples randomly selected from the projected region, and varied our regularisation multipliers from 0.5 to 5.0 in increments of 0.5. We included all feature classes (L, Q, H and P; L = linear, Q = quadratic, H = hinge and P = product) and their combinations, and we employed a random k-fold ($k=4$) method. The optimal model was selected based on the lowest corrected AIC (Δ AICc), indicating the best combination of feature and regularisation multiplier. After evaluating the model, we built a final model for native *R. japonica*.

In order to model the future distributions of *R. japonica* across its native and introduced ranges, we utilised bioclimatic variables from worldclim.org (Fick and Hijmans 2017) at a 5-arcmin resolution. Our projections for 2070 were based on contemporary climate conditions (1979–2013) and two future climate scenarios. We applied the same screening method as previously mentioned to identify climate variables with correlations >0.8. After excluding climate variables with a contribution degree below 0.1 and a VIF greater than 10, we used temperature annual range (bio7), mean temperature of coldest quarter (bio11), annual precipitation (bio12) and precipitation of driest quarter (bio17). The Maxent model employed the Community Climate System Model (CCSM5) with two levels of CO_2 concentrations. We used the stringent mitigation scenario of Representative Concentration Pathway (RCP) 2.6 and the very high greenhouse gas emissions scenario of RCP8.5, which are the two extreme climate change scenarios that were formally adopted by the Intergovernmental Panel on Climate Change (IPCC) in the Fifth Assessment Report (AR5; IPCC 2013).

3 | Results

3.1 | cpDNA Diversity Within *R. japonica*

The alignment of seven concatenated plastid markers (*rbcL, matK, rbcL-accD, accD-psaI, ndhF, accD, trnL-intron*) yielded a consensus length of 7142 bp and identified 46 haplotypes (Figure 1) based on 84 variable sites (Table S6). We found 26 haplotypes in Chinese populations (H1–H26), seven in South Korean populations (H27–H33), 12 in Japanese populations (H34–H45), but only one in European populations (H45) and two in North American populations (H45 and H46) (Table 1). The distribution of haplotypes reflected a strong cpDNA phylogeographic structure ($N_{ST}=0.690>G_{ST}=0.330$). There were no shared haplotypes between Chinese and Japanese populations (Figure 1). The single haplotype H45 found in Europe was also the most abundant haplotype in North America, and it was also present in Japan, supporting the hypothesis that this region was the origin of introduced populations (Figure 1).

3.2 | Phylogeographical and Phylogenetic Surveys

In our phylogenetic analysis, *R. sachalinensis* emerged as a sister species to *R. japonica*, with significant divergence of both species from *R. multiflora*. Within *R. japonica*, both the ML (Figure 2a) and Bayesian trees (Figure 2b) identified three major clades, each with well-supported (> 80%) bootstrap values in the ML tree. *R. japonica* haplotypes evolved first in two main lineages. The first one (clade I) consisted of the five haplotypes H40–H44, all from the southern-most island of Kyushu, Japan (Figure 1). The second lineage was composed of two sister clades: clade II included the five haplotypes H34–H38 plus H45 from Japan (note that H45 is also the haplotype dominating Europe and North America), and clade III encompassed all remaining *R. japonica* haplotypes from China, Korea, Japan and North America. Most bootstrap values within this third clade were generally low, but the ML-based relationships were consistent with the Bayesian tree (Figure 2b). Haplotype H16 from China was the sister to the remaining haplotypes from clade III. Within clade III, we further

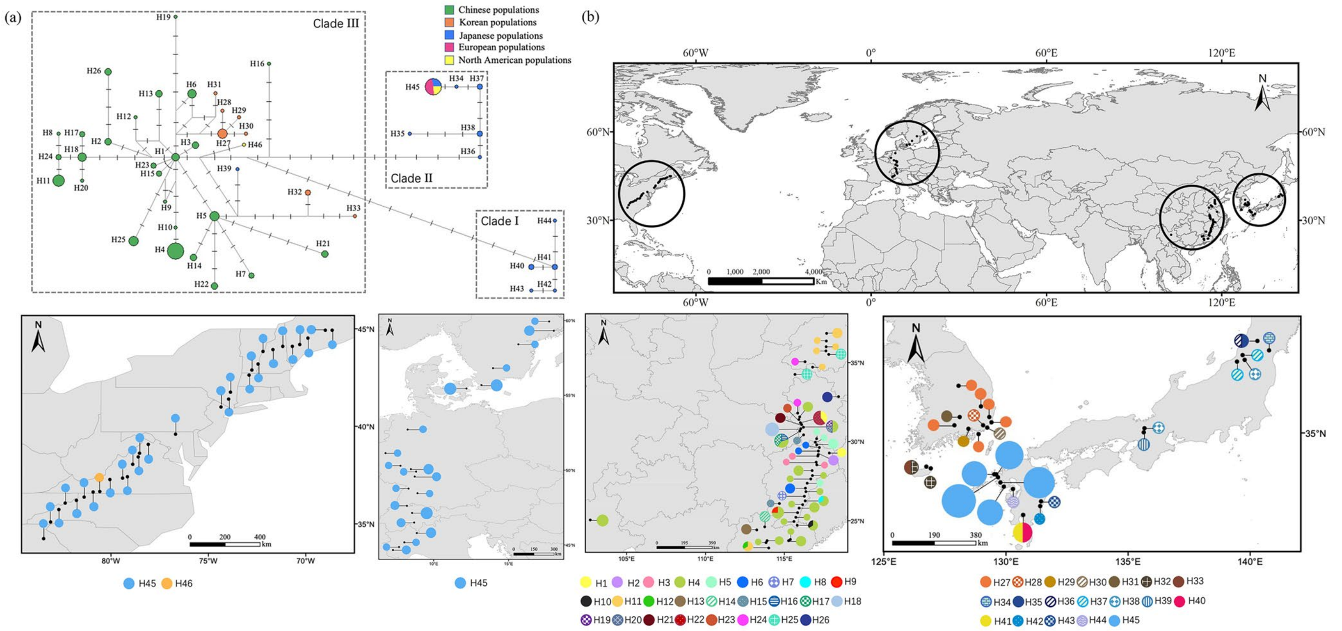

FIGURE 1 | Haplotype network and distribution of sampling for *Reynoutria japonica*. (a) Minimum spanning network of the 46 cpDNA haplotypes we identified across 265 global samples of *R. japonica*. The circle size corresponds to the frequency of each haplotype, and different colours represent the different geographical regions. (b) Geographical distribution of 46 *R. japonica* haplotypes detected around the world, with different colours representing different haplotypes (see legend). The haplotype names in the map are the same as in Figures 2 and 3b; Tables S1 and S6. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 1 | Samples sizes, numbers of polymorphic sites and haplotypes, nucleotide diversity (P_i), haplotype diversity (H_d) and average number of differences (K) for all analysed *Reynoutria japonica* samples, and separately for each region.

	All	China	South Korea	Japan	Europe	North America
Sample size	265	110	13	51	61	30
Population numbers	130	51	12	16	21	30
Polymorphic sites	84	47	16	38	0	17
Haplotypes	46	26	7	12	1	2
Nucleotide diversity (P_i)	0.00162	0.00093	0.00062	0.00109	0.00000	0.00016
Haplotype diversity (H_d)	0.752	0.869	0.795	0.503	0.000	0.067
Average number of differences (K)	11.338	6.477	4.333	7.570	0.000	1.133

identified two subclades: (i) subclade IIIa contained haplotypes from China (H6, H19) and Korea (H27–H31), and (ii) subclade IIIb included two haplotypes from Korea (H32/H33), one from Japan (H39), one from North America (H46) and the remaining haplotypes from China. It should be noted, though, that the bootstrap support for the two subclades was rather low (<60%).

3.3 | Divergence Time Estimates and Ancestral State Reconstruction

We used BEAST (Drummond and Rambaut 2007) to construct a time-calibrated tree (relaxed clock model) for the Polygonaceae plus several outgroups based on the concatenated cpDNA matrix. The tree estimated the divergence between the Polygonaceae and Plumbaginaceae (*Limonium tenellum*) at 42.25–44.57 Ma (95% highest posterior density), which was close to the time we set (i.e., 42 Ma), indicating that the result was reasonable. *Knorringia sibirica* and *Muehlenbeckia platyclada* diverged at 10.2–37.34 Ma, *Muehlenbeckia platyclada* and *R. multiflora* diverged at 3.75–25.72 Ma and the split between *R. sachalinensis* and *R. multiflora* was estimated at 2.51–20.64 Ma (node ages, 10.16 Ma) (Figure S1). The node ages between *R. sachalinensis* and *R. multiflora* were then estimated more precisely for all *Reynoutria* haplotypes using a strict clock model (Figure 2b). This model estimated the split between *R. sachalinensis* and *R. multiflora* at 10.43–12.37 Ma. The crown node of all Japanese and Chinese *R. japonica* populations was dated at

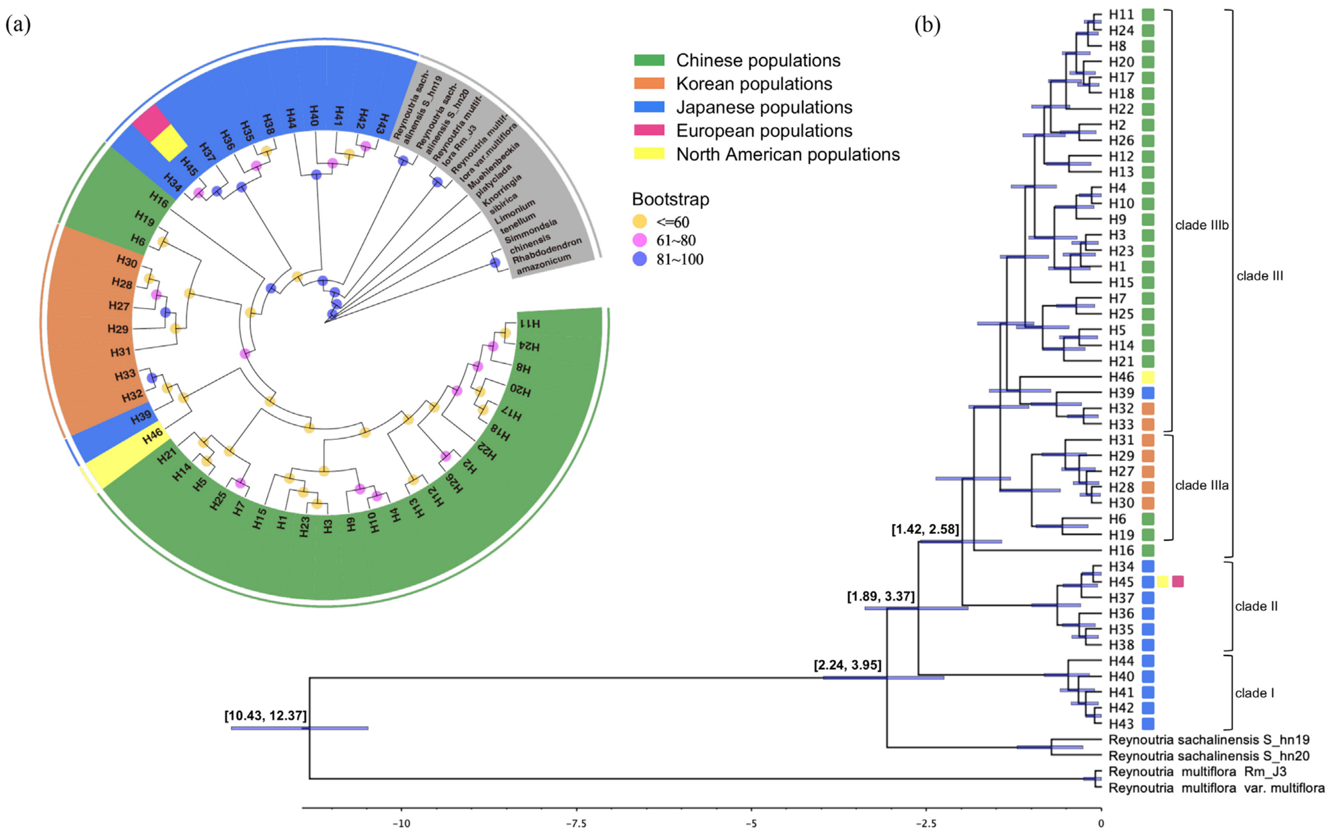

FIGURE 2 | Phylogenetic trees based on the concatenated data matrix. (a) CpDNA-based phylogenetic tree for the 46 *Reynoutria japonica* haplotypes as well as several other *Reynoutria* species and outgroups. The coloured circles on the nodes indicate different levels of maximum likelihood bootstrap support, and the colours in the outer circle represent geographical regions of sampling. For haplotypes identities see Table S1. (b) Phylogeny and divergence time estimates based on a Bayesian analysis for the same set of samples. The numbers and purple intervals at the nodes indicate 95% HPD for node ages (Ma). Colours of squares represent geographical regions of sampling and they are consistent with Figure (a).

1.42–2.58 Ma, and the most recent common ancestor of *R. japonica* at 2.24–3.95 Ma (Figure 2b).

The biogeographical reconstruction supported Japan as the likely evolutionary origin of *R. japonica* (Figure 3). An early divergence in the species resulted in two main lineages, that is, node 1 (Figure 3b). The ancestral lineage remained in Japan and then gradually migrated westward to China, with the descendant populations in China further spreading to the Korean peninsula (node 10). Most introduced populations in North America and Europe originated from Japan, with one exception (H46) which might have come from Japan or Korea (sharing a recent common ancestor with Japanese populations H39, and South Korean populations H32 and H33).

3.4 | Ecological Niche Modelling

Our model projections for the current distribution of *R. japonica* fit very well with the existing data for the East Asian region (Figure 4a), which confirmed the robustness of our ecological niche modelling. For the three historical periods (130 ka, 787 ka and 3.205 Ma), the projected distributions were generally smaller than the current ranges, especially during the two glacial periods (130 and 787 ka), with glacial refugia at lower latitudes of China and Japan (Figure 4b,c). During the late Pliocene warm period climate (3.205 Ma), our model suggested a disjunct but climatically suitable additional area in mainland Asia (Figure 4d). Thus, the climate of mainland Asia might have been suitable for colonisation by *R. japonica* at the time when the land bridge existed.

The ecological niche modelling also projected the current global distribution of *R. japonica* very well (Figure 5a). When we modelled the distributions in 2070 based on the IPCC scenarios RCP 2.6 (baseline low emissions) or RCP 8.5 (high emissions) (IPCC 2013), we found substantial increases of habitat suitability in both models at higher latitudes of Europe and North America, for example, European regions above 60° latitude as well as the northeast and northwest coast of Canada, with generally stronger changes under the RCP 8.5 scenario (Figure 5c). In East Asia, there was a projected shift northward, with substantial habitat losses in Southern China and some habitat gains in North East Russia, particularly on Sakhalin Island and the Kamchatka peninsula (Figure 5b,c).

4 | Discussion

In this study, we conducted an extensive, cross-continental investigation into the geographical origins, historical colonisation and spatiotemporal dynamics of *R. japonica*, one of the most important invasive plants worldwide. The phylogenetic analyses,

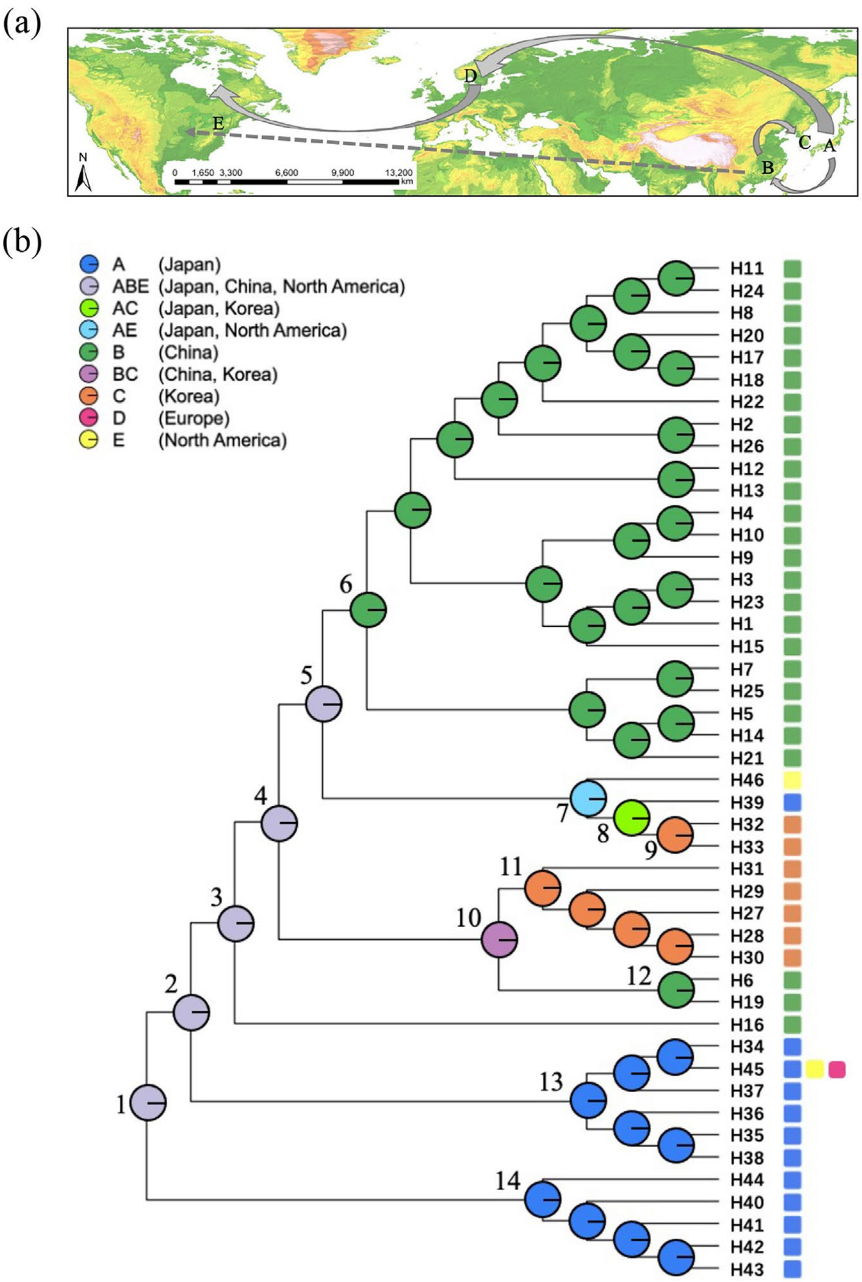

FIGURE 3 | Ancestral area reconstructions and the inferred migration routes of *Reynoutria japonica*. (a) Inferred migration routes of *R. japonica* based on RASP analysis. (b) Ancestral area reconstruction of *R. japonica* based on RASP analysis. The haplotypes are labelled as H1–H46 (see Table S1 for details). Squares in different colours represent the sampling locations in different areas. The numbers on the nodes are used in the description of the results. The areas (A–E) with different colours are defined according to the physical geographical regions in (a) and (b), with area A as putative ancestral area. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

combined with ecological niche modelling, provided evidence that past climate fluctuations and sea level changes likely led to an expansion of *R. japonica* from southern Japan to continental East Asia, followed by a contraction of the East Asian populations. Under the influence of human activities, the species was recently introduced from Japan to Europe and North America, ultimately resulting in the establishment of three major genetic clades worldwide. Future climate scenarios indicated a northward expansion of *R. japonica* in Europe and North America, but shrinking of its range in China. In summary, our study represents the largest study to date on this species and highlights the roles of historical climate shifts, topography, sea level rise and human activities in the large-scale geographic structure of this species, and the spatiotemporal dynamics of its distribution.

4.1 | Phylogenetic Relationships Within *R. japonica*

We discovered a complex phylogeography of *R. japonica*, particularly in its native East Asian range, with multiple major clades: one (clade I) restricted to Japanese populations, another one

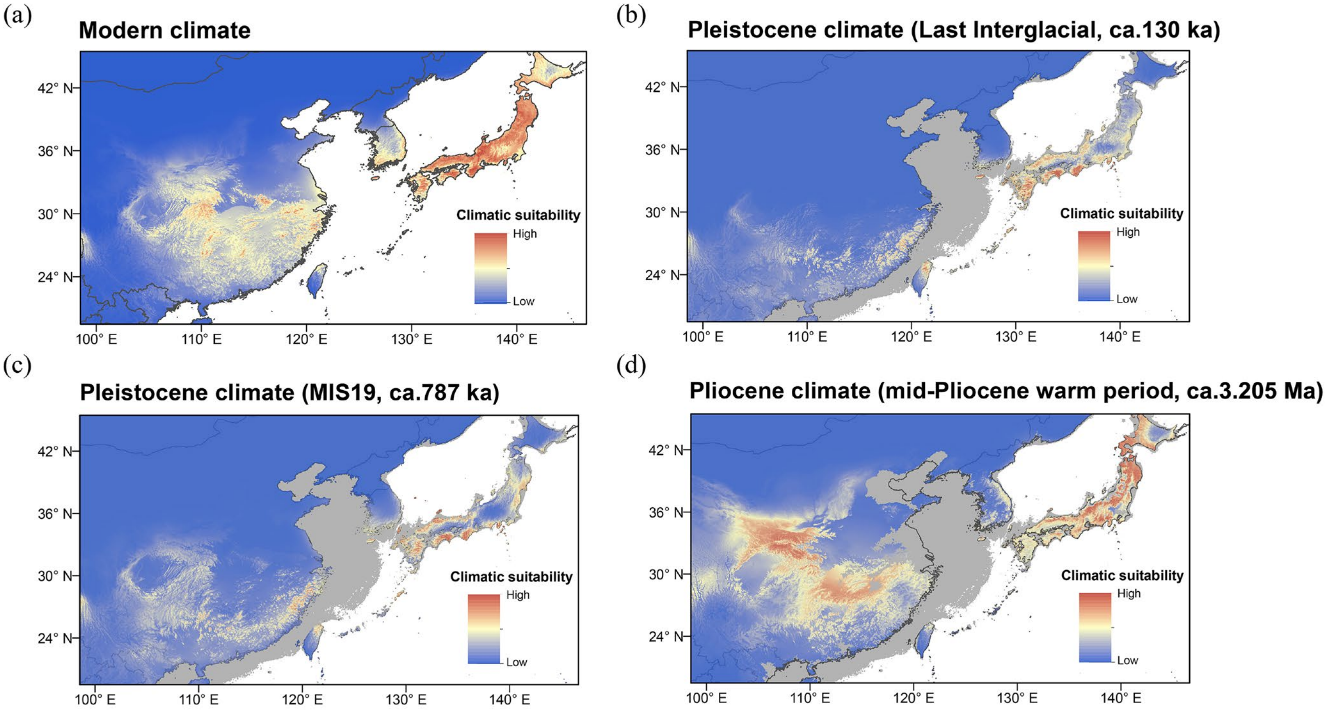

FIGURE 4 | Current and past distributions of *Reynoutria japonica* in East Asia, as projected with Maxent ecological niche modelling for (a) modern climate, (b) Pleistocene climate around 130 ka—representing conditions at the end of the land bridge formation, (c) Pleistocene climate at 787 ka and (d) the Pliocene warm period climate around 3.205 Ma—at the start of the land bridge formation. Colour scales from blue (least suitable climates) to red (most suitable climates). The grey background in panels (b–d) represents additional land available during these periods, and thus potential dispersal routes from southern Japan to mainland Asia. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

(clade II) combining other Japanese populations with almost all European and North American ones, and a third (clade III) that included mainly Chinese and South Korean populations but also a few individuals from Japan and North America (Figure 2). The Japanese populations from the southern part of Kyushu Island (all clade I) appeared to have diverged early from all other examined *R. japonica* samples. This genetic divergence was further reflected in the morphological variation observed in our collection: offspring of Japanese populations from clade I had thicker leaves, less above-ground biomass and more ramets than the Chinese populations when grown in common gardens (Cao et al. 2023; Irimia et al. 2023; Wang et al. 2024). This suggested that the genetic divergence of Chinese and South Korean populations might also have resulted in functional divergence from the Japanese populations.

We found that, compared to East Asian populations, levels of haplotype diversity were extremely low in *R. japonica* populations from North America and Europe. This corroborates several previous studies that also found very low levels of molecular marker diversity in European and North American populations (Grimsby et al. 2007; Richards, Schrey, and Pigliucci 2012; Zhang et al. 2016; Tippery, Olson, and Wendtlandt 2021). The genetic diversity of exotic species in their introduced ranges is influenced by their introduction history (e.g., founder effects, and number of introduction events; Bock et al. 2015). Analyses of historical documents and herbaria suggest that a single genotype of *R. japonica* was introduced from Japan to Europe in the 1840s and a few years later to the United States with cuttings of rhizomes (Del Tredici 2017). Our phylogenetic analysis found that all European samples and almost all North American samples formed a single, well-supported clade together with the Japanese haplotype H45. This result supports a single founder event for all European populations and most US populations, resulting in very low levels of nucleotide diversity in the introduced ranges. A similar drastic reduction in genetic diversity in the introduced ranges has also been reported in other invasive plants such as *Pennisetum setaceum* (Poulin, Weller, and Sakai 2005), *Rubus alceifolius* (Amsellem et al. 2000) and *Alternanthera philoxeroides* (Geng et al. 2016). In all of these cases, the colonisation of new ranges was mostly likely based on only a small number of initially introduced (or surviving) genotypes, thereby strongly reducing genetic diversity in the introduced ranges. Such genetic bottlenecks often lead to reduced adaptive potential (Willi, Van Buskirk, and Hoffmann 2006), inbreeding and subsequent loss of heterozygosity (Charlesworth and Charlesworth 1987) and stochastic increases in the frequency of deleterious alleles (Lynch, Conery, and Burger 1995). These processes, in turn, are expected to reduce the fitness of founding populations and thereby hinder their establishment and further spread. However, the successful colonisation of *R. japonica* and other invasive plants in spite of strong genetic bottlenecks does not meet this expectation and is known as the 'genetic paradox of invasion' (Allendorf and Lundquist 2003). It appears that at least for some highly successful clonal invasive plants (e.g., *A. philoxeroides*) (Geng et al. 2016), levels of genetic diversity may not be a critical factor limiting their distribution and abundance (Mounger et al. 2021).

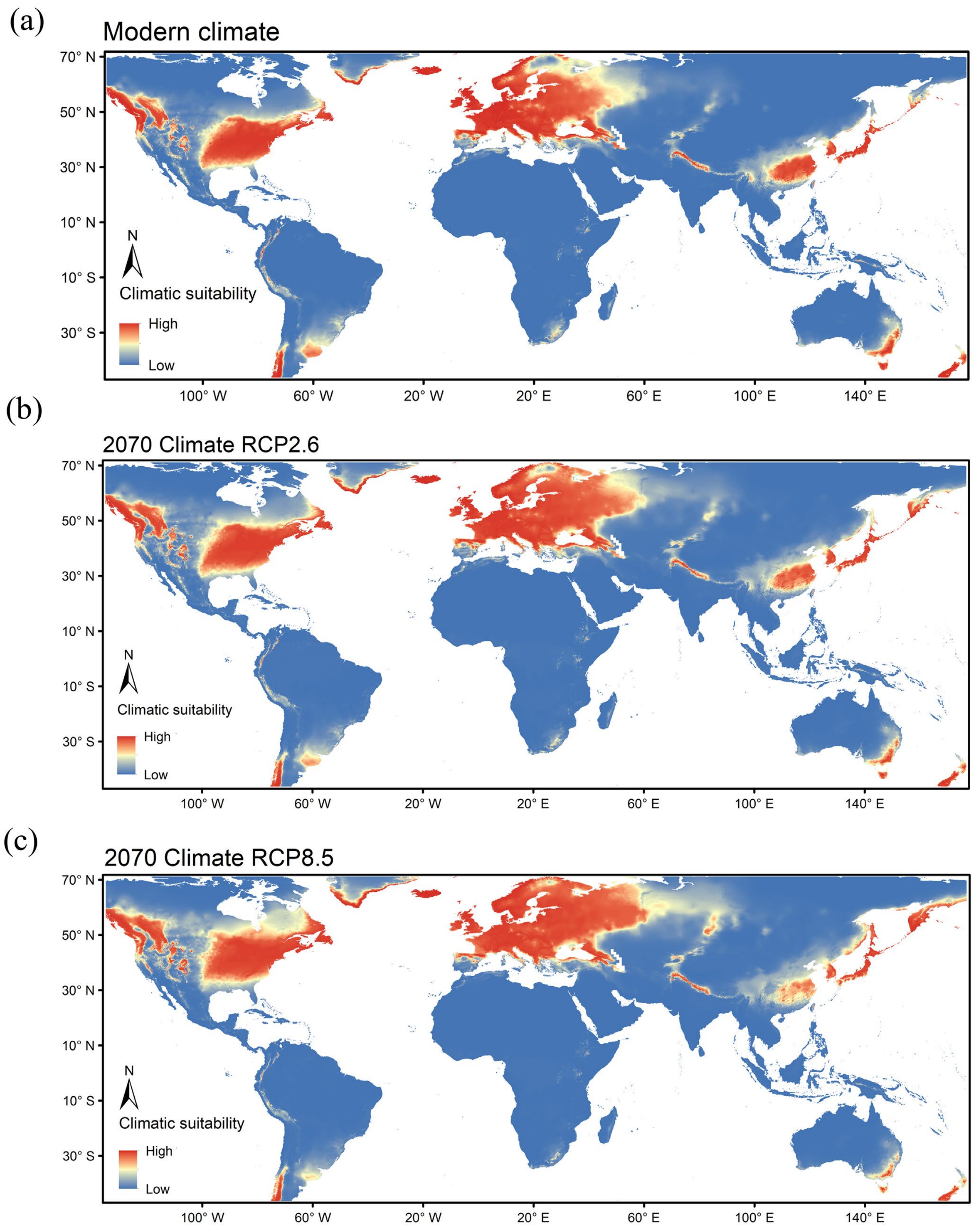

FIGURE 5 | Global habitat suitability modelled for *Reynoutria japonica* in (a) modern climate or future climates under (b) RCP 2.6 or (c) RCP 8.5 scenarios in 2070. Red colour indicates the highest projected habitat suitabilities. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

We identified one North American population that was not part of the large clade, which was consistent with previous studies in which there had been multiple introductions of *R. japonica* into North America (Grimsby et al. 2007; Tippery, Olson, and Wendtlandt 2021). We could not pinpoint the source of this North American haplotype (H46), but from our data, an introduction from Japan or Korea seemed most likely. More extensive and more high-resolution surveys of East Asian and North American populations are still needed to resolve this introduction, and to identify additional rare haplotype variation in North America. Furthermore, we used cpDNA markers that do not involve the nuclear DNA of *R. japonica*, and we, thus, did not capture the complete genetic diversity and evolutionary history of the species. However, since the main focus of our study was on large-scale and longer term patterns, we considered cpDNA markers sufficient for our research objectives. We are preparing a much more detailed molecular global analysis based on nuclear DNA markers, which may shed further light on the species' evolution and adaptation.

4.2 | Intraspecific Divergence and Spatiotemporal Dynamics of Distribution in the Past

Our ancestral reconstruction of *R. japonica* indicated a Japanese origin of the mainland Asian populations. The same was true for the closely related *R. sachalinensis* which originated from northern Japan and/or Sakhalin Island (Park et al. 2018). Such a Japanese origin is a rather uncommon pattern for plants in the Sino-Japanese Floristic Region, where most taxa originated from mainland China and later colonised Japan, such as *Cephalotaxus oliveri* (Wang, Wang, and Su 2014), *Heterotropa* sp. (Takahashi et al. 2021) and *Cardiocrinum* sp. (Yang et al. 2017). *R. japonica* may be one of the few cases with the opposite biogeographic pattern, together with some other exceptions, for example, *Diabelia* sp. (Wang et al. 2020) and *Kirengeshoma* sp. (Qiu et al. 2009).

For a more accurate understanding of evolutionary history, we used a molecular clock to refine our phylogenetic tree based on geological evidence. Our results further supported the hypothesis that ancient divergence of *R. japonica* occurred in the Sino-Japanese Floristic Region around the Plio-Pleistocene boundary (*c.* 2.58 Ma). This aligned closely with previous estimates of the formation of Chinese *R. japonica* at *c.* 2.2 Ma based on chloroplast data (Chen et al. 2022), and it coincided with the opening of the Tsushima/Korean Strait between South Japan and mainland China during 1.7–3.5 Ma (Kitamura and Kimoto 2006). However, we did not find any shared haplotypes between China and Japan, suggesting that the two regions did represent genetically distinct units, and that *R. japonica* evolved allopatrically for a long period of time. These ideas were further supported by our ecological niche modelling, suggesting a more widespread distribution across mainland China during the late Pliocene (*c.* 3.205 Ma), but a range contraction and fragmentation at the beginning of the Pleistocene. This range contraction might have reduced gene flow between Chinese and Japanese populations, leading to the observed genetic divergence (Nelson and Platnick 1981; Humphries and Parenti 1984).

We found that some regions in China, in particular the Dabie Mountains bordering the Hubei and Anhui provinces of China, had particularly high cpDNA diversity (Figure 1b). It is possible that this genetic diversity might have resulted from habitat fragmentation where populations were regionally diversified in different refugia. Previous studies have indicated that during the Pleistocene the Dabie Mountain region might have served as a refugium for many plant species such as *Quercus* spp. (Hao et al. 2023). *R. japonica* might have spread from the Hubei province into other Chinese regions (Chen et al. 2022). The results of our ecological niche modelling also indirectly indicated the presence of large patchy suitable habitats in southeastern China during the glacial period. However, to fully understand the complex intraspecific divergence patterns of *R. japonica* and confirm the existence of multiple refugia, future research is needed to incorporate more populations from both China and Japan.

The low resolution of cpDNA markers makes it difficult to precisely date *R. japonica*'s recent introductions into Europe and North America. Nevertheless, our ancestral reconstruction, together with existing literature, strongly indicated that European and most North American populations were introduced from Japan (Grimsby et al. 2007; Del Tredici 2017). The history of the North American introductions appeared to be somewhat more complex though, with a dominant genotype matching the one in Europe, but recent molecular work (Tippery, Olson, and Wendtlandt 2021) as well as historical analyses (Del Tredici 2017) indicated multiple introduction events, most likely two from Europe and one directly from Japan. Our phylogenetic analysis identified one individual in North America (H46) that did not specifically match any of the populations in Japan, China or Korea, but was most closely related to populations in Japan (H39) and Korea (H32 and H33). Further sampling from the native ranges is required to identify the exact source of this additional North American introduction.

Understanding the population spread and genetic differentiation of *R. japonica* can also inform us of its biological control. Current biocontrol efforts use biological control agents from Japan like *Aphalara itadori* (Camargo et al. 2022) and *Mycosphaerella polygoni-cuspidati* (Kurose et al. 2016, 2017). We found that most populations in Europe and North America share the same haplotype as those in Japan. Since these long-lived, clonal plants were introduced only recently, they are unlikely to have substantially genetically diverged from their source populations. The long coevolution between *R. japonica* and its specialist natural enemies in Japan might have resulted in high levels of defences against these herbivores. These evolved defences may still be maintained in European and North American populations reducing control effectiveness. In contrast, Chinese *R. japonica* populations, separated from Japan for nearly 2 million years, exhibited high genetic diversity, suggesting that China might offer more effective biological control agents such as *Gallerucida bifasciata* (Wang, Ding, and Zhang 2008).

4.3 | Response to Future Climatic Change

Numerous previous studies have indicated that global climate change can weaken the climatic constraints on geographic distributions, and lead to a tropicalisation of ecosystems and poleward shifts of invasive species (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003; Hickling et al. 2006; Chen et al. 2011; Christina, Limbada, and Atlan 2020). This aligns with our model projections that under the baseline-RCP 2.6 and 8.5 scenarios, the habitat suitabilities for *R. japonica* would significantly increase until 2070, particularly at higher latitudes. Field observations support such shifts: while *R. japonica* was once thought incapable of producing viable seeds at its northern limit in the Americas because of its late flowering, recent surveys have found seed production near its northern limit, possibly due to a climate-change driven extension of the growing season (Groeneveld, Belzile, and Lavoie 2014).

In contrast to the introduced ranges, the suitable habitats for native Chinese populations were projected to shrink by 2070 compared to currently suitable habitats, especially under the baseline-RCP 8.5 scenarios. The limited range expansion in East Asia might be attributed to contrasting climatic situations and future projections for China versus Europe and North America. The IPCC forecasts increased drought frequencies in the south of the Yangtze River (IPCC 2023), which may pose significant challenges for species like *R. japonica* that requires consistent water availability (Bailey and Wisskirchen 2004; Jovanovic et al. 2018). These climatic challenges may be exacerbated by intraspecific trait variation. Ongoing research indicates that Chinese populations of *R. japonica* have on average a lower leaf toughness than populations in Japan, Europe and Northern America (Cao et al. 2023). This is critical, since plants with softer leaves generally tend to be less drought-resistant (Wright et al. 2004). In another study, we have also found that these Chinese populations are less plastic in response to different environmental conditions (Wang et al. 2024). These trait discrepancies could further increase the susceptibility of Chinese *R. japonica* populations to climate change.

The observed differences in leaf traits between Chinese plants and others could also be a result of their distinct glacial histories. Our analyses suggest that Chinese *R. japonica* populations were confined to glacial refugia for longer periods than other native populations. The conditions in these refugia may have been more stable than in other areas, so the species in these long-term refugia might have reduced its capacity to tolerate harsh environmental conditions such as severe droughts. Such effects of glacial histories on intraspecific variation in leaf traits have been observed in other plant species like *Ulmus glabra* (Myking and Yakovlev 2006), *Campanula barbata* (Scheepens and Stoecklin 2011) and *Quercus coccifera* (de Casas et al. 2009). However, it should be acknowledged that most ecological niche modelling implementations are founded on the Eltonian noise hypothesis. This hypothesis states that biotic interactions at fine spatial scales within local communities are predicted to not significantly modify the abiotic signals extracted from coarser-scale environmental data used over large spatial areas (Soberon and Nakamura 2009; Lira-Noriega, Soberon, and Miller 2013). However, crucial biotic interactions may impact the resolution and extent of abiotic information pertinent to niche modelling (Wisz et al. 2013). As a result, niche modelling based on native range distributions might overpredict potential and future distributions, especially when genetic diversity is diminished in introduced ranges, as observed in *R. japonica*. Currently, integrating biotic interactions into niche modelling remains challenging, and future research should address interactions of biotic factors with abiotic predictors or historical factors like past extinctions and dispersal barriers (Warton et al. 2015; Dormann et al. 2018; Early and Keith 2019; Soley-Guardia, Alvarado-Serrano, and Anderson 2024).

5 | Conclusions

We have used a unique global data set to investigate the phylogeography, evolutionary history and spatiotemporal dynamics of the invasive *R. japonica*. Our results support a Japanese origin of the species in the late Pliocene, with subsequent spread to continental Eastern Asia. Our findings also support genetic divergence between ancestors and Chinese and Korean descendants after the disconnection of the land bridge during the Pleistocene, followed by a contraction in East Asian populations. The recent introductions and subsequent spread of *R. japonica* into Europe and North America have also been mostly of Japanese origin. Ongoing global climatic changes will likely drive European and North American populations to expand northward, while its native Chinese ranges are predicted to shrink in the future. Further research is necessary to investigate the evolutionary mechanisms underlying the differential responses to climate change between native and introduced populations of *R. japonica*. More broadly, understanding the evolutionary history of invasive plants is important to predict how they can adjust to challenging environmental changes, which necessitates additional empirical research.

Author Contributions

Lei Zhang: data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Isolde van Riemsdijk:** conceptualization, formal analysis, investigation, methodology, resources. **Mu Liu:** conceptualization, methodology, writing – original draft, writing – review and editing. **Zhiyong Liao:** investigation, methodology, resources, writing – review and editing. **Armand Cavé-Radet:** methodology, resources, writing – review and editing. **Jingwen Bi:** writing – review and editing. **Shengyu Wang:** writing – review and editing. **Yujie Zhao:** writing – review and editing. **Peipei Cao:** writing – review and editing. **Madalin Parepa:** conceptualization, writing – review and editing. **Oliver Bossdorf:** conceptualization, supervision, writing – review and editing. **Armel Salmon:** methodology, supervision. **Malika Aïnouche:** writing – review and editing. **Rui-Ting Ju:** formal analysis, methodology, writing – review and editing. **Jihua Wu:** methodology, writing – review and editing. **Christina L. Richards:** writing – review and editing. **Bo Li:** funding acquisition, methodology, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.27919170.v1, https://doi.org/10.6084/m9.figshare.27919167.v1, https://doi.org/10.6084/m9.figshare.27919161.v1, https://doi.org/10.6084/m9.figshare.27919164.v1, https://doi.org/10.6084/m9.figshare.27919155.v1, https://doi.org/10.6084/m9.figshare.27919176.v1, and https://doi.org/10.6084/m9.figshare.27919173.v1. The model code that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.27854592.v1 and NCBI with the accession numbers PP066065–PP066093, PP094309–PP094480, PP101881–PP101887. https://doi.org/10.6084/m9.figshare.27854592. The distribution data is available from GBIF at https://doi.org/10.15468/dl.knv9vd. The sources of cpDNA data obtained from the NCBI database are detailed in the supplemental material.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.