Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography
A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

The Nature of Oceanic Dispersal in the Diversification Process on Insular Systems in Asia

Takumi Saito[1] | Yasuto Ishii[2] | Shun Ito[3] | T. Mason Linscott[4] | Bin Ye[5] | Do Van Tu[6,7] | Shovon Mohammad Shariar[8] | Larisa Prozorova[9] | Purevdorj Surenkhorloo[10] | Aileen Shau Hwai Tan[11,12] | Yuma Fujino[13] | Takeru Uechi[14] | Shota Uchida[2] | Daishi Yamazaki[15] | Yuta Morii[16] | Kazuki Kimura[17,18] | Hiroshi Fukuda[19] | Osamu Miura[20] | Takahiro Hirano[21] | Satoshi Chiba[2,17]

[1]Faculty of Science, Ecology & Evolution, Amsterdam Institute for Life and Environment (A-LIFE), Vrije Universiteit, Amsterdam, the Netherlands | [2]Graduate School of Life Sciences, Tohoku University, Sendai, Miyagi, Japan | [3]College of Science, Academic Institute, Shizuoka University, Shizuoka, Shizuoka, Japan | [4]Department of Biological Sciences, Virginia Polytechnic Institute and State University, Blacksburg, USA | [5]Institutes of Physical Science and Information Technology, Anhui University, Hefei, Anhui, China | [6]Institute of Biology, Vietnam Academy of Science and Technology, Ha Noi, Vietnam | [7]Graduate University of Science and Technology, Vietnam Academy of Science and Technology, Ha Noi, Vietnam | [8]Department of Biochemistry and Molecular Biology, University of Rajshahi, Rajshahi, Bangladesh | [9]Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia | [10]Mongolian Benthological Society-MOBS, Ulaanbaatar, Mongolia | [11]School of Biological Sciences, Universiti Sains Malaysia, Penang, Malaysia | [12]Centre for Marine and Coastal Studies, Universiti Sains Malaysia, Penang, Malaysia | [13]Fukui City Museum of Natural History, Fukui, Fukui, Japan | [14]Marino Research co., Ltd., Kuwana, Mie, Japan | [15]Department of Environmental Science, Faculty of Science, Toho University, Chiba, Japan | [16]Department of Biology, Faculty of Agriculture and Life Science, Hirosaki University, Hirosaki, Japan | [17]Center for Northeast Asian Studies, Tohoku University, Sendai, Miyagi, Japan | [18]Department of Biology, Kyungpook National University, Daegu, South Korea | [19]Conservation of Aquatic Biodiversity, Faculty of Agriculture, Okayama University, Okayama, Japan | [20]Faculty of Agriculture and Marine Science, Kochi University, Nankoku, Kochi, Japan | [21]Biology Program, Faculty of Science, University of the Ryukyus, Okinawa, Japan

Correspondence: Takumi Saito (saito.zef@gmail.com)

Received: 29 April 2025 | **Revised:** 5 August 2025 | **Accepted:** 27 August 2025

Handling Editor: Juan Carvajal-Quintero

Funding: This work was supported by Japan Society for the Promotion of Science, KAKENHI 17H04611, KAKENHI 18H02506, KAKENHI 20K15866, KAKENHI 20K15872, KAKENHI 23K14261, Overseas Research Fellowship.

Keywords: continental island | diversification | freshwater snail | *Gyraulus* | island biogeography | Japan | long-distance dispersal | oceanic island | transoceanic dispersal

ABSTRACT

Aim: To clarify the characteristics and contribution of oceanic dispersal (OD), a representative of long-distance dispersal, to phylogenetic diversification on insular systems.
Location: Eastern Eurasia.
Time Period: Post-Neogene.
Major Taxa Studied: Freshwater snails of the genus *Gyraulus* (Mollusca: Gastropoda).
Methods: We conducted comprehensive sampling across the entire distribution range of *G. chinensis* group, including several continental and oceanic islands. To evaluate the evolutionary history of the group and the role of OD in diversification, we obtained genome-wide data using high-throughput sequencing and conducted phylogenetic analyses using three analytical approaches. We then assessed the relationship between phylogenetic and geographic distance separately in three distinct regions, using model fitting to evaluate the impact of dispersal mode on current phylogenetic diversity. The frequency and characteristics

of OD events were then estimated by conducting biogeographic analyses on two time-calibrated phylogenies produced using two separate geographic calibration events.

Results: Phylogenies revealed a well-supported monophyletic *Gyraulus* clade with a broad distribution across Eastern Eurasia and the presence of several internal geographic lineages. On the two insular regions, a power-law model best described the relationship between phylogenetic and geographic distances, suggesting limited dispersal and diversification through infrequent OD events. Divergence time estimations suggested that *Gyraulus* diversification originated after the late Miocene. The Oriental region of Eurasia was the most frequent source of dispersal. Across all trees, 6–8 OD events were estimated throughout the entire period, primarily on oceanic islands, with a single exception on a continental island at high latitudes. OD frequently originated from non-adjacent regions, in contrast to other dispersal events. Longitudinal dispersal was more frequent than latitudinal dispersal, and geographic lineages exhibited widespread longitudinal distributions.

Main Conclusions: OD exhibits a distinctive nature compared to other forms of dispersal. The interplay of oceanic barriers and rare OD events has shaped current biodiversity patterns on Asian insular systems.

1 | Introduction

Dispersal plays a fundamental role in shaping and maintaining spatial biodiversity patterns and has been extensively studied in the fields of ecology and evolution (Clobert et al. 2012; Stevens et al. 2014). Long-distance dispersal (LDD; *sensu* Jordano 2017), including oceanic dispersal (OD; see de Queiroz 2005), has been a central focus in biogeography due to its vital role in facilitating the colonisation of less mobile organisms to isolated environments, such as oceanic islands (de Queiroz 2005; Cowie and Holland 2006; Gillespie et al. 2012). Moreover, accumulating evidence suggests that LDD can contribute significantly to both species and genetic diversification across biological systems and geographic contexts, not limited to oceanic islands (de Queiroz 2005; Yuan et al. 2005; Hendriks et al. 2019; Korábek et al. 2022; Horsák et al. 2024).

However, despite increasing attention, our understanding of the general role of LDD in the diversification process remains limited and many questions regarding the impact of LDD on diversification persist (Matzke 2014; Dupin et al. 2017). For example, how often does LDD-associated diversification occur? Is LDD a major driver of current patterns of genetic structure in natural populations? Does LDD have specific properties that differ from other dispersals in shaping the process of diversification? Furthermore, progress in resolving these questions is hindered by the tendency of phylogeographic and diversification studies of LDD to focus on deep phylogenetic timescales where LDD is more easily detected, which limits our ability to determine LDD's influence on more recent evolutionary dynamics (see Graham et al. 2018). As genetic diversification within species or closely related lineages can profoundly shape current biodiversity patterns (Baselga et al. 2015), these phylogenetic scale biases present a major challenge to our ability to understand the impact of LDD on diversification. Consequently, the contribution of LDD to recent population structure and associated diversification remains poorly understood. To address these gaps, the nature of LDD, such as the frequency, directionality, and dispersal route, must be assessed in comparison with other forms of dispersal in phylogenetic and biogeographic contexts.

Here, we investigate the role of OD within the genus *Gyraulus*, a freshwater snail in the family Planorbidae (Hygrophila: Mollusca), in eastern Eurasia, with a particular emphasis on the Japanese archipelago. Small freshwater molluscs generally exhibit limited active dispersal abilities but possess high passive dispersal potential (Kappes and Haase 2012), and thus several species or species complexes are characterised by broad distributional ranges (e.g., Bespalaya et al. 2024). Simultaneously, the population and phylogenetic structure of freshwater mollusc species often mirror the geologic history of the region, which reflects the impact of biogeography on diversification (e.g., Schultheiß et al. 2014; Zielske et al. 2017). Indeed, *Gyraulus* species population structure appears to be affected by dispersal barriers such as oceans and mountains, despite their wide distribution (von Oheimb et al. 2013; Saito, Sasaki, et al. 2022). Previous phylogenetic and taxonomic studies of *Gyraulus* have revealed the presence of multiple clades in eastern Eurasia, and one of these monophyletic clades (clade A in Saito, Hirano, et al. 2018) is broadly distributed across eastern Eurasia, including much of the Japanese archipelago (Saito, Hirano, et al. 2018; Saito, Sasaki, et al. 2022). Although the taxonomy of most *Gyraulus* remains unresolved, this monophyletic clade seemingly corresponds to the recognised species *Gyraulus chinensis* (Dunker, 1848) or a species complex encompassing closely related lineages (Saito et al. 2020). The differentiation of these *Gyraulus* lineages in the Japanese archipelago may also have been driven by recurrent periods of isolation of the Japanese archipelago from the Eurasian continent (Saito, Hirano, et al. 2018). However, the role of OD vs. intraregional dispersal in the diversification process of *Gyraulus* remains unclear. The *Gyraulus* lineages on the continental islands of eastern Eurasia therefore provide an ideal model system to clarify the characteristics and impacts of OD on diversification among closely related lineages.

In this study, we examine LDD in the form of OD within *Gyraulus* freshwater snails from the Japanese Archipelago to assess how LDD shapes diversification across both shallow and deep phylogenetic timescales in insular systems. By combining comprehensive geographic sampling with genome-wide data and phylogenetic and biogeographic analyses, we estimate the propensity of OD and other factors to influence diversification across the evolutionary history of *Gyraulus*. We then compare our estimated rates and OD dispersal events to other studies of LDD in previously published studies of insular systems.

2 | Materials and Methods

2.1 | Location, Sampling and DNA Isolation

The Japanese archipelago primarily consists of several' large continental islands on the eastern edge of the Eurasian continent, as well as a few smaller oceanic islands. The geologic history of the archipelago is complex and is characterised by repeated connections and isolations from the Eurasian continent (Ninomiya et al. 2014). This complex geographic history has fostered exceptional biodiversity, making the Japanese archipelago one of the world's recognised biodiversity hotspots (Motokawa and Kajihara 2017). The region's high species diversity and well-documented geologic history make it an excellent model system for understanding the formation of insular biodiversity (Pietsch et al. 2003). Furthermore, the presence of numerous isolated islands provides a clear opportunity to identify OD events in *Gyraulus*, as a representative of LDD, through the integration of geological and divergence time data (Patiño et al. 2017).

We sampled *Gyraulus* specimens from 182 localities, including 33 islands and the Eurasian continent, covering the entire Japanese archipelago and most of the continental distribution range of the lineage (Figure 1 and Table S1). A total of 227 samples (up to three individuals per locality) were used, and these duplicate samples (two for 27 and three for three localities) were employed to verify whether multiple lineages coexist at the same locality. Additionally, samples were collected from artificial aquaria to evaluate introduced lineages that could potentially skew phylogeographic interpretations. All sampling localities were mapped using 'ggOceanMaps 1.3.4' (Vihtakari 2022) on R version 4.2.2 (R Core Team 2022). Samples were stored in 99.5% ethanol, and the total DNA was isolated from the tissue using

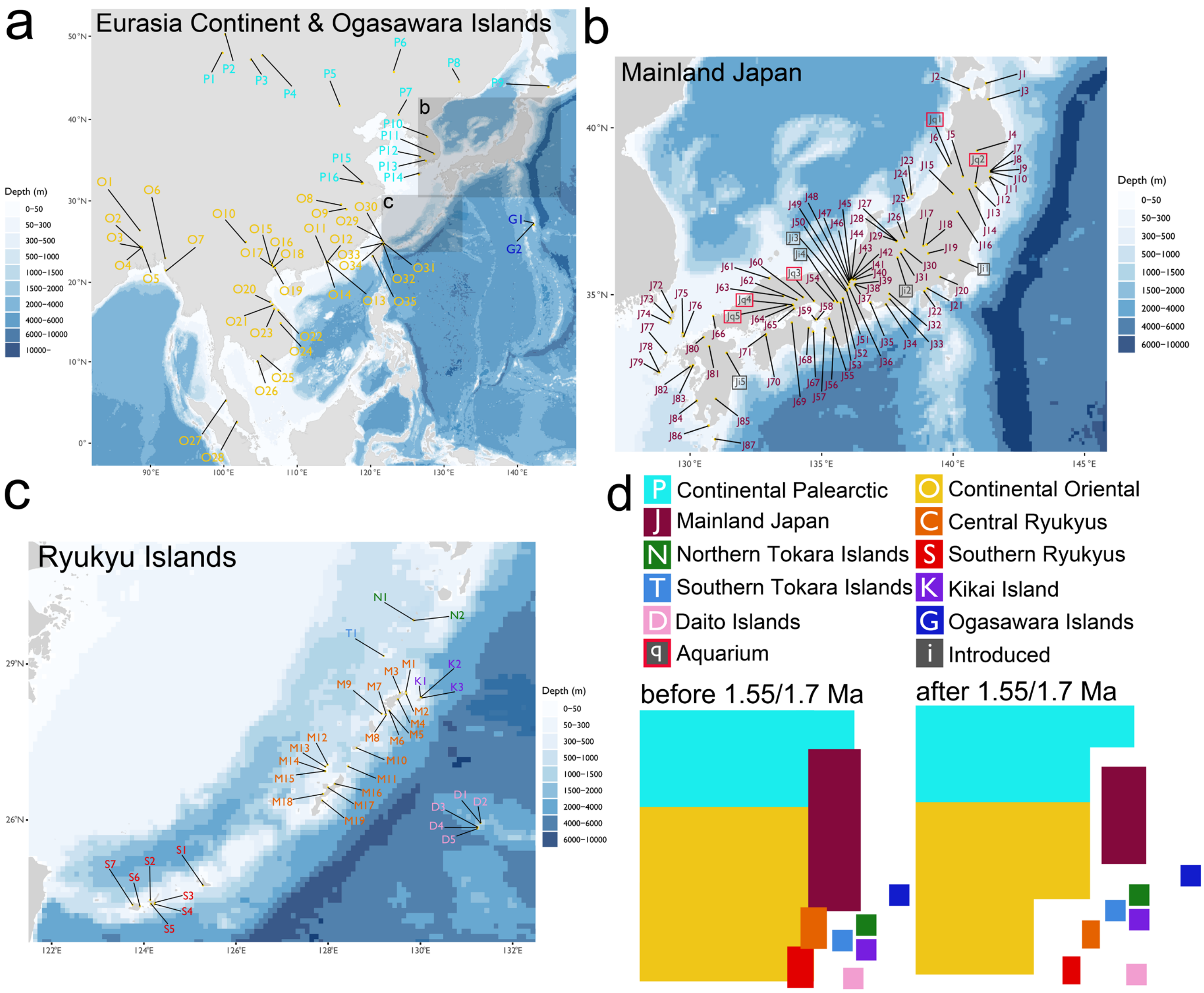

FIGURE 1 | (a–c) Geographic maps showing the sample locations used in this study. Letters and colours indicate geographic regions or sample origins (including aquarium and introduced populations). Maps were generated using the 'ggOceanMaps' in R version 4.2.2. For detailed sample information, refer to Table S1. (d) Geographical frameworks applied in this study. Detailed explanations on the geographic frameworks and classification can be found in Document S1.

the DNeasy Blood & Tissue Kit (Qiagen Inc., Germany) following the manufacturer's standard protocol.

2.2 | SNPs Detection and Phylogenetic Analyses

Previous phylogeographic studies in this region often relied on only a few markers like mitochondrial genes and risked misrepresenting evolutionary history due to their inability to infer and distinguish evolutionary artefacts (e.g., introgression, incomplete lineage sorting; Degnan and Rosenberg 2009; Toews and Brelsford 2012) and insufficient resolution to capture recent diversification events (Parks et al. 2009), potentially overlooking OD processes. Here, we utilise a phylogenomics approach using high-throughput sequencing which can offer reliable and high-resolution phylogeographic insights (e.g., Amador et al. 2022; Sano et al. 2022). To obtain genome-wide single nucleotide polymorphisms (SNPs), we performed double-digest restriction site-associated DNA sequencing (ddRAD-seq; Peterson et al. 2012) with slight modifications described in Sano et al. (2022). Briefly, a total of 30 ng of genomic DNA was used for digestion, and the size selection was conducted using Pippin Prep (Sage Science, MA, USA) within the 300–350 bp range. DNA fragments were amplified through PCR for 8 cycles, and final products were sequenced at the University of Oregon (OR, USA) and Northwestern University (IL, USA) using Illumina HiSeq 4000 (Illumina, CA, USA) with 100 bp single-end reads. Sequenced reads were assembled *de novo* using ipyrad 0.7.29 (Eaton and Overcast 2020). We specified a minimum coverage (min_samples_locus) of 40%, a maximum of 50% SNPs per locus, and a maximum of 20% indels per locus, with default settings for other parameters. This process yielded 404,548 bp and 137,797 SNPs across 2710 loci.

Based on the concatenated sequences, phylogenetic analysis was conducted using a maximum likelihood (ML) approach in IQ-TREE 2.1.3 (Minh et al. 2020). The substitution model was selected using ModelFinder (Kalyaanamoorthy et al. 2017) implemented in IQ-TREE2 under the Bayesian information criterion, and the ML phylogeny was estimated under the GTR + F model. The tree topology was assessed using ultrafast bootstrapping (UFBoot; Hoang et al. 2018) with 1000 replicates, Shimodaira–Hasegawa approximate likelihood ratio test (SH-aLRT; Shimodaira and Hasegawa 1999) with 1000 replicates, and a Bayesian-like transformation of aLRT (aBayes; Anisimova et al. 2011). UFBoot was conducted with the -bnni option to avoid overestimation of branch supports.

In addition to the ML approach, two additional phylogenetic approaches (i.e., locus tree-based and SNPs-based approaches) were employed to consider potential discordance between each gene/locus tree in biogeographic estimations. For the locus tree-based approach, trees of each locus were reconstructed using IQ-TREE2 with the same settings as described above, and a summarised phylogeny was estimated using ASTRAL III (ASTRAL; Zhang et al. 2017). The ASTRAL algorithm provides a robust phylogenetic estimation under the presence of discordance between each locus (Mirarab et al. 2014; Chou et al. 2015). The topological reliability was assessed using a coalescent-based computation (Sayyari and Mirarab 2016).

For the SNPs-based approach, we conducted SVDquartets (SVD; Chifman and Kubatko 2014) implemented in PAUP* 4.0. The SVDquartets algorithm can estimate robust relationships for a set of four taxa (quartet) using site pattern probability distributions of unlinked multi-locus data, and the estimation can be extended for arbitrary taxa using the agglomeration technique (Long and Kubatko 2019). All quartets were estimated under the multispecies coalescent model and were assembled and summarised using the quartet Fiduccia and Mattheyses algorithm (Reaz et al. 2014). Node supports were evaluated using 100 bootstrap replicates.

2.3 | Model Fitting for Current Biogeographic Pattern

We assessed the impacts of past OD events on phylogenetic history using several approaches. Dispersal ability often constrains the genetic structures of populations within space, particularly within species or closely related lineages exhibiting few niche differences (Gómez-Rodríguez and Baselga 2018; Gómez-Rodríguez et al. 2020). Consequently, the dispersal mode strongly influences the relationship between genetic and geographic structure within species (Chust et al. 2016); therefore, OD, despite its accidental nature, is also expected to affect this relationship when species diversify following OD events as it leaves a distinct spatial and genetic signature from other diversification processes.

Generalised linear models (GLMs; response variable: phylogenetic distance based on the ML tree; predictor variable: geographic distance) were fitted to characterise the relationship between phylogenetic distance and Euclidean geographic distance across three geographic areas: the Ryukyu Islands, Mainland Japan, and the Eurasian continent (see Document S1 for details of geographic grouping). Two oceanic islands, Ogasawara and Daito, were excluded from the analysis as outliers due to their high isolation. In addition, introduced lineages were also excluded (as detailed in Document S2). Three models were fitted using different parameters: linear (Gaussian error and identity link), exponential (Gaussian error and log link) and power-law (Gaussian error, log link and log-transformed spatial distance). Phylogenetic distances were calculated using the R package 'ape 5.0' (Paradis and Schliep 2019), and geodesic distances were obtained from the coordinates of each sample locality using the 'geopy 2.3.0' Python library under the WGS84 model with the Karney method (Karney 2013). Models were fitted using 'betapart 1.6' on R. The best-fit model was selected using the Akaike Information Criterion (AIC) whose weight (Wagenmakers and Farrell 2004) was calculated for each model. This framework was adapted from community ecology (Nekola and McGill 2014; Gómez-Rodríguez et al. 2020). An asymptotic relationship suggests restricted dispersal, while a linear relationship indicates no dispersal limitation (Hutchison and Templeton 1999; Gómez-Rodríguez et al. 2020).

2.4 | Divergence Time Analyses

To estimate the phylogeographic and colonisation history of a species group, a time-calibrated tree is required to understand how phylogenetic divergence aligns with changes in geographic setting.

However, as computational power and time requirements increase exponentially with the number and length of sequences for divergence estimation (Costa et al. 2022), we conducted divergence time dating using MCMCtree (Yang and Rannala 2006) implemented in PAML4 as this method is practical for large phylogenomic datasets (dos Reis and Yang 2019). For time calibration, we used two geographic constraints, instead of fossil calibration, as assigning phylogenetic positions to fossils at the intraspecific level is generally challenging (Kimura et al. 2021) and the fossil record of *Gyraulus* in eastern Eurasia may not be well resolved. We opted for a geographic constraint as fossil assignments and calibrations are almost impossible for *Gyraulus*, given the poor diagnostic traits of their shells (Meier-Brook 1983). The first calibration was based on the emergence of the Daito Islands, oceanic islands formed approximately 1.89 Ma (Iryu et al. 2023). Our taxon sampling covered both the Northern and Southern Daito Islands, and the divergence between the Northern and Southern Daito Islands must have occurred after the emergence of the Daito Islands.

The second calibration was the expansion of Lake Biwa to its present location. Lake Biwa, the largest ancient lake in Japan, has many endemic species and lineages (Kawanabe et al. 2020). Before the current Lake Biwa formed, a smaller, unstable lake (Paleo-Katata Lake) existed in the southern part of the present Lake Biwa area. This lake expanded and shifted to its current size and location after 0.43 Ma (Kawanabe et al. 2020). Thus, we set a skewed *t*-distribution (0.0043, 0.001. −2, 1) for the basal node of the Lake Biwa endemic lineage, which is well supported by all phylogenetic approaches (Figure S1; see Document S3 for complementary details of the calibration).

Using these calibrations and concatenated sequences, the gradient of branch length (g) and the Hessian matrix (H) were estimated for each tree on MCMCtree (usedata = 3) under the correlated clock model. The GTR model, selected as the best model in ML analysis, was applied for the substitution model. Then, using estimated g and H, divergence times were estimated for each tree on MCMCtree (usedata = 2). The substitution rate was roughly estimated using BASEML in PAML4 for the parameters of the prior distribution. For this estimation, the tree from IQ-TREE2 without branch lengths was rooted at 3.75 Ma based on a previous divergence time estimate for Asian *Gyraulus* (Saito, Hirano, et al. 2018). Based on this substitution rate (3.10/100 Ma), the prior gamma distribution for the rate (rgene_gamma) was set as 1, 0.32 and the prior gamma distribution for sigma (sigma2_gamma) was set at 1, 4.5 for each analysis. Each MCMC run was performed for 15,000,000 iterations, with the first 5,000,000 discarded as burn-in, and parameters were sampled every 1000 iterations. Convergence of chains was assessed using Tracer v1.7 (Rambaut et al. 2018) to ensure effective sample sizes (ESS > 100). We replicated two additional MCMC runs and confirmed convergence across analyses (ESS total > 200). Time-calibrated trees from a single MCMC run for each phylogenetic method (IQ-TREE2/ASTRAL/SVD) were used and these three time-calibrated phylogenetic trees were then used for biogeographic estimation.

2.5 | Biogeographic Estimation

First, we trimmed our tree so that a single sample from the same locality was randomly selected and the remaining shared site samples were removed from the resulting time trees using 'ape' in R. In addition, samples from the aquarium trade and samples suspected of artificial introduction based on the information from the aquarium lineages were also excluded to increase tree reliability for subsequent biogeographic analyses (as detailed in Document S2). Outgroups were removed and three time-calibrated trees (IQ-TREE2/ASTRAL/SVD) were used for subsequent analyses.

The resulting trees, containing 177 samples, were utilised to estimate ancestral geographic regions and dispersal events. These samples represent small populations rather than species, and to avoid spurious 'speciation' events, we employed the Markov-*k* model (M*k*; Lewis 2001), which treats geographic regions as unordered discrete traits. Using BioGeoBEARS (Matzke 2014), we compared multiple M*k* models incorporating time-stratification, dispersal probabilities (+*w*), and distances between regions (+*x*).

Ten geographic regions, including five oceanic islands (Daito Islands, Ogasawara Islands, Kikai Island, Northern Tokara Islands, and Southern Tokara Islands), were defined based on the past and present geographic connectivity (Figure 1). Based on microfossil data, the Tsushima/Korea Strait which isolates Mainland Japan and the Eurasian continent formed around 1.7 Ma and persisted during the last glacial period (Park et al. 2000; Kitamura and Kimoto 2006; Hoiles et al. 2012). On the other hand, a paleogeographic review of the Ryukyu Islands indicated a synchronous isolation of islands around 1.55 Ma, and this review presumed that the formation of the Tsushima/Korea Strait has occurred synchronously at 1.55 Ma (Osozawa et al. 2012). Therefore, we set two time scenarios: isolation of the Japanese and Ryukyu Islands synchronously at 1.55 or 1.7 Ma, implemented as the time stratifications in BioGeoBEARS. Note that Hokkaido Island was grouped in the continental Palearctic region, and Taiwan Island was included in the continental Oriental region, due to frequent connections to the continent during low sea level periods (Voris 2000; Artemova et al. 2019). Further details of the geographic frameworks are provided in Document S1.

Dispersal rate (a) was made to be a function of two matrices: distance between regions and probability of OD events compared to other distribution expansion. The distances were scaled as '1' for distances < 100 km, '2' for 100–500 km, and '3' for > 500 km, based on current minimum geographic distances, as no drastic land shifts occurred within the studied time scale. For the OD probability compared to other distribution expansion between connected regions, we set 10% (high), 1% (medium) and 0.1% (low) respectively. These matrices were then tuned by each hyper-parameter (*x* for the distance and *w* for the OD probability; Van Dam and Matzke 2016). Therefore, note that the difference in OD probability is a complement to the ML search as a variable initial value, and it is not a deterministic parameter. In total, eight models (M*k*/M*k* + distance-weighted/M*k* + TS + high_OD_prob/M*k* + TS + medium_OD_prob/M*k* + TS + low_OD_prob/M*k* + TS + distance-weighted+high_OD_prob/M*k* + TS + distance-weighted+medium_OD_prob/M*k* + TS + distance-weighted+low_OD_prob) with two time scenarios (i.e., TS = 1.55 or 1.7 Ma) were compared based on the relative weights of AIC with correction for small sample size (AICc weight) for three trees.

The models with the highest AICc weight were used to estimate the ancestral regions. Biogeographical stochastic mapping (BSM; Dupin et al. 2017) was performed with 100 replicates under the models with AICc weight ranking 1st to 3rd to calculate the estimated average numbers of OD/other dispersal events before and after 1.55/1.7 Ma. In addition, average geographic distances between regions per OD/other dispersal event were calculated. We visualised the results of the ancestral regions and the distributions of dominant clades in the time-calibrated tree from IQ-TREE2 using 'ggOceanMaps', showing the relationships between phylogenetic diversification and geographic location.

3 | Results

3.1 | Phylogenetic Analyses

Our phylogenetic analyses (Figure S1) showed a well-supported monophyletic clade (UFBoot/SH-aLRT/aBayes/SVD/ASTRAL = 98/99/1.00/99/100) for *Gyraulus* samples from eastern Eurasia, including the entire Japanese archipelago. Excluding introduced and aquarium-collected samples, samples from geographically close regions tended to form monophyletic clades. These clades were frequently well-supported in three or four supporting trees or measures of support. However, the ASTRAL tree exhibited notable topological differences across these clades (Figure S2). Furthermore, all samples from the same localities demonstrated genetically close relationships, and these terminal monophyletic clades were well-supported in most cases. By contrast, branches between the entire *Gyraulus* spp. from eastern Eurasia and the geographic clades varied among phylogenetic methods (Figure S2).

3.2 | Model Fitting

In both the Ryukyu Islands and Mainland Japan, the power-law model had the lowest AIC (Figure 2 and Table 1), with substantial AIC differences (AIC weight = 1.000) compared to the second-best model. In contrast, the exponential model represented the lowest AIC for the Eurasian continental samples, although fewer AIC differences from the second-best model (linear) were observed (AIC weight = 0.818 vs. 0.182).

3.3 | Divergence Time Estimation and Biogeographic Analyses

The root age of the *Gyraulus* spp. analysed in this study was estimated to be 6.49 Ma (95% CI: 5.12–6.90) in the case of the tree from IQ-TREE2 (Figure 3). From the root, 13 geographic clades were estimated to have diversified by the end of the Pliocene, and the ages of the most crown group for each lineage were dated to the Late Pliocene. For ancestral range estimation, the M*k* + TS + high_OD_prob model (1.55 Ma scenario: Figure 3) and M*k* + TS + low_OD_prob model (1.7 Ma scenario: Figure S3a) were selected based on AICc weight (Table 2) and few differences were observed between these scenarios (Figure 3 vs. Figure S3a). In both time scenarios, the modified OD probability (10/1/0.1% to the power of *w*) under the maximum likelihood parameters was stable at 5%–6% between each initial value (Table 2). In both selected models, the most likely ancestral regions for initial divergences were in the continental Oriental or Palearctic regions.

On the SVD tree (Figure S2a), the root age was estimated to be 6.87 Ma (5.85–7.91). Geographic lineages were sequentially diversified by the end of the Pliocene, and the most crown group ages of each lineage were estimated to be around the Late Pliocene. The M*k* + TS + *w*1% model (1.55 Ma scenario: Figure S2a) and M*k* + TS + high_OD_prob model (1.7 Ma scenario: Figure S3b) were selected based on AICc weight (Table 2), again with limited differences between these scenarios (Figure S2a vs. Figure S3b). Ancestral regions for initial divergences were most likely the continental Palearctic or Oriental regions.

The ASTRAL tree (Figure S2b) yielded an older root age estimate (8.91 Ma [7.85–9.91]). Geographic lineages were diversified until the early Pliocene, with the most crown group ages dating to the Pliocene. The M*k* + TS + low_OD_prob model (1.55 Ma scenario: Figure S2b) and M*k* + TS + distance-weighted + low_OD_prob model (1.7 Ma scenario: Figure S3c) were selected based on AICc weight (Table 2), with limited differences between scenarios (Figure S2b vs. Figure S3c). The most likely ancestral regions for initial divergence were the continental mainland Japan.

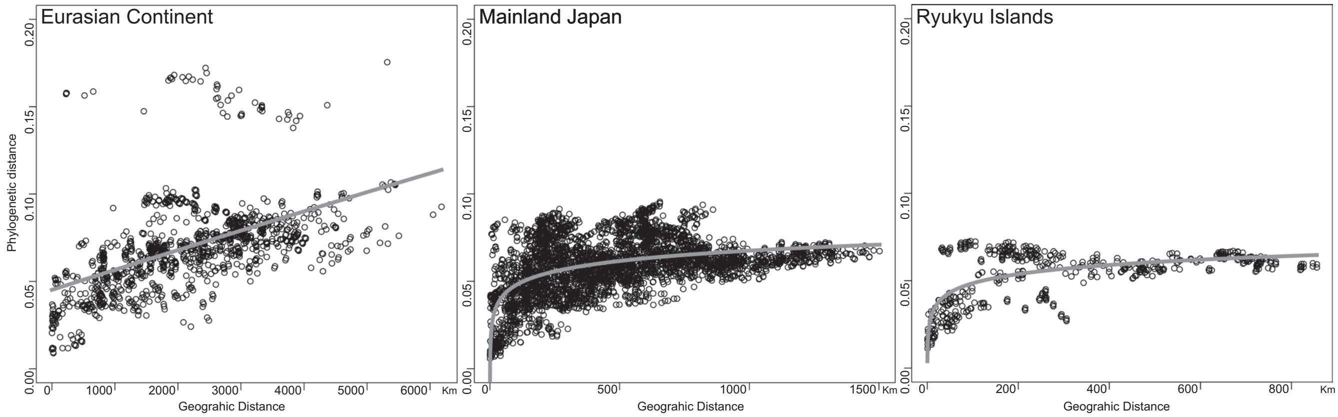

FIGURE 2 | Scatter plots illustrating the relationships between phylogenetic and geographic distances for each sample. Regression lines were derived based on the best-fit models identified using Akaike Information Criterion.

TABLE 1 | Results of model fitting for the relationship between phylogenetic and geographic distances.

Region	Ryukyu Islands				Mainland Japan				Eurasian continent			
Formula	**AIC**	**AIC_*w***	**Pseudo-R^2**	**Slope**	**AIC**	**AIC_*w***	**Pseudo-R^2**	**Slope**	**AIC**	**AIC_*w***	**Pseudo-R^2**	**Slope**
Linear	−2871	0	2.18×10^{-1}	2.86×10^{-5}	−20,960	0	1.74×10^{-1}	2.09×10^{-5}	−6110	0.182	2.62×10^{-1}	1.11×10^{-5}
Exponential	−2871	0	2.21×10^{-1}	3.05×10^{-5}	−20,960	0	1.76×10^{-1}	2.24×10^{-5}	**−6113**	**0.818**	$\mathbf{2.65\times10^{-1}}$	$\mathbf{1.21\times10^{-5}}$
Power-law	**−3034**	**1.000**	$\mathbf{4.39\times10^{-1}}$	$\mathbf{7.99\times10^{-3}}$	**−21,590**	**1.000**	$\mathbf{3.03\times10^{-1}}$	$\mathbf{9.12\times10^{-3}}$	−6084	0	2.48×10^{-1}	1.24×10^{-2}

Note: Bold letters indicate the model with the highest AIC weight.

3.4 | Dispersal Stochastic Mapping

On the tree from IQ-TREE2, the continental Oriental region seemed to be the most frequent source of dispersal before 1.55 Ma (Figure 4 and Table S3). Approximately two average dispersal events were estimated from the Oriental region to Central and Southern Ryukyus (2.03 and 1.92 events), and one or two dispersal events to Mainland Japan (1.24) and the continental Palearctic region (1.72). The Oriental region was inferred as a source of OD to the Northern Tokara Islands (0.40 events). Conversely, dispersal from Mainland Japan to the Oriental region (0.85 events) and from the Palearctic region to the Oriental region (1.89) were also estimated. The dominant source regions for OD to the Daito Islands were estimated as the Oriental region and Southern Ryukyus (0.53 and 0.37 events), and those to the Ogasawara Islands were estimated as the Oriental region and Palearctic region (0.28 and 0.23). After 1.55 Ma, approximately a single OD was estimated from Mainland Japan to the Palearctic region (0.99 events). In addition, the Central Ryukyus seemed to be the dominant dispersal source regions for Kikai Island (0.98 events) and the Southern Tokara Islands (0.86), while the Oriental region remained to be the possible source for the Northern Tokara Islands (0.43). In total, 6–7 OD events (6.59) were estimated, representing 32.9% within all dispersal events. The average geographic distance between regions per a single OD event was approximately 553 km, while the distance per other dispersal was 190 km (Figure 4). Similar estimations were obtained from the 1.7 Ma scenario (Figure S4 and Table S3).

The results on SVD suggested the Oriental region as the most frequent dispersal source before 1.55 Ma (to Mainland Japan: 2.96 events; Palearctic region: 2.12; Central Ryukyus: 2.01; Southern Ryukyus: 2.59; Northern Tokara Islands: 0.44; Daito Islands: 0.64; Figure 4 and Table S3). After 1.55 Ma, approximately a single OD was estimated from Mainland Japan to the Palearctic region (0.98 events), and more than a single OD event was estimated from Central Ryukyus to Kikai Island (1.63). Furthermore, approximately two dispersal events were estimated from the Oriental region to the Palearctic region, and the Oriental region seemed to be the most likely source region for the Southern Tokara Islands and the Northern Tokara Islands (0.57 and 0.34 events). In total, approximately eight OD events (7.91) were estimated, representing 32.4% within all dispersal events, and the distance for OD was 549 km and for others was 217 km (Figure 4). Similar estimations were observed in the 1.7 Ma scenario, although slightly more OD events were estimated (8.91 events and 35.8%; Figure S4 and Table S3). The estimations on the tree from ASTRAL suggested 5–6 OD events (5.64) in total, representing 21.9% within all dispersal events (distance: 642 km vs. 318 km; Figure 4), with similar estimates in the 1.7 Ma scenario (Figure S4 and Table S3 in details). Similar results were obtained with the second and third AICc weight models from each tree and time scenario (Table S4).

4 | Discussion

4.1 | Divergence Timescale and Discordance Between Phylogenetic Methods

Divergence time estimations indicate that the dominant diversification of eastern Asian *Gyraulus* primarily occurred during the Pliocene and Pleistocene. Although these estimates relied on

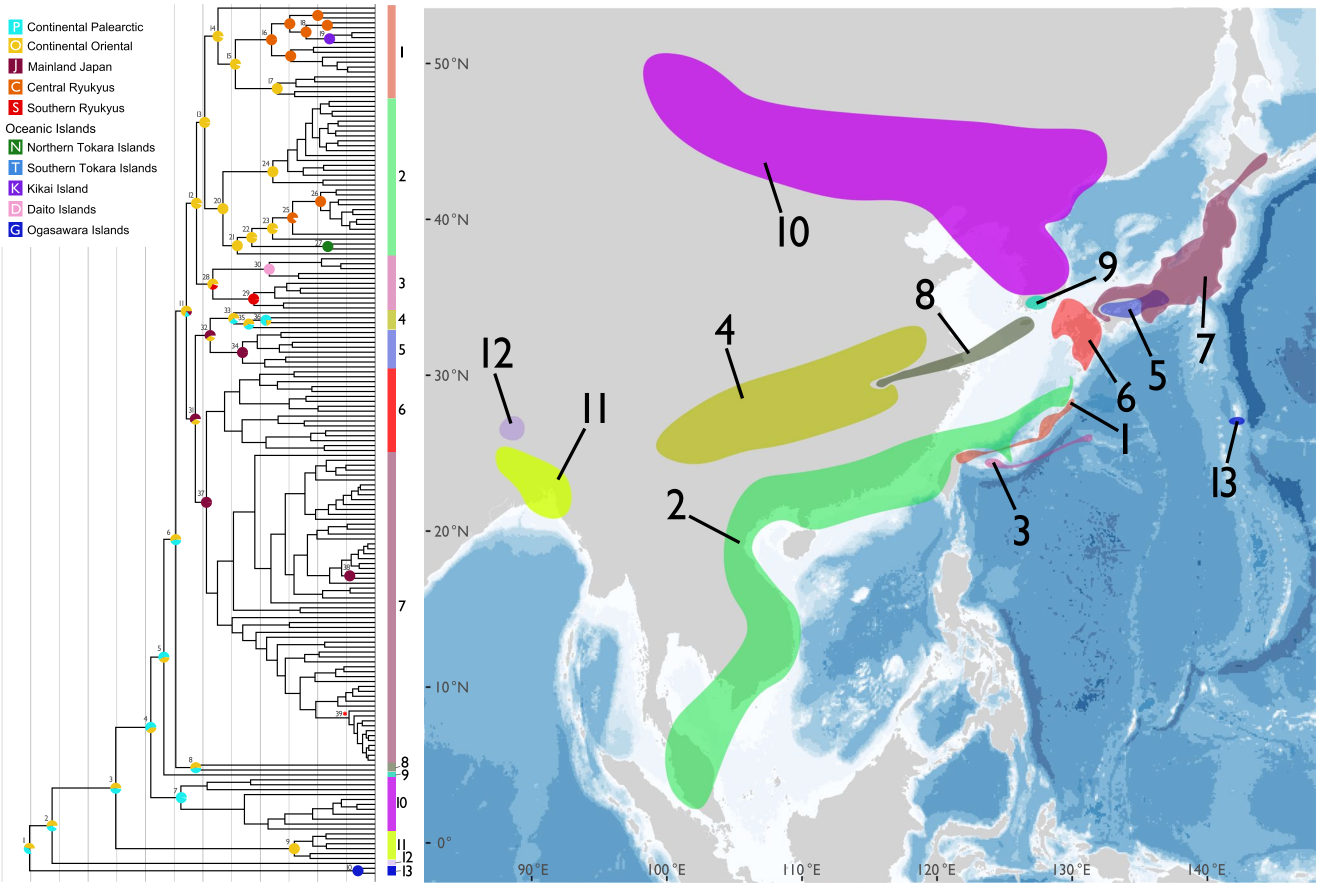

FIGURE 3 | Results of divergence time estimation and ancestral region estimation on the maximum likelihood tree generated by IQ-TREE2 (Minh et al. 2020). Ancestral region estimation was performed under the $\mathrm{M}k + \mathrm{TS} + \mathrm{high\_OD\_prob}$ model with time-stratification at 1.55 Ma. Letters and colours correspond to geographic regions for the samples. Coloured pie chart slices at each node represent the estimated ancestral region, with the central angle of the arc indicating the probability. Areas with a probability of less than 10% were omitted from each pie chart for visibility. Vertical bars on the right side of the tree denote thirteen geographic clades, and the distributions of these clades are shown on the map to the left.

two geographic calibrations, the estimated crown age of endemic lineage on the Ogasawara Islands closely aligns with previous results (Saito, Sasaki, et al. 2022) obtained from approximate Bayesian computation using different genome-wide data (mean estimates in our analyses: 0.30–0.41 Ma [95% CIs 0.06–0.83]; previous analyses: 0.35–0.39 Ma [0.16–0.50]). The divergence between the Eurasian continent and the Japanese archipelago likely occurred before the 1.55/1.7 Ma isolation, mainly during the Pliocene, followed by regional diversification (e.g., within Mainland Japan) during the Late Pliocene to Pleistocene. This timescale suggests that rather than the initial formation of the Japanese archipelago in the Early Miocene (Martin 2011), repeated connections and isolations between the continent and the archipelago during the Pliocene, and the subsequent land fragmentation within the archipelago played important roles in the diversification of *Gyraulus*.

This Pliocene–Pleistocene timescale is broadly consistent with previous estimates for other freshwater molluscs in eastern Asia, particularly those in the Japanese archipelago (e.g., Sphaeriidae: Saito, Fujimoto, et al. 2022; Valvatidae: Saito, Prozorova, et al. 2018; Viviparidae: Hirano, Saito, et al. 2019). In contrast, older divergence times have been suggested for other aquatic taxa such as aquatic insects (Tojo et al. 2017; Gamboa et al. 2019), crustaceans (Tomikawa et al. 2022), and fish (Watanabe et al. 2017). These differences may reflect variations in ecological traits, including dispersal ability and environmental constraints. For instance, even among molluscs, unionid mussels—which rely on fish to disperse their larvae—show an older diversification timescale, often predating the Pliocene (Sano et al. 2020, 2022). Across freshwater taxa, few studies have integrated genome-wide data with geographic sampling across both continental and island regions in Asia. Therefore, our results contribute to a more comprehensive understanding of the timescale of biodiversity formation of freshwater organisms in eastern Asia.

Although the overall timescale was generally consistent across phylogenetic methods, notable topological differences were also observed. In particular, the ASTRAL tree produced a different arrangement of basal nodes for samples from Mainland Japan. These differences can result from various factors such as incomplete lineage sorting, introgressive hybridization, or the compatibility between methods used and the number and length of genomic loci analysed (Chou et al. 2015). The ASTRAL topology had a particular impact on inferring dispersal direction between the Eurasian continent and the Japanese archipelago prior to the 1.55/1.7 isolation,

TABLE 2 | Results of model selection for biogeographic analyses using BioGeoBEARS.

Models	No. of parameters	*a*	*x*	*w*	Log-likelihood	AICc	AICc_*w*
Scenario: 1.55							
Method: IQ-TREE2							
M*k*	1	7.79×10^{-3}	—	—	−93.36362	188.7499	0
M*k*+distance-weighted	2	2.23×10^{-2}	−1.64	—	−90.26291	184.5829	0
M*k*+TS+high_OD_prob	**2**	$\mathbf{5.84\times10^{-2}}$	—	**1.25**	**−81.30923**	**166.6756**	**0.2360**
M*k*+TS+medium_OD_prob	2	5.82×10^{-2}	—	6.24×10^{-1}	−81.30945	166.6760	0.2360
M*k*+TS+low_OD_prob	2	5.83×10^{-2}	—	4.16×10^{-1}	−81.30946	166.6760	0.2360
M*k*+TS+distance-weighted+high_OD_prob	3	6.03×10^{-2}	-8.05×10^{-2}	1.24	−81.23611	168.5756	0.0913
M*k*+TS+distance-weighted+medium_OD_prob	3	6.95×10^{-2}	-5.54×10^{-1}	5.71×10^{-1}	−81.07541	168.2542	0.1071
M*k*+TS+distance-weighted+low_OD_prob	3	6.14×10^{-2}	-1.59×10^{-1}	4.23×10^{-1}	−81.2125	168.5284	0.0935
Method: SVDQuartets							
M*k*	1	9.02×10^{-3}	—	—	−109.76841	221.5595	0
M*k*+distance-weighted	2	2.10×10^{-2}	−1.25	—	−107.2331	218.5233	0
M*k*+TS+high_OD_prob	2	5.99×10^{-2}	—	1.20	−96.77484	197.6068	0.2448
M*k*+TS+medium_OD_prob	**2**	$\mathbf{6.02\times10^{-2}}$	—	$\mathbf{6.02\times10^{-1}}$	**−96.7744**	**197.6059**	**0.2449**
M*k*+TS+low_OD_prob	2	6.03×10^{-2}	—	4.02×10^{-1}	−96.77442	197.6059	0.2449
M*k*+TS+distance-weighted+high_OD_prob	3	5.92×10^{-2}	-3.76×10^{-2}	1.18	−96.79323	199.6899	0.0864
M*k*+TS+distance-weighted+medium_OD_prob	3	5.88×10^{-2}	6.56×10^{-2}	6.09×10^{-1}	−96.75923	199.6219	0.0894
M*k*+TS+distance-weighted+low_OD_prob	3	5.72×10^{-2}	1.22×10^{-1}	4.08×10^{-1}	−96.75524	199.6139	0.0897
Method: ASTRAL							
M*k*	1	5.90×10^{-3}	—	—	−115.6184	233.2594	0
M*k*+*x*	2	6.69×10^{-3}	-1.67×10^{-1}	—	−115.5415	235.1401	0
M*k*+TS+high_OD_prob	2	3.02×10^{-2}	—	1.24	−101.0998	206.2567	0.1688
M*k*+TS+medium_OD_prob	2	2.99×10^{-2}	—	6.16×10^{-1}	−101.0997	206.2566	0.1688
M*k*+TS+low_OD_prob	**2**	$\mathbf{3.00\times10^{-2}}$	—	**0.4128751**	**−101.0995**	**206.2562**	**0.1689**
M*k*+TS+distance-weighted+high_OD_prob	3	1.81×10^{-2}	8.51×10^{-1}	1.35	−100.1012	206.3058	0.1647
M*k*+TS+distance-weighted+medium_OD_prob	3	1.83×10^{-2}	8.16×10^{-1}	6.63×10^{-1}	−100.105	206.3133	0.1641

(Continues)

TABLE 2 | (Continued)

Models	No. of parameters	*a*	*x*	*w*	Log-likelihood	AICc	AICc_*w*
M*k* + TS + distance-weighted+low_OD_prob	3	1.83×10^{-2}	8.30×10^{-1}	4.47×10^{-1}	−100.1023	206.3080	0.1646
Scenario: 1.7							
Method: IQ-TREE2							
M*k*	1	7.79×10^{-3}	—	—	−93.36341	188.7495	0
M*k* + *x*	2	2.23×10^{-2}	−1.64	—	−90.2627	184.5825	0
M*k* + TS + high_OD_prob	2	6.20×10^{-2}	—	1.26	−81.09928	166.2557	0.2419
M*k* + TS + medium_OD_prob	2	6.59×10^{-2}	—	6.49×10^{-1}	−81.09163	166.2404	0.2438
M*k* + TS + low_OD_prob	**2**	$\mathbf{6.42\times10^{-2}}$	**—**	$\mathbf{4.26\times10^{-1}}$	**−81.09078**	**166.2387**	**0.2440**
M*k* + TS + distance-weighted+high_OD_prob	3	6.68×10^{-2}	-8.29×10^{-2}	1.28	−81.0401	168.1836	0.0923
M*k* + TS + distance-weighted+medium_OD_prob	3	6.48×10^{-2}	2.48×10^{-2}	6.53×10^{-1}	−81.10937	168.3221	0.0861
M*k* + TS + distance-weighted+low_OD_prob	3	6.54×10^{-2}	-7.75×10^{-2}	4.20×10^{-1}	−81.04304	168.1895	0.0920
Method: SVDQuartets							
M*k*	1	9.02×10^{-3}	—	—	−109.76832	221.5593	0
M*k* + *x*	2	2.02×10^{-2}	−1.17	—	−107.24534	218.5478	0
M*k* + TS + high_OD_prob	**2**	$\mathbf{6.49\times10^{-2}}$	**—**	**1.21**	**−97.04899**	**198.1551**	**0.2448**
M*k* + TS + medium_OD_prob	2	6.53×10^{-2}	—	6.06×10^{-1}	−97.04958	198.1563	0.2447
M*k* + TS + low_OD_prob	2	6.40×10^{-2}	—	3.98×10^{-1}	−97.05003	198.1572	0.2445
M*k* + TS + distance-weighted+high_OD_prob	3	6.31×10^{-2}	-2.34×10^{-2}	1.17	−97.06412	200.2316	0.0867
M*k* + TS + distance-weighted+medium_OD_prob	3	6.36×10^{-2}	8.79×10^{-2}	6.17×10^{-1}	−97.03177	200.1669	0.0895
M*k* + TS + distance-weighted+low_OD_prob	3	6.22×10^{-2}	1.18×10^{-1}	4.11×10^{-1}	−97.02907	200.1615	0.0898
Method: ASTRAL							
M*k*	1	5.90×10^{-3}	—	—	−115.61766	233.2580	0
M*k* + *x*	2	8.04×10^{-3}	-4.20×10^{-1}	—	−115.5552	235.1675	0
M*k* + TS + high_OD_prob	2	3.24×10^{-2}	—	1.27	−100.513	205.0831	0.1753
M*k* + TS + medium_OD_prob	2	3.24×10^{-2}	—	6.34×10^{-1}	−100.51301	205.0831	0.1753
M*k* + TS + low_OD_prob	2	3.23×10^{-2}	—	4.22×10^{-1}	−100.51318	205.0835	0.1753
M*k* + TS + distance-weighted+high_OD_prob	3	1.31×10^{-2}	1.43	1.45	−99.75954	205.6225	0.1339

(Continues)

TABLE 2 | (Continued)

Models	No. of parameters	***a***	***x***	***w***	Log-likelihood	AICc	AICc_*w*
Mk + TS + distance-weighted+medium_OD_prob	3	2.32×10^{-2}	5.18×10^{-1}	6.36×10^{-1}	−99.64791	205.3992	0.1500
***Mk* + TS + distance-weighted + low_OD_prob**	**3**	**1.89×10^{-2}**	**8.95×10^{-1}**	**4.59×10^{-1}**	**−99.40703**	**204.9175**	**0.1904**

Note: Eight models were tested with two different time stratification scenarios across three trees based on distant analytical approaches.

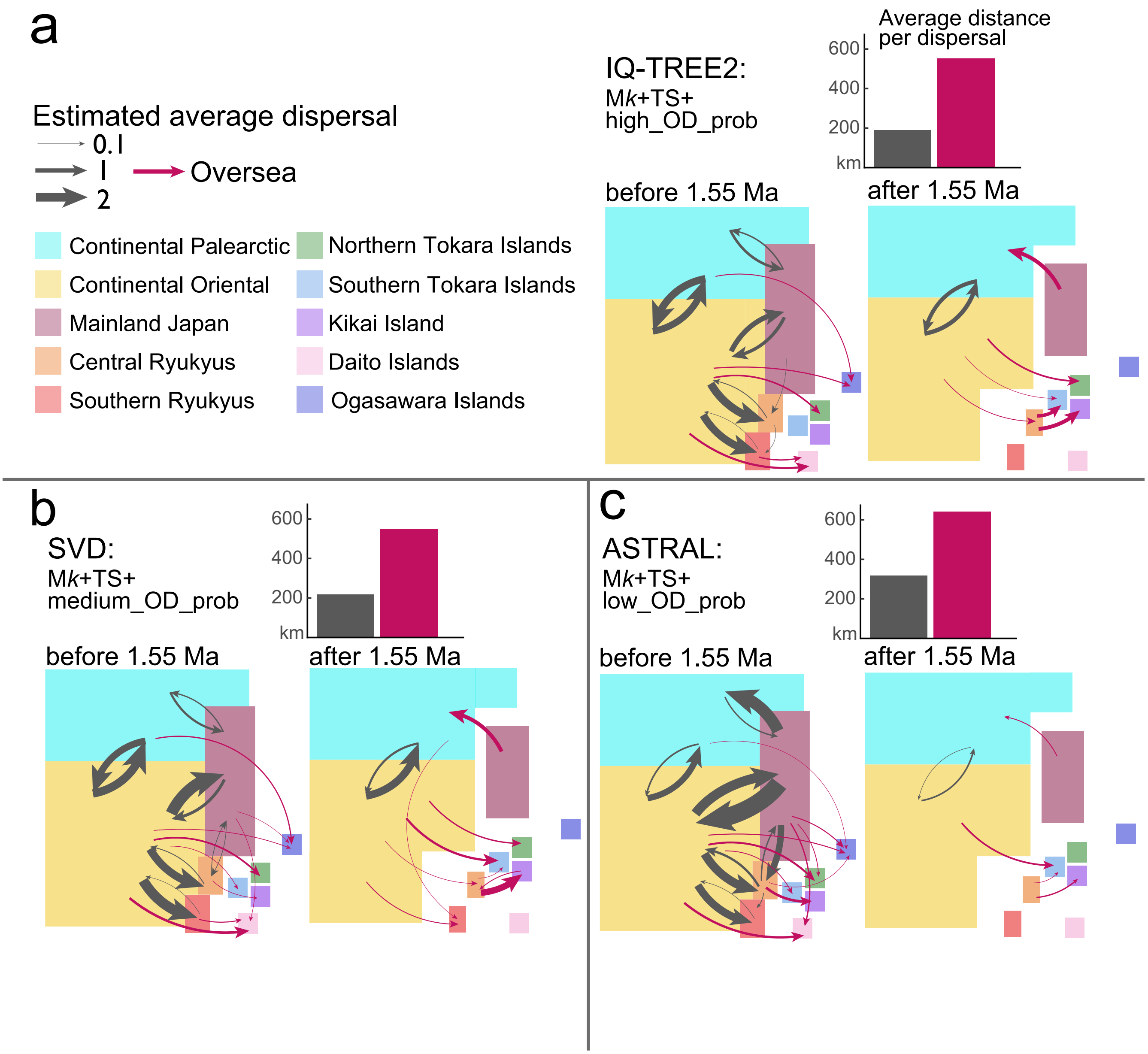

FIGURE 4 | (a) Estimated average dispersal events under the time-stratification at 1.55 Ma, based on 100 biogeographical stochastic mappings using BioGeoBEARS. Background boxes depict schematic representations of eastern Eurasia, with colours indicating geographic regions. Red arrows represent oceanic dispersal events, and letters represent abbreviations for the geographic regions. Vertical bars above each schematic represent the geographic distance between regions per OD or other dispersal event. For visibility, dispersal events with frequencies below 0.1 are omitted. Full results are provided in Table S3. (b) Results on the SVDQuartets tree. (c) Results on the ASTRAL tree.

and several dispersals from Mainland Japan to the Eurasian continent were estimated. Given the broader distribution of the *Gyraulus chinensis* group on the Eurasian continent, such results likely reflect methodological artefacts rather than actual biogeographic signals. In contrast, estimations of the OD nature (e.g., estimated number, direction and distance) were relatively consistent across three phylogenetic methods. Therefore, our interpretations focus on patterns consistently supported across methods, excluding the reverse dispersals suggested by the ASTRAL tree.

4.2 | General Pattern of Dispersal and Diversification

Dispersals between regions prior to 1.55/1.7 Ma were predominantly inferred as originating from neighbouring regions. These dispersals often followed a west-to-east direction (i.e., from the continental Oriental region to the Ryukyus and Mainland Japan) despite the sampling imbalance between the continental and Japanese regions, and the dominant geographic lineages are distributed across longitudinal gradients. As environmental differences can influence the establishment of freshwater molluscs (i.e., environmental filtering; Hauffe et al. 2016), these patterns may reflect limitations on latitudinal distribution expansion due to climatic niche conservatism (Wiens and Graham 2005), as previously shown in a freshwater snail (Saito et al. 2021). Furthermore, the dispersal directions may result from several factors such as the connectivity and directionality of freshwater systems and movement of dispersal vectors, including migratory birds.

Within regions, particularly in the insular regions (i.e., the Ryukyus and Mainland Japan), *Gyraulus* exhibits clear geographic structures, with ocean and mountain barriers often defining geographic boundaries. On many small islands that were likely connected to other areas during marine regression periods, monophyletic lineages are distributed, with their sister groups located in geographically adjacent areas. This pattern suggests that diversification results from distribution expansion via dispersal from adjacent areas and subsequent differentiation through isolation. Similarly, geographic diversification bounded by mountain ranges may reflect the same pattern of distribution expansion followed by isolation, consistent with the timing of mountain ranges' uplift in Mainland Japan (after the Pleistocene; Ota et al. 2010). Geographic diversification caused by such barriers has been documented in many terrestrial organisms in the Japanese archipelago (e.g., Pietsch et al. 2003; Tabata 2022) and may represent a general mechanism of genetic diversification in this region.

4.3 | Characteristics and Contribution of Oceanic Dispersal

Our biogeographic analyses estimated at least 6–8 OD events across all phylogenetic trees under optimal biogeographic models. Differences in these estimates were influenced more strongly by phylogenetic estimation approaches than by time scenarios (1.55/1.7 Ma). Nonetheless, all estimations consistently demonstrated that most diversification via OD occurred on oceanic islands. While *Gyraulus* has been documented on the Ogasawara Islands (Saito, Sasaki, et al. 2022), our findings revealed the substantial contribution of OD events in the divergence of endemic lineages on oceanic islands during the Pliocene–Pleistocene.

In contrast, OD events were rarely inferred for continental islands, with the exception of a recent dispersal from Mainland Japan to Hokkaido Island. Considering the several ODs to highly isolated oceanic islands, dispersal to continental islands remains possible. Thus, certain obstacles to the establishment of the *Gyraulus* lineages may be assumed on continental islands. One of the key differences between continental and oceanic islands is the presence of prior-resident organisms, and a plausible explanation for the obstacles may be extinction caused by competition and hybridisation (Silvertown 2004; Silvertown et al. 2005) with existing *Gyraulus* lineages. Competition within species or between closely related lineages is common in freshwater snails (Brown 1982), and a plausible case of inter-lineage hybridisation in other *Gyraulus* species has been documented (Klobušická et al. 2025). Additionally, inter-lineage mating has been observed under experimental conditions between some *Gyraulus* lineages (e.g., lineages 2 and 7 herein; Saito et al. personal observation). Moreover, bottlenecks following dispersal likely increase the vulnerability of newly immigrated populations to extinction through interactions with prior-resident populations. Our sampling detected no coexistence of different lineages at the same locality and revealed minimal geographic overlap between lineages. These patterns support the existence of exclusionary interactions between lineages. This competition/hybridisation hypothesis may also explain the OD event estimated in Hokkaido Island. The distribution of *Gyraulus* in our study is largely restricted to temperate and subtropical regions, indicating limited tolerance to cold environments. High-latitude populations, such as those in Hokkaido Island, are prone to local extinction during glacial periods (e.g., Horsák et al. 2020). Following such extinctions, these high-latitude regions may have resembled oceanic islands, providing opportunities for immigration via OD.

Furthermore, this hypothesis may partially explain the diversification observed in regions with multiple LDDs on deeper phylogenetic trees, as documented in previous studies (e.g., Tolley et al. 2013; Horsák et al. 2024). Evolution of ecological niches and the reproductive isolation following the phylogenetic divergence between closely related lineages could provide opportunities for new colonisation via LDDs, including ODs, without intraspecies competition and hybridisation. This mechanism implies that LDDs may occur more frequently at deep phylogenetic scales (e.g., species tree within a genus) than within species-level trees, even over similar time scales.

Our biogeographic estimations highlight distinctive characteristics of OD compared to other dispersals. The origins of oceanic island lineages were predominantly traced to the Eurasian continent rather than geographically adjacent regions. This finding suggests that the frequency of OD does not follow a simple linear relationship with distance from the source. In fact, the distance parameter (x) was rarely adopted in the best-fit models for biogeographic estimations. The probability of OD could be extremely low, even over short distances, while stochastic fluctuations associated with transoceanic distances may remain relatively minor. These dynamics of OD suggest that oceanic barriers function as binary thresholds, beyond geographical proximity. This relationship may parallel the long-tailed dispersal kernels often associated with LDD in seed dispersal of plants (Bullock et al. 2017), and a similar dispersal kernel could apply to freshwater snails. Additionally, larger population sizes and numbers in the continental Oriental region, due to its greater geographic area, may have increased the probability of dispersal from this region compared to smaller insular regions. Consequently, dispersal from more distant and larger regions may have occurred more frequently than dispersal from closer and smaller regions. Thus, one of the key characteristics of OD may be its stochastic nature.

These findings basically align with our model fitting results. On the Eurasian continent, phylogenetic distance was linearly related to geographic distance, except for the South Asian lineages, which are geographically isolated by several mountain regions (e.g., Qinghai-Tibet Plateau and Yunnan-Guizhou Plateau), whereas in insular regions, especially the Ryukyus, a power-law relationship emerged which could be explained by the limited dispersal and rare LDD diversification (Gómez-Rodríguez et al. 2020).

In addition, dispersal vectors can also influence the mode of OD. The lack of south-to-north ODs, often documented for other organisms in the Ryukyu Islands (Yang et al. 2018; Hirano, Kameda, et al. 2019; Hirano et al. 2022), suggests that ocean currents from south to north are unlikely to be the dominant vector of OD in our case. *Gyraulus* exhibits low salt tolerance (Zinchenko and Golovatyuk 2013) and conversely has certain tolerance to desiccation and gut passage through birds (van Leeuwen and van der Velde 2012; vanLeeuwen et al. 2012). These observations imply that birds may serve as an alternative vector for OD of *Gyraulus*. A migratory bird, for instance, has been documented carrying a planorbid snail over thousands of kilometres, from Oceania to Japan (Saito et al. 2023). Bird-mediated OD may better explain the observed dispersal patterns from remote regions (e.g., Gittenberger et al. 2006; Harzhauser et al. 2015; Yu et al. 2021).

4.4 | Implications, Limitations and Future Perspectives

Incorporating all findings, the underlying process of *Gyraulus* diversification in Asian insular systems is shaped by a combination of dispersal between connected regions, isolations driven by ocean barriers, and highly stochastic OD events. While OD is not the most frequent contributor to diversification in terms of frequency, its unique nature introduces a distinct process to the diversification of Asian insular systems. As a result, OD has significant implications in various research contexts, such as biogeographical interpretation and biodiversity conservation, and explicitly addressing OD as a distinct process is critical for ecological research on insular systems.

This study presents one of the most geographically and phylogenetically comprehensive reconstructions of biogeographic events in the Asian insular region to date. Nevertheless, major limitations to phylogeography—such as the accuracy of phylogenies, completeness of sampling, and uncertainty in fossil calibrations—also apply here. We addressed these through genome-wide SNP data, the multifaceted analytical approach, expanded sampling, and the geographic calibrations; however, it should be acknowledged that the limitations are inherent. These challenges can be complemented in future research through validation with independent data, including palaeontology and geology. Finally, the hypotheses and findings suggested here will be verified through comparative phylogeography with other taxonomic groups and meta-analysis based on accumulated phylogeographic data, and this study may serve as a model case to guide such future efforts.

Acknowledgements

We are grateful to Kameda Y, Otani JU, Isao S, Kagawa O, Pak JH, Akiyama K, Sato T, Quang NX, Dong Z, Shiraishi K, Murai Y, Fujimoto K, Aota T, Koseki J, Ozawa S, Nagao K, Tanchangya RTS, Sasaki T, and Okayama Prefectural Nature Conservation Center for taxon sampling. We also thank Iryu Y for valuable comments about the geological history of Daito Islands, and Tatani M for valuable comments about migratory birds. Moreover, we sincerely appreciate Dr. Michal Horsák and an anonymous reviewer, and the editor, Dr. Juan Carvajal-Quintero for valuable comments and suggestions on the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data are included in the published article, Supporting Information S1, and deposited in GenBank (SAMN48155944–SAMN48156170) and Zenodo (10.5281/zenodo.15855840).

References

Amador, L., A. D. Leaché, P. F. Victoriano, M. J. Hickerson, and G. D'Elía. 2022. "Genomic Scale Data Shows That *Parastacus nicoleti* Encompasses More Than One Species of Burrowing Continental Crayfishes and That Lineage Divergence Occurred With and Without Gene Flow." *Molecular Phylogenetics and Evolution* 169: 107443. https://doi.org/10.1016/j.ympev.2022.107443.

Anisimova, M., M. Gil, J.-F. Dufayard, C. Dessimoz, and O. Gascuel. 2011. "Survey of Branch Support Methods Demonstrates Accuracy, Power, and Robustness of Fast Likelihood-Based Approximation Schemes." *Systematic Biology* 60: 685–699. https://doi.org/10.1093/sysbio/syr041.

Artemova, A. V., Y. P. Vasilenko, S. A. Gorbarenko, A. A. Bosin, and V. V. Sattarova. 2019. "Climatic and Oceanological Changes in the Southwestern Part of the Sea of Okhotsk During the Last 94 Kyr." *Progress in Oceanography* 179: 102215. https://doi.org/10.1016/j.pocean.2019.102215.

Baselga, A., C. Gómez-Rodríguez, and A. P. Vogler. 2015. "Multi-hierarchical Macroecology at Species and Genetic Levels to Discern Neutral and Non-neutral Processes." *Global Ecology and Biogeography* 24, no. 8: 873–882. Portico. https://doi.org/10.1111/geb.12322.

Bespalaya, Y. V., M. V. Vinarski, O. V. Aksenova, et al. 2024. "Phylogeny, Taxonomy, and Biogeography of the Sphaeriinae (Bivalvia: Sphaeriidae)." *Zoological Journal of the Linnean Society* 201: 305–338. https://doi.org/10.1093/zoolinnean/zlad139.

Brown, K. M. 1982. "Resource Overlap and Competition in Pond Snails: An Experimental Analysis." *Ecology* 63: 412–422. https://doi.org/10.2307/1938959.

Bullock, J. M., L. Mallada González, R. Tamme, et al. 2017. "A Synthesis of Empirical Plant Dispersal Kernels." *Journal of Ecology* 105: 6–19. https://doi.org/10.1111/1365-2745.12666.

Chifman, J., and L. Kubatko. 2014. "Quartet Inference From SNP Data Under the Coalescent Model." *Bioinformatics* 30: 3317–3324. https://doi.org/10.1093/bioinformatics/btu530.

Chou, J., A. Gupta, S. Yaduvanshi, et al. 2015. "A Comparative Study of SVDquartets and Other Coalescent-Based Species Tree Estimation Methods." *BMC Genomics* 16: S2. https://doi.org/10.1186/1471-2164-16-S10-S2.

Chust, G., E. Villarino, A. Chenuil, et al. 2016. "Dispersal Similarly Shapes Both Population Genetics and Community Patterns in the Marine Realm." *Scientific Reports* 6: 28730. https://doi.org/10.1038/srep28730.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock, eds. 2012. *Dispersal Ecology and Evolution*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199608898.001.0001.

Costa, F. P., C. G. Schrago, and B. Mello. 2022. "Assessing the Relative Performance of Fast Molecular Dating Methods for Phylogenomic Data." *BMC Genomics* 23: 798. https://doi.org/10.1186/s12864-022-09030-5.

Cowie, R. H., and B. S. Holland. 2006. "Dispersal Is Fundamental to Biogeography and the Evolution of Biodiversity on Oceanic Islands." *Journal of Biogeography* 33: 193–198. https://doi.org/10.1111/j.1365-2699.2005.01383.x.

de Queiroz, A. 2005. "The Resurrection of Oceanic Dispersal in Historical Biogeography." *Trends in Ecology & Evolution* 20: 68–73. https://doi.org/10.1016/j.tree.2004.11.006.

Degnan, J. H., and N. A. Rosenberg. 2009. "Gene Tree Discordance, Phylogenetic Inference and the Multispecies Coalescent." *Trends in Ecology & Evolution* 24: 332–340. https://doi.org/10.1016/j.tree.2009.01.009.

dos Reis, M., and Z. Yang. 2019. "Bayesian Molecular Clock Dating Using Genome-Scale Datasets." In *Evolutionary Genomics*, edited by M. Anisimova, vol. 1910, 309–330. Springer New York. https://doi.org/10.1007/978-1-4939-9074-0_10.

Dupin, J., N. J. Matzke, T. Särkinen, et al. 2017. "Bayesian Estimation of the Global Biogeographical History of the Solanaceae." *Journal of Biogeography* 44: 887–899. https://doi.org/10.1111/jbi.12898.

Eaton, D. A. R., and I. Overcast. 2020. "Ipyrad: Interactive Assembly and Analysis of RADseq Datasets." *Bioinformatics* 36: 2592–2594. https://doi.org/10.1093/bioinformatics/btz966.

Gamboa, M., D. Muranyi, S. Kanmori, and K. Watanabe. 2019. "Molecular Phylogeny and Diversification Timing of the Nemouridae Family (Insecta, Plecoptera) in the Japanese Archipelago." *PLoS One* 14: e0210269. https://doi.org/10.1371/journal.pone.0210269.

Gillespie, R. G., B. G. Baldwin, J. M. Waters, C. I. Fraser, R. Nikula, and G. K. Roderick. 2012. "Long-Distance Dispersal: A Framework for Hypothesis Testing." *Trends in Ecology & Evolution* 27: 47–56. https://doi.org/10.1016/j.tree.2011.08.009.

Gittenberger, E., D. S. J. Groenenberg, B. Kokshoorn, and R. C. Preece. 2006. "Molecular Trails From Hitch-Hiking Snails." *Nature* 439: 409. https://doi.org/10.1038/439409a.

Gómez-Rodríguez, C., and A. Baselga. 2018. "Variation Among European Beetle Taxa in Patterns of Distance Decay of Similarity Suggests a Major Role of Dispersal Processes." *Ecography* 41: 1825–1834. https://doi.org/10.1111/ecog.03693.

Gómez-Rodríguez, C., K. E. Miller, J. Castillejo, J. Iglesias-Piñeiro, and A. Baselga. 2020. "Disparate Dispersal Limitation in *Geomalacus* Slugs Unveiled by the Shape and Slope of the Genetic–Spatial Distance Relationship." *Ecography* 43: 1229–1240. https://doi.org/10.1111/ecog.05142.

Graham, C. H., D. Storch, and A. Machac. 2018. "Phylogenetic Scale in Ecology and Evolution." *Global Ecology and Biogeography* 27: 175–187. https://doi.org/10.1111/geb.12686.

Harzhauser, M., O. Mandic, T. A. Neubauer, E. Georgopoulou, and A. Hassler. 2015. "Disjunct Distribution of the Miocene Limpet-Like Freshwater Gastropod Genus *Delminiella*." *Journal of Molluscan Studies* 82: 129–136. https://doi.org/10.1093/mollus/eyv040.

Hauffe, T., C. Albrecht, and T. Wilke. 2016. "Assembly Processes of Gastropod Community Change With Horizontal and Vertical Zonation in Ancient Lake Ohrid: A Metacommunity Speciation Perspective." *Biogeosciences* 13: 2901–2911. https://doi.org/10.5194/bg-13-2901-2016.

Hendriks, K. P., G. Alciatore, M. Schilthuizen, and R. S. Etienne. 2019. "Phylogeography of Bornean Land Snails Suggests Long-Distance Dispersal as a Cause of Endemism." *Journal of Biogeography* 46: 932–944. https://doi.org/10.1111/jbi.13546.

Hirano, T., Y. Kameda, T. Saito, and S. Chiba. 2019. "Divergence Before and After the Isolation of Islands: Phylogeography of the *Bradybaena* Land Snails on the Ryukyu Islands of Japan." *Journal of Biogeography* 46: 1197–1213. https://doi.org/10.1111/jbi.13575.

Hirano, T., T. Saito, Y. Tsunamoto, et al. 2019. "Enigmatic Incongruence Between mtDNA and nDNA Revealed by Multi-Locus Phylogenomic Analyses in Freshwater Snails." *Scientific Reports* 9: 6223. https://doi.org/10.1038/s41598-019-42682-0.

Hirano, T., T. Saito, P. V. von Oheimb, et al. 2022. "Patterns of Diversification of the Operculate Land Snail Genus *Cyclophorus* (Caenogastropoda: Cyclophoridae) on the Ryukyu Islands, Japan." *Molecular Phylogenetics and Evolution* 169: 107407. https://doi.org/10.1016/j.ympev.2022.107407.

Hoang, D. T., O. Chernomor, A. Von Haeseler, B. Q. Minh, and L. S. Vinh. 2018. "UFBoot2: Improving the Ultrafast Bootstrap Approximation." *Molecular Biology and Evolution* 35: 518–522. https://doi.org/10.1093/molbev/msx281.

Hoiles, P. W., S. J. Gallagher, A. Kitamura, and J. M. Southwood. 2012. "The Evolution of the Tsushima Current During the Early Pleistocene in the Sea of Japan: An Example From Marine Isotope Stage (MIS) 47." *Global and Planetary Change* 92: 162–178. https://doi.org/10.1016/j.gloplacha.2012.05.015.

Horsák, M., N. Limondin-Lozouet, S. Granai, J. Dabkowski, J. Divíšek, and P. Hájková. 2020. "Colonisation Dynamic and Diversity Patterns of Holocene Forest Snail Fauna Across Temperate Europe: The Imprint of Palaeoclimate Changes." *Quaternary Science Reviews* 240: 106367. https://doi.org/10.1016/j.quascirev.2020.106367.

Horsák, M., D. Ortiz, J. C. Nekola, and B. Van Bocxlaer. 2024. "Intercontinental Dispersal and Niche Fidelity Drive 50 Million Years of Global Diversification in *Vertigo* Land Snails." *Global Ecology and Biogeography* 33: e13820. https://doi.org/10.1111/geb.13820.

Hutchison, D. W., and A. R. Templeton. 1999. "Correlation of Pairwise Genetic and Geographic Distance Measures: Inferring the Relative Influences of Gene Flow and Drift on the Distribution of Genetic Variability." *Evolution* 53: 1898–1914. https://doi.org/10.1111/j.1558-5646.1999.tb04571.x.

Iryu, Y., H. Takayanagi, T. Ishikawa, et al. 2023. "Uplift Rate of Kitadaito Jima Island on the Lithospheric Forebulge of the Philippine Sea Plate." *Progress in Earth and Planetary Science* 10: 4. https://doi.org/10.1186/s40645-023-00535-5.

Jordano, P. 2017. "What Is Long-Distance Dispersal? And a Taxonomy of Dispersal Events." *Journal of Ecology* 105: 75–84. https://doi.org/10.1111/1365-2745.12690.

Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermiin. 2017. "ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates." *Nature Methods* 14, no. 6: 587–589. https://doi.org/10.1038/nmeth.4285.

Kappes, H., and P. Haase. 2012. "Slow, but Steady: Dispersal of Freshwater Molluscs." *Aquatic Sciences* 74: 1–14. https://doi.org/10.1007/s00027-011-0187-6.

Karney, C. F. F. 2013. "Algorithms for Geodesics." *Journal of Geodesy* 87: 43–55. https://doi.org/10.1007/s00190-012-0578-z.

Kawanabe, H., M. Nishino, and M. Maehata. 2020. *Lake Biwa: Interactions Between Nature and People*. 2nd ed. Springer International Publishing. https://doi.org/10.1007/978-3-030-16969-5.

Kimura, Y., L. J. Flynn, and L. L. Jacobs. 2021. "Tempo and Mode: Evidence on a Protracted Split From a Dense Fossil Record." *Frontiers in Ecology and Evolution* 9: 642814. https://doi.org/10.3389/fevo.2021.642814.

Kitamura, A., and K. Kimoto. 2006. "History of the Inflow of the Warm Tsushima Current Into the Sea of Japan Between 3.5 and 0.8 ma." *Palaeogeography, Palaeoclimatology, Palaeoecology* 236: 355–366. https://doi.org/10.1016/j.palaeo.2005.11.015.

Klobušická, V., E. Šlachtová, M. van Wieringen, L. Beran, V. Horsáková, and M. Horsák. 2025. "Can Tentacle Pigmentation Help Distinguish Between Non-Native and Native Populations of *Gyraulus Parvus* in Europe?" *Journal of Molluscan Studies* 91: eyaf005.

Korábek, O., M. Glaubrecht, B. Hausdorf, and M. T. Neiber. 2022. "Phylogeny of the Land Snail *Levantina* Reveals Long-Distance Dispersal in the Middle East." *Zoologica Scripta* 51: 161–172. https://doi.org/10.1111/zsc.12526.

Lewis, P. O. 2001. "A Likelihood Approach to Estimating Phylogeny From Discrete Morphological Character Data." *Systematic Biology* 50: 913–925. https://doi.org/10.1080/106351501753462876.

Long, C., and L. Kubatko. 2019. "Identifiability and Reconstructibility of Species Phylogenies Under a Modified Coalescent." *Bulletin of Mathematical Biology* 81: 408–430. https://doi.org/10.1007/s11538-018-0456-9.

Martin, A. K. 2011. "Double Saloon Door Tectonics in the Japan Sea, Fossa Magna, and the Japanese Island Arc." *Tectonophysics* 498: 45–65. https://doi.org/10.1016/j.tecto.2010.11.016.

Matzke, N. J. 2014. "Model Selection in Historical Biogeography Reveals That Founder-Event Speciation Is a Crucial Process in Island Clades." *Systematic Biology* 63: 951–970. https://doi.org/10.1093/sysbio/syu056.

Meier-Brook, C. 1983. "Taxonomic Studies on *Gyraulus* (Gastropoda: Planorbidae)." *Malacologia* 24: 1–113.

Minh, B. Q., H. A. Schmidt, O. Chernomor, et al. 2020. "IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era." *Molecular Biology and Evolution* 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015.

Mirarab, S., R. Reaz, M. S. Bayzid, T. Zimmermann, M. S. Swenson, and T. Warnow. 2014. "ASTRAL: Genome-Scale Coalescent-Based Species Tree Estimation." *Bioinformatics* 30: i541–i548. https://doi.org/10.1093/bioinformatics/btu462.

Motokawa, M., and H. Kajihara. 2017. *Species Diversity of Animals in Japan*. Springer Japan. https://doi.org/10.1007/978-4-431-56432-4.

Nekola, J. C., and B. J. McGill. 2014. "Scale Dependency in the Functional Form of the Distance Decay Relationship." *Ecography* 37: 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x.

Ninomiya, T., S. Shimoyama, K. Watanabe, K. Horie, D. J. Dunkley, and K. Shiraishi. 2014. "Age of the Taishu Group, Southwestern Japan, and Implications for the Origin and Evolution of the Japan Sea." *Island Arc* 23: 206–220. https://doi.org/10.1111/iar.12072.

Osozawa, S., R. Shinjo, A. Armid, Y. Watanabe, T. Horiguchi, and J. Wakabayashi. 2012. "Palaeogeographic Reconstruction of the 1.55 ma Synchronous Isolation of the Ryukyu Islands, Japan, and Taiwan and Inflow of the Kuroshio Warm Current." *International Geology Review* 54: 1369–1388. https://doi.org/10.1080/00206814.2011.639954.

Ota, Y., K. Koike, K. Chinzei, M. Nogami, H. Machida, and T. Matsuda. 2010. *Geomorphology of the Japanese Islands*. University of Tokyo Press (in Japanese).

Paradis, E., and K. Schliep. 2019. "Ape 5.0: An Environment for Modern Phylogenetics and Evolutionary Analyses in R." *Bioinformatics* 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633.

Park, S.-C., D.-G. Yoo, C.-W. Lee, and E.-I. Lee. 2000. "Last Glacial Sea-Level Changes and Paleogeography of the Korea (Tsushima) Strait." *Geo-Marine Letters* 20: 64–71. https://doi.org/10.1007/s003670000039.

Parks, M., R. Cronn, and A. Liston. 2009. "Increasing Phylogenetic Resolution at Low Taxonomic Levels Using Massively Parallel Sequencing of Chloroplast Genomes." *BMC Biology* 7: 84. https://doi.org/10.1186/1741-7007-7-84.

Patiño, J., R. J. Whittaker, P. A. V. Borges, et al. 2017. "A Roadmap for Island Biology: 50 Fundamental Questions After 50 Years of the Theory of Island Biogeography." *Journal of Biogeography* 44: 963–983. https://doi.org/10.1111/jbi.12986.

Peterson, B. K., J. N. Weber, E. H. Kay, H. S. Fisher, and H. E. Hoekstra. 2012. "Double Digest RADseq: An Inexpensive Method for *de Novo* SNP Discovery and Genotyping in Model and Non-Model Species." *PLoS One* 7: e37135. https://doi.org/10.1371/journal.pone.0037135.

Pietsch, T. W., V. V. Bogatov, K. Amaoka, et al. 2003. "Biodiversity and Biogeography of the Islands of the Kuril Archipelago." *Journal of Biogeography* 30: 1297–1310. https://doi.org/10.1046/j.1365-2699.2003.00956.x.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rambaut, A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard. 2018. "Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7." *Systematic Biology* 67: 901–904. https://doi.org/10.1093/sysbio/syy032.

Reaz, R., M. S. Bayzid, and M. S. Rahman. 2014. "Accurate Phylogenetic Tree Reconstruction From Quartets: A Heuristic Approach." *PLoS One* 9: e104008. https://doi.org/10.1371/journal.pone.0104008.

Saito, T., S. Chiba, and H. Fukuda. 2020. "Type Materials of the Species of the Planorbidae (Mollusca, Gastropoda, Hygrophila) Described by Shuichi Mori." *Molluscan Research* 40: 169–182. https://doi.org/10.1080/13235818.2020.1724604.

Saito, T., K. Fujimoto, S. Uchida, et al. 2022. "Uncovering Overlooked Diversity Using Molecular Phylogenetic Approach: A Case of Japanese Sphaeriid Clams (Bivalvia: Sphaeriidae)." *Molecular Phylogenetics and Evolution* 173: 107508. https://doi.org/10.1016/j.ympev.2022.107508.

Saito, T., T. Hirano, L. Prozorova, et al. 2018. "Phylogeography of Freshwater Planorbid Snails Reveals Diversification Patterns in Eurasian Continental Islands." *BMC Evolutionary Biology* 18: 164. https://doi.org/10.1186/s12862-018-1273-3.

Saito, T., T. Hirano, B. Ye, et al. 2021. "A Comprehensive Phylogeography of the Widespread Pond Snail Genus *Radix* Revealed Restricted Colonization due to Niche Conservatism." *Ecology and Evolution* 11: 18446–18459. https://doi.org/10.1002/ece3.8434.

Saito, T., L. Prozorova, T. Sitnikova, et al. 2018. "Molecular Phylogeny of Glacial Relict Species: A Case of Freshwater Valvatidae Molluscs (Mollusca: Gastropoda) in North and East Asia." *Hydrobiologia* 818: 105–118. https://doi.org/10.1007/s10750-018-3595-y.

Saito, T., T. Sasaki, Y. Tsunamoto, et al. 2022. "Even Short-Distance Dispersal Over a Barrier Can Affect Genetic Differentiation in *Gyraulus*, an Island Freshwater Snail." *Freshwater Biology* 67: 1971–1983. https://doi.org/10.1111/fwb.13990.

Saito, T., M. Tatani, Y. Odaya, and S. Chiba. 2023. "Direct Evidence for Intercontinental Dispersal of a Snail via a Bird." *Ecography* 2023: e06771. https://doi.org/10.1111/ecog.06771.

Sano, I., T. Saito, S. Ito, et al. 2022. “Resolving Species-Level Diversity of *Beringiana* and *Sinanodonta* Mussels (Bivalvia: Unionidae) in the Japanese Archipelago Using Genome-Wide Data.” *Molecular Phylogenetics and Evolution* 175: 107563. https://doi.org/10.1016/j.ympev.2022.107563.

Sano, I., T. Saito, J.-I. Miyazaki, et al. 2020. “Evolutionary History and Diversity of Unionoid Mussels (Mollusca: Bivalvia) in the Japanese Archipelago.” *Plankton and Benthos Research* 15: 97–111. https://doi.org/10.3800/pbr.15.97.

Sayyari, E., and S. Mirarab. 2016. “Fast Coalescent-Based Computation of Local Branch Support From Quartet Frequencies.” *Molecular Biology and Evolution* 33: 1654–1668. https://doi.org/10.1093/molbev/msw079.

Schultheiß, R., B. Van Bocxlaer, F. Riedel, T. Von Rintelen, and C. Albrecht. 2014. “Disjunct Distributions of Freshwater Snails Testify to a Central Role of the Congo System in Shaping Biogeographical Patterns in Africa.” *BMC Evolutionary Biology* 14: 42. https://doi.org/10.1186/1471-2148-14-42.

Shimodaira, H., and M. Hasegawa. 1999. “Multiple Comparisons of Log-Likelihoods With Applications to Phylogenetic Inference.” *Molecular Biology and Evolution* 16: 1114–1116. https://doi.org/10.1093/oxfordjournals.molbev.a026201.

Silvertown, J. 2004. “The Ghost of Competition Past in the Phylogeny of Island Endemic Plants.” *Journal of Ecology* 92: 168–173. https://doi.org/10.1111/j.1365-2745.2004.00853.x.

Silvertown, J., J. Francisco-Ortega, and M. Carine. 2005. “The Monophyly of Island Radiations: An Evaluation of Niche Pre-Emption and Some Alternative Explanations.” *Journal of Ecology* 93: 653–657. https://doi.org/10.1111/j.1365-2745.2005.01038.x.

Stevens, V. M., S. Whitmee, J. Le Galliard, et al. 2014. “A Comparative Analysis of Dispersal Syndromes in Terrestrial and Semi-Terrestrial Animals.” *Ecology Letters* 17: 1039–1052. https://doi.org/10.1111/ele.12303.

Tabata, R. 2022. “Lake Biwa and the Phylogeography of Freshwater Fishes in Japan.” In *Fish Diversity of Japan*, edited by Y. Kai, H. Motomura, and K. Matsuura, 205–218. Springer Nature Singapore. https://doi.org/10.1007/978-981-16-7427-3_12.

Toews, D. P. L., and A. Brelsford. 2012. “The Biogeography of Mitochondrial and Nuclear Discordance in Animals.” *Molecular Ecology* 21: 3907–3930. https://doi.org/10.1111/j.1365-294X.2012.05664.x.

Tojo, K., K. Sekiné, M. Takenaka, et al. 2017. “Species Diversity of Insects in Japan: Their Origins and Diversification Processes.” *Entomological Science* 20: 357–381. https://doi.org/10.1111/ens.12261.

Tolley, K. A., T. M. Townsend, and M. Vences. 2013. “Large-Scale Phylogeny of Chameleons Suggests African Origins and Eocene Diversification.” *Proceedings of the Royal Society B: Biological Sciences* 280: 20130184. https://doi.org/10.1098/rspb.2013.0184.

Tomikawa, K., Y. Nishimoto, N. Nakahama, and T. Nakano. 2022. “A New Species of the Genus *Pseudocrangonyx* (Crustacea: Amphipoda: Pseudocrangonyctidae) From Yonaguni Island, Southwestern Japan, and Historical Biogeographic Insights of Pseudocrangonyctids.” *Zoological Science* 39: 489–499. https://doi.org/10.2108/zs220030.

Van Dam, M. H., and N. J. Matzke. 2016. “Evaluating the Influence of Connectivity and Distance on Biogeographical Patterns in the South-Western Deserts of North America.” *Journal of Biogeography* 43: 1514–1532. https://doi.org/10.1111/jbi.12727.

van Leeuwen, C. H. A., and G. van der Velde. 2012. “Prerequisites for Flying Snails: External Transport Potential of Aquatic Snails by Waterbirds.” *Freshwater Science* 31: 963–972. https://doi.org/10.1899/12-023.1.

van Leeuwen, C. H. A., G. van der Velde, B. van Lith, and M. Klaassen. 2012. “Experimental Quantification of Long Distance Dispersal Potential of Aquatic Snails in the Gut of Migratory Birds.” *PLoS One* 7: e32292. https://doi.org/10.1371/journal.pone.0032292.

Vihtakari, M. 2022. ggOceanMaps: Plot Data on Oceanographic Maps Using ‘ggplot2’. https://CRAN.R-project.org/package=ggOceanMaps.

von Oheimb, P. V., C. Albrecht, F. Riedel, U. Bössneck, H. Zhang, and T. Wilke. 2013. “Testing the Role of the Himalaya Mountains as a Dispersal Barrier in Freshwater Gastropods (*Gyraulus* spp.).” *Biological Journal of the Linnean Society* 109: 526–534. https://doi.org/10.1111/bij.12068.

Voris, H. K. 2000. “Maps of Pleistocene Sea Levels in Southeast Asia: Shorelines, River Systems and Time Durations.” *Journal of Biogeography* 27: 1153–1167. https://doi.org/10.1046/j.1365-2699.2000.00489.x.

Wagenmakers, E.-J., and S. Farrell. 2004. “AIC Model Selection Using Akaike Weights.” *Psychonomic Bulletin & Review* 11: 192–196. https://doi.org/10.3758/BF03206482.

Watanabe, K., K. Tominaga, J. Nakajima, R. Kakioka, and R. Tabata. 2017. “Japanese Freshwater Fishes: Biogeography and Cryptic Diversity.” In *Species Diversity of Animals in Japan*, edited by M. Motokawa and H. Kajihara, 183–227. Springer Japan. https://doi.org/10.1007/978-4-431-56432-4_7.

Wiens, J. J., and C. H. Graham. 2005. “Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology.” *Annual Review of Ecology, Evolution, and Systematics* 36: 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431.

Yang, S., S. Komaki, R. M. Brown, and S. Lin. 2018. “Riding the Kuroshio Current: Stepping Stone Dispersal of the Okinawa Tree Lizard Across the East Asian Island Arc.” *Journal of Biogeography* 45: 37–50. https://doi.org/10.1111/jbi.13111.

Yang, Z., and B. Rannala. 2006. “Bayesian Estimation of Species Divergence Times Under a Molecular Clock Using Multiple Fossil Calibrations With Soft Bounds.” *Molecular Biology and Evolution* 23: 212–226. https://doi.org/10.1093/molbev/msj024.

Yu, T., T. A. Neubauer, and A. Jochum. 2021. “First Freshwater Gastropod Preserved in Amber Suggests Long-Distance Dispersal During the Cretaceous Period.” *Geological Magazine* 158: 1327–1334. https://doi.org/10.1017/S0016756821000285.

Yuan, Y.-M., S. Wohlhauser, M. Möller, J. Klackenberg, M. W. Callmander, and P. Küpfer. 2005. “Phylogeny and Biogeography of *Exacum* (Gentianaceae): A Disjunctive Distribution in the Indian Ocean Basin Resulted From Long Distance Dispersal and Extensive Radiation.” *Systematic Biology* 54: 21–34. https://doi.org/10.1080/10635150590905867.

Zhang, C., E. Sayyari, and S. Mirarab. 2017. “ASTRAL-III: Increased Scalability and Impacts of Contracting Low Support Branches.” In *Comparative Genomics*, edited by J. Meidanis and L. Nakhleh, vol. 10562, 53–75. Springer International Publishing. https://doi.org/10.1007/978-3-319-67979-2_4.

Zielske, S., W. F. Ponder, and M. Haase. 2017. “The Enigmatic Pattern of Long-Distance Dispersal of Minute Freshwater Gastropods (Caenogastropoda, Truncatelloidea, Tateidae) Across the South Pacific.” *Journal of Biogeography* 44: 195–206. https://doi.org/10.1111/jbi.12800.

Zinchenko, T. D., and L. V. Golovatyuk. 2013. “Salinity Tolerance of Macroinvertebrates in Stream Waters (Review).” *Arid Ecosystems* 3: 113–121. https://doi.org/10.1134/S2079096113030116.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Maximum likelihood phylogeny estimated using IQ-TREE2. Circles in black, grey and white indicate support values for each branch. Letters and colours denote geographic regions for the samples. **Figure S2:** (a) Divergence time estimates and inferred ancestral regions on the SVDQuartets tree. Ancestral region estimation was performed separately under the

M*k* + TS + medium_OD_prob and M*k* + TS + low_OD_prob models with time-stratification at 1.55 Ma. Letters and colours correspond to geographic regions for the samples. Coloured circular arcs at each node indicates the estimated ancestral region, with the central angle representing the probability. (b) Results on the ASTRAL tree. **Figure S3:** (a) Divergence time estimates and inferred ancestral regions based on the maximum likelihood tree. Ancestral region estimation was conducted severally under the M*k* + TS + low_OD_prob, M*k* + TS + high_OD_prob and M*k* + TS + distance-weighted + low_OD_prob models with time-stratification at 1.7 Ma. Letters and colours indicate geographic regions, with coloured circular arcs at each node representing the estimated ancestral region, and the central angle indicating the probability. (b) Results on the SVDQuartets tree. (c) Results on the ASTRAL tree. **Figure S4:** (a) Estimated average dispersal events under time- stratification at 1.7 Ma, based on 100 biogeographical stochastic mappings using BioGeoBEARS. Background boxes depict schematic representations of eastern Eurasia, with colours indicating geographic regions. Red arrows represent oceanic dispersal events, and letters represent abbreviations for the geographic regions. For visibility, dispersal events with frequencies below 0.1 are omitted. Full results are provided in Table S3. (b) Results on the SVDQuartets tree. (c) Results on the ASTRAL tree. **Table S1:** Sample information used in this study. **Table S2:** Detail estimates for divergence time analyses using MCMCtree (Yang and Rannala 2006). Node numbers correspond to those indicated in Figure 3 and Figure S2. **Table S3:** Estimated dispersal events of the best AICc weight models. All estimates of dispersal events on 100 biogeographical stochastic mapping using BioGeoBEARS. Red text indicates oceanic dispersal events, and letters denote abbreviations for the geographic regions. **Table S4:** Estimated dispersal events of the second/third best AICc weight models. All estimates of dispersal event on 100 biogeographical stochastic mapping using BioGeoBEARS. Red letters represent oversea dispersal event and alphabets represent abbreviation for geographic regions. **Data S1:** Supporting Information.