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RESEARCH ARTICLE

Synergistic polyploidization and long-distance dispersal enable the global diversification of yellowcress herbs

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Abstract

Aim: Long-distance dispersal (LDD) plays an important role in shaping the distribution of global biodiversity. Polyploidy could favour invasion and thereby facilitate LDD. However, how and to what extent polyploidy interacts with LDD remain unclear. Here, we test the putative role of polyploidy in the global dispersal of a cosmopolitan genus *Rorippa*.

Location: Global.

Time Period: Late Miocene to present.

Major Taxa Studied: *Rorippa* Scop., Brassicaceae.

Methods: We traced the biogeographical and speciation history for 17 diploids and 41 polyploids of *Rorippa* using variation from plastid genomes and multiple nuclear loci. The ploidy role in dispersal rate difference was demonstrated using trait-dependent biogeographical modelling.

Results: LDD shaped the amphitropical disjunction of *Rorippa*, during which polyploids showed higher dispersal rates than those of diploids, with 5.6× increase under the best-fitted model. Five diploids and 21 polyploids were identified as products of transoceanic speciation events. Polyploidy-involved LDD was more common in terms of polyploidization following LDD than those preceding LDD.

Main Conclusions: We demonstrate that polyploidy would be not only a driver but also a responder of LDD in *Rorippa*, highlighting a synergistic relationship between them. Our results provide a framework to uncover the biogeographical consequences of polyploidization and the joint roles of polyploidy and LDD in shaping the distribution of biodiversity.

KEYWORDS
dispersal trait, global biogeography, hybridization, ploidy diversity, polyploid speciation, trait-dependent biogeography

1 | INTRODUCTION

Long-distance dispersal (LDD) is one of the most important biogeographical processes (Carlquist, 1966; Wu et al., 2023), shaping the global distribution of diversity in plants and animals (Luo et al., 2020; Wu et al., 2018). However, the underlying drivers of LDD are still elusive. Polyploidy, or whole-genome duplication, has long been proposed as an intrinsic attribute of LDD (Mummenhoff & Franzke, 2007), being reported in several plants such as cotton (Wendel & Cronn, 2003), Danthonioideae grasses (Linder & Barker, 2014), Microlepidieae crucifers (Mandáková et al., 2017) or flora on islands (Meudt et al., 2021). These studies speculated that: (1) polyploidy may interact with LDD, either preceding or following LDD (Linder & Barker, 2014) (Figure 1); (2) polyploidy may facilitate the success of a diaspore through its invasive advantage or interaction with trait or niche shifts during post-dispersal establishment (Moura et al., 2021; Pyšek et al., 2023; te Beest et al., 2012) and (3) LDD would promote polyploid speciation as a result of instantly geographical or genetic isolation from population-of-origin (Mummenhoff & Franzke, 2007; Taylor et al., 2001). However, due to the difficulties in deciphering polyploid speciation and its links with biogeographical history, the relationship between polyploidy and LDD has remained controversial. For example, LDD would be underestimated and biogeographical clues for polyploid evolution would be inadequate if biparentally inherited nuclear variation was not incorporated into polyploid phylogenetic construction or if different genome types (i.e. subgenome of polyploidy) were confounded during biogeographical inference (Marhold & Lihová, 2006).

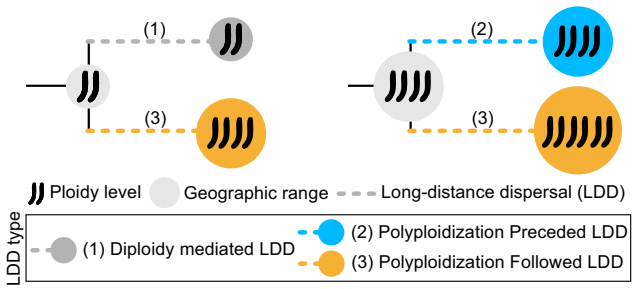

FIGURE 1 Hypotheses about the relationship between polyploidy and LDD. The possible combinations of LDD-associated polyploidization: (1) LDD occurs without polyploidization (i.e. diploidy mediated LDD, DM-LDD, dashed line with pie in dark grey); (2) polyploid lineages are more likely involved in LDD than diploid lineages (Polyploidization Preceded LDD, PP-LDD, dashed line with pie in blue) or (3) ploidy changes more frequently co-occur with LDD (Polyploidization Followed LDD, PF-LDD, dashed line with pie in orange). Only process (3) has experienced ploidy changes from either diploidy (along the left tree) or polyploidy (along the right tree) to a new polyploidy after LDD. LDD process is shown as dashed and coloured line, including DM-LDD in dark grey (1), PP-LDD in blue (2), PF-LDD in orange (3) along the branch of simplified phylogenetic tree, with coloured pies at the nodes or tips reflecting the different geographical regions, and different number of pairs of chromosomes revealing changes in ploidy levels.

Therefore, it is still unclear how and to what extent polyploidy interacts with LDD in a focal group.

Since most intrageneric ploidy changes from lower to higher levels are intuitively irreversible, polyploid complexes involving both diploidy and polyploidy are ideal systems to make biogeographical inference (Stebbins, 1971). Recent methods have been developed to specifically trace the speciation and biogeographical history for polyploid complexes. For example, approaches using a backbone phylogeny of diploid progenitors followed by polyploid phylogenetic modelling can effectively untangle the speciation mode of polyploid complexes (Rothfels, 2021; Thomas et al., 2017). Alternatively, the level of ploidy-mediated dispersal rate differences can be evaluated using trait-dependent biogeographical modelling (Klaus & Matzke, 2020), with ploidy state (e.g. diploid vs. polyploid) as a potential variable affecting biome shift probability (Liddell et al., 2021). An integrated framework employing both approaches makes estimating the tempo and mode of polyploidy-impacted LDD more reliable (Figure 1).

Here we test the putative role of polyploidy in the global dispersal of yellowcress (*Rorippa* Scop.), a Brassicaceae genus with an accepted 86 species and a worldwide distribution characterized by amphitropical disjunction (Bleeker et al., 2002). Most of *Rorippa* species have affinity for wet habitats (Les, 2018), where migrating birds may transit their seeds or propagules far from local populations (Bleeker et al., 2002; Chater & Rich, 1995). They also have robust tolerance to whole-genomic changes, such as interspecific hybridization and polyploidization (Bleeker, 2007). About 70% of *Rorippa* are polyploids, and 90% of them are endemic to specific continents (Figures S1 and S2). *Rorippa* polyploids are globally distributed but more prevalent in the Southern Hemisphere (accounting for 91% of species) (Figure S1). These observations highlight a potential role of LDD in shaping the amphitropical disjunction of *Rorippa* and suggest that polyploidy may have promoted effective LDD.

To test the polyploid role in LDD, we first built well-resolved and dated phylogenies for 58 *Rorippa* species using nucleotide data from both plastid genomes and multiple low-copy nuclear loci. We then classified different genome groups across ploidies and traced their dispersal tempos and modes around the world. This study will widen our knowledge about the biogeographical consequences of polyploidization and the joint roles of polyploidy and LDD in shaping the global distribution of biodiversity.

2 | METHODS

2.1 | Sampling

A total of 58 *Rorippa* species were sampled from 177 accessions across the world, including 17 diploids and 41 polyploids (Table S1). Chromosome data were obtained from PloiDB (http://ploidb.tau.ac.il/) (Halabi et al., 2023). DNA was extracted using modified CTAB method or obtained from previous study (Nakayama et al., 2018). High-quality DNA from 46 accessions covering 22

Rorippa species was sequenced on an Illumina NovaSeq 6000 platform, achieving a minimum of 2 Gb data for each sample (about 8× coverage for *Rorippa* diploidy) with 150 bp paired-end reads. Ploidy level for sample with genomic sequence was estimated using nQuire (Weiß et al., 2018). For samples without enough well-reserved DNA, sequences from four plastid markers (*psbC-trnS*, *trnG-trnM*, *trnL* and *trnL-trnF*), 12 low-copy nuclear loci (*ACO*1, *CHS*, *CIP7*, *CRD*1, *FTSZ*1-1, *HY*4, *MCM*5, *MLH*1, *SMC*2, *SYP*61, AT3G50910 and AT5G52810) and ITS were obtained following our previous study (Han et al., 2022). We cloned and sequenced the 12 low-copy nuclear loci and ITS for at least one sample of each species, during which sequences of 8–16 clones were gathered for each locus and sample. Variation from cloned sequences was processed by PURC pipelines using reported methods (Han et al., 2022; Rothfels et al., 2017), with the cloned sequences as input reads for PURC analysis. Ploidy level for each sample was rechecked according to the mean number of PURC-phased homoeologues across loci (Rothfels et al., 2017).

2.2 | Plastid genome assembly

The assembly of plastid genomes was performed using GetOrganelle v.1.4.0j (Jin et al., 2020). The published 15 plastid genomes from Capparaceae and Brassicaceae were downloaded from GenBank and used as outgroups (Table S1). We annotated each plastid genome using CPGAVAS2 (Shi et al., 2019). In accordance with previous work (Guo et al., 2017), coding regions for 77 protein-coding genes were extracted and aligned using Geneious Prime v.2019.0.3 (Kearse et al., 2012).

2.3 | Phylogenetic analysis

To untangle the evolution of *Rorippa* species, we integrated multiple approaches, including homoeologue phasing (Rothfels et al., 2017), polyploid phylogenetics (Rothfels, 2021) and polyploid speciation modelling (Thomas et al., 2017). The workflow used plastid- or diploid-first methods followed by polyploid phylogenetic modelling, including a total of seven steps for plastid and nuclear data (see Appendix S1 in Supporting Information for details).

2.3.1 | Plastid phylogeny

To generate a well-resolved plastid phylogeny backbone, a *plastome tree* was built in BEAST v.1.8.4 (Drummond et al., 2012) using the concatenated coding sequences for *Rorippa* species and outgroups. The nucleotide substitution rate variation model was fitted using the ModelFinder tool in IQ-TREE v.1.6.12 (Nguyen et al., 2015). Secondary calibration was used to constrain the crown nodes of Brassicaceae and core Brassicaceae as 30.0–42.5 million years (Myr) and 21.7–29.7 Myr (Guo et al., 2017) respectively. An uncorrelated relaxed clock with a lognormal distribution was used as a clock model, together with uniform prior distributions for the calibration points. Four independent runs were performed, with 200 million Markov Chain Monte Carlo (MCMC) simulations for each run. Convergence was checked according to the effective sample size of parameters >200. A total of 1000 trees were resampled and annotated to produce a final maximum clade credibility (MCC) tree in TreeAnnotator v.1.8.4 (BEAST Developers) under mean node heights.

We then placed 131 extra samples into the plastome tree through phylogenetic placement (Czech et al., 2020). Concatenated sequences of plastid markers were used as queries (Table S1). All queries were placed into the resampled 1000 plastome trees described above. Values of the likelihood weight ratio (LWR) were calculated to evaluate the model performance. The placed trees were rescaled using penalized likelihood and maximum likelihood methods under the selected relaxed model of substitution rate variation in R package ape v.5.5 (Paradis & Schliep, 2019). The crown age of *Rorippa* was recalibrated according to the plastome tree (5.3–9.3 Myr). A *final rescaled placed-tree* was annotated as a consensus MCC tree of the 1000 rescaled placed-trees in TreeAnnotator v.1.8.4. To obtain a *final plastid tree*, only one tip or one sample representing the species was kept. We selected the sample based on the criteria of node age (i.e. the earliest diverged tip) and geographical information (i.e. from a native region).

2.3.2 | Nuclear phylogeny

We resolved the reticulate relationships and clarified the genome types (i.e. subgenome of polyploidy) among *Rorippa* species. The *ITS Bayesian tree* was built on all PURC-phased ITS sequences, using the same settings as described above for the *plastome tree* in BEAST v.1.8.4. Secondary calibration was implemented to constrain the crown nodes of Brassicaceae and core Brassicaceae as 36.3–37.8 Myr and 29.1–30.3 Myr (Huang et al., 2015) respectively.

A group of methods were used to analyse variation from the cloned sequences for 12 low-copy nuclear loci (Appendix S1). First, an initial *diploid backbone tree* was built with only diploid progenitors, using a concatenated sequence matrix of single PURC-phased homoeologues across loci. We clarified genome types according to their phylogenetic positions, species ages, phenotypic or geographical representativeness, as well as section classifications (Bleeker et al., 2002). Second, to assign genome types for homoeologues of polyploids, a group of *raw single-gene trees* covering all samples was constructed using the PURC-phased sequences for each locus. Species with more than one PURC-phased sequence were placed into the diploid backbone tree for each locus to generate a *placed single-gene tree* using phylogenetic placement (Czech et al., 2020). Genome types for each homoeologue were assigned according to the diploid backbone tree and the raw or the placed single-gene trees. Third, to obtain a *final*

nuclear tree, we generated a new concatenated sequence matrix for each species based on the classified homoeologues and constructed a Bayesian tree in BEAST v.1.8.4. Given the different mutation rate or selective pressure between plastid and nuclear genomes, we applied secondary calibration to constrain the crown node of *Rorippa* along the concatenated nuclear tree as 4.2–10.3 Myr, according to the estimated time from the *ITS Bayesian tree*. The final nuclear tree was then split into a *nuclear homoeologous tree* for each genome type using the drop.tip() function in ape v.5.5. Finally, we used the topology-based gene-tree reconciliation algorithm implemented in GRAMPA (Thomas et al., 2017) to infer speciation mode for each species, according to the best-fitted multi-labelled tree (MUL-tree) with a minimum parsimony score. Speciation mode was clarified as autopolyploidy or allopolyploidy (polyploidy without or with hybridization), homoploid hybrid (hybrid without polyploidization) or no polyploidy respectively.

2.4 | Biogeographical history and identification of LDD

We inferred the biogeographical history of *Rorippa* species along the final plastid tree and the nuclear homoeologous trees for each genome type under a group of biogeographical models, including BAYAREA, DEC, DIVALIKE and their jump-dispersal models (+ *j*) implemented in BioGeoBEARS (Matzke, 2018). The most fitted model was selected using AIC value corrected for sample size (AICc) and its weight (*wt*). The number of maximum ranges was constrained to two based on the extant distribution of species (Figures S1 and S2). The five geographical regions were classified as Eurasia (EUA), North America region (NAR), South America region (SAR), Africa (AFR) and Oceania (OEA). *Rorippa* species could be assigned to these regions because 90% of them are endemic to specific continents (Figures S1 and S2). LDD was referred to as a dispersal event between geographical regions or across ocean basins (Gillespie et al., 2012; Wu et al., 2018). Accordingly, we identified LDD as any dispersal of a lineage between any two defined geographical regions above. In addition, to quantify the spatial extent of LDD, relationships between pairwise geographical and phylogenetic distances were assessed. We located outliers that informed us about the spatial scale of genetic divergence beyond the expectation of isolation-by-distance (Jordano, 2017). Geographical distances were calculated between centroids of species' minimum convex polygons using letsR v.4.0 (Vilela & Villalobos, 2015). Phylogenetic distances between tips were estimated from the branch lengths of the plastid species tree using ape v.5.5.

2.5 | Trait evolution of ploidy state

To decipher the evolutionary history of ploidy state changes and account for mixed-ploidy variation across ancestral populations, we performed ancestral state reconstruction of ploidy along the final plastid tree and the nuclear homoeologous trees for each genome type using ape v.5.5 and phytools v.1.0-3 (Revell, 2012) (Appendix S1). Two kinds of models were used to specify the transition probabilities between ploidy states, including the two ploidy levels model (TPL) and the multiple ploidy levels model (MPL) associated with three hard-wired models: equal rate model (ER), all rates different model (ARD) and symmetric model (SYM) respectively. Given the intrageneric irreversibility from diploid to polyploid level (Stebbins, 1971), transition between states can only happen from low to high ploidy but not the reverse. For each analysis, 1000 simulations were performed under each evolutionary model.

2.6 | Level and type of polyploidy-involved LDD

To test whether ploidy changes have influenced dispersal rate variation along the phylogenetic tree, we jointly modelled their interaction using trait-based biogeographical models (Klaus & Matzke, 2020). A standard two-rate transition model was built according to the parsimonious model under two ploidy levels (i.e. diploid vs. polyploid), with transition only from diploid to polyploid state but not the reverse. The effect of ploidy changes on dispersal possibility was estimated as a multiplier (*m*) on the anagenetic dispersal rate of range expansion. Here, the multiplier for diploid lineages (m_1) was fixed to 1, and the multiplier for polyploid lineages (m_2) was variable. These trait-based modellings were run along the plastid species tree under six biogeographical models: BAYAREA, DEC, DIVALIKE and their jump-dispersal models (+ *j*). The best fitted model was selected using the scaled AICc value corrected for sample size (AICc_scaled).

LDD types were distinguished as DM-LDD (diploidy mediated LDD), PP-LDD (polyploidization preceded LDD) or PF-LDD (polyploidization followed LDD), based on the cooccurrence of LDD and the inferred ploidy changes from node to tips (Figure 1). LDD regardless of ploidy changes were assigned as DM or PP type, and those with ploidy changes as PF type. LDD on the early divergent node and without direct evidence on speciation mode was assigned as undetermined type. Correspondingly, the dispersed species were assigned as a product of either DM, PP or PF type of LDD.

2.7 | Phenotypic features of polyploidy-involved LDD

Effective LDD would be influenced by a group of traits associated with dispersal. Since polyploidization was suggested to evolve with shifts in lifespan (annual or perennial), mating system types (self-compatibility or self-incompatibility) and the ability of clonal reproduction (sexual or asexual) (Van Drunen & Husband, 2019), we gathered these information and combined them together as a dataset of ploidy-involved dispersal trait (DT). We assigned each species with a specific DT type, including DT1–DT6 for polyploidy and DT7–DT11 for diploidy (Appendix S1; Table S2).

3 | RESULTS

3.1 | Phylogeny and speciation mode

Based on the well-resolved and dated plastome tree (Figures 2 and S3), *Rorippa* originated *c*. 7.10 million years ago (Ma) (95% HPD: 9.32–5.26 Ma) in the late Miocene. Two main clades were identified, the Eurasian clade and North American clade, with continent-specific diploids embedded in each of them (Figure 2). A similar classification of clades can also be observed in the ITS Bayesian tree (Figure S4). A total of 131 samples were placed into the plastome tree with high certainty (mean ± *SE* of LWR = 0.68 ± 0.17).

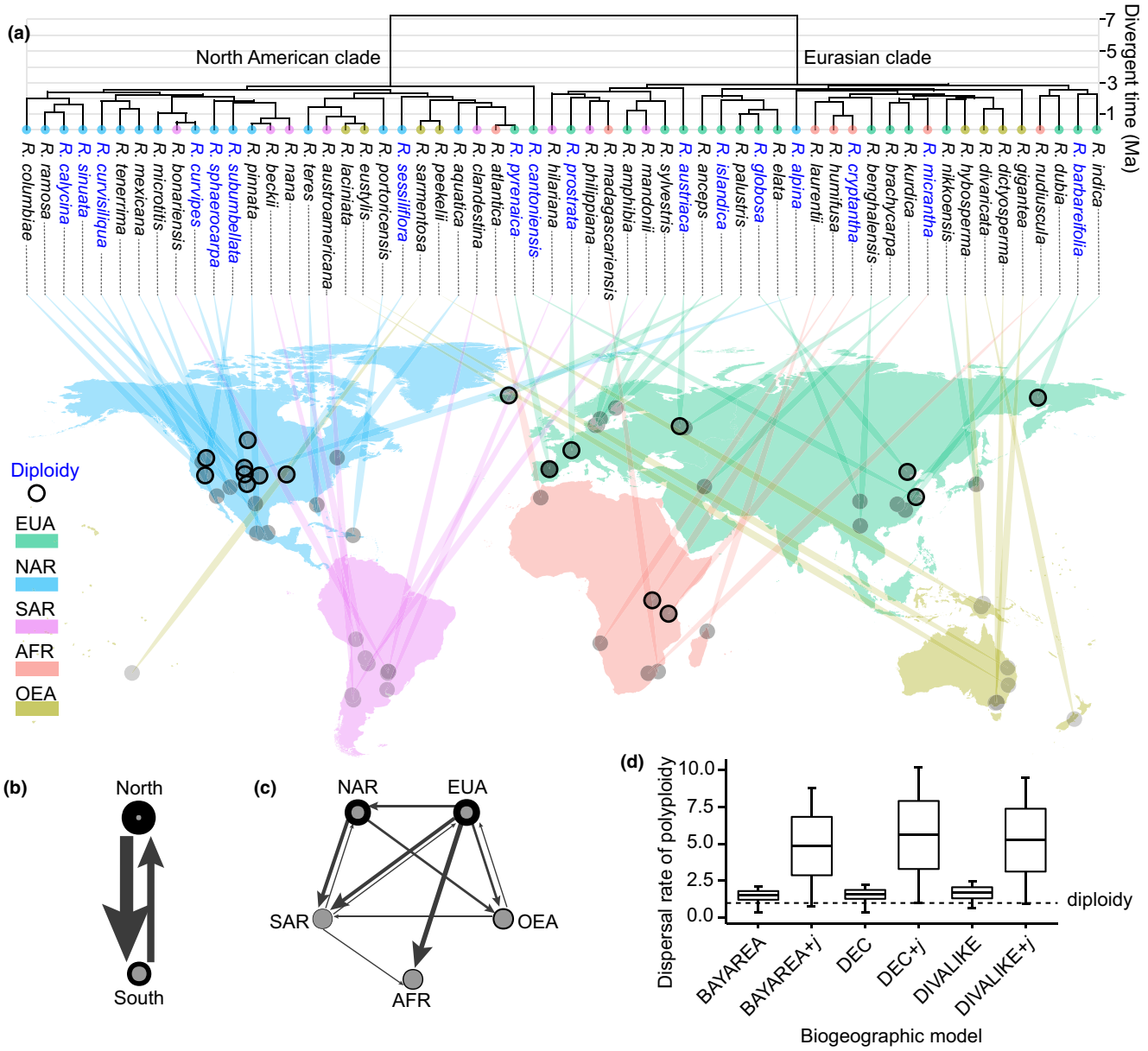

FIGURE 2 The plastid *Rorippa* phylogeny and biogeographical inference. The plastid *Rorippa* phylogeny projected to a global map (a). Geographical regions are classified as Eurasia (EUA), North America region (NAR), South America region (SAR), Africa (AFR) and Oceania (OEA). The geographical location for each species (circles) is indicated by the centroid of polygon of occurrence. Diploid species are denoted by black circles, with the remainder representing polyploids. Links between phylogenetic tips and corresponding geographical centroids are shown as coloured solid lines, with the name of diploid species labelled in blue. The biogeographical flows between the Northern and Southern Hemispheres (b) or among continents (c); the dispersal rate estimated by multiplier values for polyploid lineages across different biogeographical models (d). In (b, c), the extent of biogeographical flows is proportional to the thickness of black lines, with arrows indicating their direction; the black borders of circles representing each continent indicate speciation events, with their thickness proportional to the number of speciation events. In (d), multiplier values are shown as percent of AICc support on each model, indicated as box-and-whisker plots with the median (horizontal line), 25th and 75th percentiles (bottom and top of the box), and limits of the 95% confidence intervals (lower and upper whiskers), with the multiplier value for diploid lineages fixed as 1.0 and shown with a dashed line. Estimators or model tests for each biogeographical model are listed in Tables S3 and S4.

The final plastid species tree harboured a total of 58 *Rorippa* species, with polyploids scattered along the phylogeny (Figure 2). The Eurasian and North American clades originated *c*. 2.71 Ma (3.61–1.59 Ma) and *c*. 2.59 Ma (3.46–1.51 Ma) respectively. Polyploids (mean ± *SE*, 1.05 ± 0.10 Myr) were significantly younger than diploids (1.55 ± 0.14 Myr; Wilcoxon rank-sum test, $W = 495.5$, $p = 0.012$) (Table S2).

Based on the nuclear phylogenies, a total of 91 homoeologous types were phased (Figures S5 and S6), from which six genome groups (A–F) were identified (Figure 3). Compatible with the identification of plastid clades (Figure 2), diploids with AA–DD genomes were mainly found in Eurasia and with globose (AA–BB) to oblong (CC–DD) fruits, including *R. austriaca* (AA), *R. globosa* (BB), *R. cantoniensis* (CC) and *R. islandica* (DD); diploids with EE–FF genomes were only found in North America and with oblong to linear fruits, including *R. sessiliflora* (EE) and *R. sinuata* (FF). Genome group B had the highest occurrence rate (32.50%), followed by genome groups F (21.25%) and D (20.00%) (Table S2; Figure 3).

Out of the sampled 58 species, 20 speciation events were detected with hybrid origin, comprising six homoploid hybrids and 14 allopolyploids (Table S2; Figures S7 and S8). Potential maternal progenitors can be identified for 12 hybrid species according to the plastid trees (Table S2; Figure 3a). Chloroplast capture (i.e. the interspecific introgression of chloroplast in plants) was detected for seven species from South America, Oceania, Eurasia or Africa. About 65.85% of polyploids are of autopolyploid origins (27 species) and 34.15% are of allopolyploid origins (14 species). The most frequent combination of genome types for hybrids was BD (5 species) or BBDD (3 species), and the most frequent genome type for autopolyploidy was BBBB (8 species). Dating results indicated that polyploids were younger than diploids for both the youngest (mean ± *SE*, polyploidy vs. diploidy, 1.03 ± 0.15 vs. 1.88 ± 0.49 Myr) and the oldest homeologues (1.71 ± 0.26 vs. 2.29 ± 0.47 Myr) (Table S2). Taken together, the well-resolved plastid and nuclear phylogenies provide a relatively complete picture of the speciation history in *Rorippa*.

3.2 | Biogeography

3.2.1 | Plastid biogeography

Biogeographical inference under DEC + *j* model statistically fitted better than those under the other models (Table S3; likelihood ratio test, $p \leq 2.4e{-}19$), but the inferred biogeographical patterns were mostly consistent with each other. Under DEC + *j* model, biogeographical analysis along the final plastid tree indicated that the ancestral range for *Rorippa* was located in the Northern Hemisphere (Figure S9). The potential biogeographical origin was identified as Eurasia (probability = 45.52%) or Eurasia together with North America (44.91%). That said, species from all continents were found within each main clade.

A total of 21 LDD events for *Rorippa* species were detected across continents, especially from the Northern to the Southern Hemisphere (percent = 80%) (Table 1; Figures 2b and S9). More than half of LDD (55%) occurred from Eurasia to other continents, and about 25% of LDD occurred from North America to South America or Oceania (Figure 2c). The mean multipliers of dispersal probability for polyploid lineages (m_2) were >1.33× higher than the designated value for diploid lineages ($m_1 = 1$) across models (Table S4; Figure 2d). Under the selected DEC + *j* model, the mean dispersal multiplier of polyploid lineages predicted 5.60× increase (Table S4; Figure 2d). Stochastic character mapping analysis on ploidy state revealed congruent evolutionary trends under models of two or multiple ploidy levels (Figure S10). Under the selected two ploidy levels model, we identified three occurrences of PP-LDD (polyploidization preceded LDD), nine occurrences of PF-LDD (polyploidization followed LDD), and four occurrences of DM-LDD (diploidy-mediated LDD) (Table 1; Figure S10). These dispersal events are also reflected by observations of species pairs with close phylogenetic relationships but geographical separation as far as 7500–9000 km and 10,000–13,000 km from each other (Figure S11). In summary, the plastid biogeography of *Rorippa* suggests frequent LDD may have shaped the amphitropical disjunction of its species and polyploidy played a significant role during LDD.

3.2.2 | Nuclear homoeologous biogeography

Under the selected DEC + *j* biogeographical modelling along nuclear homoeologous trees (Table S3), we identified the different dispersal modes associated with each genome type and their different contributions to the diversification of *Rorippa* (Figures 3b, S12 and S13). A total of 41 LDD events were identified, including 10 polyploidization preceded (PP) types, 14 polyploidization followed (PF) types and four diploidy-mediated (DM) types of LDD (Table 1; Figure S13). Under these LDD events, about 26 species (45% out of the total sampled species) were identified as products of LDD, including 21 polyploids (Table S5; Figure 4). The median age of LDD-mediated species was 1.466 Myr, ranging from 0.384 to 3.789 Myr. At the level of genome types, A–D originated from Eurasia and dispersed into the other continents through recurrent LDD; E–F originated from North America and dispersed into South America or Oceania (Figure 3b). In general, genome type B had the most frequent intercontinental dispersals (Figures 3b and S12), leading to speciation outside its origin range in Eurasia, such as those species with unique genome types, including *R. austroamericana* (BBEE) in South America, and *R. laciniata* (BBDDFF) in Oceania.

Integrative evidence demonstrated the asymmetric biogeographical flows among continents across either plastid or nuclear trees (Figure 4). In *Rorippa*, more LDD events were inferred to have occurred when using nuclear than plastid markers. Biogeographical flows mainly occurred from Eurasia or North America to Africa, Oceania or South America, but bidirectional nuclear biogeographical

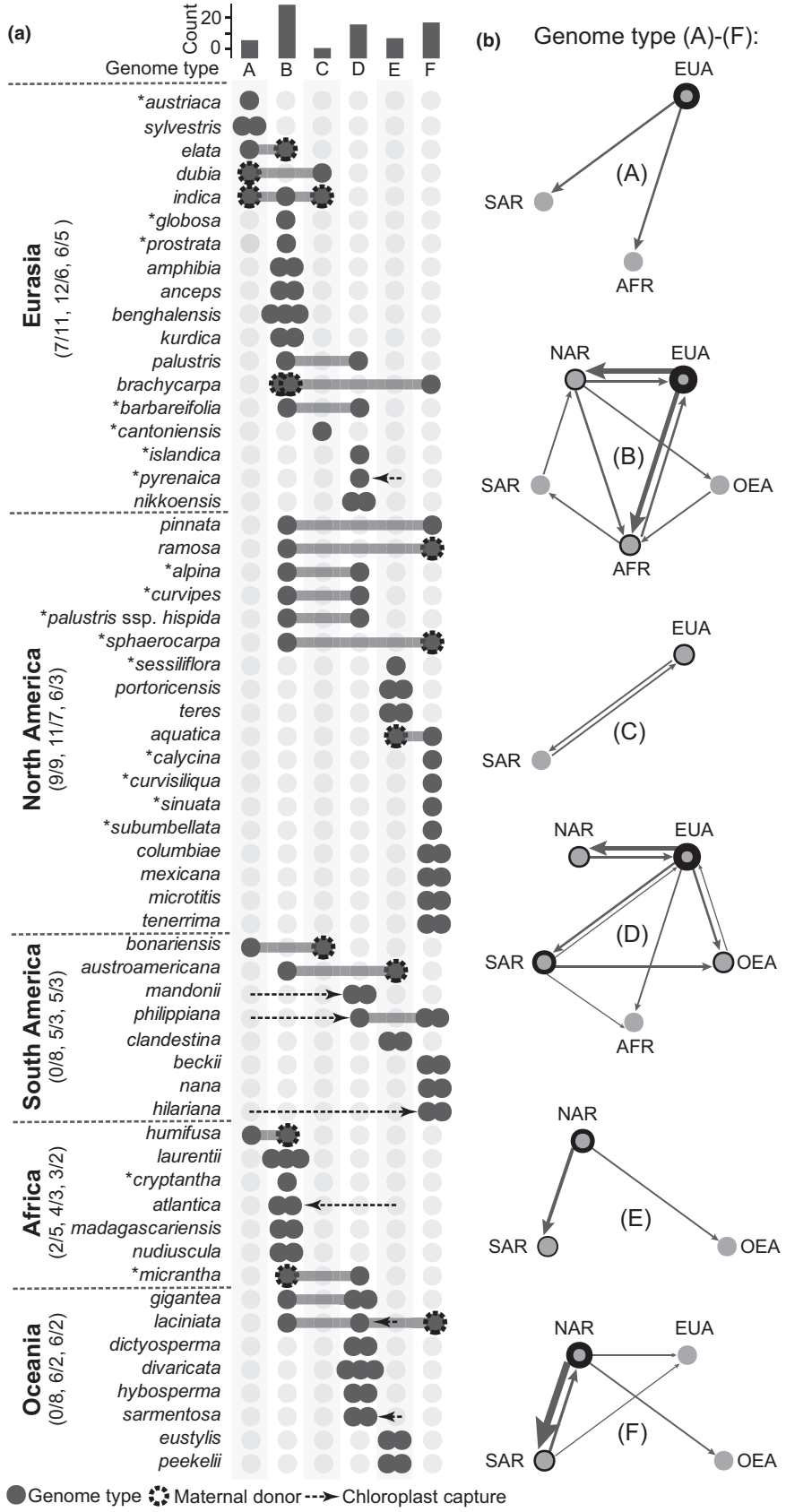

FIGURE 3 Speciation mode and biogeographical inference for *Rorippa* species. Speciation mode and composition of genome types are shown as dumbbell chart (a), with numbers in the parentheses showing the counts of diploidy/polyploidy, non-hybrid/hybrid and autopolyploidy/allopolyploidy in each region. Events of chloroplast capture are shown as dashed line with arrow, and potential maternal donors are revealed by dashed circles. The biogeographical flows among continents inferred along trees for each nuclear genome type (A)–(F) (b). Geographical regions are Eurasia (EUA), North America region (NAR), South America region (SAR), Africa (AFR) and Oceania (OEA).

flows were detected equally between Eurasia and North America. In the Southern Hemisphere, 18 species were involved in LDD (accounting for 78% of its total species), 16 of which are polyploids. In short, the overall global biogeography of *Rorippa* indicates that polyploidy may have mediated the success of LDD in the Southern Hemisphere.

TABLE 1 The number of identified long-distance dispersal (LDD) types in *Rorippa*.

LDD type	Plastid	Nuclear genome type						
		A	B	C	D	E	F	Total
Polyploidization preceded LDD/PP-LDD	3	1	3	0	1	1	4	10
Polyploidization followed LDD/PF-LDD	9	1	6	1	2	0	4	14
Diploidy-mediated LDD/DM-LDD	4	0	2	0	2	0	0	4
Undetermined LDD	5	0	5	1	6	0	1	13
Total	21	2	16	2	11	1	9	41

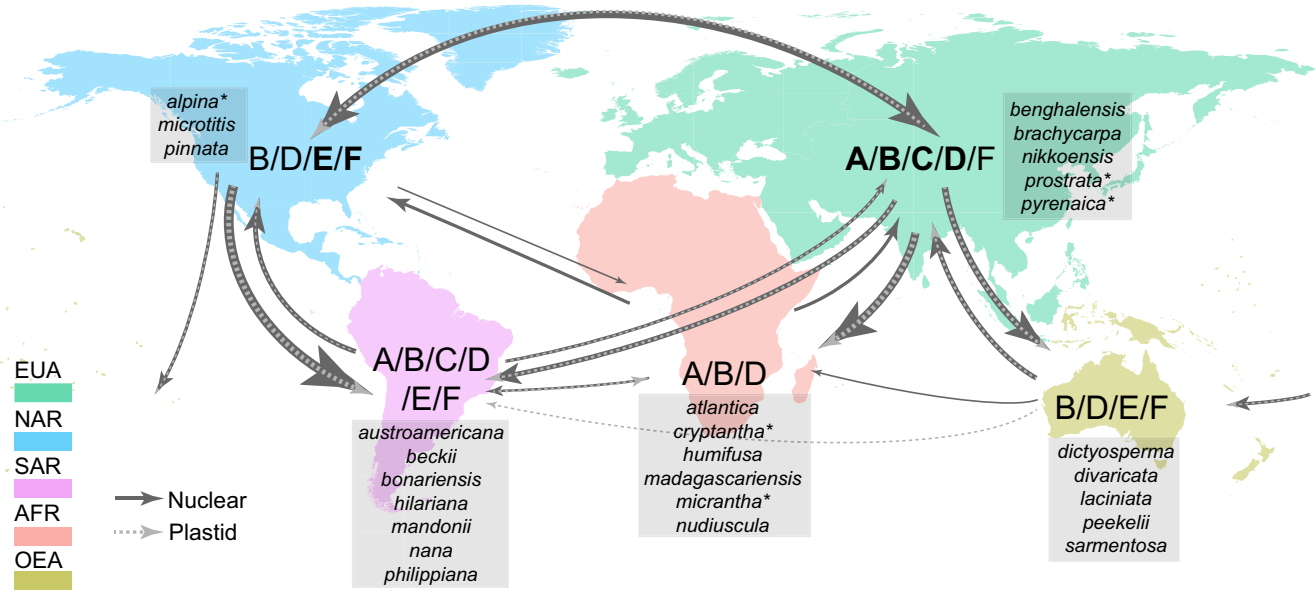

FIGURE 4 Summary of global biogeographical flows in *Rorippa*. Geographical flows inferred from the plastid tree are indicated by light grey and dashed lines; geographical flows inferred from nuclear tree are indicated by dark grey and solid lines. Lines with arrows indicate only the possible directions of biogeographical flows and may not represent the actual dispersal routes in nature. Genome types A–D from Eurasia and E–F from North America are shown in bold, indicating their putative places of origin. Name lists show the 26 *Rorippa* species that experienced LDD. Diploid species are labelled with an asterisk (*). Geographical regions are Eurasia (EUA), North America region (NAR), South America region (SAR), Africa (AFR) and Oceania (OEA).

3.3 | Features of polyploidy-impacted LDD

Lineage dispersal of *Rorippa* species may have been aided by a group of ploidy-involved dispersal trait (DT). A total of 11 DT-types (coded as DT1–11) were identified (Table S2). Three DT-types were associated with 81% of LDD events, including DT1 (selfing polyploidy, covering 54% of LDD events), DT2 (selfing and perennial polyploidy, 15%), and DT4 (perennial polyploidy, 12%) (Table S5).

4 | DISCUSSION

Polyploidization is an important mechanism driving speciation and transoceanic dispersal, but integrative analyses of these processes have been lacking. Here, we developed a unified framework to test the putative role of polyploidy in the global biogeography of *Rorippa*. We found that polyploidy may have facilitated the success of LDD and the subsequent persistence of those dispersed lineages in new environments.

4.1 | Global biogeography of *Rorippa* mediated by polyploidization and LDD

Rorippa is a globally distributed genus in Brassicaceae, with species occurring on all continents except for Antarctica (Jonsell, 1968). However, its geographical origin and evolutionary history are still enigmatic. We inferred that the *Rorippa* genus originated in Eurasia and North America in the late Miocene (*c.* 7.10 Ma) and then dispersed into other continents, particularly in the Southern Hemisphere, by LDD on multiple occasions (Figure 2). Polyploids are prevalent among *Rorippa* species and accounting for 91% of species in the Southern Hemisphere, suggesting polyploidization and LDD may have jointly shaped the global biogeography of *Rorippa*. Similar patterns have also been observed in other Brassicaceae genera,

such as *Draba* (Jordon-Thaden et al., 2013) and *Cardamine* (Carlsen et al., 2009).

LDD in *Rorippa* was assumed to be achieved via migrating shorebirds (Bleeker et al., 2002). *Rorippa* plants have strong affinity for wet habitats and extreme flooding tolerance (Akman et al., 2014; Chater & Rich, 1995; Ikematsu et al., 2023; Les, 2018), which made LDD of *Rorippa* seeds or propagules more feasible by floods or migrating shorebirds (Boere & Stroud, 2006; Green et al., 2023). Other characters, such as the mucilage covering or hollows on seeds or the ability of self-fertilization and clonal regeneration (Chater & Rich, 1995; Jonsell, 1968), may also have facilitated the transoceanic voyage of *Rorippa* diaspores (Table S5).

Hybridization may also play a significant role during the evolution of *Rorippa* species (Bleeker, 2007). Benefited from the incorporation of biparentally inherited nuclear variation into phylogenetic construction, about 34.48% of species were detected as hybrid origins, comprising six homoploid hybrids (10.34%) and 14 allopolyploids (24.13%) (Table S2; Figures 3 and S8). Besides, interspecific introgression of chloroplast genome (i.e. chloroplast capture) was observed for species mainly distributed in the Southern Hemisphere, such as South America or Oceania (Table S2; Figure 3a). Since hybridization between organisms only happened in their contact zones, species combining genomes from different geographical origins may provide empirical evidence for the occurrence of LDD in *Rorippa*.

4.2 | Polyploidy is not only a driver but also a responder of LDD

Understanding drivers of effective dispersal would help in predicting LDD and examining their consequences (Gillespie et al., 2012; Waters et al., 2020). Polyploids could favour invasion and LDD (Figure 1), which may have jointly mediated the transoceanic establishment of several plant groups (Linder & Barker, 2014; Mandáková et al., 2017; Meudt et al., 2021; Wendel & Cronn, 2003). Among the eight invasive *Rorippa* species, six species are polyploids (Figure S1), partially supporting the robust invasiveness of polyploidy (Moura et al., 2021; Pyšek et al., 2023; te Beest et al., 2012). However, we still know little about the level and pattern of polyploid interaction with LDD.

In *Rorippa*, polyploids are generally younger and prevalent during LDD in the Southern Hemisphere (Table S2; Figure 2). A higher dispersal rate was estimated for polyploid lineages compared to diploid lineages (Table S4; Figure 2d). Furthermore, 21 out of the total 26 events identified as LDD products were polyploids (Table S5; Figure 4). Contrary to a previous finding (Linder & Barker, 2014), polyploidy-impacted LDD was slightly more common in terms of polyploidization following LDD (PF-LDD) than those preceding LDD (PP-LDD) here in *Rorippa* (Table 1; Figures S10 and S13), suggesting that polyploids may be bolstered by LDD and affect the post-dispersal effectiveness of LDD (i.e. the successful establishment of reproductive individuals). The fact that most *Rorippa* polyploids were younger than diploids may provide additional evidence for these detected polyploidization events following rather than preceding LDD events (Table S2). These observations indicate that polyploidy could be not only an intrinsic driver but also a responder of LDD, highlighting a synergistic relationship between them.

4.3 | Synergistic polyploidization and LDD

Mechanistically, polyploidy and LDD may interact synergistically during the evolution of globally distributed groups such as *Rorippa* (Marhold & Lihová, 2006). This inference is reinforced by the fact that polyploids are well-suited to be pioneers in novel environments (Baniaga et al., 2020; te Beest et al., 2012). Polyploids have duplicated genomes, providing them with high robustness to cope with stresses imposed by long-distance travels. Furthermore, polyploidy-mediated LDD would be influenced by trait shifts in mating system or life history (Baker, 1955), which may emerge after polyploidization (Van Drunen & Husband, 2019). Given the stochasticity of LDD, the possibility of mating of early-arrived founders would be extremely rare due to their small population sizes. However, specific trait shifts following polyploidization can provide several ways to cope with the reproductive difficulties. In *Rorippa*, for example, post-dispersal populations can be established by providing propagules with reproductive assurance (e.g. 52% of LDD occurred in selfing polyploids), or sufficient time to withstand stress and find suitable mates (e.g. 32% of LDD occurred in perennial polyploids) (Table S5). Overall, these observations suggest that the success of polyploidy-impacted LDD would be influenced by both polyploid advantages and environment-dependent trait shifts.

Meanwhile, polyploid lineages are more likely to speciate because of LDD, such as those polyploid endemics on islands (Meudt et al., 2021) or *Rorippa* species in the Southern Hemisphere (Table S5; Figure 2). First, recurrent LDD may bring polyploids with different genotypes together, resulting in new hybrids during contact (e.g. chloroplast capture) (Table S2; Figure 3). For example, the AD-genomic cottons in the New World were produced by allopolyploidization following the LDD of their A-genome progenitors from Africa or Asia (Wendel & Cronn, 2003). Combined with observations in *Rorippa*, these results suggest that LDD may promote polyploid speciation. Second, through LDD, geographical isolation can be established instantly between population-of-origin and the newly established population (Jordano, 2017; Meudt et al., 2021), avoiding risks of genetic swamping from diploid progenitors. In *Rorippa*, lineages under LDD can be transferred more than 7500 km away from their population-of-origin (Figure S11), making subsequent contact unrealistic (Gillespie et al., 2012). Third, together with the independent gain or loss of duplicated genes among populations (divergent resolution) (Taylor et al., 2001), genetic divergence would accumulate and lead to polyploid speciation in lineages following LDD (e.g. type of polyploidization followed LDD, accounting for 43% and 34% of LDD events along plastid and nuclear trees respectively; Tables 1 and S5). However, the importance of LDD in polyploid diversification

is still controversial due to its rarity (but see Meudt et al., 2021). Therefore, more work is needed to fill the gap between speciation inference and biogeographical reconstruction for those globally distributed polyploid complexes.

5 | CONCLUSION

Characteristics that confer strong adaptability to diaspores could enhance their effective dispersal. Therefore, factors facilitating post-dispersal success are critical in predicting effective LDD (Wu et al., 2023). Here we uncovered the synergistic relationship between polyploidy and LDD and provided insights into their joint roles in shaping the global species diversification in a plant genus *Rorippa* that originated in the late Miocene (*c.* 7.10 Ma). *Rorippa* polyploids mainly originated in the Pleistocene around 1.71–1.03 Ma and spread as products of LDD around 1.47 Ma. Global changes during the Pleistocene and the establishment of modern ecosystems may have provided the conditions for polyploids to colonize new areas. However, reduced dispersal ability has been predicted as one of the key drivers of diversification under climate changes in the future (Waters et al., 2020). Therefore, we propose that the predictive role of polyploidy in LDD would deepen our understanding about the mechanisms underlying global biodiversity in a changing world.

AUTHOR CONTRIBUTIONS

Ting-Shen Han and Yao-Wu Xing conceived the project. Ting-Shen Han collected the data, developed the model, performed analyses and drafted the manuscript. Chih-Chieh Yu interpreted results and contributed intellectual content. Quan-Jing Zheng collected the data and did the phylogenetic analyses. Seisuke Kimura provided materials and revised the manuscript. Renske E. Onstein revised the manuscript. All authors reviewed the final manuscript and provided critical feedbacks.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The sequences can be accessed by GenBank IDs: plastid genomes (ON564273–ON564277, ON892566–ON892601), low-copy nuclear loci (ON563925–ON564272, ON572549–ON573012), ITS (ON616541–ON616690) and plastid fragments (ON585120–ON585560). Custom scripts, data and appendix files are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.n02v6wx44).

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REFERENCES

Akman, M., Bhikharie, A. V., Mustroph, A., & Sasidharan, R. (2014). Extreme flooding tolerance in *Rorippa*. *Plant Signaling & Behavior*, *9*(2), e27847. https://doi.org/10.4161/psb.27847

Baker, H. G. (1955). Self-compatibility and establishment after 'long-distance' dispersal. *Evolution*, *9*(3), 347–349. https://doi.org/10.1111/j.1558-5646.1955.tb01544.x

Baniaga, A. E., Marx, H. E., Arrigo, N., & Barker, M. S. (2020). Polyploid plants have faster rates of multivariate niche differentiation than their diploid relatives. *Ecology Letters*, *23*(1), 68–78. https://doi.org/10.1111/ele.13402

Bleeker, W. (2007). Interspecific hybridization in *Rorippa* (Brassicaceae): Patterns and processes. *Systematics and Biodiversity*, *5*(3), 311–319. https://doi.org/10.1017/S1477200007002411

Bleeker, W., Weber-Sparenberg, C., & Hurka, H. (2002). Chloroplast DNA variation and biogeography in the genus *Rorippa* Scop. (Brassicaceae). *Plant Biology*, *4*(1), 104–111. https://doi.org/10.1055/s-2002-20442

Boere, G. C., & Stroud, D. A. (2006). The flyway concept: What it is and what it isn't. In G.C. Boere, C.A. Galbraith, & D.A. Stroud (eds.), *Waterbirds around the world* (pp. 40–47). The Stationery Office Limited, Edingburgh, UK.

Carlquist, S. (1966). The biota of long-distance dispersal. I. Principles of dispersal and evolution. *The Quarterly Review of Biology*, *41*(3), 247–270. https://doi.org/10.1086/405054

Carlsen, T., Bleeker, W., Hurka, H., Elven, R., & Brochmann, C. (2009). Biogeography and phylogeny of *Cardamine* (Brassicaceae). *Annals of the Missouri Botanical Garden*, *96*(2), 215–236. https://doi.org/10.3417/2007047

Chater, A. O., & Rich, T. C. G. (1995). *Rorippa islandica* (Oeder ex Murray) Borbas (Brassicaceae) in Wales. *Walsonia*, *20*, 229–238.

Czech, L., Barbera, P., & Stamatakis, A. (2020). Genesis and Gappa: Processing, analyzing and visualizing phylogenetic (placement) data. *Bioinformatics*, *36*(10), 3263–3265. https://doi.org/10.1093/bioinformatics/btaa070

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*(8), 1969–1973. https://doi.org/10.1093/molbev/mss075

Gillespie, R. G., Baldwin, B. G., Waters, J. M., Fraser, C. I., Nikula, R., & Roderick, G. K. (2012). Long-distance dispersal: A framework for hypothesis testing. *Trends in Ecology & Evolution*, *27*(1), 47–56. https://doi.org/10.1016/j.tree.2011.08.009

Green, A. J., Lovas-Kiss, Á., Reynolds, C., Sebastián-González, E., Silva, G. G., van Leeuwen, C. H. A., & Wilkinson, D. M. (2023). Dispersal of aquatic and terrestrial organisms by waterbirds: A review of current knowledge and future priorities. *Freshwater Biology*, *68*(2), 173–190. https://doi.org/10.1111/fwb.14038

Guo, X., Liu, J., Hao, G., Zhang, L., Mao, K., Wang, X., Zhang, D., Ma, T., Hu, Q., & Al-Shehbaz, I. A. (2017). Plastome phylogeny and early diversification of Brassicaceae. *BMC Genomics*, *18*(1), 1–9. https://doi.org/10.1186/s12864-017-3555-3

Halabi, K., Shafir, A., & Mayrose, I. (2023). PloiDB: The plant ploidy database. *New Phytologist*, *240*, 918–927. https://doi.org/10.1111/nph.19057

Han, T.-S., Hu, Z.-Y., Du, Z.-Q., Zheng, Q.-J., Liu, J., Mitchell-Olds, T., & Xing, Y.-W. (2022). Adaptive responses drive the success of polyploid yellowcresses (*Rorippa*, Brassicaceae) in the Hengduan Mountains, a temperate biodiversity hotspot. *Plant Diversity*, *44*(5), 455–467. https://doi.org/10.1016/j.pld.2022.02.002

Huang, C.-H., Sun, R., Hu, Y., Zeng, L., Zhang, N., Cai, L., Zhang, Q., Koch, M. A., Al-Shehbaz, I., & Edger, P. P. (2015). Resolution of Brassicaceae phylogeny using nuclear genes uncovers nested radiations and supports convergent morphological evolution. *Molecular Biology and Evolution*, *33*(2), 394–412. https://doi.org/10.1093/molbev/msv226

Ikematsu, S., Umase, T., Shiozaki, M., Nakayama, S., Noguchi, F., Sakamoto, T., Hou, H., Gohari, G., Kimura, S., & Torii, K. U. (2023). Rewiring of hormones and light response pathways underlies the inhibition of stomatal development in an amphibious plant *Rorippa aquatica* underwater. *Current Biology*, *33*(3), 543–556. https://doi.org/10.1016/j.cub.2022.12.064

Jin, J.-J., Yu, W.-B., Yang, J.-B., Song, Y., de Pamphilis, C. W., Yi, T.-S., & Li, D.-Z. (2020). GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. *Genome Biology*, *21*(1), 241. https://doi.org/10.1186/s13059-020-02154-5

Jonsell, B. (1968). *Studies in the North-West European species of Rorippa s. str.* (Doctoral dissertation), Acta Universitatis Upsaliensis, Uppsala, Sweden. (0082-0644).

Jordano, P. (2017). What is long-distance dispersal? And a taxonomy of dispersal events. *Journal of Ecology*, *105*(1), 75–84. https://doi.org/10.1111/1365-2745.12690

Jordon-Thaden, I. E., Al-Shehbaz, I. A., & Koch, M. A. (2013). Species richness of the globally distributed, arctic–alpine genus *Draba* L. (Brassicaceae). *Alpine Botany*, *123*(2), 97–106.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., & Duran, C. (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics*, *28*(12), 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Klaus, K. V., & Matzke, N. J. (2020). Statistical comparison of trait-dependent biogeographical models indicates that Podocarpaceae dispersal is influenced by both seed cone traits and geographical distance. *Systematic Biology*, *69*(1), 61–75. https://doi.org/10.1093/sysbio/syz034

Les, D. H. (2018). Core eudicots: Dicotyledons IV: "Rosid" tricolpates: Malvid Rosids (Eurosids II): Order 9: Brassicales: Family 2: Brassicaceae: 7. *Rorippa*. In D.H. Les (eds.), *Aquatic dicotyledons of North America: Ecology, life history, and systematics* (pp. 398–406). CRC Press.

Liddell, L. G., Lee, W. G., Dale, E. E., Meudt, H. M., & Matzke, N. J. (2021). Pioneering polyploids: The impact of whole-genome duplication on biome shifting in New Zealand *Coprosma* (Rubiaceae) and *Veronica* (Plantaginaceae). *Biology Letters*, *17*(9), 20210297. https://doi.org/10.1098/rsbl.2021.0297

Linder, H. P., & Barker, N. P. (2014). Does polyploidy facilitate long-distance dispersal? *Annals of Botany*, *113*(7), 1175–1183. https://doi.org/10.1093/aob/mcu047

Luo, Y., Goh, S. P., Li, D., Gonzaga, M. O., Santos, A. J., Tanikawa, A., Yoshida, H., Haddad, C. R., May-Collado, L. J., Gregorič, M., Turk, E., Kuntner, M., & Agnarsson, I. (2020). Global diversification of *Anelosimus* spiders driven by long distance overwater dispersal and Neogene climate oscillations. *Systematic Biology*, *69*(6), 1122–1136. https://doi.org/10.1093/sysbio/syaa017

Mandáková, T., Pouch, M., Harmanová, K., Zhan, S. H., Mayrose, I., & Lysak, M. A. (2017). Multispeed genome diploidization and diversification after an ancient allopolyploidization. *Molecular Ecology*, *26*(22), 6445–6462. https://doi.org/10.1111/mec.14379

Marhold, K., & Lihová, J. (2006). Polyploidy, hybridization and reticulate evolution: Lessons from the Brassicaceae. *Plant Systematics and Evolution*, *259*(2), 143–174. https://doi.org/10.1007/s00606-006-0417-x

Matzke, N. J. (2018). BioGeoBEARS: BioGeography with Bayesian (and likelihood) Evolutionary Analysis with R Scripts. version 1.1.1. https://doi.org/10.5281/zenodo.1478250

Meudt, H. M., Albach, D. C., Tanentzap, A. J., Igea, J., Newmarch, S. C., Brandt, A. J., Lee, W. G., & Tate, J. A. (2021). Polyploidy on islands: Its emergence and importance for diversification. *Frontiers in Plant Science*, *12*(336), 637214. https://doi.org/10.3389/fpls.2021.637214

Moura, R. F., Queiroga, D., Vilela, E., & Moraes, A. P. (2021). Polyploidy and high environmental tolerance increase the invasive success of plants. *Journal of Plant Research*, *134*(1), 105–114. https://doi.org/10.1007/s10265-020-01236-6

Mummenhoff, K., & Franzke, A. (2007). Gone with the bird: Late tertiary and quaternary intercontinental long-distance dispersal and allopolyploidization in plants. *Systematics and Biodiversity*, *5*(3), 255–260. https://doi.org/10.1017/S1477200007002393

Nakayama, H., Sakamoto, T., Okegawa, Y., Kaminoyama, K., Fujie, M., Ichihashi, Y., Kurata, T., Motohashi, K., Al-Shehbaz, I., & Sinha, N. (2018). Comparative transcriptomics with self-organizing map reveals cryptic photosynthetic differences between two accessions of North American Lake cress. *Scientific Reports*, *8*(1), 3302. https://doi.org/10.1038/s41598-018-21646-w

Nguyen, L. T., Schmidt, H. A., von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, *32*(1), 268–274. https://doi.org/10.1093/molbev/msu300

Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*(3), 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pyšek, P., Lučanová, M., Dawson, W., Essl, F., Kreft, H., Leitch, I. J., Lenzner, B., Meyerson, L. A., Pergl, J., van Kleunen, M., Weigelt, P., Winter, M., & Guo, W.-Y. (2023). Small genome size and variation in ploidy levels support the naturalization of vascular plants but constrain their invasive spread. *New Phytologist*, *239*, 2389–2403. https://doi.org/10.1111/nph.19135

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*(2), 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rothfels, C. J. (2021). Polyploid phylogenetics. *New Phytologist*, *230*(1), 66–72. https://doi.org/10.1111/nph.17105

Rothfels, C. J., Pryer, K. M., & Li, F. W. (2017). Next-generation polyploid phylogenetics: Rapid resolution of hybrid polyploid complexes using PacBio single-molecule sequencing. *New Phytologist*, *213*(1), 413–429. https://doi.org/10.1111/nph.14111

Shi, L., Chen, H., Jiang, M., Wang, L., Wu, X., Huang, L., & Liu, C. (2019). CPGAVAS2, an integrated plastome sequence annotator and analyzer. *Nucleic Acids Research*, *47*(W1), W65–W73. https://doi.org/10.1093/nar/gkz345

Stebbins, G. L. (1971). *Chromosomal evolution in higher plants*. Edward Arnold (Publishers) Ltd.

Taylor, J. S., Van de Peer, Y., & Meyer, A. (2001). Genome duplication, divergent resolution and speciation. *Trends in Genetics*, *17*(6), 299–301. https://doi.org/10.1016/S0168-9525(01)02318-6

te Beest, M., Le Roux, J. J., Richardson, D. M., Brysting, A. K., Suda, J., Kubešová, M., & Pyšek, P. (2012). The more the better? The role of

polyploidy in facilitating plant invasions. *Annals of Botany*, *109*(1), 19–45. https://doi.org/10.1093/aob/mcr277

Thomas, G. W. C., Ather, S. H., & Hahn, M. W. (2017). Gene-tree reconciliation with MUL-trees to resolve polyploidy events. *Systematic Biology*, *66*(6), 1007–1018. https://doi.org/10.1093/sysbio/syx044

Van Drunen, W. E., & Husband, B. C. (2019). Evolutionary associations between polyploidy, clonal reproduction, and perenniality in the angiosperms. *New Phytologist*, *224*(3), 1266–1277. https://doi.org/10.1111/nph.15999

Vilela, B., & Villalobos, F. (2015). letsR: A new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, *6*(10), 1229–1234. https://doi.org/10.1111/2041-210X.12401

Waters, J. M., Emerson, B. C., Arribas, P., & McCulloch, G. A. (2020). Dispersal reduction: Causes, genomic mechanisms, and evolutionary consequences. *Trends in Ecology & Evolution*, *35*(6), 512–522. https://doi.org/10.1016/j.tree.2020.01.012

Weiß, C. L., Pais, M., Cano, L. M., Kamoun, S., & Burbano, H. A. (2018). nQuire: A statistical framework for ploidy estimation using next generation sequencing. *BMC Bioinformatics*, *19*(1), 122. https://doi.org/10.1186/s12859-018-2128-z

Wendel, J. F., & Cronn, R. C. (2003). Polyploidy and the evolutionary history of cotton. *Advances in Agronomy*, *78*, 139–186.

Wu, Z.-Y., Liu, J., Provan, J., Wang, H., Chen, C. J., Cadotte, M. W., Luo, Y. H., Amorim, B. S., Li, D. Z., & Milne, R. I. (2018). Testing Darwin's transoceanic dispersal hypothesis for the inland nettle family (Urticaceae). *Ecology Letters*, *21*(10), 1515–1529. https://doi.org/10.1111/ele.13132

Wu, Z.-Y., Milne, R. I., Liu, J., Nathan, R., Corlett, R. T., & Li, D.-Z. (2023). The establishment of plants following long-distance dispersal. *Trends in Ecology & Evolution*, *38*(3), 289–300. https://doi.org/10.1016/j.tree.2022.11.003

BIOSKETCH

Ting-Shen Han is interested in ploidy diversity of plants, devoting to look into the mystery of polyploid fate at either species or population levels. **Yao-Wu Xing** is keen to exploring the biogeographical pattern and mechanism of plant diversity, by integrating fossil and molecular evidence. All authors are interested in describing and interpreting the biodiversity at molecular, population or community levels, and across local, regional or global scales.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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