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Cold Origins Limit the Establishment of Northern Temperate Plants in the Southern Hemisphere

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Abstract.—Plants with amphitropical distributions have closely related populations in both Northern and Southern Hemispheres, but are absent from the intervening tropics. They provide a unique opportunity to study the constraints shaping the distribution of temperate lineages through time. Using grasses from the ecologically diverse supertribe Melicodae, an emerging study system with species distributed throughout the temperate regions, we test the hypothesis that geography and/or environmental niche constrain which lineages successfully cross the tropics to establish in the opposite hemisphere. Biogeographic and evolutionary modelling was conducted on well resolved plastid and nuclear phylogenies constructed from whole-genome sequencing of 178 accessions of 103 Melicodae species. Results show that species from cold regions are much less likely to successfully cross the tropics, with successful lineages all sharing warmer niches that evolved prior to their establishment in the opposite hemisphere. Evidence suggests that this result is explained both by the greater distances that high-latitude, cold-origin lineages must disperse to cross the tropics, and inherent limitations associated with colder thermal niches. In particular, our results suggest that traits allowing species to cope with cold winters, rather than an inability to cope with warm summers, limit their ability to establish in the opposite hemisphere, hinting at important trade-offs between cold-tolerance and biogeographic potential. These results provide insight into the drivers of the distribution and diversity of plants, and the challenges facing cold-origin lineages in a rapidly warming world. If cold-origin species occupy a smaller proportion of their potential range, and are unlikely to establish in new areas with suitable climates, their ability to track preferred habitat as climates warm may be worse than currently expected. [amphitropical distribution; *Melica*; *Glyceria*; biogeography; cold tolerance; dispersal.]

Where an organism lives is a consequence of multiple processes, and the distribution of organisms can reveal much about the processes shaping Earth's biosphere. One critical factor determining a species distribution is the range of environmental conditions it can tolerate (Wiens and Donoghue 2004; Banasiak et al. 2013; Linder et al. 2013). This environmental niche may remain relatively stable or change through time. Niche conservatism, the tendency for organisms to maintain stable environmental preferences and move to track them through space and time, has historically been viewed as a major determinant of biogeographical patterns (e.g., Ricklefs and Latham 1992; Prinzing et al. 2001; Wiens and Graham 2005), although recent work increasingly highlights the importance of niche shifts (e.g., Wasof et al. 2013; Atwater et al. 2018; Nürk et al. 2018; Quiroga et al. 2018; 2021). To occupy more than a small fraction of the suitable habitat available worldwide, species must be able to effectively disperse, potentially over long distances (Wen and Ickert-Bond 2009; Linder et al. 2013; Klaus and Matzke 2020; Huang et al. 2024). Although other factors, such as the rise and fall of geographic barriers (e.g., Bacon et al. 2015), also shape distributions, environmental niche and dispersal ability are central to our understanding of the mechanisms shaping species distributions.

An extreme case highlighting the importance of both environmental niche and dispersal ability, are amphitropical distributions, where closely related lineages (e.g., populations within a single species or groups of closely related species) occupy habitats at similar latitudes on either side of the tropics (e.g., Raven 1963; Thorne 1972; Simpson et al. 2017). These distributions arise in temperate lineages via both their exclusion from warmer tropical regions (i.e., lowland habitats between 23.5 ° N and ° S, where cold month temperature is generally > 18 ° C; Beck et al. 2023), and their ability to disperse great distances to reach mid- or high-latitudes in the opposite hemisphere. Amphitropical distributions have a long history of study (e.g., Humboldt 1817; Darwin 1859; Gray and Hooker 1880; Wallace 1880; Bray 1898; Du Rietz 1940; Raven 1963; Thorne 1972; Allred 1981; Wen and Ickert-Bond 2009; Quiroga et al. 2021). Previous work suggests that most amphitropical distributions arise via recent (< c. 5 Ma) long-distance dispersal events, rather than step-wise dispersal through the tropics or via vicariance (e.g., Raven 1963; Mitchell et al. 2016; Simpson et al. 2017), although this may be biased by the emphasis often placed on disjunctions at lower taxonomic levels (e.g., Raven 1963; Wen and Ickert-Bond 2009; Drew et al. 2017; Simpson et al. 2017). A body of work also suggests disjunctions occur disproportionately among certain groups (e.g., perennial herbs; Raven 1963; Thorne 1972; Drew et al. 2017; Simpson et al. 2017), and authors have extensively explored the dispersal processes that initiate disjunctions, and the role that changing climates have in facilitating dispersal or fragmenting once-continuous ranges (e.g., Darwin 1859; Wallace 1880; Bray 1898; Jürgens 1997; Wen and Ickert-Bond 2009; Schenk and Saunders 2017). The role of climate is particularly topical because temperate species, particularly those of polar and montane regions, are among the hardest hit by warming climates in the present day (Wang et al. 2016; Rantanen et al. 2022). The shifting of cold environments to higher latitudes and elevations may have dire consequences for these taxa (Kaplan and New 2006; Araújo et al. 2011; Pearson et al. 2013), and understanding the factors that have helped some temperate lineages establish hemisphere-spanning ranges will help develop understanding of the factors shaping the risk or resilience of species to anthropogenic climate change.

Although most temperate species in theory have a suitable habitat at a similar latitude in the opposite hemisphere, the majority do not occupy both the northern and southern portions of their theoretical range (Raven 1963; Thorne 1972; Simpson et al. 2017). Why certain species and not others form these distributions has received a great deal of attention. Much of this research has focused on dispersal mechanisms, including the direction of dispersal (e.g., Simpson et al. 2017), timing of dispersal (e.g., Drew et al. 2017; Kamiński et al. 2022), and intrinsic (e.g., dispersal syndrome, Schenk and Saunders 2017) or extrinsic (e.g., dispersal corridors, McGuire and Kron 2005; Mitchell et al. 2016) factors facilitating dispersal. However, in addition to dispersal across the tropics, the creation of disjunct distributions requires populations to become successfully established in the opposite hemisphere. This depends on a range of non-dispersal factors including degree of self-compatibility, environmental conditions at the destination, the lineage's present environmental niche, and its ability to acclimate or adapt to new conditions (Simpson et al. 2017; Villaverde et al. 2017; Quiroga et al. 2018; 2021). Although evidence suggests that amphitropical lineages disproportionately possess high degrees of self-compatibility and occupy certain habitats (e.g., wetlands; Henslow 1879; Raven 1963; Schenk and Saunders 2017; Simpson et al. 2017), many of these non-dispersal factors have received less attention in the study of how these distributions are established (Villaverde et al. 2017).

One largely untested hypothesis is that thermal niche plays an important role in determining which lineages form amphitropical distributions. A number of observations suggest that thermal niche is likely important. For example, there are relatively few lineages disjunct between the northern and southern polar regions compared to mid-latitude disjuncts (Raven 1963), and several amphitropical species in the Americas show evidence of shifts in thermal niche between northern and southern populations (Quiroga et al. 2018; 2021). In addition, the latitudinal distribution of terrestrial habitats differs markedly between hemispheres, with the Southern Hemisphere having less total land mass, and a greater proportion of its terrestrial area at low latitudes (< c. 30°). Furthermore, the relatively small land area and consequently more maritime climates of the Southern Hemisphere mean that winters are generally milder than their Northern Hemisphere equivalents (Beard 1990; Gaston and Chown 1999; Beck et al. 2023). Ultimately, this means there may be large differences in the amount of suitable habitat for a given temperate plant in the Northern and Southern Hemispheres.

Cold-origin lineages, in particular, may be less likely to establish amphitropical disjunctions than their warm-temperate counterparts for several reasons. First, cold-adapted species are generally located at higher latitudes (Casler et al. 2004; Humphreys and Linder 2013; Zanne et al. 2018; Birkeland et al. 2020; Chang et al. 2021), and must travel farther to reach the opposite hemisphere than species at lower latitudes. Second, there is significantly less temperate land mass in the Southern Hemisphere, meaning seed rain from cold-origin lineages in the Northern Hemisphere is less likely to arrive in an area of equivalent habitat in the Southern Hemisphere. Finally, the tropics may form a more impenetrable barrier to cold-adapted lineages whose thermal niche is less similar to that of the tropics than is the thermal niche of their warm-temperate relatives. This might effectively narrow corridors through the tropics (e.g., along highlands; Mitchell et al. 2016; Simpson et al. 2017) for some species, making dispersal less viable. The first mechanism implies patterns primarily driven by dispersal limitation, with thermal niche correlated only as a byproduct. In contrast, the latter two mechanisms imply a more direct role of thermal niche in determining which lineages successfully establish in the opposite hemisphere.

If thermal niche directly impacts potential to establish in the opposite hemisphere, several niche axes may have important effects. One barrier to cold-origin lineages may be the effects of high summer temperatures and resulting heat stress, which plants can experience at temperatures only c. 5 ° C above their optimum growth temperature (Bita and Gerats 2013). Heat stress causes a host of negative effects, ranging from cellular reorganization and changes to normal enzyme activity, to the creation of harmful reactive oxygen species (ROS). Together these effects reduce productivity and can eventually lead to plant death (Wahid et al. 2007; Bita and Gerats 2013). The ability to mitigate these effects is correlated with species realized niche, with species from hot regions generally faring better than species from cold ones (Zhu et al. 2018; Feeley et al. 2020; Li et al. 2022). Cold-origin species might also be disadvantaged in warmer regions if traits conferring cold tolerance negatively impact their ability to establish in regions where cold stress is rare. For example, in many taxa extended cold periods are required to break seed dormancy (e.g., Schütz and Rave 1999; Baskin and Baskin 2004; Cavieres and Sierra-Almeida 2018) or promote flowering (e.g., Michaels and Amasino 2000; McKeown et al. 2016), and high-latitude species may also be reliant on long-summer days to realize their full growth potential (e.g., Savage and Cavender-Bares 2013). Tradeoffs with growth rate may also mean that species investing in costly cold tolerance mechanisms could be at a competitive disadvantage to other taxa, a pattern commonly used to explain the lower range limits of high-latitude and alpine species (Loehle 1998; Brodribb and Feild 2008; Pellissier et al. 2018; Leites et al. 2019; Willi and Buskirk 2022; Moore et al. 2023).

In this study, we test the extent to which the formation of disjunct distributions can be explained by dispersal limitation and ancestral thermal niche versus post-dispersal niche shifts using the diverse grass supertribe Melicodae Soreng (Poaceae: Pooideae) as a model. Melicodae consists of c. 150 species distributed across two tribes and eight genera, with species native to every continent except Antarctica. Apart from a handful of species found at high elevations, the group is largely absent from tropical latitudes. Its two most speciose genera, *Melica* L. and *Glyceria* R. Br. (>85% of species), have ranges resembling classic amphitropical disjunctions, although a pair of Andean *Melica* narrow the gap in the Americas (POWO 2025). The supertribe is an excellent model system because it displays a wide diversity of environmental niches from subarctic to subtropical, and wetland to desert (Schick 1983; Barkworth et al. 2007; Hempel 2011). Although previous studies have identified the group as useful for studying a range of morphological and physiological traits (Khodaverdi et al. 2023; Brightly et al. 2024) and despite a number of species having been sampled in at least one focused study (e.g., Winterfield et al. 2025) and several broader phylogenetic studies (e.g., Schubert et al. 2019a; Schneider et al. 2011; Orton et al. 2021; Grass Phylogeny Working Group III 2025), previous work has been limited by the absence of a robust phylogenetic treatment for the supertribe. To test predictions of our biogeographical hypotheses, we start by inferring a robust phylogeny of the group based on whole genome sequencing, and use time-calibrated trees to reconstruct the evolution of the group's biogeography and thermal niche, with an emphasis on the formation of disjunctions between the Northern and Southern Hemispheres.

Methods

Sample Collection and Preparation

Leaf tissue samples for DNA extraction were collected from dried specimens obtained from herbaria and field collections (Supplementary Material Supplementary Table S1). Taxonomic determinations were verified for all plants prior to sampling. Fresh tissue samples from field collections were placed on silica gel until completely dry (c. 48 hours), at which point the silica gel was removed.

We collected tissue samples for 178 individuals from 103 species of the supertribe Melicodae (68% of recognized species). This included 61 *Melica* L. (of c. 91 recognized species), 30 *Glyceria* R. Br. (of c. 41 recognized species), all six recognized species of *Pleuropogon* R. Br., two *Triniochloa* Hitchc. (of c. six recognized species), two *Schizachne* (Torr.) Swallen (of c. three recognized species), and *Koordersiochloa longiarista* (A. Rich.) Veldkamp (one of two recognized *Koordersiochloa* Merr. species) from the tribe Meliceae Link ex Endl. The sole species in the tribe Brylkinieae Tateoka, *Brylkinia caudata* (Munro) F. Schmidt, was also sampled (Soreng et al. 2022; POWO 2025). The only genus not sampled was the monotypic *Lycochloa* Samuelsson, due to scarcity of material.

Leaf tissue samples were ground by hand in a mortar and pestle with the aid of sterile silica sand. DNA extraction was then conducted using a QIAGEN (Hilden, Germany) DNeasy Plant Mini Kit (69,106). Standard kit instructions were followed, with the exception of an extended hourlong incubation at 65 ° C, to increase the number of cells lysed, which was expected to constrain DNA yields in samples up to 100 years old. Prior to library preparation, all extractions were quality checked for DNA concentration and fragment size using an Invitrogen (Waltham, MA) Qubit 3 Fluorometer and gel electrophoresis, respectively.

Illumina libraries were prepared using New England BioLabs (Ipswitch, Massachusetts) NEBNext Ultra II FS DNA (NEB #E6177L) library prep kits with single index primers (NEB #E6609S). Owing to the wide range of quality in DNA extractions obtained, library prep followed one of three protocols. Samples with average fragment size > 1000 bp were fragmented and size-selected following normal kit instructions to produce libraries with insert sizes of 200–350 bp given 200 ng of DNA input. Samples with average fragment size 200–1000 bp and DNA concentration > 5 ng/μL were prepared with the exclusion of fragmentation steps, while samples with either fragment size < 200 bp or DNA concentration < 5 ng/µL were prepared without fragmentation or size selection steps. Paired end sequencing was conducted by BGI Tech Solutions (Warsaw, Poland) on four lanes of a DNBSEQ-T7 to an average yield of 25 Gb/sample.

Chloroplast Assembly and Phylogenetic Analysis

Chloroplast assembly was conducted on adaptor trimmed reads using the GetOrganelle genome assembly toolkit (v. 1.7.7.1; Jin et al. 2020), with dependencies Bowtie2 (v. 2.5.3; Langmead and Salzberg 2012), SPAdes (v. 3.15.5; Bankevich et al. 2012), and Blast (v. 2.15.0; Camacho et al. 2009). Most assemblies were successfully completed using default parameters. For those that failed to assemble, modifications such as changing default kmer values (see code in Supporting Materials) were necessary to optimize performance. For each sample, assembly graphs were visually inspected using the visualization software Bandage (v. 0.9.0; Wick et al. 2015). Assembly statistics are provided in the Supplementary Material (Supplementary Table S1).

Newly produced sequence data were supplemented by previously published full plastid genomes obtained from the NIH GenBank (Supplementary Material Supplementary Table S2), representing seven Melicodae and 28 outgroup taxa, the latter representing all major groups within the Pooideae subfamily of grasses. Previously published chloroplast assemblies were used as a reference to rearrange de novo assemblies, and save a single final assembly per sample with the short single copy (SSC) region in the same orientation as published assemblies. This was conducted in Geneious Prime (Geneious Prime 2024.0.7), via a combination of manual editing and MAFFT alignment (Katoh and Standley 2013). For *Pleuropogon oregonus* Chase, we were unable to successfully assemble a complete chloroplast genome. In this case we assembled a partial chloroplast genome using contigs extracted from the assembly graphs in Bandage (Wick et al. 2015). First, the highest coverage contigs were selected, and BLASTed (Altschul et al. 1990; Camacho et al. 2009; Wick et al. 2015) against the remaining dataset, retaining only those with best matches inside *Pleuropogon*. In Geneious Prime (v. 2024.0.7) contigs were then mapped to a previously published chloroplast genome of *Pleuropogon hooverianus* (G.T.Benson) Howell (NC_059,983, with the Inverted Repeat A removed), to determine their order and orientation, and then concatenated into a partial chloroplast genome (111,983 bp) which was aligned with the remaining, full chloroplast assemblies.

All chloroplast genome assemblies (178 of our de novo assemblies, seven Melicodae and 28 outgroup taxa from GenBank) were then aligned in Geneious Prime using the MAFFT plugin and FFT-NS-i x1000 algorithm (Katoh and Standley 2013), with all parameters left at their default values. Minor manual corrections to this initial alignment were then made and the Inverted Repeat Region A removed. Poorly aligned regions were removed from this initial alignment using trimAl (v. 1.5.0; Capella-Gutiérrez et al. 2009), by trimming gap-rich sites with the "gappyout" algorithm, chosen by the program's automatic heuristic. The resulting alignment of 213 taxa and 115,429 bp was used for subsequent phylogenetic analysis.

Maximum likelihood trees were reconstructed using iQtree (v. 2.3.4; Minh et al. 2020). Akaike information criterion (AIC; Akaike 1974) scores obtained from the iQtree implementation of ModelFinder (Kalyaanamoorthy et al. 2017) supported GTR + F + I + G4 as the best model for these reconstructions. A bootstrap consensus tree was generated from 25 independent runs, each with 500 non-parametric bootstrap replicates.

Divergence time estimation and Bayesian phylogenetic reconstruction was conducted using BEAST (v. 2.7.6; Drummond and Rambaut 2007) run on the CIPRES science gateway (Miller et al. 2010). We used the same GTR + F + I + G4 model as in ML analyses, with a Calibrated Yule tree prior (Heled and Drummond 2012). Because no fossils are known for the Melicodae, divergence time estimation used an optimized relaxed clock model (Douglas et al. 2021) with a single secondary calibration point placed on the most recent common ancestor (MRCA) of Pooideae. We assigned a log-normal prior ($\mu = 84.8$, $\sigma = 0.06$) to this node, to match its posterior age estimate in Orton et al. (2021). Dating in Orton et al. (2021) was based on 14 fossil calibrations, and was chosen because it was based upon full chloroplast genomes and included similar sampling of early diverging Pooideae lineages to the present study. Default values were retained for the remaining priors with the exception of the birth-rate of the Yule process (lognormal, $\mu = 0.047$, $\sigma = 1.5$) and proportion of invariant sites (beta, $a = b = 2$), for which we assigned new, more informative priors following preliminary runs. Sampling was completed via two rounds of Metropolis-coupled Markov chain Monte Carlo sampling (MCMCMC; Geyer 1991; Müller and Bouckaert 2020). Each MCMCMC round included six chains with a target acceptance ratio of 0.18 (default values were used for the remaining parameters), and was run for 175 million generations, sampling every 10,000 generations, and the first 35 million discarded as burn-in. Chains were checked for convergence and adequate sampling of the posterior using Tracer (v. 1.7.2; Rambaut et al. 2018), and a maximum clade credibility tree was computed from the posterior sample using TreeAnnotator (v. 2.7.6; Drummond and Rambaut 2007), with the "Common Ancestor" option used to compute node heights. For analyses requiring a single tip per taxon, the maximum clade credibility tree was trimmed by randomly dropping all but a single representative from each taxon.

Nuclear Marker Assembly and Phylogenetic Analysis

For analyses on nuclear data, we generated alignments for 4,460 complete Benchmarking Universal Single-Copy Orthologs (BUSCO, Simão et al. 2015) present in an annotated reference genome of *Melica nutans* L. (see Data Availability Statement). BUSCOs were initially located in the reference genome using annotations and BUSCO (v 5.7.1; Manni et al. 2021). Reads from our samples were then mapped to the reference genome using bowtie2 (v. 2.5.3; Langmead et al. 2019), sorted with SAMtools (v. 1.2.0; Li et al. 2009), and consensus sequences subsequently generated and aligned following the approach of Dunning et al. (2022). SNPs were called only at sites where reads provided a coverage depth > 3 and when present in > 1 read (Dunning et al. 2019). Poorly aligned regions and sequences with low overlap were removed from gene alignments using trimAl (v 1.5.0; Capella-Gutiérrez et al. 2009). Sequences < 200 bp and alignments < 500 bp were discarded, and alignments including less than half of the samples were dropped. We then estimated maximum likelihood trees for the remaining 2,837 gene alignments separately using iQtree (v. 2.3.4), with 1000 ultrafast bootstrap replicates (Hoang et al. 2017), and substitution models automatically selected for each alignment using the iQtree implementation of ModelFinder (Kalyaanamoorthy et al. 2017). Gene trees were then used to infer a coalescent species tree using the hybrid weighted ASTRAL (v. 1.16; Zhang and Mirarab 2022), a method which takes into account both node support and branch lengths of individual gene trees to infer the coalescent species tree.

Temperature Niche Reconstruction

To characterize temperature niches we obtained median warm quarter (WQT), cold quarter (CQT), and mean annual temperature (MAT) data using georeferenced occurrence records. For each species, occurrence records were downloaded from the Global Biodiversity Information Facility (GBIF; Supplementary Material Methods S1) between March and October of 2023. Records outside each species' known native range (following POWO 2025) were manually excluded using GBIF's polygon selection tool. Records were then vetted (for more detail see Supporting Info Methods S1) to ensure correct taxonomy and to remove records with dubious geospatial data using a combination of GBIF quality flags and tests available in the R package CoordinateCleaner (v. 3.0.1; Zizka et al. 2019). Vetted occurrence records were used to extract WQT, CQT, and MAT from WorldClim 2 climate surfaces (Fick and Hijmans 2017), using the R packages terra (v 1.7–78; Hijmans 2024) and exactextractr (v 0.10.0; Baston 2025). The evolution of all three aspects of temperature niche was reconstructed using the R package Rphylopars (v. 0.3.1, Goolsby et al. 2017), which incorporates intraspecific variation and correlation between niche axes into reconstructions. Ancestral states were estimated under Brownian motion, Ornstein-Uhlenbeck, early burst, and lambda models of trait evolution. Fit was compared using AIC, with lambda model reconstructions kept for subsequent analyses. For each taxon, reconstructions were based on up to 500 randomly selected individuals where sample sizes permitted. Remaining taxa were represented by all available climate data.

Biogeographic Analyses

To reconstruct the biogeographic history of supertribe Melicodae and test whether the establishment of amphitropical disjunctions was correlated with temperature niche, we conducted three sets of analyses. To classify biogeographic range, species were listed as present or absent from six geographic areas based on their native ranges. In order of species richness in our dataset, regions were as follows: Palearctic including Mediterranean Africa (41 species), North and Central America (38), South America (27), sub-Saharan Africa (3), Australia (2), and the island of Tristan da Cunha (1). To reduce the number of areas in the analyses, Indo-Malayan populations of *Koordersiochloa longiarista* were grouped with the species' larger African range.

For the first set of analyses, we used phytools (v 2.3–0, Revell 2024) to fit Bayesian threshold models to test for correlation between WQT, CQT, or MAT and transitions between the Northern and Southern Hemispheres. For each model we ran four chains of 10 million generations, with the first two million discarded as burnin. We confirmed chains were run for long enough, using rstan (v 2.32.6; Stan Development Team 2024) to calculate the $\hat{R}$ convergence diagnostic and effective sample sizes (ESS) for each model parameter ($\hat{R} \approx 1.0$ and ESS > 400).

For the second set of analyses, we used OUwie (v. 2.13; Beaulieu and O'Meara 2024) to fit a series of evolutionary models to test whether there are differences in the evolution of thermal niche between Northern and Southern Hemisphere lineages. Our model fitting approach was as follows. First, we fit six different models of evolution to each temperature variable. These were 1) a single global Brownian Motion model (BM1), 2) a Brownian Motion model with different rates (σ^2) for Northern and Southern Hemisphere lineages (BMS), 3) an Ornstein-Uhlenbeck model with a single global optimum (θ) (OU1), 4) an Ornstein-Uhlenbeck model with different optima (θ) for Northern and Southern Hemisphere lineages (OUM), 5) an Ornstein-Uhlenbeck model with different trait optima (θ) and rates (σ^2) for Northern and Southern Hemisphere lineages (OUMV), and 6) an Ornstein-Uhlenbeck model with different trait optima (θ) and selection strengths (α) for Northern and Southern Hemisphere lineages (OUMA). Models allowing all three parameters (i.e., α, σ^2, and θ) to vary between Northern and Southern Hemisphere lineages failed to reliably estimate the maximum likelihood value of one or more model parameters, and were excluded from further consideration. After model fitting, the relative strength of fit was compared between models using corrected AIC scores calculated using MuMIn (v. 1.48.4; Bartoń 2024). We then conducted 100 parametric bootstrap replicates for each model and used the output to obtain evolutionary parameter estimates weighted by model AIC scores. Models with weight < 0.01 were excluded from this step. To evaluate whether evolutionary differences in thermal niche between hemispheres predate the establishment of disjunct distributions, this model fitting process was repeated twice, with Southern Hemisphere lineages expanded to include their Northern Hemisphere sister lineages by artificially moving the origin of southern populations back in time by one or two nodes. Original node placement was based on ancestral state reconstruction using the phytools function *make.simmap* (Revell 2024) with equal rates and 100 simulations.

For the final set of analyses, we used BioGeoBEARS (v. 1.1; Matzke 2013) to conduct ancestral range estimation under four alternative dispersal-extinction-cladogenesis (DEC) models, following the approach of Klaus and Matzke (2020; see also Garcia-R and Matzke 2021). The models employed were as follows: 1) range and temperature niche as independently evolving characters (DEC + t_{12}).; 2) range and temperature niche as independently evolving characters with dispersal rate proportional to distance between areas (DEC + x + t_{12}); 3) range and temperature niche as correlated characters (DEC + t_{12} + m); and 4) range and temperature niche as correlated characters with dispersal rate proportional to distance between areas (DEC + x + t_{12} + m). Distances between areas were calculated using the geodesic distance between the centroids of species ranges that fell within each area. This was favored over alternative approaches, such as the distance between area edges, because substantial portions of most geographic areas are unoccupied. Models incorporating distance were run twice, either incorporating the minimum or mean distance between centroids in each region.

To directly evaluate the link between likely dispersal distances and thermal niche, we used phylogenetically informed Bayesian mixed effect models (brms v. 2.22.0; Bürkner 2017) to reconstruct the correlation between species thermal niche (MAT, WQT, and CQT) and the minimum distance to a range centroid found in the opposite hemisphere. Species was treated as a random effect grouping factor over which model intercept varied, with effects correlated via a phylogenetic covariance matrix (Paradis and Schliep 2019). Responses were modeled with a normal distribution and identity link, using default priors, and four chains of 8000 generations with a 20% burn-in. After model fitting, effective sample sizes and $\hat{R}$ convergence diagnostics were used to confirm chain convergence and adequate sampling of the posterior for all model parameters (i.e., ESS > 400 per chain; $\hat{R} \approx 1.0$; Bürkner 2017). Bayesian R^2 estimates were also obtained for each model (performance v. 0.7.3; Gelman et al. 2019; Lüdecke et al. 2021).

Because the DEC modelling framework only accommodates categorical data, thermal niche was classified as either warm or cold. We defined this as having a CQT greater than or less than 0 ° C respectively. Although cold stress for individual plants varies through space and time across a species range, species falling below this threshold ($n = 40$) experience more frequent and extended periods of freezing temperatures than their relatives. For convenience, we refer to plants falling below this threshold as "cold-origin", but stress that thermal niche was only discretized for DEC analyses where model limitations required it. An additional set of analyses using a higher temperature threshold (CQT = 3.2 ° C, resulting in the reclassification of 10 species) was also conducted to test whether results were sensitive to the value chosen to discretize thermal niche. We focused on CQT because it was the niche axis most strongly correlated with amphitropical disjunctions (see Results). Preliminary analysis of temperature niche evolution showed higher support for equal rates models than models allowing warm to cold and cold to warm transitions to occur at different rates ($AIC_{ER} = 121.6$, $AIC_{ARD} = 122.8$, $weight_{ER} = 0.65$). We thus treated temperature niche as evolving via an equal rates model for all primary DEC analyses. To reduce the state space, DEC models were run with a maximum allowable range size of four areas, which is double the largest range observed among extant taxa. We ran models both with (DEC) and without (DEC∗) the null range included within the possible state space (Massana et al. 2015). For all models, we reran model optimization steps using seven sets of initial parameter values (Supplementary Material Supplementary Table S3). Results from these runs were compared to ensure stability, and the result with highest log-likelihood was saved for subsequent analyses. Model support was evaluated using AIC, and the best fitting DEC and DEC∗ models were used to conduct biogeographic stochastic mapping to estimate the number of dispersal events between each geographic area (Dupin et al. 2017).

Preliminary results suggested that dispersal events between southern landmasses were relatively rare, while transitions between northern landmasses occurred more frequently (see Results). Because our hypothesis specifically concerns the influence of temperature niche on the establishment of amphitropical disjunctions, we reran DEC modelling analyses with Northern Hemisphere areas combined. This effectively removed dispersal events between northern landmasses, and their effect on any correlation between thermal niche and dispersal rate.

RESULTS

Well Resolved Nuclear and Plastid Phylogenies Reconstruct Congruent History of Melicodae

Phylogenetic analyses returned well-supported species trees with relationships generally congruent between plastid and nuclear datasets (Fig. 1; Supplementary Material Figs. S1–S2). In the chloroplast trees, the Melicodae is reconstructed as sister to a clade including the Stipeae and core Pooideae, consistent with other recent reconstructions of the Pooideae (e.g., Orton et al. 2021; Gallaher et al. 2022; Grass Phylogeny Working Group III 2025). With the exception of *Glyceria*, all genera within the Melicodae are strongly supported as monophyletic in both datasets (>99% bootstrap or local posterior probability support).

Glyceria is paraphyletic due to the inclusion of *Pleuropogon*, which forms a strongly supported clade sister to *Glyceria* sect. *Glyceria* R. Br. (Fig. 1). *Glyceria latispicea* (F.Muell.) F. Muell. ex Benth. is placed outside the Meliceae, consistent with the suggestions of previous authors (Weiller and Walsh 2009). The *Glyceria*-*Pleuropogon* group is separated into four strongly supported clades in both analyses, three corresponding to the traditional sections of *Glyceria* (*Glyceria* sect. *Glyceria* R. Br., *Glyceria* sect. *Hydropoa* Dumort., and *Glyceria* sect. *Striatae* G.L. Church; Church 1949; Fig. 1) and the fourth including all *Pleuropogon* species.

Melica is separated into eight well supported clades, and within each clade species generally share similar geographic ranges (Fig. 1; Fig. 2). Relationships between *Melica* clades are largely congruent between chloroplast and nuclear datasets, with the exception of the three American clades (i.e., sect. *Melicula,* sect. *Bromelica*, and the *M. mutica* clade). Nuclear data support a sister relationship between sect. *Melicula* and the *M. mutica* clade, where chloroplast data instead reconstruct sects. *Melicula* and *Bromelica* as sisters (Fig. 1; Supplementary Material Supplementary Fig. S1). Outside of these differences, the two datasets largely agreed (Supplementary Material Supplementary Fig. S2). The maximum clade credibility tree obtained during divergence time analyses in BEAST had an identical topology to maximum likelihood chloroplast trees. Age estimates for major divergences within the group of interest are broadly consistent with previous publications (e.g., Schubert et al. 2019a; Gallaher et al. 2022). The crown Melicodae are dated to 41.1 Ma (95% highest posterior density: 28.2–54.9) with Meliceae dated to 32.5 Ma (21.7–43.7), *Glyceria* dated to 23.5 Ma (15.2–32.0) and *Melica* dated to 14.1 Ma (9.2–19.2).

Melicodae Show Diverse Temperature Niches & A Palearctic Origin

Extant Melicodae show a large degree of thermal niche diversity. Within species' native distributions, average MAT ranges from ∓12.4 to 20.8 °C (mean 10.4 °C), WQT ranges from 3.5 to 27.4 °C (mean 18.7 °C), and CQT ranges from ∓28.9 to 17.5 °C (mean 2.1 °C). The ancestral temperature niche of the melicgrasses was reconstructed to be moderate/cool (MAT = 9 °C, $\sigma = 3$; WQT = 18 °C, $\sigma = 2$; CQT = 0 °C, $\sigma = 5$), with cooler niches independently acquired in *Schizachne* and *Glyceria*, and within *Melica* in sects. *Agonomelica*, *Bromelica*, and *Melica* (Supplementary Material Supplementary Fig. S3; Supplementary Table S4).

The best fitting dispersal-extinction-cladogenesis (DEC) model (see below) reconstructed a Palearctic origin for the supertribe Melicodae (albeit with high uncertainty), tribe Meliceae, and both *Melica* and *Glyceria* (Fig. 2). Biogeographic stochastic mapping using this model infers that a majority of dispersal events in the group occurred between the Palearctic and North America (the number of inferred dispersal events is higher when the null range is excluded; Fig. 3). With the exception of the island of Tristan da Cunha, all Southern Hemisphere areas are inferred to have been occupied by separate dispersal events from North America (South America) or the Palearctic (Africa and Australia). Populations on Tristan da Cunha were inferred to have originated in South America, although longer distance dispersal from the Palearctic is also a possibility (Fig. 2; Fig. 3).

Distance and Thermal Niche Both Influence Dispersal Between Hemispheres

The geodesic distance between species ranges and the closest occupied portion of the opposite hemisphere was negatively correlated with all three aspects of thermal niche (Fig. 4a): MAT—[$E(\beta|x) = \mp0.17$; SE = 0.04; $R^2 = 0.15$], WQT—[$E(\beta|x) = \mp0.07$; SE = 0.03; $R^2 = 0.06$], CQT—[$E(\beta|x) = \mp0.26$; SE = 0.07; $R^2 = 0.16$], as expected given the correlation that both have with latitude (Supplementary Material Supplementary Fig. S4).

For BioGeoBEARS analyses including all six geographic areas, models incorporating minimum distance between areas and excluding the null range had the best overall fit ($\text{DEC}{*}{+}\text{x}{+}\text{t}_{12}$; Table 1). These inferred a negative effect of distance on dispersal rate ($x = \mp2.36$), which was also recovered by models incorporating mean distances and/or including the null range. Modelling a correlation between dispersal probability and thermal niche did not noticeably improve fit ($\text{DEC}{*}{+}\text{x}{+}\text{t}_{12} + \text{m}$; Table 1). In contrast, the best fitting model from BioGeoBEARS analyses combining Northern Hemisphere regions included minimum distance between areas, a correlation between dispersal and thermal niche, and excluded the null range ($\text{DEC}{*}{+}\text{x}{+}\text{t}_{12} + \text{m}$; Table 1). Models inferred a negative effect of distance ($x = \mp2.32$) and cold niche ($m = 0$) on dispersal rates, the latter effectively disallowing dispersal in lineages with cold thermal niches (i.e., $\text{CQT} < 0$ °C). Similar penalties were recovered by models incorpo-

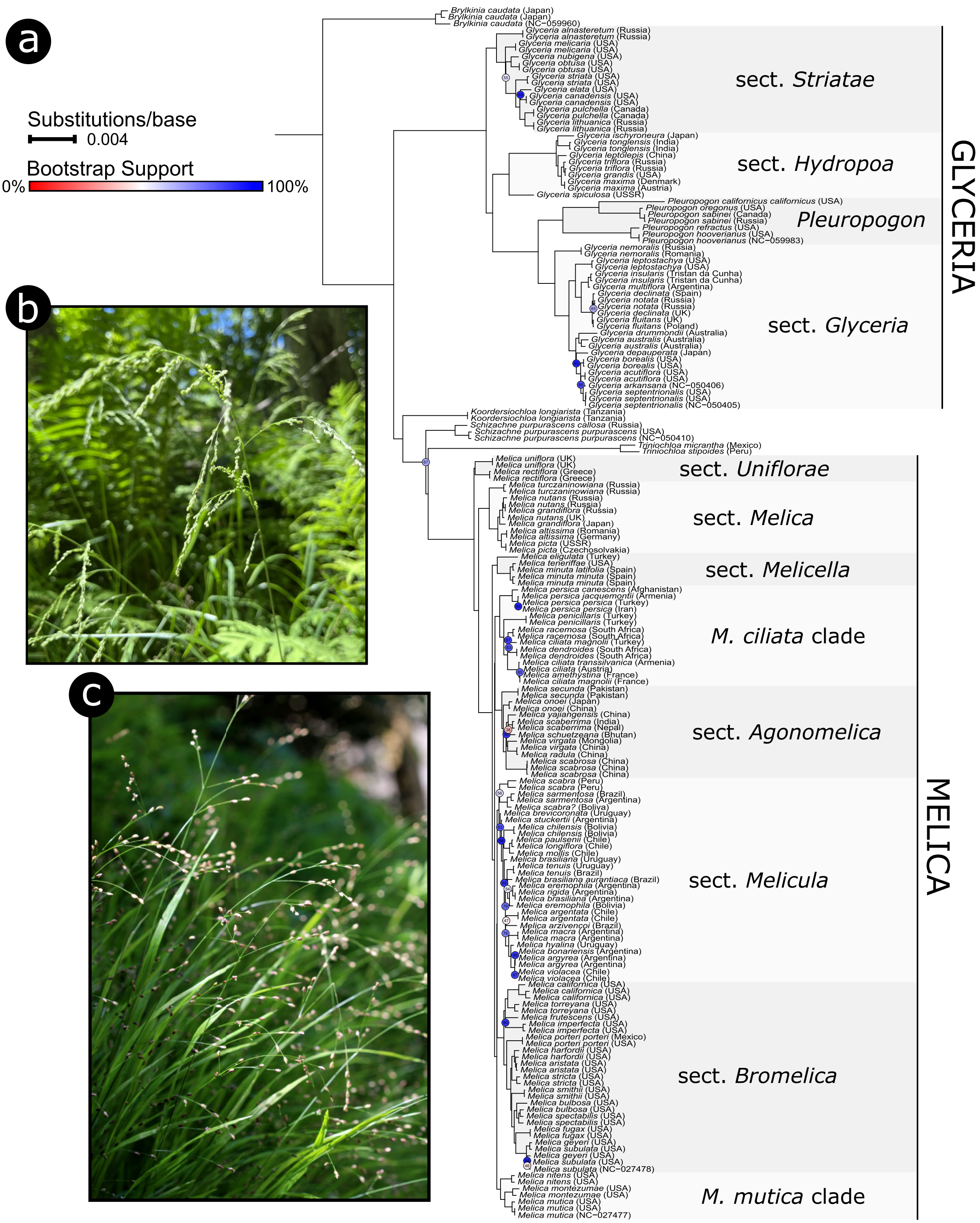

FIGURE 1. Maximum likelihood bootstrap consensus tree of Melicodae constructed from chloroplast sequence data, with major clades identified. Newly sequenced individuals are provided with their country of origin (in some cases reflecting the historic nature of sampled specimens), and GenBank accession numbers are provided for previously published sequences. Within *Glyceria*, group labels indicate traditional section boundaries (and *Pleuropogon*). Within *Melica*, labels indicate section boundaries recently proposed by Winterfield et al. (2025), and informal group names where this new taxonomic treatment is incongruous with our results. Bootstrap support values for internal nodes are provided for all nodes with less than 95% support. Inset images show examples of *Glyceria grandis* (b) and *Melica uniflora* (c) growing in the wild.

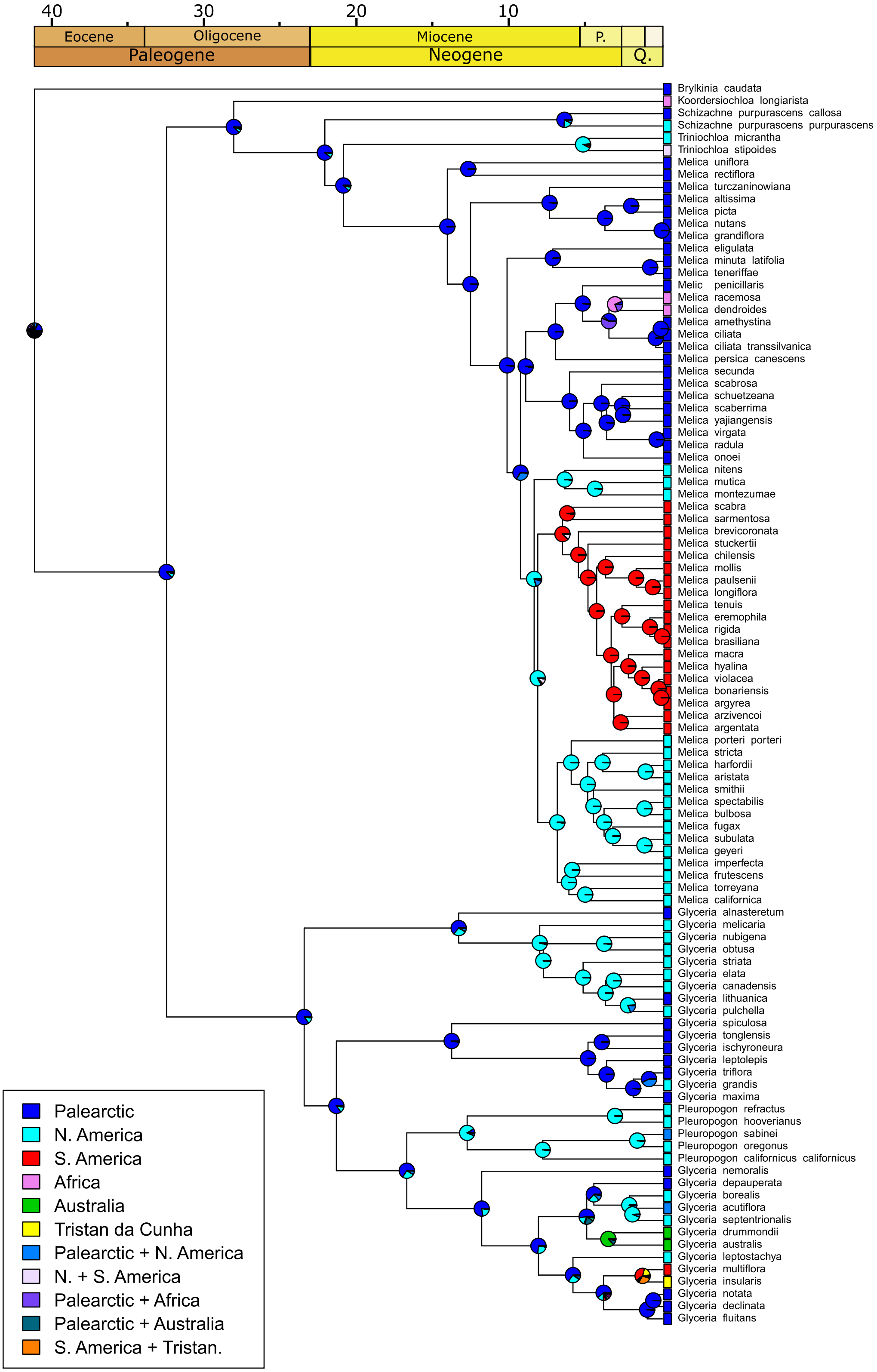

FIGURE 2. Ancestral range estimation for the Melicodae on time calibrated chloroplast tree, based on the best fitting six area model in BioGeoBEARS (DEC$*$+x+t_{12}; see Table 1). Internal nodes show the probability of reconstructed ranges, and tips show observed native ranges of sampled species.

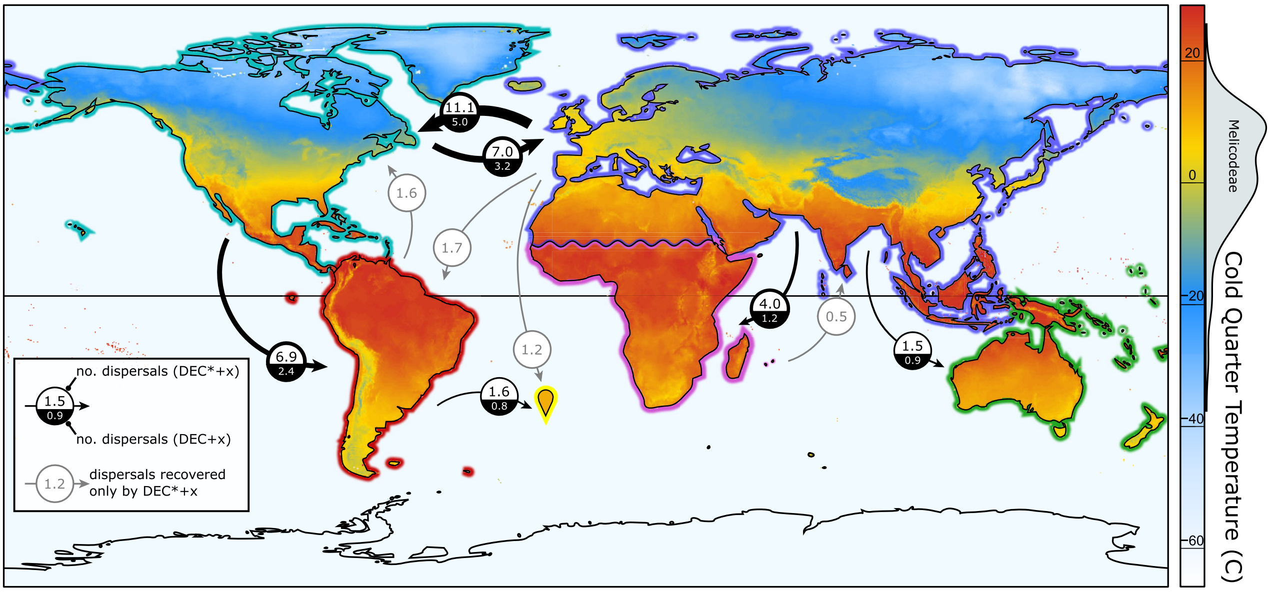

FIGURE 3. Summary of Biogeographic Stochastic Mapping results overlain on a map of Cold Quarter Temperature (WGS84; Fick and Hijmans 2017), showing the average number of dispersal events between areas per simulation, obtained from dispersal-extinction-cladogenesis (DEC) models. Results from simulations including (DEC + x) and excluding (DEC∗+x) the null range are both given. Dispersal events between areas that were present in $<$ 50% of simulations are not shown. Note that all Southern to Northern dispersal events inferred by DEC∗ models did not persist (i.e., were subsequently extirpated), and no extant Northern Hemisphere Meliceae show evidence of a Southern Hemisphere origin in these models (Fig. 2). The enlarged pin in the South Atlantic indicates the location (and CQT) of Tristan da Cunha. The distribution of average CQT observed among sampled species is overlain on the scale to right.

rating mean distances and/or including the null range (Table 1). Unlike six area analyses, several models received moderate support. However, these largely varied in treatment of distance and a majority of support was given to models imposing a strong penalty of cold niche on dispersal probability (Table 1). Additional analyses combining Northern Hemisphere regions, but using a different threshold for defining warm and cold thermal niches (i.e., CQT $< 3.2^\circ$ C) returned results congruent with those presented here (Supplementary Material Supplementary Table S5).

Modelling Supports Disjunct Taxa Evolve from Warm Winter Northern Ancestors

Threshold models revealed evolutionary correlations between biogeography and some, but not all, aspects of thermal niche. WQT was not correlated with movement between Northern and Southern Hemispheres ($r = \mp 0.06$, 95% HPD $= \mp 0.59$, 0.50), and neither was MAT ($r = 0.44$, 95% HPD $= \mp 0.22$, 0.81). In contrast, CQT showed a strong correlation ($r = 0.66$, 95% HPD $= 0.14$, 0.90), with Southern Hemisphere taxa having thermal niches characterized by warmer winters than their northern relatives.

Evolutionary models support ancestrally warm and slowly evolving thermal niches in southern lineages.— Evolutionary model fitting results showed support for Ornstein-Uhlenbeck (OU) models over Brownian Motion (BM) models for all three temperature variables (Table 2). However, which OU model provided the best fit, and model-weighted evolutionary parameter values varied substantially between temperature variables (Table 2; Table 3). For MAT, model-weighted parameter estimates broadly showed similar selection strength (α) for Northern and Southern Hemisphere lineages, but inferred substantially higher rates of thermal niche evolution and a colder (c. 6° C difference; Table 3) optimum MAT for northern lineages. Similar patterns were returned when the origins of Southern Hemisphere lineages were pushed back to older nodes (i.e., SH + 1, SH + 2; Supplementary Material Supplementary Fig. S5), although differences between Northern and Southern Hemisphere lineages decreased marginally (Table 3). In contrast, WQT model-weighted parameter estimates showed similar selection strength, rates, and optimum trait values for both Northern and Southern Hemisphere lineages, with patterns unchanged by expansion of southern lineages (Table 3). Model-weighted parameter estimates for CQT showed similar selection strength between Northern and Southern Hemisphere lineages, but inferred higher evolutionary rates and a colder (c. 10° C difference; Table 3) optimum for northern lineages. When the origins of Southern Hemisphere lineages were pushed back to older nodes, differences in evolutionary rates between northern and southern lineages became much less pronounced, while differences between optima remained relatively stable (Table 3; Fig.

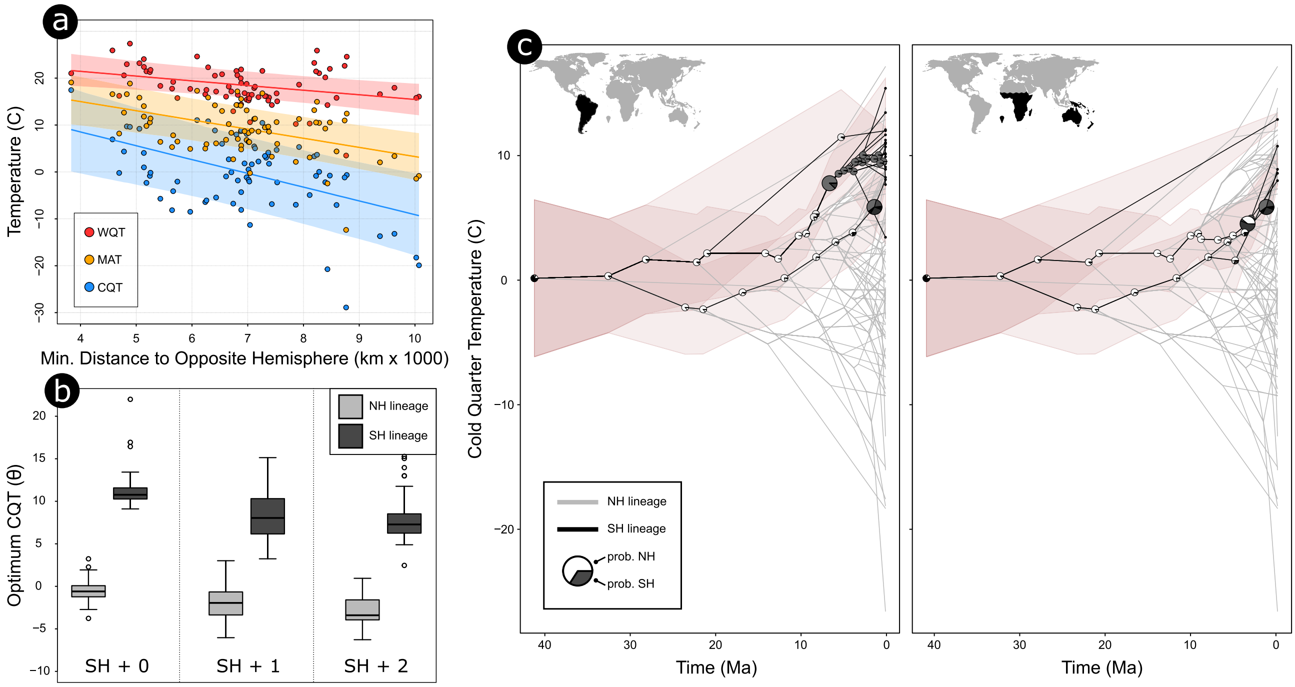

FIGURE 4. Results of analyses comparing thermal niche and biogeography in the Melicodae. (a) Relationship between species' thermal niche and the geodesic distance between the centroid of its geographic range and the closest species in the opposite hemisphere. Thermal niche is defined by warm quarter (WQT), mean annual (MAT), and cold quarter temperature (CQT). (b) Inferred evolutionary optimum cold quarter temperature (CQT) values for Northern (NH) and Southern (SH) Hemisphere lineages from model fitting analyses. To evaluate whether evolutionary differences in thermal niche between hemispheres predate the establishment of disjunct distributions, three sets of analyses were completed, using present distribution of taxa between hemispheres (SH + 0), or with Southern Hemisphere lineages expanded by a single node (SH + 1), or by two nodes (SH + 2), to include their Northern Hemisphere sister lineages. (c) Phenograms showing reconstructed evolution of CQT in Southern Hemisphere lineages, with standard deviation of CQT estimates shaded in red. Pie charts show probability of ranges including (dark grey) or excluding (white) Southern Hemisphere areas (from DEC modelling results—see Fig. 2). For each Southern Hemisphere lineage, the earliest internal node at which a southern range is reconstructed as the most likely state is enlarged. Note in some cases dispersal to the Southern Hemisphere is reconstructed along terminal branches so the number of enlarged pie charts is less than the total number of independent Southern Hemisphere lineages.

4b). Taken together, these results suggest that disjunct taxa evolved from warm winter Northern Hemisphere ancestors and rates of thermal niche evolution were generally depressed in the Southern Hemisphere. Thus, post-establishment niche shifts do not appear to explain the warmer niches of Southern Hemisphere lineages.

DISCUSSION

Amphitropical Distributions are Established by Long-Distance Dispersal from the Northern Hemisphere

Our phylogenetic reconstruction is the most comprehensive yet for the study group, and relationships are resolved with strong agreement between nuclear and chloroplast markers. Elaboration on the taxonomic ramifications of our results is largely confined to the Supplementary Material (Discussion S1), but two points warrant brief mention here. First, consistent with recent work (e.g., Brightly et al. 2024; Tkach et al. 2026) our results suggest that *Glyceria* is not monophyletic as traditionally circumscribed. *Pleuropogon* is placed within *Glyceria* in both nuclear and chloroplast trees (Fig. 1; Supplementary Material Supplementary Fig. S1; see also Tkach et al. 2026), and *Glyceria latispicea* is reconstructed outside the Melicodae entirely (Weiller and Walsh 2009; Gillespie et al. 2022; Supplementary Material Discussion S1; Supplementary Fig. S6). Second, we find that major divisions within *Melica* are largely biogeographic (Fig. 1; Fig. 2; Khodaverdi et al. 2023), rather than along the morphological lines used in most previous classifications (e.g., Papp 1928; Boyle 1945; Mejía-Saulés and Bisby 2003; Hempel 2011; Supplementary Material Discussion S1; Supplementary Fig. S7). The composition of these clades generally conforms to the newly proposed sections of Winterfield et al. (2025), although relationships between sections differ more markedly (Supplementary material Discussion S1).

We infer a Palearctic origin and initial diversification for the Melicodae, with independent northern origins for all Southern Hemisphere lineages, except the Tristan da Cunha endemic *Glyceria insularis* C.E. Hubb. (Fig. 2, Fig. 3). Range evolution and diversification within the Melicodae appears to have largely occurred from the late middle Miocene onward, with the establishment

Table 1. Dispersal-extinction-cladogenesis (DEC) model results.

	model	distance	d	e	x	t_{12}	m	lnL	np	AIC	weight
SIX AREA ANALYSES					**Null Included**						
	DEC + x + t_{12}	min.	0.23	$1.0{*}10^{-12}$	−2.49	0.07	–	−161.06	4	330.11	0.64
	DEC + x + t_{12} + m	min.	0.05	$1.0{*}10^{-12}$	−2.55	0.07	9.07	−160.72	5	331.44	0.33
	DEC + x + t_{12}	mean	0.30	$1.0{*}10^{-12}$	−1.84	0.07	–	−165.08	4	338.16	0.01
	DEC + x + t_{12} + m	mean	0.26	$1.0{*}10^{-12}$	−2.36	0.07	7.16	−164.24	5	338.47	0.01
	DEC + t_{12}	–	$3.9{*}10^{-3}$	$1.0{*}10^{-12}$	–	0.07	–	−167.29	3	340.57	0.00
	DEC + t_{12} + m	–	$4.0{*}10^{-3}$	$1.0{*}10^{-12}$	–	0.07	0.91	−167.28	4	342.57	0.00
					Null Excluded						
	DEC∗+x+t_{12}	min.	0.53	0.89	−2.36	0.07	–	−145.87	4	299.74	0.71
	DEC∗+x+t_{12} + m	min.	0.52	0.88	−2.32	0.07	0.92	−145.86	5	301.72	0.26
	DEC∗+x+t_{12}	mean	2.86	0.99	−2.34	0.07	–	−149.75	4	307.50	0.01
	DEC∗+x+t_{12} + m	mean	3.34	0.95	−2.47	0.07	1.35	−149.68	5	309.35	0.01
	DEC∗+t_{12}	–	0.01	0.83	–	0.07	–	−153.59	3	313.18	0.00
	DEC∗+t_{12} + m	–	0.01	0.82	–	0.07	0.85	−153.56	4	315.11	0.00
FIVE AREA ANALYSES					**Null Included**						
	DEC + x + t_{12} + m	min.	0.21	$1.0{*}10^{-12}$	−2.47	0.06	0.00	−106.43	5	222.85	0.40
	DEC + t_{12} + m	–	$4.1{*}10^{-3}$	$1.0{*}10^{-12}$	–	0.06	0.00	−107.79	4	223.58	0.28
	DEC + x + t_{12} + m	mean	0.03	$1.0{*}10^{-12}$	−0.83	0.06	0.00	−107.71	5	225.42	0.11
	DEC + x + t_{12}	min.	0.08	$1.0{*}10^{-12}$	−2.22	0.07	–	−108.74	4	225.48	0.11
	DEC + t_{12}	–	$2.3{*}10^{-3}$	$1.1{*}10^{-12}$	–	0.07	–	−110.15	3	226.31	0.07
	DEC + x + t_{12}	mean	0.04	$1.0{*}10^{-12}$	−1.13	0.07	–	−109.84	4	227.68	0.04
					Null Excluded						
	DEC∗+x+t_{12} + m	min.	0.39	0.83	−2.32	0.06	0.00	−98.10	5	206.20	0.43
	DEC∗+t_{12} + m	–	0.01	0.77	–	0.06	0.00	−99.40	4	206.81	0.32
	DEC∗+x+t_{12} + m	mean	0.07	0.84	−0.86	0.06	0.00	−99.31	5	208.61	0.13
	DEC∗+x+t_{12}	min.	0.20	0.62	−2.31	0.07	–	−101.06	4	210.12	0.06
	DEC∗+t_{12}	–	$4.8{*}10^{-3}$	0.57	–	0.07	–	−102.42	3	210.85	0.04
	DEC∗+x+t_{12}	mean	0.21	0.67	−1.54	0.07	–	−101.94	4	211.89	0.02

Notes: Results area shown for analyses with all six biogeographic areas included (with or without the null range included in the potential range space), and for analyses with northern landmasses combined to highlight north to south dispersal events (five area analyses). For each model the following is indicated: model type (model; see Methods), whether the minimum or mean distance between areas was used (distance), estimates of model parameters for dispersal (d), extinction (e), distance scalar (x; values < 0 indicate a distance penalty on dispersal), rate of thermal niche change (t12), and correlation coefficient between thermal niche and dispersal (m; values < 1 indicate a dispersal penalty of cold-adaptation). Model support is indicated by computed log-Likelihood values (lnL), number of free model parameters (np), AIC scores (AIC) and resulting model weights (weight).

of Southern Hemisphere lineages within the last c. 9 Ma (with the possible exception of *Koordersiochloa*; Fig. 2). Therefore, dispersal to the Southern Hemisphere approximately coincides with, or postdates, the establishment of more or less modern global climates and temperature gradients following the Miocene Climate Transition and subsequent late Miocene cooling (Herbert et al. 2016; Frigola et al. 2018; Steinthorsdottir et al. 2021).

In the Americas, establishment in the Southern Hemisphere coincides with or postdates the closure of the Central American Seaway, the initial establishment of a land connection between North and South America (c. 10 Ma; Bacon et al. 2015; Montes et al. 2015; Jaramillo 2018), and uplift that brought the northern Andes to approximately modern heights by the end of the Miocene (Boschman 2021). Thus, a temperate corridor linking North and South America likely existed around the time the latter was first occupied by the supertribe, although its size and permeability would have changed with climate fluctuations through time (Bacon et al. 2016). Extant South American *Melica* occur as far north as the Colombian Andes (Renvoize 1998; POWO 2025), and the most northerly species, *M. scabra* and *M. sarmentosa,* form a clade sister to the remaining South American taxa in chloroplast trees (Fig. 1). Thus, we cannot rule out a stepping-stone migration of *Melica* into temperate South America along high elevation habitats. The range of *Triniochloa* may reflect a similar migration (Mejía-Sualés and Gómez-Sánchez 2001; POWO 2025), but improved species sampling is necessary to resolve its biogeographic history.

Consistent with previous work (Thorne 1972; Wen and Ickert-Bond 2009; Drew et al. 2017; Schenk and Saunders 2017; Simpson et al. 2017), long distance dispersal appears to explain the origins of remaining Southern Hemisphere populations (Fig. 2, Fig. 3). The Melicodae produce a diverse array of dispersal structures (Brightly et al. 2024), some of which are traditionally

TABLE 2. Model weights computed from corrected Akaike information criterion scores for evolutionary model fitting analyses.

hemisphere	BM1	BMS	OU1	OUM	OUMV	OUMA
Mean Annual Temperature (MAT)						
SH + 0	0	0	0	0	0.876	0.123
SH + 1	0	0	0	0.029	0.954	0.017
SH + 2	0	0	0	0.05	0.95	0
Warm Quarter Temperature (WQT)						
SH + 0	0	0	0.438	0.313	0.249	UNR
SH + 1	0	0	0.195	0.09	0.498	0.215
SH + 2	0	0	0.159	0.387	0.369	0.085
Cold Quarter Temperature (CQT)						
SH + 0	0	0	0	0	0.705	0.295
SH + 1	0	0	0	0.004	0.421	0.575
SH + 2	0	0	0	0.002	0.536	0.461

Notes: Results are shown for models explaining the evolution of mean annual temperature (MAT), warm quarter temperature (WQT), and cold quarter temperature (CQT). To evaluate whether evolutionary differences in thermal niche between hemispheres predate the establishment of disjunct distributions, three sets of analyses were completed, using present distribution of taxa between hemispheres (SH + 0), or with Southern Hemisphere lineages expanded by a single node (SH + 1), or by two nodes (SH + 2), to include their Northern Hemisphere sister lineages. Models are as follows: BM1–a single global Brownian Motion model, BMS—a Brownian Motion model with different rates (σ^2) for Northern and Southern Hemisphere lineages, OU1–an Ornstein-Uhlenbeck model with a single global optimum (θ) (OU1), OUM—an Ornstein-Uhlenbeck model with different optima (θ) for Northern and Southern Hemisphere lineages (OUM), OUMV—an Ornstein-Uhlenbeck model with different trait optima (θ) and rates (σ^2) for Northern and Southern Hemisphere lineages, and OUMA—an Ornstein-Uhlenbeck model with different trait optima (θ) and selection strengths (α) for Northern and Southern Hemisphere lineages. UNR—analysis failed to return a reliable estimate for one or more parameters.

TABLE 3. Results from evolutionary model fitting, showing model weighted parameter values of selection strength (α), evolutionary rate (σ^2), and optimum trait value (θ) for Northern (NH) and Southern Hemisphere (SH) lineages.

hemisphere	α	σ^2	θ
Mean Annual Temperature (MAT)			
NH	1.25 +/− 0.64	71.15 +/− 38.83	8.93 +/− 0.59
SH + 0	1.23 +/− 0.52	16.25 +/− 6.95	15.08 +/− 0.67
NH	0.95 +/− 0.43	71.15 +/− 32.47	8.25 +/− 0.95
SH + 1	0.98 +/− 0.29	31.60 +/− 12.81	12.50 +/− 0.55
NH	1.06 +/− 0.37	79.73 +/− 28.71	7.62 +/− 0.85
SH + 2	1.04 +/− 0.35	33.17 +/− 10.82	12.57 +/− 0.62
Warm Quarter Temperature (WQT)			
NH	2.59 +/− 1.10	72.47 +/− 40.81	18.46 +/− 0.36
SH + 0	2.66 +/− 1.13	78.85 +/− 31.36	18.89 +/− 0.77
NH	1.47 +/− 1.11	54.064 +/− 35.90	18.39 +/− 0.48
SH + 1	1.78 +/− 1.20	40.17 +/− 26.24	18.85 +/− 0.49
NH	2.33 +/− 1.49	64.95 +/− 38.99	18.00 +/− 0.75
SH + 2	1.95 +/− 1.25	67.53 +/− 48.14	19.20 +/− 0.56
Cold Quarter Temperature (CQT)			
NH	0.73 +/− 0.19	84.91 +/− 22.37	−0.60 +/− 0.97
SH + 0	0.67 +/− 0.22	18.03 +/− 8.87	10.77 +/− 0.82
NH	0.24 +/− 0.08	51.87 +/− 17.72	−1.95 +/− 1.99
SH + 1	0.27 +/− 0.10	33.05 +/− 18.63	8.04 +/− 2.80
NH	0.29 +/− 0.13	52.14 +/− 28.25	−3.40 +/− 1.38
SH + 2	0.29 +/− 0.14	26.12 +/− 10.83	7.28 +/− 1.63

Notes: To evaluate whether evolutionary differences in thermal niche between hemispheres predate the establishment of disjunct distributions, Northern and Southern Hemisphere lineages were defined based upon present distribution of taxa between hemispheres (SH + 0) or by expanding Southern Hemisphere lineages by a single node (SH + 1), or two nodes (SH + 2), to include their immediate Northern Hemisphere sister lineages. Results are provided for mean annual, warm quarter, and cold quarter temperature.

viewed as facilitating long distance dispersal. *Glyceria* is a wetland genus, and some species produce seeds that are readily consumed by waterfowl (Quattrochi 2006; Cope and Gray 2009). Wetland species are disproportionately represented among plants with amphitropical distributions, and waterfowl are commonly cited as their likely dispersers (Raven 1963; Schenk and Saunders 2017; Simpson et al. 2017). South American and South African *Melica* have traits promoting wind dispersal (Brightly et al. 2024). Although wind is less commonly viewed as an efficient long distance dispersal mechanism, it is employed by many wide-ranging taxa (Ridley 1930; Schenk and Saunders 2017) and single long distance dispersal events may not be necessary to explain the distribution of South American *Melica*. Other dispersal mechanisms are also attested in the supertribe (e.g., epizoochory in *Koordersiochloa*; Ridley 1930; van der Pijl 1982), but the dispersal potential of most species is poorly understood and requires further work (Brightly et al. 2024).

Dispersal Distance and Cold Origins per se Explain Bias Towards Warm Winter Niches in Southern Taxa

Although there is evidence of some thermal niche diversification following establishment in the Southern Hemisphere (Fig. 4c), results from evolutionary model fitting (Fig. 4b; Table 3), DEC analyses (Table 1), and ancestral state reconstructions (Fig. 4c) suggest that warm winter thermal niches are ancestral to all Southern Hemisphere lineages in the Melicodae. Thus, plants that established in the Southern Hemisphere were drawn from northern lineages already putatively adapted to warmer winters rather than cold-origin lineages (here roughly defined as those where average winter temperatures are below freezing).

Because cold-origin plants are generally found at higher latitudes, it is possible that this pattern is driven by the greater dispersal distances required for these plants to cross the tropics (Fig. 4a; Supplementary Material Supplementary Fig. S4; Lancaster and Humphreys 2020). Our results support this hypothesis by showing that dispersal probabilities scale strongly with the minimum distance between regions—halving distance increases dispersal probability by a factor of approximately six (Table 1). Furthermore, the smaller land area and more maritime climates of the temperate Southern Hemisphere mean that there is a limited area matching the climate niche of cold-origin plants dispersing from the north (Fig. 3; Beard 1990; Gaston and Chown 1999; Beck et al. 2023). Targets are thus smaller and more distant. Dispersal limitation is one of the primary factors shaping species ranges (e.g., Linder et al. 2013; Klaus and Matzke 2020; Garcia-R and Matzke 2021), and the evidence presented here suggests that the lack of cold-origin Southern Hemisphere Melicodae is at least partly caused by the greater difficulty high-latitude Northern Hemisphere species have reaching southern temperate regions.

In addition to constraints imposed by dispersal distance, our results also imply that there are direct impacts of thermal niche on which lineages successfully establish amphitropical distributions. This is suggested by the fact that biogeographic models incorporating species thermal niche consistently outperform other models at predicting the probability of north-south dispersal events (i.e., five area analyses; Table 1). These models all impose a strict penalty disallowing transtropical dispersal in lineages with colder niches (i.e., CQT < 0; Table 1; Supplementary Table S5). Both threshold and evolutionary model fitting results (Table 3) suggest that winter temperature is the most important axis of this thermal niche. Indeed, sites occupied by the warm-origin Melicodae from the Southern Hemisphere generally fall within the annual range of temperatures cold-origin lineages experience (Supplementary Material Supplementary Fig. S8). Thus, it appears that species are limited by mechanisms allowing them to cope with more frequent and/or extreme periods of cold (Rezende et al. 2014), rather than an inability to cope with high summer temperatures.

Although few members of the Melicodae have been studied in detail, there is a growing body of research into cold tolerance in grasses (e.g., Schubert et al. 2019b; Sandve et al. 2011; Schubert et al. 2020; Schat et al. 2025). Grasses cope with exposure to chilling and freezing in a range of ways, including the accumulation of soluble sugars, particularly fructans, which mitigate cold damage via several pathways (e.g., stabilizing membranes; Versluys et al. 2018; Schubert et al. 2020). Fructan levels have been surveyed in a handful of *Melica* spp., with known accumulators (e.g., *M. nutans*) generally showing colder realized niches than non-accumulators (e.g., *M. imperfecta*) (Landsem 2021; Supplementary Material Supplementary Fig. S3). Phenological adaptations tailored to the short growing seasons and long summer days of high latitudes are also evident in the Melicodae, with a number of species flowering more rapidly after vernalization (McKeown et al. 2016; Hjertaas 2020; Khodaverdi et al. 2023). Although data are limited, some taxa also apparently require extended periods of cold stratification to germinate (Darris 2005; St John and Tilley 2012). However, this is not a universal requirement and others need only short cold periods, or require no stratification at all (Lloyd-Reilley et al. 2002; Darris 2005; Mugwedi et al. 2015; Khodaverdi et al. 2023).

Although it is unclear from the available data exactly how these cold tolerance mechanisms might limit ability to establish in remote regions, several plausible hypotheses can be made. The environmental cues plants use to align growth and reproduction with ideal conditions are dramatically affected by winter temperatures. For example, although dormancy mechanisms preventing premature germination are common throughout regions with temperature seasonality, strategies can differ depending on the length and extremity of cold periods (Fernández-Pascual et al. 2021; Zhang et al. 2022). Alpine species disproportionately exhibit warm-cue germination (Fernández-Pascual et al. 2021), which helps avoid damaging spring frosts, but may also limit growth potential in milder regions. Vernalization requirements can also be stricter in colder regions (Boudry et al. 2002; Preston and Fjellheim 2022), and some high-latitude plants require long summer days to reach their full growth potential (Savage and Cavender-Bares 2013). Thus, differences in phenological cues may mean that plants adapted to regions with colder winters may fail to effectively accumulate biomass and flower as reliably under superficially amenable climates.

Herbivore pressure may also vary with latitude, and cold-origin lineages often possess weaker defenses than other plants (Pellissier et al. 2012; Pellissier et al. 2014; Willi and Buskirk 2022). Regions with mild winters can also harbor higher rates of disease, in part because the distribution of many pathogens is limited by the frequency and severity of frost (e.g., Marcais et al. 2004). Depending on moisture and host availability, warming in alpine and arctic communities has been shown to increase pathogen load and diversity (Liu et al. 2019; Yang et al. 2024; Hu et al. 2025; Lin et al. 2025), and in temperate regions with mesic climates, warmer winters are correlated with greater fungal pathogen loads (Vacher et al. 2008; Kumar et al. 2024). Although the extent to which cold-origin taxa are more poorly equipped than other taxa to cope with high pathogen loads is unclear, the potential that a greater exposure and/or susceptibility to herbivory and disease may limit the establishment of cold-origin lineages deserves further investigation.

Even if the above stressors are insufficient to directly prevent the establishment of cold-origin lineages in the temperate Southern Hemisphere, they may put them at a disadvantage relative to plants already established in the region (e.g., Loehle 1998; Kraft et al. 2015; Cadotte and Tucker 2017). Evidence suggests that cold habitats are difficult to invade and additional external factors like anthropogenic disturbance may be required to facilitate establishment of non-native taxa (Lembrechts et al. 2016; 2018). That high-latitude and alpine plants have a competitive disadvantage in warmer regions is also widely believed to influence the lower boundaries of their ranges (Loehle 1998; Pellissier et al. 2018; Leites et al. 2019; Willi and Buskirk 2022). In the case of cold-origin Melicodae, temperature conditions may directly impede their establishment through environmental filtering, indirectly through modifications to biotic interactions, or through a combination of both. Ultimately, disentangling these mechanisms requires additional data (Kraft et al. 2015; Cadotte and Tucker 2017).

Limitations, Broader Implications, and Future Work

Overall, the available evidence is consistent with the hypothesis that ancestral thermal niche is correlated with potential to establish in the Southern Hemisphere both through inherent limits associated with cold tolerance and indirectly through dispersal limitation. These mechanisms are not mutually exclusive. However, because dispersal distances and thermal niche covary through their shared link with latitude (Fig. 4a; Supplementary Material Supplementary Fig. S4) it is difficult to resolve their relative contributions. This is partly a limitation of the available methods. For example, dispersal limitation is most appropriately modelled for individual lineages, rather than areas, but the former cannot be easily integrated into our analytical framework. Similarly, currently available DEC methods require thermal niche traits to be discretized, collapsing the variation observed in the group and introducing potentially arbitrary distinctions between which species occupy warm and cold thermal niches. Furthermore, temperature is not the only aspect of environmental niche that shapes the distribution of the sampled taxa, and other niche axes not considered in this study may influence potential for dispersal across the tropics. The Melicodae are found in an extremely wide range of habitats (e.g., Hempel 2011), and although our results suggest thermal niche is broadly important, other lineage specific aspects of habitat may also play an important role. Finally, we are limited by what can be inferred from patterns in extant taxa, due to a lack of fossil evidence. Our reconstructions may therefore represent an incomplete or biased view of niche and/or biogeographic evolution in the group (e.g., Finarelli and Flynn 2006; Wood et al. 2013; Herrera et al. 2024). Resolving these issues may be achieved through new methodological approaches, and/or through further testing of predictions made by each hypothesized mechanism.

Melicgrasses are not the only taxa which show these distributions, and the mechanisms proposed to explain the temperature biases in their formation are universal. Dispersal limitation is one of the primary factors shaping species ranges, and its effects have been demonstrated in a diverse set of taxa with highly variable dispersal abilities (e.g., marine invertebrates–Lester et al. 2007; mammals–Munguía et al. 2008; grasses–Linder et al. 2013; podocarps–Klaus and Matzke 2020; rails–Garcia-R and Matzke 2021; woody angiosperms–Huang et al. 2024). Thus, a similar bias against cold-origin lineages should be expected within most clades forming amphitropical distributions. Furthermore, the implication of our results that cold-origin taxa are inherently worse at colonizing new regions, no matter how remote, has broad significance. Although more work is clearly needed to elucidate the underlying mechanisms, none of those discussed are unique to grasses. Indeed, insects, ectothermic vertebrates, and a wide range of plants all show similar patterns of diverging cold-tolerance strategies between hemispheres, and in at least some cases these have been linked to physiological tradeoffs between the ability to cope with chronic and acute temperature stresses (e.g., Sinclair and Chown 2005; Bannister

2007; Sunday et al. 2011; Rezende et al. 2014; Lehmann et al. 2015).

Both of these processes have important implications for global diversity patterns. If cold-origin lineages occupy a smaller proportion of their potential range and/or struggle to establish in regions with similar climates, they may be more susceptible to extinction (Saupe et al. 2015; Staude et al. 2020). Over time this may contribute to the lower diversity of cold-origin floras and thus latitudinal diversity gradients more generally (Moreau and Bell 2013; Rangel et al. 2018; Hagen et al. 2019; Dagallier et al. 2020; Lorcery et al. 2025). Today, high-latitude and alpine communities are among the hardest hit by anthropogenic climate change. Both are experiencing faster rates of warming than adjacent regions, resulting in shrinking habitat area and communities being pushed to higher latitudes and/or elevations (Kaplan and New 2006; Araújo et al. 2011; Pearson et al. 2013; Wang et al. 2016; Rantanen et al. 2022). This reduces the total amount of suitable habitat and increases the distance between patches (Araújo et al. 2011; Rehnus et al. 2018; Guan et al. 2021). Our results reinforce that cold-origin lineages may be less likely to successfully establish in new regions, particularly when they are separated by areas of warmer climates. More work is necessary to understand the mechanistic underpinnings of this pattern, but our results suggest that the ability of many cold-origin species to track their preferred habitat as climates warm may be worse than currently expected.

Conclusions

Using grasses from the diverse supertribe Melicodae, we evaluated the role that thermal niche and dispersal limitation have in constraining migration across the tropics. Biogeographic and evolutionary modelling show that species putatively adapted to cold winters are much less likely to successfully cross the tropics. Lineages that successfully established in the Southern Hemisphere share warmer niches, which evolved prior to their establishment outside of their ancestral northern temperate habitats. Evidence suggests that this is a result of both the greater distances that cold-origin lineages must disperse to cross the tropics, and inherent limitations associated with colder thermal niches. Cold-origin lineages face many challenges in a rapidly warming world, and these results provide important insight into the mechanisms by which they establish new populations in remote regions. If cold-origin species disproportionately struggle to establish areas with suitable climates, their ability to move in response to warming climates may be worse than expected.

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Supplementary data

Supplementary material is available at *SYSBIO* online.

Conflict of interest

None declared.

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Data availability

The raw sequence data, assembled chloroplast genomes, and *Melica nutans* reference and annotation are deposited on GenBank (Supplementary Material Supplementary Table S1; BioProject PRJNA1457356) and Zenodo, and all data and code necessary to replicate our results are available on Dryad and Zenodo respectively (https://doi.org/10.5061/dryad.dz08kps7q).

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