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Multiple Trans-Marine Dispersals and Niche Conservatism Underlie the Pantropical Distribution of Eugeniinae (Myrtaceae)

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ABSTRACT

Aim: The factors underlying large disjunct distributions among closely related species have long been debated by biogeographers. In general, lineages crossing several trans-marine barriers should be able to establish more easily where conditions are similar to their ancestral environments, while adaptation to diverse environmental conditions would be more frequent where dispersal is less limited by geographical barriers, such as within landmasses. Here, we test this assumption by contrasting biogeographical history and environmental niche evolution in the large tree clade Eugeniinae (Myrtaceae).

Location: Pantropical.

Taxon: Subtribe Eugeniinae, including the genera *Eugenia* and *Myrcianthes* (Myrtaceae).

Methods: We employed the largest available phylogeny of subtribe Eugeniinae to date in a comparative framework for biogeographical models to assess the likelihood of different dispersal routes. We then integrated soil and climatic data to estimate species' environmental niches and used trait evolution models to obtain rates of niche evolution across different regimes and within Eugeniinae clades. Finally, we compared the number of dispersals with rates of niche evolution within each clade.

Results: Eugeniinae originated in South America and achieved a pantropical distribution through a series of predominantly easterly trans-marine dispersals in the last 25 million years. In general, colonisations of new areas were decoupled from accelerated changes in environmental preferences. Old World Eugeniinae exhibited the highest rates of colonisation of new landmasses and more conserved environmental niches than many exclusively New World clades of the subtribe. High rates of niche evolution in Neotropical Eugeniinae seem to be associated with diversification along elevational gradients and into soils of diverse properties. Finally, the persistence of Eugeniinae within the tropical zone during its geographic expansion may reflect slow evolution of temperature tolerance across all clades.

Main Conclusion: Our findings show that a complex interaction between geographical movement and niche evolution explains the modern distribution of Eugeniinae. Different factors are likely responsible for each trans-marine long-distance dispersal event, and further comparative studies across diverse pantropical clades will be useful for determining whether general patterns exist that explain why certain lineages are particularly successful at dispersing across long distances globally.

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1 | Introduction

Lineages move in space over time, and even populations of sessile organisms, such as plants, can disperse large distances over many generations (Nathan et al. 2009). While pollen dispersal is responsible for inter-populational genetic structuration, hybridisation and introgression, dispersal of seeds and vegetative propagules are important for the colonisation of new areas (Nathan 2006; Cervantes et al. 2025). These propagules are often able to overcome strong geographic barriers for terrestrial organisms, such as salt water, leading descendant populations to establish themselves disjointly from the ancestral ones through trans-marine dispersal events (e.g., Renner 2004).

Trans-marine dispersals can involve short distances, such as between continental islands and the associated mainland (hereinafter short-range trans-marine jumps), and extreme cases of trans-continental shifts, with crossing of large oceanic barriers (hereinafter long-distance dispersal and establishment; LDDE). In both cases, trans-marine dispersals may occur via stepping-stones (i.e., sequentially through a series of habitable islands) or as a single and direct event, often following oceanic currents or via 'sweepstakes' routes (i.e., rare events by chance and not following any pattern, usually due to exceptional conditions; Simpson 1940). Dispersal vectors can be several, but in most cases, they are animals, wind or ephemeral floating islands formed by vegetation, debris and soil (Katinas et al. 2013). With improvement in molecular phylogenetic techniques and the consequent escalation in the inference of dated phylogenies, trans-marine dispersals have been recognised as more relevant in plant evolution than previously thought (Sanmartín and Ronquist 2004; Pennington et al. 2006). For example, broad modern distributions of several plant clades have been attributed to LDDE, from amphi-Atlantic disjunctions (Givnish et al. 2004; Dick et al. 2007; Lopes et al. 2024) to global spans (Wu et al. 2018). A higher number of trans-marine dispersals in plants compared to other groups of terrestrial organisms may be related to the presence of resistant seeds and the ability of many plant lineages to propagate vegetatively and self-pollinate, leading to higher chances of establishment in isolated areas (Pennington et al. 2006; Pannell et al. 2015).

Notwithstanding the growing recognition of the contribution of trans-marine dispersals to global plant distribution patterns and biogeography, little is known about the interplay between these events and changes in rates of environmental niche evolution. Usually, lineages are found in environments similar to those of their ancestors and close relatives, even when separated by long geographical distances (Crisp et al. 2009). On the other hand, occupation of a wealth of distinct environments by closely related species or clades is less common (Wiens and Graham 2005). This tendency has been referred to as phylogenetic niche conservatism (Donoghue 2008) and appears to be especially pronounced in wide-ranging tropical clades, whose species are split across continents yet restricted to warmer conditions of lower latitudes around the globe (e.g., Baker and Couvreur 2013).

It is intuitive to think that only a few lineages would be capable of both founding viable populations in diverse new landmasses while simultaneously adapting to distinct environmental conditions. Thus, clades transposing several trans-marine barriers should be able to establish more easily where they are already adapted for survival, while environmental shifts would be more frequent where dispersal across geographic barriers is less of a limiting factor (e.g., within a landmass) (Crisp et al. 2009; Donoghue and Edwards 2014). In other words, slower rates of environmental niche evolution should be observed in lineages capable of moving long distances compared to those evolving within a single, large landmass. A deeper understanding of biogeographical disjunctions and environmental niche evolution in plants depends on exploring these patterns in diverse and globally spread plant lineages.

Here, we aim to answer the question: is environmental niche evolution more constrained in lineages with frequent trans-marine dispersal events when compared to clades that diversified mainly within large continental landmasses? To test this idea, we describe the biogeographical history and assess environmental niche evolution in Eugeniinae, a large clade of South American origin (Mazine et al. 2018) within the family Myrtaceae. Eugeniinae is an ideal system to address these questions: its pantropical distribution, including isolated islands in the Indian and Pacific oceans, combined with its relatively recent origin suggest that trans-marine dispersal events have been common throughout its evolutionary history. At the same time, much of the diversification within this group took place within South America, allowing the comparison of niche evolution between lineages that diversified within the continent and those that repeatedly dispersed across oceans. Thus, in the present work we describe the route and mode of dispersal of Eugeniinae out of South America by employing the most comprehensive phylogenetic hypothesis of the clade to date in ancestral biogeographic range reconstructions, accounting for differential dispersal probabilities between bioregions. Then, we use climatic and edaphic data associated with geographic occurrences to characterise species' realised environmental niches and compare niche evolutionary dynamics across clades.

2 | Material and Methods

2.1 | Study System

Myrtaceae is a flowering plant family dated to c. 85 Ma, with modern pantropical and subtropical distribution (Thornhill et al. 2015; Lucas 2020). The majority of Myrtaceae tribe Myrteae (c. 2800 species; WFO 2025) belongs to the New World Myrteae lineage (c. 2500 species; Lucas et al. 2019), a clade dating back to c. 40 Ma that probably originated by vicariance with the dissolution of the land bridge once connecting the Antarctic Peninsula to South America, now submerged beneath the Drake Passage (Thornhill et al. 2015; Vasconcelos et al. 2017). The New World clade of Myrteae is distributed in the Americas from southern Mexico to Argentina, Chile and Uruguay, with some species also occurring in other continents (Lucas et al. 2019).

Myrteae subtribe Eugeniinae (Figure 1) is composed of the woody genera *Myrcianthes* (39 species; POWO 2025) and *Eugenia* (1239 species; POWO 2025), with the latter being the second largest tree genus in the world (Beech et al. 2017). Eugeniinae is known to have originated in the Atlantic Forest of South America,

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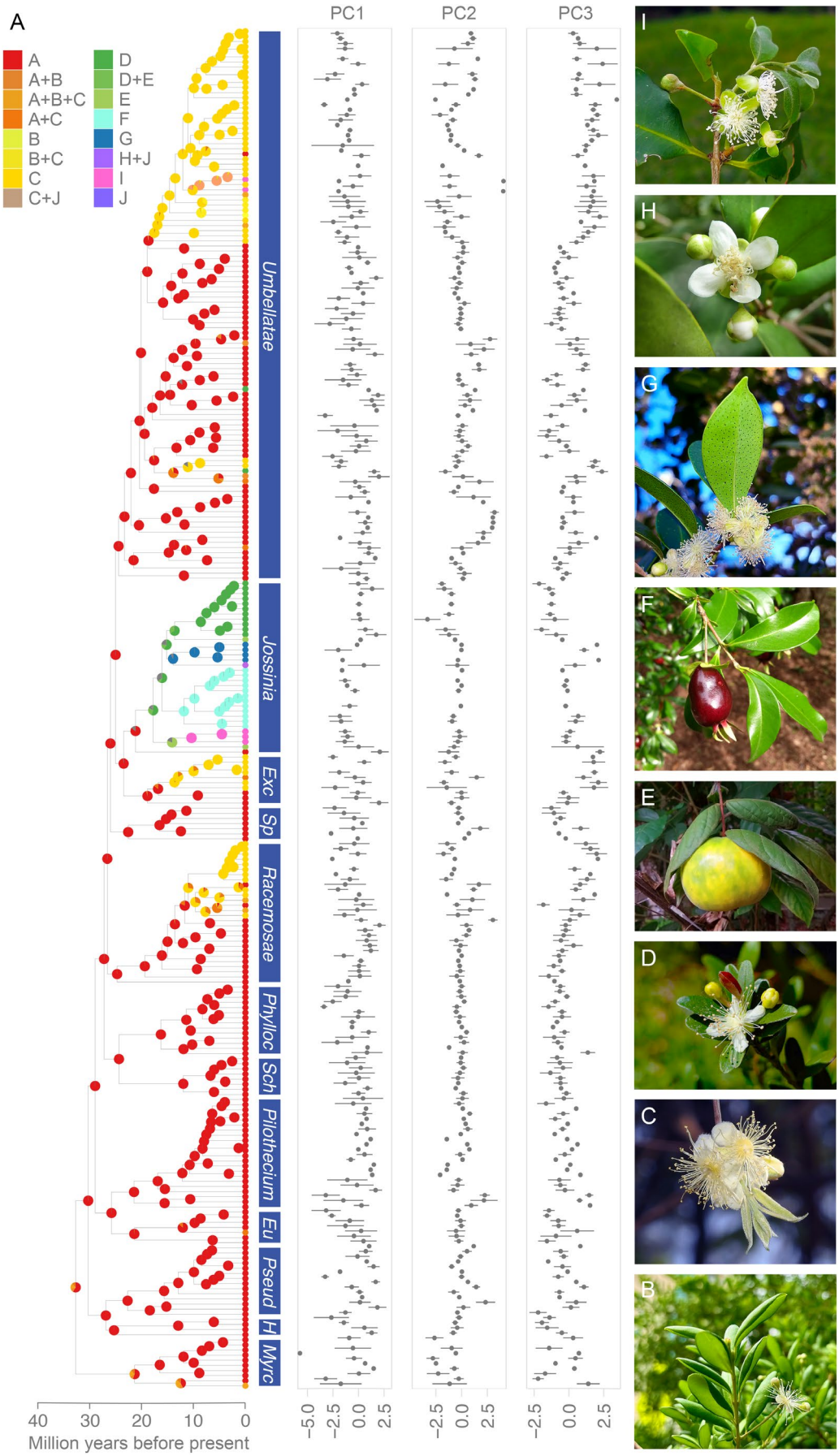


FIGURE 1 | Legend on next page.

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FIGURE 1 | Biogeographical reconstruction, abiotic characterisation of species and morphology of Eugeniinae (Myrtaceae). (A) Ancestral range estimation with the DEC+J-Eastbound model implemented in BioGeoBEARS. Pie charts on nodes depict ancestral state probabilities and circles on terminals indicate the current range of extant taxa. A—South America; B—continental Central America and Mexico; C—the Caribbean and southern Florida; D—continental Africa; E—Madagascar; F—Mascarene Islands; G—South Asia; H—South-East Asia, the Malay Archipelago and Australia; I—New Caledonia; and J—the Pacific islands. *Eu*, *Eugenia*; *Exc*, *Excelsae*; *H*, *Hexachlamys*; *Myrc*, *Myrcianthes*; *Phylloc*, *Phyllocalyx*; *Pseud*, *Pseudeugenia*; *Sch*, *Schizocalomyrtus*; *Sp*, *Speciosae*. Tip mean score and standard deviation in the three first eigenvectors of a principal component analysis of climatic and edaphic data. PC1: primarily soil fertility and precipitation seasonality; PC2: mainly moisture, soil acidity and temperature seasonality; PC3: temperature seasonality and annual averages. (B) *Myrcianthes fragrans*. (C) *Eugenia myrcianthes*. (D) *E. mattosii*. (E) *E. stipitata*. (F) *E. involucrata*. (G) *E. stigmatosa*. (H) *E. coronata* (J. Flickinger). (I) *E. cerasiflora*. All photos, except (H), by the authors.

subsequently spreading to other regions around the globe (Mazine et al. 2018). So far, dated phylogenies have included only a few representatives of the palaeotropical Eugeniinae and have suggested that geographical disjunctions in this clade are young enough to be attributed to LDDE, with biogeographical reconstructions suggesting a westward colonisation pattern (Vasconcelos et al. 2017; Mazine et al. 2018). Species of this clade occurring outside tropical America also inhabit other tropical and subtropical regions of the globe, suggesting that they have retained environmental requirements similar to those of their ancestors as they colonised new areas, resulting in its current pantropical distribution. Species of Eugeniinae are abundant in neotropical forests (Mori 1983), where individuals provide floral resources and fleshy fruits to the fauna year-round (Staggemeier et al. 2017; Martins et al. 2023). The Eugeniinae are also important components of sociodiversity, with plants being cultivated in gardens for fruit consumption and, less often, also commercialised (Vieira et al. 2016). Thus, studying the evolution of their environmental preferences may help uncover the potential challenges to the persistence of their valuable resources in a rapidly changing world.

2.2 | Phylogenetic and Taxonomic Basis

Unless otherwise stated, all analyses were performed in R (R Core Team 2025). For this work, we employed the taxonomically verified phylogenetic hypothesis of the Neotropical Myrtaceae Working Group (NMWG 2024). We clipped the Eugeniinae clade from the authors' original time-calibrated super-matrix tree that contains one tip per species and combines ETS, ITS and seven plastid markers (i.e., their Appendix S7). Our pruned Eugeniinae tree consisted of 266 single-taxon tips, of which 256 represented *Eugenia* and 10 belonged to *Myrcianthes*, corresponding to 20% of the ca. 1300 Eugeniinae species known to date (POWO 2025). The operational taxonomic units (OTUs) used in the present work also match those of NMWG (2024), comprehending 240 species, 2 subspecies, 2 varieties and 22 entities identified to the genus level. All OTUs were preserved to obtain the largest possible tree.

2.3 | Occurrence Data

We extracted geographic distributions of OTUs named to the species level or lower taxonomic ranks (hereinafter 'fully named OTUs') as occurrence points from the Global Biodiversity Information Facility (GBIF.org 2025) using the R package 'rgbif' (Chamberlain et al. 2025), keeping only observations linked to preserved museum specimens and those cited in the literature. We cleaned the resulting 52,015 raw coordinates in two steps. First, we filtered the raw dataset using the package 'CoordinateCleaner', which automatically flags common spatial errors in occurrence points (Zizka et al. 2019). Second, we filtered occurrence data to the species' native ranges, as defined by the Plants of the World Online database (POWO 2025), using the 'rWCVP' pipeline (Brown et al. 2023). Final distribution maps of fully named OTUs are available at https://doi.org/10.5281/zenodo.21495669. For OTUs identified to the genus level, we manually extracted single-occurrence points from herbarium specimens linked to these terminals in the phylogeny. In total, 246 of the 266 OTUs were represented by at least one occurrence in the curated geographic dataset, totalling 44,970 points (i.e., 86% of the original dataset).

2.4 | Bioregions and Biogeographical Inference

We first explored the biogeographical regionalisation of all 266 OTUs using Infomap Bioregions, an online application that uses network theory to generate data-specific bioregions (Edler et al. 2017). To this end, we uploaded the cleaned occurrence dataset to the application's website and subsequently inspected the output (Appendix S1, Supporting Information). Because our biogeographical question is linked to trans-marine dispersals, we subsequently modified the bioregions obtained from Infomap Bioregions so that each was likely isolated from other bioregions by sea at the time of dispersal events. Thus, we merged the two originally identified South American and African bioregions into single bioregions and separated the Caribbean from Central America and Madagascar from continental Africa. Although separated from one another, South-East Asia, the Malay Archipelago and Australia were kept together because they are represented in our dataset by a single, shared species, *Eugenia reinwardtiana*. Furthermore, New Caledonia is treated separately from the rest of the Pacific islands due to the high diversity and endemism of Eugeniinae species, as identified by Infomap Bioregions. Finally, Cocos Island (Costa Rica), despite being closer to Central America than the remaining Pacific islands, is considered part of the same bioregion as the latter because of its volcanic origin (Rojas and Alvarado 2012), therefore not being connected to continental Central America in recent history. Our final bioregions were: (A) South America; (B) continental Central America and Mexico (hereinafter simply Central America); (C) the Caribbean, including southern Florida; (D) continental Africa; (E) Madagascar; (F) the Mascarene Islands; (G) South Asia; (H) South-East Asia, the Malay Archipelago and Australia; (I) New Caledonia; and (J) the Pacific islands. We classified

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species as belonging to one or more bioregions manually (see Appendix S2) based on their native distribution maps.

We reconstructed the biogeographical history of Eugeniinae using 'BioGeoBEARS' (Matzke 2013), an R package and pipeline that permits testing different biogeographical evolution models while incorporating dispersal constraints between areas. We assessed the fit of six models implemented in the package via maximum likelihood—namely, DEC, DIVA-LIKE and BAYAREA-LIKE, and their extensions incorporating the jump speciation parameter 'J' (Matzke 2014). Models in BioGeoBEARS permit assessing geographic range evolution in light of distinct processes during cladogenesis; differences between models are explained elsewhere (e.g., Martins et al. 2025). Despite the controversy in employing jump speciation in biogeographical analyses (e.g., Ree and Sanmartín 2018), we run models that include this parameter because it can represent events of colonisation of new environments followed by independent diversification from the source area (i.e., founder events), especially in LDDE, which may have been important in the biogeographical history of Eugeniinae. We presented ancestral area reconstructions obtained with all models either in the main text (for the model with the lowest Akaike Information Criterion value corrected for sample size; AICc) or in the Supporting Information (for the remaining models). To assess the significance of including the jump speciation parameter to model fit, we also conducted likelihood ratio tests between each standard model and its '+J' extension.

Because our biogeographical question includes the dispersal route of *Eugenia* out of the Neotropics, we tested three dispersal scenarios for each model: (1) Unconstrained models, in which all dispersal probabilities across bioregions are equal; (2) Eastbound route, where eastward colonisation is facilitated; and (3) Westbound route, where westward dispersal is favoured (see Appendix S3). In the constrained models, we considered the sizes and distances of destination landmasses to categorise dispersals as highly likely (1), likely (0.5) and unlikely (0.01). For the South America-Pacific Islands connection, dispersals were assigned as unlikely in both directions due to the small size and isolation of the Pacific Islands as potential destinations from South America, as well as the large geographic distance between the two in both directions. Because all dispersals have occurred within the last 25 million years, when most continents had essentially reached their modern relative positions (Sanmartín and Ronquist 2004), and because island availability in this timeframe is highly variable, we did not stratify our dispersal probabilities into time slices. In all cases, we identified geographic range changes by analysing differences between two subsequent nodes in the phylogeny, using the age of the older one as a proxy for the earliest instance at which a range change event may have occurred. We did not consider alternative ranges in our biogeographic reconstruction because they did not present relevant probabilities (i.e., $p \leq 0.3$). We extracted nodes' mean ages and confidence intervals from appendix S5 of NMWG (2024), but unless otherwise stated our results are interpreted based on mean node ages. When inferring the types of events responsible for range expansions or shifts, we considered the positions of continents and the presence or absence of dry-land passages at the time of dispersals (e.g., Thiede 1977; Bermingham and Martin 1998; Pennington and Dick 2004).

2.5 | Environmental Niche Analyses

We performed environmental niche analyses with the 246 OTUs for which occurrence data were obtained. Niche conservatism is often addressed via analyses of niche evolution, requiring, in the case of abiotic niches, the characterisation of the environments where species occur. Together with climatic data, these analyses should also include, for example, edaphic preferences, since soil conditions are important for seed germination, successful plant development and reproduction (Velazco et al. 2017). Thus, to investigate the evolution of environmental niches in Eugeniinae, we extracted environmental data based on our curated occurrence points and used them in phylogenetic comparative analyses. For this, we employed CHELSA-bioclim (Karger et al. 2017, 2021) variables 'bio1' (mean annual air temperature), 'bio4' (temperature seasonality), 'bio12' (annual precipitation amount) and 'bio15' (precipitation seasonality), along with SoilGrids (Poggio et al. 2021; Turek et al. 2023) variables 'bdod' (soil bulk density), 'cfvo' (coarse fragments volume, percentage), 'clay' (clay content, percentage), 'sand' (sand content, percentage), 'silt' (silt content, percentage), 'nitrogen' (total nitrogen content, percentage), 'ocd' (soil organic carbon density) and 'phh2o' (soil pH in water solution). We extracted soil values for six depths and averaged them to obtain single values of each variable for each occurrence point using functions of the R packages 'dplyr' (Wickham et al. 2025) and 'terra' (Hijmans 2025).

We tested for correlations between pairs of abiotic variables using Pearson's correlation coefficient, removing a variable whenever it was highly correlated with another (i.e., $r \geq 0.7$); this was the case for sand, which was highly correlated with both clay and silt. We summarised the climatic and edaphic descriptors via principal component analysis (PCA) using functions of the R package 'stats' (R Core Team). We considered the first three PCA eigenvectors as combined environmental descriptors in our niche analyses. Since most OTUs were represented in the PCA space by more than one point, we calculated the average and standard deviation for each OTU across all analysed eigenvectors.

We investigated the relationship between colonisation of new landmasses and niche evolution in Eugeniinae using functions of the R package 'OUwie' (Beaulieu and O'Meara 2025) in two different approaches. In Approach A, we tested whether environmental niches evolve differently in palaeotropical versus neotropical Eugeniinae, based on the assumption that the Eugeniinae have achieved their pantropical distribution through trans-marine dispersals from the Neotropics. For this, we labelled each terminal on our Eugeniinae tree as either neotropical or palaeotropical and used these as discrete regimes to fit evolutionary models, using our three combined environmental descriptors as continuous traits of interest. OUwie models Brownian motion (BM) and Ornstein–Uhlenbeck (OU) processes, as well as derivations thereof. BM is a random walk model for trait evolution in which the evolutionary rate (σ^2) is constant, and the total change is proportional to time; in contrast, OU extends BM by incorporating a restoring force ($\alpha > 0$) pulling traits back to an adaptive optimum (θ) (Blomberg et al. 2020). Under this framework, we interpreted comparatively lower σ^2 values as evidence of environmental niche conservatism and higher values as indicative of niche lability. Additionally, we considered the presence of a

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restoring force ($\alpha > 0$) as further support for niche conservatism, as it suggests the maintenance of ancestral environmental preferences against the pressure of stochastic niche divergence. We considered the following models: BM1 (simple BM, with a single σ^2 for both regimes), BMS (BM with a different σ^2 for each regime), OU1 (a simple OU model, with a single σ^2, α and θ), OUM (a multi-peak OU model with a single σ^2 and α, but different θ for each regime) and OUMV (a multi-peak and multi-rate OU model with a single α, but different σ^2 and θ). Likelihood functions of OUMA (a multi-peak OU model with a single σ^2, but different α and θ) and OUMVA (an all-variable OU model, with all three parameters differing between regimes) require revision (Beaulieu and O'Meara 2025); thus, these models were excluded from our analyses. For each combined environmental descriptor, we ranked all models by AICc, selecting the model with the lowest value as the best fit to our data.

In Approach B, we compared clade-specific evolutionary rates. To this aim, we extracted the clades corresponding to *Myrcianthes* and the 11 sections of *Eugenia* sensu Mazine et al. (2018) and NMWG (2024) from our phylogeny. We merged single species or small clades not assigned to any formally described lineage to their sister clades to ensure that all species with available environmental data were included in the analyses. For each combined environmental descriptor, we ran simple BM1 models for all clades and ranked them from the highest to lowest σ^2. Because evolutionary rates permit investigation of niche conservatism within a clade-comparison framework (Münkemüller et al. 2014), we inferred environmental niche conservatism for clades with a low σ^2 rank and lability for clades with a high σ^2 rank. Finally, to inspect if colonisation of new areas (as inferred from historical biogeographical analyses) is linked to higher rates of environmental niche change, we plotted each clade's σ^2 against the number of biogeographical range expansions or shifts within the same clade. In both approaches, we calculated confidence intervals for the estimated parameters using the OUwie.boot function available in OUwie (Beaulieu and O'Meara 2025).

3 | Results

3.1 | Biogeographical History

Six of the 12 Eugeniinae clades diversified exclusively within South America, while the remainder expanded northwards (4 clades) or both north and eastwards (2 clades). A pantropical distribution has been achieved only by *Eugenia* sect. *Jossinia* (Figure 1).

Our data is best explained by the DEC+J-Eastbound model (Appendix S4). The Eastbound route was consistently preferred over both the Westbound route and the Unconstrained model for all models (Appendix S4). Likelihood ratio tests indicate that including the J parameter significantly improved model fit ($p < 10^{-3}$ in all cases; Appendix S5). Biogeographical reconstructions are similar in all pairs of any given model and its respective '+J' extension, and when considering only models that do not allow jump dispersals, our data is best explained by the DEC-Eastbound model (Appendix S4), describing the same dispersal route as the best model including the J parameter.

The MRCA (most recent common ancestor) of Eugeniinae was recovered in South America ($p = 0.59$), during the Early Oligocene, at 33.2 (36.1–30.2) Ma (Figures 1A and 2). The

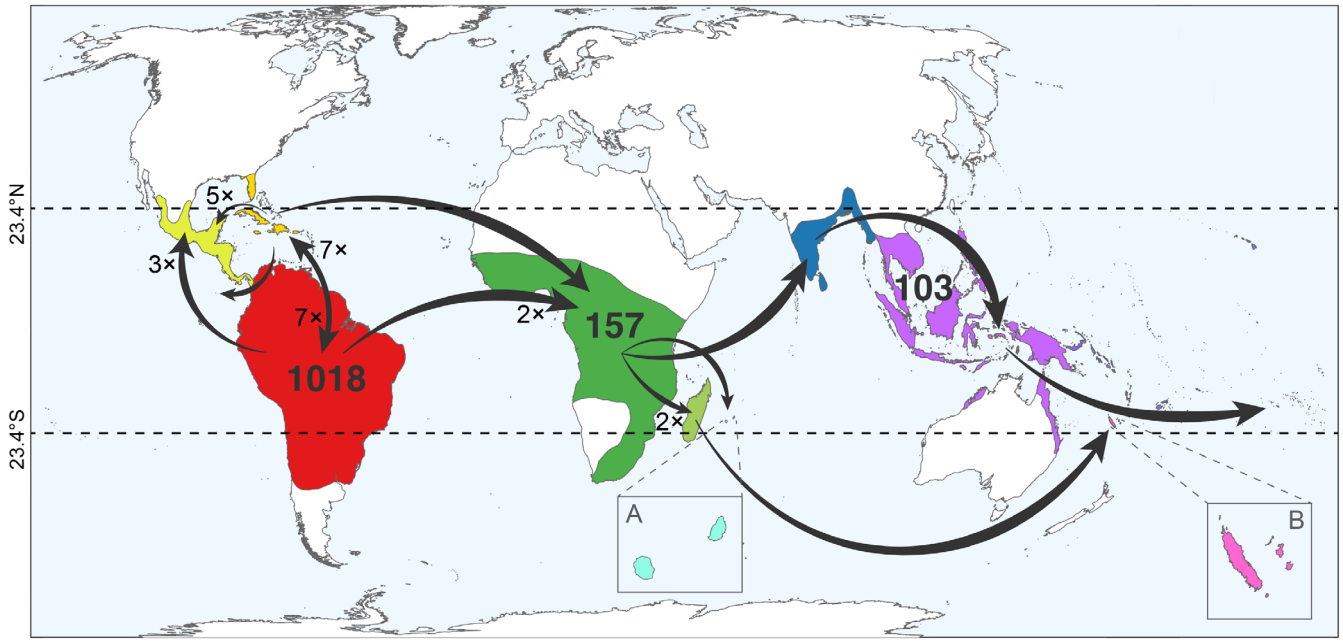


FIGURE 2 | Schematic of the pantropical geographical distribution of Eugeniinae, species richness per region and dispersal route inferred based on biogeographical range estimation with the best fit model via BioGeoBEARS. Geographical distribution of clade based on species' occurrence information. Number of species in the Neotropics, Africa and Asia + Oceania from Plants of the World Online. Bioregion colours match Figure 1. The number of repeated movements is indicated next to the arrow tips. Inserts depict insular bioregions with high endemism of Eugeniinae species: (A) Mascarene Islands and (B) New Caledonia.

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MRCA of *Myrcianthes* dated to 21.7 (28.1–15.5) Ma, in the Early Miocene, also from South America ($p = 0.55$). In *Myrcianthes*, at least one range expansion into Central America and the Caribbean occurred at 12.6 Ma (19.8–6 Ma), as indicated by the modern distribution of *M. fragrans*. The MRCA of *Eugenia* and all its sections lived in South America ($p = 0.85$–1), with the former dated to 30.8 (33.6–27.8) Ma, in the Early Oligocene, and the latter emerging between c. 26 and 12 Ma, between the Oligocene and the Miocene. Range expansions from South America northwards between 12.3 and 4.8 Ma are recovered in species with modern widespread distributions in *Eugenia* sections *Eugenia* (*E. ligustrina*, to the Caribbean) and *Umbellatae* (*E. punicifolia*, to the Caribbean and *E. egensis*, to Central America). Major range shifts from South America to the Caribbean are recorded during the Miocene in *Eugenia* sections *Excelsae* (*E. confusa* clade, 17.1 [21.1–13.1] Ma [$p = 0.59$]), *Racemosae* (*E. linearis* clade, 11.9 [14.6–9.4] Ma [$p = 0.72$]) and *Umbellatae* (*E. dictyophylla* clade, 19 [21.2–16.6] Ma [$p = 0.95$]); in all cases, further shifts and/or expansions to Central America and back to South America were recorded. In *Eugenia* sect. *Umbellatae*, a further expansion from the Caribbean to the Cocos Island of Costa Rica in the Pacific Islands bioregion was recorded in the *E. pacifica* clade c. 10.3 (12.8–7.8) Ma ($p = 1$), followed by two independent shifts to the latter represented by *E. cocosensis* and *E. pacifica*.

Eugenia talbotii and *E. coronata* feature two range shifts from the Neotropics to continental Africa in *E.* sect. *Umbellatae* in the Miocene, at c. 12–11 Ma. A further shift is evident in the main lineage of *Eugenia* sect. *Jossinia* (i.e., excluding *E. umbellulifera*), whose MRCA probably lived in South America but gave origin to a continental African lineage ($p = 0.55$). The first clade to diverge within the 'core' *Eugenia* sect. *Jossinia* features a range shift from continental Africa to Madagascar (*E. tropophylla* clade; $p = 0.81$), followed by a shift from Madagascar to New Caledonia (*E. brongniartiana* subclade; $p = 1$). An independent shift to Madagascar was recorded in *Eugenia roseopetiolata*, diverging from the African clade of *E.* sect. *Jossinia* at 13.9 (17.2–10.4) Ma. In the remainder of the core *Eugenia* sect. *Jossinia*, range shifts from continental Africa to the Mascarene Islands (*E. bojeri* clade; $p = 1$) and South Asia (*E. calcadensis* clade; $p = 0.91$) occurred, as well as a further shift from the latter to South-East Asia + the Malay Archipelago + Australia, followed by a range expansion to the Pacific Islands, represented by *E. reinwardtiana*. All range shifts in *Eugenia* sect. *Jossinia* described above date to c. 24.6–10.1 Ma, spanning the Late Oligocene to the Late Miocene, when continents already had a spatial arrangement similar to the present. All major events are summarised in Appendix S6. Biogeographical reconstructions produced by all models fitted with BioGeoBEARS are available in Appendices S7–S12 and the above-mentioned named clades within sections are shown in Appendices S13–S14.

3.2 | Environmental Niche Evolution

The first three PCA eigenvectors explain together 59.3% of the total variation of our environmental data (Figure 3). The PC1 axis appears to capture a gradient primarily related to soil fertility and precipitation seasonality (Appendix S15). Overall, species within the Eugeniinae clades presented high variance along the first eigenvector (Figure 3), indicating that lineages within this subtribe evolved to occupy an array of soil fertility conditions and precipitation regimes. The second eigenvector translates an environmental gradient of moisture, soil acidity and temperature seasonality. In *Eugenia* sections *Eugenia*, *Hexachlamys*, *Phyllocalyx* and *Schizocalomyrtus*, taxa tend to populate the portion of PC2 around zero, suggesting that they prefer mesic conditions and neutral soils (Figure 3). In contrast, species of *E.* sections *Pilothecium*, *Racemosae* and *Umbellatae* are over-dispersed along the second eigenvector (Figure 3), showing that they have adapted to diverse temperature seasonality, humidity and soil pH conditions. Finally, the third combined environmental descriptor translates a gradient varying from highly seasonal temperatures with lower annual averages to more homogeneous temperatures yearly with higher averages.

In the environmental niche evolution analysis Approach A, evolutionary dynamics along PC1 were best explained by OUMV (Figure 4; Appendix S16). In this case, σ^2_{Palaeo} was four times slower than σ^2_{Neotr} (i.e., 0.05 [0.03–0.1] vs. 0.2 [0.14–0.3] square units per million years), suggesting lower rates of evolution of soil fertility and precipitation seasonality preferences in palaeotropical Eugeniinae. This model also presented an $\alpha = 0.06$ [0.04–0.11] million years^{-1}, indicating overall niche conservatism within each regime. The values of θ_{Palaeo} were, on average, smaller than those of θ_{Neotr}. Still, their confidence intervals substantially overlap (i.e., −0.64 [−1.85 to 0.11] vs. −0.3 [−0.76 to 0.05] units), implying that in both regimes lineages are evolving towards occupying equivalent, intermediate PC1 conditions. For PC2, BMS was the best model, with σ^2_{Palaeo} being, on average, eight times faster than σ^2_{Neotr} (0.35 [0.19–0.53] vs. 0.04 [0.04–0.05] square units per million years). The fastest rate of evolution across all models fitted in Approach A, together with $\alpha = 0$, suggests lability in temperature seasonality, annual precipitation and soil pH requirements in palaeotropical Eugeniinae. Finally, the best-fit model for PC3 was BM1, with $\sigma^2 = 0.03$ (0.03–0.04) square units per million years, which is among the lowest of all models fitted in Approach A and implies slow evolution in temperature preferences shared by neotropical and palaeotropical Eugeniinae. Parameter estimates of the best models are summarised in Figure 4 and details of all fitted models are presented in Appendix S16.

In Approach B, Eugeniinae clades ranked differently for each combined environmental descriptor according to rates of niche evolution (Appendix S17), but *Myrcianthes* and *Eugenia* sections *Pseudeugenia*, *Racemosae* and *Umbellatae* frequently emerged within the five highest positions in the ranking, suggesting overall high evolutionary lability to different environments in these clades. *Eugenia* sect. *Jossinia*, the only lineage of Eugeniinae spanning the entire Pantropics and the associated subtropical areas as here defined, ranked in overall median or low positions, with less labile niches than many exclusively neotropical clades (Figure 5, Appendix S17). Overall, *Eugenia* sections *Eugenia*, *Hexachlamys* and *Schizocalomyrtus* ranked low in all or most combined environmental descriptors, suggesting conservatism in soil, temperature and precipitation preferences in these clades over time.

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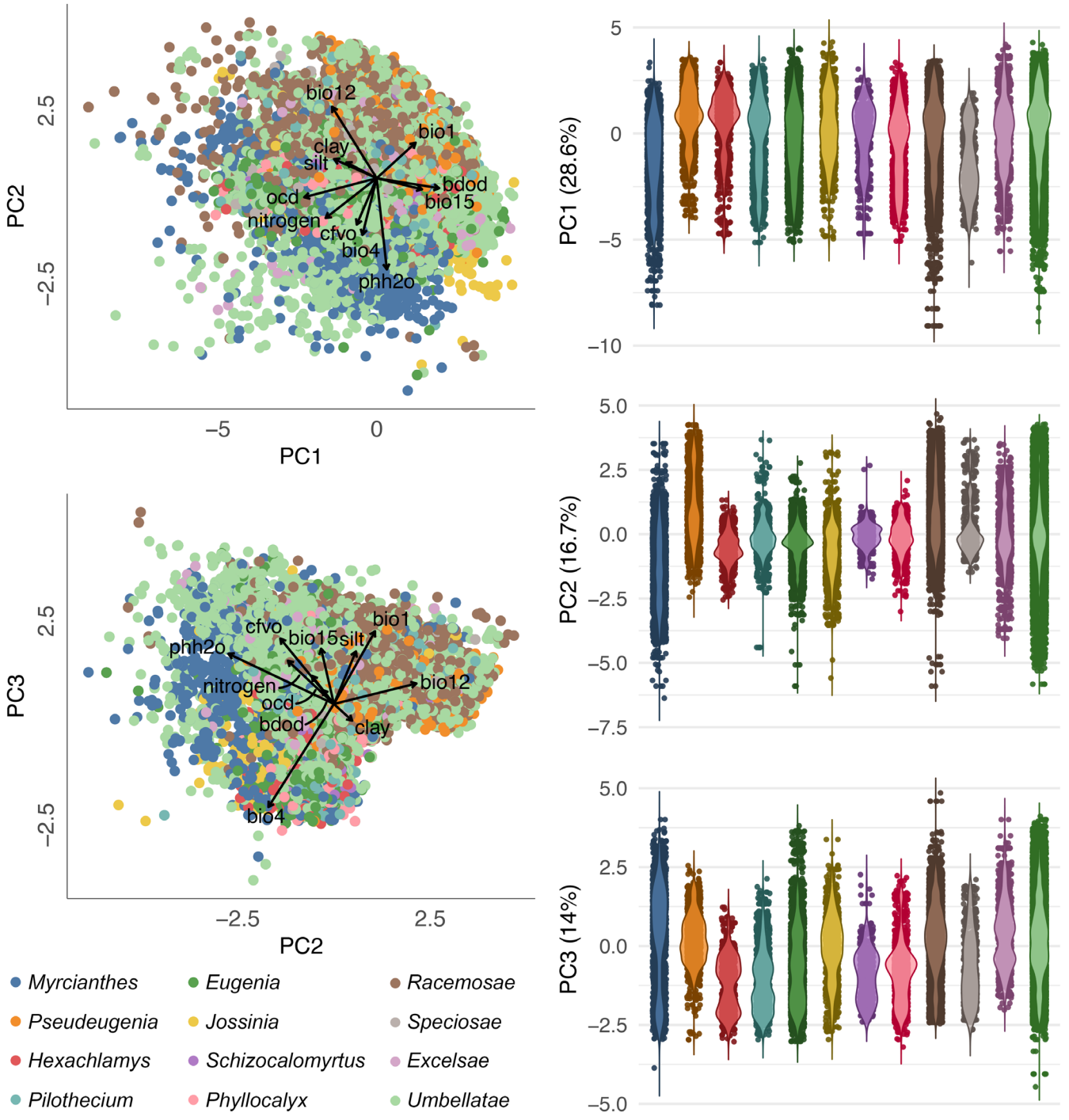


FIGURE 3 | Principal component analysis of abiotic CHELSA-bioclim and SoilGrids variables extracted from curated occurrence points of species of *Myrcianthes* and the 11 sections of *Eugenia* (Eugeniinae, Myrtaceae). Left panels: Biplots of single occurrences along the three first eigenvectors. Arrows represent loadings of abiotic variables onto the principal components. bdod, soil bulk density; bio1, mean annual air temperature; bio12, annual precipitation amount; bio15, precipitation seasonality; bio4, temperature seasonality; cfvo, coarse fragments volume, percentage; clay, clay content percentage; nitrogen, total nitrogen content, percentage; ocd, soil organic carbon density; phh2o, soil pH in water solution; silt, silt content, percentage. Right panels: Violin plots depicting distributions of scores for the first three principal components across the 12 clades.

4 | Discussion

As detailed geographical and environmental data from diverse plant lineages become more widely available, it is possible to better understand how geographic movement interacts with niche evolution over time. In the present study, we investigated this interplay by reconstructing the historical biogeographic history and assessing the evolution of environmental niches in the ecologically important subtribe Eugeniinae (Myrtaceae). We found that Eugeniinae's pantropical distribution has been achieved through an origin in South America followed by multiple trans-marine dispersals to other land masses, primarily in an easterly direction. We also found that geographic movement in Eugeniinae was generally decoupled from accelerated changes

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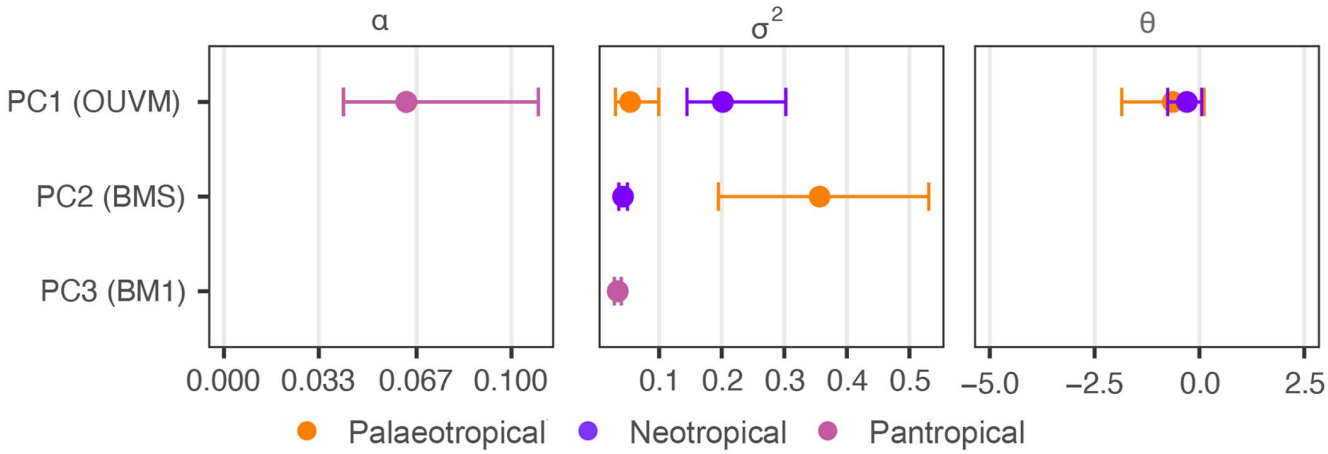


FIGURE 4 | Parameter estimates for the best models fitted with OUwie in environmental niche evolution analyses of Eugeniinae (Myrtaceae) along the three first combined environmental descriptors (i.e., three first PCA eigenvectors). Error bars indicate confidence intervals. Parameters identical in the palaeotropical and neotropical regimes are referred to as pantropical. Parameters: σ^2—evolutionary rate; α—restoring force; θ—adaptive optimum.

in environmental preferences, with the latter occurring predominantly in clades characterised by few or no new landmass colonisation events. These findings suggest that niche conservatism can be a key driver of successful trans-marine dispersals, aligning with patterns observed across other plant lineages (Crisp et al. 2009; Donoghue and Edwards 2014), with environmental shifts primarily associated with intracontinental diversification.

4.1 | A Pantropical Distribution Shaped Mostly by Eastward Trans-Marine Dispersals

Exchanges between South America, Central America and the Caribbean in *Eugenia* and *Myrcianthes* during the Miocene (19–10 Ma) precede the closure of the Isthmus of Panama, in the Pliocene (c. 3 Ma; Coates and Obando 1996), but are too young to have benefitted from other land bridges thought to have existed in the region in the past. Hence, these movements likely resulted from trans-marine dispersals, being carried either by migratory birds via air or floating islands via the North Brazil Current in the Atlantic Ocean (Stramma and England 1999).

Our results support a predominantly eastward biogeographical pattern, rather than a westward route, as proposed by Vasconcelos et al. (2017) and Mazine et al. (2018), shaping the pantropical distribution of Eugeniinae. Migrations from the New World to Africa are dated to the Miocene (22–11 Ma), being thereby unlikely to result from vicariance, inland dispersal or island hopping. Thus, LDDE is the most plausible dispersal mechanism of Eugeniinae from the Americas to the Old World, with vectors possibly including floating islands (see Katinas et al. 2013) being carried by long-standing oceanic currents (Renner 2004).

Eugeniinae migrated from Africa to Madagascar at least twice in the Miocene (18–13.9 Ma), when the landmass and the island were well separated by the Mozambique Channel (Rabinowitz et al. 1983). Because no land bridge is known to have existed between the two during the Cenozoic (Yoder and Nowak 2006), these shifts were probably also trans-marine. In this case, seeds were possibly carried by birds via aerial migration (see Yoder and Nowak 2006) or on floating islands, either as part of the vegetation mats or inside small frugivores (Ali and Huber 2010). If true, those rafts could have developed during extreme weather conditions (e.g., storms, floods or cyclones).

The dispersal event from Madagascar to New Caledonia in the *Eugenia brongniartiana* subclade, also in the Miocene (c. 14.3 Ma), is perplexing because of the very long distance involved and the absence of known major oceanic currents flowing eastwards in the Indian Ocean during that time (Herold et al. 2012). Thus, sweepstakes events might also have been responsible for that range shift. At least one more case of plant dispersal from Madagascar to New Caledonia during the Miocene has been recorded in the literature (Davis et al. 2002), and further examples may become available in the future, potentially aiding in identifying the mechanisms behind these seemingly anomalous trans-oceanic shifts.

South Asian Eugeniinae originated, according to our results, from a migration from Africa during the Miocene at 15.4 (18.4–12.4) Ma, aligning temporally with the existence of the Gomphotherium Land Bridge (19–15 Ma), which is thought to have been responsible for extensive biotic exchanges between Africa and Asia in that period (Harzhauser et al. 2007). The dispersal event also coincides with the Middle Miocene Climatic Optimum (MMCO; 17–14 Ma), when north-east Africa, Arabia and adjacent Eurasia were covered by mosaics of grasslands, savannahs and forests (Kingston and Hill 1999). Therefore, South Asian Eugeniinae may have originated via overland dispersal by zoochoric agents, although oceanic LDDE cannot be ruled out.

Finally, the range shift from South Asia to South-East Asia + the Malay Archipelago + Australia at c. 14.2 Ma can be attributed to a combination of inland dispersals and island hopping across the complex island mosaic that developed in the region during the Miocene (Hall 2009). In this sense, intense tectonic activity and fluctuating sea levels may have established a series of island-hopping routes utilised by frugivores, which may have acted as dispersal agents, as discussed in similar studies targeting other

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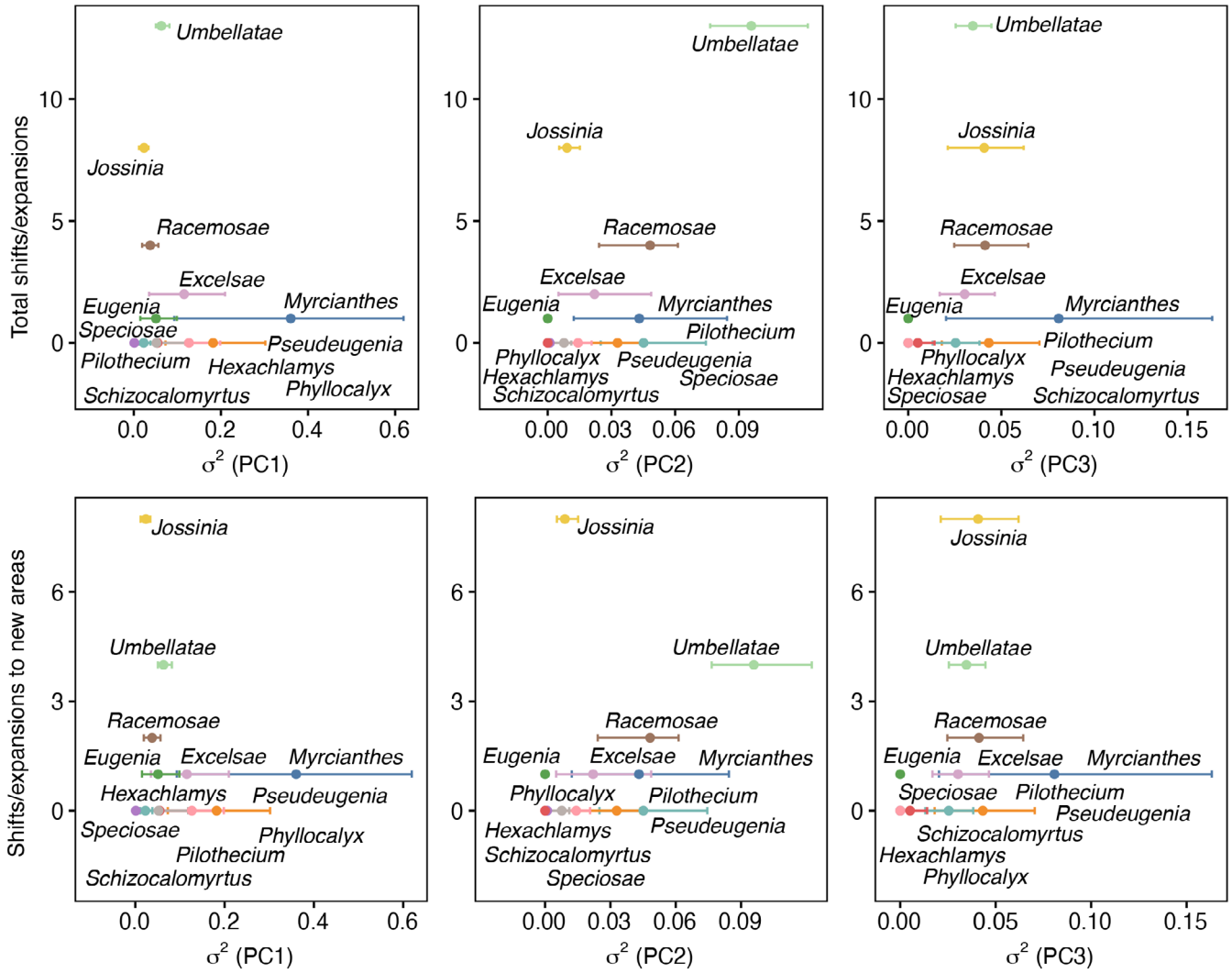


FIGURE 5 | Rates of environmental niche evolution in Brownian motion models of clades representing *Myrcianthes* and the 11 sections of *Eugenia* along the 3 first combined environmental descriptors (PC1–3) versus total number of geographic range shifts or expansions observed in each clade (top row) and range shifts or expansions to new areas only (bottom row). Error bars indicate confidence intervals. Clades' colours match Figure 3.

plant clades (Lauraceae, Huang et al. 2016; Araliaceae, Shee et al. 2020).

Therefore, we argue that Eugeniinae probably achieved its modern pantropical distribution by repeatedly overcoming marine barriers. Trans-marine dispersals are thought to have been pivotal to broad modern distributions of other tropical plant clades (Rubiaceae, Kainulainen et al. 2017; Ochnaceae, Schneider et al. 2022) and further studies are needed to quantify the overall contribution of this phenomenon to tropical plant biogeography. Importantly, our results also emphasise the value of increasingly complete species-level phylogenies for inferring biogeographical histories. The topology employed in our analyses is 2.7 times more densely sampled than the one used in the most recent biogeographical inference for this group (98 OTUs; Mazine et al. 2018). Consequently, this is also the first time that three independent dispersal events from South America to Africa—one in *Eugenia* sect. *Jossinia* and two in *E.* sect. *Umbellatae*—are reported in Eugeniinae. Because *Eugenia* sect. *Umbellatae* does not disperse beyond Africa, this may have contributed to the model identifying an eastward dispersal direction as the best fit. In any case, an initial successful dispersal from South America to Africa is also more plausible given the proximity and size of the two landmasses, in contrast to the route from South America to New Caledonia, which was inferred in previous studies (Vasconcelos et al. 2017; Mazine et al. 2018). Finally, dispersal events between South America and Africa are common in other plant lineages (Renner 2004), which further supports our interpretation.

4.2 | An Evolutionary History Shaped by Both Niche Conservatism and Lability

Based on the parameters of the evolutionary models, we argue that Eugeniinae probably conserved most aspects of their abiotic niches while crossing marine barriers to achieve their modern pantropical distribution. Our results show conserved niches for all lineages with higher rates of dispersal (i.e., *Eugenia* sections *Jossinia* and *Umbellatae*) along PC1 and PC3 in both Approaches A and B. *Eugenia* sect. *Jossinia*, the clade with by far the highest number of dispersals to new areas, including the

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vast majority of trans-marine long-distance dispersal events, has relatively low rates of niche evolution across all three PCs in Approach B (Appendix S17), consistent with the idea that successful trans-marine events are more likely when lineages encounter conditions to which they are already adapted upon arrival (Crisp et al. 2009). In this scenario, low rates can be related to limited genetic variation available for adaptive response to novel environments due to strong genetic bottleneck effects (Mayr 1963), since carriers involved in events that result in colonisation of new landmasses usually transport only a few individuals (Simpson 1940). Added to successive founder events, trans-marine dispersals within *Eugenia* sect. *Jossinia* are relatively recent; consequently, these populations may also not have had sufficient time to diversify in situ to the extent observed in the Neotropics.

Results of niche evolution analyses also indicate the highest rates of environmental shifts in Eugeniinae lineages that remained in South America or the Neotropics. This was most pronounced in Approach A for PC1, the eigenvector accounting for the highest proportion of environmental variation, and in Approach B across all combined environmental descriptors, except for *Eugenia* sect. *Umbellatae* ranking the highest for PC2. In South America, where Eugeniinae originated and diversified for most of its history, significant environmental changes have occurred in the last 35 million years, such as the rise of the Andes, the formation of the South American Dry Diagonal (SADD) and Pleistocene climatic fluctuations (Pennington et al. 2000; Hoorn et al. 2010). These historical events may have allowed Eugeniinae lineages to spread and diversify extensively across many biomes, occupying much of tropical and subtropical America. Furthermore, Eugeniinae lineages diversifying in such a large landmass likely underwent less severe populational bottlenecks than those colonising new areas sequentially. This may have resulted in higher levels of standing genetic diversity that may have facilitated colonisation and persistence across different environments, for example, by recruitment of advantageous alleles via hybridisation and introgression (Mayr 1963).

This dynamic could explain the rapidly evolving environmental niches observed in clades such as *Myrcianthes* and *Eugenia* sect. *Pseudeugenia*. *Myrcianthes* presents elevational and latitudinal ranges that are exceptionally broad for Eugeniinae (Proença et al. 2025), and our results reflect this diversity given that the genus had the highest environmental niche evolution rate along PC1, representing in part soil fertility, which varies along elevational gradients (Soethe et al. 2008). The genus also presented the fastest evolving environmental niche on PC3, which captures a gradient of temperature seasonality and annual averages, which is also tightly linked to latitudinal variation. Therefore, much of the diversification of *Myrcianthes* may be related to Andean uplift in South America. In parallel, *Eugenia* sect. *Pseudeugenia* occurs across seasonal SADD ecosystems and adjacent mesic forests, as well as environments of various soil fertility properties and annual temperature regimes, but its species are usually restricted to one or few vegetation types characterised by certain environmental conditions (Mazine et al. 2020). This distribution pattern aligns with the section's position as the second highest in environmental niche evolution rates along both PC1 and PC3, of which soil fertility, precipitation seasonality and temperature annual averages and seasonality are important drivers. Thus, it is possible that the accelerated evolution of environmental niches in *Eugenia* sect. *Pseudeugenia* is related to the opening of the SADD.

Our results demonstrate the geographical expansion of Eugeniinae during the Miocene, when temperate floras were already established in higher latitudes (Wen 1999). Nevertheless, the absence of fossil evidence of Eugeniinae species in these areas and a modern pantropical and subtropical distribution suggest that this lineage either never established long-term, viable populations in temperate environments or experienced higher rates of extinction there, precluding a Boreotropical route of migration, unlike in other tropical clades (Davis et al. 2004). This idea is corroborated by the slow pace at which temperature preferences have evolved in Eugeniinae, as indicated by the best fit model for PC3, suggesting limited thermal tolerance in this clade over time. If true, this restriction is more likely due to functional constraints rather than the lack of evolutionary accessibility (see Edwards and Donoghue 2013), since regions where Eugeniinae species occur in North America and Asia are in direct contact with temperate forests (Olson et al. 2001), although these contact zones were probably positioned in higher latitudes during the MMCO (Herold et al. 2010).

Our results illustrate that a thorough characterisation of environmental niches of plants, including soil variables, can reveal a more complex picture of abiotic niche evolution than analyses that include only climatic data (e.g., Moro et al. 2015). While climate is indeed important, soil variables are especially critical for angiosperms, which are tightly linked to soil conditions (Hulshof and Spasojevic 2020). In the case of Eugeniinae, the central role of edaphic characteristics in shaping environmental niches is shown by their high relative contributions to the first two combined environmental descriptors, especially soil density and pH and carbon and nitrogen contents. In fact, many plant lineages are known to specialise in particular soil types, pH levels and nutrient availability (Rajakanura 2018), and similar patterns are evident in our results. Therefore, our findings show the importance of employing comprehensive abiotic datasets to understand environmental niche conservatism on a global scale.

5 | Conclusions

Our results support multiple short-range trans-marine jumps and LDDE events coupled with slowly evolving, conserved environmental niches in explaining the modern distribution of Eugeniinae. They also suggest an important role of historical events of the last 35 million years in South America in the rapid evolution of niches in Neotropical Eugeniinae. Several lines of research may build on our findings. First, a recently achieved pantropical distribution that is coherent with multiple events of trans-oceanic long-distance dispersal is not exclusive to Eugeniinae and has likely happened in many plant lineages (see Givnish and Renner 2004). Since these events can occur through multiple distinct modes and vectors, it would be interesting to test whether general patterns emerge when comparing many such clades for which comprehensive phylogenetic frameworks are available. These future investigations should consider biological traits that may facilitate trans-marine

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dispersals—for instance, associations with migratory animals or anemochory—but also extrinsic factors, like oceanic currents. Quantifying how often plant lineages have achieved pantropical distributions by overcoming oceanic barriers compared to other modes (e.g., land bridges via higher latitudes), would also be important in terms of understanding global generalities. Second, future works could investigate whether the premise related to the interplay between geographic movement and niche evolution, tested in the present work, is a generality by testing it with similar methods in different plant clades.

In the specific context of Eugeniinae, future works should include an increasingly complete phylogeny with more terminals representing poorly sampled sections and species from the Old World, potentially improving estimates of evolutionary parameters. Future works should also investigate potential evolutionary innovations that may have enabled frequent LDDE in *Eugenia* sect. *Jossinia*.

Author Contributions

P.H.G., S.A.S. and T.V. conceived the study. P.H.G., J.D.B., F.F.M. and K.S.V. collected and/or analysed data. P.H.G. wrote the first draft and all authors contributed to revising and editing the original text.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code needed to implement our methods and replicate our results can be found at https://doi.org/10.5281/zenodo.21495669.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Global bioregionalisation of Eugeniinae (Myrtaceae) derived from curated Global Biodiversity Information Facility (GBIF) coordinates and calculated via Infomap Bioregions. **Appendix S2:** Final bioregion assignment of Eugeniinae (Myrtaceae) phylogeny terminals employed in biogeographical reconstruction analyses. **Appendix S3:** Dispersal probability matrices employed in biogeographical hypothesis testing in BioGeoBEARS. **Appendix S4:** Biogeographical model fit results from BioGeoBEARS for Eugeniinae (Myrtaceae). **Appendix S5:** One-tailed chi-squared Likelihood Ratio Test results from BioGeoBEARS for Eugeniinae (Myrtaceae). **Appendix S6:** Reconstruction of biogeographical history of Eugeniinae (Myrtaceae) with BioGeoBEARS. **Appendix S7:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the DEC model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S8:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the DEC+J model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S9:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the DIVALIKE model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S10:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the DIVALIKE+J model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S11:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the BAYAREALIKE model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S12:** Ancestral range estimations for Eugeniinae (Myrtaceae) according to the BAYAREALIKE+J model implemented in BioGeoBEARS testing three different dispersal probability schemes. **Appendix S13:** Detail of ancestral range estimations for Eugeniinae (Myrtaceae) according to the DEC+J model implemented in BioGeoBEARS, focusing on named clades within *Eugenia* sections *Excelsae*, *Jossinia* and *Racemosae*. **Appendix S14:** Detail of ancestral range estimations for Eugeniinae (Myrtaceae) according to the DEC+J model implemented in BioGeoBEARS, focusing on named clades within *Eugenia* sect. *Umbellatae*. **Appendix S15:** Principal components analysis of CHELSA-bioclim and SoilGrids data obtained from curated Eugeniinae (Myrtaceae) occurrences. **Appendix S16:** Two-regime environmental niche evolution analyses implemented in OUwie with combined environmental descriptors (i.e., PCA eigenvectors of CHELSA-bioclim and SoilGrids data obtained from curated Eugeniinae [Myrtaceae] occurrences). **Appendix S17:** Per-clade environmental niche evolution analyses implemented in OUwie with combined environmental descriptors (i.e., PCA eigenvectors of CHELSA-bioclim and SoilGrids data obtained from curated Eugeniinae occurrences).

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