

Biomes as evolutionary arenas structuring the global floristic assembly

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Title: Biomes as evolutionary arenas structuring the global floristic assembly

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27 **Abstract**

28 Global plant diversity is distributed unevenly across terrestrial biomes. While the effects of
29 environmental differences on species distributions have been well studied, how the spatial
30 configuration of biomes structures the macroevolutionary assembly of the global flora remains
31 unclear. Here, we introduce a biome-centred framework for elucidating global floristic
32 assembly based on joint reconstructions of biome and geographic occupancy across 160 plant
33 lineages comprising ~20,000 species. We demonstrate that global plant diversity is assembled
34 predominantly through within-biome speciation (~86% of variation in biome-level plant
35 richness) rather than biome shifts (~12%), revealing pervasive phylogenetic biome
36 conservatism. Transitions among biomes are asymmetric and jointly governed by their
37 biogeographic configurations and evolutionary histories: species-rich biomes with deeper
38 evolutionary histories act as major evolutionary sources that disproportionately export lineages
39 to other biomes, with biotic interchange increasing with biome area and declining with
40 geographic and environmental distance. These results identify biomes as fundamental
41 evolutionary arenas that both constrain diversification and mediate the biotic exchange of plant
42 lineages, providing an integrative framework for understanding the spatiotemporal dynamics
43 of global plant diversity.

44 **Key words:** biomes, biogeographic reconstruction, floristic assembly, plant diversity.

45 **Main text**

46 Understanding the processes underlying the broad-scale assembly of global biodiversity
47 remains a central goal in macroecology and biogeography¹⁻⁴. Global biodiversity is not
48 randomly distributed across space but organized by past and contemporary environmental
49 conditions and, critically, by their spatial structure and organization—that is, how different
50 environmental conditions are distributed and arranged across Earth’s surface⁵⁻⁷. This spatial
51 structure determines the degree to which environmentally similar or distinct habitats are
52 connected or isolated, thereby defining the geographic and environmental context in which
53 species disperse, persist, and diversify. While the effects of global environmental conditions on
54 biodiversity have been extensively studied, it remains poorly understood whether and how their
55 spatial structure shapes the eco-evolutionary processes through which biodiversity emerges,
56 evolves, and assembles to generate contemporary global patterns⁸.

57 Biomes characterize assemblages of vegetation that have experienced convergent evolution
58 under similar environmental conditions, resulting in broadly similar plant functional traits and
59 structural properties⁹⁻¹¹. As fundamental biogeographic units that encapsulate the spatial
60 structure of global environmental conditions, biomes are therefore expected to strongly
61 structure global patterns of plant diversity through mediating the underlying eco-evolutionary
62 processes^{12,13}. They have been hypothesized to represent evolutionary arenas – regions with
63 distinct evolutionary histories and unique biotic and abiotic conditions that confine the
64 evolution and distribution of the lineages they host¹⁴⁻¹⁶. Such constrained evolutionary
65 processes are expected to lead to a pattern of phylogenetic biome conservatism, the tendency
66 of lineages to retain their ancestral biome occupancies during diversification^{12,13,17,18}. Under
67 this hypothesis, the emergence of plant diversity in a certain biome would be driven primarily
68 by speciation that occurred within its boundaries, rather than by shifts among biomes¹⁸.

Although numerous studies have provided evidence for phylogenetic biome conservatism^{12,14,19,20}, the generality of this pattern at a global scale remains contested. Some lineages (e.g., Bombacoideae) exhibit frequent biome shifts²¹, i.e., the expansion or change of biome occupancies through dispersal and adaptation. Further, most studies are clade-specific^{14,19,22–25}, taxonomically limited or confined to a particular region (e.g., the Southern Hemisphere¹² or Neotropics²⁶) and a subset of the global biomes. Establishing phylogenetic biome conservatism as a prevalent, global pattern would support the view of biomes as relatively impermeable evolutionary arenas. This functional analogy to islands provides a critical theoretical foundation for extending the Theory of Island Biogeography to interpret the macroevolutionary dynamics of the global flora.

The Theory of Island Biogeography emphasizes the roles of area and isolation in shaping diversity and has therefore been extended occasionally to other isolated systems, such as sky islands^{27,28}. If biomes with contrasting environments also follow the predictions of island biogeography, larger and better-connected biomes should receive more lineages from other biomes (i.e., immigration events)^{26,27,29}. Furthermore, dispersal between biomes is likely constrained by both geographic and environmental distance; geographically proximate and environmentally similar biomes should experience more frequent floristic interchange¹³. However, biomes do not function just as analogs of islands, as for biomes there is no “mainland” serving as the external source of biodiversity. Consequently, the evolutionary dynamics of biomes are likely to be more complex than those of isolated islands, influenced by the interplay of within-biome diversification, extinction, immigration, the contribution of lineages to other biomes (i.e., emigration events), and the dynamics of the biome distribution through time⁸. Given the complex evolutionary dynamics, the intrinsic evolutionary histories of biomes may substantially influence biome-shift processes in addition to their biogeographic attributes^{13,26,30,31}. Examining the relative roles of speciation and dispersal, together with the

94 evolutionary and (bio-)geographic factors underlying them, is therefore essential for
95 understanding the macroevolutionary processes that shaped the diversity and assembly of
96 modern biotas.

97 Here, we aim to explore how the spatial structure of environmental conditions mediates the
98 emergence of plant diversity by testing the generality of biomes as evolutionary arenas and
99 investigating the dynamics of biome shifts. To capture this complexity, we utilize well-dated
100 phylogenies from 160 vascular plant lineages and analyze these across ten widely recognized
101 biomes³² and six floristic realms³³. Because patches of the same biome type can differ
102 substantially in area, species richness, and evolutionary history across different regions, this
103 explicit geographic context is vital to prevent obscuring underlying shift mechanisms. Using
104 an extended phylogenetic comparative model that jointly reconstructs the evolutionary
105 histories of biome occupancy and floristic realm affiliation across clades, we tested the
106 phylogenetic biome conservatism hypothesis by quantifying biome shift frequencies and
107 comparing them against null expectations. We then partitioned the relative contribution of
108 speciation and dispersal in shaping current plant diversity and assessed the effect of area,
109 connectivity, evolutionary history, species richness, as well as geographic and environmental
110 distance on biome shift dynamics. Building on these results, we propose a framework
111 illustrating how biomes, as evolutionary arenas, structure the accumulation and interchange of
112 global plant biodiversity through their environmental boundaries, spatial configurations, and
113 evolutionary histories, providing an integrated perspective on the formation of global
114 biodiversity.

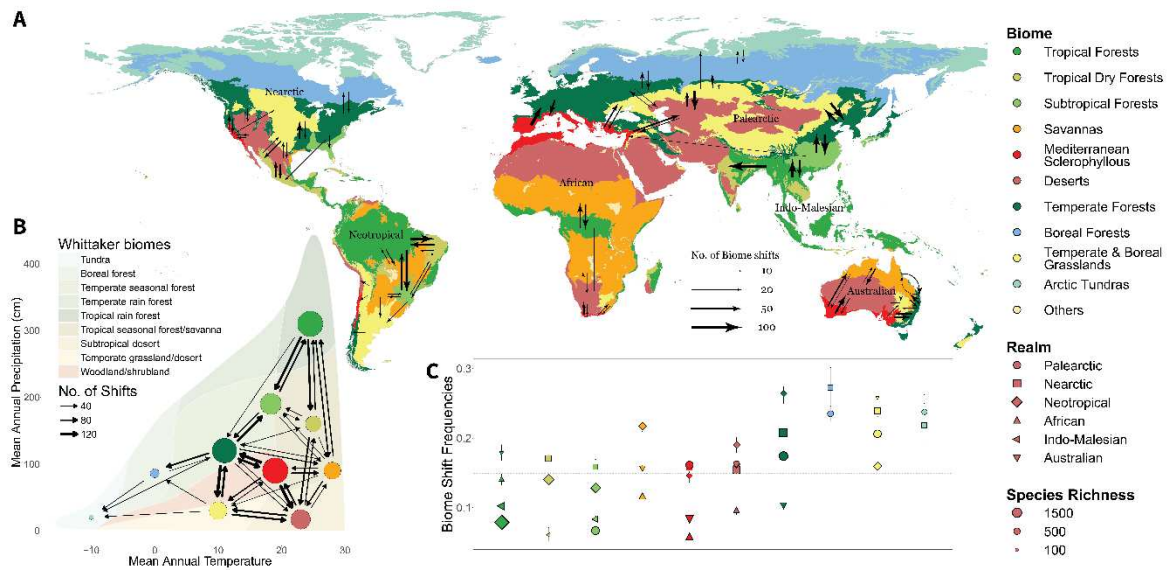


Fig. 1. General assessment of biome conservatism and frequencies of biome shifts. (A) Biome map (modified from Olsen et al.) showing six floristic realms (“Others” refer to other biome types that are azonal (Flooded Grasslands and Mangroves) and are thus not included in our analysis). Shifts between biomes within each realm are indicated by arrow width. Very rare shifts (<5) are not shown for figure clarity. Biome patches of the same type within a realm are treated as a single unit. For example, arrows showing shifts between temperate grasslands and temperate forests in the Palearctic are drawn toward temperate forests in East Asia, but the underlying counts also include shifts involving temperate forests in Europe. **(B)** Shifts between biomes across all six floristic realms projected onto Whittaker’s biome framework in environmental space defined by mean annual temperature and mean annual precipitation. Positions of some circles were slightly adjusted for figure clarity. Circle size represents the number of extant species studied within each biome; arrow width reflects the absolute number of shifts between two biomes. Very rare shifts (<30) are excluded for figure clarity. **(C)** Biome shift frequencies across biomes and floristic realms, based on 100 randomly sampled reconstruction results. Solid dots indicate mean biome shift frequencies, and error bars indicate

the 25 to 75% quantile intervals of estimated frequencies. The black dashed line indicates the mean realized biome shift frequency.

Phylogenetic biome conservatism confirms biomes as evolutionary arenas

Analyzing 160 plant clades representing ~20,000 species from ~20% of all vascular plant families (>60% of all plant orders) across all major global biomes (Table S9), we identify a pervasive pattern of biome conservatism. Based on ancestral state reconstructions, we calculated biome shift frequencies as the proportion of phylogenetic branches where a descendant node occupies a different biome than its ancestor²⁰. Cross-realm dispersals were identified similarly. An observed biome shift frequency of ~14.8% indicates that a descendant lineage is more than 6 times more likely to remain within the same biome than to colonize a new one. This observed frequency is, on average, 30% lower than the null expectations with randomized tip states (Fig. 1C, Fig. S1), providing strong evidence for biome conservatism as the prevailing global pattern in plant speciation¹⁹. This finding is robust to incomplete species sampling: randomly dropping up to 70% of species across 99 ancestral state reconstructions revealed a significant negative relationship between sampling fractions and the estimated biome shift frequencies (Fig. S2, Pearson's $r = -0.94$, $p < 0.01$). Thus, actual biome shift frequencies are likely even rarer than our global estimates indicate, solidifying the support for phylogenetic biome conservatism.

Consequently, biome-level plant diversity is driven primarily by in situ speciation rather than cross-biome shifts (Fig. 2A), underscoring the central role of speciation in generating biodiversity at large spatial scales³⁴. By quantifying the relative contributions of speciation events, within-realm biome shifts, and cross-realm dispersal events (including both with and without biome shifts) to global floristic assembly, we evaluated their explanatory power for

contemporary biome-level richness. Speciation emerges as both the most frequent historical process and the strongest predictor, explaining ~86% of the variance in biome-level richness of plants (Fig. 2, B and C). Biome shifts contribute substantially but more modestly, accounting for ~12% of the observed variation (Fig. 2B). In contrast, cross-realm dispersals are generally rare (~3%, Fig. 2A) and explain little (~2%) of the standing richness, with the notable exception of cold biomes in the Nearctic and Palearctic, which exhibit frequent exchanges, likely via Beringia (Fig. 2A).

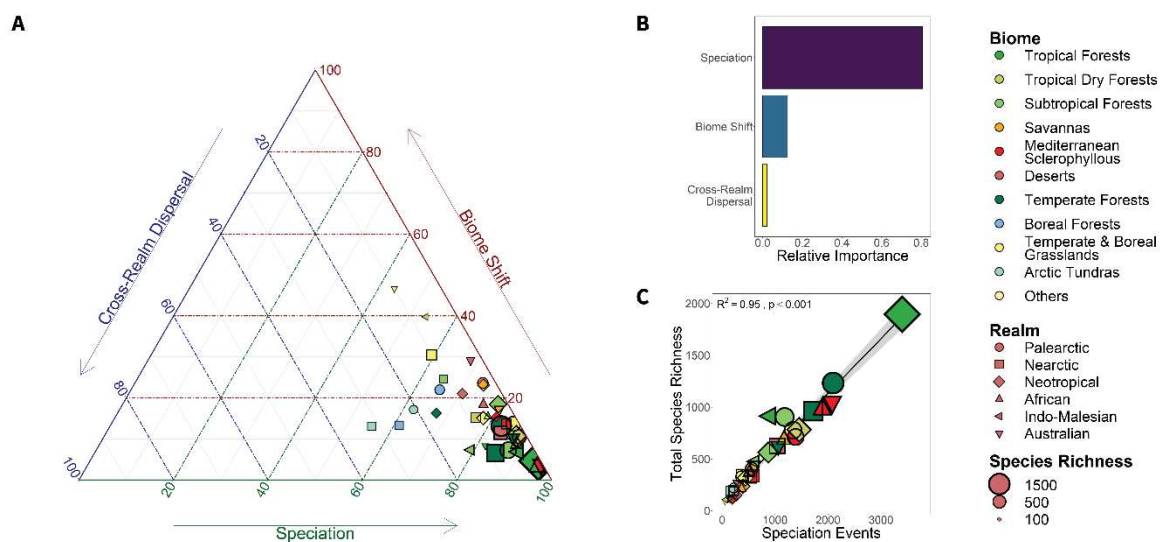


Fig. 2. Relative contributions of historical biogeographic processes to the assembly of contemporary biome-level plant diversity. (A) Proportions of within-biome speciation, within-realm biome shifts, and cross-realm dispersals (including realm dispersals both with and without biome shifts) occurring across different biomes. (B) Relative importance of the frequencies of different historical events in explaining current biome-level biodiversity patterns. (C) Relationship between the number of within-biome speciation events and current total plant richness across biomes.

Asymmetric biome shifts mediated by biogeographic configurations and evolutionary histories

While phylogenetic biome conservatism emerges as a prevailing pattern, the biome shift frequencies vary substantially among biomes and floristic realms, revealing pronounced asymmetry. Tropical forests and Mediterranean sclerophyllous ecosystems consistently contribute more lineages than they received, acting as evolutionary sources, whereas boreal forests and arctic tundra primarily act as sinks (Fig. 1B). Temperate forests exhibited high levels of both emigration and immigration, suggesting a distinct role as macroevolutionary crossroads (Fig. 1B).

To investigate hypothesized mechanisms underlying the varying degree of biome shifts¹³, we used Bayesian linear regression to model biome shifts as a function of biome area, connectivity, evolutionary time, and biome-specific cumulative branch lengths. These biogeographic and evolutionary attributes strongly explain biome shift dynamics (Bayesian $R^2 = 0.78$ for emigration events, 0.49 for immigration events, and 0.58 for the log-ratio of emigration to immigration events). Residuals of cumulative branch lengths against evolutionary time and area emerge as the strongest predictors of both emigration and immigration events (emigration: standardized coefficient = 0.67, highest posterior density [HPD] interval = 0.63–0.71; immigration: standardized coefficient = 0.32, HPD interval = 0.27–0.35). Biomes harboring greater cumulative lineage diversity within a given area and period exhibit more frequent biome shifts (Fig. 3, A, B, E, and F). Furthermore, the directionality of biome shifts is also governed by cumulative branch lengths (log-ratio: standardized coefficient = 0.33, HPD interval = 0.16–0.49), alongside a significant effect of evolutionary time (standardized coefficient = 0.42, HPD interval = 0.25–0.58) (Fig. 3 I-L). Species-rich biomes that were occupied earlier in evolutionary history were more likely to function as donors, whereas recently colonized,

species-poor biomes tend to act as sinks, likely reflecting a greater availability of unfilled ecological niches. For instance, boreal forests and Arctic tundra have experienced substantial climatic instability^{35,36}, making them susceptible to lineage turnover. This reduced niche saturation may predispose these biomes to function as macroevolutionary sinks³⁷ (Fig. 3, I, J and K).

Consistent with the Theory of Island Biogeography²⁷, larger and more connected biomes tend to receive more lineages (area: standardized coefficient = 0.25, HPD interval = 0.21–0.29; connectivity: standardized coefficient = 0.04, HPD interval = 0.01–0.07) (Fig. 3, E and H). This helps explain the high influx of lineages into temperate forests, which encompass 14% of the total terrestrial biome areas and are highly connected, particularly within the Palearctic (Fig. 3H). Conversely, the effects of area and connectivity on emigration are much weaker (area: standardized coefficient = 0.19, HPD interval = 0.15–0.24; connectivity: standardized coefficient = 0.02, HPD interval = –0.01–0.04). Instead, historical factors play the prominent role in emigration (standardized coefficient = 0.60, HPD interval = 0.56–0.64), with biomes possessing longer evolutionary histories accumulating more donor contributions over time (Fig. 3, A and C).

Overall, beyond the dominant pattern of biome conservatism, biome shift dynamics are strongly mediated by biotic, biogeographic, and historical attributes of the biomes themselves. By considering biome shifts as a key process of global floristic assembly alongside within-biome speciation and deriving implications from island biogeography, our results provide evidence for a highly structured, biome-centred framework on global floristic assembly.

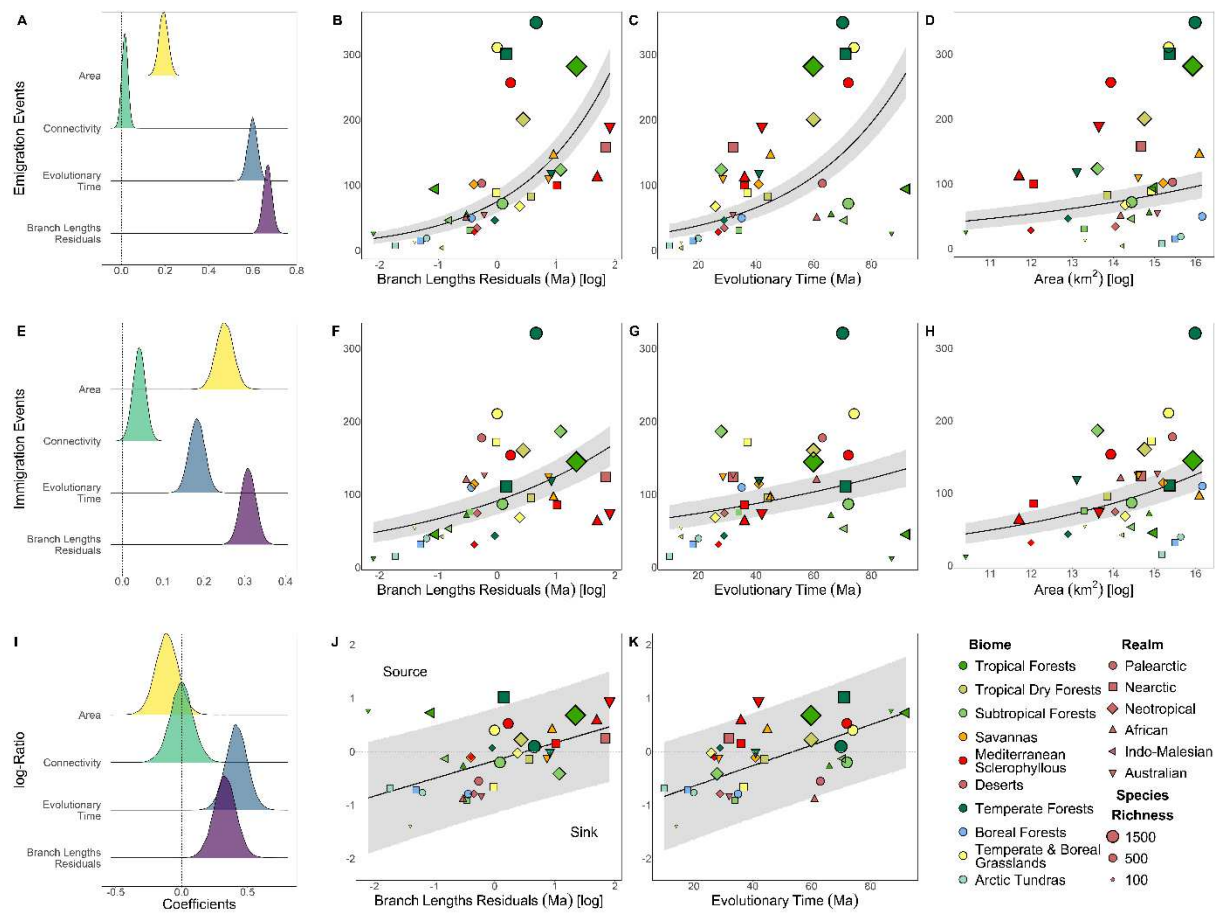


Fig. 3. Biome shift dynamics mediated by biogeographic, historical, and biotic attributes.

(A, E, I) Posterior distributions of Bayesian regression coefficients for predictor variables of (A) Emigration events, (E) Immigration events, and (I) the log-ratio of immigration to emigration events. Black dashed lines indicate 0. (B-D, F-H, J-K) Partial effect plots for (B-D) Emigration events, (F-H) Immigration events, and (J-K) the log-ratio of the number of emigration to immigration events, shown for variables with >90% of the posterior distribution either above or below. This threshold indicates strong support for coefficients differing from zero (Bayes factor > 10) and thus a directional effect of the predictor variables. Gray dashed lines in (J-K) indicate a log-ratio value of zero, suggesting balanced emigration and immigration. Points above this line represent biomes functioning as sources of biome shifts (more emigration than immigration), whereas points below represent sinks. Point size is proportional to the total number of included species in occurring in the biome. The fitted Lines

indicate posterior mean predictions with the other predictor variables fixed at mean values; shaded areas denote 95% credible intervals.

Pairwise biome exchange structured by geographic and environmental distance

In addition to the role of individual biome properties, we further investigated the mechanisms governing transitions between specific biome pairs. Floristic interchange is most frequent between environmentally similar biomes (Fig. 1B). Notably, we observe more than 200 shifts between biomes with comparable environmental conditions, such as tropical and subtropical forests³⁸. In contrast, transitions decrease between environmentally dissimilar biomes (e.g., tropical and temperate forests) and are rare between highly distinct biomes, such as tropical and boreal forests (Fig. 1B). However, environmental similarity alone does not fully explain these patterns. For example, transitions between tropical dry forests and subtropical forests are rare despite the proximity in environmental conditions, especially when contrasted with the frequent shifts between subtropical and temperate forests (Fig. 1B). This reduced shift frequency is likely due to limited geographic proximity: tropical dry forests are concentrated in the Indian subcontinent and Mexico, largely isolated from major subtropical forests systems of East Asia, Australia, and Florida (Fig. 1A). Therefore, environmental similarity and geographic proximity act jointly, yet partly independently, in offering opportunities for floristic interchange¹³.

This joint role was also confirmed by a Bayesian model explaining pairwise biome shift frequencies while controlling for combined branch lengths within biomes (Bayesian $R^2 = 0.66$). Geographic proximity exerts the strongest influence (standardized coefficient = 0.56, HPD interval = 0.52–0.60), with more frequent shifts occurring between biome pairs sharing longer boundaries (Fig. 4A). This supports previous findings that niche and biome shifts tend to follow

geographically available opportunities³⁹, explaining, for example, the high frequency of shifts from tropical forests to savannas in Africa and to tropical dry forests in the Neotropics (Fig. 4B)^{40,41}. Environmental similarity also significantly predicts biome shift patterns (thermal similarity: standardized coefficient = 0.14, HPD interval = 0.10–0.18; moisture similarity: standardized coefficient = 0.02, HPD interval = –0.02–0.05) (Fig. 4A) and can substantially facilitate transitions between biomes lacking shared boundaries. For instance, despite extreme geographic isolation between Mediterranean sclerophyllous forests and Palearctic subtropical forests, notable shifts occur between them, likely facilitated by pre-existing traits that enable adaptation to similar environments¹³ (Fig. 4C).

Together, our results highlight how geographic proximity increases opportunities for dispersal, while environmental similarity reduces ecological barriers to establishment^{13,42}, emphasizing the profound role of spatial and environmental structures in shaping macroevolutionary dynamics.

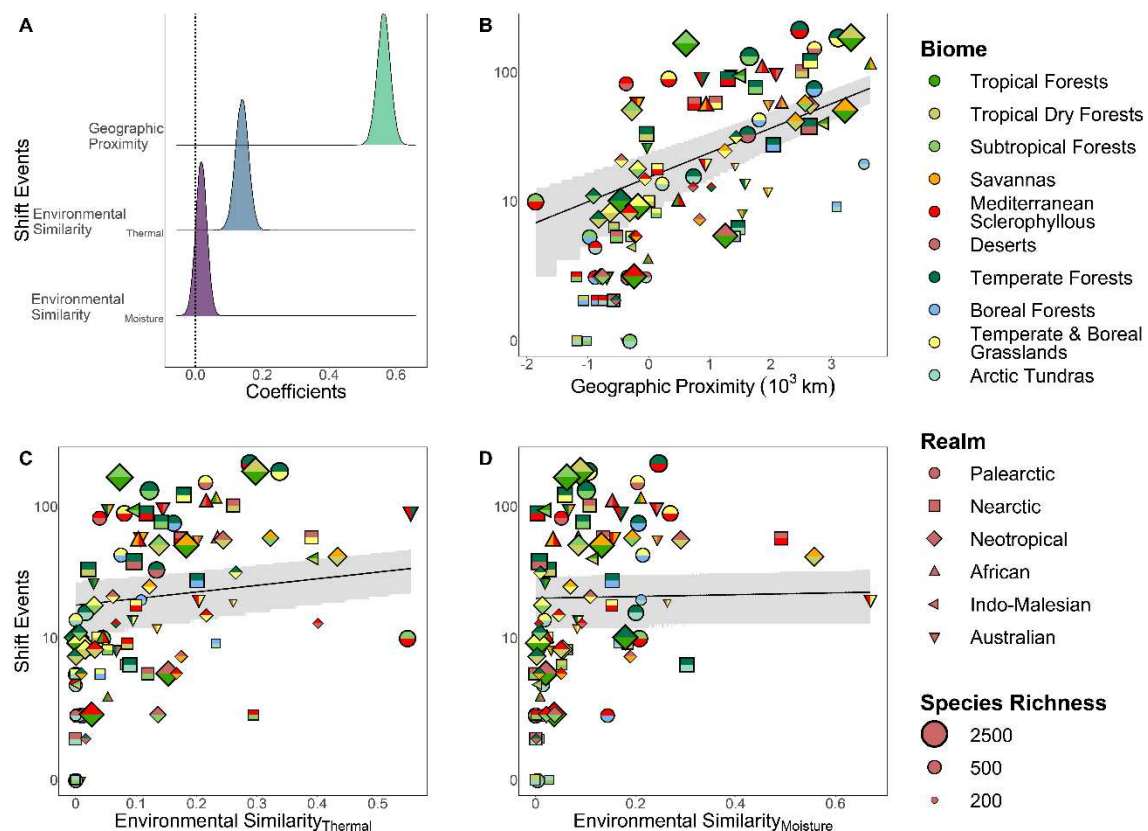


Fig. 4. Geographically closer and environmentally similar biomes exhibited more biotic interchange. (A) Posterior distributions of Bayesian regression coefficients for the effects of geographic proximity and environmental similarity on biome shifts between biome pairs. Black dashed line indicates 0. (B-D) Partial effect plots of biome shifts for (B) Geographic proximity, (C) Thermal similarity, and (D) Moisture similarity. Points represent the number of biome shifts between biome pairs indicated by the two inner fill colours. Point size is proportional to the total number of species included in occurring in the paired biomes. The fitted Lines indicate posterior mean predictions with the other predictor variables fixed at mean values; shaded areas denote 95% credible intervals.

A biome-centred biogeographic framework on global floristic assembly

Geographically isolated regions (e.g., islands or most floristic realms) fundamentally shape the evolution of biodiversity^{33,43,44}. Our analyses reveal that, alongside geographic constraints, the emergence of plant diversity is heavily structured by the environmental boundaries defined by biomes. Biodiversity assembly is largely constrained within the environmental space of individual biomes, whereas biotic interchange follows predictable patterns determined by biome spatial configurations. These findings underscore the necessity of integrating the spatial organization of environmental conditions into models of global floristic assembly^{5,42}. Synthesizing data across multiple plant lineages, floristic realms, and biomes, we propose a coherent biome-centred framework: biomes function as evolutionary arenas that structure the emergence of global plant diversity through two complementary processes: diversification constrained within environmental boundaries and predictable biome shifts mediated by spatial biome configurations and evolutionary history (Fig. 5).

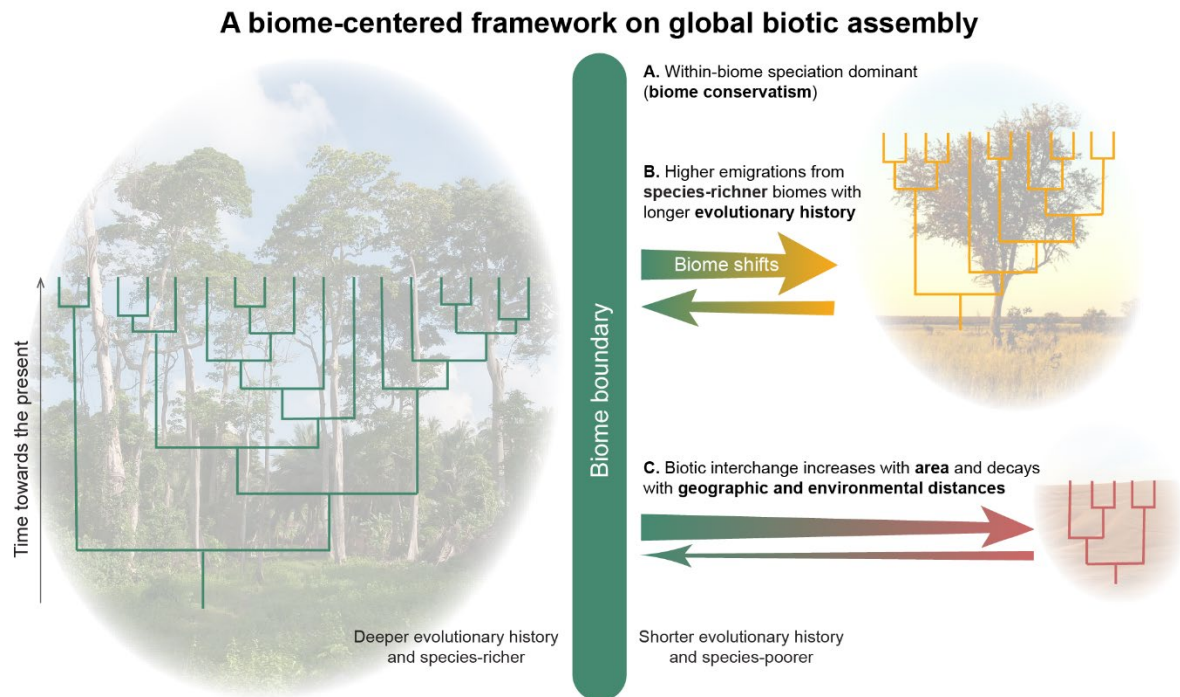


Fig. 5. A biome-centred synthesis framework on global floristic assembly. Plant diversity across biomes arises from two fundamental processes: the origination of new lineages through speciation and their interchange among biomes through biome shifts. Three biomes (tropical forests, left; savannas, upper right; deserts, lower right) are illustrated within a conceptual geographic space. The vertical green bar indicates biome boundaries of tropical forests with respect to the other two biomes. Phylogenetic trees illustrate within-biome lineages, with a higher number of tip nodes indicating greater species richness and longer branch lengths indicating deeper evolutionary history. Arrows represent biome shifts between biomes, with arrow widths indicating biome shift frequencies. Colours at trailing end of arrows correspond to the colours of phylogenetic trees in the donor biome, while colours at the tipping end correspond to those of recipient biomes. Three major rules (**A-C**) structure the global floristic assembly processes. (**A**) Biome conservatism: most speciation occurs within biome boundaries. As a result, within-biome speciation serves as the primary source of biodiversity at the biome level. (**B**) Effect of evolutionary history and resident plant diversity on biome shift dynamics:

biomes with longer evolutionary histories and greater species richness (e.g., tropical forests) tend to experience more emigration events, acting as sources of biome shifts. In contrast, biomes with shorter histories and lower biodiversity (e.g., savannas and deserts) exhibit fewer emigration events and function as sinks. (C) Insights from and similarities to the theory of island biogeography applied to biome shifts: larger and better-connected biomes (here, savannas) tend to receive more immigrations, while smaller, more isolated biomes (here, deserts) receive fewer. In consequence, biotic interchange between biomes declines with both geographic and environmental distance and increases with area. Image credits: Tropical forest photograph by Vyacheslav Argenberg (CC BY 4.0); Savanna photograph by Javier Puig Ochoa (CC BY 3.0); Desert photograph by Aidas U. (CC BY 3.0).

By confirming biomes as evolutionary arenas^{14,16} (Fig. 5A), we show that despite frequent biome shifts in certain clades, phylogenetic biome conservatism remains the dominant global pattern. Robust to sampling bias and consistent with smaller scale studies^{14,19,23}, the confirmed biome conservatism confines most diversification within biome boundaries, with lineages retaining ancestral biome occupancy over evolutionary timescales. Biomes are therefore not merely products of contemporary environments: they impose persistent constraints on macroevolutionary processes, structuring where diversification occurs, how lineages disperse, and why biodiversity is globally unevenly distributed^{15,16}.

Consequently, biome-scale biodiversity is primarily assembled through within-biome speciation, complemented by predictable shifts between differing environments (Fig. 5, B and C) that provide source elements for further speciation, acting as pumps of evolutionary innovation^{16,45,46}. Since biomes and islands similarly impose evolutionary constraints, the Theory of Island Biogeography offers valuable predictive power in explaining biome shift

329 dynamics: larger and better-connected biomes experience more immigration^{27,47}, and biomes
330 closer in geographic and environmental space exhibit greater biotic interchange (Fig. 5B).
331 However, unlike islands that rely on a mainland source^{27,47,48}, biomes rely on in situ speciation,
332 harboring far more complex evolutionary dynamics. Our framework extends island
333 biogeography by explicitly incorporating distinct evolutionary histories of biomes.
334 Evolutionary diversity provides the biological foundation for biome transitions, while
335 evolutionary time since occupancy exerts a cumulative effect. Biomes of larger size, longer
336 evolutionary histories, and greater accumulated species richness experience more emigration
337 and immigration, functioning as primary sources of biome shifts (Fig. 5C).

338 Ultimately, this study lays the groundwork for a mechanistic understanding of how
339 macroevolutionary processes and long-term changes in the spatial structure of global
340 environmental conditions have jointly shaped the assembly of global flora⁵. Future realizations
341 of this framework's full potential will require expanded phylogenetic sampling, particularly in
342 the tropics, and the explicit modelling of biome dynamics over evolutionary timescales that
343 consider changes in biome distribution, area, and connectivity^{49,50}.

Methods

Data preparation

We compiled dated phylogenies of biome-representative plant clades from public repositories and requests to authors of published studies. In total, our dataset comprises 160 well-dated, well-sampled phylogenies, representing approximately 20,000 species (~6% of all vascular plants), 84 families (~20%), and 40 orders (62.5%) (Table. S8). The total dataset provides broad coverage across geographic regions and biomes, as well as diverse life forms, ensuring representativeness of global vascular plants (Table. S9). For each clade, we standardized species names using the plants of the world (POWO) database via the R package rWCVP and removed duplicate synonyms to prevent overestimation of biome conservatism⁵¹. All climate variables were taken from the Climatologies at high resolution (1 km) for the earth's land surface areas (CHELSA) data⁵². All species distribution data were requested from the Global Biodiversity Information Facility (GBIF)⁵³ and combined with nativeness information at the level of botanical countries⁵⁴ provided by the World Checklist of Vascular Plants (WCVP)^{51, 55}. For each species, all occurrences were extracted from the GBIF download and filtered by record type (HUMAN_OBSERVATION, OCCURRENCE, OBSERVATION, MACHINE_OBSERVATION, or PRESERVED_SPECIMEN), observation year (≥ 1900), coordinate uncertainty (≤ 5 km or missing), CoordinateCleaner v3.0.1 (with the tests 'capitals', 'centroids', 'gbif', 'institutions', 'seas', and 'zeros')⁵⁶, and restricted to the species' native botanical countries. Finally, the filtered occurrences were rasterized into species-specific presence-only layers at the 1-km spatial resolution of the CHELSA climate data [*these data have been deposited in Zenodo (reserved DOI: 10.5281/zenodo.20555413) and will be made publicly available upon acceptance, together with a GBIF DOI of a derived dataset to ensure appropriate attribution of GBIF data contributors*].

Joint reconstruction of range and biome evolution with ClaSSE model

To investigate biome conservatism across plant lineages, we reconstructed biome evolutionary histories using biogeographic comparative methods. While approaches modelling biome evolution (e.g., DEC, DIVA)⁵⁷ have been widely applied, previous studies often overlooked two critical factors:

- **Geographic Context:** Prior studies typically treated the same biome type across continents as a single entity, ignoring dispersal and speciation events within the same biome but across distinct geographic regions. This simplification may obscure biogeographic drivers of biome conservatism.
- **Mountain Biomes:** Mountain systems, which create unique environmental gradients and opportunities for adaptation, were rarely explicitly modelled. Their exclusion limited our understanding of how lineages diversified across various habitats in mountain systems.

To address these gaps, we developed a novel framework using cladogenetic state-dependent speciation-extinction (ClaSSE) models⁵⁸, which jointly simulated biome occupancy, geographic range evolution, and lineage diversification (birth-death processes), while incorporating mountain biomes as distinct states. This approach statistically accounted for unobserved speciation/extinction events and incomplete sampling, providing, what we consider, a more robust inference of biome evolution.

Species assignment to biomes and geographic ranges

To implement our model, each species needed to be assigned to one or more biogeographic ranges and biomes. This required defining and delineating biogeographic areas and biomes on a global scale.

The classification and delineation of biomes have long been controversial due to the lack of consensus on a biome's definition and standard criteria for biome mapping, leading to multiple biome schemes with varying biome classifications. To minimize bias in biome delineation, we did not refer to a single biome scheme. Instead, we synthesized insights from prior research and our expertise to define 10 focal biomes for further analysis³². The 10 biomes are: Tropical Forest, Tropical Dry Forest, Savanna, Subtropical Forest, Mediterranean Sclerophyllous, Temperate Forest, Boreal Forest, Temperate and Boreal Grassland, Arctic Tundra, Dessert.

Additionally, we identified 5 distinct mountain biomes based on global patterns of elevational vegetation belts. Although these biomes share environmental and floristic characteristics with their corresponding lowland counterparts and were therefore classified under the same biome types, we modelled them separately to account for their unique evolutionary histories. The mountain biomes include Laurel Forest (corresponding to Subtropical Forest), Cloud Forest (Temperate Forest), Subalpine Forest (Boreal Forest), Montane and Subalpine Grassland (Temperate and Boreal Grassland), and Alpine Tundra (Arctic Tundra).

To create a global biome map, we adapted the OneEarth biome classification system⁵⁹ due to its strong alignment with our scheme and its demonstrated mapping accuracy. Where necessary, we implemented the following modifications. For biomes present in its scheme but not in ours, we reclassified them as follows:

- Tropical Conifer Forest: Merged into Tropical Dry Forest in the Americas due to moisture constraints, and into Tropical Forest in Asia, where it occurs at higher elevations with sufficient moisture but lower temperatures.
- Temperate Conifer Forest: Merged into Temperate Forest.

For the biome that was only in our scheme, delineation was based on our expertise knowledge:

- Subtropical Forest: defined to include three main regions: Middle-South China, Florida, and Paraná.

We delineated geographic ranges by synthesizing the updated floristic regions from Liu et al.³⁶ with zoogeographic realms from Holt et al.⁶², identifying six biogeographic realms: Palearctic (Eurasia and North Africa), Nearctic (North America), African (Sub-Saharan Africa), Neotropical (South America), Australian, and Indo-Malesian (Indian subcontinent and islands). Given that realm boundaries are often transitional, we additionally identified three transitional zones: Palearctic-Indo-Malesian, Palearctic-African, and Nearctic-Neotropical.

To map these realms globally, we adapted the biogeographic realm maps from Liu et al. and Holt et al., with the following modifications:

- The Holarctic realm in Liu et al. was divided into two realms, Palearctic and Nearctic, following Holt et al.
- The Australian and Novozealandic realms in Liu et al. were merged as Australian realm.
- The Neotropical and Chile-Patagonian realms in Liu et al. were merged as Neotropical realm.
- The Saharo-Arabian realm in Liu et al. was designated as the transitional zones between Palearctic and African.
- The Sino-Japanese and Panamanian realms in Holt et al. were designated as the transitional zones of Palearctic-Indo-Malesian and Nearctic-Neotropical, respectively.

To assign species to the biomes and realms, we used a two-step approach: (1) occurrence-based mapping followed by (2) expertise-based manual check. For realm assignment, native ranges were extracted from POWO and mapped to our biogeographic realms. For biome assignment,

GBIF occurrences were overlaid with our modified biome map. While species may occur across multiple biomes, we did not consider all biomes in which there was an occurrence as biomes the species truly occupied. This decision was based on two key considerations: (1) limitations in the geospatial accuracy of biome mapping and occurrence records, and (2) our focus on identifying biomes where species are more abundant and likely to thrive, rather than marginal habitats where they may occur but with lower fitness. To this end, we applied a simple filtering rule: only biomes with an occurrence proportion over 50% of that of the most-occupied biome were retained as the species' final biome assignment. We also recorded the total number of valid occurrences and the proportion of occurrences within mountain regions, based on the GMBA mountain map⁶¹.

Following this initial assignment, we conducted a manual review to ensure the reliability of the assignments. For realm assignment, if a species is assigned to one of the transitional zones, it was re-assigned to one of the relevant core realms based on the general distribution of the genus or its sister species. For example, several *Abies* species were assigned to the transitional zone between Indo-Malesian and Palearctic. Given the genus' general distribution in the Holarctic, we reassigned these species to the Palearctic realm. Additionally, recognizing the distinct biogeographic character of islands, we also identified whether each species was primarily distributed on continents, islands, or both, within its respective realms.

For biome assignment, if more than 50% of a species' occurrences were in mountain regions, or if the species had fewer than 50 total occurrences, we manually reviewed its assignment by checking local floras (e.g., eFlora, www.efloras.org) or relevant literature, adjusting the biome occupancies when necessary, and documenting the used sources. Specifically, for mountain species, we reviewed their elevational ranges and assigned them to corresponding mountain biomes based on global patterns of elevational vegetation belts.

460 *Model design*

461 The model integrated the following processes in biome and geographic evolution (Fig. S4).
462 Here, uppercase letters A and B represent different geographic ranges represented by different
463 floristic realms, lowercase letters i and j denote different biomes, combinations like A_i denote
464 species occupying specific biome i within range A , 0 represents extinction (null distribution),
465 and $\rightarrow$ indicates biogeographic processes:

466 i. Anagenetic processes

467 a. Extinction: This process includes global extinction ($A_i \rightarrow 0$), range contraction
468 ($AB_i \rightarrow A_i$), and biome contraction ($A_{ij} \rightarrow A_i$). These processes were all
469 parameterized by an extinction rate e .

470 b. Range Expansion: Colonization of new geographic ranges within the same biome
471 ($A_i \rightarrow AB_i$) is modelled. This process was parameterized by a range dispersal rate
472 d_r .

473 c. Biome Expansion: Colonization of new biomes within the same geographic range
474 ($A_i \rightarrow A_{ij}$) is modelled. This process was parameterized by a biome dispersal rate
475 by d_b .

476 ii. Cladogenetic processes

477 a. Sympatric speciation: Both descendants inherit the distribution range and biome
478 occupation of the ancestor ($A_i \rightarrow A_i, A_i$). This process was parameterized by a
479 sympatric speciation rate λ_{sym} .

480 b. Subset sympatric speciation: One descendant inherits the full distribution ranges
481 and biome occupations of the ancestor while the other inherits only one distribution

482 range ($AB_i \rightarrow AB_i, A_i$), or one biome occupation ($A_{ij} \rightarrow A_{ij}, A_i$), or both
483 ($AB_{ij} \rightarrow AB_{ij}, A_i$). This process was parameterized by a sympatric speciation rate
484 λ_{subsym} .

485 c. Allopatric speciation: One descendant inherits a single range or biome, while the
486 other inherits the remaining ranges ($AB_i \rightarrow A_i, B_i$) or biomes ($A_{ij} \rightarrow A_i, A_j$).
487 This process was parameterized by a sympatric speciation rate λ_{allo} .

488 For cladogenetic processes, we enumerated the m possible cladogenetic scenarios and assigned
489 each the rate λ/m .

490 It is worth noting here that:

491 i. Full sympatric speciation was not considered: We excluded speciation processes in which
492 the two descendants both inherit the multiple distribution ranges and/or biome occupations
493 of the ancestor ($AB_i \rightarrow AB_i, AB_i / A_{ij} \rightarrow A_{ij}, A_{ij}$), as this would require simultaneous
494 speciation in multiple ranges or biomes, which does not make much sense biologically in
495 our context.

496 ii. Jump dispersal was not considered: We excluded speciation processes in which one
497 descendant inherits the distribution range or biome occupation of the ancestor while the
498 other colonizes an unoccupied distribution range or biome ($A_i \rightarrow A_i, B_i / A_i \rightarrow A_i, A_j$).
499 Instead, such scenarios were modelled as sequential processes: dispersal followed by
500 allopatric speciation ($A_i \rightarrow AB_i \rightarrow A_i, B_i$).

501 iii. Dispersal between zonal biomes and mountain biomes of the same type was treated as
502 range expansion rather than biome shift: In dispersal event ($A_i \rightarrow A_{ij}$), when i and j
503 represent a zonal biome and a mountain biome of the same type (e.g., Arctic Tundra and

Alpine Tundra, respectively), this event was classified as a range dispersal instead of a biome transition. It was also parametrized by the range dispersal rate d_r .

Model implementation

For each clade, the model incorporated discrete states representing all possible combinations of realms and biomes it occupied. For a clade occupying n realms and m biomes, theoretically there should be $2^n - 1$ possible geographic ranges and each range is associated with $2^m - 1$ possible biome occupancies. When a clade occupied multiple realms and biomes, the number of states might become computationally prohibitive (e.g., 961 states for a clade occupying 5 realms and 5 biomes). Therefore, we applied several constraints to control the number of states and maintain computational feasibility:

- i. Limiting number of realm and biome: States associated with more than two realms or biomes were excluded unless they were observed in at least one extant species within the clade.
- ii. Removing impossible combinations: States combining realms and biomes that do not co-occur were excluded. For example, if a clade spanned the Indo-Malesian realm and occupied Mediterranean sclerophyllous biomes (in other realms), any state combining the two was removed, as Mediterranean sclerophyllous does not occur in the Indo-Malesian realm.
- iii. Excluding biologically implausible co-occurrence: States indicating co-occurrence of biomes with highly contrasting environments or realms with distinct evolutionary histories were excluded (Table. S10, Table. S11). For instance, combinations such as tropical forests and tundra, or the Australian and Nearctic realms, were deemed ecologically and biogeographically implausible for single species.

iv. Filtering mountain biome states across multiple realms: States associated with mountain biomes and multiple realms were excluded, as mountain species rarely have broad cross-realm distributions.

The model was implemented in RevBayes⁶². We specified informative priors according to previous studies⁶³ (Table S12). For each clade, we estimated the Bayesian posterior distribution using Markov chain Monte Carlo (MCMC) sampling. A preliminary run was performed to tune proposal parameters, followed by a main MCMC run of 2000 generations, with a burn-in of 200 generations. All posterior estimates had effective sample sizes (ESS) well over or near 200. We then used stochastic mapping⁶⁴ to generate posterior simulations of range and biome evolution consistent with each clade's phylogeny and observed tip states.

Synthetic analysis

To account for model uncertainties, all subsequent analyses were repeated 100 times by randomly sampling 100 out of 2000 generations from the MCMC chains for each clade and applying the analysis to each randomly sampled result. Given that islands and mountain biomes often have distinct evolutionary histories and unique climatic conditions, and that common principles underlying biome shifts proposed by previous studies may not apply to transitions from continents to islands or along elevational gradients, all island biomes and all mountain biomes were excluded from following analysis. All follow-up analysis was performed in R 4.4.1.

Identifying biome shifts

Biome shift events were identified based on ancestral state reconstructions by comparing biome occupancy between ancestral nodes and their descendants. Specifically, each speciation event in the phylogeny involves an ancestral node and two descendant nodes. A transition was defined

as the evolutionary path between an ancestral node and each of its descendant nodes (thus, each speciation event corresponds to two transitions). For each transition, we compared the biome occupancy of the ancestral and descendant nodes. A transition was classified as a biome shift if the descendant node occupied a biome that does not present in the ancestor (Fig. S5)²⁰. The biome shift frequency was then calculated as the proportion of biome shift transitions relative to the total number of transitions.

To further explore variations in biome shifts frequencies across biomes and biogeographic realms, we calculated biome shift frequencies separately for each biome and realm. For each biome, we first identified all transitions where the ancestral node occupied that biome and then computed the shift frequency of this biome type as the proportion of those transitions identified as biome shift. Similarly, for each biogeographic realm, we considered transitions where both the ancestral and descendant nodes were confined to that realm and calculated the biome shift frequency of this realm as the proportion of biome shifts within those transitions

Additionally, for each biome shift transition, we recorded the specific biome pair involved (i.e., from which biome to which other) and quantified the bi-directional numbers of shifts occurring between each biome pair. We also counted, for each biome in each realm, the number of biome shifts with the biome as donors (i.e., *Emigration* events) and that of biome shifts with the biome as recipients (i.e., *Immigration* events). The *LogRatio* of immigration versus emigration events was also calculated for each biome, with a positive value indicating the biome receive more than it donates, thus more likely to be the sink instead of source of biome shift.

Assessing biome conservatism

Frequencies of biome shifts are often used as indicators of biome conservatism. However, there is little consensus on the absolute threshold at which biome occupancy can be considered

“conserved”. For example, one study inferred low biome conservatism from just three biome shifts within a clade of 17 species²², whereas another considered biome occupancy conserved despite biome shift frequencies approaching 50%²⁰. To better assess biome conservatism, we did not rely solely on absolute biome shift frequencies. Instead, we compared observed frequencies with a null distribution generated by randomizing tip states. Specifically, for each clade, we randomized tip states and re-ran ancestral state reconstructions 99 times using a shorter MCMC length (200) for computational feasibility. The resulting biome shift frequencies from randomization formed the null distribution, against which we compared the observed values. Observed frequencies lower than the null expectation indicated that biome assemblages were more phylogenetically clustered than expected by chance, supporting the biome conservatism hypothesis.

Ideally, biome shift identification should be based on complete sampling of all extant species within a lineage, as incomplete sampling can bias biome shift frequency estimates. In particular, neglecting species that occupy unique biome types may lead to underestimation of biome shifts, potentially weakening conclusions about conservatism. Because perfectly or near-perfectly sampled phylogenies were rarely available for our focal clades, we evaluated the potential bias by randomly removing up to 70% of species and re-running ancestral state reconstructions 99 times using a shorter MCMC length (200) for computational feasibility. We then calculated biome shift frequencies for each subsampled dataset and examined their correlation with sampling fraction. A positive correlation indicated that incomplete sampling underestimated biome shift frequencies, whereas a negative correlation suggested the opposite.

Evaluating contributions of different historical biogeographic processes to floristic assembly

To elucidate the relative contributions of different historical biogeographic processes to floristic assembly, we quantified the occurrence of three major processes: local speciation,

biome shifts, and cross-realm dispersal (realm shifts), across biome types and floristic realms. For each phylogenetic transition, we compared the biome and realm occupancy of ancestral and descendant nodes. Transitions in which all biomes occupied by the descendant node were already occupied by its ancestor were classified as speciation events occurring within the descendant's biomes. Transitions in which the descendant occupied at least one biome not occupied by its ancestor were classified as biome shift events. Likewise, transitions in which the descendant occupied at least one new floristic realm were classified as realm shift events. Because biome shifts and realm shifts can co-occur within a single transition, we restricted biome shifts to within-realm events, whereas realm shifts include transitions both with and without biome shifts. To assess the contributions of these processes to contemporary biodiversity patterns, we fitted linear models relating total species richness to the frequencies of the three processes and partitioned their relative importance using the R package relaimpo⁶⁵.

Investigating mechanisms underlying biome shift dynamics

Given that realm shifts are both rare and explain little of the variance in contemporary biome-level biodiversity compared with within-realm biome shifts, subsequent analyses focus exclusively on within-realm biome shifts.

To investigate the mechanisms underlying biome-shift dynamics, we evaluated a set of factors hypothesized to have a potential effect on the biome shifts dynamics (Table. S13-15). These factors included two broad categories: (1) characteristics of individual biomes and (2) properties that describe the proximity or similarity between biome pairs. For factors regarding a single biome, we considered:

- i. Biogeographic factors

To capture basic biogeographic properties, we measured biome area and connectivity following the island biogeography theory.

a. *Area*: the total surface area occupied by each biome (km²).

b. *Connectivity*: quantified as the additive inverse of the mean minimum distance (km) from a focal biome to all other biomes within the same realm.

ii. Historical factor

As a measure of historical context, we estimated the evolutionary *Time* of each biome within each floristic realm, defined as the timing of first colonization in our analyses.

iii. Biotic factor

We used biotic factors to represent the biotic prosperity of each biome. Because simply counting species ignores the evolutionary history, we quantified biotic diversity as the total *Branch Length*.

For factors describing relationships between pairs of biomes, we considered:

i. Geographic proximity

Geographic proximity represents how close two biomes are in physical space. Proximity between biome types *i* and *j* was defined as:

$$GeoProx_{ij} = \begin{cases} b_{ij}, & \text{when } i \text{ and } j \text{ are adjacent} \\ -d_{ij}, & \text{when } i \text{ and } j \text{ are not adjacent} \end{cases}$$

Where b_{ij} is the length of the shared boundary (km) between biomes *i* and *j*, and d_{ij} is the minimum distance (km) between biomes *i* and *j*.

ii. Environmental similarity

Environmental similarity was quantified across two major climatic dimensions relevant to plant distributions: thermal similarity ($ThermalSimi_{ij}$) and moisture similarity ($MositureSimi_{ij}$). We measured ecological similarity as the degree of climatic overlap⁶⁶, using the first 12 bioclimatic variables for the thermal dimension, and the last 7 for the moisture dimension.

To assess how these factors mediate biome-shift dynamics, we used linear models to test their associations with different measures of biome shifts. To identify which biomes are more likely to contribute or receive biological novelty, we modelled the number of shift events involving each biome and the log-ratio of received vs. contributed species as functions of the biogeographic, historical, and biotic predictors (as *Branch Length* might be affected by *Area* and evolutionary *Time*, we hereby used the residuals of *Branch Length* from a linear regression model against *Area* and evolutionary *Time*):

$$Emigration/Immigration/LogRatio \sim Area + Connectivity + Time \\ + Branch Length Residuals$$

To analyse factors influencing pairwise interchange between biomes, we modelled the number of biome shifts between biome pairs (n_{ij}) as:

$$n_{ij} \sim GeoProx_{ij} + ThermalSimi_{ij} + MositureSimi_{ij} + Branch Length_{i+j}$$

We implemented all models in a Bayesian framework using the R package brms^{67–69}. We evaluated multicollinearity among predictors to make sure no variables were with correlations exceeding 0.6. Skewed predictors (*Area*, *Connectivity*, *Branch Length*, *GeoProx*) were $\log(x+1)$ -transformed to improve data normality, and all predictors were standardized to zero mean and unit variance to allow comparison of coefficients. For Count response variables (*Emigration*, *Immigration*, n_{ij}), we fit the model using Poisson distribution. We used

663 weakly informative priors for all coefficients (mean = 0, Sd = 5). Each model was run for
664 1000000 MCMC iterations, with the first 20% discarded as burn-in.

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Data, code, and materials availability: All data and code are available on Dryad (http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/01lj-zWrOOLxrYv6CcezFiW1b5ommEJlQcrXUDyc1Eo). Please note that all phylogenies used in this study were not reconstructed by us. Anyone wishing to use these phylogenies should refer to and cite the original papers (Table. S8) that generated the phylogenies, rather than this study. Specifically, the phylogeny of *Carex* is deposited at Repositorio Institucional Olavide (<https://hdl.handle.net/10433/26944>).

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