

Integrative biogeography: Validating hypotheses of species distribution

DEAR EDITOR,

Biogeography is a scientific field dedicated to the investigation of the origins and distribution patterns of organisms, as well as predicting future alterations in their geographical distributions (Cox & Moore, 2005). However, the majority of conclusions drawn within the field of biogeography are hypothetical. Rigorous testing of these biogeographic hypotheses remains a considerable challenge. This paper presents the concept of “integrative biogeography”, which emphasizes the experimental testing of biogeographic hypotheses through studies on geological history, as well as biotic and abiotic factors (Figure 1).

Geological events have long been recognized as key factors shaping biodiversity patterns (Rahbek et al., 2019). Landmass fragmentation has resulted in the extensive separation of lineages, while landmass collisions have brought together groups with diverse origins. These geological processes increase similarities in the diversity patterns of biotic assemblages. The geological vicariance hypothesis can be evaluated based on congruence between biogeographic reconstructions and geographic history, employing evidence from fossils and molecular phylogenies. The presence of similar fossils in distinct regions enables robust analyses of how continental plate collision and convergence have affected diversity patterns (Hou & Li, 2018). Phylogenetic inferences can also serve to evaluate overarching biogeographic patterns at broad taxonomic, spatial, and temporal scales.

The first step in testing geological hypotheses involves the collection of data pertaining to the focal organisms, their distributions, and related geological events and climatic fluctuations. Subsequently, time-calibrated phylogenetic trees are constructed, which are essential for biogeographic reconstruction and diversification analyses, as well as accurate interpretation of results within an evolutionary framework. Finally, sensitivity analyses are applied to test correlations between geological and paleoclimatic transformation with both species richness and speciation rates.

An increasing body of research has examined geological hypotheses. For example, diversification analyses of pollen fossils combined with molecular data of dipterocarp plants have elucidated how the India-Asia collision facilitated the

dispersal of dipterocarps from India to analogous climatic zones in Southeast Asia (Bansal et al., 2022). Furthermore, phylogenetic reconstructions and observed shifts in the geographic ranges of flowering plants have demonstrated the impact of mountain formation and Asian monsoon intensification on the rich diversity of alpine flora on the Xizang Plateau (Ding et al., 2020). Thus, these studies highlight the substantial influence of geological events on biological patterns, and further demonstrate the utility of evolutionary patterns in deducing geological processes (Zhao et al., 2022).

Environmental variables, such as climatic factors, soil composition, and land cover, are regarded as influential determinants that constrain species distribution and shape species richness gradients (Manel et al., 2020). The latitudinal diversity gradient, wherein species richness peaks near the equator and decreases toward the poles, is one of the most widespread large-scale patterns (Rabosky et al., 2018). One plausible hypothesis accounting for this gradient suggests that temperature affects species richness by increasing speciation rates and reducing extinction rates.

Abiotic hypothesis assessment involves the study of how environmental predictors impact spatial diversity patterns using georeferenced data. Studies exploring abiotic hypotheses typically employ newly generated genetic data or data from public repositories (e.g., GenBank and Dryad), as well as environmental data on potential predictors derived from global databases (e.g., WorldClim, Global Biodiversity Information Facility), to conduct phylogenetic comparative analyses across broad taxonomic and spatial scales. Statistical analyses are then performed to evaluate the robustness of the correlations between key abiotic factors (e.g., annual mean temperature) with species richness and speciation rates within each grid cell. Comparative genomic analyses are conducted to identify potential genes related to thermoregulation. Finally, experiments are undertaken to test the thermal acclimation capabilities of the focal organisms, accomplished through comparisons of gene expression patterns between control and experimental groups.

The proliferation of open datasets and the availability of advanced statistical computing packages such as R have enabled researchers to address groundbreaking questions. Notably, studies have established that annual sea surface temperature plays a pivotal role in shaping the patterns of intraspecific genetic variation and species richness in fish (Manel et al., 2020), including the latitudinal diversity gradient.

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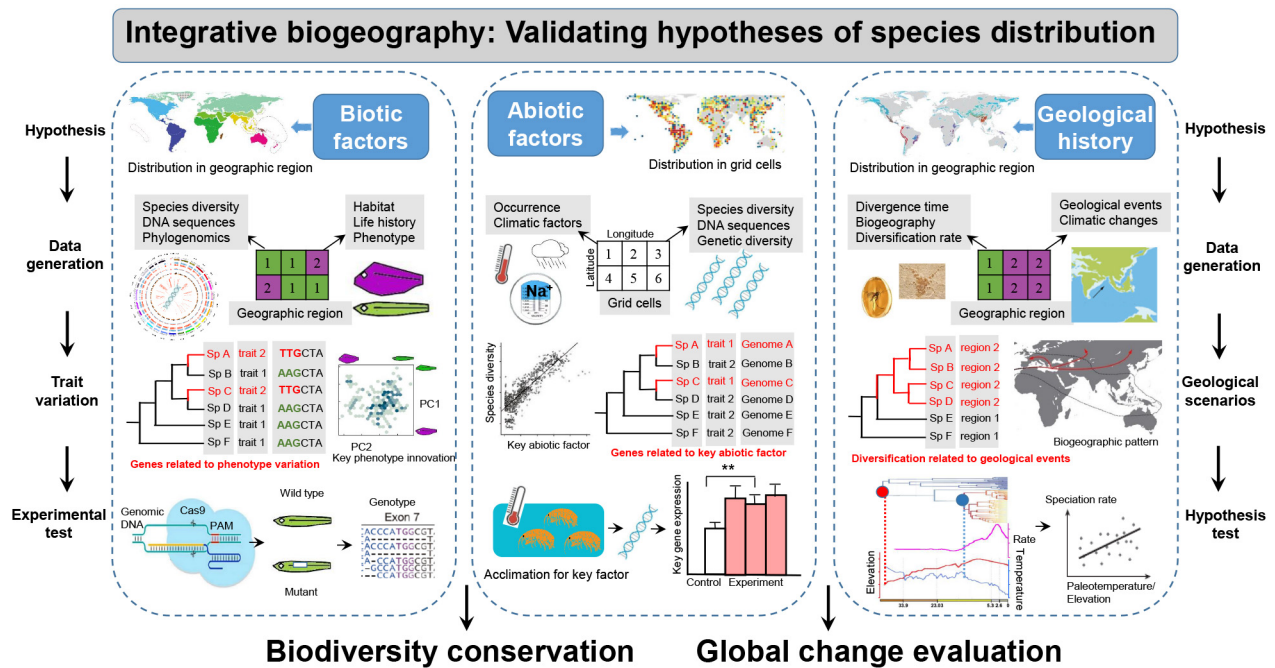


Figure 1 Workflow for integrative biogeography incorporating study of geological history and abiotic and biotic factors to explain biodiversity distribution patterns

Additionally, a robust negative association between speciation rates and both species richness and annual sea surface temperature has been observed, with speciation rates peaking at higher latitudes (Rabosky et al., 2018). The genetic mechanisms underpinning rapid speciation in the cold oceanic regions of the world warrant further investigation. Recent research has focused on clarifying the physiological and genetic mechanisms underlying biogeographic patterns via acclimation experiments, driven by advancements in genome sequencing technologies. For instance, research into the thermal acclimation of intertidal gastropods has revealed that heart rate responses to temperature increases and the up-regulation of genes involved in the protein-folding process have facilitated range expansion (Wang et al., 2022). These studies not only enhance our understanding of the complex correlations between diversity and environmental predictors, but also provide genetic insights into acclimation responses to environmental fluctuations.

While geological events and abiotic factors can help elucidate whether geographic regions are suitable for studied species, their physiology, morphology, and genetics ultimately shape their evolutionary success. Among these factors, morphological innovations are important triggers of organismal diversification, especially lineage-restricted morphological traits that serve novel functions (Li et al., 2021). The evolutionary emergence of such innovations provides organisms with the opportunity to exploit new ecological niches.

Biotic factors can be assessed by evaluating correlations between biogeographic patterns and the evolution of key morphological innovations, as well as by editing potential candidate genes responsible for morphological variation. The importance of biotic factors in shaping species distributions can be evaluated via a three-step approach. First, comprehensive data on DNA sequences, genomics, key morphological traits, and habitat and distribution characteristics are collected for the focal animals. Second, a

phylogenetic tree is constructed using DNA or genomic sequences, with distribution areas and morphological traits subsequently mapped to the phylogeny to visualize trait variation under different biogeographic scenarios. Third, genomic analyses are conducted to identify genes involved in the development of key traits. Subsequent functional validation can be achieved through knockout experiments utilizing the CRISPR-Cas9 system. These knockout mutants enable the observation of loss-of-function phenotypes, which will undoubtedly reveal the genetic basis of key traits.

Significant advances in multi-omics technologies and genome-editing tools, especially the CRISPR-Cas system, have aided investigations into the global patterns and morphological diversity of non-model organisms. For example, the radiation of cichlid fish in Lake Tanganyika is attributed to diversifications in body shape and jaw morphology, with species richness shown to be positively correlated with per-individual heterozygosity (Ronco et al., 2021). Research on seahorses has also revealed that the evolution of protective dermal spines is a response to predation pressure, thereby promoting their global diversification. Comparative genomic analyses have shown that the bone morphogenetic protein 3 (*bmp3*) gene experienced positive selection in spiny seahorse lineages, as confirmed by knockout experiments (Li et al., 2021). In a recent study, biogeographic analysis and genome editing demonstrated that marine-montane transitions were accompanied by gill innovation, potentially under the regulation of the *SMC3* gene (Liu et al., 2023). The integration of morphological analyses and genome-editing validation into biogeographic studies will enhance our understanding of the molecular mechanisms underlying global diversity patterns.

Although knowledge regarding global biodiversity patterns and the vulnerability of biodiversity to global changes is expanding, the fundamental ecological and evolutionary processes that have shaped the complex diversity and biogeography of continental biotas remain unclear. The adoption of integrative biogeographical approaches has the

potential to offer novel insights to facilitate the development of strategies for conserving biodiversity in the face of rapid climate change.

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

Both authors participated in writing the manuscript. All authors read and approved the final version of the manuscript.

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