Botany and Geogenomics: constraining geological hypotheses in the Neotropics with large-scale genetic data derived from plants

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Abstract

Decades of empirical research have revealed how the geological history of our planet shaped plant evolution by establishing well-known patterns (e.g., how mountain uplift resulted in high rates of diversification and replicate radiations in montane plant taxa). Under this approach, information is passed from geology to botany by interpreting data in light of geological processes. Instead, in this synthesis, I describe how by integrating natural history, phylogenetics, and population genetics, botanical research can inform our understanding of past geological and climatic processes. This conceptual shift aligns with the goals of the emerging field of geogenomics. In the Neotropics, plant geogenomics is a powerful tool for the reciprocal exploration of two long standing questions in biology and geology: how the dynamic landscape of the region came to be and how it shaped the evolution of the richest flora. Current challenges that are specific to analytical approaches for plant geogenomics are discussed. I describe the scale at which various geological questions can be addressed from biological data, and what makes some groups of plants excellent model systems for geogenomics research. Although plant geogenomics is discussed with reference to the Neotropics, the recommendations given here for approaches to plant geogenomics can and should be expanded to exploring long-standing questions on how the earth evolved with the use of plant DNA.

Key words: admixture, biogeography, demographic modeling, geogenomics, geology, Neotropics, orogeny, phylogenetic networks, plant phylogenomics

Geological history in the Neotropics has played a key role in shaping the evolution of the world's richest flora (Gentry, 1982; Hughes et al., 2013). Geomorphic processes in the region —driven greatly by rapid mountain building (Hoorn et al., 2010; Boschman, 2021)—, have led to identifiable evolutionary patterns. These patterns include accelerated diversification (e.g., explosive radiations in Andean bellflowers, *Lupinus,* and several other taxa living at high-elevations*;* (Hughes and Eastwood, 2006; Madriñán et al., 2013; Lagomarsino et al., 2016; Tribble et al., 2023), limited gene flow across landscape units (e.g., in *Amphirrox longifolia* and two species of *Marathrum* across the Rio Negro and Andean mountains respectively; Nazareno et al., 2017; Bedoya et al., 2021), and replicated radiations (e.g., repeated evolution of leaf ecomorphs in a Neotropical clade of *Viburnum*; Donoghue et al., 2022). Plant evolution research has shed light on such patterns by interpreting biological data in reference to known geological events. Although past geological studies have provided insight into the timing of processes that led to the configuration of the dynamic and heterogeneous landscape matrix in the Neotropics (e.g., Hoorn et al., 2010; Montes et al., 2015), precise landscape models for the region carry large uncertainty and are unavailable across most landscape units through time.

The massive amount of genomic data currently being generated, the long-recognized role of landscape change in shaping the evolution of the Neotropical flora, and the current gap in our knowledge about the timing and process of formation of many landscape units in the region, presents an opportunity to use patterns inferred from large-scale genetic data to generate, constrain, or reduce uncertainty in landscape evolution models in the Neotropics. This approach aligns with the goal of Geogenomics, an emerging field (Baker et al., 2014) that involves the reciprocal integration of geologic, climatic, ecological, paleontological, and genomic data to test landscape evolution hypotheses from biological data (Badgley et al., 2017; Rahbek et al., 2019; Dolby et al., 2022). The reciprocal investigation and testing of biological and geomorphic processes in geogenomics research, sets it apart from other fields like comparative phylogeography, which search for landscape and climatic features that are correlated with patterns of genomic variation in co-distributed taxa (Edwards et al., 2022), without explicitly testing models of landscape or climatic evolution.

Here I review recent contributions to plant geogenomics in the Neotropics that show how by integrating natural history, phylogenetics, and population genetics, botanical research can go beyond investigating patterns in light of landscape change and inform our understanding of past geologic and climatic processes in the Neotropics. I also discuss what makes some groups of plants ideal model systems for learning about past landscapes with the use of plant DNA, and offer practical considerations for plant geogenomics, including the scale at which geological hypotheses can be tested from genomic data. Research aligned with the goals of geogenomics and using animals as study systems (e.g., birds, mammals, and amphibians), has tested landscape hypotheses in the Neotropics (Albert et al., 2006; Boubli et al., 2015; Thom and Aleixo, 2015; Godinho and Da Silva, 2018; Naka et al., 2022; Rodriguez-Muñoz et al., 2022). However, responses to a common geological or climatic event across taxa are idiosyncratic (Donoghue and Smith, 2004; Bacon et al., 2015; Antonelli et al., 2018). Geogenomics research in plants is fundamental to a more holistic understanding of the geophysical history of the Neotropics, and instrumental to our understanding of how landscape changes contributed to the high plant richness in the region.

WHY AND HOW TO SHIFT THE PARADIGM?

Plant evolutionary patterns can inform paleogeograhic dynamics— Since the proposal of the 'riverine barrier' hypothesis by A.R. Wallace in 1852, historical biogeography has aimed to study distributional patterns of organisms with reference to landscape units. Research in this area has tremendously advanced our understanding of plant evolution on our constantly changing planet. Examples where dated phylogenies were interpreted according to landscape model reconstructions abound (e.g., biogeographic studies in Asteraceae, Bromeliaceae, Lamiaceae, Malpighiaceae, Myristicaceae, Orchidaceae, and Solanaceae (Davis et al., 2002; Bell, 2005; Givnish et al., 2011, 2016; Dupin et al., 2017; Frost et al., 2017, 2022; Mandel et al., 2019; Rose et al., 2022). A more recent approach to modeling species geographic ranges is biogeographic dating, a time-stratified framework where molecular, paleogeographic, and biogeographic evidenced are jointly modeled to estimate time-calibrated phylogenies and species ancestral ranges. Under this approach, paleogeographic hypotheses impose constraints on the rates of biogeographic change and vice versa (Landis, 2017). For example, estimated dates of island formation in the Hawaiian archipelago (Lim and Marshall, 2017) were incorporated as the maximum ages at which dispersal to each island could have taken place in a biogeographic study of Hawaiian silverswords (Asteraceae; Landis et al., 2018; Fig. 1A). This analytical framework was expanded to re-examine the ancestral biome reconstruction of *Viburnum* (Landis et al., 2021).

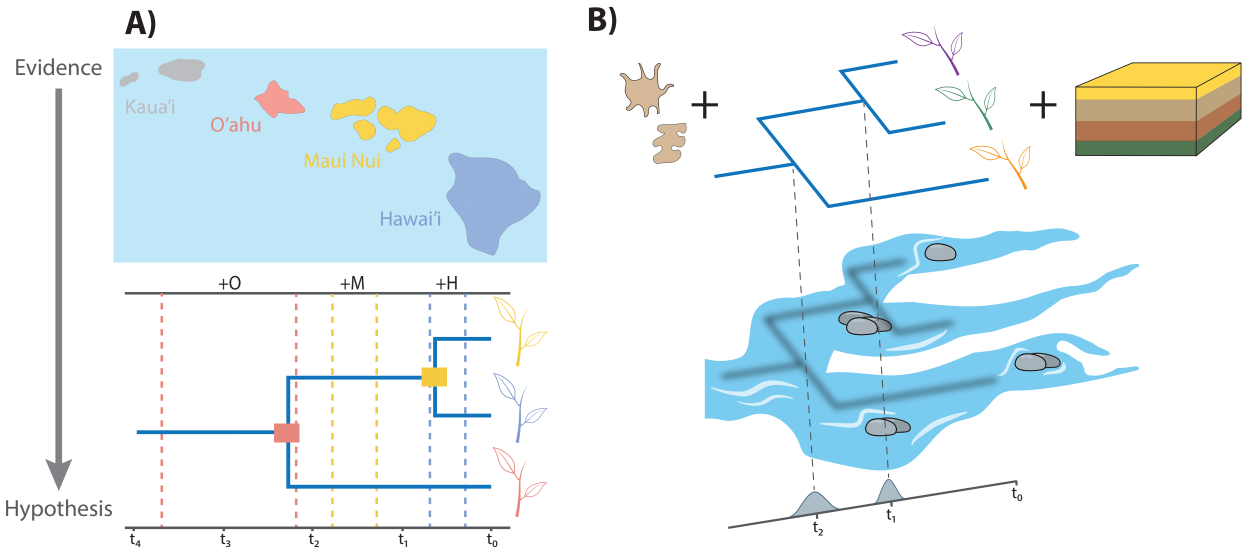

Figure 1. Approaches to questions at the intersection of geology and plant evolution, from evidence to hypothesis generation. A) Biogeographic dating *sensu* Landis et al., 2017; 2018. Modeling of ancestral ranges is conducted by imposing proposed times for the formation of islands in the Hawaiian archipelago (top) as constraints on the rates of biogeographic change (bottom). B) A geogenomics approach, where divergence times for three populations of river plants are used to constrain the approximate timing and pattern of connections of paleodrainages through time. Fossil (e.g., phytoliths) and geologic (e.g., stratigraphic) data would further provide support for the formulated hypothesis.

A major assumption of these approaches is that there is a model of the context in which plants evolved in a given area. The example above is unusual in the extent to which we know the exact timing of island formation in the Hawaiian archipelago. However, unifying, accurate, and precise landscape or climatic models are unavailable for a majority of regions and time scales. This gap can be explained by uncertainty in analytical tools for dating strata (Schoene et al., 2013), the complexity of past landscape dynamics, and the high degree of heterogeneity of topographic units. While geological advances continue to improve paleogeographic reconstructions, biological information can be used for inference of geologic events (Wegener, 1966). Today's exponential growth of genomic data presents an opportunity to improve what we know about landscape configurations over time using a geogenomics approach. In the Neotropics, plant geogenomics research is a tool for the reciprocal exploration of how the dynamic landscape of the region came to be and how it shaped the evolution of the richest flora.

Selection of study systems, reciprocity in geogenomics and the problem of scale — Figure 1B shows how inferred divergence times of river plants could be used to propose a hypothesis for fluvial connections in the past. The efficacy of this approach is dependent on the temporal and spatial concordance of geological and biological processes. In other words, geogenomics research requires careful selection of model systems whose evolutionary histories reflect that of landscape units, as organismal responses to geomorphic barriers are highly heterogeneous (Araya-Donoso et al., 2022; Rodriguez-Muñoz et al., 2022). A famous example of this heterogeneity is the variable timing of dispersal in terrestrial organisms (i.e., plants, birds, mammals, reptiles, amphibians, and arthropods) across the isthmus of Panama (Bacon et al., 2015). The hypothesis-testing approach shown in Figure 1B would necessitate that the plants studied live strictly in riverine habitats, are naturally distributed across rivers, and have limited gene flow across drainage basins (e.g., low dispersal ability, unsuccessful establishment of migrant populations, or other pre or pro-zygotic barriers to gene flow).

By concurrently interpreting geological and biological data, geogenomics reduces biases introduced from using geological data alone —which inherently carry uncertainty— to constrain biological processes (e.g., divergence times). It also better informs the interpretation of biological data (e.g., dated phylogenies or algorithms for detection of gene flow events) to constrain geological hypotheses. For example, although both geological and biological models carry uncertainty, a temporal and spatial correspondence between a geological hypothesis (i.e., timing of mountain building) and biological processes for a given study system (i.e., inferred divergence times), would support such geological hypothesis. Patterns inferred from genomic data (Fig. 2C-E) for allopatric operational taxonomic units would further inform the study system's responses to mountain building. Then, biological patterns inferred for this same study system can be used to formulate hypotheses of mountain building of a different topographic unit, or of other landscape events linked to mountain building. The paleontological record could further inform plant responses to some geological events (e.g., (Strömberg, 2005; Stiles et al., 2020; Carvalho et al., 2021).

Estimating the timing of geomorphic events from genomic data is scale-dependent. The example shown in Figure 1B is an oversimplification of a deep time (i.e., millions of years) event spanning large geographic distances. Here, the connections of river drainages— not of single rivers—are inferred. On the other end of the spectrum, the genomic signature of a landscape event (Fig. 2) could be erased by demographic processes and the strong influence of genetic drift on plants with small population sizes. Thus, geologic events may be reconstructed most reliably only if occurring at shallow time scales. For example, using genomic data to estimate the timing of connections across high-elevation ecosystems in topographically complex landscapes is likely to be limited to recent dispersal and vicariance events. For example, páramo plants experienced demographic changes due to the contraction and expansion of high-elevation ecosystems during the Pleistocene glaciations (Flantua et al., 2019), only the most recent of which may be identifiable from genomic data (Nevado et al., 2018).

Genomic approaches to plant geogenomics— Genomic signatures of past geologic events may be identified with four main approaches: 1) estimation of divergence times of species/populations distributed across landscape units (Fig. 1B); 2) identification of the distribution of genetic variation across the landscape (i.e., genetic structure; Fig. 2C); 3) investigation of introgression events (e.g., phylogenetic network inference, summary methods for the detection of gene flow from site patterns, and likelihood-based methods for inference of introgression; Fig. 2D; Green et al., 2010; Durand et al., 2011; Blischak et al., 2018; Nauheimer et al., 2021; Ji et al., 2023); and 4) demographic modeling (i.e., using site frequency spectra and whole genomes; Fig. 2E; Adams and Hudson, 2004; Gutenkunst et al., 2009; Li and Durbin, 2011; Schiffels and Durbin, 2014).

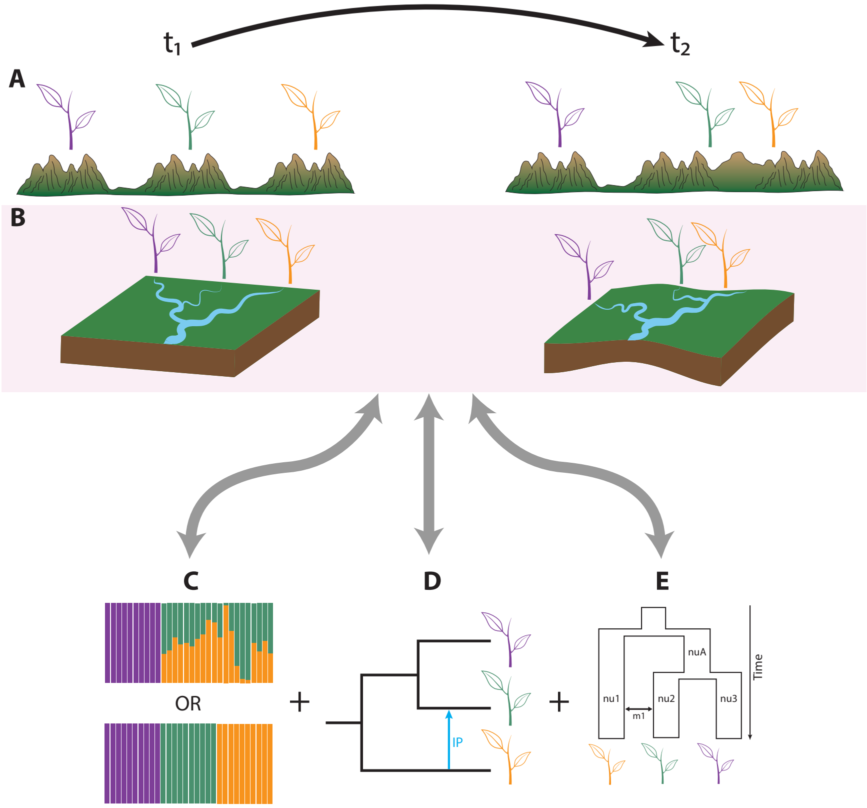

Figure 2. Hypothetical example of three lines of genomic evidence that can be used to identify landscape change events from biological data. Two hypothetical examples presented correspond to uplift and connection of mountain segments A), and a river capture event B) taking place at time t_2. These events resulted in secondary contact and admixture of two previously isolated plant populations (orange and green). Admixture linked to geologic processes, leaves a signature in the genetic constitution of populations that may be identifiable from C) inference of admixture proportions, D) identification of introgression events through phylogenetic network inference, and E) modeling of past demographic dynamics. Bidirectional arrows indicate how geologic processes can inform the interpretation of genomic patterns, which can then be used to test geologic hypotheses (see '*Selection of study systems, reciprocity in geogenomics and the problem of scale'* for how geogenomics avoids circularity). IP: Inheritance probability, or the proportion of genes contributed by each parental population to a reticulation node, if gene trees are used for network inference.

Figure 2 shows a hypothetical example of uplift and connection of mountain segments (A) and a river capture event (B) taking place at time t_2 and generating patterns of genomic variation that can be identified with the approaches mentioned above. The examples assume lack of plant dispersal across landscape units. The hypothetical events resulted in secondary contact and admixture of two previously isolated populations of plants (green and orange), exemplifying spatial and temporal correspondence of geological and biological processes. Gene flow following secondary contact may be revealed by an admixture plot (Fig. 2C, top). However, signatures of admixture could be eroded by subsequent events such as genetic drift (Fig. 2C, bottom), particularly in small populations (e.g., plant populations in savanna pockets within the Amazon, sky islands like the páramos, or river-rapids). Exploration of non-bifurcating relationships through phylogenetic network inference could also detect the branches of the tree involved in the reticulation event (green and orange populations; Fig. 2D), and the inheritance probability (IP; the proportion of genes contributed by each parental population to a reticulation node, if gene trees are used for network inference; Solís-Lemus et al., 2017). Ideally, the demographic model in Fig. 2E would be identified as the best fit for genomic data generated from the three populations. Variations of this model would include permitting changes in population size and asymmetric gene flow.

Concordant patterns across approaches would facilitate interpretation of the resulting patterns as indicators of a specific past geomorphic process (recent connections of previously disconnected mountain segments (Fig. 2A) and river capture events (Fig. 2B). However, the gene flow patterns detected in Fig. 2 could also result from long-distance dispersal across landscape units. Phylogeographic and population structure analyses of the study systems would be necessary to determine the extent and direction of gene flow across populations/species. This would inform the extent to which these patterns are indicative of an underlying landscape change event. Sedimentological and stratigraphic data in the area where the species are distributed would further support the landscape change hypothesis formulated. The above highlights the reciprocal integration of geologic, climatic, and genomic data to test landscape evolution hypotheses from biological data *sensu* Dolby et al., 2022.

Rigorously constraining landscape and climatic hypotheses with the use of time-trees, admixture plots, phylogenetic networks, and inferred demographic models requires the joint application of at least two of the four approaches for various reasons. Putative hybrid ancestry in admixture proportions might instead result from the retention of ancestral polymorphisms from shared ancestry (Lawson et al., 2018), scenarios that can often be distinguished through demographic modeling. Furthermore, the signatures of polymorphism in truly admixed populations are expected to be removed with time (Clark, 1997). There are also practical limits to existing algorithms: phylogenetic network inference is computationally feasible only for a small number of terminal taxa, does not identify the direction at which gene flow took place, and may suffer from non-identifiability as complexity of the model increases (Yu et al., 2014; Pardi and Scornavacca, 2015; Solís-Lemus and Ané, 2016; Solís-Lemus et al., 2017). Similarly, demographic models inferred from genetic data can only be applied to a limited number of populations (Farleigh et al., 2021), suffer from non-identifiability (Terhorst and Song, 2015), and require *a priori* specifications of parameters and demographic events (unknown in most empirical systems; Li and Durbin, 2011; Loog, 2021).

Caveats important but not exclusive to plant geogenomics include the scarcity of fossil evidence useful for calibration for many taxa. (Crane et al., 2004; Schenk, 2016). Dated phylogenies for a large number of plant groups are inferred from secondary calibrations and are subject to potential bias (Schenk, 2016). Gene flow can also affect inference of divergence times (Leaché et al., 2014). Inferred chronograms are a means to exploring plausible evolutionary and landscape change scenarios, but they should be taken cautiously and re-examined as more sources of data and analytical tools become available. Issues more specific to plants include escalating costs of sequencing of genomic-scale data for taxa with big genomes, widespread hybridization, polyploidization, and various mating systems (Stebbins, 1950), as well as the difficulty of developing analytical tools that accommodate these complexities (Blischak et al., 2023; but see Garrison and Marth, 2012; Serang et al., 2012; Blischak et al., 2018b; Gerard et al., 2018; Clark et al., 2019 for genotyping tools that enable ploidy specification and algorithms for genotype likelihood estimation). Other challenges include the identification of paralogous and orthologous loci prior to phylogenetic inference (Yang and Smith, 2014; Johnson et al., 2016; Gardner et al., 2021; Morales-Briones et al., 2022; Freyman et al., 2023; Mendez-Reneau et al., 2023), a scarcity of resources for analysis of shared ancestry in polyploids (but see Kolář, 2021; Shastry et al., 2021), and demographic modeling under various ploidy and mating systems scenarios (but see Roux and Pannell, 2015; Blischak et al., 2023; Roux et al., 2023). Simulation studies testing the effect of strategies and violations of model assumptions in plant geogenomics research (Schenk, 2016; Stift et al., 2019) are critical to better constrain and propose plausible geological scenarios from biological data in light of uncertainty.

PLANT EVOLUTION AND GEOGENOMICS IN THE NEOTROPICS, OR, HOW ELSE ARE PLANTS SPECIAL

The original proposal of the geogenomics neologism (Baker et al., 2014) identified major geologic questions in the Neotropics to be addressed with biological data. The groundwork for many of these questions consists of a model of the geologic history of northern South America since the Paleogene by Hoorn et al., 2010, who provided a review of paleontological, sedimentological, ecological, and geological data for the region. Below I show how plant evolution research conducted over the past decade, exemplify how the hypotheses laid out by Hoorn et al., 2010, by Baker et al., 2014, and by the several prior studies that they were based on, can be constrained from biological data.

Fine-scale uplift history of different segments and Cordilleras of the Northern Andes— Landscape models indicate that the uplift of the Andes (which in northern South America are split into the Western, Central, and Eastern Cordilleras) was an asynchronous process that started in the Late Cretaceous (Horton, 2018; Gianni et al., 2020). A current challenge is to generate a finer-scale geological model that reflects the asynchrony and spatial heterogeneity of the Andes, particularly for the Western and Central cordilleras (Sanín et al., 2022b). A recent study by Sanín et al., 2022b tackled this challenge and revised the geologic history of uplift across the three mountain ranges that constitute the northern

Andes, using genomic data generated for the *Geonoma undata–G. orbignyana* species complex (Arecaceae).

The study integrated inference of genetic structure, phylogenetic relationships, divergence times, and demographic modeling with information from past geological studies in the region (Velandia et al., 2005; Mora et al., 2008; Veloza et al., 2012; Anderson et al., 2016; Montes et al., 2019, 2021; Mora-Páez et al., 2019; Noriega-Londoño et al., 2020). They provide evidence for a scenario where mountain segments were already uplifted but disconnected until the Pliocene, when continuous cordilleras were formed.

Phylogeographic breaks coincide with the location of strike-slip faults (i.e., vertical fractures where blocks have moved horizontally). The authors suggest that extensional and compressional features of the faults may represent initial negative topography that is subsequently inverted (Dewey et al., 1998; Veloza et al., 2012; Montes et al., 2019; Zapata et al., 2023). This resulted in the connection of previously isolated mountain segments during the Pliocene. Geological samples of ignimbritic rocks (i.e., a type volcanic rocks) further indicate that vulcanism contributed to mountain connectivity and the closure of low mountain passes in the Plio-Pleistocene (< ~2 Ma; Sanín et al., 2022a). This resulted in increased dispersal of high-elevation mountain palms (i.e., *Ceroxylon*) throughout the northern Andean cordilleras. Phylogeographic inference in the *Tococa-Azteca* plant-ant mutualism (Torres Jimenez et al., 2021) and biogeographic modeling in the Rubiaceae (Antonelli et al., 2009) further support the prior existence of lowland passes across the Andean mountains, and the dispersal through lowland portals in frogs, mammals, and non-avian reptiles (Rodriguez-Muñoz et al., 2022).

Drainage basin reconfiguration through time— In addition to being a major driver of Neotropical diversification (Antonelli et al., 2009; Antonelli and Sanmartín, 2011; Sklenář et al., 2011; Smith et al., 2014; Hoorn et al., 2018), Andean uplift reconfigured watersheds across South America (Albert et al., 2006; Hoorn et al., 2010; Ruokolainen et al., 2019). However, the configuration of paleodrainages through time remains largely unknown. To propose a hypotheses for past river connections in northern South America, I have used two species of strictly riverine plants (*Marathrum*, Podostemaceae) with broad distributions across the Andes as a model system. Collecting genomic data for populations from different drainage basins, I inferred population structure, phylogenetic networks, divergence dates, and population summary statistics (Bedoya et al., 2021). After establishing that gene flow is limited in populations across drainage basins via population structure analyses, I used the timing and pattern of population divergence across river drainages as evidence to argue that drainage basins became separated at ~12 and ~4 Ma as a result of major pulses of Andean uplift (Gregory-Woodzicki, 2000; Garzione et al., 2008; Hoorn et al., 2010; Mora et al., 2010; Anderson et al., 2016; Boschman, 2021). This paleodrainage model was subsequently validated by a paleogeographic model of northern South America through the Miocene, built from geochronological, petrographic, and thermochronological data (Zapata et al., 2023). Strictly riverine plants are a great study system in geogenomics in the Neotropics. Limited gene flow has been reported for various species in the Podostemaceae (Baggio et al., 2013; Katayama et al., 2016). However, long-distance dispersal may explain the pantropical distribution of some groups in the family (Kita and Kato, 2004; Koi et al., 2015; Ruhfel et al., 2016). Research in this group should be expanded to investigate the link between river structure, distance between river rapids within and across rivers, and plant dispersal. This to better understand the prevalence of range evolution through river capture events and long distance dispersal in the group, and assess to what extent geologic hypotheses can be formulated from genomic data across space in the group.

Additional botanical studies have introduced promising study systems to constrain hypotheses for river reconfiguration in the past, including *Mauritia flexuosa* (Arecaceae), whose populations are inferred to have strong genetic structure across drainage basins in the Amazon (Sander et al., 2018). Other examples include *Amphirrox longifolia* (Violaceae) and *Buchenavia oxycarpa* (Combretaceae), tree species with limited gene flow across broad portions of the Rio Negro in the Amazon basin (Nazareno et al., 2017, 2019).

Neogene and Pleistocene marine incursions in the Neotropics— Landscape change models developed from palynological, sedimentological, geochemical, and macrofossil data indicate that Pebas

Lake, a vast wetland-like system of > 1 million km^2, was in place in northern and central South America from ca. 23–10 Ma (Hoorn, 1993; Wesselingh et al., 2002; Hoorn et al., 2010; Linhares et al., 2017; Jaramillo, 2023). Isotopic and palynological evidence shows a marine influence on this water body, but conflicting interpretations of the Miocene depositional environment and extent of marine incursions at the time remain unresolved (Frailey et al., 1988; Hoorn, 1993, 2006; Räsänen et al., 1995; Webb, 1995; Vonhof et al., 2003; Latrubesse et al., 2007, 2010; Jaramillo et al., 2017).

Based on distributional information, dispersal biology, and calibrated phylogenies of plant taxa, Bernal et al., (2019) proposed the hypothesis that the current occurrence of plants from estuarine or coastal zones in western Amazonia is the legacy of Miocene marine incursions in the region. Divergence times of populations of *Pachira aquatica* (Malvaceae) and *Manicaria saccifera* (Arecaceae) suggest that Amazonian and costal populations differentiated as a result of the complete retreat of the marine-influenced embayment. Appropiate testing of this hypothesis to reconstruct the extent of past estuarine environments requires further geogenomics studies, for which the authors provide a list of 28 candidate species from deltaic or estuarine environments in the region. Evidence for past estuarine connections from botanical data also include a study of a relict inland mangrove ecosystem (*Rhizophora mangle*) in the Yucatán peninsula (Aburto-Oropeza et al., 2021). Population genetic analyses of genotyping-by-sequencing data, together with floristics, sedimentological, paleontological evidence, and sea-level modeling, point to the mangrove relict reaching its current inland location in the Yucatán peninsula during last interglacial (ca. 120 K years).

FUTURE CONSIDERATIONS FOR PLANT GEOGENOMICS

Given their putatively limited gene flow across landscape units, distributional patterns, and affinity to specific habitats, many plant groups are excellent systems for geogenomics research. Recent botanical investigations demonstrate that the analysis of data derived from plant DNA can improve our knowledge of topography, riverine, and habitat connections through time.

Geogenomics research advocates for building interdisciplinary networks (e.g., Sanín et al., 2022a and the Baja GeoGenomics consortium; https://bajageogenomics.org). Future questions in geogenomics would necessitate such integrative collaborations. For example, investigating the extent of expansion, contraction, and flickering connectivity of high elevation Neotropical grasslands (i.e., páramos) requires reciprocally testing the concordance of inferred timing and patterns of gene flow (e.g., in *Lupinus;* Nevado et al., 2018), and landscape models derived from palynological evidence during the Pleistocene (e.g., Flantua et al., 2019). Exploring concordance across other páramo plant taxa, may further support or reject landscape hypotheses for how high-elevation grasslands connected and disconnected in the past.

The timing of formation, long-term persistence, geographical isolation, and expansion or contraction of seasonally dry topical forests (SDTFs), are other future questions to be addressed with plant geogenomics in the Neotropics. To explore these questions, biological (e.g., divergence time estimation from sequence data and biogeographic modeling; Pennington et al., 2004; Särkinen et al., 2012; Fernandes et al., 2022) and paleontological data (Toby Pennington et al., 2000; Burnham and Carranco, 2004; Mayle et al., 2004; Werneck et al., 2011; Martínez et al., 2020, 2021), have been provided independently. Integrating these findings into a geogenomics framework would involve selecting study systems in the SDTFs where geomorphic, ecological (Pennington et al., 2006), and evolutionary processes are concordant, and applying the approaches here described.

This synthesis focuses on recent and future approaches to understanding how the richest flora and one of the most species-rich landscapes evolved through time. However, the recommendations given here for plant geogenomics would allow for the exploration of questions at the intersection of geology and biology across the globe (e.g., the origin of disjunct arid and semi-arid regions across the Americas, and the evolution of arid-adapted species with amphitropical distributions). At a time when rapid technological innovation allows for the generation of massive amounts of genomic data, classical botanical knowledge is critical for identifying good study systems where plant DNA can help us address long-standing questions on earth's geologic history.

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