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The emerging field of *geogenomics*: Constraining geological problems with genetic data

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ABSTRACT

The development of a genomics-derived discipline within geology is timely, as a result of major advances in acquiring and processing geologically relevant genetic data. This paper articulates the emerging field of "geogenomics", which involves the use of large-scale genetic data to constrain geological hypotheses. The paper introduces geogenomics and discusses how hypotheses can be addressed through collaboration between geologists and evolutionary biologists. As an example, geogenomic methods are applied to evaluate competing hypotheses regarding the timing of the Andean uplift, the closure of the Isthmus of Panama, the onset of trans-Amazon drainage, and Quaternary climate variation in the Neotropics.

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1. Introduction

In the past decade, DNA sequencing of plant and animal **taxa** (Box 1) has generated vast amounts of genetic data. In light of advancing

Box 1
Essential biological vocabulary.

Calibration: In phylogenetics, a calibration is a fossil with a known or approximately known age that is used to aid in the conversion of molecular units of change into units of chronological time.

Clade: A taxonomic group consisting of an ancestor and all its descendants, representing a single "branch" on the "tree of life".

Crown group: A group of taxa that includes all living members, as well as all of their ancestors back to the last common ancestor of all living species in the group. The crown group also includes all extinct taxa that also trace their ancestry back to the last common ancestor of all living taxa in the group

Diversification: The generic process by which evolutionary lineages arise from common ancestors to produce extant taxa. Also defined as the sum of taxa produced within a clade by speciation minus extinction.

Endemic: A taxon with a distribution that is restricted to a particular geographic area or environment.

Gene: A DNA sequence of nucleotides in the genome of an organism that forms the physical unit of heredity and that affects some aspect of the organism by coding for the building blocks of proteins or functional RNA molecules.

Gene tree: A bifurcating graph composed of edges and nodes that define the evolutionary relationships among a set of genes from multiple taxa.

Genome: The entirety of an organism's hereditary (DNA) information, often subcategorized by location in the nucleus (nuclear genome) or plastids (mitochondrial or chloroplast genomes).

Nodes: In the context of a phylogeny, nodes represent the branching points representing recent or ancestral speciation events.

Molecular clock: A hypothesis that the rate at which mutations occur is constant, or at least linear through time, so that there exists a linear relationship between the number of accumulated mutations between two taxa and chronological time.

Population: A group of interbreeding individuals located at a common geographical location.

Species tree: A bifurcating graph composed of edges and nodes that define the evolutionary relationships (i.e. phylogeny) among a set of species (see also Supplementary Information: Geogenomic hypothesis tests).

Stem group: A group of taxa that includes all of the lineages that predate the last common ancestor of all living members of the group, but that are still distinct from the closest living relative of the crown group. A good example would be theropod dinosaurs, which are part of the stem group of modern birds. In this case, theropod dinosaurs are more closely related to extant birds than to extant crocodilians, which are the closest living relatives of birds.

Taxon: A taxonomic group at any level in the Linnaean hierarchy (e.g. species).

technologies, it is certain that data collection will compound exponentially, and it is conceivable, even likely, that complete **genomes** of taxa from across the tree of life will become available in the next decade. Genetically distinct **populations** and species arise in response to environmental variation as a consequence of evolutionary processes, such as natural selection; conversely the genetic composition of modern taxa retains information about their environmental past. As a result of this linkage between genetic composition and environmental history, *phylogenetics* (Box 2) represents a major opportunity for qualitative advance in geologic reconstruction, particularly given the development of new bioinformatics approaches for the collection and interpretation of large genetic data sets. In this paper, biologists and geologists collaborate to envision an emergent field called "geogenomics", which we define as the use of large-scale genetic data to test or constrain geological hypotheses (Fig. 1). By imagining this future, we hope to hasten its realization and illuminate possible pitfalls in its application. We anticipate that geogenomics will be most useful for (1) providing an independent chronology for a variety of past geologic events, some of which may be otherwise extremely difficult or impossible to date, and (2) providing constraint and nuance to paleo-environmental interpretations.

Geogenomics is deeply rooted in the field of *biogeography*. From its earliest history (Wallace, 1852), biogeographers sought patterns in the distribution of plant and animal taxa to infer their geographic history and related these patterns to the geological processes that shaped their evolution. Geological processes that produce vicariance – isolation of populations in response to the formation of a geographic barrier to migration and consequent genetic divergence between these populations – are central in biogeography as drivers of evolutionary change.

Box 2
Key scaling concepts.

Genetics and genomics — Genetics is a biological discipline investigating genes, heritability, and variation. Genomics is the study of the structure and function of the entire **genome**. Genomic data comprise whole genome sequences or a broad representative sample (Elshire et al., 2011).

Molecular phylogenetics and population genetics — Phylogenetics is the study of the evolutionary history of a set of taxa, including the patterning, timing, and causes of **diversification** events. Population genetics is the study of processes leading to the genetic differentiation within and among **populations**, including demographic and evolutionary processes leading to observed patterns.

Biogeography and phylogeography — Biogeography is the study of the distribution of **taxa** through space and time. Phylogeography is a specialized branch of biogeography that examines geographic patterns in the distribution of lineages within or among closely related taxa (Hickerson et al., 2010). The focus on relative "closeness" (i.e. time elapsed from a common ancestor) affects the temporal scale of hypotheses that can be investigated. For example, the distribution of related plant and animal taxa on different continents led to the hypothesis of continental drift (Wegener, 1924), whereas phylogeographic analyses provided evidence for refugia formation during glacial periods (Emerson and Kolm, 2005).
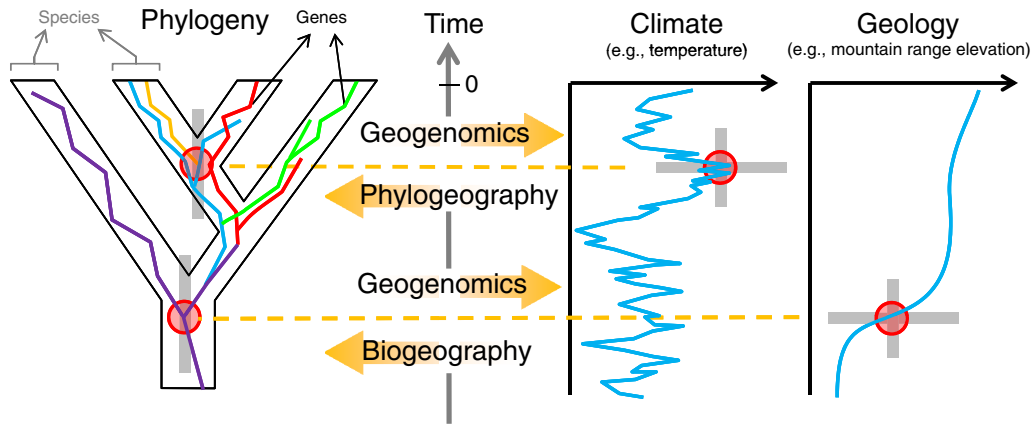
Fig. 1. Conceptual illustration of how geogenomics can constrain geologic or climatic scenarios. In the phylogenetic tree (left), black 'tubes' represent species (i.e. the **species tree**), whose individuals are characterized by genes with different mutational histories (color lines within tubes; i.e. the **gene tree**). On the right, a climatic time series and temporal variation of a geologic feature are represented. Red circles and orange dashed lines highlight the correspondence between evolutionary and climatic/geologic events; gray bars represent confidence intervals for the timing of divergence (left) or the geologic/climatic events (right). Note also that the **nodes** in the phylogenetic tree on the left have uncertainty associated with them (i.e. the equivalent error depicted by horizontal error bars in the graphs to the right). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Cladistic or phylogenetic *biogeography* (focused above the species level) and *phylogeography* (focused within or among closely related species) introduced phylogenies into biogeographic analyses. Time-calibrated phylogenies (Fig. 2) are used to determine if **clades** arose through vicariance or if they attained disjunct (fragmented) distributions by dispersing across geographic barriers. Comparing the age of disjunction with the accepted age of barrier formation can help to constrain these alternative hypotheses. Hence, in these disciplines geologic information is used to constrain evolutionary histories (Fig. 1).

Whereas the concept of "reciprocal illumination" (Hennig, 1966), when applied to historical biogeography, describes the search for congruence between phylogenetic hypotheses and earth history, geogenomics encourages the flow of information from biology to geology. Thus, it builds upon the historic use of biotic patterns to infer geologic processes, such as the distribution of the *Glossopteris* flora and Permo-Triassic vertebrates, which contributed to the development of plate tectonics (Wegener, 1924). Geogenomics is timely, because of recent advances in methodologies used to obtain and analyze phylogenetic data. In particular, novel platforms for DNA sequencing ("next generation" approaches) can rapidly provide millions of DNA sequences from non-model organisms (see Supplementary Information). The profusion of genomic data and new bioinformatics methods promises greater phylogenetic precision and the ability to address novel questions of interest to biologists and geologists.

In this paper we present four examples of outstanding geological problems that have been addressed by classical geological methods, but only recently by biogeographic or phylogenetic methods that provide new insight. In each case we briefly review the problem and

alternative explanatory hypotheses. Exemplary published biological studies are presented, followed by our own suggestions for possible future geogenomic research. Key vocabulary (bolded text) and concepts (italicized text) are defined in boxes, and additional detail about methods for geogenomic hypothesis testing is provided in the Supplementary Information. All of our examples are taken from the New World tropics, but the global generality of these methods should be clear to all readers.

2. Geogenomic perspectives on Neotropical geology and paleoclimate

2.1. Andean uplift

2.1.1. Geological problem

As a major topographic barrier and source of eroded sediment, the tropical Andes (Fig. 3) are a critical agent of vicariance, habitat creation, and climate control in the Amazon basin, montane uplands, and Pacific lowlands. Construction of both the Western and Eastern Cordilleras has long been considered the product of Cenozoic shortening, crustal thickening, and isostatic uplift related to subduction of the oceanic Nazca plate beneath South America. Modern elevation correlates relatively well with documented shortening and crustal thickness (Isacks, 1988; Kley and Monaldi, 1998; McQuarrie, 2002), and records of faulting, exhumation, and associated basin evolution indicate shortening and flexural loading since Paleocene–Eocene time (Lamb and Hoke, 1997; Oncken et al., 2006; Horton, 2012; Parra et al., 2012). This conceptual framework, however, has been recently challenged on the basis of
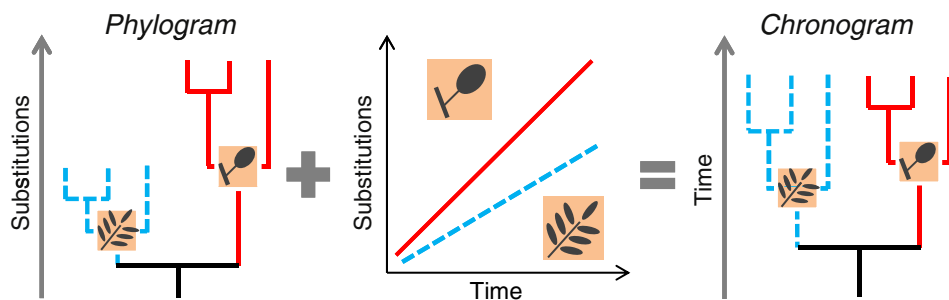
Fig. 2. Construction of a dated phylogenetic tree (chronogram, constrained branch lengths) based on a tree representing cumulated molecular changes (phylogram, variable branch lengths). Fossil records of known age (schematic leaves) are used to calibrate selected nodes and thus infer the relationship between substitutions and chronologic time.
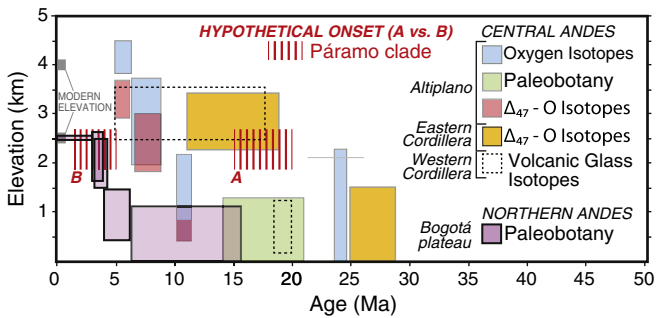
Fig. 3. Topographic relief map (SRTM30) of tropical and sub-tropical South America, showing the Amazon Basin and the northern and central Andes. Indicated on the map are the Eastern Cordillera (EC) and Western Cordillera (WC) of the Andes, the Altiplano, and the Bogotá plateau (BP).

new stable isotopic and paleobotanic datasets (Fig. 4) suggesting rapid pulses of high-magnitude uplift over the past 10–20 Myr across parts of the central and northern Andes (Gregory-Wodzicki, 2000; Garzione et al., 2006; Ghosh et al., 2006; Garzione et al., 2008; Mulch et al., 2010; Leier et al., 2013; Garzione et al., 2014; Saylor and Horton, 2014). Additional studies have used indirect means to evaluate the location, timing and magnitude of surface uplift of the Andes, such as sediment provenance studies (Roddaz et al., 2005; Horton et al., 2010),

Fig. 4. Age-elevation plot showing the range of paleoelevation estimates (color rectangles) for the 4 km-high Central Andean plateau (Bolivia) and 2.5 km-high Northern Andean plateau (Colombia) based on proxy data from oxygen and clumped C–O isotopes (Garzione et al., 2006; Ghosh et al., 2006; Leier et al., 2013), volcanic glass H isotopes (Saylor and Horton, 2014), and paleobotany (Gregory-Wodzicki, 2000; Hooghiemstra et al., 2006). Contrasting paleoelevation estimates for the Altiplano, Eastern Cordillera, Western Cordillera, and Bogotá plateau (see Fig. 3) highlight the debate over the absolute timing (early vs. late), tempo (slow vs. rapid), and spatial variability of surface uplift. Ruled red rectangles depict two hypothetical results that would be consistent with (A) early vs. (B) late onset of high-elevation conditions necessary for the onset of páramo clades using a geogenomic approach in testing geological hypotheses (see text for details). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

river incision histories (e.g., Hoke et al., 2007; Schildgen et al., 2007), aridification and structural tilting of the western slope (e.g., Rech et al., 2006; Jordan et al., 2010), and these studies generally agree with the quantitative estimates of surface elevation change. Such a punctuated history would support an alternative mechanism of surface uplift operating at shorter timescales and largely decoupled from shortening, crustal thickening, and basin flexure. Removal of lower lithosphere is considered the most reasonable alternative and is consistent with geophysical evidence for large-scale lithospheric thinning or delamination (Kay et al., 1994; Whitman et al., 1996; Allmendinger et al., 1997) and local piecemeal removal (Beck and Zandt, 2002).

These exciting new datasets and interpretations are not without debate and help to underscore several critical outstanding and unresolved issues. First, the long-lived Andean arc shows evidence of protracted magmatism since the Late Cretaceous. The latest phase of magmatism, focused in the Western Cordillera over the past ~30 Myr (Haschke et al., 2006), must have been associated with significant positive topography. No detailed studies have addressed paleoelevation of the magmatic arc forming the western flank of the Andean chain, because most indicators of past elevation are restricted to sedimentary materials (e.g. paleosol carbonates, fossil leaves, bone, and teeth) further east. Yet, if high altitudes were attained early in the Western Cordillera, then the creation of high-elevation habitat and the influence of topographic barriers on climate and delivery of sediments and nutrients to the eastern lowlands may all date tens of Myr earlier than commonly assumed. Further concerns include the recognition of competing influences (rather than purely surface elevation) on the stable isotopic composition used to deduce paleoelevation. For example, general circulation model simulations show that long-term climate change or the presence of large water bodies in the adjacent lowlands could also produce significant isotopic shifts in the Andean geologic record (Ehlers and Poulsen, 2009; Poulsen et al., 2010; Jeffery et al., 2012).

2.1.2. Biological constraints

The Andes contains distinct montane biomes restricted by temperature and elevation; thus the history of biota **endemic** to these biomes can be used as biological proxies for elevation through time. The Andean páramo, which is the tropical analog of an alpine tundra ecosystem and is presently located at 3000–5000 m elevation, occurs above the closed canopy forest and extends to the upper elevation limit of plant life (Luteyn, 1999). The páramo is characterized by several endemic plant radiations, whose life forms include dwarf trees and shrubs, rosette plants, bunch grasses, and cushion plants. In the northern Andes, a palynological reconstruction from the Bogotá plateau (reviewed in Van der Hammen and Cleef, 1986) indicates a Plio-Pleistocene (last 5.3 Myr) origin of the páramo.

The current geological debate about the timing of the Andean uplift provides two distinct scenarios, which can be constrained by time-calibrated phylogenies of higher elevation Andean clades (see Picard et al., 2008 for a case study in a lower region). If the Andes experienced punctuated uplift during the past 10 Myr (Fig. 4), then the age of the Colombian páramo should apply broadly to indicate a relatively recent origin of páramo-restricted lineages. In contrast, under the model of earlier and more gradual uplift, the most recent ancestors of páramo clades should be older than the Plio-Pleistocene, extending perhaps to the Oligocene–early Miocene (Fig. 4). Moreover, the pattern of **diversification** can be used to examine how rates of uplift differed between the Central and Northern Andes. If páramo originated in the Central Andes, then the earliest branching clades of páramo organisms could be expected to occur farther south, as shown for several plant and bird taxa from other Andean habitats.

Phylogenetic studies of groups of páramo plants and birds from the central and northern Andes agree in showing recent **stem** ages of about 5 to 9 Ma for birds (Bates and Zink, 1994; Quintero et al., 2012) and less than 4 Ma for plants (Saerkinen et al., 2012). Diversification within the páramo started between 3 and 6 Ma for birds (Quintero et al., 2012); current species of both plants and birds originated in the last 1 Myr (Ribas et al., 2007; Quintero et al., 2012; Saerkinen et al., 2012; Madriñan et al., 2013). This evidence suggests that initial diversification of the studied páramo clades is consistent with a recent origin of the páramo biomes, although the origin of contemporary clades may reflect climate change within already uplifted highlands. Analysis of additional clades may uncover earlier diversification patterns.

2.2. Great American Biotic Interchange

2.2.1. Geological problem

The great exchange of vertebrates between North and South America is widely ascribed to the ~3 Ma closure of the Central American seaway and emergence of the Isthmus of Panama (e.g. Simpson, 1940; Duque-Caro, 1990; Coates et al., 1992; Coates et al., 2004; Woodburne, 2010). In addition to the biologic effects of this "Great American Biotic Interchange" (Marshall et al., 1982; Webb, 1991), the presumed late Pliocene closure event has been implicated as a primary trigger of glaciation in the Northern Hemisphere (Burton et al., 1997; Haug and Tiedemann, 1998). The isthmus debate, which many considered to be "solved," has been re-energized by emerging geological evidence that suggests a much earlier closure of the seaway. On the basis of new structural, stratigraphic, and thermochronologic signatures of shortening, sedimentation, and erosional exhumation, Montes et al. (2012) suggest a long, complex collision of the Panama volcanic arc with northwestern South America since mid-Cenozoic time. Although available plate tectonic reconstructions do not permit precise placement of the isthmus, recent workers reconstruct an uninterrupted Central American volcanic chain that was above sea level by the late Eocene and had collided with northwestern South America by ~25 Ma (Farris et al., 2011; Montes et al., 2012).

If correct, the interpretation of much earlier closure for the isthmus would require that previous age estimates of biologic exchange are grossly in error or that additional non-topographic barriers may have delayed such interchange. For example, perhaps favorable climatic conditions, such as aridification of Central America and establishment of savanna environments, were required for large-scale mammal interchange (Molnar, 2008). Accurately resolving this debate is important not only for reconstructing the late Cenozoic history of North and South America but also for assessing potential linkages between tectonic or climatic events and changes in biodiversity (e.g. Cane and Molnar, 2001).

2.2.2. Biological constraints

Faunal exchange represents one of the most important events in the diversification and extinction of late Cenozoic and modern species in North America, South America, and the Caribbean region. Accurate reconstruction of molecular phylogenies can better define the Neogene (last 23 Myr) record of extinction and speciation in these regions and help discriminate between competing geologic models of the closure of the Central American seaway.

In support of an older Isthmus of Panama, Bacon et al. (2013) attributed relatively early divergence of Central and South American palms to an earlier landbridge available for palm dispersal. A major flaw in this argument, however, is that palms and many other tropical tree taxa (Cody et al., 2010) do not require land bridges to disperse over marine barriers. This is evidenced by the extreme geographic dispersal of members of the same palm clade to Hawaii and South Pacific and Caribbean islands (Bacon et al., 2013). Nevertheless, similar application of **molecular clocks** could address the dynamic responses of both marine and nonmarine organisms in relationship to isthmus closure (Jackson et al., 1993).

In addition to its role in facilitating interchange for terrestrial biota, the isthmus is a geographic barrier for marine organisms. Interpretation of a long-lived isthmus may be confirmed or falsified by molecular data from cross-isthmian divergence times of marine organisms. In a comprehensive review, Lessios (2008) reported on 34 trans-isthmian sister clades of fish, crustaceans, and mollusks with molecular divergence dated to the late Pliocene (5.3–2.6 Ma). These data imply the absence of a marine dispersal barrier between the Caribbean and Pacific until the late Neogene and provide compelling evidence against an older isthmus model. Some circularity in the dating of these divergences exists, however, because several authors **calibrated** their molecular clock estimates assuming a 3 Ma isthmian closure. But in a significant subset of the data, fossil-calibrated molecular clocks provided comparable divergence times, which suggest that the divergence time estimates are robust.

2.3. Late Cenozoic history of the Amazon River

2.3.1. Geological problem

The Amazon River is by far the greatest transcontinental river on Earth, yet geologists remain perplexed about many aspects of its history. Eastward drainage of the Amazon has been linked to rapid uplift of the Andes and sedimentary "overfilling" of Andean foreland basins (Mora et al., 2010). Knowing both the timing of Andean uplift and the age of the river is critical to testing this proposed origination mechanism. Variable estimates of the development of trans-continental drainage of the Amazon River basin have been generated from different types of evidence. A mid-Miocene age has been posited based on changes in sedimentation rate and sediment geochemistry in marine cores immediately east of the mouth of the Amazon River. For example, Figueiredo et al. (2009) studied industry drill cores from the Amazon continental margin and concluded that the Amazon River originated at 11.8–11.3 Ma on the basis of Nd isotopic evidence for Andean provenance and a concurrent slight increase in Amazon Fan mass accumulation rate (MAR). However, although Nd isotopic ratios shift slightly toward "Andean values" sometime after 12.5 Ma, they implausibly return to "non-Andean values" after 5 Ma. A significant MAR increase

did not begin on the Amazon Fan until ca 7 Ma, and MARs generally continued to increase during the Pleistocene (after 2.6 Ma). In drill cores (ODP Leg 154) from the Ceara Rise in the tropical Atlantic Ocean (Shackleton et al., 1997), a bathymetric high on the distal eastern margin of the Amazon Fan, a slight increase in MAR and shift in minor element composition of terrestrial sediments ca. 10 Ma were ascribed to Andean erosion and initiation of transcontinental Amazon drainage (Dobson et al., 2001). However, both the Ceara Rise and Amazon Fan sequences are greatly influenced by sea level and oceanographic currents (as well as climate and hydrology, Harris and Mix, 2002) and therefore do not provide a simple answer to the age of the through-going Amazon River (Campbell et al., 2006).

Other data suggest a later, late-Miocene to Pliocene, age for the origins of the modern Amazon drainage system. Latrubesse and co-workers (Latrubesse et al., 1997, 2007, 2010) conclude that trans-Amazon drainage occurred sometime between 6.5 and 5 Ma, soon after deposition of the Solimões Formation ceased in the Solimões basin of the western Brazilian Amazon. Leguizamon Vega et al. (2006) used sedimentological evidence to conclude that the Purus Arch was an effective barrier to eastward, transcontinental Amazon drainage until at least the late Miocene. In contrast, Campbell and co-workers (Campbell et al., 2006, 2010) suggested that the transcontinental Amazon only developed in the late Pliocene. They posit that a huge paleo "Lago Amazonas" filled most of the lowland Amazon until the end of the Pliocene, when an imagined divide in the far eastern Amazon was finally breached, forming the Amazon River and Amazon Fan.

### 2.3.2. Biological constraints

The riverine barrier hypothesis, first proposed by Wallace (1852), asserts that large rivers act as barriers between populations and lead to biological differentiation and eventual speciation. Wallace observed that the main-stem Amazon separated phenotypically distinct species of monkeys on its north and south banks. Similar observations have been made for other taxa, including birds (Haffer, 1974; Cracraft, 1985), butterflies (Brown, 1979), and additional primate species (Silva et al., 2005). If Amazonian rivers were indeed the drivers of vicariance for these taxa, it follows that dated phylogenies of the separated sister taxa can place limits on the age of river establishment.

For example, the genus *Psophia* (Aves, Gruiformes) occurs throughout the Amazon Basin, with species distributions clearly delimited by the main Amazonian rivers. Ribas et al. (2012) showed that the diversification events within *Psophia* suggest a sequence of drainage evolution during the last 3 Myr involving an initial split related to the lower Amazon River, subsequent splits related to the upper Negro and Madeira rivers, and more recent splits between adjacent interfluves on the Brazilian shield (Fig. 5). Additionally, ages of diversification events in other Amazonian avian and primate groups that show strong spatial correlation between lineage distributions and large Amazonian rivers indicate that current species originated during the Plio-Pleistocene (Ribas et al., 2005; Boubli et al., 2012; d'Horta et al., 2013). These data suggest the possibility that the Amazonian drainage has been very dynamic during the Plio-Pleistocene and played an important role in the origin of current species. Nonetheless improved geological data and interpretation are needed to inform phylogenetic studies, while further geogenomic study is poised to place significant constraints on Amazon geological history.

2.4. Quaternary climate variation and vegetation history

2.4.1. Geological problem

The large-scale Quaternary (last 2.6 Myr) climate variation evident in the waxing and waning of continental ice sheets in the Northern Hemisphere and globally changing atmospheric CO_2, temperature, and sea level has long been presumed to drive massive moisture changes in the Neotropics and in turn affect the past distribution of landscapes and associated biomes. The inferred environmental changes have been
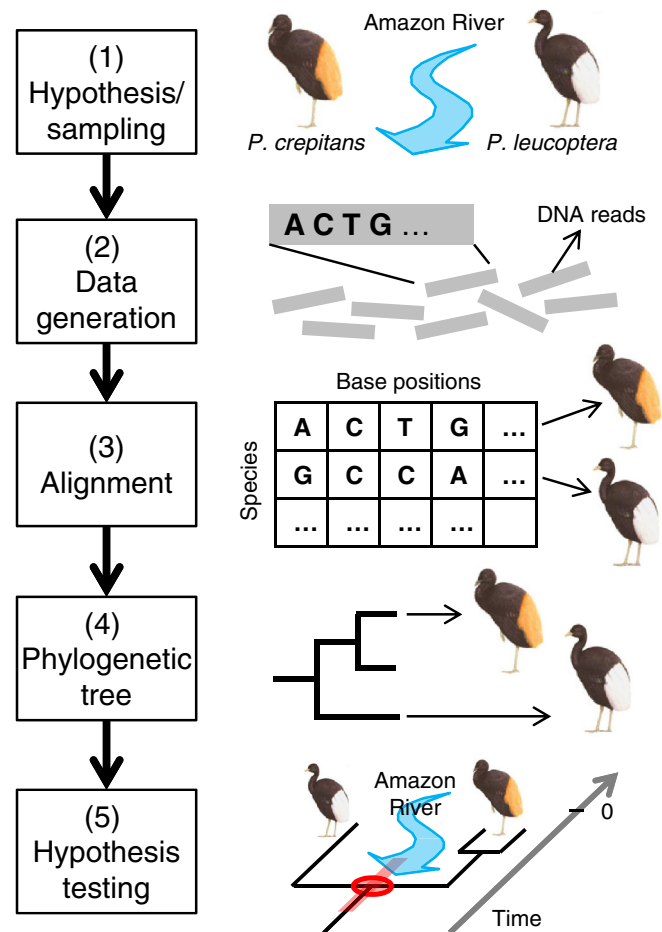
Fig. 5. Schematic illustration of the workflow for genetic or genomic analyses that yield phylogenetic trees and ultimately testing of geologic hypotheses (see Supplementary Information for details). Testing of geologic hypotheses can be carried out with (as shown) or without time calibrated phylogenetic trees (Fig. 2). This example depicts the origins of two trumpeter bird species (*Psophia crepitans* and *Psophia leucoptera*) following the establishment of the Amazon River as a geographic barrier (Ribas et al., 2012).

invoked as factors driving the distribution of organisms and their subsequent diversification and extinction. One of the most prominent hypotheses linking climate change to the generation of tropical biodiversity is the Amazon refugia hypothesis (Haffer, 1969), which stated that during Pleistocene dry periods fragments of Amazon forest persisted in regions of high rainfall (refugia) separated by vast savannah and that populations isolated in these refugia underwent accelerated rates of allopatric speciation. Thus, refugia became species pumps and centers of endemism (Haffer and Prance, 2001). Haffer's hypothesis has subsequently been disputed on several grounds — his centers of purported endemism overlap with areas of high collection intensity and may be artifacts of sampling (Nelson et al., 1990); many species complexes originated prior to the Pleistocene (reviewed in Moritz et al., 2000); and there is no strong evidence that the Amazon forest was fragmented, at least during the latest significant cold period, the Last Glacial Maximum ~20 Ka (reviewed in Mayle et al., 2009). However, some of these counter-arguments are also disputed.

During the past few decades, many late Quaternary pollen records have been generated from tropical South America to evaluate how plant populations responded to Quaternary climate variation and whether or not tropical biomes were fragmented. These records portray spatially diverse patterns of vegetation change at various temporal scales. During the last glacial period (~20–60 Ka), Andean forest taxa moved downslope, and savannah or dry tropical forest expanded at the eastern and southern margins of the Amazon Basin (Mayle et al.,

2009). Although no paleoecological evidence supports widespread contraction of mesic tropical forests or expansion of savannah in the Amazon basin during glacial times, it is not yet clear if this is merely a shortcoming of paleoecological sampling, as the majority of paleoecological records are from the margins of the Amazon, no central Amazonian records contain sediments from the Last Glacial Maximum, and most Quaternary records span <50 Kyr (Mayle et al., 2009).

Recent high-resolution records of paleoclimate, particularly from speleothems and lake sediment cores, are generating greatly improved understanding of late Quaternary climate variation and demonstrate that large-scale moisture variation occurred in the Amazon and adjoining Andes. The largest changes in moisture availability occurred on ~100 Kyr (eccentricity) cycles, synchronous with global glaciation: the southern tropical Andes and western Amazon were the wettest (maximum precipitation minus evaporation) during glacial stages and the driest during interglacial stages (Fritz et al., 2007). Large precipitation changes were paced by the 20-Kyr precession cycles: in the western Amazon and tropical Andes, high precipitation rates, associated with increased intensity of the South American summer monsoon, coincided with austral summer seasonal insolation maxima (Baker et al., 2001; Cruz et al., 2005; Wang et al., 2006). Precipitation north of the equator was anti-phased with that farther south (Peterson et al., 2000). However, precipitation variation was also anti-phased between the western Amazon and eastern Amazon/Nordeste of Brazil (Cruz et al., 2009; Cheng et al., 2013). The spatial patterns of millennial moisture changes were different from those at precessional scales: whereas northern hemisphere cold events were dry in northern South America, the tropics south of the equator were wet (no evidence of an east–west dipole) (Peterson et al., 2000; Cruz et al., 2005; Wang et al., 2006; Fritz et al., 2010; Kanner et al., 2012; Mosblech et al., 2012; Cheng et al., 2013).

2.4.2. Biological constraints

How these large and spatially variable changes in moisture affected Quaternary expansion, contraction, and connectedness of populations of neotropical organisms and subsequent diversification and extinction are insufficiently explored; thus key aspects of the refugia hypothesis in its broadest sense remain untested. Cheng et al. (2013) set out the provocative hypothesis that during past wet periods forest corridors connected presently disjunct regions: the western Amazon with the southwestern Atlantic rainforest of Brazil or the southeastern Amazon with the eastern Atlantic rainforest. Their data imply that the presently wet western equatorial Amazon was a likely wet "refugium" during some phases of the Pleistocene, while the presently drier eastern Amazon (as well as the northern and southern ecotones) was a likely dry "refugium", where rain forest fragmentation, population decline, and species loss would have been greatest, but where dry-adapted species would have thrived.

The pattern and tempo of tropical diversification have been illuminated by the recent proliferation of phylogenetic data. Phylogenetic analyses of complexes of extant species (**crown groups** or clades) suggest that the origination of most studied Amazon clades dates from the Neogene or earlier. This perspective highlights pre-Quaternary geological processes, such as mountain building and river evolution, in the generation of neotropical biodiversity (Hoorn et al., 2010; Bennett et al., 2012). However, other analyses considering the age of extant species (instead of crown clades) suggest considerable speciation during the Quaternary and approximately constant diversification rates throughout the Neogene and Quaternary (Rull, 2008, 2011). This suggests a substantive role for Quaternary processes in speciation and in shaping present biodiversity patterns. This relationship is best evidenced by phylogenetic analyses that sample closely related species.

Population genetic data used within a coalescent framework (Supplemental Information) permit reconstruction of the expansion, contraction, and connectedness of populations of Neotropical organisms during the late Quaternary and can test predictions about environmental history derived from paleoclimatic studies, because it is possible to detect from the current distribution of genetic diversity whether a population has gone through recent changes in size (Beaumont et al., 2002). The concept behind this approach is to fit mathematical models of population demographics (e.g. growth rate) to observed patterns of genetic diversity. During dry periods, mesic forest taxa should be negatively affected, with reduced ranges and population sizes. In contrast, populations adapted to dry or open areas would expand and become more connected in periods of dry climate, allowing greater **gene** flow.

At present, few species have been sufficiently sampled or studied to approach these questions, but there are examples of forest taxa (Carnaval et al., 2009; d'Horta et al., 2011; Ribas et al., 2012; d'Horta et al., 2013; Jones et al., 2013) that show signs of recent population expansion in Amazonia, Central America, and the southern Atlantic forest, but population retraction in the northern Atlantic forest (d'Horta et al., 2011). Also, currently isolated populations that occur in open areas within or around Amazonia seem to have been more connected during the Late Pleistocene (Wuster et al., 2005; Bonvicino et al., 2009; Vargas-Ramírez et al., 2010; Capurucho et al., 2013).

3. Discussion

The concept of reciprocal illumination highlights the potential knowledge that can be gained through interactions between biologists and geologists (Fig. 1). One outcome of a more thorough integration of biology and geology will be better reasoned and better vetted development of the mechanistic links between Earth history and biotic diversification. Research programs that are framed within the context of both biological and geological scenarios from the start and that simultaneously seek reliable data from both fields will be more successful in understanding the evolution of the highly complex environments that arise from the interaction between life and Earth. Too often, probably due to lack of communication between the disciplines, biogeographic studies create a narrative for the causes of diversification making overly simplistic and sometimes incorrect assumptions about complex geological processes. On the other hand, geologists are generally not aware of how biological data can inform major debates regarding tectonics, landscape evolution, and climate history. Although we have presented only four examples of the "reciprocal illumination" between geology and biology, all from the Neotropics, it is clear that many other geological problems from many other geographic settings are equally amenable to geogenomic approaches (e.g. Genner et al., 2010).

Several of our examples underscore the importance of retaining some level of independence, at least in approaches to determining the timing of events. For example, biologists often use the timing of biogeographic events determined from the geological literature to calibrate molecular clocks, which subsequently may be used as an independent age estimate by geologists interested in the same phenomena. We cited one such example — molecular clock estimates for marine taxa that explicitly assumed 3 Ma closure of the Isthmus. It is generally problematic to use biogeographic events (such as the emergence of migration barriers) to calibrate molecular clocks, because one must then assume a vicariance history, thereby ignoring alternative hypotheses, such as more recent cross-barrier dispersal. Alternatively, such biogeographic events can be used as maximum divergence times, thereby allowing for the possibilities of more recent dispersal.

Circularity between geological events and phylogenetic dating can be further minimized through sampling designs and analytical methods that allow the use of fossils and/or biogeographic events that are as independent as is reasonable to the question at hand. For example, statistical methods are available for use of single or multiple calibration points in molecular phylogenies that incorporate fossils that are distantly related to the focal taxon (Wertheim et al., 2010; Yang and Rannala, 2012). These methods work by allowing the statistical transformation of molecular divergence into divergence times to vary throughout a phylogeny (i.e. molecular rates of evolution vary within the phylogeny).

Such calibrations, depending on the global context of the geological events under scrutiny, should be independent of the geological questions under study.

As articulated by Avise (2000) as "taxonomic congruence", time estimates from multiple time-calibrated phylogenies should be used to robustly evaluate geological hypotheses. While the number of time estimates (i.e. the number of time-calibrated phylogenies) obviously affects the reliability of a mean across estimates, efforts should be made to provide multiple time estimates that are phylogenetically independent, representing different groups that are affected by the same barrier. In the end, congruence across estimates may be more informative when they are made from phylogenetically independent taxa that have differing life histories rather than just a large number of taxa.

In some cases, time estimates derived from time-calibrated phylogenies have associated variances that can preclude them from being useful in a geogenomic context. This variance results from three sources: sampling variance (e.g. sampling some but not all species within a clade), evolutionary variance (i.e. the variance resulting from the evolutionary process, see Nei, 1987), and variance associated with age of the fossil or biogeographic events used for calibration (Graur and Martin, 2004). For example, it may be difficult to differentiate between geological hypotheses that are temporally adjacent, especially when variance is correctly taken into account. This does not mean, however, that molecular data are uninformative about the timing of events, just that the events under scrutiny are not differentiated enough temporally (e.g. see Eckert et al., 2008 for an example with testing hypotheses based on Holocene versus Pleistocene events). In practice, this typically means that the hypotheses being tested should have dates separated by hundreds of thousands to millions of years. It is the responsibility of the researcher to fully report uncertainty associated with time estimates (Bromham and Penny, 2003; Graur and Martin, 2004; Parham, 2012). Uncertainty associated with fossil ages and strata can be easily incorporated as priors in Bayesian phylogenetic analyses (e.g. Drummond et al., 2006). This kind of uncertainty is often better understood by geologists and paleontologists than by evolutionary biologists, thus providing another important point of collaboration.

Looking ahead, we can expect great methodological advances in generating and analyzing genomic data, which will provide great opportunities for earth scientists who are prepared to understand modern genetic methodologies and results. Therefore, we encourage geoscientists to learn the basis and assumptions involved in the use of phylogenetic data, to construct hypotheses that can be tested with genomic data, and to collaborate with biologists to undertake these tests. We believe that the application of geogenomics has the potential to revolutionize many fields of Earth sciences.

Author contributions

PB first suggested the idea of geogenomics, and PB, SF, and CD organized the NESCent and OTS workshops that gave rise to this paper. All authors contributed to the development of the ideas contained in this paper. PB, SF, CD, AE, BH, SM, and CR wrote the majority of the text during an OTS Emerging Frontiers workshop, with subsequent contributions from CG and DB.

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