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EDITORIAL

Geogenomics: Toward synthesis

Ours is an often integrative undertaking, a discipline peppered with combinatorial neologisms that reflect the formation and advances of practice and of thought: bio·geography, phylo·geography (Avise et al., 1987) and macro·ecology (Brown & Maurer, 1989), for example. When coined, these new words described an idea—perhaps a technologically enabled way of asking new questions, as in the case of phylogeography, or a novel way of conceptualizing existing data, as in macroecology—in the previously inaccessible interstices or remote reaches of existing thought. In the earliest stages, the idea is rare, precariously placed, and has an uncertain future; it is only assured a place in history if the approach and its contributions are sufficiently accessible and insightful that the principles are adopted more broadly. Adoption and growth is at first slow, but if intriguing and fruitful, the approach will spread and the new field will gain critique and refinements as it develops and matures. Such has been, of course, the fate of the two examples mentioned here. And in time they may go on to seed additional fields.

A more recent neologism is geo·genomics (Baker et al., 2014). While drawing on similar etymons, the origins of geogenomics and phylogeography emphasize distinct characteristics. Whereas phylogeography originated with innovations in molecular biology—specifically the techniques that made mtDNA widely accessible—at the intersection of population genetic and phylogenetic thought, geogenomics' core idea lies in interdisciplinary approaches. Although geogenomics eponymously acknowledges advances in high-throughput sequencing that enabled sampling the breadth of genetic information in organisms, its intersection with geographical and geological thinking is the source of novelty in geogenomics hypothesis testing. As defined by Baker et al. (2014), geogenomics was conceived as 'the use of large-scale genetic data to test or to constrain geological hypotheses … through collaboration between geologists and evolutionary biologists'. They saw it as being 'deeply rooted in … biogeography' and '(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'. While geogenomics, thus, was established with an emphasis on the flow of information from biology to geology, that is, in testing geological hypotheses using genomic data (Baker et al., 2014), it nonetheless recognized the value of reciprocal illumination (*sensu* Hennig, 1966). In a biogeographical context, reciprocal illumination was understood to mean that hypotheses to be tested using the biological (genomic) datasets would be built using detailed knowledge about geological processes; that is, hypotheses would be realistically framed in space and time and their mechanistic outcomes would be well understood by both biologists and geologists.

Intriguingly, Sargeant et al. (2014) also coined the term 'geogenomics' but from a very different perspective, specifically the geography of pathogens, and emphasizing finer spatial and temporal scales. Sargeant et al. (2014) defined geogenomics as the 'examin[ation of] the geographic distribution of … genomes … with a particular emphasis on those mutations that give rise to [adaptations]'; their vision of geogenomics was an extension of evolutionary biology, historical and phylogenetic biogeography, and phylogeography. The differences between these two visions—one explicitly hypothesis driven (Baker et al., 2014), and the other largely descriptive (Sargeant et al., 2014)—and their fates are perhaps illuminating: Baker et al. (2014) has been well cited (Figure 1), whereas Sargeant et al. (2014) has been cited only once. Geogenomics *sensu* Baker et al. (2014) brought something new, something for which phylogeography had long been critiqued as lacking (Nielsen, 2006), that is, a focus on rigorously articulating causal mechanisms linking the coupled evolution of biodiversity and landscapes through time (Dolby et al., 2022; see also Dong, 2022; Figure 2).

One of the great potentials of genomic data is providing information about ecological and evolutionary processes across a range of timescales, so one may be able to look at the interaction of geology with biology, and biology with geology. The continuity of ecological and evolutionary processes has long been appreciated (Marske et al., 2013), but geogenomics arguably extends this further, considering how geological and evolutionary relationships can be nested in time and recorded as superimposed signals in the record of each (Figure 2). At the deep-time end of the spectrum, such things are the purview of classical historical (phylogenetic) biogeography and include questions surrounding Gondwanan vicariance, uplift of the Andes (and every other mountain chain), emergence of the Isthmus of Panama and so on. At the shallowest time spectrum, it includes allele frequency distributions that may hold information about generational changes, including changes in connectivity and diversity of populations responding to landscape and anthropogenic change and the evolution of plant niche construction traits in biogeomorphic landscapes (Dong, 2022), wherein mutual feedbacks over short times may structure both biotic and abiotic environments. These processes must occur on ecological scales throughout evolutionary time (Marske et al., 2013), leading to questions of eco-evolutionary meandering (Thompson, 1999), and the extent to which large-scale interspecific biogeographical patterns are ineluctably extrapolations of small-scale population-level biogeographical processes (Avise

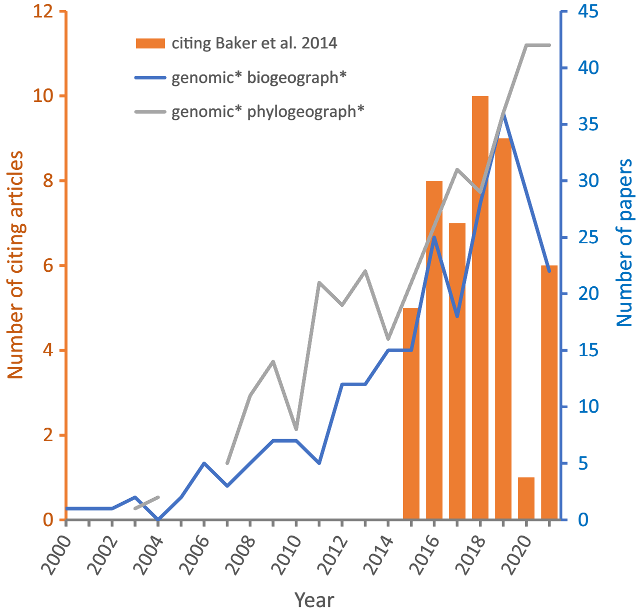

FIGURE 1 The publication history of geogenomics and related fields. The term 'geogenomics' was introduced by Baker et al. (2014) among a background of biogeographical and phylogeographical studies increasingly applying genomic methods. Data are from Web of Science searches on 23 March 2022 conducted as follows: [1] "Genomic* (All Fields) and Biogeograph* (Title)", [2] "Genomic* (All Fields) and Phylogeograph* (Title)", and [3] by listing the articles citing Baker et al. (2014). A fourth search for "Genomic* (All Fields) and Biogeograph* (Title) and Phylogeograph* (All Fields)" indicates mean and median 22% overlap between [1] and [2].

et al., 1987). But how biogeographical processes scale—from local microevolutionary processes to regional macroevolutionary patterns—is something we still do not know, and must yet become tractable as genomic and geological information become better integrated, and as in situ and remotely sensed data become more available on finer scales and more continuously through time and across places. If geogenomics can provide a robust framework for integrating such diverse data streams, perhaps it can precipitate a truly synthetic biogeography?

It is in this spirit of development and refinement of a still young (only 8 years!) and emerging field that we invited contributions to a collection of papers at the intersection of geology, geobiology, earth system science, genomics and higher-level biodiversity studies. Through an expansion of its original definition, we explicitly targeted the potential for geogenomics to yield reciprocal illumination (Hennig, 1966), noting that 'Geogenomics employs genomic data to solve geologic problems or constrain geological hypotheses … [and that] phylogenetics and phylogeography seek to use the geological record … for formulating diversification hypotheses'. Improving mutual appreciation of limits and opportunities within explicit frameworks is key. In interdisciplinary scientific pursuits, it is easy to understand nuances and uncertainties in one's own field, but to presume greater certainty in another. Yet uncertainty, like the processes it describes, is distributed heterogeneously; absolute uncertainty is generally higher on deep timescales and lower (but rarely absent) on recent timescales. Yet a 'coefficient of uncertainty', as an analogue of the 'coefficient of variance', would suggest that uncertainty remains substantial at many scales: reconstructions of the palaeogeographical history of the Amazon are imprecise, as are predictions of gene flow from marine larval transport. Better constraining such uncertainties will enable more mechanistic integration across all scales and beckons a unified and intersectional approach—looking from deep time forward, and from contemporary time backward—where mutual strengths are combined to inform the hypothesis-space and leverage a synergistic understanding of the dynamic, sometimes deterministic and sometimes stochastic, world.

We publish the first papers in the geogenomics special collection here to explore some of these matters. Our goal is to provide a sampling of what geogenomics is currently perceived to be (and therefore what it is?) and also to drive advancement in this synthetic field. This section begins with six papers that examine genetic structure in fish, insects, plants and birds, including studies rooted in Africa, Australia, Eurasia and South America. Several papers examine how the genetic structure of populations is related to changes in landscape structure driven by Quaternary climate variability. Luna et al. (2021) use explicit hypothesis testing to discover that the genetic differentiation in an endemic bird of the Amazon floodplains is related to changing connectivity of drainages associated with Pleistocene climate change, instead of strong gradients in contemporary environmental or river characteristics. Similarly, Barbosa et al. (2021) show that floodplain habitats differing in long-term persistence and connectivity led to different demographic histories for sympatric ovenbird species with distinct habitat affinities. Changes in connectivity also were inferred to drive genetic diversification in thermophilous grasshoppers in Iberia and North Africa as a result of fluctuating sea level and suitable climate during glacial–interglacial cycles (Ortego et al., 2021), and in a widely distributed migratory freshwater fish in Australia as a result of aridification during Pleistocene glacial periods (Bootha et al., 2022). Sanín et al. (2022) reveal that tectonic faulting dynamics, rather than recent mountain uplift, likely shaped phylogeographical breaks in Andean palms. Barthelemy and Munoz (2022) evaluated processes in deeper time and examined whether the proportion of shared lineages of woody plants between India and Madagascar changed following the period of separation and isolation of Madagascar from the Indian-Malagasy plate. Their analysis indicates that Madagascar maintained more of the ancient flora than the Western Ghats of India, likely because of expanded biotic interchange following the collision of India with Eurasia.

What these contributions imply for the future of geogenomics is something to consider again when all the papers in the collection are available. In the meantime, we re-focus briefly on geogenomics' origins in Baker et al. (2014) and the counterpoint of Sargeant et al. (2014) as food for thought. Whereas Sargeant et al. (2014) appeared largely an extension of existing practice, Baker et al. (2014) joined a chorus for updating and extending phylogeography *sensu lato* (Dawson, 2014; Hickerson et al., 2010; Knowles & Maddison, 2002;

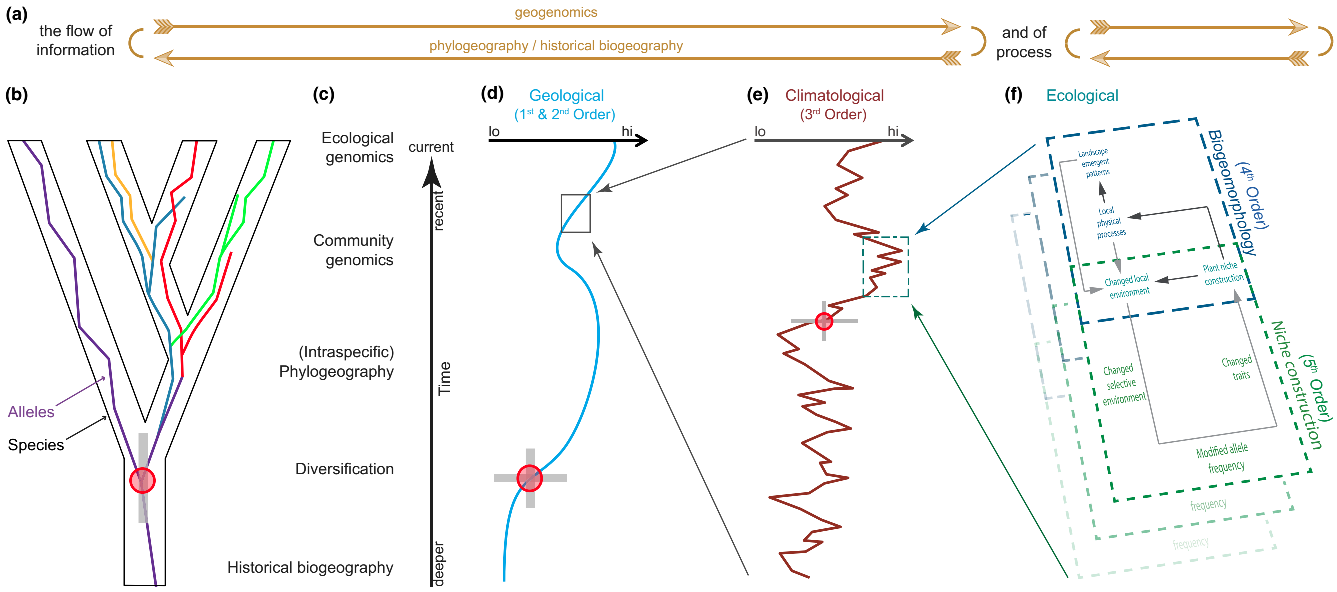

FIGURE 2 Key attributes in geogenomic thinking. (a) The original concept of geogenomic analyses (Baker et al., 2014) used phylogenetic information to test hypotheses about geologic or climatic history. In a manner of speaking, geogenomics was reciprocal to phylogeography and historical biogeography, which tended to employ geologic or climatic history to interpret phylogenetic patterns. The complementarity of these two perspectives, and their potential for reciprocal illumination, however, is self-evident, and speaks to mechanistic intersection in one, another, or both directions across various scales, or 'orders' (*sensu* Dolby et al., 2015). (b) Schematic representation of the phylogenetic context for geogenomics, emphasizing the integration of allelic through species to clade levels, and emergence of macroevolutionary patterns from population-level micro-evolutionary processes. (c) The approximate relative scales of some inter-related subdisciplines in biogeography, and the direction of time in the adjacent four panels, (b) and (d–f). (d) Geological processes, such as rifting and mountain building and opening/closing of seaways, typically are 'large' scale, occurring across regions of the planet and taking tens-of-millions (first order) or millions (second order) of years to complete. (e) Climatological processes, such as glacial cycles, can be shaped by continental-scale geological changes but are more typically conceived of as mid-scale processes occurring over tens to hundreds-of-thousands of years (third order). (f) Extending the geogenomic timeline introduced by Baker et al. (2014), a suite of 'ecological' processes develop trends over shorter time periods—nominally decades to millenia—and at more local spatial scales, for example as conceptualized in the complementary field of biogeomorphology. Biogeomorphology emphasizes the potential interactions between earth and life processes in which evolutionary trajectories are influenced by the geomorphic context, which, in turn, is altered as the niche-construction traits of the biota evolve (Dong, 2022). Red circles and bars in (b, d) and (e) emphasize that assessing variance around estimates of historical and current processes—whether biological, climatological or geological—is essential whether the focus is on applying phylogenies to constrain geological/climatological scenarios or vice versa. In (d) and (e), 'lo' and 'hi' are used to suggest the range of values, from low to high, across which the relative processes vary; the 'blow-out' boxes indicated the nested scales of subsequent panels. This representation of geogenomics emphasizes the iterative nature of processes through time, and that relatively short-term processes act throughout the longer term arcs of climatological and geological history, shaping genomic variation between times and places.

Marske et al., 2013; Papadopoulou & Knowles, 2016), and perhaps because Baker et al. (2014) expounded a new core idea and identified a specific audience, it had greater impact. Yet, many papers in the special issue include components that are not encapsulated by the original definition of geogenomics (*sensu* Baker et al., 2014), as they do not test or constrain specific geological hypotheses, but use geological data to build predictions about biological processes (e.g. demography, migration), often in recent times, thus articulating a finer scale of reciprocal illumination. Is this evidence that geogenomics is misunderstood? Or that it is evolving? Or, perhaps its potential is not yet widely recognized by geologists, and thus that these papers represent a largely biological point of view? Should geogenomics take this opportunity to reaffirm itself as genomics clarifying geology? Or should it broaden its embrace while emphasizing the central tenet of using rich interdisciplinary quantitative data in hypothesis-driven frameworks? Reciprocally? These seem, to us, to be key questions for this special collection to address.

And what of the consequences? Can geogenomics catalyse rethinking of the direction of information flow—not only in biogeography but also in nature—and a revolution in our practice *sui generis*? Or will the ingrained anecdotal approach to phylogeography prevail, co-opting 'geogenomics' simply as shorthand for work that draws on both geo(-logical or -graphical) and genomic datasets but not substantially amending practice? Others have already noted that 'phylogeography' may have passed its peak as a term, even if its essence lives on in other guises (Edwards et al., 2021; but see Figure 1). But does it, and, in its current common configuration, should it? Or is it time to reflect fondly on the many advances made by phylogeography while looking now to a different neologism—geogenomics—for better ways to understand the coupled evolution of Life and Earth?

KEYWORDS

genomics, geology, phylogenetics, phylogeography, population genetics, speciation

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CONFLICTS OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data for Figure S1 are presented in supplementary online documentation.

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BIOSKETCH

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