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PERSPECTIVE

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Building up biogeography: Pattern to process

Abstract

Linking pattern to process across spatial and temporal scales has been a key goal of the field of biogeography. In January 2017, the 8th biennial conference of the International Biogeography Society sponsored a symposium on *Building up biogeography—process to pattern* that aimed to review progress towards this goal. Here we present a summary of the symposium, in which we identified promising areas of current research and suggested future research directions. We focus on (1) emerging types of data such as behavioural observations and ancient DNA, (2) how to better incorporate historical data (such as fossils) to move beyond what we term "footprint measures" of past dynamics and (3) the role that novel modelling approaches (e.g. maximum entropy theory of ecology and approximate Bayesian computation) and conceptual frameworks can play in the unification of disciplines. We suggest that the gaps separating pattern and process are shrinking, and that we can better bridge these aspects by considering the dimensions of space and time simultaneously.

1 | INTRODUCTION

Linking pattern to its underlying process has long been the Holy Grail of macroecology. However, mechanistic and process-based models are often formulated at small spatio-temporal scales, whereas biogeographical patterns usually emerge at broader scales. Historically, statistical models have offered a unifying, predictive framework that can operate across scales, but to do so often requires that we sacrifice explicit consideration of ecological and evolutionary mechanisms (see McGill, 2010). For example, while regional variation in species richness is often readily predicted by environmental conditions (Currie, Francis, & Kerr, 1999), the precise evolutionary and ecological processes underlying such relationships remain unresolved. It is often difficult to understand any kind of pattern in a biogeographical context because it is impossible to conduct experiments at the appropriate temporal *and* spatial scales, such that we biogeographers (unlike other biologists) are often limited to correlative and observational studies. New approaches offer possibilities to integrate evolutionary and biogeographical processes of dispersal, speciation and extinction into dynamic models of community structure (such as the "DAMOCLES" approach described by Pigot & Etienne, 2015; see Figure 1). Scaling up such models to encompass regional biodiversity gradients is an important next step (Cabral, Valente, & Hartig, 2017). In this and many other cases, we believe that it is possible to better link underlying processes to emerging patterns, and our symposium on *Building up biogeography—process to pattern* held at the 8th biennial conference of the International Biogeography Society in Tucson, Arizona, described recent progress in this direction. Here, we summarize these advances. Three themes emerge throughout this discussion: (1) the importance of incorporating data from multiple sources and disciplines (e.g. behavioural observations and minisatellites), (2) the need to move beyond "footprint measures" by incorporating historical processes into models of contemporary data and (3) the power of recently developed models to address biogeographical questions across spatial and temporal scales. We address each of these themes in the sections below. Our intention is not to provide a thorough review of all the ways in which biogeographical processes act across scales (c.f. Cabral et al., 2017; Cavender-Bares, Kozak, Fine, & Kembel, 2009; Chave, 2013; Levin, 1992), but within Figure 1 we show how these concepts fit within the broader biogeography framework linking the drivers of biogeographical patterns and processes. We focus on how processes interact across different spatial and temporal scales, not on ascribing processes to particular spatio-temporal scales (c.f. Cavender-Bares et al., 2009; Swenson, Enquist, Thompson, & Zimmerman, 2007; Weiher & Keddy, 2001), and we believe focusing in this way holds promise in making practical progress fitting mechanistic models to data. We conclude that we are moving towards a productive synthesis of pattern- and process-based methods that will provide new and more generalizable insights into the spatial and temporal distributions of biodiversity.

2 | NON-TRADITIONAL DATA IN BIOGEOGRAPHY

2.1 | Targeted collection of observational data

While macroecology has traditionally advanced through drawing inference from pre-existing data (i.e. data the researcher did not collect themselves), it is increasingly recognized that experiments can also be placed within a macroecological context (Alexander, Diez, Hart, & Levine, 2016; Paine, 2010). Such experiments form one non-traditional source of data in biogeography, but we (uncontroversially, we hope) suggest that macroecologists should not forget the importance of collecting new, carefully considered, observational data. Collecting data that directly address a question or mechanism of interest is a more efficient way to understand a problem than implementing post-hoc statistical corrections. For example, Keith et al. (2016) collected data on the timing of coral spawning in 34 reefs throughout the Indian and Pacific Oceans and, through a combination of careful site selection and the collection of relevant explanatory data, identified the likely cues of coral spawning (namely, seasonal rise in ocean temperature). These data move us closer towards an understanding of the ecological and physiological processes behind spawning through the explicit collection of small-grain large-extent data, which in turn can shed light on the spatio-temporal biogeographical distribution of corals. Moreover, this work uses traditional biogeography to set the agenda for future experimental tests (e.g. temperature manipulations)—an approach that is potentially fruitful across biogeography more widely. Such precise data on the timing of coral spawning could (almost certainly) not have been collated from existing sources: testing different *mechanisms* often requires targeted data collection, not simply the collation of ever-larger data that elucidate general *patterns*.

2.2 | Behavioural data

One type of data that has been incorporated only rarely in biogeographical studies is behavioural observations. While behavioural data might be measured on very different spatial scales to the data usually included in biogeographical models, such data could provide invaluable insight into the link between pattern and process. Individuals make cognitive decisions to enact particular behaviours given a combination of external stimuli and internal motivation. For instance, the presence of food and motivation of hunger could initiate foraging behaviour. However, these behaviours, and their underlying decision-making processes, can become suboptimal in novel environments because of an inability to accurately process novel external information (such as mistaken mate identification as described by Gwynne & Rentz, 1983; see also Whitehead, Rendell, Osborne, & Würsig, 2004). Sub-optimal behaviour at the individual level could feasibly scale up to cause population level declines and subsequent shifts in biogeographical patterns such as species' distributions. Using, for example, coupled dynamic individual-based and species distribution models it is possible to propagate the outcomes of such local-scale behavioural dynamics to produce biogeographical patterns (see "behavioral dynamics" in Figure 1). For example, individual-based models can be used to generate decision rules that can inform about species' environmental preferences and tolerances, which can be propagated through distribution models to improve predictions, and to test whether behaviour is constant through space and time (reviewed in Keith & Bull, 2017). The kinds of behavioural data to best inform such models will depend on the particular question and study system, but as we discuss in *targeted collection of observation data* above, these data may be best gathered specifically to shed light on, for example, the dispersal mechanisms for the clade of interest. Data on phenology or other physiological responses to changing environmental stimuli are already informing the study of biogeography in organisms other than animals (Chuine, 2010).

2.3 | Emerging data sources

There are perhaps three additional kinds of data that, we believe, have the potential to fundamentally change the way in which biogeography operates, but it is of course too soon to be certain. The first is ancient DNA: DNA extracted and sequenced from historical specimens (Gugerli, Parducci, & Petit, 2005; Pääbo et al., 2004). Such data form a natural bridge between phylodynamic models commonly used to infer historical population size (Archie, Luikart, & Ezenwa, 2009; Lemey, Rambaut, Welch, & Suchard, 2010; which are commonly used in epidemiology) and the fossil data whose use we advocate below. The second is intraspecific trait variation; advances in automated image analysis and measurement protocols (Bucksch et al., 2014; Pearse et al., 2018) allow researchers to collect more data than previously thought possible. This has given biogeographers the data to move beyond the simplifying assumption that variation within a species is negligible and random with respect to environment (Bolnick et al., 2011). It is difficult (but, of course, not impossible) to extend modelling approaches to incorporate variation of species traits in response to environmental conditions; it may be more straightforward to do so by collecting data on how species' traits vary and modelling those data themselves. Finally, drones (Anderson & Gaston, 2013; Linchant, Lisein, Semeki, Lejeune, & Vermeulen, 2015) and small satellites (Baker & Worden, 2008; Sandau, 2010) are expanding both the temporal and spatial grain across which we can measure biogeographical patterns. If we are to truly bridge spatial scales and wish to model uncertainty in species' distributions (particularly using quantum approaches—see below), then the increased resolution provided by these new tools will be critical.

3 | BEYOND "FOOTPRINT MEASURES" OF PAST DYNAMICS

3.1 | Integrating phylogenetic information

Biogeographers often try to infer underlying processes from stationary present-day patterns, but it is increasingly clear that deep-time history is important (Ricklefs, 2004; Wiens & Donoghue, 2004). Such deep-time history has been accounted for in two key ways: by measuring (1) species' shared evolutionary history (Webb, Ackerly, McPeek, & Donoghue, 2002), or (2) past environmental change and dispersal lags (e.g. Kissling, Blach-Overgaard, Zwaan, & Wagner, 2016; Sandel et al., 2011). Yet in both of these cases, biogeographical history, macroevolutionary processes or past environmental dynamics are reduced to *footprint measures* that sum up accumulated change (see "beyond footprint measures" in Figure 1). Thus, for purposes here, we consider any metric that sums across an entire time series or phylogeny and reduces it to a single datum as a "footprint measure." Historical data have transformed our understanding of *recent* environmental change (Foley et al., 2005; Parmesan, 2006) and species' invasions (Dehnen-Schmutz, Touza, Perrings, & Williamson, 2007; Duncan, Blackburn, & Sol, 2003), but new data and methods mean there is no need to limit ourselves to historical footprints when addressing processes operating over longer time-scales (Hunt & Slater, 2016). For example, Fritz et al. (2016) use long-term palaeontological datasets to show a consistent diversity–productivity relationship within North American and European mammal and plant fossil records between 23 and 2 million years ago. Present-day data do not match this relationship, likely because Pleistocene climatic

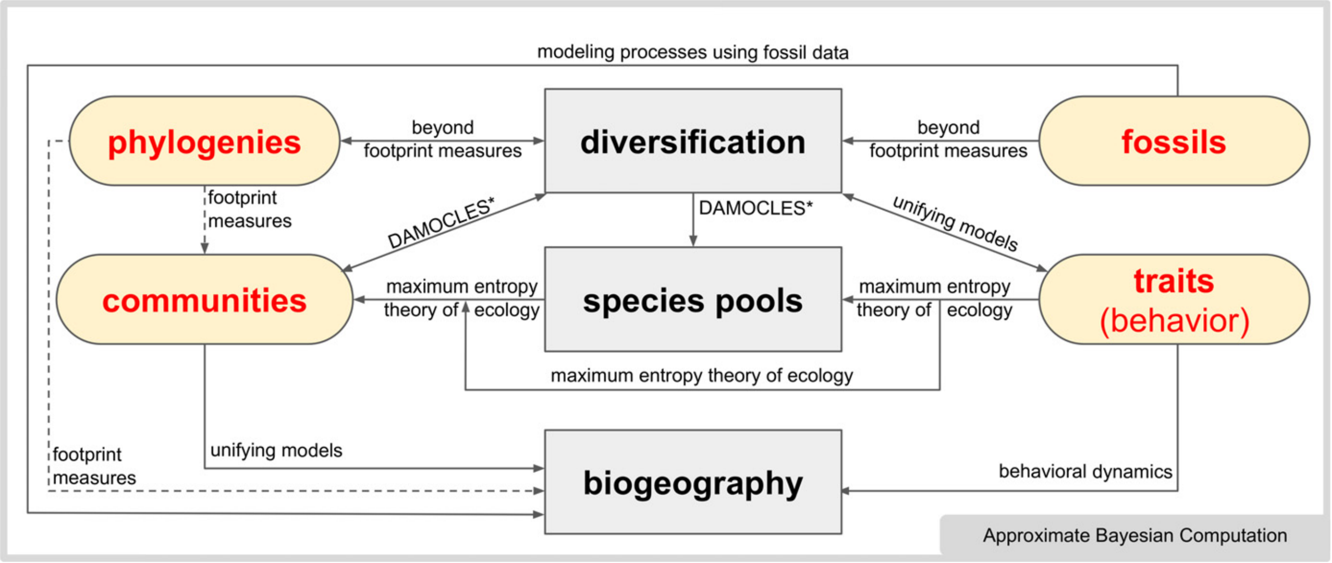

FIGURE 1 Conceptual overview of the processes involved in the assembly of biogeographical patterns. We focus on how data (rounded corners) integrate with biological concepts (square corners) through modelling approaches (labelled arrows) that we describe within the text. Although numerous previous reviews of spatial scaling biogeography have focused on mapping processes onto particular spatial and temporal scales (e.g. Cavender-Bares et al., 2009; Chave, 2013; Levin, 1992; Weiher & Keddy, 2001), here we represent the mapping between each process. This allows scale-dependent processes to interact *across different scales simultaneously*, and provides more information than the traditional placement of processes within a two-dimensional space–time mapping allows. As discussed in the text, approximate Bayesian computation has the potential to incorporate all these processes, and each modelling arrow represents, to some extent, an over-simplification of the processes captured by that model. The dashed lines represent an approach that, as we discuss in the text, we believe the field is currently moving beyond. We emphasize that each label is intended to direct the reader towards the relevant section of this essay, and the intention of this diagram is not to outline all, or even necessarily the most important, patterns, processes and approaches in biogeography. An example of such a missing link might be the study of fossil assemblages (e.g. Gill, Williams, Jackson, Lininger, & Robinson, 2009; Goldberg, Roy, Lande, & Jablonski, 2005; Williams et al., 2013). There are many potential missing links that could be placed linking “communities” to “biogeography,” such as environmental filtering (reviewed in Kraft et al., 2015) and character displacement (reviewed in Dayan & Simberloff, 2005). *DAMOCLES is a method developed by Pigot and Etienne (2015), and is described in the introduction [Colour figure can be viewed at wileyonlinelibrary.com]

oscillations and human impacts reduced mammalian diversity and terrestrial primary production (Barnosky, 2008; Doughty, Faurby, Wolf, Malhi, & Svenning, 2016; Faurby & Svenning, 2015). Similarly, Pearse, Jones, and Purvis (2013) used information from phylogeny to show a tendency for members of younger clades to co-occur with one-another more often than older clades, even millions of years after the clade originated. This perhaps reflects rapid niche evolution of diversifying clades, and, by examining the interaction between evolutionary history and community structure, exposes an observable link between niche evolution and ecological assembly (see “unifying models” in Figure 1). More work is needed to see whether younger clades that have diversified more rapidly in the recent evolutionary past, in terms of both number of species and traits, co-occur more frequently or form more/less stable assemblages in the present day. Both these examples show how general ecological rules ought not to be inferred exclusively from past or extant data, but rather from the mapping of past onto extant data.

3.2 | Modelling processes using fossil data

Another aspect of biogeography that is being revolutionized by moving beyond footprints is the evolution of species’ geographical ranges, where (unlike the examples given above) process-based models are increasingly being fit to data. While methodological development in this field has been tremendous (e.g. Matzke, 2014; Tagliacollo, Duke-Sylvester, Matamoros, Chakrabarty, & Albert, 2015), the ability of purely phylogenetic methods to reliably infer rates of dispersal and extirpation remains limited, even when we simulate data under very simple models (e.g. constant and symmetrical rates). Fossil occurrence data provide an alternative source of information about the evolution of biogeographical ranges through time, and arguably represent the most direct evidence of the processes under study, but fossil data are notoriously incomplete. Silvestro et al. (2016) have shown that dispersal and extirpation rates can be accurately estimated from fossil lineages if fossil preservation is explicitly modelled, and that dispersal rates are more variable through time and between geographical areas than commonly assumed in purely phylogenetic models. Perhaps most importantly, Silvestro et al. also show that fossil-estimated extirpation rates are much higher than the near-zero estimates typically obtained from neontological data. Thus fossil data need not only be used to improve the dating of phylogenetic trees (as is common; reviewed in Donoghue, Doyle, Gauthier, Kluge, & Rowe, 1989; Rutschmann, 2006), but can also be used to augment phylogenetic inferences of historical biogeography and more accurately measure variation in dispersal and extinction through time. Fossils provide data that shed light on the processes that affect diversification (of species and of traits) and range evolution, providing information on both time and place that can inform models fit jointly to phylogenetic and fossil data (Hunt & Slater, 2016). Many open access databases of fossils that contain data on location, age and morphology/traits are now available (e.g. Goring et al., 2015, and *PaleoDB*—https://paleobiodb.org/), making this a rich seam for biogeographical analysis.

4 | UNIFYING MODELS AND CONCEPTS

4.1 | Maximum entropy theory in ecology

The integration of mechanism into statistical models has long been a major challenge in macroecology. Rapid progress means that we now possess conceptual frameworks that combine the explanatory power of statistical tools with the biological insight that mechanistic models can provide. Starting only with a small number of measured state variables and no parameters, the maximum entropy theory in ecology (METE; Harte, Rominger, & Zhang, 2015; see also "METE" in Figure 1) predicts the functional form of multiple macroecological patterns, such as the species abundance distribution and variation in individual body size. These statistical insights have informed debates that have raged for decades within ecology, such as what underlies variation in the species–area curve (Harte, Smith, & Storch, 2009). From hundreds of empirical tests a generalization has emerged: in ecosystems with constant state variables METE performs well, but in ecosystems undergoing shifts METE fits data poorly. For those ecosystems in which the state variables are changing, a hybrid METE–mechanism-based approach (DynaMETE) might be more appropriate, in which dynamic state variables are driven by explicit mechanisms. This promising theory of ecosystems undergoing change, either in response to human influence or to natural disturbance regimes, has the potential to unify statistical and mechanistic approaches. More detail on the expanding range of METE-like models that can incorporate non-equilibrium dynamics can be found in Rominger et al. (2017).

4.2 | Quantum biogeography

An alternative framework which, like METE, also draws from the physics literature, is to treat species as analogous to quantum particles. As species distributions are dynamic, precise locations are only known when they are observed and thus provide an incomplete portrait of the entire species' distribution. Consequently, a species' distribution may be better represented by a wave function, or an analogous distribution function, that describes the relative likelihood of presence at given locations (see "quantum biogeography" in Figure 1; Real, Barbosa, & Bull, 2017). Acknowledging that species' likelihood of occurrence is continuous, not discrete, has advanced prediction and inference of species' distributions (Guillera-Arroita et al., 2015) and assembly patterns (Karger et al., 2016) and quantum-inspired approaches may continue this trend. A fruitful next step may be to incorporate behaviour into similar waveform functions, unifying uncertainty, behaviour and macro-scale distribution data.

4.3 | Approximate Bayesian computation

METE and the frameworks developed from it have been criticized for their mathematical complexity. For those who prefer to simulate rather than to solve, approximate Bayesian computation (ABC) has emerged as a way to contrast the influence of different mechanisms (see Beaumont, 2010 for a thorough review; but also Robert, Cornuet, Marin, and Pillai, 2011). Informally, ABC involves simulating a system (e.g. populations migrating at specified rates) with existing data as starting points under different parameters (e.g. migration rates) and defined statistical metrics (e.g. average range size). ABC is thus a model-fitting framework, like maximum likelihood, and not a particular model formulation. An ABC model is declared a good fit if the metrics of the simulations and data are similar, and so ABC does require the careful selection of sensitive and appropriate summary statistics. While ABC is computationally intensive, its flexibility allows the testing of almost any model we can conceive and implement. Clarke, Thomas, and Freckleton (2017) used ABC to model interspecific competition on phylogenies, addressing theory that has proven difficult to test (Nuismer and Harmon, 2015; but see Drury, Clavel, Manceau, and Morlon, 2016. There is a pressing need for more such work, testing, for example, whether clades whose trait evolution has been shaped by competition are still competing in the present, or whether that past evolution has mitigated competition in the present.

4.4 | Integration through concepts rather than equations

Building cross-scale models that produce broad-scale patterns from process-based models may seem challenging, but it can be done. Alongside the approaches outlined above, Albert, Schoolmaster, Tagliacollo, and Duke-Sylvester (2017) provide another excellent example of cross-scale modelling. Focusing on a single process—the effects of river capture in changing species' geographical distributions—Albert et al. simulate realistic broad-scale diversification dynamics using local-scale dispersal limitation. Such approaches that connect disparate ideas and processes (in this case, dispersal limitation and river capture) have more potential than approaches that only connect to specific patterns (e.g. changes in diversification rate). Scales and disciplines are united by concepts formalized as equations, but even if two disciplines use similar terms it does not necessarily follow that the processes are the same. For example, Ornstein–Uhlenbeck (OU) models of trait evolution have a parameter, α, that describes the tendency of evolution to remain near some optimum. This parameter is often referred to as a "selection" parameter, largely because OU models are used to represent constant stabilizing selection in quantitative genetics. However, empirical studies have shown conclusively that the quantitative genetics version of OU models differs from the macroevolutionary version (e.g. Harmon et al., 2010, but see also Uyeda and Harmon, 2014). Shared terminology and models alone do not unify the two fields of quantitative genetics and macroevolution: unification comes not from models or equations, but from concepts. To give another example, incorporating equations from quantum theory into species distribution modelling, as proposed by Real et al. (2017), may be a useful way to advance one field by borrowing concepts from another, but does not reflect a meaningful unification of quantum and biogeographical theory. Biogeography has greatly benefited from the sharing of theory across disciplines, and we hope that this continues, but such exchange will be more fruitful when we consider whether not just mathematics but also concepts are comparable across fields.

5 | CONCLUSION AND FUTURE DIRECTIONS

We frequently consider biogeographical processes operating at different temporal and/or spatial scales, but it is often difficult in practice to "scale up" (or down). By including new data into process-based models, especially those with a temporal dimension, we might be able to better connect across scales. The palaeontological record has always informed our understanding of species' biogeographical histories and can greatly enhance inference from phylogeny (Brewer, Jackson, & Williams, 2012; Fritz et al., 2013; Jackson & Erwin, 2006; Lieberman, 2002), but the integration of fossil data within newer macroecological methods has tended to lag behind that of phylogenetic data. Data not typically incorporated within biogeographical analyses, such as species' behavioural responses, provide information at a much finer temporal resolution, but can similarly be used to construct scale-able process-based models. Despite recent advances and exciting prospects for the future, the identification of generalizable models that can improve the link from process to pattern remains elusive (Cabral et al., 2017). However, the gaps that artificially separate pattern and process in our concepts and analyses are shrinking, and by considering the dimensions of space and time simultaneously, we will be able to link them with stronger bridges. The development of new methodological frameworks, such as METE and ABC, provides the power and flexibility to move us towards a more complete understanding of how processes produce patterns across spatio-temporal scales. It is exciting to think that many of the conceptual linkages we outlined in Figure 1 can now be explicitly modelled, as we outline in Figure 2. What strikes us most when looking at this figure is the *linkages* across data-types: it is now possible to integrating so many different kinds of data in a single model that the range of questions we can now ask has increased substantially.

We do not wish to suggest that the concepts we discuss here encompass all the exciting new advances in the field of biogeography, but throughout this essay we have articulated three areas that we have focused upon in our own research and that inspired our symposium at the International Biogeography Society meeting in Arizona. (1) The collection or inclusion of non-traditional data, such as the dispersal behaviours of species on a landscape, which has improved our understanding of the mechanisms underlying biogeographical patterns. (2) Moving beyond "footprint measures" of deep-time patterns to shed light on how past mechanisms have shaped

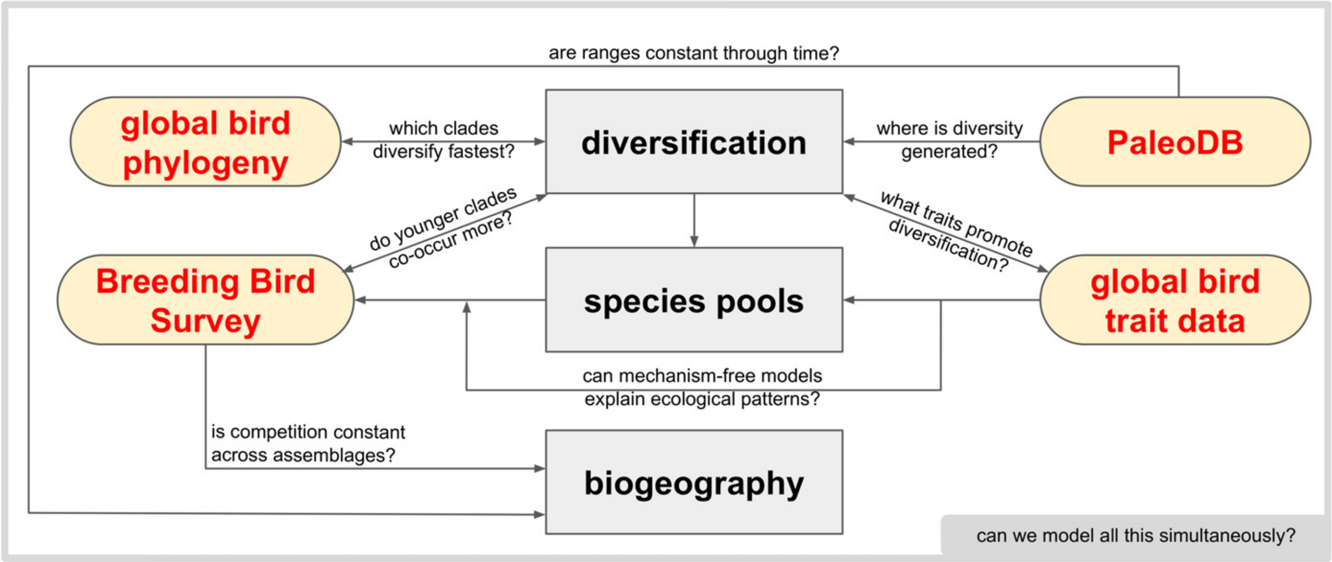

FIGURE 2 Questions that can be answered about the nature of spatio-temporal scaling using the approaches outlined in this essay. As an accompaniment to Figure 1, we present here a figure with the same layout, only now each source of data has been replaced with a published dataset (Breeding Bird Survey—Sauer, Hines, & Fallon, 1966; PaleoDB—https://paleobiodb.org/; global bird phylogeny—Jetz, Thomas, Joy, Hartmann, & Mooers, 2012; global bird traits—Wilman et al., 2014) and each methodological arrow with a question that can be answered [Colour figure can be viewed at wileyonlinelibrary.com]

present-day ecological dynamics. (3) Utilizing empirical frameworks such as METE and ABC to test specific hypotheses that, even a decade ago, were only conceptual frameworks (e.g. Figure 1). It is our hope that these three avenues provide a way forward for biogeographers to continue to advance our understanding of how processes vary across spatial and temporal scales.

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approximate Bayesian computation (ABC), behaviour, fossils, macroecology, maximum entropy theory, mechanism, phylogeny, scale, space, time

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