

1 **Title page**

2 **Article type:** Perspectives

3 **Article title:** Building up biogeography: pattern to process

4 **Running head:** Building up biogeography: pattern to process

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32 **Word-count:** 5680 (abstract, main text, acknowledgements, and references)

## 33 Abstract

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

46 **Keywords:** approximate Bayesian computation (ABC), behavior, fossils, macroecology,  
47 maximum entropy theory, mechanism, phylogeny, scale, space, time

## 48 Introduction

49 Linking pattern to its underlying process has long been the Holy Grail of macroecology. How-  
50 ever, mechanistic and process-based models are often formulated at small spatio-temporal  
51 scales, whereas biogeographic patterns usually emerge at broader scales. Historically, sta-  
52 tistical models have offered a unifying, predictive framework that can operate across scales,  
53 but to do so often requires that we sacrifice explicit consideration of ecological and evo-  
54 lutionary mechanisms (see McGill 2010). For example, while regional variation in species  
55 richness is often readily predicted by environmental conditions (Currie et al. 1999), the pre-  
56 cise evolutionary and ecological processes underlying such relationships remain unresolved.  
57 It is often difficult to understand any kind of pattern in a biogeographical context because  
58 it is impossible to conduct experiments at the appropriate temporal *and* spatial scales, such  
59 that we biogeographers (unlike other biologists) are often limited to correlative and observa-  
60 tional studies. New approaches offer possibilities to integrate evolutionary and biogeographic  
61 processes of dispersal, speciation and extinction into dynamic models of community struc-  
62 ture (such as the ‘DAMOCLES’ approach described by Pigot & Etienne 2015, see figure  
63 1). Scaling up such models to encompass regional biodiversity gradients is an important  
64 next step (Cabral et al. 2017). In this and many other cases, we believe that it is possible  
65 to better link underlying processes to emerging patterns, and our symposium on *Building*  
66 *up biogeography—process to pattern* held at the 8<sup>th</sup> biennial conference of the International  
67 Biogeography Society in Tucson, Arizona, described recent progress in this direction. Here,  
68 we summarize these advances. Three themes emerge throughout this discussion: (1) the  
69 importance of incorporating data from multiple sources and disciplines (*e.g.*, behavioral  
70 observations and mini-satellites), (2) the need to move beyond ‘footprint measures’ by incor-  
71 porating historic processes into models of contemporary data and (3) the power of recently  
72 developed models to address biogeographical questions across spatial and temporal scales.  
73 We address each of these themes in the sections below. Our intention is not to provide a

74 thorough review of all the ways in which biogeographic processes act across scales (*c.f.* Levin  
75 1992; Cavender-Bares et al. 2009; Chave 2013; Cabral et al. 2017), but within figure 1 we  
76 show how these concepts fit within the broader biogeography framework linking the drivers  
77 of biogeographic patterns and processes. We focus on how processes interact across different  
78 spatial and temporal scales, not on ascribing processes to particular spatio-temporal scales  
79 (*c.f.* Weiher & Keddy 2001; Swenson et al. 2007; Cavender-Bares et al. 2009), and we believe  
80 focusing in this way holds promise in making practical progress fitting mechanistic models  
81 to data. We conclude that we are moving towards a productive synthesis of pattern- and  
82 process-based methods that will provide new and more generalizable insights into the spatial  
83 and temporal distributions of biodiversity.

## 84 **Non-traditional data in biogeography**

85 **Targeted collection of observational data.** While macroecology has traditionally ad-  
86 vanced through drawing inference from pre-existing data (*i.e.*, data the researcher did not  
87 collect themselves), it is increasingly recognized that experiments can also be placed within  
88 a macroecological context (Paine 2010; Alexander et al. 2016). Such experiments form one  
89 non-traditional source of data in biogeography, but we (uncontroversially, we hope) suggest  
90 that macroecologists should not forget the importance of collecting new, carefully consid-  
91 ered, observational data. Collecting data that directly address a question or mechanism of  
92 interest is a more efficient way to understand a problem than implementing *post-hoc* sta-  
93 tistical corrections. For example, Keith et al. (2016) collected data on the timing of coral  
94 spawning in 34 reefs throughout the Indian and Pacific Oceans and, through a combination  
95 of careful site selection and the collection of relevant explanatory data, identified the likely  
96 cues of coral spawning (namely, seasonal rise in ocean temperature). These data move us  
97 closer towards an understanding of the ecological and physiological processes behind spawn-

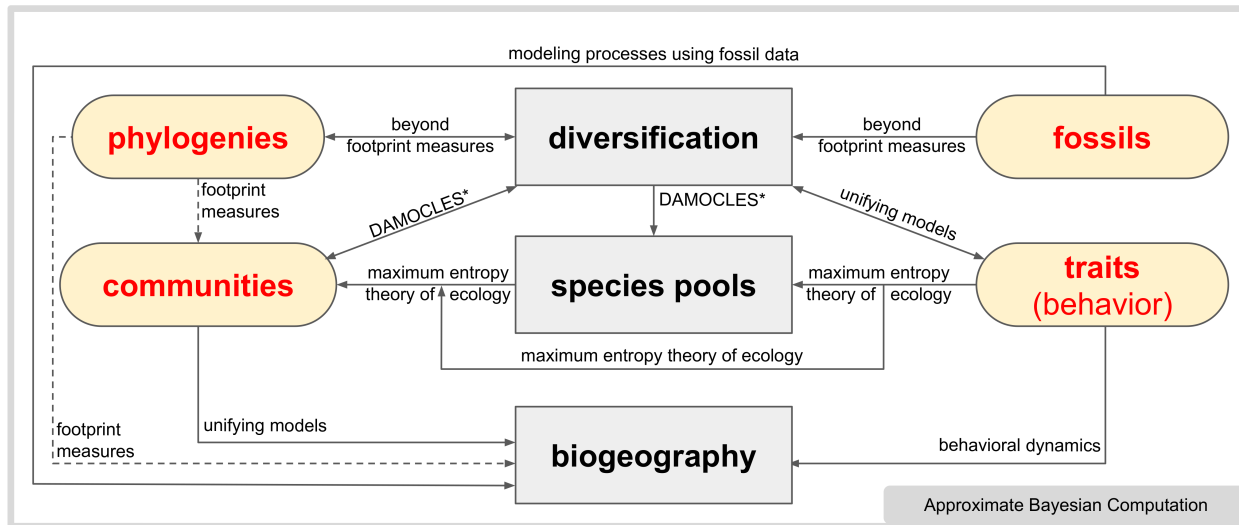


Figure 1: **Conceptual overview of the processes involved in the assembly of biogeographical patterns.** We focus on how data (rounded corners) integrate with biological concepts (square corners) through modeling approaches (labeled arrows) that we describe within the text. Whereas numerous previous reviews of spatial scaling biogeography have focused on mapping processes onto particular spatial and temporal scales (*e.g.*, Levin 1992; Weiher & Keddy 2001; Cavender-Bares et al. 2009; Chave 2013), 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 that each modeling 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.*, Goldberg et al. 2005; Gill et al. 2009; 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 & Etienne (2015), and is described in the introduction.

98 ing through the explicit collection of small-grain large-extent data, which in turn can shed  
99 light on the spatio-temporal biogeographic distribution of corals. Moreover, this work uses  
100 traditional biogeography to set the agenda for future experimental tests (*e.g.*, temperature  
101 manipulations)—an approach that is potentially fruitful across biogeography more widely.  
102 Such precise data on the timing of coral spawning could (almost certainly) not have been  
103 collated from existing sources: testing different *mechanisms* often requires targeted data  
104 collection, not simply the collation of ever-larger data that elucidate general *patterns*.

105 **Behavioral data.** One type of data that has been incorporated only rarely in biogeographic  
106 studies is behavioral observations. While behavioral data might be measured on very different  
107 spatial scales to the data usually included in biogeographic models, such data could provide  
108 invaluable insight into the link between pattern and process. Individuals make cognitive  
109 decisions to enact particular behaviors given a combination of external stimuli and internal  
110 motivation. For instance, the presence of food and motivation of hunger could initiate  
111 foraging behavior. However, these behaviors, and their underlying decision-making processes,  
112 can become sub-optimal in novel environments because of an inability to accurately process  
113 novel external information [such as mistaken mate identification as described by Gwynne  
114 & Rentz (1983); see also Whitehead et al. (2004)]. Sub-optimal behavior at the individual  
115 level could feasibly scale up to cause population level declines and subsequent shifts in  
116 biogeographical patterns such as species' distributions. Using, for example, coupled dynamic  
117 individual-based and species distribution models it is possible to propagate the outcomes  
118 of such local-scale behavioral dynamics to produce biogeographic patterns (see 'behavioral  
119 dynamics' in figure 1). For example, individual-based models can be used to generate decision  
120 rules that can inform about species' environmental preferences and tolerances, which can be  
121 propagated through into distribution models to improve predictions, and to test whether  
122 behavior is constant through space and time (reviewed in Keith & Bull 2017). The kinds  
123 of behavioral data to best inform such models will depend on the particular question and  
124 study system, but as we discuss in '*targeted collection of observation data*' above, these data

125 may be best gathered specifically to shed light on, for example, the dispersal mechanisms  
126 for the clade of interest. Data on phenology or other physiological responses to changing  
127 environmental stimuli are already informing the study of biogeography in organisms other  
128 than animals (Chuine 2010).

129 **Emerging data sources.** There are perhaps three additional kinds of data that, we be-  
130 lieve, have the potential to fundamentally change the way in which biogeography operates,  
131 but it is of course too soon to be certain. The first is ancient DNA: DNA extracted and  
132 sequenced from historic specimens (Gugerli et al. 2005; Pääbo et al. 2004). Such data form  
133 a natural bridge between phylodynamic models commonly used to infer historic population  
134 size (Archie et al. 2009; Lemey et al. 2010, which are commonly used in epidemiology;) and  
135 the fossil data whose use we advocate below. The second is intra-specific trait variation; ad-  
136 vances in automated image analysis and measurement protocols (Bucksch et al. 2014; Pearse  
137 et al. 2016) allow researchers to collect more data than previously thought possible. This  
138 has given biogeographers the data to move beyond the simplifying assumption that varia-  
139 tion within a species is negligible and random with respect to environment (Bolnick et al.  
140 2011). It is difficult (but, of course, not impossible) to extend the modeling approaches to  
141 incorporate variation of species traits in response to environmental conditions; it may be  
142 more straightforward to do so by collecting data on how species' traits are non-stationary  
143 and modeling those data themselves. Finally, drones (Anderson & Gaston 2013; Linchant  
144 et al. 2015) and small satellites (Baker & Worden 2008; Sandau 2010) are expanding both  
145 the temporal and spatial grain across which we can measure biogeographical patterns. If  
146 we are to truly bridge spatial scales and wish to model uncertainty in species' distributions  
147 (particularly using quantum approaches—see below), then the increased resolution provided  
148 by these new tools will be critical.



## 149 Beyond ‘footprint measures’ of past dynamics

150 **Integrating phylogenetic information.** Biogeographers often try to infer underlying  
151 processes from stationary present-day patterns, but it is increasingly clear that deep-time  
152 history is important (Ricklefs 2004; Wiens & Donoghue 2004). Such deep-time history have  
153 been accounted for in two key ways: by measuring (1) species’ shared evolutionary history  
154 (Webb et al. 2002), or (2) past environmental change and dispersal lags (*e.g.*, Sandel et al.  
155 2011; Kissling et al. 2016). Yet in both of these cases, biogeographic history, macroevolution-  
156 ary processes, or past environmental dynamics are reduced to “*footprint measures*” that sum  
157 up accumulated change [see ‘(beyond) footprint measures’ in figure 1]. Thus, for purposes  
158 here, we consider any metric that sums across an entire time series or phylogeny and reduces  
159 it to a single datum as a ‘footprint measure’. Historical data have transformed our under-  
160 standing of *recent* environmental change (Foley et al. 2005; Parmesan 2006) and species’  
161 invasions (Duncan et al. 2003; Dehnen-Schmutz et al. 2007), but new data and methods  
162 mean there is no need to limit ourselves to historical footprints when addressing processes  
163 operating over longer timescales (Hunt & Slater 2016). For example, Fritz et al. (2016) use  
164 long-term paleontological datasets to show a consistent diversity-productivity relationship  
165 within North American and European mammal and plant fossil records between 23 and 2  
166 million years ago. Present-day data do not match this relationship, likely because Pleis-  
167 tocene climatic oscillations and human impacts reduced mammalian diversity and terrestrial  
168 primary production (Barnosky 2008; Faurby & Svenning 2015; Doughty et al. 2016). Simi-  
169 larly, Pearse et al. (2013) used information from phylogeny to show a tendency for members  
170 of younger clades to co-occur with one-another more often than older clades, even millions  
171 of years after the clade originated. This perhaps reflects rapid niche evolution of diversify-  
172 ing clades, and, by examining the interaction between evolutionary history and community  
173 structure, exposes an observable link between niche evolution and ecological assembly (see  
174 ‘unifying models’ in figure 1). More work is needed to see whether younger clades that have

175 diversified more rapidly in the recent evolutionary past, in terms of both number of species  
176 and traits, co-occur more frequently or form more/less stable assemblages in the present day.  
177 Both these examples show how general ecological rules ought not to be inferred exclusively  
178 from past or extant data, but rather from the mapping of past onto extant data.

179 **Modeling processes using fossil data.** Another aspect of biogeography that is being  
180 revolutionized by moving beyond footprints is the evolution of species' geographic ranges,  
181 where (unlike the examples given above) process-based models are increasingly being fit to  
182 data. While methodological development in this field has been tremendous (*e.g.*, Matzke  
183 2014; Tagliacollo et al. 2015), the ability of purely phylogenetic methods to reliably infer  
184 rates of dispersal and extirpation remains limited, even when we simulate data under very  
185 simple models (*e.g.*, constant and symmetric rates). Fossil occurrence data provide an al-  
186 ternative source of information about the evolution of biogeographic ranges through time,  
187 and arguably represent the most direct evidence of the processes under study, but fossil data  
188 are notoriously incomplete. Silvestro et al. (2016) have shown that dispersal and extirpation  
189 rates can be accurately estimated from fossil lineages if fossil preservation is explicitly mod-  
190 eled, and that dispersal rates are more variable through time and between geographic areas  
191 than commonly assumed in purely phylogenetic models. Perhaps most importantly, Silvestro  
192 et al. also show that fossil-estimated extirpation rates are much higher than the near-zero  
193 estimates typically obtained from neontological data. Thus fossil data need not only be used  
194 to improve the dating of phylogenetic trees (as is common; reviewed in Donoghue et al. 1989;  
195 Rutschmann 2006), but can also be used to augment phylogenetic inferences of historical bio-  
196 geography and more accurately measure variation in dispersal and extinction through time.  
197 Fossils provide data that shed light on the processes that affect diversification (of species  
198 and of traits) and range evolution, providing information on both time and place that can  
199 inform models fit jointly to phylogenetic and fossil data (Hunt & Slater 2016). Many open  
200 access databases of fossils that contain data on location, age, and morphology/traits are now  
201 available (*e.g.*, Goring et al. 2015, and *PaleoDB*—<https://paleobiodb.org/>), making this a

202 rich seam for biogeographical analysis.

## 203 **Unifying models and concepts**

204 **Maximum entropy theory in ecology (METE).** The integration of mechanism into  
205 statistical models has long been a major challenge in macroecology. Rapid progress means  
206 that we now possess conceptual frameworks that combine the explanatory power of statis-  
207 tical tools with the biological insight that mechanistic models can provide. Starting only  
208 with a small number of measured state variables and no parameters, the maximum entropy  
209 theory in ecology (METE; Harte et al. 2015, ; see also ‘METE’ in figure 1) predicts the func-  
210 tional form of multiple macroecological patterns, such as the species abundance distribution  
211 and variation in individual body size. These statistical insights have informed debates that  
212 have raged for decades within ecology, such as what underlies variation in the species-area  
213 curve (Harte et al. 2009). From hundreds of empirical tests a generalization has emerged:  
214 in ecosystems with constant state variables METE performs well, but in ecosystems under-  
215 going shifts METE fits data poorly. For those ecosystems in which the state variables are  
216 changing, a hybrid METE–mechanism-based approach (DynaMETE) might be more appro-  
217 priate, in which dynamic state variables are driven by explicit mechanisms. This promising  
218 theory of ecosystems undergoing change, either in response to human influence or to natural  
219 disturbance regimes, has the potential to unify statistical and mechanistic approaches. More  
220 detail on the expanding range of METE-like models that can incorporate non-equilibrium  
221 dynamics can be found in (Rominger et al. 2017).

222 **Quantum biogeography.** An alternative framework which, like METE, also draws from  
223 the physics literature, is to treat species as analogous to quantum particles. As species  
224 distributions are dynamic, precise locations are only known when they are observed and  
225 thus provide an incomplete portrait of the entire species’ distribution. Consequently, a

226 species' distribution may be better represented by a wave-function, or an analogous dis-  
227 tribution function, that describes the relative likelihood of presence at given locations (see  
228 'quantum biogeography' in figure 1; Real et al. 2017). Acknowledging that species' like-  
229 lihood of occurrence is continuous, not discrete, has advanced prediction and inference of  
230 species' distributions (Guillera-Arroita et al. 2015) and assembly patterns (Karger et al.  
231 2016), and quantum-inspired approaches may continue this trend. A fruitful next step may  
232 be to incorporate behavior into similar waveform functions, unifying uncertainty, behavior,  
233 and macro-scale distribution data.

234 **Approximate Bayesian computation.** METE and the frameworks developed from it  
235 have been criticized for their mathematical complexity. For those who prefer to simulate  
236 rather than to solve, approximate Bayesian computation (ABC) has emerged as a way to  
237 contrast the influence of different mechanisms [see Beaumont (2010) for a thorough review;  
238 but also Robert et al. (2011)]. Informally, ABC involves simulating a system (*e.g.*, pop-  
239 ulations migrating at specified rates) with existing data as starting points under different  
240 parameters (*e.g.*, migration rates) and defined statistical metrics (*e.g.*, average range size).  
241 ABC is thus a model-fitting framework, like maximum likelihood, and not a particular model  
242 formulation. An ABC model is declared a good fit if the metrics of the simulations and data  
243 are similar, and so ABC does require the careful selection of sensitive and appropriate sum-  
244 mary statistics. While ABC is computationally intensive, its flexibility allows the testing of  
245 almost any model we can conceive and implement. Clarke et al. (2017) used ABC to model  
246 inter-specific competition on phylogenies, addressing theory that has proven difficult to test  
247 [Nuismer & Harmon (2015); but see Drury et al. (2016)]. There is a pressing need for more  
248 such work, testing, for example, whether clades whose trait evolution has been shaped by  
249 competition are still competing in the present, or whether that past evolution has mitigated  
250 competition in the present.

251 **Integration through concepts rather than equations.** Building cross-scale models

252 that produce broad-scale patterns from process-based models may seem challenging, but it  
253 can be done. Alongside the approaches outlined above, Albert et al. (2017) provide another  
254 excellent example of cross-scale modeling. Focusing on a single process—the effects of river  
255 capture in changing species’ geographic distributions—Albert et al. simulate realistic broad-  
256 scale diversification dynamics using local-scale dispersal limitation. Such approaches that  
257 connect disparate ideas and processes (in this case, dispersal limitation and river capture)  
258 have more potential than approaches that only connect to specific patterns (*e.g.*, changes  
259 in diversification rate). Scales and disciplines are united by concepts formalized as equa-  
260 tions, but even if two disciplines use similar terms it does not necessarily follow that the  
261 processes are the same. For example, Ornstein-Uhlenbeck (OU) models of trait evolution  
262 have a parameter,  $\alpha$ , that describes the tendency of evolution to remain near some optimum.  
263 This parameter is often referred to as a ‘selection’ parameter, largely because OU models  
264 are used to represent constant stabilizing selection in quantitative genetics. However, em-  
265 pirical studies have shown conclusively that the quantitative genetics version of OU models  
266 differs from the macroevolutionary version [*e.g.*, Harmon et al. (2010), but see also Uyeda  
267 & Harmon (2014)]. Shared terminology and models alone do not unify the two fields of  
268 quantitative genetics and macroevolution: unification comes not from models or equations,  
269 but from concepts. To give another example, incorporating equations from quantum theory  
270 into species distribution modeling, as proposed by Real et al. (2017), may be a useful way  
271 to advance one field by borrowing concepts from another, but does not reflect a meaningful  
272 unification of quantum and biogeographic theory. Biogeography has greatly benefited from  
273 the sharing of theory across disciplines, and we hope that this continues, but such exchange  
274 will be more fruitful when we consider whether not just mathematics but also concepts are  
275 comparable across fields.

## 276 Conclusion and future directions

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

298 We do not wish to suggest that the concepts we discuss here encompass all the exciting new  
299 advances in the field of biogeography, but throughout this essay we have articulated three  
300 areas that we have focused upon in our own research and that inspired our symposium at  
301 the International Biogeography Society meeting in Arizona. (1) The collection or inclusion

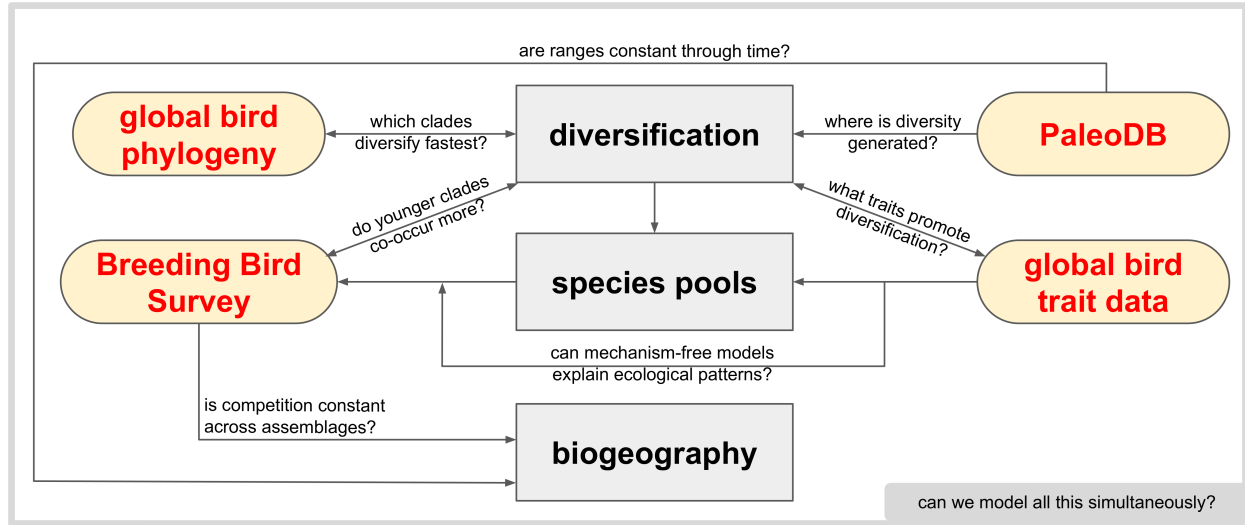


Figure 2: **Questions that can be answered about the nature of spatio-temporal scaling using the approaches outlined in this essay.** As an accompaniment to figure 1, we present here a figure with the same layout, only now each source of data has been replaced with a published dataset [Breeding Bird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

302 of non-traditional data, such as the dispersal behaviors of species on a landscape, which  
 303 has improved our understanding of the mechanisms underlying biogeographical patterns.  
 304 (2) Moving beyond ‘footprint measures’ of deep-time patterns to shed light on how past  
 305 mechanisms have shaped present-day ecological dynamics. (3) Utilizing empirical frameworks  
 306 such as METE and ABC to test specific hypotheses that, even a decade ago, were only  
 307 conceptual frameworks (*e.g.*, figure 1). It is our hope that these three avenues provide a way  
 308 forward for biogeographers to continue to advance our understanding of how processes vary  
 309 across spatial and temporal scales.

## 310 Acknowledgements

311 We are grateful to the International Biogeography Society for funding and organizing the  
 312 2017 symposium at their annual meeting that this article summarizes, and to the editor

313 (Peter Linder) for encouraging us to submit this summary. We are grateful to all who  
314 attended the symposium, and in particular James Albert. BG Waring provided useful feed-  
315 back, as did two anonymous reviewers and Juliano Sarmiento Cabral. AMB is supported  
316 by FCT (Portugal) and by FEDER/COMPETE 2020 through contract IF/00266/2013, ex-  
317 ploratory project CP1168/CT0001, and funds POCI-01-0145-FEDER-006821 to research  
318 unit UID/BIA/50027. SAK is supported by the VILLUM Foundation (grant number 10114)  
319 and the Danish National Research Foundation through support to the Center for Macroecol-  
320 ogy, Evolution and Climate (grant number DNRF96). LJH is supported under a grant from  
321 the National Science Foundation (NSF DEB 1208912). DS is supported by a grant from the  
322 Swedish Research Council (2015-04748). SF is supported by the German Research Foun-  
323 dation (DFG Emmy Noether grant FR 3246/2-1). TJD is funded by *Fonds de Recherche*  
324 *Nature et Technologies* grant number 168004.



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