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# The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models

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## ► To cite this version:

Mikael Pontarp, Lynsey Bunnefeld, Juliano Sarmiento Cabral, Rampal Etienne, Susanne Fritz, et al.. The Latitudinal Diversity Gradient: Novel Understanding through Mechanistic Eco-evolutionary Models. *Trends in Ecology & Evolution*, 2019, 34 (3), pp.211-223. 10.1016/j.tree.2018.11.009 . hal-02301521

**HAL Id: hal-02301521**

**<https://hal.univ-grenoble-alpes.fr/hal-02301521>**

Submitted on 25 May 2020

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**Highlights Box (870 characters including space)**

The latitudinal diversity gradient (LDG) is one of the most widely debated patterns in ecology and evolution, associated with hundreds of papers, dozens of hypotheses, and disagreements about its underlying processes.

The lack of agreement stems from 1) the verbal nature of existing hypotheses, 2) the failure to mechanistically integrate all relevant ecological and evolutionary processes to the LDG, and 3) the degree to which many empirical patterns are consistent with multiple LDG explanations.

We show how mapping LDG hypotheses to a set of key ecological and evolutionary processes leads to a better understanding of the internal logic of those hypotheses. The codification of those processes within a mechanistic eco-evolutionary model is essential for contrasting support for hypotheses and for understanding the relative importance of the processes themselves.

## **Outstanding Questions**

What are the underlying causes of the latitudinal diversity gradient (LDG)? Multiple hypotheses have been formulated to answer this question but a consensus remains elusive, partly due to hidden assumptions that are associated with these primarily verbal hypotheses.

What key processes, describing how organisms interact with their biotic and abiotic environment, are necessary and sufficient for modeling biodiversity patterns associated with the LDG? We argue for eco-evolutionary processes: selection, dispersal, ecological drift, and speciation, but researchers need to explore the tradeoffs associated with modeling these processes in greater or lesser detail.

How are eco-evolutionary simulation models best confronted with empirical data (e.g. phylogenies, species ranges, rank abundances, and functional trait distributions)? Pattern oriented modeling and novel Bayesian statistics may be the key for such a quantification of the link between process and LDG patterns.

1 **Title:**

2 **The latitudinal diversity gradient - novel understanding through**  
3 **mechanistic eco-evolutionary models**

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49

50 **Keywords (max 6):**

51 diversity-patterns, mechanistic-modeling, ecology, evolution, biogeography, macroecology

## 52 **Abstract**

53 The latitudinal diversity gradient (LDG) is one of the most widely studied patterns in ecology,  
54 yet no consensus has been reached about its underlying causes. We argue that the reasons are  
55 the verbal nature of existing hypotheses, the failure to mechanistically link interacting  
56 ecological and evolutionary processes to the LDG, and the fact that empirical patterns are  
57 often consistent with multiple explanations. To address this issue, we synthesize current LDG  
58 hypotheses, uncovering their eco-evolutionary mechanisms, hidden assumptions, and  
59 commonalities. Furthermore, we propose mechanistic eco-evolutionary modeling and an  
60 inferential approach that makes use of geographic, phylogenetic, and trait-based patterns to  
61 assess the relative importance of different processes for generating the LDG.

62

## 63 **State of the art and calls for novel mechanistic approaches**

64 The increase in species diversity from the poles to the equator, commonly referred to as the  
65 latitudinal diversity gradient (LDG), is one of the most pervasive [1, 2] and widely debated  
66 biological patterns, with at least 26 listed hypotheses associated with it [3-5]. These  
67 hypotheses can be classified into three higher-level categories related to latitudinal variation  
68 in **ecological limits** (See Glossary), **diversification rates**, and time for species accumulation  
69 (Table 1). Empirical evidence seems compatible with many of these hypotheses. For example,  
70 species richness is correlated with purported proxies for ecological limits such as net primary  
71 productivity [6-8], diversification rate can vary latitudinally due to gradients in temperature  
72 [9, 10], and diversity is greatest in regions where diversification has occurred over a longer  
73 period [11-13]. These and similar studies have improved our understanding of the LDG and  
74 macroevolutionary patterns in general, but the diffuse support for different hypotheses reveals  
75 a lack of consensus and points to challenges in testing and evaluating these hypotheses.

76

77 We argue that reconciling the causes of the LDG requires moving beyond verbal chains of  
78 logic, which are inherently prone to error with respect to how assumptions result in their  
79 predicted effect [14], and towards a more formal and mechanistic framework. Verbal  
80 hypotheses often contain hidden assumptions that go untested and lack specificity with  
81 respect to the mechanistic underpinning of relevant **ecological** and **evolutionary processes**.  
82 Verbal hypotheses also tend to focus on a single driver to predict just one or a few patterns  
83 related to that driver. Consequently, these predictions alone may not be sufficient to  
84 distinguish competing hypotheses [15, 16]. A more explicit description of the processes  
85 underlying all hypotheses will generate a wider range of predictions which can be used to  
86 disentangle possibly non-mutually exclusive hypotheses and evaluate the relative importance  
87 of these processes.

88

89 We, therefore, call for a transformation in the way biologists think about and study the LDG.  
90 The classification of hypotheses (Table 1) is an important first step, but it does not resolve the  
91 difficulty of identifying and quantifying the relative strength of the processes underlying the  
92 LDG. We propose moving towards a mechanistic framework, founded on key processes that  
93 describe how individual organisms interact with their biotic and abiotic environments, and  
94 how these interactions scale up to result in the LDG and other **secondary biodiversity**  
95 **patterns**. Ultimately, revealing the nature of these **eco-evolutionary processes** will yield  
96 more insight than continuing to argue about non-mutually exclusive LDG hypotheses.

97

## 98 **Examining the LDG through the lens of mechanistic macroecology**

### 99 **Key processes across levels of biological organization**

100 We recognize four key processes, as defined by [17], that necessarily underpin the LDG and  
101 thus should be included as components of any LDG model that aims to capture variation in  
102 species richness, abundance, and composition over a spatially and temporally variable

103 environment: 1) selection, 2) ecological drift, 3) dispersal, and 4) speciation. Selection, drift,  
104 and dispersal can all influence the birth, death, and movement of individuals over small  
105 spatial and temporal scales. Selection (sensu [17]) encompasses any process that results in  
106 the differential survival and reproduction of individuals, based on how **environmental**  
107 **filtering** [18] and biotic interactions select for specific traits. Ecological drift manifests itself  
108 via stochastic variation in the births and deaths of individuals. Dispersal of individuals is  
109 influenced by the spatial structure of the landscape as well as individual dispersal capabilities  
110 and can lead to species colonizing new regions. Each of these individual-level ecological and  
111 microevolutionary processes is propagated throughout higher levels of biological  
112 organization, resulting in discrete patterns at the level of populations, species, and  
113 communities (Figure 1).

114

115 Over longer timescales, environmental conditions have fluctuated with glacial/interglacial  
116 oscillations, cooler and warmer periods in Earth's history, orogenic events, volcanic activity,  
117 and shifts in tectonic plates, all of which can affect diversity dynamics [19-21]. At these  
118 spatial and temporal scales selection, ecological drift, and dispersal determine where species  
119 or even whole clades are able to persist geographically and how traits evolve. Species that  
120 become poorly adapted to the environment or that are poor competitors for resources are  
121 expected to have low fitness and ultimately go extinct, reflecting critical eco-evolutionary  
122 feedbacks [22, 23]. Speciation becomes especially relevant with increasing temporal and  
123 spatial scales. The details of how speciation occurs are complex and the critical question in a  
124 LDG context becomes how and why speciation mode or rate varies along geographic  
125 gradients. All of the processes described above necessarily interact with each other and with  
126 the spatiotemporal environment, resulting in the broad range of geographic and phylogenetic  
127 biodiversity patterns that we observe today. As highlighted below, these processes can help us  
128 compare and disentangle LDG hypotheses.



129

### 130 **Classical LDG hypotheses revisited**

131 Characterizing LDG hypotheses based on the key processes described above helps to clarify  
132 the internal logic of those hypotheses, and highlights how they differ. All hypotheses invoke  
133 an explicit driver or condition that varies latitudinally (Figure 1), but considering the  
134 processes related to this driver, often below the level of biological organization at which the  
135 hypothesis was formulated, can reveal previously unrecognized assumptions and predictions.  
136 Below we discuss four examples, chosen to represent hypotheses invoking variation in limits,  
137 rates, and time. These examples may also serve as a guide for better understanding other  
138 hypotheses.

139

#### 140 *The more individuals hypothesis*

141 The “more individuals hypothesis” invokes latitudinal variation in ecological limits and a  
142 positive relationship between the number of species and resource availability [24]. If  
143 resources are finite and a zero-sum constraint on the total amount of biomass or individuals  
144 applies, any increase in diversity over time results in a decrease in average biomass or  
145 abundance per species. Extinction rates will thus be diversity-dependent and richness will be  
146 regulated around some equilibrium value that scales with the total number of individuals that  
147 can be supported [24, 25]. This hypothesis implicitly invokes interspecific competition and  
148 the resultant allocation of resources across species (Table 1). The argument does not invoke  
149 selection (Fig. 1) and can be applied equally to ecologically neutral or non-neutral species. An  
150 important and unstated assumption is that the response of the biota to environmental change is  
151 fast enough that richness is at equilibrium across the latitudinal gradient.

152

#### 153 *The seasonality hypothesis*

154 The seasonality hypothesis argues that the within-year environmental stability of the tropics  
155 results in either greater diversification rates or higher ecological limits via increased niche  
156 packing (Table 1 and Fig. 1). The first argument suggests that in the less seasonal tropics,  
157 organisms experience a smaller range of conditions and hence evolve narrower thermal niches  
158 compared to the temperate zone. The idea that “mountain passes are higher in the tropics”  
159 [26] suggests that dispersal barriers were effectively greater there, increasing the chance of  
160 population divergence and allopatric speciation [27, 28]. Selection thus dictates the  
161 environmental conditions that a species can tolerate, but it is speciation rate that varies with  
162 latitude and ultimately generates the LDG. The second version of the seasonality hypothesis  
163 suggests that stability-driven specialization promotes intense niche packing, and hence more  
164 species can coexist in the tropics [29, 30]. Species are then hypothesized to evolve narrower  
165 resource breadths rather than narrow thermal niches, assuming that resources are limited and  
166 that diversity actually emerges from niche packing [29] (Table 1, Figure 1). Implicit in both  
167 hypotheses is a performance tradeoff between specialists and generalists, such that specialists  
168 evolve and outcompete generalists in aseasonal environments.

169

#### 170 *The temperature-dependent speciation rates hypothesis*

171 The hypothesis that higher temperature elevates evolutionary rates has been used to explain  
172 global diversity patterns in both land and sea [31, 32]. One version of the hypothesis [33]  
173 follows from the metabolic theory of ecology [34], stating that temperature positively affects  
174 all biological rates including mutation rates, which can lead to speciation and ultimately  
175 diversity accumulation. This assumes that speciation rates directly follow from mutation rates,  
176 which may be problematic if other factors (e.g. existence of geographic barriers, assortative  
177 mating) are limiting speciation. The hypothesis makes no specific predictions regarding  
178 selection or dispersal. Importantly, this hypothesis could be invoked in either an equilibrium  
179 or non-equilibrium world. In a non-equilibrium world, speciation rates alone could explain

180 variation in richness between regions if all regions were similarly old, and extinction rates  
181 were equal across regions [10]. In an equilibrium world, increased speciation rates in the  
182 tropics can lead to higher equilibrium richness, as in Hubbell [35] neutral model of  
183 biodiversity.

184

#### 185 *The tropical niche conservatism hypothesis*

186 The tropical **niche conservatism** hypothesis [36, 37] states that diversity is higher in the  
187 tropics because of the infrequency of colonisations of the cooler temperate zone by a tropical  
188 ancestor due to strongly conserved thermal niches and tropical origins of most taxa, and hence  
189 the longer time available for diversification in the tropics. The hypothesis assumes that,  
190 barring major disturbances or climatic shifts, species richness will continue to increase  
191 unbounded over time [37]. This hypothesis has only ever been formulated at the species level,  
192 and yet it inherently implies a particular set of rules by which individuals interact with the  
193 environment and each other. Selection by the environment is by definition strong, with  
194 individuals unable to survive and reproduce under conditions different from their optima, and  
195 evolution of a new optimum is rare. Less obvious are the implications of the hypothesis for  
196 resource competition between individuals. Unbounded, or diversity-independent,  
197 diversification is only possible in the absence of an overarching zero-sum constraint [25]. The  
198 absence of such a constraint implies that while the population size of a species might be  
199 affected by the fit between the environment and environmental performance traits, it is  
200 independent of the population sizes of potential competitors and of interspecific competition  
201 more broadly.

202

#### 203 **The utility of a mechanistic framework**

204 The examples presented above illustrate three insights gained by adopting a generalized eco-  
205 evolutionary framework. First, many of the fundamental rules by which organisms are

206 assumed to interact with each other and with their environment will be qualitatively similar  
207 regardless of LDG hypothesis. For example, individual survival and reproduction must be  
208 functions of how well adapted the individuals are to their environment relative to their intra-  
209 and interspecific competitors. Second, latitudinal differences in ecological limits,  
210 diversification rates, and time for diversification may emerge via different **mechanisms**  
211 integrated into the same framework. For example, diversification rates may be higher due to  
212 the temperature-dependence of mutation rates [9, 38] or due to the increased reproductive  
213 isolation in aseasonal environments [27, 39]. Third, although each hypothesis invokes a  
214 primary driver or process, we have shown that these hypotheses also make unstated  
215 assumptions about other processes and mechanisms which need to be considered in concert to  
216 fully understand the emergence of the LDG and other macroecological and macroevolutionary  
217 patterns.

218

## 219 **Mechanistic eco-evolutionary models as a quantitative tool for** 220 **understanding LDG patterns**

221 The mechanistic framing of processes that underpin the LDG naturally facilitates the  
222 translation from heuristic thinking to mechanistic eco-evolutionary models (Box 1). We  
223 believe that building these models will be essential to making progress on the LDG and  
224 biodiversity patterns in general because they allow quantitative analyses and predictions of  
225 the various secondary patterns. Secondary patterns are key for more powerful inference about  
226 the origin of species richness patterns. Below we provide concrete examples of components of  
227 a mechanistic LDG model and associated patterns followed by a discussion about how to use  
228 such a model for inference with the available data.

229

## 230 **Mechanistic models for studying the LDG**

231 *The spatiotemporal environmental template*

232 The basic driver of an LDG model is the spatiotemporal environmental template. It can be  
233 viewed as the theater in which the eco-evolutionary play unfolds, and the spatiotemporal  
234 variation in that template (Earth's climatic, geologic, and tectonic history) may be as critical  
235 to emergent diversity patterns as the mechanisms and processes governing how organisms  
236 interact and evolve [40-42]. Explaining the LDG with eco-evolutionary **simulation models**,  
237 therefore, benefits from suitable paleoenvironmental reconstructions [43] and the integration  
238 of global data sets on continental topography and paleoshorelines [44, 45].

239

240 *Trait-based local population dynamics*

241 Traits are essential for individual survival and reproduction (fitness) and mechanistic models  
242 that include interactions of organismal traits and the abiotic and biotic environment, below the  
243 level of species (i.e. at the individual, population or metapopulation level), is thus  
244 appropriate. Local population dynamics can, for example be assumed to be trait-dependent  
245 [46, 47]. One set of traits might determine an organism's fitness dictated by the abiotic  
246 environment, a different set of traits may influence relative fitness associated with the suite of  
247 potential competitors present at any point in time [48]. Such a modeling approach requires  
248 making basic assumptions that facilitate the link between environmental conditions, available  
249 resources, and ecological interactions, and population dynamics then emerge from those  
250 assumptions.

251

252 *Spatial and eco-evolutionary metacommunity dynamics*

253 For modeling eco-evolutionary metacommunity dynamics, trait-based models need to be  
254 implemented in a larger spatial context, allowing individuals to disperse over geographically  
255 relevant extents. Metacommunity dynamics will arise from eco-evolutionary feedbacks  
256 between dispersing individuals and recipient communities within the context of the

257 spatiotemporal template [49]. Evolutionary dynamics result from natural selection by both  
258 abiotic and biotic conditions, ecological drift, dispersal, and speciation. Speciation can be  
259 modeled using a phenomenological approach or more complex allele-based models in which  
260 phenotypic trait variability is completely or partially heritable and the accumulation of genetic  
261 incompatibilities may drive differentiation of daughter species (Box 2). Each of these  
262 modeling components is necessary for capturing the suite of processes invoked by LDG  
263 hypotheses (Box 1), they can be modeled with varying degrees of complexity and they come  
264 with a set of low-level assumptions that need to be clearly stated (Box 2).

265

### 266 **Understanding patterns and inferring processes**

267 Above we have shown that a mechanistic mindset is useful to better understand the internal  
268 logic and consequences of the different hypotheses, as well as the interactions among them. In  
269 addition, a **mechanistic model** can clarify the biodiversity patterns expected under different  
270 combinations of spatiotemporal environmental templates, biotic interactions, and other eco-  
271 evolutionary rules [e.g. 16, 48, 50]. This ability to simulate very different worldviews of how  
272 the LDG arises (e.g., “ecological limits”, “niche conservatism”, etc.) within the same  
273 comparative framework is a critical element of our approach as different types of processes  
274 modeled with varying degrees of mechanistic detail can be explored and contrasted.

275

276 Ultimately, we need mechanistic models to understand the details of the emerging eco-  
277 evolutionary patterns at a sufficient resolution to be able to quantitatively confront them with  
278 data. The more secondary patterns (e.g. phylogenies, species ranges, distributions of  
279 abundance or functional traits) that can be modeled, the greater the diagnostic power of the  
280 model for exploring parameter space and for inferring the strength and interactions of  
281 different processes. The examination of these patterns will also point to the type of data that  
282 will be most valuable for reliable inference of a given process [51].

283

284 While we believe that confronting different model scenarios with multiple observed patterns  
285 (described in Box 3) is the only way to make progress in understanding the LDG, we realize  
286 that substantial conceptual, statistical, and computational challenges are associated with this  
287 task [52]. The complexity of the suggested models often makes it difficult to understand the  
288 consequences of the underlying assumptions. Ways of overcoming such challenges are to  
289 build on known ecological models (e.g. Lotka-Volterra equations) and evolutionary theory  
290 (e.g. Adaptive Dynamics theory) that has been studied extensively. The models should also be  
291 built and analyzed in a sequential manner of increased complexity to shed light on the  
292 consequences of the key model assumptions and their interactions. While it is not our aim to  
293 detail these and other methodological challenges here, we nevertheless highlight two basic  
294 inferential approaches that seem particularly promising. First, qualitative matching of multiple  
295 patterns gives an indication of whether the modeled processes can produce the patterns that  
296 we observe [15, 25, 41, 53]. Pattern matching is conceptually straightforward and easily  
297 allows combining the LDG with multiple observed secondary patterns to compare alternative  
298 model or parameter choices. Second, models like the ones suggested above can be fitted to a  
299 range of patterns in data using simulation-based methods such as **Approximate Bayesian**  
300 **Computation** [54-57] or synthetic likelihood [58, 59]. Regardless of which inferential  
301 approach is used, any empirical patterns that a model is unable to reproduce can be instructive  
302 in the iterative process of model improvement.

303

### 304 **Concluding remarks**

305 Progress in understanding the processes that underlie LDG patterns and associated diversity  
306 patterns has been slow (see also Outstanding Questions). We repeat calls for a transition in  
307 biodiversity research, translating verbal models into a unified mechanistic framework that can  
308 be implemented in quantitative computer simulations [52, 53, 60]. In such a framework,

309 researchers can focus on measuring and inferring the ecological and evolutionary processes  
310 that govern the interaction of organisms with each other and their environment in time and  
311 space, which must ultimately underpin the LDG. By applying this framework, hidden  
312 assumptions in current hypotheses are exposed, revealing how the hypotheses relate to each  
313 other and how they might be distinguished (Table 1, Figure 1). More importantly, this  
314 framework is a roadmap for flexible eco-evolutionary simulation models (Box 1-2) that can  
315 generate a rich set of empirical patterns from the same underlying processes. We believe that  
316 this ability to produce multiple diagnostic patterns will be crucial for inference (Box 3), and  
317 ultimately for converting the available data into new knowledge about macroecology and  
318 macroevolution. Challenges associated with model construction and the way models are  
319 confronted with data will arise, but such challenges are inherent and inevitable to all sciences  
320 that deal with complex systems. We are confident that, with time, these challenges can be  
321 addressed, and models combining realistic spatiotemporal environmental templates with trait  
322 based eco-evolutionary implementation under an iterative procedure of model design,  
323 evaluation and improvement, will advance our understanding and quantitative inference of the  
324 processes underlying the LDG.

325

## 326 **Acknowledgments**

327 This paper is an outcome of the sELDiG working group kindly supported by sDiv,  
328 the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-  
329 Jena-Leipzig (DFG FZT 118). SH thanks the Alexander von Humboldt Foundation for  
330 funding support through a postdoctoral fellowship; SAF was funded by the German Research  
331 Foundation (DFG FR 3246/2-1). DS was supported by the Czech Science Foundation (grant  
332 no. 16-26369S).

333



334 **Box 1 (text)**

335 **Box 1. An LDG simulation model in action**

336 Any simulation model of the processes that result in patterns at the biogeographic scale [e.g.  
337 52, 60] must incorporate several fundamental processes (Figure I.A). Hurlbert and Stegen [16,  
338 25] provide one example of such an eco-evolutionary simulation model in an LDG context  
339 (Figure I.B). In the model, species have different thermal optima (initially assigned randomly,  
340 but subject to selection). The difference between a species' thermal optimum and the  
341 temperature of the region determines that species' local population size. Species may  
342 experience implicit competition via a regional zero-sum constraint, and the probability of  
343 speciation, dispersal, and extinction are each functions of regional population size. The  
344 simulation results in spatial richness patterns, regional trait distributions, and a phylogenetic  
345 tree (Figure I.C).

346

347 The simulation model was run under different parameter combinations that mimic distinct  
348 LDG hypotheses ("Niche Conservatism", "Ecological Limits", "Diversification Rates"), and  
349 the emergent geographic, trait and phylogenetic data were used to derive further metrics and  
350 patterns that provide diagnostic support for each hypothesis (Figure I.D, only two patterns  
351 shown). Simulated and observed patterns were compared informally. This study demonstrated  
352 the utility of comparing expectations for multiple hypotheses, confirming that many patterns  
353 like the diversity gradient itself and measures of phylogenetic tree imbalance were shared  
354 across hypotheses. Conversely, patterns like the relationship between speciation rate and  
355 latitude or mean root distance and richness were potentially diagnostic of the processes that  
356 generated them [16].

357

358 While exemplifying many of the desirable properties of a mechanistic model for the LDG,  
359 there are several ways in which the model in Hurlbert and Stegen [16, 25] could be improved.

360 First, the geographic representation of the model was a simple one-dimensional spatial  
361 gradient with no long-term climate dynamics. Second, the model has no means of  
362 representing a trophic niche in particular, or niche specialization in general, both of which are  
363 invoked by various LDG hypotheses (Table 1). Third, speciation is modeled as a point  
364 mutation process which may impact simulated phylogenetic patterns (Box 2). Finally, to make  
365 more quantitative inferences about the support for the respective hypotheses, a formal  
366 statistical parameter estimation, and model selection would be desirable [53, 61, 62]. We  
367 discuss methods of fitting empirical patterns to simulations in Box 3.

368

## 369 **Box 2 (text)**

### 370 **Box 2: Modeling decisions: the example of speciation**

371 Modeling each of the components in Box 1, Figure IA requires a wealth of implementation  
372 decisions. These decisions may have consequences for how well a given hypothesis is  
373 represented, and what types of patterns emerge. As an example, we consider the case of  
374 speciation, which can be modeled with varying degrees of complexity [63], from a purely  
375 phenomenological approach to more complex allele-based models. For example, spatial  
376 processes combined with drift may induce speciation through Dobzhansky-Müller  
377 Incompatibilities [64] while abiotic and ecological factors can induce disruptive selection and  
378 speciation both in allopatry [e.g. 41, 65] or sympatry [e.g. 66, 67]. For complete divergence  
379 and the formation of proper (biological) species, mechanisms for reproductive isolation,  
380 including sexual selection and assortative mating, also adds to the complexity.

381

382 After making decisions about what speciation mode to model (e.g. sympatric versus  
383 allopatric), modelers face a range of implementation choices from purely phenomenological  
384 models of point mutation speciation as in Box 1 to more mechanistic models, where species

385 diversification emerges from evolved trait divergence [48, 68-70], or the accumulation of  
386 genetic differences that arise as a function of vicariant events or divergent selection (Figure I).  
387 These implementation decisions can impact emergent phylogenetic patterns. For example,  
388 Davies et al [42] showed that measures of tree imbalance and branch stemminess were  
389 sensitive to whether speciation occurred via point mutation or various types of range fission.  
390  
391 More generally, to draw a reliable inference, researchers should assess their possible  
392 implementation options and evaluate the sensitivity of the patterns of interest to these choices.  
393 Some patterns will inevitably be more sensitive to implementation decisions than the others.  
394 For example, the topology of a phylogeny captures the relative branching pattern but is  
395 agnostic about branch lengths, and so topology may be less sensitive than branch length-based  
396 metrics to decisions that affect the timing and rate of speciation events. When attempting to  
397 infer process from empirical data, patterns sensitive to those implementation decisions should  
398 either be disregarded, or the implementation decision itself can be included as alternative  
399 submodels that are then inferred by data. A more general discussion of fitting models to data  
400 is provided in Box 3.

401

402

### 403 **Box 3 (text)**

#### 404 **Box 3. Inference**

405 Possibly the most crucial step in using mechanistic eco-evolutionary models for inference  
406 about the origin of the LDG is the way we confront them to data, for example, to compare  
407 alternative parameterizations and model structures. Starting from a set of alternative model  
408 formulations (Box 1, Figure I.A), we can compare the patterns produced by the model  
409 alternatives to observed patterns (Box 1, Figure I.B). The alternative model formulations may

410 correspond to particular hypotheses, as shown in the figure, or to different parts of parameter  
411 space independent of existing hypotheses. The fit to the different patterns can be combined  
412 and weighted, or assessed independently, to identify the support for the different alternatives,  
413 or specific model inadequacies that need to be addressed (Box 1, Figure I.C).

414

415 In detail, however, there are various challenges to achieve correct inference. How to weigh  
416 the different patterns, and account for their uncertainty, is one of them [71, 72]. Another  
417 challenge is how to deal with uncertainties in parameters and subprocesses. As most model  
418 parameters cannot be measured directly, any model comparison has to account for their  
419 uncertainty, such that the support assigned to any of the model alternatives is not contingent  
420 on arbitrary parameter choices. One possibility would be to test whether output patterns are  
421 dependent on model parameters and only use patterns that are independent for inference about  
422 the model alternatives. However, that would likely severely reduce the number of patterns that  
423 can be used for inference. A better, albeit computationally more expensive alternative, is to  
424 use techniques of inverse modeling to calibrate each model alternative [e.g. 56], and then  
425 compare their support using established statistical model selection methods that account for  
426 parameter uncertainty (e.g. the Bayes factor; Figure I). This more complete approach to model  
427 comparison is also the preferred solution in other research fields dealing with comparable  
428 problems (large complex system, no replicate observation), such as cosmological models of  
429 the early Universe [73]. Another solution would be to avoid the model selection problem  
430 altogether, and instead phrase the inferential problem as a problem of parameter inference for  
431 a “supermodel” that includes all the possible pathways (i.e. model alternatives) and processes  
432 leading to the LDG, and through which we estimate relative strength of each pathway, instead  
433 of testing fixed hypotheses.

434

435

436 **Glossary Box**

437 **Approximate Bayesian Computation (ABC)**: a simulation-based approach to create  
438 approximate likelihoods for model selection and parameter estimation of complex models,  
439 possibly with multiple data sources.

440

441 **Diversification rate**: the net rate of production of new lineages, i.e. the difference between  
442 origination and extinction rate. It usually applies to species (i.e. speciation minus extinction  
443 rate) but can be equally applied to higher or lower taxonomic levels.

444

445 **Ecological limits**: a limit to the number of individuals and/or taxa that can coexist within an  
446 ecosystem due to abiotic settings and biotic interactions such as competition for limited  
447 resources.

448

449 **Ecological processes**: interactions between individuals of the same or different species  
450 driving the dynamics of populations, communities and ecosystems within an ecological  
451 timescale, typically within a few generations of the focal organisms.

452

453 **Eco-evolutionary processes**: the interplay of ecological and evolutionary processes that  
454 violate the assumption that timescales of ecological and evolutionary processes can be  
455 separated; ecological processes affect evolution and vice versa.

456

457 **Environmental filtering**: the differential establishment, persistence, or performance of a  
458 species determined by that species' ability to tolerate a given set of abiotic conditions.

459

460 **Evolutionary processes:** any processes leading to genetic changes in populations driving  
461 lineage divergence and persistence within an evolutionary time scale, typically spanning  
462 many generations.

463

464 **Mechanisms:** a system of causally interacting parts or sub-processes (e.g. ecological  
465 interactions) that constitute some process (e.g. eco-evolutionary process).

466

467 **Mechanistic macroecology:** The study of mechanisms describing how individual organisms  
468 interact with their biotic and abiotic environments, and how these mechanisms scale up to  
469 result in macroecological patterns, including the LDG and other secondary biodiversity  
470 patterns.

471

472 **Mechanistic model:** Mechanistic models may vary in complexity and detail, but in the  
473 context of the LDG, such a model should at a minimum specify the mechanisms by which the  
474 processes of selection, dispersal, ecological drift, and speciation operate on individuals,  
475 populations, or species.

476

477 **Niche conservatism:** the tendency for descendant lineages or species to retain their ancestral  
478 niche.

479

480 **Pattern-oriented modeling:** a modeling approach where multiple patterns observed in real  
481 systems at different hierarchical levels and scales are used systematically to optimize model  
482 complexity and to reduce uncertainty.

483

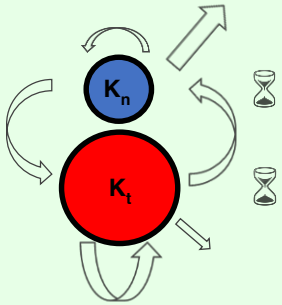
484 **Secondary biodiversity patterns:** spatial, temporal, phylogenetic or trait-based diversity  
485 patterns that emerge from the same ecological and evolutionary processes as the LDG.

486

487 **Simulation model:** a set of rules (usually formulated in a programming language) governing

488 the dynamics of artificial entities that reflect individuals, populations, or communities.

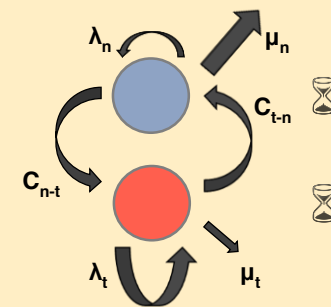
489 **Table 1. Overview of the main hypotheses proposed for explaining the LDG in recent reviews, categorized by the drivers, assumptions, and**  
 490 **rationales they invoke.** These hypotheses can be classified according to three categories: ecological limits, diversification rates, and time for  
 491 species accumulation. Some hypotheses invoke multiple distinctive (but not mutually exclusive) mechanisms and so are repeated in multiple  
 492 categories. We also distinguish the primary cause of the diversity difference between tropical (t) and non-tropical (n) regions (as parameter indices)  
 493 from secondary causes that may be explicitly or implicitly stated in the hypothesis. Subfigures illustrate the three main hypotheses categories that  
 494 predict the LDG (parameters:  $K$ , carrying capacity or limit on the number of individuals or species;  $\lambda$ , speciation rate;  $\mu$ , extinction rate;  $c$ ,  
 495 colonization rate;  $t$ , time).

Hypothesis	Drivers	Assumptions	Rationale	Parameters	Hypothesis category
<b>Area: carrying capacity</b> [74, 75]	Geographic area	Zero-sum dynamics at equilibrium due to competition	Larger area or total resource amount in the tropics can support more individuals, determining the maximum number of viable populations and therefore species.	Primary: $K_t > K_n$	<b>Ecological limits</b> 
<b>More individuals: carrying capacity</b> [24, 25]	Total amount of resources or energy	Zero-sum dynamics at equilibrium due to competition	Larger niche space in the tropics can be partitioned more finely.	Secondary: $\lambda_t > \lambda_n, \mu_t < \mu_n$	
<b>More specialization</b> [76, 77]	Resource availability	Zero-sum dynamics at equilibrium due to competition	Higher specialization in the more stable tropics allows greater niche packing.		
<b>Seasonality: coexistence</b> [29, 30]	Seasonality	Zero-sum dynamics at equilibrium due to competition; trade-offs			



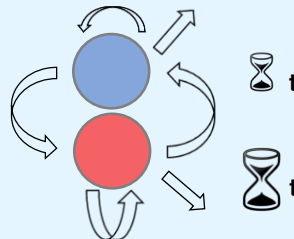
<b>Climatic stability: equilibrium</b> [26, 40]	Environmental stability (decadal to millennial)	between generalists and specialists		
<b>Temperature-dependent speciation</b> [9, 33]	Temperature	No assumption about equilibrium	Higher temperature in the tropics increases metabolic rates and mutation rates, and decreases generation times.	<p><b>Diversification rates</b></p>
<b>More individuals: more mutations</b> [75, 78]	Geographic area and resource availability	No assumption about equilibrium	Higher resource availability in the tropics supports higher population density and hence more total mutations per unit time.	
<b>Seasonality: speciation</b> [27, 28]	Seasonality and topographic relief	No assumption about equilibrium	Mountain passes are “higher” in the less seasonal tropics leading to greater isolation and allopatric speciation.	
<b>Biotic interactions</b> [79, 80]	Resource availability and environmental stability	No assumption about equilibrium	Stronger biotic interactions (e.g. competition and predation) among species in the more stable tropics increase speciation rates.	
<b>Area: diversification</b> [75, 81]	Geographic area	No assumption about equilibrium	Larger tropical area increases opportunity for allopatric speciation and decreases stochastic extinction risk.	
<b>Dispersal limitation</b> [82]	Environmental stability	No assumption about equilibrium; trade-off	More stable tropical habitats decrease stochastic extinction and select for competitive ability over	

Primary:  $\lambda_t > \lambda_n$



Primary:  $\lambda_t > \lambda_n,$

$\mu_t < \mu_n$

		between competitive and dispersal ability	dispersal ability, resulting in decreased gene flow.		
<b>Climatic stability: non-equilibrium</b> [26, 40]	Environmental stability (millennia to millions of years)	Equilibrium not reached in unstable environments; low rates of adaptive niche evolution	Frequent environmental changes (timescale: Pleistocene glacial cycles) cause extinctions, range contractions and makes gradual speciation less likely.	Primary: $\lambda_t > \lambda_n$ , $\mu_t < \mu_n$ , high $c_{n-t}$ Secondary: $t_t > t_n$	
<b>Time for speciation</b> [83, 84]	Evolutionary time since colonization or origin of clades	Longer past persistence of tropical environments	Older tropical environments allow more time for more clades to originate or colonize.	Primary: $t_t > t_n$ Secondary: $\lambda_t > \lambda_n$	<b>Time for species accumulation</b> 
<b>Niche conservatism</b> [36, 37]	Evolutionary time since colonization or origin of clades	Mostly tropical origin of clades; phylogenetically conserved niches	Climatic preferences and phylogenetic niche conservatism limit dispersal out of the region of clade origin.	Primary: $t_t > t_n$ , low $c_{t-n}$ Secondary: $\lambda_t > \lambda_n$	

496

497

498

499

500 **Figure legends**

501 **Figure 1 (in main text)**

502 **Key processes across levels of biological organization.** Illustration of our framework  
503 spanning external drivers that are associated with the spatiotemporal environment, the eco-  
504 evolutionary processes that are thought to be central to the LDG, and the emergent diagnostic  
505 patterns. We consider four key eco-evolutionary processes: selection, dispersal, ecological  
506 drift (eventually resulting in extinction), and speciation [17]; they are shown relative to  
507 spatial, temporal, and biological scales (e.g. local vs. regional, population-level vs. continent-  
508 level). Five example hypotheses from the three categories of LDG hypotheses are mapped  
509 onto this framework with their specific drivers, processes and emergent patterns (hypothesis  
510 names and categories as in Table 1). For each hypothesis, we show only the primary driver-  
511 process pathway identified in Table 1 (see main text for more detailed explanation of the  
512 mapped examples).

513

514 **Figure I (in Box 1)**

515 **An example of an eco-evolutionary simulation model in an LDG context.** A) Process  
516 classes suggested for any eco-evolutionary model of the LDG. Text inside each wedge  
517 describes how the process was modeled in [25] and [16]. B) A flowchart outlining the  
518 processes in [25] and [16], with model components colored as in (A). (C) Example  
519 simulation output displaying species richness along a spatial gradient, the distribution of  
520 species' thermal trait optima at three locations along the spatial gradient (dotted vertical lines  
521 indicate the actual temperature in those regions), and a phylogeny with branch color denoting  
522 speciation rate estimates (from low blue to high red values) from BAMM [85]. (D) Diagnostic  
523 model outputs for three different LDG hypotheses. NC - niche conservatism; EL - ecological  
524 limits; DR - diversification rates (see Table 1 for details). Patterns shown are: upper panel,  
525 temporal variation of the correlation between species richness in a region and time since the

526 region was colonized (simulations with tropical clade origin in red, temperate clade origin in  
527 blue); lower panel, phylogenies color-coded by instantaneous speciation rate as in (C).

528

### 529 **Figure I (in Box 2)**

#### 530 **Decisions about the implementation of speciation processes in mechanistic models.**

531 Examples of speciation models are schematically illustrated. The choice of model  
532 implementation may impact the pattern of interest. In this hypothetical example, allopatric  
533 and sympatric speciation result in different tree topologies, but the specific implementation of  
534 either speciation mode may additionally impact branch lengths.

535

### 536 **Figure I (in Box 3)**

537 **Inferential cycle.** (A) Theory about eco-evolutionary processes combined with data is used to  
538 build a model that can generate the observed patterns and determine its a priori support (green  
539 bars) for different combinations of eco-evolutionary processes. The models may be designed  
540 to explicitly test support for hypotheses listed in Table 1 (NC=niche conservatism,  
541 EL=ecological limits, DR=diversification rate) or some other combination of processes; (B)  
542 the competing models are parameterized and their predictions are compared to empirical data,  
543 quantifying the support lent by the model predictions for each hypothesis (pink bars) or  
544 parameter combination and providing specific information on missing or misspecified  
545 processes to be improved in further inference cycles; (C) the model can then be used for  
546 inference and prediction. The updated posterior support (blue bars) informs on the plausibility  
547 of inference given prior and empirical support and can be used as a prior in a subsequent  
548 iteration of the approach with a modified model structure and/or different input data.

549

### 550 **References**

- 551 1. Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American*  
552 *Naturalist* 163 (2), 192-211.
- 553 2. Mannion, P.D. et al. (2014) The latitudinal biodiversity gradient through deep time. *Trends*  
554 *in Ecology & Evolution* 29 (1), 42-50.
- 555 3. Lomolino, M.V. et al. (2017) *Biogeography: biological diversity across space and time*,  
556 Fifth Edition edn.
- 557 4. Fine, P.V.A. (2015) Ecological and evolutionary drivers of geographic variation in species  
558 diversity. *Annual Review of Ecology, Evolution, and Systematics* 46, 369-392.
- 559 5. Currie, D.J. et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale  
560 variation in taxonomic richness. *Ecology Letters* 7 (12), 1121-1134.
- 561 6. Hawkins, B.A. et al. (2003) Productivity and history as predictors of the latitudinal  
562 diversity gradient of terrestrial birds. *Ecology* 84 (6), 1608-1623.
- 563 7. Valentine, J.W. and Jablonski, D. (2015) A twofold role for global energy gradients in  
564 marine biodiversity trends. *Journal of Biogeography* 42 (6), 997-1005.
- 565 8. Fritz, S.A. et al. (2016) Twenty-million-year relationship between mammalian diversity  
566 and primary productivity. *Proceedings of the National Academy of Sciences of the*  
567 *United States of America* 113 (39), 10908-10913.
- 568 9. Rohde, K. (1992) Latitudinal gradients in species-diversity - the search for the primary  
569 cause. *Oikos* 65 (3), 514-527.
- 570 10. Ricklefs, R.E. (2006) Global variation in the diversification rate of passerine birds.  
571 *Ecology* 87 (10), 2468-2478.
- 572 11. Mittelbach, G.G. et al. (2007) Evolution and the latitudinal diversity gradient: speciation,  
573 extinction and biogeography. *Ecology Letters* 10 (4), 315-331.
- 574 12. Wiens, J.J. et al. (2010) Niche conservatism as an emerging principle in ecology and  
575 conservation biology. *Ecology Letters* 13 (10), 1310-1324.

- 576 13. Marin, J. et al. (2018) Evolutionary time drives global tetrapod diversity. *Proceedings of*  
577 *the Royal Society B-Biological Sciences* 285 (1872).
- 578 14. Servedio, M.R. et al. (2014) Not just a theory-the utility of mathematical models in  
579 evolutionary biology. *Plos Biology* 12 (12).
- 580 15. Grimm, V. et al. (2005) Pattern-oriented modeling of agent-based complex systems:  
581 lessons from ecology. *Science* 310 (5750), 987-991.
- 582 16. Hurlbert, A.H. and Stegen, J.C. (2014) On the processes generating latitudinal richness  
583 gradients: identifying diagnostic patterns and predictions. *Frontiers in Genetics* 5.
- 584 17. Vellend, M. (2016) *The Community of Ecological Communities*.
- 585 18. Kraft, N.J.B. et al. (2015) Community assembly, coexistence and the environmental  
586 filtering metaphor. *Functional Ecology* 29 (5), 592-599.
- 587 19. Leprieur, F. et al. (2016) Plate tectonics drive tropical reef biodiversity dynamics. *Nature*  
588 *Communications* 7.
- 589 20. Badgley, C. et al. (2017) Biodiversity and topographic complexity: modern and  
590 geohistorical perspectives. *Trends in Ecology & Evolution* 32 (3), 211-226.
- 591 21. Pellissier, L. et al. (2018) Are global hotspots of endemic richness shaped by plate  
592 tectonics? *Biological Journal of the Linnean Society* 123 (1), 247-261.
- 593 22. Urban, M.C. and Skelly, D.K. (2006) Evolving metacommunities: toward an evolutionary  
594 perspective on metacommunities. *Ecology* 87 (7), 1616-1626.
- 595 23. Urban, M.C. and De Meester, L. (2009) Community monopolization: local adaptation  
596 enhances priority effects in an evolving metacommunity. *Proceedings of the Royal*  
597 *Society B-Biological Sciences* 276 (1676), 4129-4138.
- 598 24. Storch, D. et al. (2018) The more-individuals hypothesis revisited: the role of community  
599 abundance in species richness regulation and the productivity-diversity relationship.  
600 *Ecology Letters* 21 (6), 920-937.

- 601 25. Hurlbert, A.H. and Stegen, J.C. (2014) When should species richness be energy limited,  
602 and how would we know? *Ecology Letters* 17 (4), 401-413.
- 603 26. Janzen, D.H. (1967) Why mountain passes are higher in tropics. *American Naturalist* 101  
604 (919), 233-&.
- 605 27. Ghalambor, C.K. et al. (2006) Are mountain passes higher in the tropics? Janzen's  
606 hypothesis revisited. *Integrative and Comparative Biology* 46 (1), 5-17.
- 607 28. Sheldon, K.S. et al. (2018) Fifty years of mountain passes: a perspective on Dan Janzen's  
608 classic article. *American Naturalist* 191 (5), 553-565.
- 609 29. MacArthur, R.H. (1972) *Geographical ecology*.
- 610 30. Ben-Eliahu, M.N. and Safriel, U.N. (1982) A comparison between species diversities of  
611 polychaetes from tropical and temperate structurally similar rocky inter-tidal habitats.  
612 *Journal of Biogeography* 9 (5), 371-390.
- 613 31. Antonelli, L.A. et al. (2015) An engine for global plant diversity: highest evolutionary  
614 turnover and emigration in the American tropics. *Frontiers in Genetics*.
- 615 32. Rabosky, D.L. et al. (2018) An inverse latitudinal gradient in speciation rate for marine  
616 fishes. *Nature* 559 (7714), 392-395.
- 617 33. Allen, A.P. et al. (2006) Kinetic effects of temperature on rates of genetic divergence and  
618 speciation. *Proceedings of the National Academy of Sciences of the United States of*  
619 *America* 103 (24), 9130-9135.
- 620 34. Brown, J.H. et al. (2004) Toward a metabolic theory of ecology. *Ecology* 85 (7), 1771-  
621 1789.
- 622 35. Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*.  
623 Princeton University Press.
- 624 36. Wiens, J.J. and Donoghue, M.J. (2004) Historical biogeography, ecology and species  
625 richness. *Trends in Ecology & Evolution* 19 (12), 639-644.

- 626 37. Wiens, J.J. and Graham, C.H. (2005) Niche conservatism: Integrating evolution, ecology,  
627 and conservation biology. *Annual Review of Ecology Evolution and Systematics* 36,  
628 519-539.
- 629 38. Gillooly, J.F. and Allen, A.P. (2007) Linking global patterns in biodiversity to  
630 evolutionary dynamics using metabolic theory. *Ecology* 88 (8), 1890-1894.
- 631 39. Jocque, M. et al. (2010) Climatic control of dispersal-ecological specialization trade-offs:  
632 a metacommunity process at the heart of the latitudinal diversity gradient? *Global*  
633 *Ecology and Biogeography* 19 (2), 244-252.
- 634 40. Dynesius, M. and Jansson, R. (2000) Evolutionary consequences of changes in species'  
635 geographical distributions driven by Milankovitch climate oscillations. *Proceedings of*  
636 *the National Academy of Sciences of the United States of America* 97 (16), 9115-  
637 9120.
- 638 41. Rangel, T.F. et al. (2018) Modeling the ecology and evolution of biodiversity:  
639 Biogeographical cradles, museums, and graves. *Science* 361 (6399).
- 640 42. Davies, T.J. et al. (2011) Neutral biodiversity theory can explain the imbalance of  
641 phylogenetic trees but not the tempo of their diversification. *Evolution* 65 (7), 1841-  
642 1850.
- 643 43. Descombes, P. et al. (2018) Linking species diversification to palaeo- environmental  
644 changes: a process- based modelling approach. *Global Ecology and Biogeography* 27  
645 (2), 233-244.
- 646 44. Muller, R.D. et al. (2008) Long-term sea-level fluctuations driven by ocean basin  
647 dynamics. *Science* 319 (5868), 1357-1362.
- 648 45. Chalmandrier, L. et al. (2018) Comparing spatial diversification and meta-population  
649 models in the Indo-Australian Archipelago. *Royal Society Open Science* 5 (3).



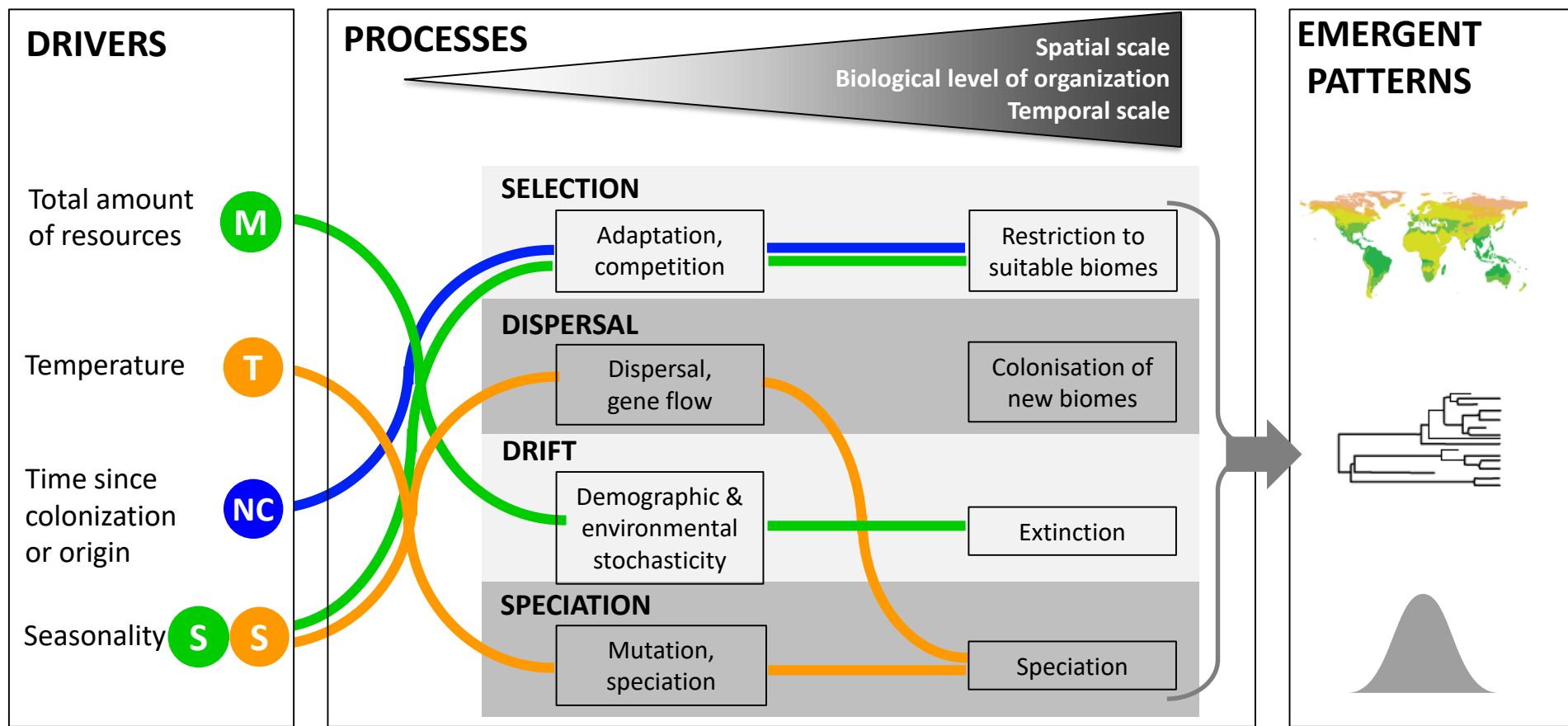
- 650 46. Brännström, A. et al. (2012) Modelling the ecology and evolution of communities: a  
651 review of past achievements, current efforts, and future promises. *Evolutionary*  
652 *Ecology Research* 14 (5), 601-625.
- 653 47. Cabral, J.S. and Kreft, H. (2012) Linking ecological niche, community ecology and  
654 biogeography: insights from a mechanistic niche model. *Journal of Biogeography* 39  
655 (12), 2212-2224.
- 656 48. Pontarp, M. and Wiens, J.J. (2017) The origin of species richness patterns along  
657 environmental gradients: uniting explanations based on time, diversification rate and  
658 carrying capacity. *Journal of Biogeography* 44 (4), 722-735.
- 659 49. Urban, M.C. (2011) The evolution of species interactions across natural landscapes.  
660 *Ecology Letters* 14 (7), 723-732.
- 661 50. Roy, K. and Goldberg, E.E. (2007) Origination, extinction, and dispersal: Integrative  
662 models for understanding present-day diversity gradients. *American Naturalist* 170,  
663 71-85.
- 664 51. Pontarp, M. and Petchey, O.L. (2016) Community trait overdispersion due to trophic  
665 interactions: concerns for assembly process inference. *Proceedings of the Royal*  
666 *Society B-Biological Sciences* 283 (1840).
- 667 52. Connolly, S.R. et al. (2017) Process, Mechanism, and modeling in macroecology. *Trends*  
668 *in Ecology & Evolution* 32 (11), 835-844.
- 669 53. Cabral, J.S. et al. (2017) Mechanistic simulation models in macroecology and  
670 biogeography: state-of-art and prospects. *Ecography* 40 (2).
- 671 54. Sisson, S.A. et al. (2007) Sequential Monte Carlo without likelihoods. *Proceedings of the*  
672 *National Academy of Sciences of the United States of America* 104 (6), 1760-1765.
- 673 55. Beaumont, M.A. (2010) Approximate Bayesian Computation in Evolution and Ecology.  
674 *Annual Review of Ecology, Evolution, and Systematics*, Vol 41 41, 379-406.

- 675 56. Hartig, F. et al. (2011) Statistical inference for stochastic simulation models - theory and  
676 application. *Ecology Letters* 14 (8), 816-827.
- 677 57. Blum, M.G.B. et al. (2013) A comparative review of dimension reduction methods in  
678 Approximate Bayesian Computation. *Statistical Science* 28 (2), 189-208.
- 679 58. Wood, S.N. (2010) Statistical inference for noisy nonlinear ecological dynamic systems.  
680 *Nature* 466 (7310), 1102-U113.
- 681 59. Hartig, F. et al. (2014) Technical note: Approximate Bayesian parameterization of a  
682 process-based tropical forest model. *Biogeosciences* 11 (4), 1261-1272.
- 683 60. Gotelli, N.J. et al. (2009) Patterns and causes of species richness: a general simulation  
684 model for macroecology. *Ecology Letters* 12 (9), 873-886.
- 685 61. Csillery, K. et al. (2010) Approximate Bayesian Computation (ABC) in practice. *Trends*  
686 *in Ecology & Evolution* 25 (7), 410-418.
- 687 62. van der Plas, F. et al. (2015) A new modeling approach estimates the relative importance  
688 of different community assembly processes. *Ecology* 96 (6), 1502-1515.
- 689 63. Rundell, R.J. and Price, T.D. (2009) Adaptive radiation, nonadaptive radiation, ecological  
690 speciation and nonecological speciation. *Trends in Ecology & Evolution* 24 (7), 394-  
691 399.
- 692 64. Orr, H.A. and Turelli, M. (2001) The evolution of postzygotic isolation: accumulating  
693 Dobzhansky-Muller incompatibilities. *Evolution* 55 (6), 1085-1094.
- 694 65. Etienne, R.S. and Haegeman, B. (2011) The neutral theory of biodiversity with random  
695 fission speciation. *Theoretical Ecology* 4 (1), 87-109.
- 696 66. Doebeli, M. and Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*  
697 421 (6920), 259-264.
- 698 67. Bolnick, D.I. and Fitzpatrick, B.M. (2007) Sympatric speciation: models and empirical  
699 evidence. *Annual Review of Ecology Evolution and Systematics* 38, 459-487.

- 700 68. Gavrillets, S. and Vose, A. (2005) Dynamic patterns of adaptive radiation. Proceedings of  
701 the National Academy of Sciences of the United States of America 102 (50), 18040-  
702 18045.
- 703 69. de Aguiar, M.A.M. et al. (2009) Global patterns of speciation and diversity. Nature 460  
704 (7253), 384-387.
- 705 70. Pontarp, M. et al. (2015) The biogeography of adaptive radiations and the geographic  
706 overlap of sister species. American Naturalist 186, 565-581.
- 707 71. Keenan, T.F. et al. (2011) The model-data fusion pitfall: assuming certainty in an  
708 uncertain world. Oecologia 167 (3), 587-597.
- 709 72. Kuppel, S. et al. (2018) What can we learn from multi-data calibration of a process-based  
710 ecohydrological model? Environmental Modelling & Software 101, 301-316.
- 711 73. Trotta, R. (2008) Bayes in the sky: Bayesian inference and model selection in cosmology.  
712 Contemporary Physics 49 (2), 71-104.
- 713 74. MacArthur, R.H. and Wilson, E.O. (1963) Equilibrium-Theory of Insular Zoogeography.  
714 Evolution 17 (4), 373-&.
- 715 75. Rosenzweig, M.L. (1995) Species diversity in space and time.
- 716 76. Abrams, P.A. (1995) Monotonic or Unimodal Diversity Productivity Gradients - What  
717 Does Competition Theory Predict. Ecology 76 (7), 2019-2027.
- 718 77. Srivastava, D.S. and Lawton, J.H. (1998) Why more productive sites have more species:  
719 An experimental test of theory using tree-hole communities. American Naturalist 152  
720 (4), 510-529.
- 721 78. Stevens, M.H.H. et al. (2007) Diversification rates increase with population size and  
722 resource concentration in an unstructured habitat. Genetics 177 (4), 2243-2250.
- 723 79. Schemske, D.W. et al. (2009) Is There a Latitudinal Gradient in the Importance of Biotic  
724 Interactions? Annual Review of Ecology Evolution and Systematics 40, 245-269.
- 725 80. Dobzhansky, T. (1950) Evolution in the tropics. American Scientist 38, 209 - 221.

- 726 81. Kisel, Y. et al. (2011) How diversification rates and diversity limits combine to create  
727 large-scale species-area relationships. *Philosophical Transactions of the Royal Society*  
728 *B-Biological Sciences* 366 (1577), 2514-2525.
- 729 82. Pellissier, L. (2015) Stability and the competition-dispersal trade-off as drivers of  
730 speciation and biodiversity gradients. *Frontiers in Ecology and Evolution*.
- 731 83. Fischer, A.G. (1960) Latitudinal Variations in Organic Diversity. *Evolution* 14 (1), 64-81.
- 732 84. Stephens, P.R. and Wiens, J.J. (2003) Explaining species richness from continents to  
733 communities: The time-for-speciation effect in emydid turtles. *American Naturalist*  
734 161 (1), 112-128.
- 735 85. Rabosky, D.L. et al. (2014) BAMMtools: an R package for the analysis of evolutionary  
736 dynamics on phylogenetic trees. *Methods in Ecology and Evolution* 5 (7), 701-707.
- 737

Figure 1 (main text)



**Ecological limits**

**M** More individuals: carrying capacity

**S** Seasonality: coexistence

**Diversification rates**

**T** Temperature-dependent speciation

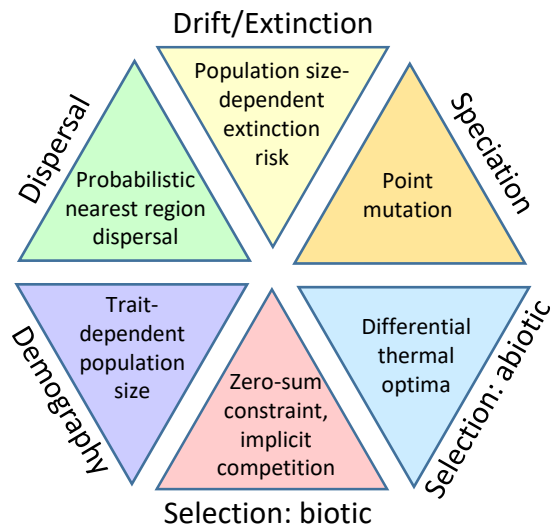
**S** Seasonality: speciation

**Time**

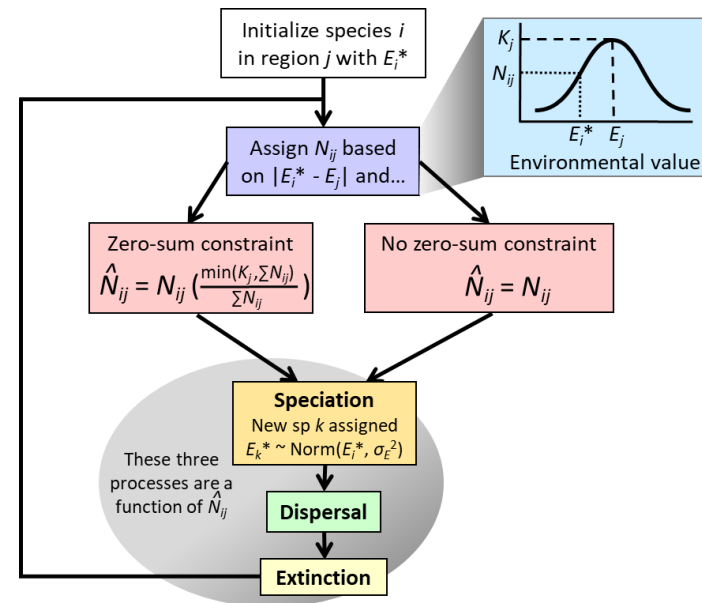
**NC** Niche conservatism

Figure 1 (in Box 1)

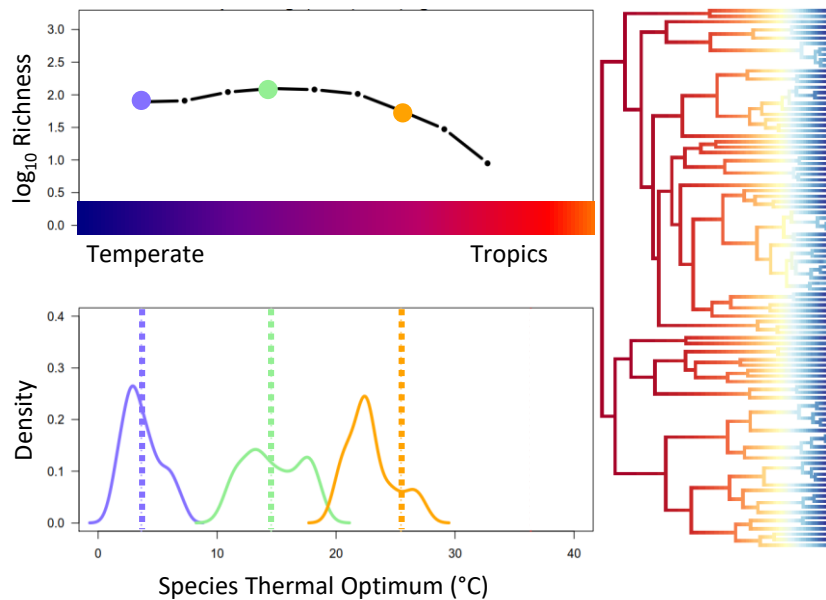
## A) Basic processes



## B) Model details



## C) Example simulation output



## D) Diagnostic patterns

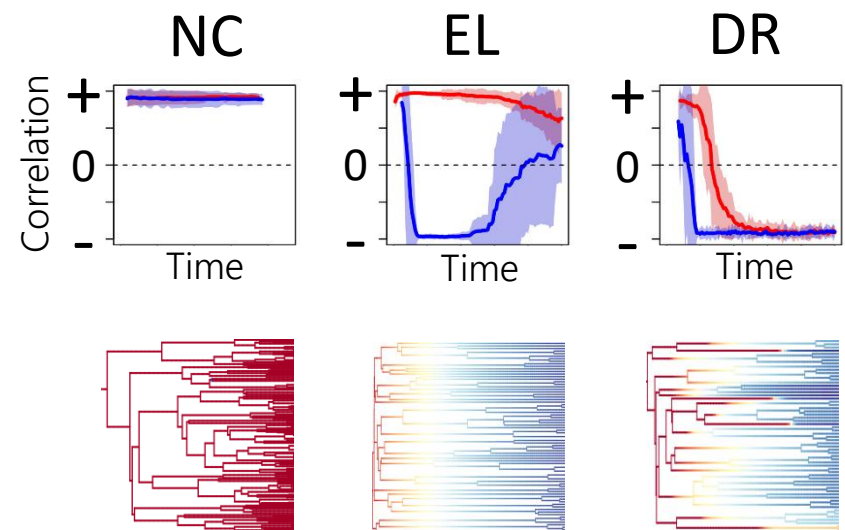


Figure 1 (in Box 2)

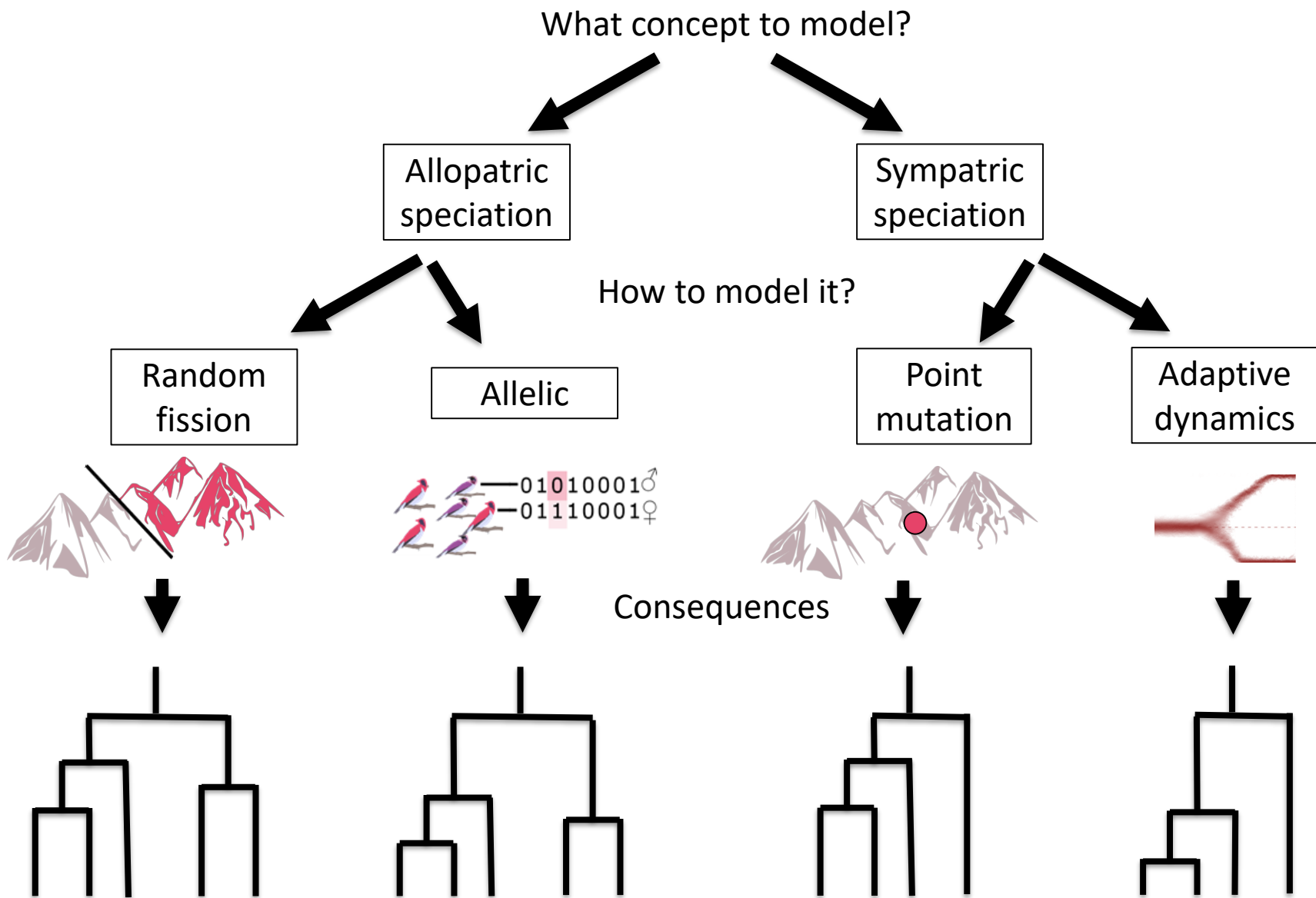


Figure I (in Box 3)

