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1 **Title:**

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

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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

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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.

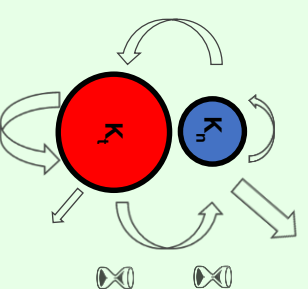
486

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; λ , speciation rate; μ , extinction rate; c ,
495 colonization rate; t , time).

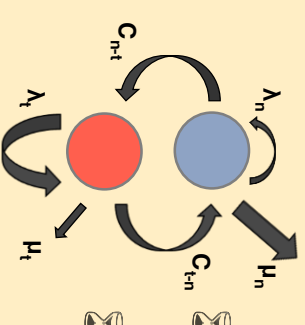
Hypothesis	Drivers	Assumptions	Rationale	Parameters	Hypothesis category
Area: carrying capacity [74, 75]	Geographic area	Zero-sum dynamics at equilibrium due to competition	Larger area or total resource amount in the tropics can support more individuals, determining the maximum number of viable populations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



Climatic stability: Equilibrium [26, 40]	Environmental stability (decadal to millennial)	between generalists and specialists	
Temperature-dependent speciation [9, 33]	Temperature	No assumption about equilibrium	Higher temperature in the tropics increases metabolic rates and mutation rates, and decreases generation times.
More individuals: more mutations [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.
Seasonality: speciation [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.
Biotic interactions [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.
Area: diversification [75, 81]	Geographic area	No assumption about equilibrium	Larger tropical area increases opportunity for allopatric speciation and decreases stochastic extinction risk.
Dispersal limitation [82]	Environmental stability	No assumption about equilibrium; trade-off	More stable tropical habitats decrease stochastic extinction and select for competitive ability over

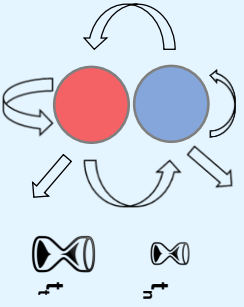
Diversification rates

Primary: $\lambda_t > \lambda_n$



$\mu_t < \mu_n$

Primary: $\lambda_t > \lambda_n$,

	between competitive and dispersal ability	dispersal ability, resulting in decreased gene flow.
Climatic stability: non-equilibrium [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: $t_t > t_n$
Time for speciation [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: $\lambda_t > \lambda_n$
Niche conservatism [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_{n-t} Secondary: $\lambda_t > \lambda_n$
		<p>Time for species accumulation</p> 

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

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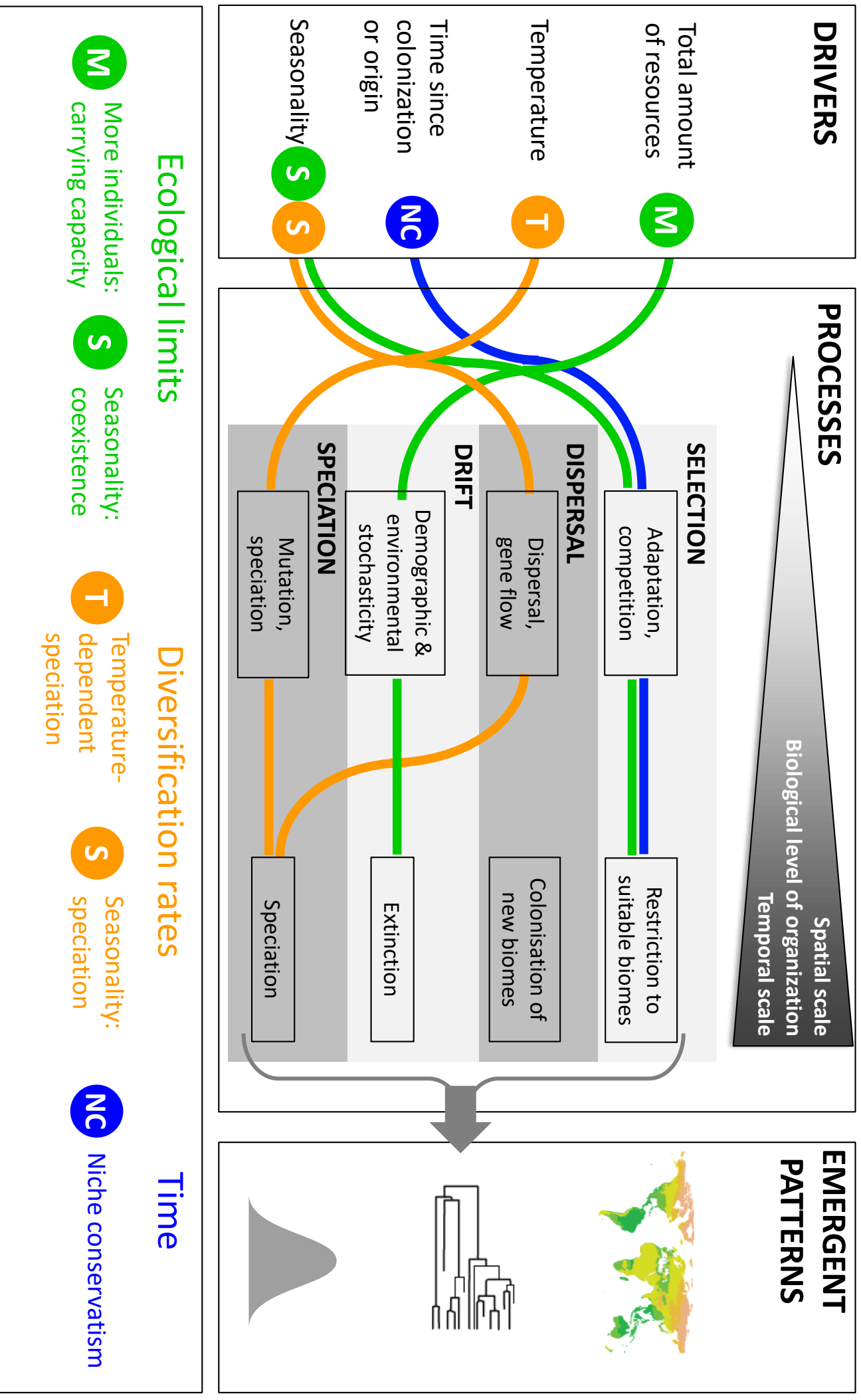
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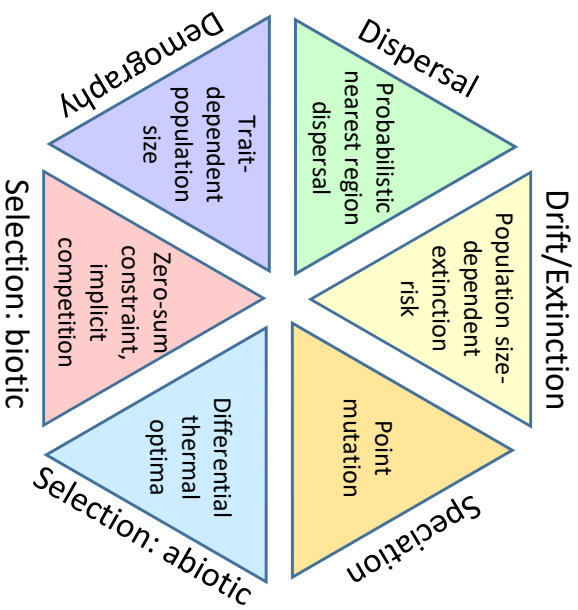
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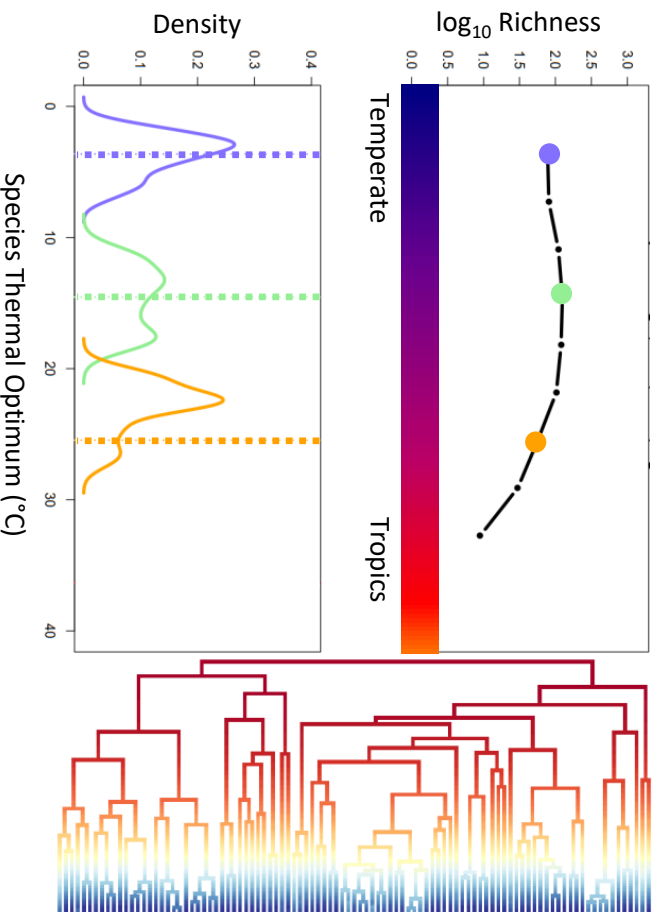
Figure 1 (main text)



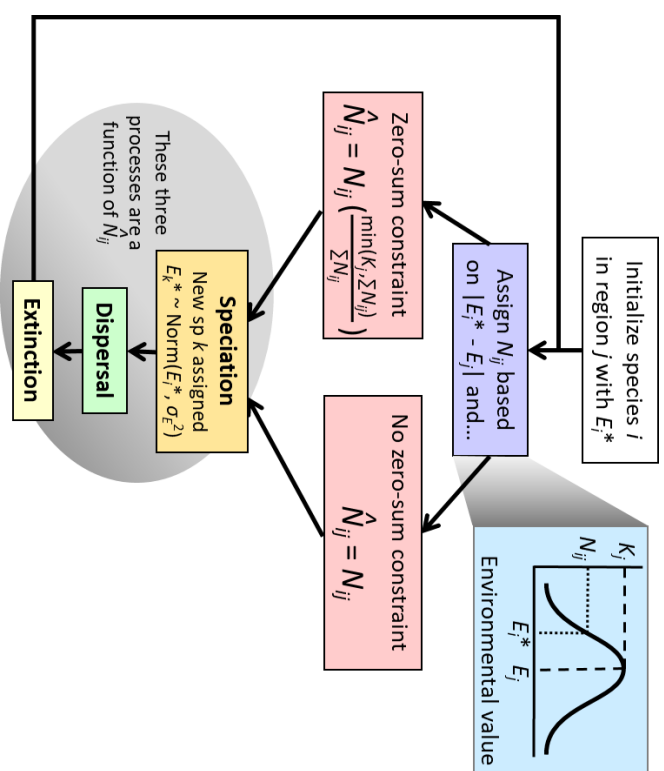
A) Basic processes



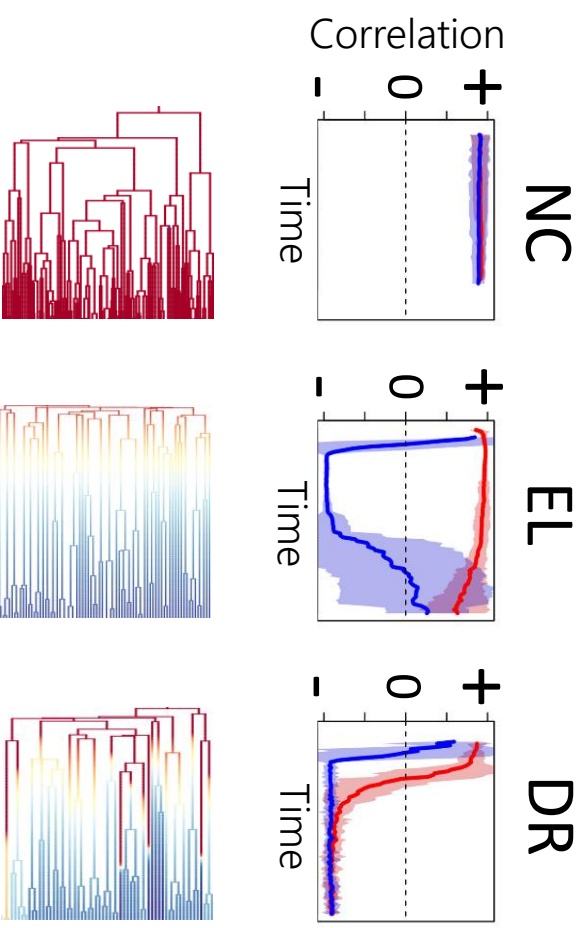
C) Example simulation output

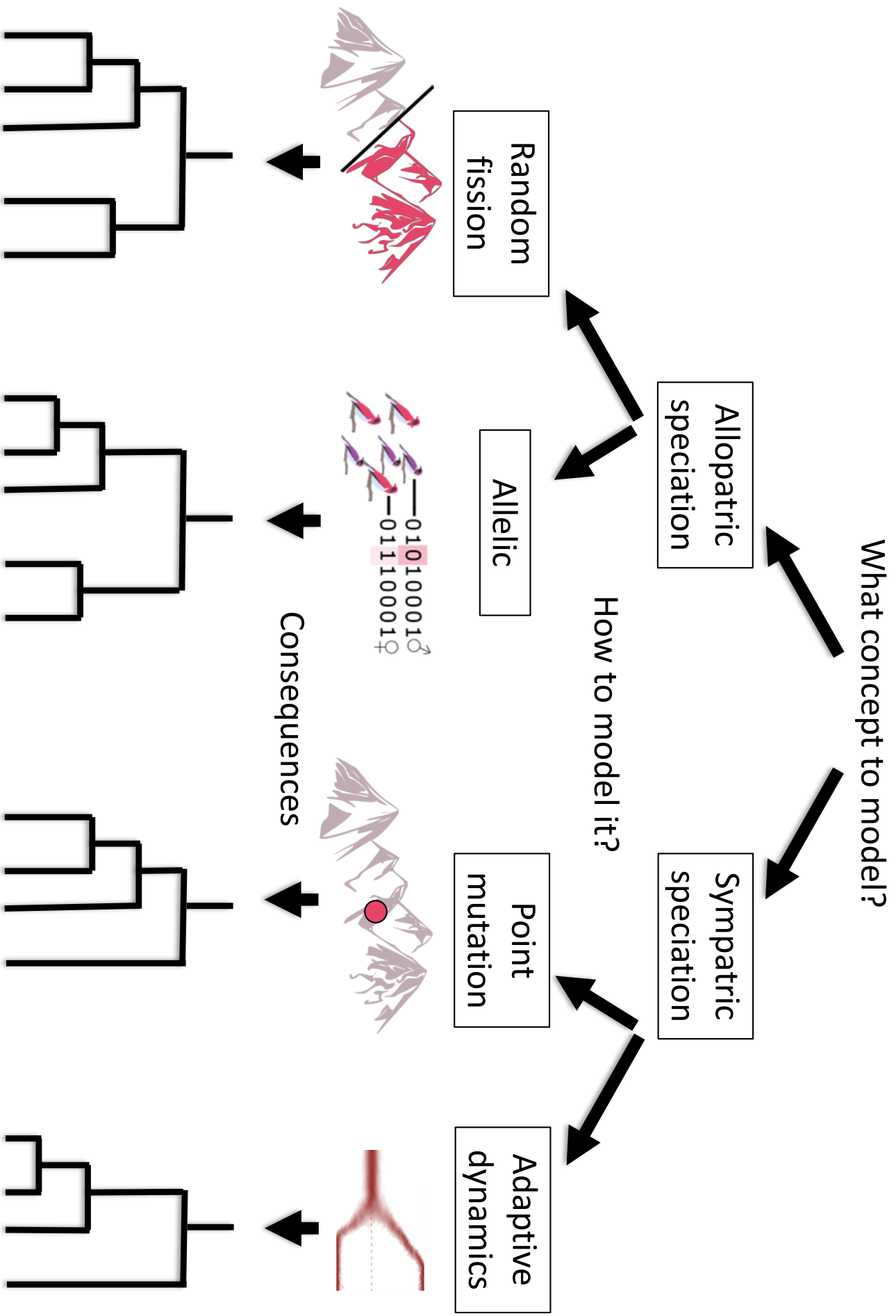


B) Model details

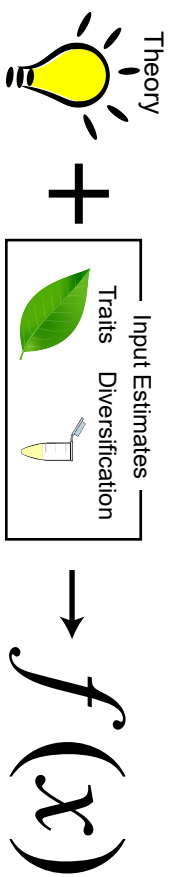


D) Diagnostic patterns

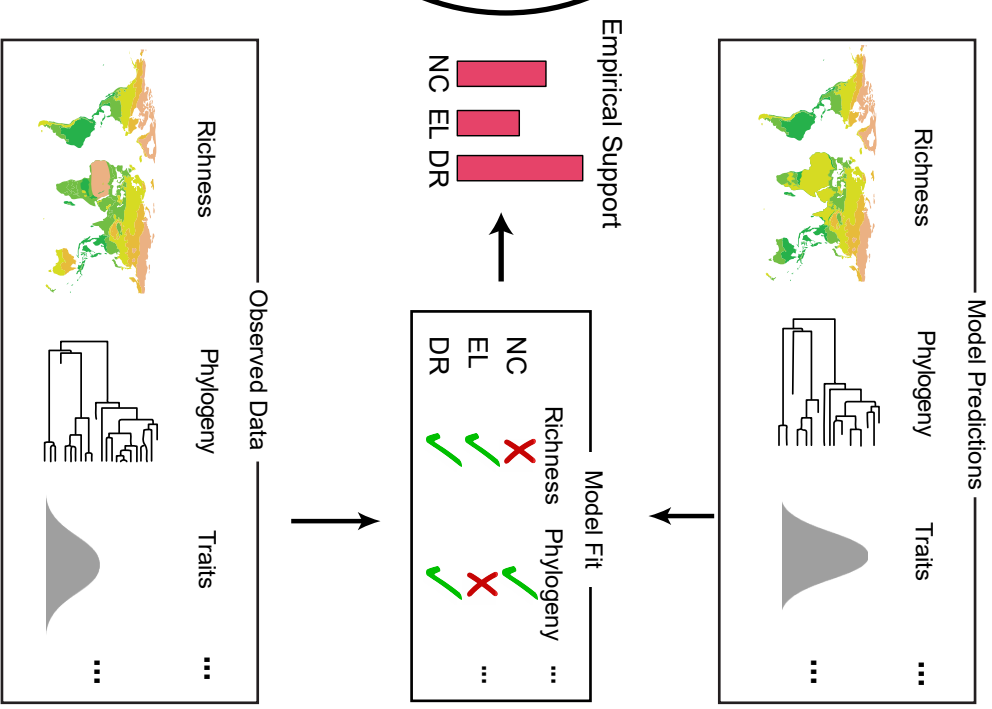




(A) Model design



(B) Model Evaluation / Test



(C) Model inference and application

