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

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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.

Title:

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

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Abstract

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

State of the art and calls for novel mechanistic approaches

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

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

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

Examining the LDG through the lens of mechanistic macroecology

Key processes across levels of biological organization

We recognize four key processes, as defined by [17], that necessarily underpin the LDG and thus should be included as components of any LDG model that aims to capture variation in species richness, abundance, and composition over a spatially and temporally variable environment: 1) selection, 2) ecological drift, 3) dispersal, and 4) speciation. Selection, drift, and dispersal can all influence the birth, death, and movement of individuals over small spatial and temporal scales. Selection (sensus [17]) encompasses any process that results in the differential survival and reproduction of individuals, based on how **environmental filtering** [18] and biotic interactions select for specific traits. Ecological drift manifests itself via stochastic variation in the births and deaths of individuals. Dispersal of individuals is influenced by the spatial structure of the landscape as well as individual dispersal capabilities and can lead to species colonizing new regions. Each of these individual-level ecological and microevolutionary processes is propagated throughout higher levels of biological organization, resulting in discrete patterns at the level of populations, species, and communities (Figure 1).

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

Classical LDG hypotheses revisited

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

The more individuals hypothesis

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

The seasonality hypothesis

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

The temperature-dependent speciation rates hypothesis

The hypothesis that higher temperature elevates evolutionary rates has been used to explain global diversity patterns in both land and sea [31, 32]. One version of the hypothesis [33] follows from the metabolic theory of ecology [34], stating that temperature positively affects all biological rates including mutation rates, which can lead to speciation and ultimately diversity accumulation. This assumes that speciation rates directly follow from mutation rates, which may be problematic if other factors (e.g. existence of geographic barriers, assortative mating) are limiting speciation. The hypothesis makes no specific predictions regarding selection or dispersal. Importantly, this hypothesis could be invoked in either an equilibrium or non-equilibrium world. In a non-equilibrium world, speciation rates alone could explain variation in richness between regions if all regions were similarly old, and extinction rates were equal across regions [10]. In an equilibrium world, increased speciation rates in the tropics can lead to higher equilibrium richness, as in Hubbell [35] neutral model of biodiversity.

The tropical niche conservatism hypothesis

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

The utility of a mechanistic framework

The examples presented above illustrate three insights gained by adopting a generalized eco-evolutionary framework. First, many of the fundamental rules by which organisms are assumed to interact with each other and with their environment will be qualitatively similar regardless of LDG hypothesis. For example, individual survival and reproduction must be functions of how well adapted the individuals are to their environment relative to their intra- and interspecific competitors. Second, latitudinal differences in ecological limits, diversification rates, and time for diversification may emerge via different **mechanisms** integrated into the same framework. For example, diversification rates may be higher due to the temperature-dependence of mutation rates [9, 38] or due to the increased reproductive isolation in aseasonal environments [27, 39]. Third, although each hypothesis invokes a primary driver or process, we have shown that these hypotheses also make unstated assumptions about other processes and mechanisms which need to be considered in concert to fully understand the emergence of the LDG and other macroecological and macroevolutionary patterns.

Mechanistic eco-evolutionary models as a quantitative tool for understanding LDG patterns

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

Mechanistic models for studying the LDG

The spatiotemporal environmental template

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

Trait-based local population dynamics

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

Spatial and eco-evolutionary metacommunity dynamics

For modeling eco-evolutionary metacommunity dynamics, trait-based models need to be implemented in a larger spatial context, allowing individuals to disperse over geographically relevant extents. Metacommunity dynamics will arise from eco-evolutionary feedbacks between dispersing individuals and recipient communities within the context of the spatiotemporal template [49]. Evolutionary dynamics result from natural selection by both abiotic and biotic conditions, ecological drift, dispersal, and speciation. Speciation can be modeled using a phenomenological approach or more complex allele-based models in which phenotypic trait variability is completely or partially heritable and the accumulation of genetic incompatibilities may drive differentiation of daughter species (Box 2). Each of these modeling components is necessary for capturing the suite of processes invoked by LDG hypotheses (Box 1), they can be modeled with varying degrees of complexity and they come with a set of low-level assumptions that need to be clearly stated (Box 2).

Understanding patterns and inferring processes

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

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

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

Concluding remarks

Progress in understanding the processes that underlie LDG patterns and associated diversity patterns has been slow (see also Outstanding Questions). We repeat calls for a transition in biodiversity research, translating verbal models into a unified mechanistic framework that can be implemented in quantitative computer simulations [52, 53, 60]. In such a framework, researchers can focus on measuring and inferring the ecological and evolutionary processes that govern the interaction of organisms with each other and their environment in time and space, which must ultimately underpin the LDG. By applying this framework, hidden assumptions in current hypotheses are exposed, revealing how the hypotheses relate to each other and how they might be distinguished (Table 1, Figure 1). More importantly, this framework is a roadmap for flexible eco-evolutionary simulation models (Box 1-2) that can generate a rich set of empirical patterns from the same underlying processes. We believe that this ability to produce multiple diagnostic patterns will be crucial for inference (Box 3), and ultimately for converting the available data into new knowledge about macroecology and macroevolution. Challenges associated with model construction and the way models are confronted with data will arise, but such challenges are inherent and inevitable to all sciences that deal with complex systems. We are confident that, with time, these challenges can be addressed, and models combining realistic spatiotemporal environmental templates with trait based eco-evolutionary implementation under an iterative procedure of model design, evaluation and improvement, will advance our understanding and quantitative inference of the processes underlying the LDG.

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Box 1 (text)

Box 1. An LDG simulation model in action

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

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

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

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

Box 2 (text)

Box 2: Modeling decisions: the example of speciation

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

After making decisions about what speciation mode to model (e.g. sympatric versus allopatric), modelers face a range of implementation choices from purely phenomenological models of point mutation speciation as in Box 1 to more mechanistic models, where species diversification emerges from evolved trait divergence [48, 68-70], or the accumulation of genetic differences that arise as a function of vicariant events or divergent selection (Figure I). These implementation decisions can impact emergent phylogenetic patterns. For example, Davies et al [42] showed that measures of tree imbalance and branch stemminess were sensitive to whether speciation occurred via point mutation or various types of range fission.

More generally, to draw a reliable inference, researchers should assess their possible implementation options and evaluate the sensitivity of the patterns of interest to these choices. Some patterns will inevitably be more sensitive to implementation decisions than the others. For example, the topology of a phylogeny captures the relative branching pattern but is agnostic about branch lengths, and so topology may be less sensitive than branch length-based metrics to decisions that affect the timing and rate of speciation events. When attempting to infer process from empirical data, patterns sensitive to those implementation decisions should either be disregarded, or the implementation decision itself can be included as alternative submodels that are then inferred by data. A more general discussion of fitting models to data is provided in Box 3.

Box 3 (text)

Box 3. Inference

Possibly the most crucial step in using mechanistic eco-evolutionary models for inference about the origin of the LDG is the way we confront them to data, for example, to compare alternative parameterizations and model structures. Starting from a set of alternative model formulations (Box 1, Figure I.A), we can compare the patterns produced by the model alternatives to observed patterns (Box 1, Figure I.B). The alternative model formulations may correspond to particular hypotheses, as shown in the figure, or to different parts of parameter space independent of existing hypotheses. The fit to the different patterns can be combined and weighted, or assessed independently, to identify the support for the different alternatives, or specific model inadequacies that need to be addressed (Box 1, Figure I.C).

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

Glossary Box

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

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

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

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

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

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

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

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

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

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

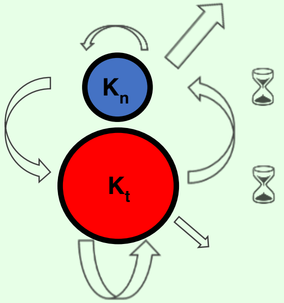
Niche conservatism: the tendency for descendant lineages or species to retain their ancestral niche.

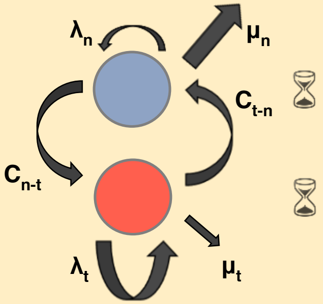
Pattern-oriented modeling: a modeling approach where multiple patterns observed in real systems at different hierarchical levels and scales are used systematically to optimize model complexity and to reduce uncertainty.

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

Simulation model: a set of rules (usually formulated in a programming language) governing the dynamics of artificial entities that reflect individuals, populations, or communities.

Table 1. Overview of the main hypotheses proposed for explaining the LDG in recent reviews, categorized by the drivers, assumptions, and rationales they invoke. These hypotheses can be classified according to three categories: ecological limits, diversification rates, and time for species accumulation. Some hypotheses invoke multiple distinctive (but not mutually exclusive) mechanisms and so are repeated in multiple categories. We also distinguish the primary cause of the diversity difference between tropical (t) and non-tropical (n) regions (as parameter indices) from secondary causes that may be explicitly or implicitly stated in the hypothesis. Subfigures illustrate the three main hypotheses categories that predict the LDG (parameters: K, carrying capacity or limit on the number of individuals or species; λ, speciation rate; μ, extinction rate; c, 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: $K_t > K_n$ Secondary: $\lambda_t > \lambda_n$, $\mu_t < \mu_n$	**Ecological limits** 
More individuals: carrying capacity [24, 25]	Total amount of resources or energy				
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.		
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.	Primary: $\lambda_t > \lambda_n$	**Diversification rates** 
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.	Primary: $\lambda_t > \lambda_n$, $\mu_t < \mu_n$	
Dispersal limitation [82]	Environmental stability	No assumption about equilibrium; trade-off	More stable tropical habitats decrease stochastic extinction and select for competitive ability over		

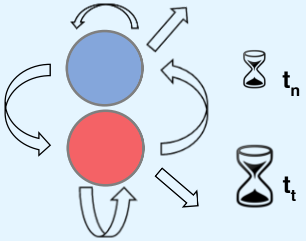
		between competitive and dispersal ability	dispersal ability, resulting in decreased gene flow.		
Climatic stability: non-equilibrium [26, 40]	Environmental stability (millennia to millions of years)	Equilibrium not reached in unstable environments; low rates of adaptive niche evolution	Frequent environmental 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: $\lambda_t > \lambda_n$	**Time for species accumulation** 
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_{t-n} Secondary: $\lambda_t > \lambda_n$	

Figure legends

Figure 1 (in main text)

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

Figure I (in Box 1)

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

Figure I (in Box 2)

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

Figure I (in Box 3)

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

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Figure 1 (main text)

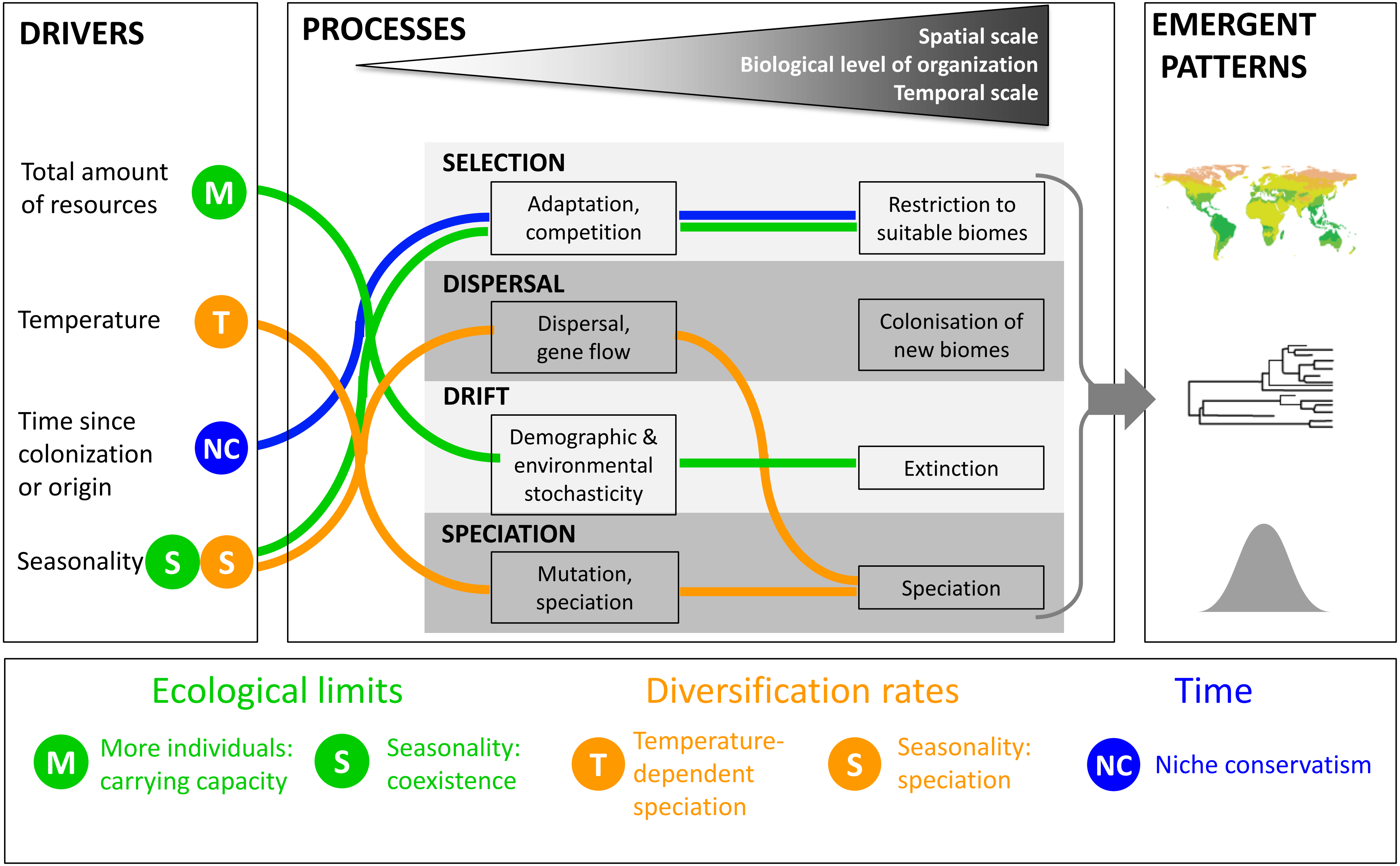

Figure I (in Box 1)

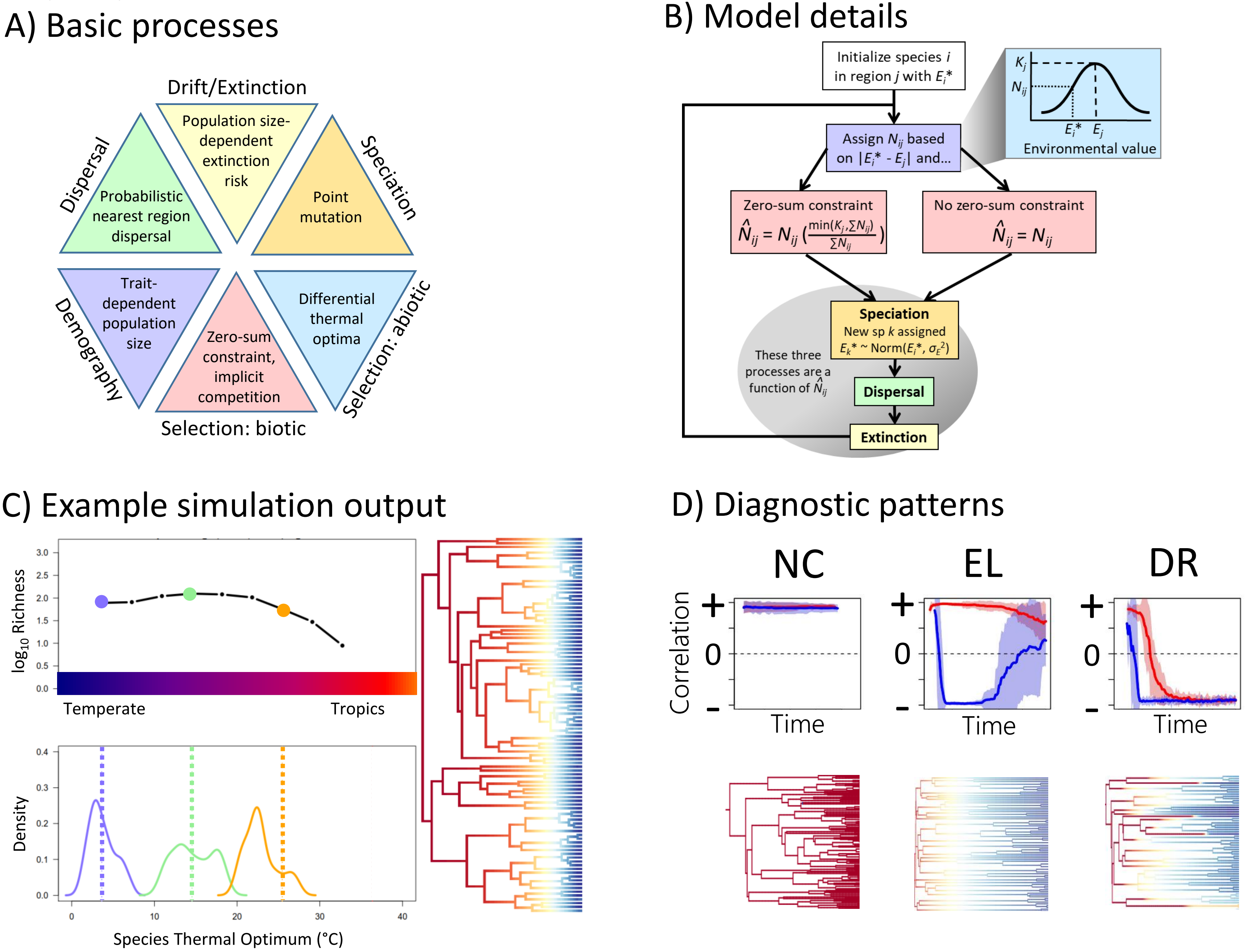

Figure I (in Box 2)

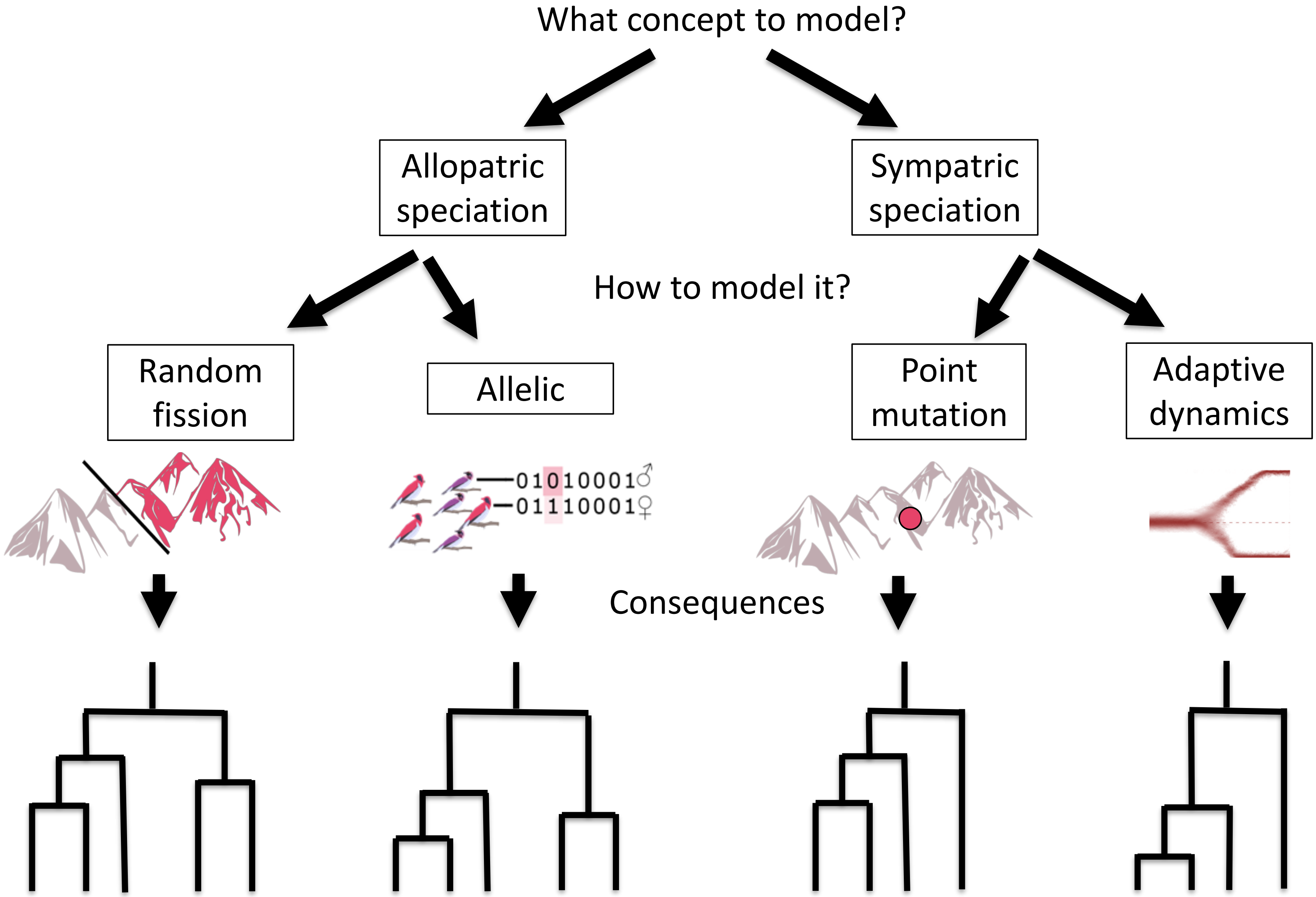

Figure I (in Box 3)