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

Pontarp, Mikael ; Bunnefeld, Lynsey ; Cabral, Juliano Sarmento ; Etienne, Rampal S ; Fritz, Susanne A ; Gillespie, Rosemary ; Graham, Catherine H ; Hagen, Oskar ; Hartig, Florian ; Huang, Shan ; Jansson, Roland ; Maliet, Odile ; Münkemüller, Tamara ; Pellissier, Loïc ; Rangel, Thiago F ; Storch, David ; Wiegand, Thorsten ; Hurlbert, Allen H

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.

1 **Title:**

2 **The latitudinal diversity gradient - novel understanding through**

3 **mechanistic eco-evolutionary models**

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5 **Mikael Pontarp**, Department of Evolutionary Biology and Environmental Studies,

6   University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

7 **Lynsey Bunnefeld**, Biological & Environmental Sciences, University of Stirling, Stirling

8   FK9 4LA, Scotland

9 **Juliano Sarmento Cabral**, Ecosystem Modeling, Center for Computational and Theoretical

10   Biology (CCTB), University of Würzburg, Emil-Fischer-Str. 32, 97074 Würzburg,

11   Germany

12 **Rampal S. Etienne**, Groningen Institute for Evolutionary Life Sciences, University of

13   Groningen, Box 11103, 9700 CC Groningen, The Netherlands

14 **Susanne A. Fritz,** Senckenberg Biodiversity and Climate Centre (BiK-F), Senckenberg

15   Gesellschaft für Naturforschung, D-60325 Frankfurt & Institute of Ecology, Evolution

16   and Diversity, Goethe-University, D-60438 Frankfurt

17 **Rosemary Gillespie**, Environmental Science, 130 Mulford Hall, University of California,

18   Berkeley, CA 94720, USA

19 **Catherine H. Graham**, Swiss Federal Research Institute WSL, CH-8903 Birmensdorf,

20   Switzerland

21 **Oskar Hagen**, Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland

22 & Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich,

23   Switzerland

24 **Florian Hartig**, Theoretical Ecology, University of Regensburg, Universitätsstr. 31, 93053

25   Regensburg, Germany

26 **Shan Huang**, Senckenberg Biodiversity Research Centre, Senckenberganlage 25, 60327,

27   Frankfurt am Main, Germany

28 **Roland Jansson**, Department of Ecology and Environmental Science, Umeå University, 901

29   87 Umeå, Sweden

30 **Odile Maliet**, Institut de biologie de l'Ecole normale supérieure (IBENS), Ecole normale

31   supérieure, CNRS, INSERM, PSL Research University, 75005 Paris, France

32 **Tamara Münkemüller**, Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, CNRS,

33   LECA, Laboratoire d'ÉcologieAlpine, F-38000 Grenoble, France

34 **Loïc Pellissier**, Swiss Federal Research Institute WSL, CH-8903 Birmensdorf, Switzerland

35   & Landscape Ecology, Institute of Terrestrial Ecosystems, ETH Zürich, CH-8092 Zürich,

36   Switzerland

37 **Thiago F. Rangel**, Department of Ecology, Federal University of Goiás, Campus

38   Samambaia, Goiânia GO, Brazil. 74690-900.

39 **David Storch**, Center for Theoretical Study, Charles University and Czech Academy of

40   Sciences. Jilská 1, 110 00 Praha 1 & Department of Ecology, Faculty of Science, Charles

41   University, Viničná 7, 128 44 Praha 2, Czech Republic

42 **Thorsten Wiegand**, Dept of Ecological Modeling, Helmholtz Centre for Environmental

43   Research – UFZ, Permoserstrasse 15, 04318 Leipzig, Germany & German Centre for

44   Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

45 **Allen H. Hurlbert**, Department of Biology and Curriculum in Environment and Ecology,

46   University of North Carolina, Chapel Hill, NC 27599, USA

47

48 **Correspondence**: mikael.pontarp@biol.lu.se (M. Pontarp)

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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.

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 (sensus [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.

5

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 equilibrial 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

7

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

8

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**

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

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

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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