

Retiring “cradles” and “museums” of biodiversity

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Abstract

In 1974, G. Ledyard Stebbins provided a metaphor illustrating how spatial gradients of biodiversity observed today are byproducts of the way environment–population interactions drive species diversification through time. We revisit the narrative behind Stebbins’ “cradles” and “museums” of biodiversity to debate two points. First, the usual “high speciation” vs. “low extinction” and “tropical” vs. “temperate” dichotomies are oversimplifications of the original metaphor and may obscure how gradients of diversity are formed. Second, the way in which we use modern gradients of biodiversity to interpret the potential historical processes that generated them are often still biased by the reasons that motivated Stebbins to propose his original metaphor. Specifically, the field has not yet abandoned the idea that species-rich areas and “basal lineages” indicate centers of origin, nor has it fully appreciated the role of traits as regulators of environment–population dynamics. We acknowledge the popularity of “cradles” and “museums” in the literature and that terminologies can evolve with the requirements of the field. However, we also argue that “cradles” and “museums” have outlived their utility in studies of biogeography and macroevolution and should be replaced by discussions of actual processes at play.

22 **Introduction**

23 The ease with which methods and various sources of data are brought together for reconstructing
24 large, well-resolved species phylogenies (Smith et al. 2009) and mapping the distribution of these
25 species in space (Hijmans and van Etten 2016) has led to a sharp increase in the number of studies
26 that investigate the historical drivers behind the assembly of biological communities (e.g.,
27 Pennington et al., 2006; Donoghue, 2008; Simon et al., 2009; Antonelli et al., 2018; Vasconcelos
28 et al., 2020). The metaphor of “cradles” and “museums” of biodiversity is frequently invoked to
29 describe the prevalent evolutionary processes behind particularly high species richness in some
30 areas (e.g., Chown et al. 2000; Arita and Vázquez-Domínguez 2008; Moreau and Bell 2013;
31 Eiserhardt et al. 2017; Rangel et al. 2018; Azevedo et al. 2020; Dagallier et al. 2020).

32 The renewed interest in identifying “cradles” and “museums” in a spatial context opens up
33 an opportunity to revisit the original intentions of those who first introduced these terms to the
34 field (i.e., Dobzhansky 1950; Axelrod 1970; Stebbins 1974). G. Ledyard Stebbins is credited with
35 popularizing the metaphor in his 1974 book, *Flowering Plants: Evolution Above the Species Level*.
36 In it, he presents a long essay about his views on angiosperm macroevolution, where he developed
37 the “museums” hypothesis as a means of countering the idea that centers of diversity reflect centers
38 of origin, particularly with respect to the putative origins of flowering plants. Today, the “cradles”
39 and “museums” metaphor is most often interpreted as differences in rates of origination (i.e., high
40 speciation) or persistence (i.e., low extinction) between geographical areas, which implies a
41 decoupling of both speciation and extinction rates. Even though the original metaphor touches
42 these ideas, Stebbins' argument was far richer, and integrative, involving rates of not only
43 speciation and extinction, but also migration and fossil preservation as well. It emphasized the role

44 of environmental stability and instability in misleading inferences of the past and also how lineage-
45 specific traits act as regulators in these dynamics.

46 In this historical perspective, we revisit the arguments that led Stebbins to characterize
47 areas as either “cradles” or “museums” of biodiversity. We evaluate whether there is still a place
48 for simple binary categories in modern studies of biogeography and macroevolution and argue that
49 the field will benefit from a de-emphasis of the “cradles” and “museums” dichotomy, especially
50 in studies that simply array rates across spatial gradients. The metaphor has outlived its usefulness.

51 **Revisiting Stebbins’ “cradles” and “museums” of biodiversity**

52 Stebbins’ 1974 book was an ambitious attempt to link micro- and macroevolutionary scales. In
53 fact, the foundation of Stebbins’ arguments come from the field of population genetics and his
54 concept of *genetical uniformitarianism* (Stebbins 1974:13), which he borrowed from the principle
55 of geological uniformitarianism—that is, the rates and mechanisms of geological processes
56 operating today can explain patterns seen in the geological record (Hutton 1785; Lyell 1830).
57 Stebbins recognized that the evolutionary processes—for instance drift, mutation, recombination,
58 and natural selection—observed in modern populations are the same processes that took place
59 throughout the history of life, no matter the time slice under consideration. Importantly, this does
60 not mean that the rates of these processes are constant, rather that they proceed in the same manner
61 through time.

62 The concept of genetical uniformitarianism led Stebbins to propose two important
63 corollaries that are the theoretical pillars of his book. The first is that the origins of the biological
64 variation and the sets of traits that distinguish higher taxonomic units are simply the result of the
65 same set of processes operating in modern populations of those groups. That is, there were no
66 processes at play at the origin of, say, a taxonomic group that we call a “family”, that are not also

67 occurring today in a single species (see also Stebbins and Ayala 1981). Following this reasoning,
68 his second corollary is that there is a greater chance that the origin of major groups took place
69 under similar conditions that today promote maximal potential for diversification in modern
70 populations. Here it is important to note that, although Stebbins recognized the role of chance in
71 evolution, he viewed the world largely through the adaptationist lens and thus placed particular
72 emphasis on the role of natural selection over other evolutionary processes.

73 *“Cradles”: biological novelties arise in areas of environmental instability*

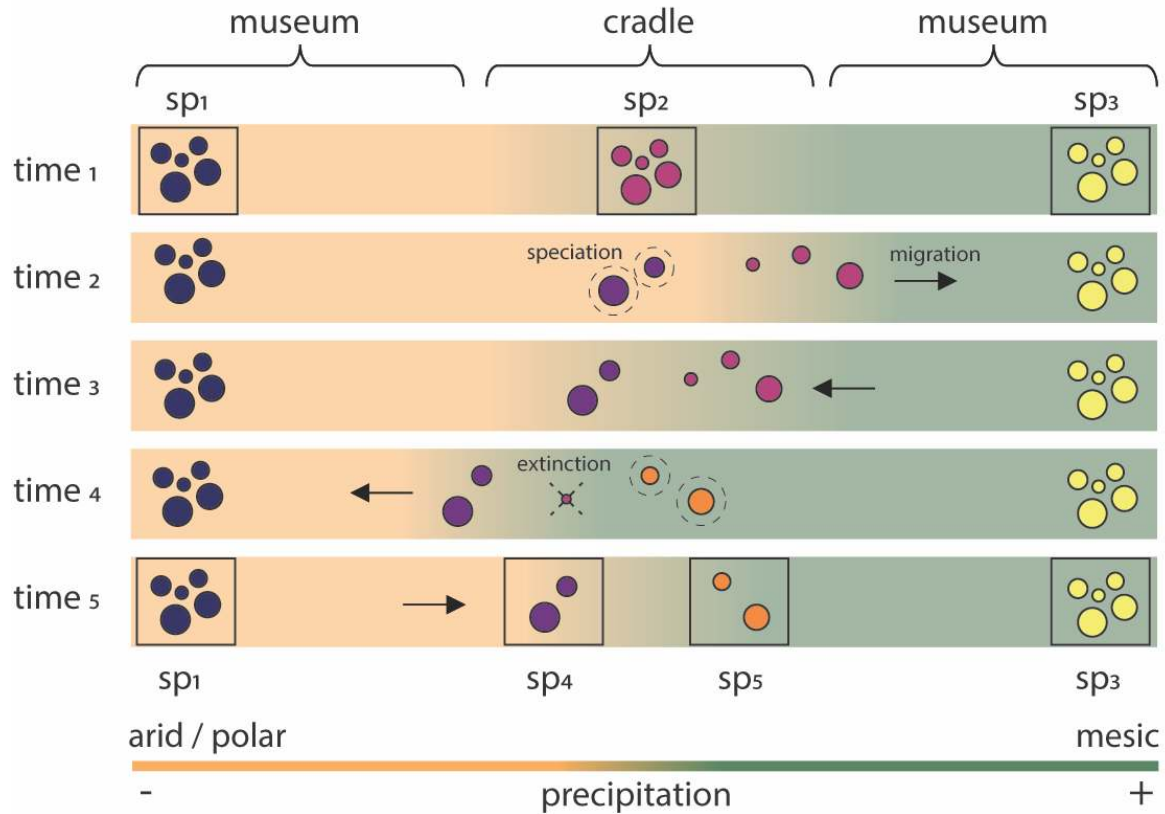
74 Stebbins referred to **cradles** (Stebbins 1974:14, discussed thoroughly in chapter 8) as geographical
75 areas that present a particular set of characteristics that maximize potential for diversification –
76 that is, the origination of biological novelties in terms of new species and traits. The rationale
77 behind this argument is strongly based on models of geographical speciation and can be
78 summarized as follows: traits that characterize the biological entities we call “species” result
79 mainly from the accumulation of adaptations to survive and reproduce under particular ecological
80 and environmental conditions. These conditions, or the combination of environmental challenges
81 in terms of the selection pressures they impose, are not static in time and periods of environmental
82 change triggered by orogeny, tectonics, or climatic cycles can make conditions shift in space.
83 Populations are faced with either migrating, following the spatial shifts of their preferred habitats,
84 or perish and eventually become extinct, in local or global scales. Occasionally, however, changes
85 that result in the partial or total fragmentation of a species’ preferred habitat may break up of
86 populations into a patchwork geographically. If the ecological and environmental conditions in
87 each of these patches are different, diversifying selection, followed by directional selection, may
88 lead to the appearance of new adaptations for habitat exploitation in different ways in these
89 populations. Depending on the selective pressures, these changes may affect only specific organs

90 (e.g., only leaves, but not flowers; “mosaic evolution” Stebbins 1974:123, 141) or lead to changes
91 in traits that are not under direct selection (e.g., due to pleiotropy; Stebbins 1974:102), but will
92 always depend on past adaptations inherited by that lineage. In other words, evolution happens
93 “along the lines of least resistance” (Stebbins, 1974:31). This is a simplified description of how
94 population–environment–genetics interactions may lead to adaptive radiations in the views of
95 Stebbins (Stebbins 1974:13).

96 Stebbins went on to argue that certain combinations of adaptations and environmental
97 conditions might accelerate or slow new adaptive radiations. The inherited adaptations are variable
98 among lineages, but for the sake of argument we will ignore how they can change this dynamic
99 for now (but see the last paragraph of the next section). Stebbins argued that the environmental
100 conditions that most often trigger new adaptive radiations have two characteristics: (1) they are
101 unstable in time, meaning that the preferable habitat of a species shifts in space frequently,
102 increasing chances of population fragmentation and reproductive isolation; (2) they are
103 heterogeneous in space, meaning that external selective pressures that lead to population
104 differentiation over time (e.g., differences in soil, temperature and precipitation) are more diverse
105 in a relatively small area. In other words, these areas increase chances of triggering new adaptive
106 radiations by both leading to constant opportunity for geographical isolation of populations and
107 imposing external selective pressure to change.

108 This combination of characteristics is often found in mosaic communities of ecotones,
109 which for flowering plants are represented by mountains, areas of rugged topography or regions
110 where occasional fire, drought, and frost are frequent but not excessive. Because environmental
111 conditions in these areas change more dramatically over time due to climatic cycles, orogeny, and
112 erosion, species populations move around frequently to follow their preferable niches (Figure 1).

113 The frequent movement in space coupled with general environmental heterogeneity can result in
114 small populations restricted to narrow favorable sites. Stebbins assumed that these isolated
115 populations would “respond more quickly than large ones to radical changes in the environment,
116 and can undergo more drastic alterations of genetic composition, since gene frequencies can be
117 altered more rapidly by similar selection pressures” (Stebbins 1974:158), which in turn would lead
118 more rapid fixation of new adaptations. This follows the thinking of Mayr (1963) and others
119 (reviewed in Maynard Smith 1983) that large population size *inhibits* adaptive evolution, an idea
120 at odds with our current understanding of evolution but common in thinking at the time of the
121 modern synthesis. However, these recently formed micro-endemic species would also be more
122 fragile and prone to extinction in scenarios of environmental instability, so that “the proportion of
123 extinctions were vastly greater in these ecotonal and transition regions than in more stable
124 communities” (Stebbins 1974:166). Using his principle of genetical uniformitarianism, Stebbins
125 proposed that the majority of new, complex adaptations, including those that led to the origin of
126 flowering plants, may have arisen in regions with this combination of characteristics, which, for
127 him, justified the “cradle” metaphor. “Cradles” are then not only areas where lineages speciate
128 frequently but are also more likely to become the areas of early radiation of major clades.
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131 Figure 1: An example of how environmental instability can trigger higher rates of both speciation
 132 and extinction in “cradle” areas according to Stebbins (1974). Stebbins characterized “cradles”
 133 and “museums” loosely, but he made a case for ecotones of intermediate precipitation, marked
 134 seasonality, and rugged topography as his model for “cradle”. “Museums”, on the other hand, are
 135 described as bimodal and distributed in the two extremes of a climatic gradient, particularly in
 136 relation to precipitation regimes. Sp₁ to sp₅ indicate populations of five hypothetical species (sp₄
 137 and sp₅ are descendants of sp₂, which goes extinct in time₄).

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“Museums”: lineages are preserved in areas of environmental stability

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There are many reasons why botanists contemporaneous to Stebbins, and possibly even today,
 would feel uncomfortable saying that early angiosperm evolution happened in unstable and
 heterogeneous regions. The main reason, Stebbins argued, comes from the idea of “center of

142 diversity” by Willis (1922) in which areas where species richness is greatest today are assumed to
143 be areas where a group first originated. This led to the idea that tropical rainforests are the ancestral
144 habitats of flowering plants, since these generally are the most species-rich today (an argument
145 also discussed previously by Wallace 1878). This idea was reinforced by suggestions that many of
146 the forms judged as archaic or “basal” in angiosperms, in terms of both phylogeny and morphology
147 (for instance, several lineages in order Magnoliales), are associated with tropical rainforests
148 (Cronquist 1968; Takhtajan 1969).

149 Tropical rainforests, however, are arguably too stable through time to promote the constant
150 movement of populations that are necessary to trigger new adaptive radiations, especially when
151 compared to certain ecotonal regions (Figure 1; but see a counterargument in Gentry 1982). For
152 that reason, Stebbins was critical of the so-called “centers of diversity” hypothesis and proposed
153 the “**museum** hypothesis” as an alternative. He suggested that lineages rapidly radiating in areas
154 of “cradles” occasionally evolve adaptations that allow them to move to areas of stability where
155 environmental conditions are either favorable (e.g., lowland rainforests) or unfavorable (e.g.,
156 deserts, polar regions), at least for flowering plants. These areas would have the opposite set of
157 characteristics as those found in “cradles”, because (1) the habitat is more stable through time, so
158 populations are less likely to fragment and get isolated in space, and (2) the habitat is less
159 heterogeneous across space, so external selective pressures related to the physical environment are
160 less divergent. When lineages enter these areas of stability, or “museums”, Stebbins argued that
161 spatial fragmentation and selection for new traits will occur less often, and consequently, there is
162 less opportunity for the appearance of novel biological forms. The environmental stability in these
163 areas facilitates the persistence of unchanged lineages for longer periods of time, so that chances
164 of extinction are also reduced. Speciation and extinction do not cease from occurring in areas of

165 “museums”, they just do so at a slower pace. In that way, the probability that the ancestors of major
166 lineages lived in areas of “cradles” instead of “museums” is higher simply because more species
167 evolve in the former rather than the latter.

168 In other words, areas of environmental stability are less likely to become important centers
169 of origin for major groups, but they may *appear* to be so due to a higher number of survivors from
170 early radiations that have persisted there for a long period of time. Conversely, origins of major
171 clades in areas of instability can be overlooked due to the higher extinction rates associated with
172 those areas. The essence of Stebbins’ famous question “Tropical rainforests: cradles or museums?”
173 (Stebbins 1974:165) is thus rhetorical, as most of his book is dedicated to presenting evidence that
174 the origin of angiosperms and major clades within angiosperms occurred in unstable and
175 heterogeneous regions, the true “cradles” of biodiversity. It was not a proposal for a research
176 program, but rather, a problem he believed he had solved.

177 Stebbins’ list of misleading patterns associated with his concept of “museums” is long and
178 includes both living and fossil evidence. For instance, traits that characterize species in stable
179 habitats of favorable conditions may be intuitively perceived as “unspecialized”. On the other
180 hand, traits characterizing lineages that live in areas defined as “cradles”, where environmental
181 challenges are usually higher, are often perceived as too specialized to allow reversals to more
182 favorable conditions. This interpretation, according to Stebbins, is a proven misconception, as he
183 argued with many examples that, “on the basis of principles of developmental genetics”,
184 modifications that allow colonization of more favorable conditions often require genetic
185 simplifications that tend to evolve more frequently than the other way around (Stebbins 1974:171–
186 197). Although rainforests are unfavorable in terms of fossil preservation, Stebbins suggested that
187 sites of deposition that increase chances of fossilization, such as lakes, floodable plains and stream

210 Stebbins' book for the journal *Taxon* in 1975, summarized it well by saying that “such a synthetic,
211 heuristic work with so many provocative ideas cannot prove in all respects to be right, or
212 acceptable to the author's professional colleagues”, but concluded, “I think that [Stebbins'] batting
213 average is very good, and that his swing is beautiful even when he strikes out” (Cronquist
214 1975:374). The impact of Stebbins' 1974 book is undeniable, as exemplified by comments in
215 Donoghue (2008:11549), who stated that “[Stebbins' 1974] book on the macroevolution of
216 flowering plants dominated discussions for decades”, and Givnish (2020:945), who stated that
217 “few works inspired as many of us to pursue careers in plant ecology and evolutionary biology as
218 [...] Stebbins' (1974) broad schema of angiosperm evolution above the species level”.

219 However, the near 400 pages filled with Stebbins' rich discussion on the origin and
220 diversification of angiosperms fell out of print until 2014 and is not easily accessible to many
221 botanists and evolutionary biologists working in the field today. Consequently, many of his ideas,
222 including the “cradles” and “museums” metaphor, have evolved independently from their original
223 characterization, changing their meaning or, in some cases, with key points of their original
224 framing lost along the way. Below, we will discuss how we believe this has led to the loss of what
225 we consider to be some of the most important elements of Stebbins' original metaphor.

226 *Simplifications: “high speciation” vs. “low extinction” and “tropical” vs. “temperate”*

227 Today, “cradles” and “museums” are most often used to refer to, respectively, geographical areas
228 where speciation rates are high and extinction rates are low (e.g., Rangel et al. 2018; Rahbek et al.
229 2019), or where either neo- or paleo-endemics prevail in the species composition of a biological
230 community (e.g., Azevedo et al. 2020, Dagallier et al., 2020). “Cradles” and “museums” are also
231 frequently mentioned in studies of well-known, but still poorly understood, broad-scale patterns
232 of species-richness, such as the latitudinal diversity gradient – that is, the tendency for species

233 diversity to increase as one moves from the poles towards the equator (Chow et al. 2000;
234 Mittelbach et al. 2007; Arita and Vazquez–Dominguez 2008; Moreau and Bell 2013). A question
235 that often emerges in these studies is: are the tropics particularly species-rich because they are a
236 “cradle” for the origination of new species due to high rates of speciation, or a “museum” where
237 species accumulate at a faster pace due to low rates of extinction?

238 The dichotomies of “high speciation” vs. “low extinction” and “tropics” vs. “temperate”,
239 are, however, simplifications of Stebbins’ original framing of “cradles” and “museums” of
240 biodiversity. Although the “high speciation” vs. “low extinction” duality exists in his metaphor, a
241 key element of Stebbins’ framing is the implicit correlation between those rates (table 1). Because
242 factors that lead to higher rates of speciation can also lead to higher rates of extinction, a better
243 approximation of the dichotomy presented by Stebbins (1974) is not of “high speciation” vs. “low
244 extinction”, but of unequal rates of *net turnover* — that is, speciation *plus* extinction, which
245 naturally measures the frequency of events happening over evolutionary time (see also Vrba 1993;
246 Beaulieu and O’Meara 2016). Average species lifespan, a measure considered in paleontology, is
247 just the reciprocal of net turnover rate. Although many studies published in the years following
248 Stebbins (1974) kept this meaning in their references to “cradles” and “museums” (e.g., Price
249 1977; Stenseth 1984), speciation and extinction rates are today mostly treated separately. Reasons
250 for ignoring turnover may stem from the limitations of methods to simultaneously estimate
251 speciation and extinction in a single analytical framework. For instance, most popular methods
252 used to investigate species diversification today force extinction rates to be zero or constant,
253 leading all differences between regions as being purely driven by differential rates of speciation
254 (e.g., Jetz et al. 2012; Rabosky et al. 2014).

255

	Stebbins (1974)	Simplified metaphor
“cradles”	+ turnover + speciation + extinction – fossil preservation – immigration + chance of origin of major clades	+ speciation
“museums”	– turnover – speciation – extinction + fossil preservation + immigration – chance of origin of major clades	– extinction

256 Table 1: Comparison of “cradles” and “museums” characterizations as first proposed by Stebbins
257 (1974) and as used by most studies of macroevolution and biogeography today (“Simplified
258 metaphor”). Plus signs indicate expected “higher rates of” or “higher” and minus signs indicate
259 “lower rates of” or “lower”.

260 Interestingly, recent empirical studies have typically found higher speciation rates in areas
261 that match Stebbins’ description of “cradles” (e.g., mountains, Madriñán et al. 2013; areas with a
262 Mediterranean climate, Sauquet et al. 2009) and lower speciation rates in areas that match his
263 description of “museums” (e.g., tropical rainforests, Schley et al. 2018), although not without
264 exceptions (e.g., Koenen et al. 2015). Nevertheless, it is difficult to justify the formation and
265 maintenance of large gradients of biodiversity as resulting only from differences in speciation rates
266 among areas (see also Jablonski et al. 2017; Eiserhardt et al. 2017; Pontarp et al. 2019). Accounting
267 for migration and extinction rates, and especially turnover rates, will refine the conclusions of
268 these studies to better align with the dynamics proposed by Stebbins (1974).

269 Another aspect of the original metaphor that has been oversimplified over the decades is
270 the geographical location of areas that are prevalent “cradles” or “museums” of biodiversity.

271 Stebbins (1974) emphasized specific characteristics of different biomes and habitats (for example,
272 tropical rainforests, mountains, deserts, Mediterranean climates) in his descriptions of “cradles”
273 and “museums”, but most post-hoc mentions of his metaphor have simplified it into a “temperate”
274 vs. “tropical” division. The regular use of the metaphor in the context of the latitudinal diversity
275 gradient (e.g., Chow et al. 2000; Jablonski et al. 2006; Arita and Vazquez–Dominguez 2008)
276 probably comes from the fact that Stebbins put much emphasis on rainforests occurring close to
277 the equator as his main example of a “museum”. However, Stebbins’ main intention with the
278 tropical rainforests example was not to explain the latitudinal diversity gradient, but rather to
279 emphasize that the processes that have shaped modern species distribution can be
280 counterintuitive. Extrapolations across latitudinal bins may be too sensitive to confounding factors
281 and, as a result, are perhaps poor predictors for the geographical placement of “cradles” and
282 “museums” in their original meaning. Some of the best “museums” can, in fact, occur alongside
283 some of the best “cradles”, and within the same latitudinal zone. Examples include lowland
284 tropical rainforests and tropical mountains, such as the Andes and the Amazon (Janzen 1967;
285 Gentry 1982; Hoorn et al. 2010). Having “cradles” side by side with “museums”, leading to
286 continuous cycles of new adaptive radiations and persistence in adjacent areas, might actually be
287 one of the key drivers for the exceptional biodiversity accumulation in some regions of the globe
288 (Rangel et al. 2018).

289 Extrapolations to whole latitudinal bins also overlook the critical role of lineage–specific
290 traits as regulators of environment–population interactions. Although Stebbins (1974) expected
291 that some areas would be predominantly “cradles” while others would be predominantly
292 “museums”, especially when considering a large number of lineages, it is more realistic to weight
293 the combination of both physical environment and biotic interactions when attempting to infer

294 general “rules” for how gradients of biodiversity are formed (see discussions by Givnish 2015;
295 Donoghue and Sanderson 2015; Nürk et al. 2019). If the abiotic environment was the only relevant
296 factor regulating lineage diversification, we would not see as much heterogeneity in diversification
297 rates across lineages that occupy the same habitats (for instance, in the Cape floristic region;
298 Verboom et al. 2009). Lineages that live in sympatry but have different ecologies will have
299 different environment–population diversification dynamics, affecting the results of studies that
300 overlook this nuance. To test these possibilities with empirical data, it is critical to make a clear
301 division within latitudinal bins, to consider where different mechanisms might be at play, and to
302 draw biological conclusions along these lines. That is, emphasis should be directed away from
303 latitude *per se* and towards the particular ecological attributes of habitats and lineages within the
304 same latitude.

305 *The potentially misleading nature of reconstructions of the past*

306 One of the central messages of Stebbins (1974) was to argue against the hypothesis that
307 angiosperms originated in tropical rainforests, an idea that was common among his
308 contemporaries. However, tropical rainforests as sources of biodiversity is an idea that still persists
309 today, and often for the same reasons contested by Stebbins almost half a century ago. These
310 models are popular because they are intuitive: “basal” lineages, or lineages that are considered
311 older or “primitive”, are indeed often restricted to, or at least more common in, the mesic habitats
312 of tropical and subtropical broadleaf forests (e.g., Feild et al. 2004; Ramirez–Barahona et al. 2020).
313 Although we discussed how the “tropical” vs. “temperate” dichotomy is a simplification of the
314 original metaphor, the tendency of thinking of tropical rainforests as sources of biodiversity is also
315 behind some of the most popular evolutionary hypotheses for the latitudinal diversity gradient
316 (Mittelbach et al. 2007), many of which still rely strongly on the “centers–of–origin” idea (Willis

317 et al. 1922; Wallace 1878). These studies suggest that tropical communities are generally older,
318 and that tropical niche conservatism is the reason for increased diversity in these areas. These
319 arguments are often complemented by the “out-of-the-tropics” hypothesis, where radiations of
320 non-tropical lineages are considered to be generally younger and often nested within clades that
321 are mostly tropical (Judd et al. 1994; Jablonski et al. 2006).

322 At the same time, lineages living in the types of habitats described by Stebbins as possible
323 “cradles” of flowering plant diversification, such as mountains and semi-xeric regions, are also
324 often recovered as younger in phylogenetic analyses (e.g., Hughes and Eastwood 2006; Simon et
325 al. 2009; Madrinan et al. 2013; Zizka et al. 2020). In fact, studies that evaluate habitat transitions
326 based on phylogenetic trees find frequent and sometimes unidirectional transitions from areas of
327 “museum” to areas of “cradles” *sensu* Stebbins (e.g., broadleaf forests to other biomes, Donoghue
328 and Edwards 2014; or the Amazon as the source of much of Neotropical biodiversity, Antonelli et
329 al. 2018). Moreover, the general trend of younger lineages in “cradles” is not only supported by
330 phylogenetic data but also by the recency of the habitats themselves. The orogeny of most modern
331 montane formations and changes in global climate that caused the expansion of modern xeric and
332 semi-xeric biomes, for instance, are relatively recent events in the geological history of Earth (i.e.,
333 Pliocene onwards; Hughes and Eastwood 2006; Simon et al. 2009). Climatic cycles that stimulated
334 diversity-pump events in areas of environmental instability are also often discussed in the context
335 of the time slices closest to the present, such as the Pleistocene (e.g., Gentry 1982; Flantua et al.
336 2019). How, then, could flowering plants have originated in “cradles” *sensu* Stebbins if
337 phylogenetic data suggest otherwise and these areas did not exist in the deep past?

338 One reason is that the original characterization of “cradles” and “museums” does not refer
339 to specific biomes or geographical locations that exist today, but rather to particular sets of

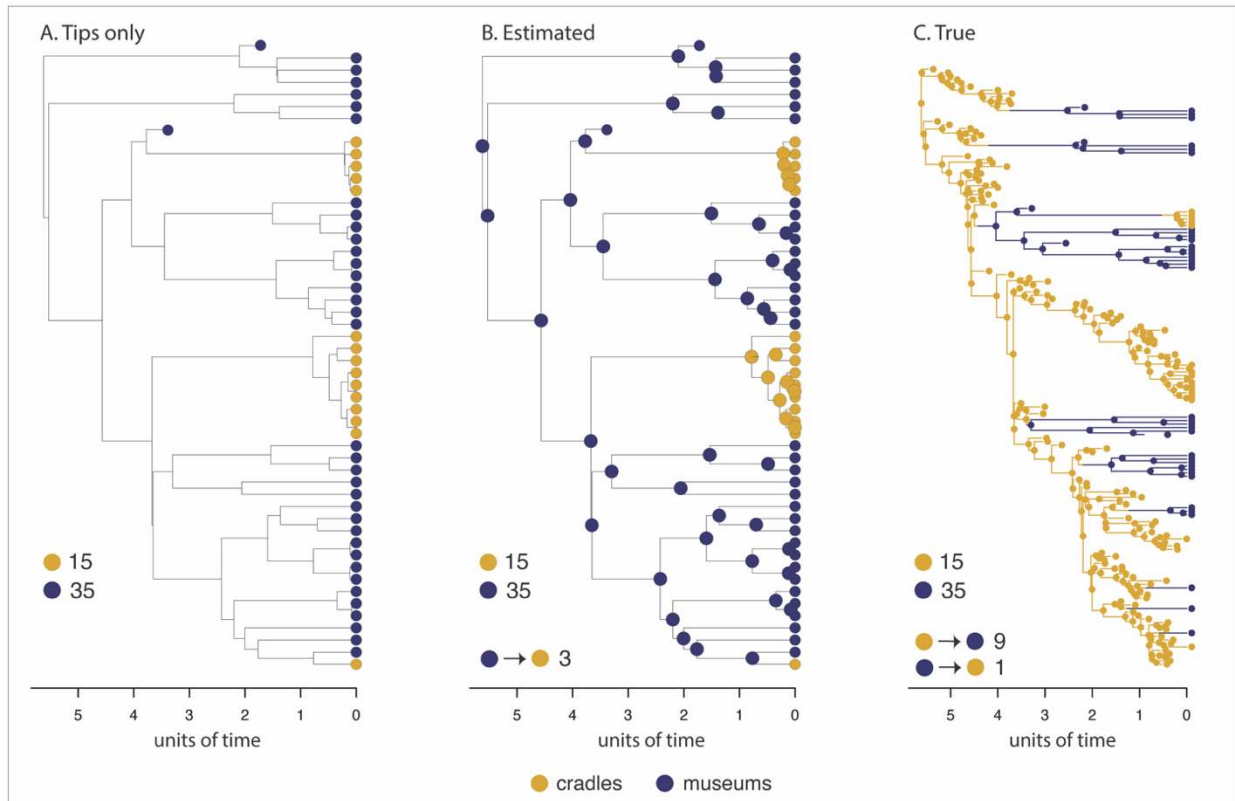
340 environmental *conditions* that accelerate or slow evolutionary processes. The fact that younger
341 radiations prevail in unstable areas today does not mean that areas with these characteristics did
342 not exist in paleo–landscapes, as many situations can trigger instability and ecotones even when
343 the climate was warmer and more humid. Mountain orogeny, mountain erosion, changes in coastal
344 areas, and areas that experience occasional frost, fire and drought may have existed in different
345 parts of the world throughout the entire evolutionary history of flowering plants (e.g., Gilluly
346 1949). The cyclical changes behind the Pleistocene climatic cycles (i.e., Milankovitch cycles) are
347 also not exclusive from recent time slices and may have played a major role in promoting
348 environmental instability during much of life’s evolutionary history (Vrba 1993; Dynesius and
349 Jansson 2000). If areas of higher latitudes have undergone higher environmental instability through
350 time, for instance, it is plausible that rates of speciation are higher in these areas (as showed
351 empirically by Rabosky et al. 2018; and Igea and Tanentzap 2020; Morales–Barbero et al. 2020)
352 with greater potential for the appearance of new adaptive radiations. The survivors of these
353 radiations that first diversified in unstable areas could be those that eventually managed to migrate
354 into stable areas, where extinction rates are lower (e.g., Meseguer and Condamine 2020). If that is
355 the case, even if modern temperate clades seem nested within mostly tropical groups, migrations
356 into stable habitats within the tropics, and not out of it, may have been higher through time. This
357 rationale, while aligned with the original framework proposed by Stebbins, may contradict both
358 the “out–of–the–tropics” and “tropical niche conservatism” hypotheses. The point is that it may
359 be more reasonable to think that areas with “cradle” characteristics have always existed, but
360 because they shift in space and appear and disappear over time at a faster pace than the stable
361 “museums”, the signal for lineages originating in these areas also disappears due to higher rates of
362 *in situ* extinction, low rates of fossil preservation and constant migration to stable areas.

363 Conversely, the original metaphor also suggests that a high frequency of “basal” lineages or older
364 fossils occurring in a certain type of habitat should not be interpreted as a hint for the center of
365 origin of that group, but instead judged as a potential case of survivorship bias.

366 The hypothetical example depicted in figure 2 shows a phylogenetic tree presenting a
367 pattern well-known to empiricists where clades are endemic or nearly endemic to two different
368 areas with distinct environmental characteristics (fig. 2A). Let’s suppose that one of these areas is
369 a “cradle” and the other is a “museum” *sensu* Stebbins. Two fossils were found and sampled, and
370 they both possess characteristics that link them to areas of “museums” (for example, large leaves
371 with entire margins, which are assumed to be more frequent in mesic habitats; but see discussion
372 in Greenwood 2005). Suppose now that we use this information to reconstruct the ancestral habitat
373 of this clade (fig. 2B), which suggests that the “museum” is the ancestral habitat, and that there
374 have been three events of migration between habitats along the history of this clade, all of them
375 from “museum” to “cradle” areas. “Museums” are inferred to be the oldest habitat and the source
376 of biodiversity to other areas. “Cradles”, on the other hand, are inferred to be the youngest habitats,
377 with no migrations observed from them to other areas (fig 2B). Fossil species added to the
378 reconstruction help support this result.

379 Let’s now compare these results with the true biogeographic history (fig. 2C). The group
380 actually originated and subsequently diversified in a “cradle”, but because extinction rates in this
381 habitat also tend to be higher through time, due to higher overall turnover rates in “cradles”, most
382 of that story is lost before the present. Also, due to lower fossil preservation rates in these areas,
383 no fossils linked to habitats with characteristics of “cradles” were sampled. Taken together, this
384 makes “cradles” appear to be younger than they really are, and, as a consequence, the number and
385 directions of transitions between areas are also estimated incorrectly. In reality, there were a total

386 of ten transitions, with only one of them from “museums” to “cradles”. In other words, “cradles”
 387 are the true source of biodiversity with nine events of migration from them to “museums”. Again,
 388 note that this does not mean that the geographical location of ancestral and modern “cradles” and
 389 “museums” is the same, only that environmental *conditions* are similar.
 390



391
 392 Figure 2. An example of how ancestral state reconstructions may be impacted by asymmetric
 393 turnover, transition and preservation rates. Numbers below each tree represent the number of tips
 394 in each state and the number of transitions between states. (A) A tree of 50 extant and two fossil
 395 tips sampled, where the tips were scored as habitats of the type “cradle” (red) or “museum” (blue).
 396 (B) Estimation of ancestral states at the nodes and frequency of transition between areas based on
 397 tree and tip states in “A”. (C) True story of the tree, including all extinct tips and transitions
 398 between states.

399 We hasten to point out that the hypothetical example above represents an extreme scenario,
400 but it illustrates the problem described by Stebbins (1974). Realistically, it is more likely that
401 lineages have experienced multiple shifts between “cradles” and “museums”, changing faster in
402 conditions of “cradles” and slower in “museums”. However, this can be challenging to test due to
403 the very nature of the processes that generate these patterns. If conditions that favor the appearance
404 of new forms of life can also drive to extinction poorly adapted ones, a correlation between
405 speciation and extinction is implied in both “cradles” and “museums” (i.e., turnover, table 1). In
406 modern “museums”, we would be more likely to observe the survivors from the original radiations
407 that may have once evolved in and migrated from ancestral “cradles”, whereas in modern “cradles”
408 we would be still observing a whole recently formed radiation, including the intermediate forms
409 that are possibly about to go extinct. Low fossil preservation rates and high extinction and
410 emigration rates in “cradles” could then mislead attempts to infer older historical biogeographical
411 events in the clade.

412

413 **Is the "cradles" and "museum" metaphor still useful?**

414 Stebbins’ arguments presented in *Flowering plants: evolution above the species level* focused on
415 multiple axes of biological evolution, including turnover, migration and fossil preservation and
416 noted how environmental changes could affect all of these. Dynamic environments led to changes
417 in all and stable environments preserved what was there without causing much change, with some
418 nuance resulting from traits and ecological interactions. By focusing primarily on latitude alone,
419 investigating speciation and extinction separately, assuming that the modern distribution of “basal”
420 lineages indicates centers of origin, or ignoring the role of traits loses the full context and nuances
421 of Stebbins’ metaphor.

422 On the whole, the arguments discussed herein lead us to the unavoidable question of: are
423 simple binary categories, such as labeling areas as “cradles” and “museums”, still useful in modern
424 studies of biogeography and macroevolution? Extensions to the metaphor (e.g., “casinos”; Arita–
425 Vazquez–Dominguez 2008; “graves”, Rangel et al. 2018) and conclusions that particular areas
426 serve as both “cradles” and “museums” even for the same lineage (e.g., Moreau and Bell, 2013)
427 are frequent because simple dichotomies rarely encompass the complex set of variables involved
428 in shaping gradients of biodiversity in space. For these reasons, we feel Stebbins' metaphor may
429 have outlived its usefulness, and instead it may be more productive to shift focus towards the actual
430 biology Stebbins was trying to describe in his book. For example, the following ideas may prove
431 to be useful for better framing future studies that wish test to the ideas central to Stebbins' (1974)
432 arguments:

- 433 1. Increased evolutionary rates occur in areas of instability. These areas can be where biomes
434 meet or in areas with heterogeneity of resources over the appropriate time and spatial scales
435 for the organisms.
- 436 2. There can be differences based on organism traits. An area that is variable for some species
437 (for instance, due to their specialist association with pollinators) might be stable for another
438 (given constant abiotic factors). Studies that aim at understanding gradients of biodiversity
439 in space must therefore also consider particularities of each lineage in their analyses, as
440 these can radically change how the environment drives diversification.
- 441 3. Instability does not correlate *only* with latitude. For instance, although glaciation caused
442 substantial disruption latitudinally, factors like the rise of the Andes caused disruption
443 longitudinally. Rather than increasingly repetitive measurements of rates by latitude, we
444 should look at where mechanisms might be at play and draw conclusions from the biology.

- 445 4. Rates of species turnover matter more than rates of speciation alone. Many factors that lead
446 to higher rates of speciation also lead to higher rates of extinction, and looking only at
447 speciation, or even only at net diversification, does not get at the processes that Stebbins
448 described.
- 449 5. We can unfortunately but easily be misled by reconstructions of the past using *both* extant
450 and fossil taxa (as well as either alone). Areas that are primarily eroding, such as
451 mountainous areas, tend to lead to fewer fossils than areas of active deposition, such as
452 valleys. The fossil record is thus a biased set of samples, often biased against collecting
453 species from areas of greatest instability. Reconstructing changes on trees using modern
454 taxa may also lead to biases as unequal rates of turnover and transition among areas may
455 incorrectly reconstruct ancestral regions being the stable ones.
- 456 6. “Basal” lineages and higher species richness do not indicate centers of origin. Number of
457 species of a clade in an area does not mean a group originated there, nor even that its overall
458 speciation rate is higher there. This can be somewhat unintuitive, but this was what
459 Stebbins tried to communicate with his “museum” metaphor: species can find it easy to
460 invade these habitats, and once there they do not change.

461

462 Stebbins’ (1974) framing of “cradles” vs. “museums” was intended to help evolutionary
463 biologists to understand that the link between processes and patterns are sometimes
464 counterintuitive, but oversimplification of important points has led the field to gradually lose sight
465 of the original intent and biological underpinnings of the metaphor. By “cradles” do we mean areas
466 of high turnover that can be hard to invade, or places with high speciation rates? More importantly,
467 is it realistic to use this dichotomy when species traits and biotic interactions play such an

468 important role in determining the diversification dynamics of a lineage? Words can change
469 meaning as understanding improves, but in this case, especially given the relative inaccessibility
470 of Stebbins' book, there has been a radiation of meanings that is anything but adaptive. It is
471 difficult to properly frame Stebbins' metaphor in modern studies of biogeography and
472 macroevolution: such metaphors are unnecessary replacements for the actual biological processes
473 at play. Focusing on the processes rather than the metaphor will advance science further.

474

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480

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