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.

Introduction

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

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

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

Revisiting Stebbins' "cradles" and "museums" of biodiversity

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

The concept of genetical uniformitarianism led Stebbins to propose two important corollaries that are the theoretical pillars of his book. The first is that the origins of the biological variation and the sets of traits that distinguish higher taxonomic units are simply the result of the same set of processes operating in modern populations of those groups. That is, there were no processes at play at the origin of, say, a taxonomic group that we call a "family", that are not also occurring today in a single species (see also Stebbins and Ayala 1981). Following this reasoning, his second corollary is that there is a greater chance that the origin of major groups took place under similar conditions that today promote maximal potential for diversification in modern populations. Here it is important to note that, although Stebbins recognized the role of chance in evolution, he viewed the world largely through the adaptationist lens and thus placed particular emphasis on the role of natural selection over other evolutionary processes.

"Cradles": biological novelties arise in areas of environmental instability

Stebbins referred to **cradles** (Stebbins 1974:14, discussed thoroughly in chapter 8) as geographical areas that present a particular set of characteristics that maximize potential for diversification – that is, the origination of biological novelties in terms of new species and traits. The rationale behind this argument is strongly based on models of geographical speciation and can be summarized as follows: traits that characterize the biological entities we call "species" result mainly from the accumulation of adaptations to survive and reproduce under particular ecological and environmental conditions. These conditions, or the combination of environmental challenges in terms of the selection pressures they impose, are not static in time and periods of environmental change triggered by orogeny, tectonics, or climatic cycles can make conditions shift in space. Populations are faced with either migrating, following the spatial shifts of their preferred habitats, or perish and eventually become extinct, in local or global scales. Occasionally, however, changes that result in the partial or total fragmentation of a species' preferred habitat may break up of populations into a patchwork geographically. If the ecological and environmental conditions in each of these patches are different, diversifying selection, followed by directional selection, may lead to the appearance of new adaptations for habitat exploitation in different ways in these populations. Depending on the selective pressures, these changes may affect only specific organs (e.g., only leaves, but not flowers; “mosaic evolution” Stebbins 1974:123, 141) or lead to changes in traits that are not under direct selection (e.g., due to pleiotropy; Stebbins 1974:102), but will always depend on past adaptations inherited by that lineage. In other words, evolution happens “along the lines of least resistance” (Stebbins, 1974:31). This is a simplified description of how population–environment-genetics interactions may lead to adaptive radiations in the views of Stebbins (Stebbins 1974:13).

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

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

The frequent movement in space coupled with general environmental heterogeneity can result in small populations restricted to narrow favorable sites. Stebbins assumed that these isolated populations would “respond more quickly than large ones to radical changes in the environment, and can undergo more drastic alterations of genetic composition, since gene frequencies can be altered more rapidly by similar selection pressures” (Stebbins 1974:158), which in turn would lead more rapid fixation of new adaptations. This follows the thinking of Mayr (1963) and others (reviewed in Maynard Smith 1983) that large population size *inhibits* adaptive evolution, an idea at odds with our current understanding of evolution but common in thinking at the time of the modern synthesis. However, these recently formed micro-endemic species would also be more fragile and prone to extinction in scenarios of environmental instability, so that “the proportion of extinctions were vastly greater in these ecotonal and transition regions than in more stable communities” (Stebbins 1974:166). Using his principle of genetical uniformitarianism, Stebbins proposed that the majority of new, complex adaptations, including those that led to the origin of flowering plants, may have arisen in regions with this combination of characteristics, which, for him, justified the “cradle” metaphor. “Cradles” are then not only areas where lineages speciate frequently but are also more likely to become the areas of early radiation of major clades.

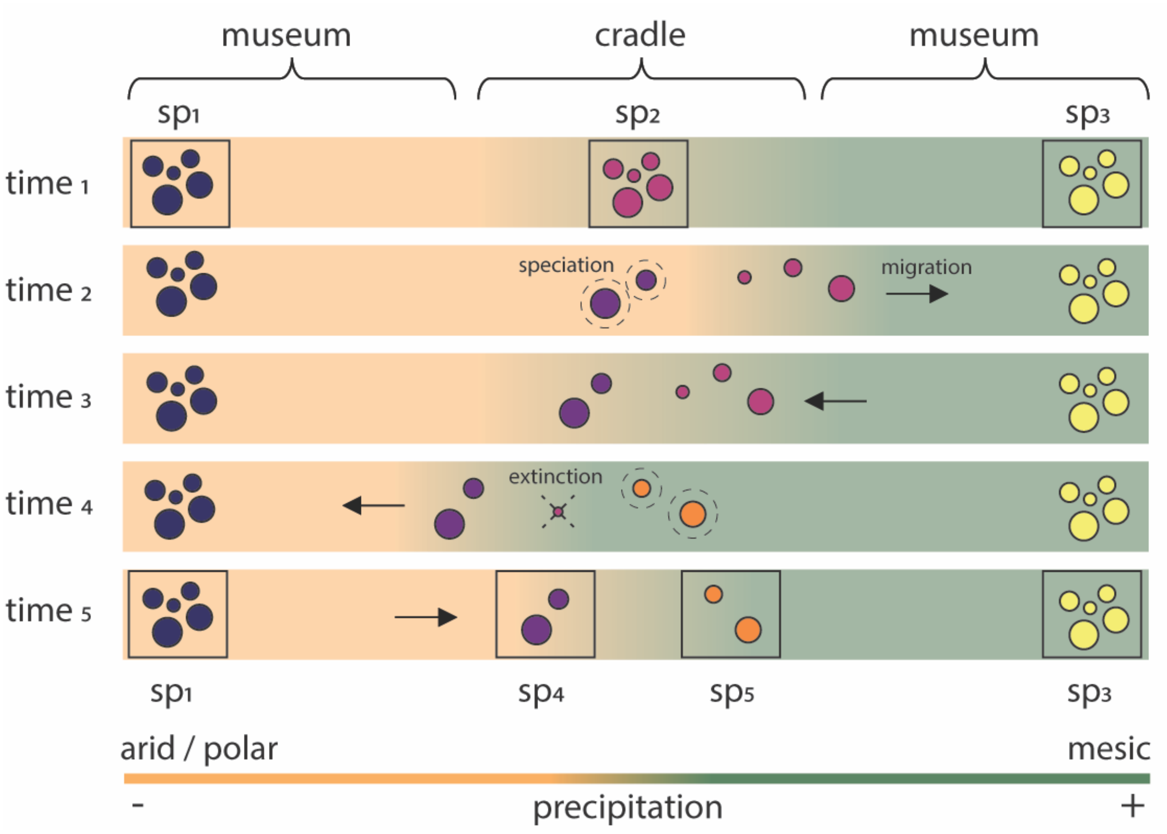

Figure 1: An example of how environmental instability can trigger higher rates of both speciation and extinction in "cradle" areas according to Stebbins (1974). Stebbins characterized "cradles" and "museums" loosely, but he made a case for ecotones of intermediate precipitation, marked seasonality, and rugged topography as his model for "cradle". "Museums", on the other hand, are described as bimodal and distributed in the two extremes of a climatic gradient, particularly in relation to precipitation regimes. Sp$_1$ to sp$_5$ indicate populations of five hypothetical species (sp$_4$ and sp$_5$ are descendants of sp$_2$, which goes extinct in time$_4$).

"Museums": lineages are preserved in areas of environmental stability

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

Tropical rainforests, however, are arguably too stable through time to promote the constant movement of populations that are necessary to trigger new adaptive radiations, especially when compared to certain ecotonal regions (Figure 1; but see a counterargument in Gentry 1982). For that reason, Stebbins was critical of the so–called "centers of diversity" hypothesis and proposed the "**museum** hypothesis" as an alternative. He suggested that lineages rapidly radiating in areas of "cradles" occasionally evolve adaptations that allow them to move to areas of stability where environmental conditions are either favorable (e.g., lowland rainforests) or unfavorable (e.g., deserts, polar regions), at least for flowering plants. These areas would have the opposite set of characteristics as those found in "cradles", because (1) the habitat is more stable through time, so populations are less likely to fragment and get isolated in space, and (2) the habitat is less heterogeneous across space, so external selective pressures related to the physical environment are less divergent. When lineages enter these areas of stability, or "museums", Stebbins argued that spatial fragmentation and selection for new traits will occur less often, and consequently, there is less opportunity for the appearance of novel biological forms. The environmental stability in these areas facilitates the persistence of unchanged lineages for longer periods of time, so that chances of extinction are also reduced. Speciation and extinction do not cease from occurring in areas of "museums", they just do so at a slower pace. In that way, the probability that the ancestors of major lineages lived in areas of "cradles" instead of "museums" is higher simply because more species evolve in the former rather than the latter.

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

Stebbins' list of misleading patterns associated with his concept of "museums" is long and includes both living and fossil evidence. For instance, traits that characterize species in stable habitats of favorable conditions may be intuitively perceived as "unspecialized". On the other hand, traits characterizing lineages that live in areas defined as "cradles", where environmental challenges are usually higher, are often perceived as too specialized to allow reversals to more favorable conditions. This interpretation, according to Stebbins, is a proven misconception, as he argued with many examples that, "on the basis of principles of developmental genetics", modifications that allow colonization of more favorable conditions often require genetic simplifications that tend to evolve more frequently than the other way around (Stebbins 1974:171–197). Although rainforests are unfavorable in terms of fossil preservation, Stebbins suggested that sites of deposition that increase chances of fossilization, such as lakes, floodable plains and stream margins, are also common *within* mesic conditions that often characterize "museums" (see also Gastaldo and Demko, 2011). Consequently, many of the oldest angiosperm fossils may have characteristics that link them to habitats that are more mesic (as previously discussed by Axelrod 1970; 1972). "Cradles", on the other hand, are often sites of erosion that hinder fossil preservation, so it is less likely to find fossils with traits that are linked to them (a consideration challenged by later paleontological findings; see Wing et al. 2015). Stebbins argued that this taphonomic bias makes it even harder to identify areas where diversification of key clades began, even with fossils.

Finally, Stebbins also recognized the role of traits and biotic interactions in his "cradles" and "museums" dynamic. In scenarios of environmental instability, for instance, niche specialists would be more likely to undergo habitat fragmentation than niche generalists, which may require a much larger area for effective isolation and differentiation, increasing chances of triggering new adaptive radiations in the former in comparison with the latter under similar conditions (Stebbins 1974:10). In the specific context of flowering plants, Stebbins highlighted the role of specialized interactions with pollinators and seed dispersers in increasing or decreasing chances of reproductive isolation in certain habitats, concluding that "many, and probably most, plant communities are 'cradles' for some of their species groups and 'museums' for others" (Stebbins 1974:14) largely depending on particular traits of each group.

"Cradles" and "museums" in the context of modern studies of macroevolution and biogeography

Flowering Plants: Evolution Above the Species Level was a popular and stimulating book when it was first published in 1974. Several of its ideas were topics of debate and criticism in the following years, as is expected with a book of such broad interest. Arthur Cronquist, when reviewing

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

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

Simplifications: "high speciation" vs. "low extinction" and "tropical" vs. "temperate"

Today, "cradles" and "museums" are most often used to refer to, respectively, geographical areas where speciation rates are high and extinction rates are low (e.g., Rangel et al. 2018; Rahbek et al. 2019), or where either neo- or paleo-endemics prevail in the species composition of a biological community (e.g., Azevedo et al. 2020, Dagallier et al., 2020). "Cradles" and "museums" are also frequently mentioned in studies of well-known, but still poorly understood, broad-scale patterns of species-richness, such as the latitudinal diversity gradient – that is, the tendency for species diversity to increase as one moves from the poles towards the equator (Chow et al. 2000; Mittelbach et al. 2007; Arita and Vazquez–Dominguez 2008; Moreau and Bell 2013). A question that often emerges in these studies is: are the tropics particularly species-rich because they are a "cradle" for the origination of new species due to high rates of speciation, or a "museum" where species accumulate at a faster pace due to low rates of extinction?

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

	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

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

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

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

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

Extrapolations to whole latitudinal bins also overlook the critical role of lineage–specific traits as regulators of environment–population interactions. Although Stebbins (1974) expected that some areas would be predominantly "cradles" while others would be predominantly "museums", especially when considering a large number of lineages, it is more realistic to weight the combination of both physical environment and biotic interactions when attempting to infer general "rules" for how gradients of biodiversity are formed (see discussions by Givnish 2015; Donoghue and Sanderson 2015; Nürk et al. 2019). If the abiotic environment was the only relevant factor regulating lineage diversification, we would not see as much heterogeneity in diversification rates across lineages that occupy the same habitats (for instance, in the Cape floristic region; Verboom et al. 2009). Lineages that live in sympatry but have different ecologies will have different environment–population diversification dynamics, affecting the results of studies that overlook this nuance. To test these possibilities with empirical data, it is critical to make a clear division within latitudinal bins, to consider where different mechanisms might be at play, and to draw biological conclusions along these lines. That is, emphasis should be directed away from latitude *per se* and towards the particular ecological attributes of habitats and lineages within the same latitude.

The potentially misleading nature of reconstructions of the past

One of the central messages of Stebbins (1974) was to argue against the hypothesis that angiosperms originated in tropical rainforests, an idea that was common among his contemporaries. However, tropical rainforests as sources of biodiversity is an idea that still persists today, and often for the same reasons contested by Stebbins almost half a century ago. These models are popular because they are intuitive: "basal" lineages, or lineages that are considered older or "primitive", are indeed often restricted to, or at least more common in, the mesic habitats of tropical and subtropical broadleaf forests (e.g., Feild et al. 2004; Ramirez–Barahona et al. 2020). Although we discussed how the "tropical" vs. "temperate" dichotomy is a simplification of the original metaphor, the tendency of thinking of tropical rainforests as sources of biodiversity is also behind some of the most popular evolutionary hypotheses for the latitudinal diversity gradient (Mittelbach et al. 2007), many of which still rely strongly on the "centers–of–origin" idea (Willis et al. 1922; Wallace 1878). These studies suggest that tropical communities are generally older, and that tropical niche conservatism is the reason for increased diversity in these areas. These arguments are often complemented by the "out–of–the–tropics" hypothesis, where radiations of non–tropical lineages are considered to be generally younger and often nested within clades that are mostly tropical (Judd et al. 1994; Jablonski et al. 2006).

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

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

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

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

Let's now compare these results with the true biogeographic history (fig. 2C). The group actually originated and subsequently diversified in a "cradle", but because extinction rates in this habitat also tend to be higher through time, due to higher overall turnover rates in "cradles", most of that story is lost before the present. Also, due to lower fossil preservation rates in these areas, no fossils linked to habitats with characteristics of "cradles" were sampled. Taken together, this makes "cradles" appear to be younger than they really are, and, as a consequence, the number and directions of transitions between areas are also estimated incorrectly. In reality, there were a total of ten transitions, with only one of them from “museums” to “cradles”. In other words, “cradles” are the true source of biodiversity with nine events of migration from them to “museums”. Again, note that this does not mean that the geographical location of ancestral and modern “cradles” and “museums” is the same, only that environmental *conditions* are similar.

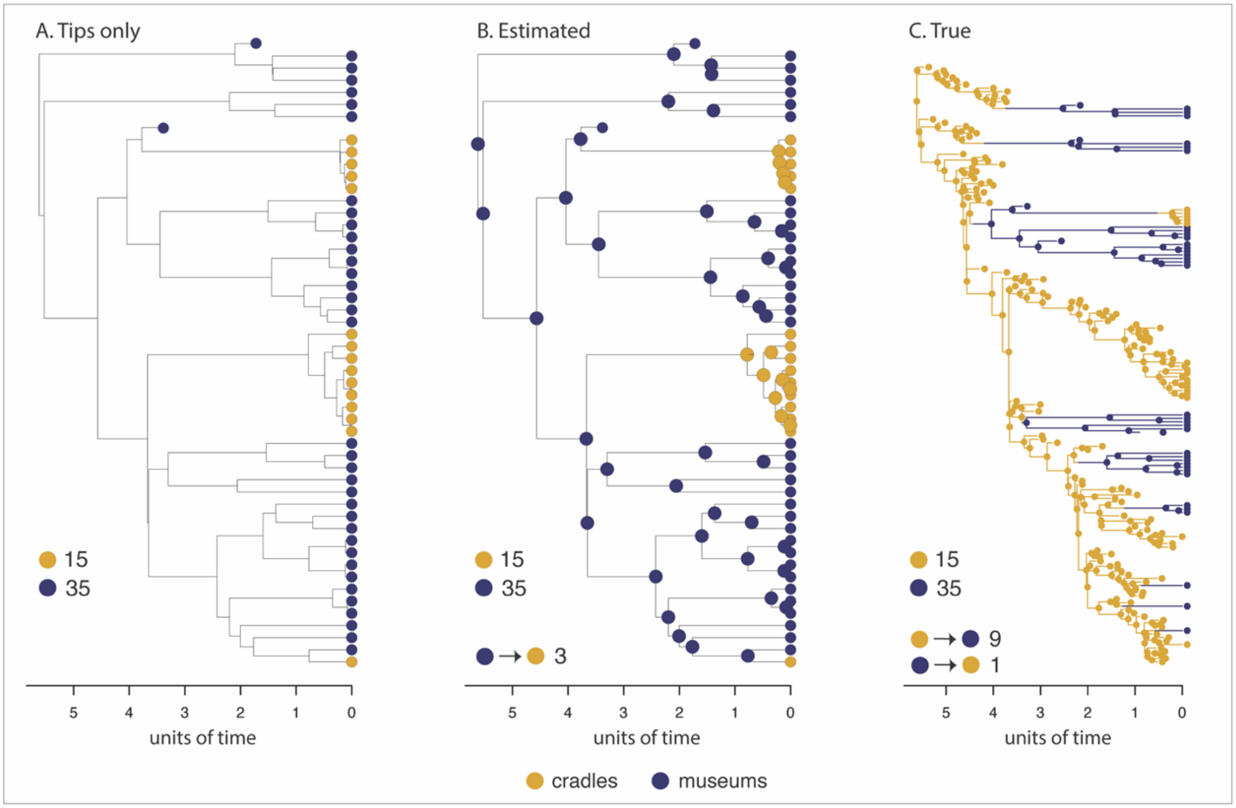

Figure 2. An example of how ancestral state reconstructions may be impacted by asymmetric turnover, transition and preservation rates. Numbers below each tree represent the number of tips in each state and the number of transitions between states. (A) A tree of 50 extant and two fossil tips sampled,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

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

Is the "cradles” and “museum” metaphor still useful?

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

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

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

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

Stebbins' (1974) framing of "cradles" vs. "museums" was intended to help evolutionary biologists to understand that the link between processes and patterns are sometimes counterintuitive, but oversimplification of important points has led the field to gradually lose sight of the original intent and biological underpinnings of the metaphor. By "cradles" do we mean areas of high turnover that can be hard to invade, or places with high speciation rates? More importantly, is it realistic to use this dichotomy when species traits and biotic interactions play such an important role in determining the diversification dynamics of a lineage? Words can change meaning as understanding improves, but in this case, especially given the relative inaccessibility of Stebbins' book, there has been a radiation of meanings that is anything but adaptive. It is difficult to properly frame Stebbins' metaphor in modern studies of biogeography and macroevolution: such metaphors are unnecessary replacements for the actual biological processes at play. Focusing on the processes rather than the metaphor will advance science further.

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