Historical Perspective

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 by-products of the way environment-population interactions drive species diversification through time. We revisit the narrative behind Stebbins's "cradles" and "museums" of biodiversity to debate two points. First, the usual high-speciation versus low-extinction and tropical versus 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 that the terms "cradles" and "museums" are popular in the literature and that terminologies can evolve with the requirements of the field. However, we also argue that the concepts of cradles and museums have outlived their utility in studies of biogeography and macroevolution and should be replaced by discussions of actual processes at play.

Keywords: extinction, latitudinal diversity gradient, turnover, speciation.

Introduction

The ease with which methods and various sources of data are brought together for reconstructing large, well-resolved species phylogenies (e.g., Smith et al. 2009), inferring rates of origination and extinction through time (e.g., Silvestro et al. 2014), and mapping the distribution of these species in time and space (e.g., 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 of both extant and fossil taxa (e.g., Pennington et al. 2006; Donoghue 2008; Simon et al. 2009; Kiessling et al. 2010; Jablonski et al. 2013; 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; Kiessling et al. 2010; Moreau and Bell 2013; Eiserhardt et al. 2017; Rangel et al. 2018; Azevedo et al. 2020; Dagallier et al. 2020).

Today, the cradle and museum 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. 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 museum hypothesis as a means of countering the idea that centers of diversity reflect centers of origin, the so-called cradles, particularly with respect to the putative origins of flowering plants. Stebbins's argument for proposing his cradle and museum metaphor was far richer—and integrative—than that currently in use by the field and involved rates of not only speciation and extinction but also migration and fossil preservation. 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. We conclude by suggesting that the metaphor has outlived its usefulness.

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Revisiting Stebbins's Cradles and Museums of Biodiversity

Stebbins's 1974 book was an ambitious attempt to link processes happening at microevolutionary scales to patterns observed at macroevolutionary scales. In fact, the foundation of Stebbins's arguments comes from the field of population genetics with his concept of "genetical uniformitarianism" (Stebbins 1974, p. 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 1788; 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, it means 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 (1974, p. 14; discussed thoroughly in chap. 8) referred to cradles 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 perishing and eventually becoming extinct, at local or global scales. Occasionally, however, changes that result in the partial or total fragmentation of a species' preferred habitat may break up 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, pp. 123, 141) or lead to changes in traits that are not under direct selection (e.g., due to pleiotropy; Stebbins 1974, p. 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, p. 31). This is a simplified description of how population-environment-genetic interactions may lead to adaptive radiations in the view of Stebbins (1974, p. 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 the chances of population fragmentation and reproductive isolation; and (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 the 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 because of climatic cycles, orogeny, and erosion, species populations move around frequently to follow their preferable niches (fig. 1). The frequent movement in space coupled with general environmental heterogeneity can result in small

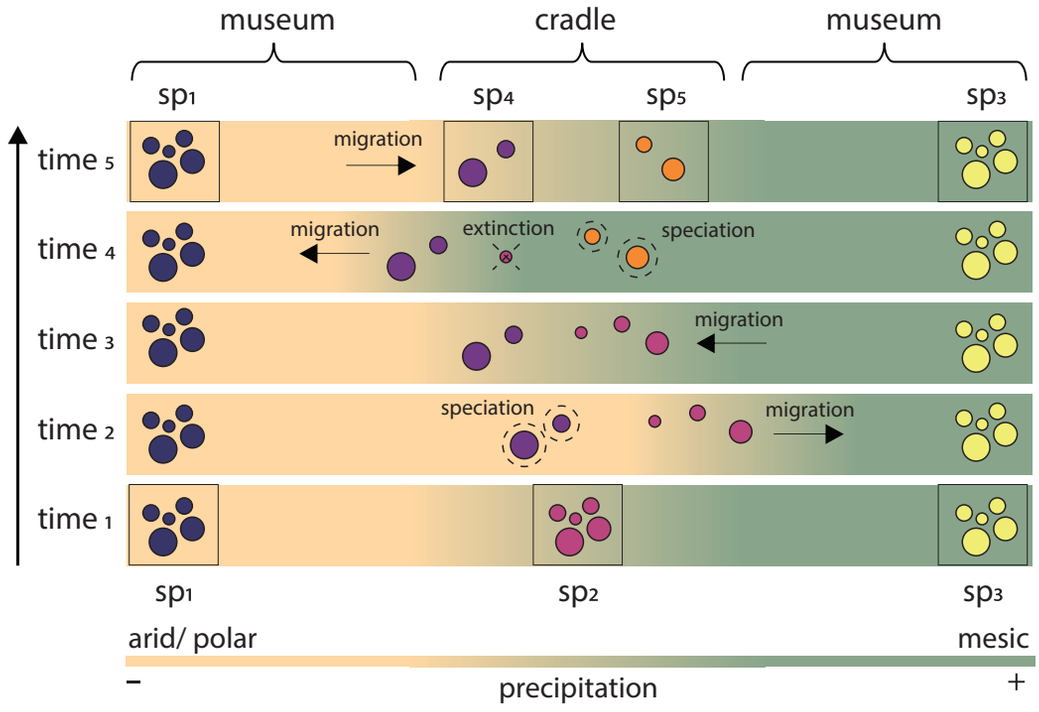

Figure 1: Example of how environmental instability can trigger higher rates of both speciation and extinction in cradle areas according to Stebbins (1974). Stebbins characterized cradles and museums loosely, but he made a case for ecotones of intermediate precipitation, marked seasonality, and rugged topography as his model for cradles. 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. Populations of five hypothetical species are indicated by sp_1 to sp_5, and a temporal series is depicted by $time_1$ to $time_5$ where climatic fluctuations make populations of species in cradle areas migrate (arrows), leading to repeated events of speciation and extinction. Climatic fluctuations are indicated by movement in the color gradient in the slices. Circles of the same color represent populations of the same species, and boxes highlight extant species at $time_1$ and $time_5$ (sp_4 and sp_5 are descendants of sp_2, which becomes extinct at $time_4$).

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, p. 158), which in turn would lead to 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 microendemic 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, p. 166; a similar description had been previously made by Simpson [1944] as areas favoring episodes of quantum evolution). 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.

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 a "center of diversity" by Willis et al. (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 (e.g., several lineages in the 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 compared with certain ecotonal regions (fig. 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 become 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 in 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 because of 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 because of the higher extinction rates associated with those areas. The essence of Stebbins's famous question "Tropical rainforests: cradles or museums?" (Stebbins 1974, p. 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's 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 showing 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, pp. 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 the 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. 2005). 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 the chances of triggering new adaptive radiations in the former in comparison with the latter under similar conditions (Stebbins 1974, p. 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, p. 14), largely depending on the 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's 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 he concluded, "I think that [Stebbins's] batting average is very good, and that his swing is beautiful even when he strikes out" (Cronquist 1975, p. 374). The impact of Stebbins's 1974 book is undeniable, as exemplified by comments from Donoghue (2008, p. 11549), who stated that "[Stebbins's 1974] book on the macroevolution of flowering plants dominated discussions for decades," and Givnish (2020, p. 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 nearly 400 pages filled with Stebbins's rich discussion on the origin and diversification of angiosperms fell out of print until 2014 and is not easily accessible to many botanists, evolutionary biologists, biogeographers, and paleontologists working in the field today. Consequently, many of his ideas, including the cradle and museum metaphor, have evolved independently from their original characterization, changing their meaning or, in some cases, losing key points of their original framing 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's original metaphor.

Simplifications: High Speciation versus Low Extinction and Tropical versus Temperate

Today, cradles and museums are most often used to refer to, respectively, geographical areas where speciation rates are high (cradles) and extinction rates are low (museums; e.g., Rangel et al. 2018; Rahbek et al. 2019) or where either neoendemics (cradles) or paleoendemics (museums) 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 toward the equator (i.e., a tropics vs. temperate dichotomy; 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 as a result of high rates of speciation or a museum where species accumulate at a faster pace as a result of low rates of extinction?

The dichotomies of high speciation versus low extinction and tropics versus temperate are, however, simplifications of Stebbins's original framing of cradles and museums of biodiversity. Although the high speciation versus low extinction duality exists in his metaphor, a key element of Stebbins's 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 versus low extinction but of unequal rates of "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). Note that turnover differs from other metrics commonly used in diversification studies, such as net diversification (i.e., speciation minus extinction) and extinction fraction (i.e., extinction divided by speciation), but has analogues in the paleontology literature, such as the concept of clade volatility (Gilinsky 1994). In fact, since observations of animal fossil series made by Stanley (1979), there is a general understanding among paleontologists that rates of speciation and extinction tend to be tightly correlated through time (see also the third law of paleontology; Marshall 2017). That researchers working in very different groups (botanists like Stebbins and zoologists like Stanley) and timescales (neontologists like Stebbins and paleontologists like Stanley) have come to similar conclusions may indicate that turnover, not each of its constituent components, is a key metric for describing major evolutionary patterns above the species level.

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),

Table 1: Comparison of cradle and museum characterizations as first proposed by Stebbins (1974) and as used by most studies of macroevolution and biogeography today ("Simplified metaphor")

	Stebbins (1974)	Simplified metaphor
Cradles	+ **Turnover**	+ Speciation
	+ Speciation	
	+ Extinction	
	− Fossil preservation	
	− Immigration	
	+ Chance of origin of major clades	
Museums	− **Turnover**	− Extinction
	− Speciation	
	− Extinction	
	+ Fossil preservation	
	+ Immigration	
	− Chance of origin of major clades	

Note: Plus signs indicate expected "higher rates of" or "higher," and minus signs indicate "lower rates of" or "lower."

speciation and extinction rates are today mostly treated separately or inferred merely by counting the number of taxa through time. Reasons for ignoring turnover may stem from the limitations of neontological methods to simultaneously estimate speciation and extinction in a single analytical framework. For instance, some of the most popular methods used to investigate species diversification from molecular phylogenies force extinction rates to be zero or constant, leading to differences in diversification between regions as being purely driven by rates of speciation (e.g., Jetz et al. 2012; Rabosky et al. 2014).

Interestingly, recent empirical studies have typically found higher speciation rates in areas that match Stebbins's description of cradles (e.g., mountains [Madriñán et al. 2013] and 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 dispersal 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 (e.g., 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 versus 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's 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 (see also Jablonski et al. 2006). 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 in 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 (e.g., 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 toward 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, 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 versus 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 (Wallace 1878; Willis et al. 1922). 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 nontropical lineages are considered to be generally younger and often nested within clades that are mostly tropical (Judd et al. 1994; Jablonski et al. 2006; Crame 2020).

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 semixeric regions, are also often recovered as younger in phylogenetic analyses (e.g., Hughes and Eastwood 2006; Simon et al. 2009; Madriñán 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 supported not only 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 semixeric biomes, for instance, are relatively recent events in the geological history of Earth (i.e., Pliocene onward; 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. That younger radiations prevail in unstable areas today does not mean that areas with these characteristics did not exist in paleolandscapes, 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 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 shown empirically by Rabosky et al. [2018], Igea and Tanentzap [2020], and Morales-Barbero et al. [2021]) 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 hypothesis and the tropical niche conservatism hypothesis. 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 because of 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 be 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. 2*A*). Let us 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 (e.g., large leaves with entire margins, which are assumed to be more frequent in mesic habitats; but see the discussion in Greenwood 2005). Suppose now that we use this information to reconstruct the ancestral habitat of this clade (fig. 2*B*), 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. 2*B*). Fossil species added to the reconstruction help support this result.

Let us now compare these results with the true biogeographic history (fig. 2*C*). The group actually originated and subsequently diversified in a cradle, but because extinction rates in this habitat also tend to be higher through time, as a result of higher overall turnover rates in cradles, most of that story is lost before the present. Also, because of lower

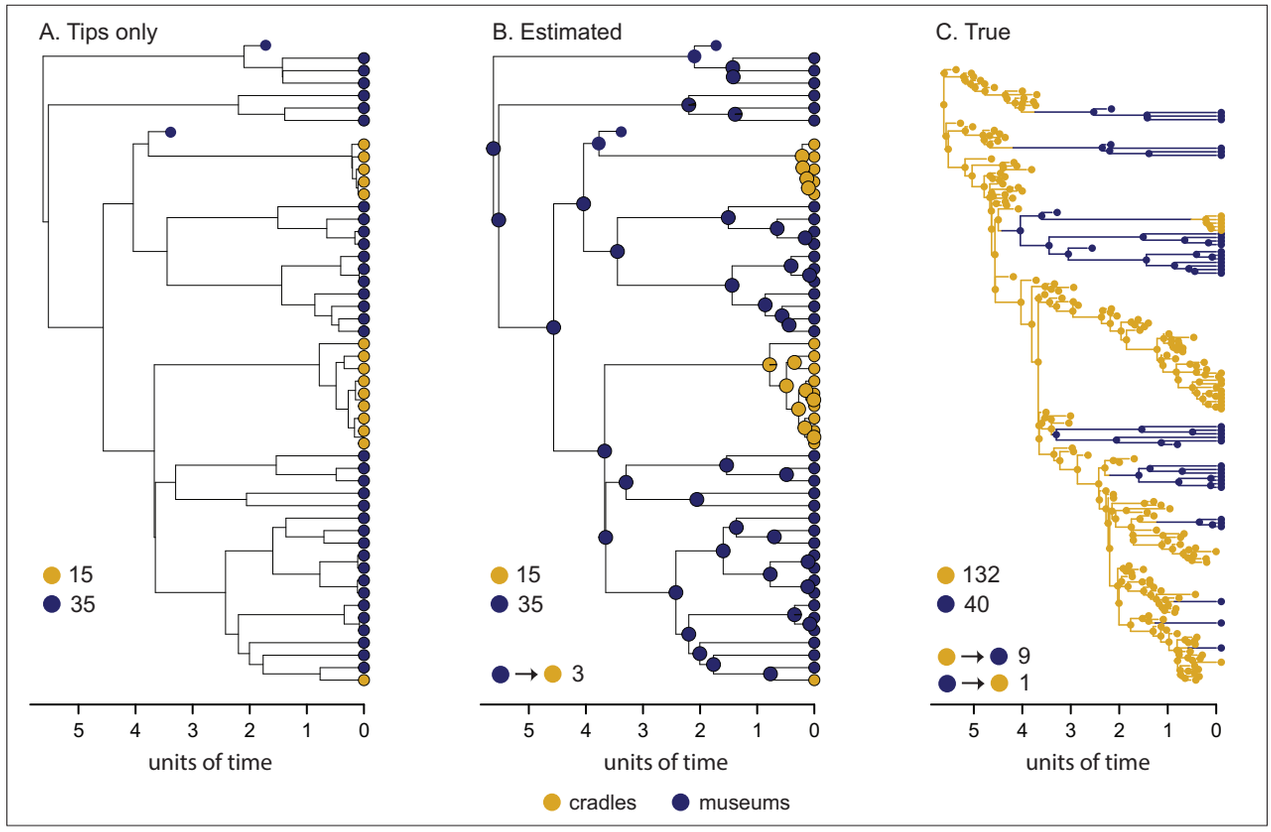

Figure 2: Example of how ancestral state reconstructions may be impacted by asymmetric turnover, transition, and fossil preservation rates. Numbers below each tree represent the number of tips in each state and the number of transitions between states. *A*, Tree of 50 extant and two fossil tips sampled, where the tips were scored as habitats of the type cradle (yellow) 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.

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 10 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.

We hasten to point out that the hypothetical example given 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 conditions of museums. However, this can be challenging to test because of 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 become 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 Cradle and Museum Metaphor Still Useful?

Stebbins's 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 lead to frequent changes, while stable environments preserve what is in 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, we lose the full context and nuances of Stebbins's metaphor.

On the whole, the arguments discussed herein lead us to the unavoidable question, 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 and Vazquez-Dominguez 2008] and "graves" [Rangel et al. 2018]) and conclusions that particular areas serve as both cradles and museums even for the same lineage (e.g., Jablonski et al. 2006; 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's metaphor may have outlived its usefulness, and instead it may be more productive to shift focus toward 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's (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 (e.g., because of 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. New methods that can accommodate this expected correlation using both extant and fossil data are necessary.

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. That does not mean that extant and fossil data have no utility to infer macroevolutionary patterns but rather that multiple lines of evidence should be combined when making inferences about the past.

6. Basal lineages and higher species richness do not indicate centers of origin. The 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's (1974) framing of cradles versus museums was intended to help evolutionary biologists 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's book, there has been a radiation of meanings that is anything but adaptive. It is difficult to properly frame Stebbins's metaphor in modern studies of biogeography and macroevolution; such metaphors are unnecessary replacements for the actual biological processes at play. We therefore discourage continued use of the terms "cradles" and "museums" in the literature, as focusing on the processes rather than the metaphor will advance science further.

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the manuscript. We are particularly grateful to Robert Colwell for sharing, in his review, a personal anecdote about his friendship with Stebbins when both were teaching in Chile in 1973, during a period of great political turmoil in that country. In his words, " 'The Book' (Stebbins, 1974) was of course done by then, but not yet released, and Ledyard was flush with excitement about the ideas in it, including prominently (at least in my memory) cradles and museums. I remember him stressing—with the Andes in constant view—that these were 'places' defined by processes, but places that were mobile with climate and orogeny, [and he] clearly located those processes solidly in the context of the Modern Synthesis." This work was funded by the National Science Foundation (grants DEB-1916558 and DEB-1916539).

Statement of Authorship

All authors were responsible for conceptualization and writing of the article.

Data and Code Availability

No new data or code was produced for this article.

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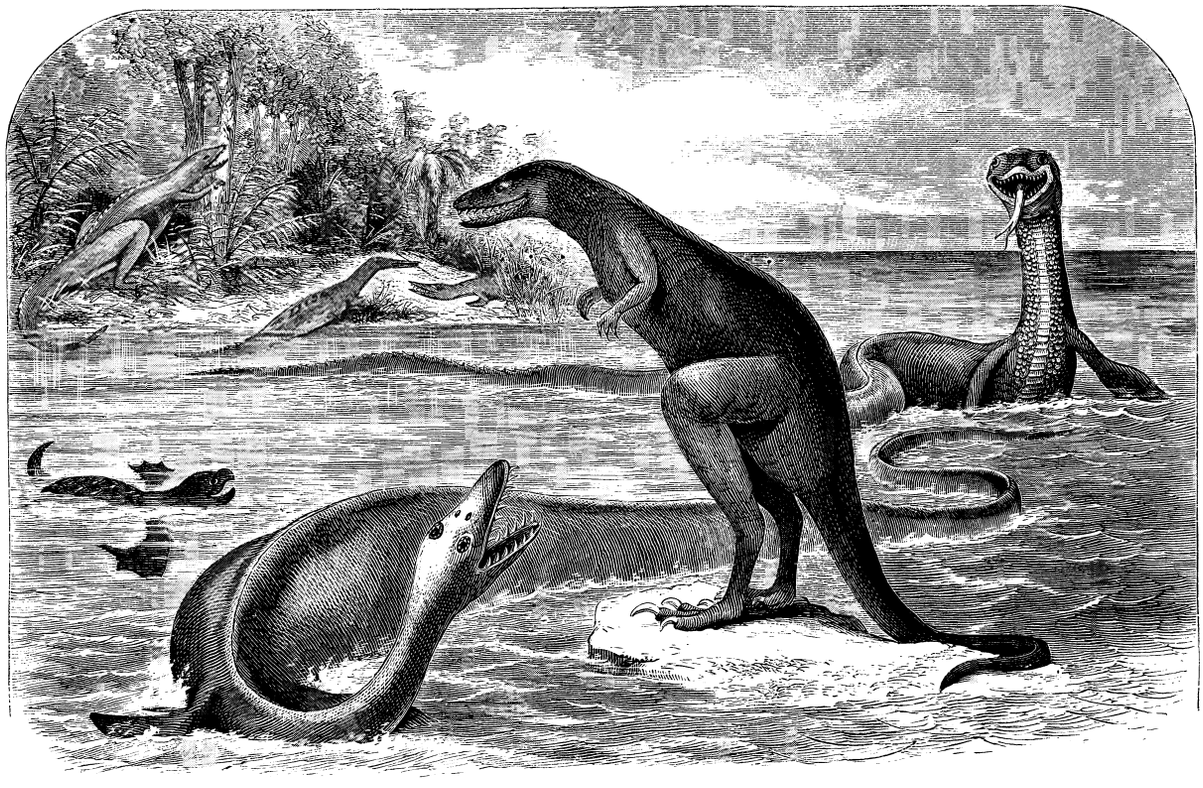

"While grim and monstrous Dinosaurs ranged the forests and flats of the coasts of the Cretaceous sea, and myriads of Gavials basked on the bars and hugged the shores, other races peopled the waters. The gigantic Mosasaurus, the longest of known reptiles, had few rivals in the ocean." From "The Fossil Reptiles of New Jersey (Continued)" by E. D. Cope (*The American Naturalist*, 1869, 3:84–91).