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Opinion

The Evolving Theory of Evolutionary Radiations

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Evolutionary radiations have intrigued biologists for more than 100 years, and our understanding of the patterns and processes associated with these radiations continues to grow and evolve. Recently it has been recognized that there are many different types of evolutionary radiation beyond the well-studied adaptive radiations. We focus here on multifarious types of evolutionary radiations, paying special attention to the abiotic factors that might trigger diversification in clades. We integrate concepts such as exaptation, species selection, coevolution, and the turnover-pulse hypothesis (TPH) into the theoretical framework of evolutionary radiations. We also discuss other phenomena that are related to, but distinct from, evolutionary radiations that have relevance for evolutionary biology.

Evolutionary Radiations – Setting the Stage: More than Merely Adaptive Radiations

Evolutionary radiations, the dramatic proliferation of taxa in a clade, are phenomena that have fascinated biologists for more than a century (e.g., [1–4]). Despite that fascination, early views on evolutionary radiations were not necessarily nuanced, and at one time all evolutionary radiations were regarded as adaptive radiations (e.g., [1–4]). However, such a view is recognized to be no longer valid [5–8]. Further, new approaches and frameworks have extended scientific understanding of adaptive radiations and evolutionary radiations (e.g., [9–11]), and it is now recognized that the diversification events subsumed under these can be complex and multifarious [12,13]. In fact, evolutionary radiations are produced by a range of biotic and abiotic factors, such that the general term ‘adaptive radiation’ is no longer universally regarded as sufficient to illuminate the plethora of processes that may be involved [6,10,12,14]. Ultimately, it has been recognized that some evolutionary radiations are adaptive radiations, but not all are. We aim here to capitalize on newly developed frameworks and approaches by developing a more holistic picture of evolutionary radiations that focuses beyond the purview of adaptive radiations. This picture is focused on distinguishing the patterns reflected in evolutionary radiation from the processes that produced them. It may be the case that evolutionary radiations account for the bulk of animal and plant diversity, but only with an accurate framework can we truly identify the processes that drive evolutionary radiations, and thereby enhance understanding of macroevolution.

Of the various types of evolutionary radiations (Figure 1), adaptive radiations have been the most intensively studied. We follow the framework of Schluter [7], Harmon *et al.* [14], Losos [3], Rundell and Price [5], Givnish *et al.* [4], and others that adaptive radiation involves an accelerating pace of diversification triggered primarily by biotic factors, generally (though not exclusively) involving sympatric speciation, and associated with ecomorphological (see [7,15]) divergence. In some studies adaptive radiations have been invoked even when ecological diversification, adaptation, and sympatric speciation are not documented (see [5,6,13]). However, because they have been subjected to so much analysis, adaptive radiations will not be our focus herein.

Trends

Evolutionary radiations involving diverse clades are of significant relevance to evolutionary biologists; as a subset they include adaptive radiations.

Several processes beyond adaptive radiation can produce highly diverse clades; a broad perspective is necessary to gain insight into the pantheon of evolutionary radiations.

A clade might be diverse because it has experienced extensive opportunities for geographic isolation and allopatric speciation.

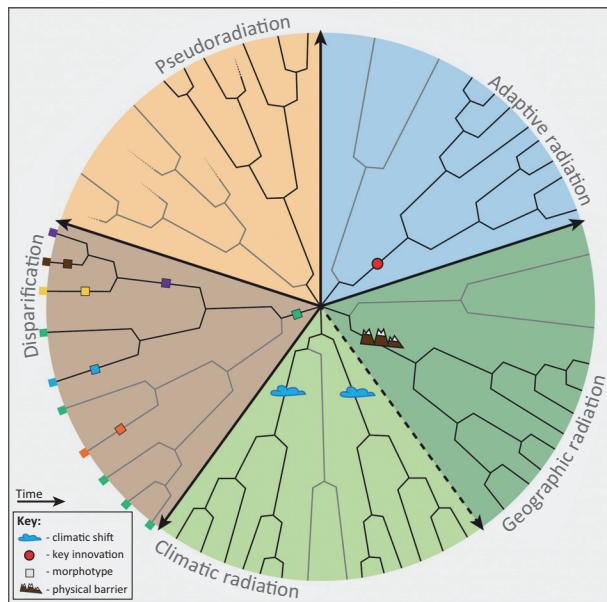
Key concepts from macroevolutionary theory such as species selection and the TPH are relevant.

Diverse clades can arise from increasing speciation rate or declining extinction rate; different processes would be involved.

Episodes of rapid speciation can be decoupled from episodes of pronounced morphological change, and signify different processes.

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Figure 1. Different Types of Evolutionary Radiations and Related Phenomena Including their Triggers and Resulting Patterns. The clades indicated by grey lines are not undergoing radiation. The adaptive radiation shown is triggered by a key innovation indicated by the red circle. An exaptive radiation may lead to a pattern very similar to that of adaptive radiation (Box 2). Different subsets of geographic radiations are shown in shades of green, and are separated by a broken arrow. The geographic radiation is triggered by a physical barrier, whereas the climatic radiation is caused by climatic shifts, but each leads to similar patterns in the affected clades. In the disparification the 'radiating' clade shows a higher diversity in morphospace, with five species and five morphotypes, compared with five species and two morphotypes in the 'non-radiating' clade. In the pseudoradiation the 'radiating' clade shows higher diversity owing to a drop in extinction rate, where extinct lineages are displayed as broken lines.

Glossary

Cospeciation: when the phylogenetic topology of the species in a clade of parasites mirrors the phylogenetic topology of the species of the host clade.

Exaptation: a trait belonging to organisms (or species) that is subjected to natural selection leading to differences in survival or reproduction of those organisms (or species). However, the selective regime that the trait is currently subjected to is different from that experienced when the trait originally evolved.

Lineage turnover: speciation or extinction within a particular clade.

Net diversification rate: the speciation rate of a clade minus its extinction rate.

We concentrate instead on the broader pantheon of evolutionary radiations that extends beyond the realm of adaptive radiations because these have been less frequently considered. In particular, we focus on the patterns and processes underlying geographic radiations [6] – radiations occurring because of increased opportunities for allopatric speciation, the related climatic radiations – those mediated by phenomena such as the TPH [16], disparifications – radiations into new areas of morphospace without concomitant increases in **net diversification rate** (see Glossary), and pseudoradiations – cases where the increasing diversity of a group is caused by a drop in extinction rate rather than by a rise in speciation rate. We will also distinguish between adaptive radiations and exaptive radiations [6,13] (definitions of evolutionary radiations and related phenomena are given in Box 1), including those evolutionary radiations mediated by

Box 1. Definitions of Evolutionary Radiations and Related Phenomena

Various Types of Evolutionary Radiation

Adaptive Radiation. Increase in the rate of speciation within a clade driven primarily by biotic factors (i.e., a 'key innovation', *sensu* [13] and references therein) occurring in sympatry and coupled with ecomorphological divergence (see [15]).

Exaptive Radiation. Increase in the rate of diversification of a clade as a result of a trait becoming advantageous after a change in selective regime (i.e., a radiation caused by exaptation).

Geographic Radiation. Increase in diversification within a clade driven by enhanced opportunities for allopatric speciation in a particular region.

Climatic Radiation. Type of geographic radiation in which allopatric speciation in the region is driven by changes in climate (see Vrba's [16] TPH).

Phenomena Related to but Distinct from Evolutionary Radiations

Disparification. Increase in morphological divergence within a clade without an increase in the clade's rate of diversification (see [47]).

Pseudoradiation. An increase in diversity within a clade caused by a drop in extinction rate rather than by a rise in speciation rate.

species selection, and consider the relationship between coevolutionary phenomena and evolutionary radiations. How abundant these various types of evolutionary radiations are in nature is not yet clear, but a broader focus on them could expand macroevolutionary synthesis.

In the perspective advanced herein, phylogenies [3,11,15] and biogeographic analyses [6,10] are absolutely essential to identify specific types of evolutionary radiations. Without understanding a group's history it is impossible to make inferences about evolutionary processes and accurately calculate speciation and extinction rates. In addition, biogeographic analyses make it possible to evaluate how a group evolves across geographic space and determine the relative amount of allopatric versus sympatric speciation, which, as we describe more fully below, is an important litmus test bearing on the type of evolutionary radiation. Finally, extensive sampling of the diversity of the clade under study is crucial because poor sampling can bias evolutionary rate calculations [17] and, further, accurate biogeographic analyses depend on such sampling [18]. Thus, when possible, one should incorporate both extant and extinct members of a radiating clade, or focus on clades that evolved recently.

Geographic Radiations

Geographic radiations comprise evolutionary radiations where allopatric speciation initiates diversification within the clade; this type of radiation seems to be common [6,10]. Allopatric speciation is accepted to be the prevailing cause of most cladogenesis ([6,10,18–20] and citations therein), and involves populations that become physically isolated due to geologic or climatic factors, and then experience divergence. Physical isolation can arise either when organisms disperse over pre-existing barriers (peripatry) or when they have their ranges divided (vicariance) [18,20]. A plethora of geographic radiations have been uncovered (e.g., [8,20–24]), and most of these were cradled in geographically complex regions such as mountain ranges, island chains, or places subjected to prolonged bouts of oscillating environmental change. Indeed, it seems that evolutionary radiations are especially likely to occur in such regions [13] not only because of the importance of allopatric speciation but also because such regions provide abundant opportunities for it to occur. Further, this has led to the recognition that it may often be the geographic milieu of a group that stimulates an evolutionary radiation.

Apposite here, a geographic driver of diversification has been found in some radiations traditionally treated as adaptive radiations: for instance, African cichlids [25] and Galapagos finches [26,27]. This could mean that, in specific instances, geographic radiations were misdiagnosed as adaptive radiations, or that factors associated with geographic radiations and adaptive radiations operate synergistically. Notably, Losos and Ricklefs [27], and Rundell and Price [5] have nicely documented instances of the latter. The more evolutionary radiations are studied the more apparent it becomes that they could involve multifactorial biotic and abiotic processes [6,11], and it is crucial to consider the factors that both initiate and sustain an evolutionary radiation. More candidate geographic radiations may be found in examples traditionally treated as adaptive radiations when it can be shown that many species within a radiating clade possess allopatric distributions [28].

There can in fact be more than one type of geographic radiation. For instance, sometimes it may be possible to identify whether geologic or climatic change is causing the geographic isolation. Consider climatic radiations and Vrba's [16] TPH (discussed in more detail below). These involve climatic changes that cause recurrent geographic isolation followed by range expansion, driving repeated and oscillating episodes of differentiation that can lead to evolutionary radiation. Coevolving systems of taxa that are undergoing evolutionary radiations also may show much in common with geographic radiations (again discussed more fully below), given that coevolutionary and biogeographic studies have much in common when it comes to theory and

methodology [18,20]. Furthermore, initiation and cessation of geographic isolation plays an important role in the differentiation of populations of coevolving species [29].

Other Evolutionary Radiations Related to Geographic Radiations

Climatic Radiations

Climatic radiations comprise a type of evolutionary radiation driven by large-scale climatic shifts. Vrba [16] developed the TPH to explain this type of radiation. The TPH predicts that a significant component of **lineage turnover** is not randomly distributed throughout the history of life, but instead has occurred in pulses correlated with climate change. Climate change can be caused by geologic changes as well as by Milankovitch cycles. The pulses arise because climate changes cause shifts in species' geographic ranges. These can further fragment populations of several species when the populations track their preferred habitats, as in the case of African bovids [16]. The net effect can be to create climate-mediated geographic barriers between different populations of species, leading to extinction, and most importantly *vis à vis* our discussion here, speciation by geographic isolation (in this case vicariance) [30]. At a later point, as climatic conditions ameliorate, the climate-mediated geographic barriers fall, the newly formed species can expand their geographic ranges, and the cycle can start all over again [16].

The TPH and associated climatic radiations are significant because they extend the geographic radiation concept from single to multiple clades [6]. In particular, patterns of diversification in several different clades could be explained by a commonly experienced episode in Earth history. With both fossil and extant taxa it is not always easy to determine the precise role that climate change plays in motivating the timing of geographic isolation and subsequent divergence [31], but climatic radiations appear to comprise a legitimate type of geographic radiation worthy of further analysis and study.

Coevolution/Cospeciation

Coevolving systems are complex and, depending on the nature of the interaction between the species involved, they can be influenced by myriad evolutionary forces. Given this complexity, we concentrate here on only one type: cospeciating hosts and their parasites (although see [32] on whether **cospeciation** necessarily indicates coevolution). Because of the importance of allopatric speciation in general, it follows that speciation within coevolving systems might also involve allopatry. This is especially true when a host speciates or a parasite switches host species, given that what happens to the parasite after either of these events is equivalent to geographic isolation [20,33,34]. Further, it has been shown that the geographic structure of populations plays an important role in coevolution [29]. Thus, when considering coevolving/cospeciating host-parasite clades in the context of evolutionary radiations, it is useful to consider their commonalities with geographic radiations. A potential example comes from the highly diverse monogenean fish parasite *Gyrodactylus*. Much of its diversity has been attributed to host-switch events because bursts of speciation seem to follow each host-switch [35]. Notably, host switching can lead to genetic isolation of populations because the reproductive strategy of *Gyrodactylus* is mainly asexual and parthenogenetic [36]. Pinning down the causes of evolutionary radiations is more challenging when parasites have multiple host species because documenting a geographic radiation entails demonstration of cospeciation across several clades. These types of systems at present are more recalcitrant to theoretical and analytical treatment, and it is clear that much remains to be learned about the relationship between evolutionary radiations and coevolution.

Exaptive Radiations

Exaptations are traits that have been co-opted for a utility distinct from the selective regime under which they originated [37], and they likely play an important role in evolutionary radiations. For instance, traits that influenced the ability of a clade to diversify into varied environments may

have originally been shaped by a different selective force. Research into the nature of so-called ‘key innovations’ has revealed that they are often highly complex and are acquired in a series of evolutionary steps that each may have contributed to diversification [38]. This suggests an exaptive dynamic, because the utility and function of these traits are likely to change over time. Lieberman [6] suggested that evolutionary radiations in which an exaptation plays a role in increasing speciation rate would be better described as ‘exaptive radiations’ because it is often difficult to determine whether a trait is exaptive or adaptive, and some previously identified adaptive radiations may in fact be exaptive radiations. In their examination of factors influencing evolutionary radiations in angiosperms, Bouchenak-Khelladi *et al.* [11] found that many radiations were associated with physiological characters that evolved before the radiations occurred, which suggests that exaptation may be a relatively prevalent dynamic in shaping evolutionary radiations. This is especially likely when there are increases in speciation rate associated with the acquisition of traits emergent at the group or species level, such as dispersal ability, population structure, or group variation [39,40]. These traits arise as side consequences of organismal features that might be adaptations at the organismal level, but, in the context of clade diversification, can be described as exaptations at the species level [41]. The prevalence and effect of species-selection has been much debated [42], and considering the nature of this debate extends beyond the purview of this paper. However, it has been recognized that species-level traits influence diversification rate [41–43]. This suggests that exaptive radiations could be common phenomena (Box 2).

Disparifications

A key facet of many studies of adaptive radiations is the notion that lineages not only increase in species richness but also in morphological disparity. This has been viewed as indicative of ecomorphological differentiation in response to adaptation [7,9,44]. Researchers (e.g., [45,46]) have highlighted the distinction between morphological disparity and species richness, and quantitative estimates of speciation rates and rates of character evolution can be used to study diversification and increases in disparity [47,48]. Of course, clades can show an increase in species diversity without a concomitant increase in disparity (and thus would not constitute examples of adaptive radiations) [46,49]; similarly, clades could undergo an increase in morphological disparity, in effect a morphospace radiation, without a proliferation in species diversity. To distinguish the latter from evolutionary radiations, we suggest the term ‘disparification’ from Ackerly [47] (see also [13]). Disparifications reflect an increase in the morphological distance between species in a clade over the course of time. They can arise not only via adaptation but also as a result of clade-level differences in variability [50], the simple accumulation of variation through time in older clades [51], and sampling error [52]. Their existence reflects just one aspect of the many interesting phenomena beyond the purview of evolutionary radiations.

Pseudoradiations

The focus of most research on evolutionary radiations has been in ascertaining what caused the increased speciation rates within the clade of interest that led to its enhanced diversity level. A

Box 2. Adaptive Radiation versus Exaptive Radiation versus Species Selection

To be considered adaptive, a radiation must be triggered by an increase in the rate of speciation driven primarily by biotic factors, often in the form of adaptations or ‘key innovations’ (*sensu* [13] and references therein) associated with both the ecological and morphological roles of the individuals (i.e., members of a species) involved. By contrast, an exaptive radiation is an increase in the rate of diversification within a clade driven by a previously acquired trait becoming advantageous under a new selective regime. Clades undergoing adaptive radiation diversify within an unchanged selective regime, whereas clades experiencing exaptive radiation only begin to diversify once a new selective regime is established. Species selection is a subset of exaptive radiation in which an exaptation nascent at the species-level promotes diversification of a clade (see [41–43] for further discussion of species selection).

group might be diverse, however, not solely because of an elevation in speciation rate, but instead because of a decline in extinction rate. Thus, we are led to the somewhat paradoxical perspective that evolutionary radiations in a clade, if inferred based on a clade's extensive diversity relative to other clades, might actually be caused by something very different; traditionally less emphasis has been placed on the role declining extinction rates might play in leading to enhanced clade diversity, but we suspect these could be an important phenomenon (see also [10]). Such clades with normal speciation rates that accumulate richness owing to a decline in extinction rate we treat as 'false' or 'pseudo' radiations, hereafter pseudoradiations. Significantly, pseudoradiations will likely have different triggers than evolutionary radiations.

It has been shown that, in some evolutionary radiations, there can be a slowdown of speciation rate through time, but not all clades exhibit diversity-dependent decline or saturation [53,54]. Such groups may be unconstrained by niche filling, and their richness could be unbound within the biotic or abiotic space of their range [55].

A potential example of a pseudoradiation comes from the study by Smith and Marcot [56] of fossil beetles, which shows that the dramatic increase in the diversity of this group through time could be attributable to a decline in extinction rate (rather than an increase in speciation rate) (by contrast, other insect orders appear to show the more traditional pattern of prodigious diversity associated with elevated speciation rate [57]). Another potential example of an ongoing pseudoradiation may come from the South American ovenbirds (Furnariidae). Within this clade, speciation rates have declined and morphological disparity has become constrained [53,58]. Despite this, ovenbird diversity has continued to increase, suggesting that a decline in extinction rate continues to propel the diversity increase. This might further mean that previously studied ecological factors may not be limiting radiations in continental tropical systems [58], and clades that remain unsaturated at the end of an evolutionary radiation may experience continued diversity increases via reduced extinction rates, and thus also undergo pseudoradiation.

The phenomenon of pseudoradiation may actually be very important if we consider the fact that many instances of evolutionary radiation are explained by the acquisition of a key anatomical character. Further, in such instances the acquisition of the character is inferred to provide organisms with a competitive advantage and lead to their experiencing reduced selection pressures. Although conceivably reduced selection pressures might increase speciation rates, theoretically it seems easier to conceive of such reduced selection pressures as leading to declining extinction rates instead. Notably, if the decline in extinction rate were to be sustained over long intervals of time, the net effect would be a clade that shows a pronounced diversity increase (this has been offered as an explanation for heightened tropical diversity [59]). More study of extinction rates within clades is needed to understand how common pseudoradiations are, but the fact that elevated clade diversity is often associated with the acquisition of organismal characters that enhance organismal fitness suggests they could be commonplace.

Concluding Remarks

Adaptive radiations are an important phenomenon linking ecology and evolution [3,9,10,26]. They have been invoked for over a century, and they still inspire debate. Perhaps adaptive radiations may have been invoked mistakenly in some cases and, further, they have not always been clearly differentiated from other types of evolutionary radiations. Understanding the conceptual foundation of evolutionary radiations leads to a greater appreciation of the range of potential triggers of diversification, and of the roles that multifarious processes play in shaping evolutionary history. To ascertain what type of evolutionary radiation a clade embodies there are several desiderata, including a time-calibrated phylogeny having accurate distributional, morphological, and ecological data for each species, together with estimates of speciation and extinction rates across the branches of the tree (see Outstanding Questions). Moreover, the

Outstanding Questions

How common are the various types of evolutionary radiation? In particular, are adaptive radiations relatively rare and geographic radiations far more pervasive?

How often have climate-mediated turn-over pulses generated multiple evolutionary radiations in the same region?

Are many adaptive radiations in fact exaptive radiations?

How frequently are evolutionary radiations caused by species selection?

Are pseudoradiations rare or common? In particular, do highly diverse clades typically arise because of increased speciation rates or decreased extinction rates?

In general, are evolutionary radiations primarily motivated by biotic factors (such as the propensity of a group to speciate) or abiotic factors (such as a group's presence in a geologically complex or climatically diverse region)?

How often do cospeciating systems produce evolutionary radiations? In such systems is the phenomenon involved generally analogous to a geographic radiation?

What are the factors driving disparifications, and how do these differ from evolutionary radiations?

In any complex system, including a clade that has undergone an evolutionary radiation, the factors involved are likely to be multifactorial. How easy will it truly be to pin down specific causes of evolutionary radiations, or to ascribe in a quantitative framework the relative contributions of different evolutionary processes?

How does the species concept used in a study impact the interpretation of an evolutionary radiation?

What is the most appropriate way to quantify physical isolation among closely related species to best ascertain the relative contributions of allopatric and sympatric speciation to an evolutionary radiation?

clade in question must have been comprehensively sampled. However, even then determining the specific type of evolutionary radiation present and the triggers involved may be tricky. This is because the more evolutionary radiations are studied the more apparent it becomes they can be caused by multifactorial biotic and abiotic processes [6,10]. Moreover, the factors that initiate evolutionary radiations can be different from those that sustain them [11]. Ultimately, the diverse variety of evolutionary radiations, in combination with the multifactorial processes that may cause any one radiation, makes research into evolutionary radiations more complicated, but also more exciting. Given the importance of the topic, we suspect that over the coming years there will be numerous advances in understanding evolutionary radiations, and greater appreciation of the myriad processes involved in precipitating them.

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