

# Thinking in continua: beyond the “adaptive radiation” metaphor

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**“Adaptive radiation” is an evocative metaphor for explosive evolutionary divergence, which for over 100 years has given a powerful heuristic to countless scientists working on all types of organisms at all phylogenetic levels. However, success has come at the price of making “adaptive radiation” so vague that it can no longer reflect the detailed results yielded by powerful new phylogeny-based techniques that quantify continuous adaptive radiation variables such as speciation rate, phylogenetic tree shape, and morphological diversity. Attempts to shoehorn the results of these techniques into categorical “adaptive radiation: yes/no” schemes lead to reification, in which arbitrary quantitative thresholds are regarded as real. Our account of the life cycle of metaphors in science suggests that it is time to exchange the spent metaphor for new concepts that better represent the full range of diversity, disparity, and speciation rate across all of life.**

**Keywords:** adaptive radiation; disparity; diversity; metaphor; reification

## Introduction

“Adaptive radiation” is a member of evolutionary biology’s pantheon of key terms. Although no consensus definition exists, biologists use the term to express all or part of the idea of the rapid evolution of many species into a wide array of ecological and morphological types, all driven by ecological opportunity. The term has been in use for over a hundred years and now stands at the height of its popularity. Recent authors such as Givnish<sup>(1)</sup> and Roff,<sup>(2)</sup> respectively declare adaptive radiation as “one of the most important processes bridging ecology and evolution” (p. 1), and “a fundamental building block of the process of speciation” (p. 519). Schluter<sup>(3)</sup> went so far as to single out the account of adaptive radiation developed in the 1940s and 1950s as “the greatest single application of the then-new modern synthesis” (p. vii). In addition to driving cutting edge research, “adaptive

radiations” cavort across the pages of introductory textbooks,<sup>(4)</sup> and the term has even been co-opted by other fields, e.g., by philosophers discussing the adaptive radiation of ideas.<sup>(5)</sup>

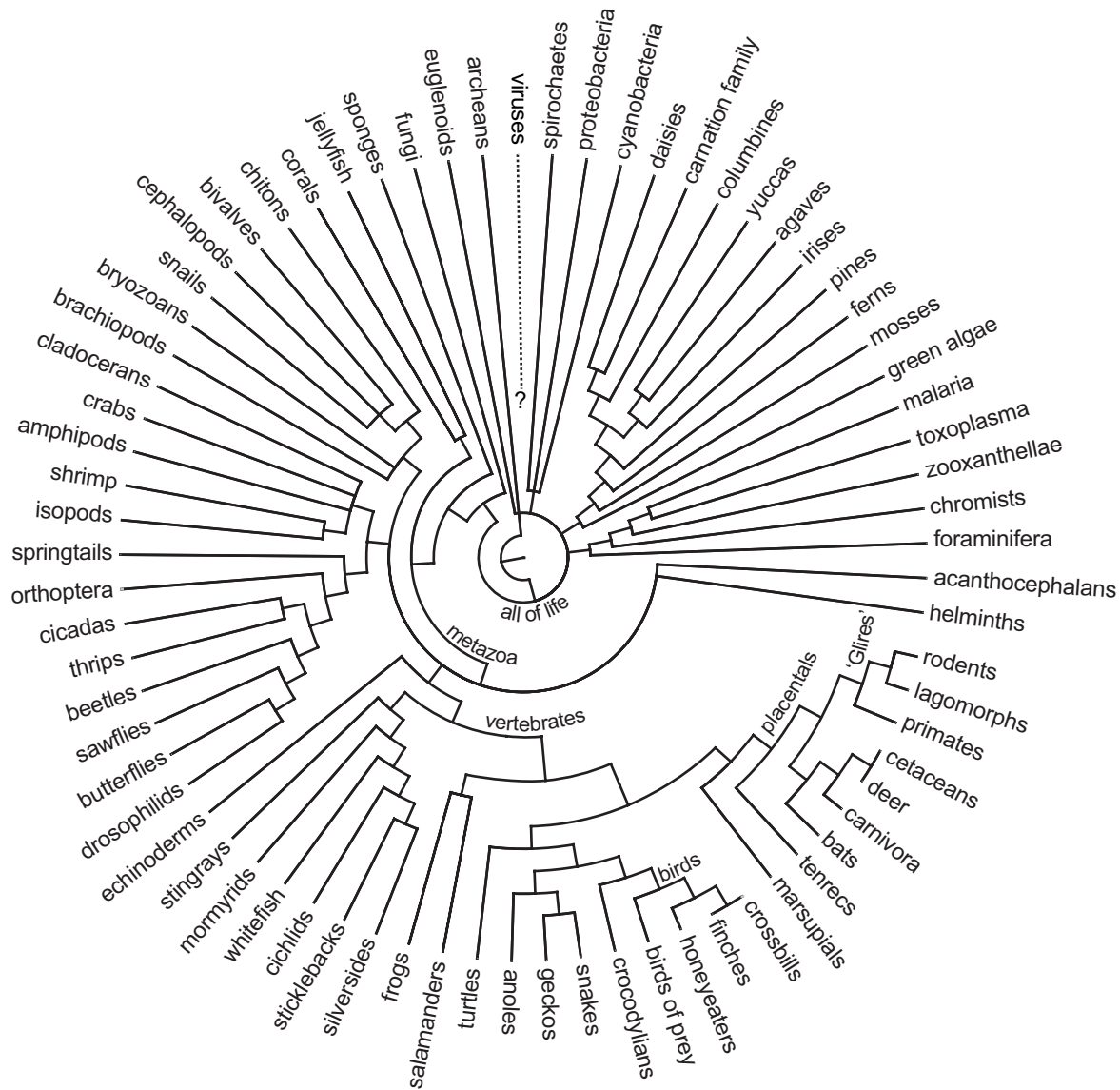
Given the importance assigned to adaptive radiation, it is no wonder that it is so frequently invoked (Fig. 1). However, we argue that the time is ripe for evolutionary biologists to discard the term. Recent years have seen an explosion of phylogeny-based techniques that quantify attributes such as speciation rate, phylogenetic tree shape, and morphological diversity, the very variables comprised by definitions of adaptive radiation. We suggest that the ability to quantify these variables renders classifying a clade as an adaptive radiation or not unnecessary for any study of the evolutionary process. Moreover, we worry that efforts to quantify the status of clades as adaptive radiations actually lead to a dangerous fallacy in which imaginary segments of nature are treated as though they were real. We advocate discarding adaptive radiation in favor of thinking in terms of continua, such as speciation rate in its full arc from the most rapid rates of divergence to the slowest, or morphological diversity in the most varied groups to the most uniform. We detail these issues below, explaining the success and predicting the decline of adaptive radiation as one of the natural fates of metaphors in science: evocative if vague metaphors often power the early stages of research programs before being superseded and discarded. We begin by asking what adaptive radiation is and what it is not.

## Lack of consensus and the variables that make up adaptive radiation

Despite the importance of the term, there is no consensus regarding what adaptive radiation is. A century ago the paleontologist Osborn<sup>(6,7)</sup> coined the term as a “law” leading to repeated arrays of similar morphological types in different animal groups. In his formulations of the 1940s and 1950s, Simpson,<sup>(8)</sup> to whom the current sense of the term is often attributed, downplayed Osborn’s law-like overtones, but emphasized the rapid proliferation of species into a multitude of morphological and ecological types. The many definitions of adaptive radiation that have been proposed since differ in

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**Figure 1.** The 78 “adaptive radiations” reflected in this tree come from the recent phylogenetic literature, and show that “adaptive radiation” is a metaphor that has given a powerful heuristic to biologists working on all groups of organisms at all levels of the phylogenetic hierarchy. More importantly, it unites the nearly 300 authors of these studies with a common theme. A version of this figure with references is given in the supplementary information.

the relative importance they assign to variables such as speciation rate, species number, and morphological diversity.<sup>(1)</sup> For example, many authors regard rapid “rate of species divergence” as a primary factor in their definitions, with adaptive radiations being nearly simultaneous “star divergences” of many species.<sup>(8–13)</sup> Exemplifying the lack of consensus on all aspects of the term, definitions of adaptive radiation that include speciation rate are defended by their proponents while being emphatically criticized by detractors who assert that the evolution of ecological divergence is driven by natural selection whether fast or slow, making rate an irrelevant variable.<sup>(1,14)</sup>

There is similar disagreement regarding the significance of high “diversity,” *i.e.*, of species number, in definitions of adaptive radiation. One common view is that an adaptive radiation is characterized by having many species.<sup>(3,8,15)</sup> With a distinct view, Givnish<sup>(1)</sup> notes that “In most instances, adaptive radiation will surely be accompanied by an increase in species number within a lineage. But including such an increase in the definition of adaptive radiation would interfere with testing the very idea that radiation [defined as the evolution of strong ecological differences] should increase speciation.” (p. 10). Similarly, Jackman *et al.*<sup>(16)</sup> argue that “even clades with relatively few species can constitute an

adaptive radiation” (p. 535) given sufficient ecological differences between species.

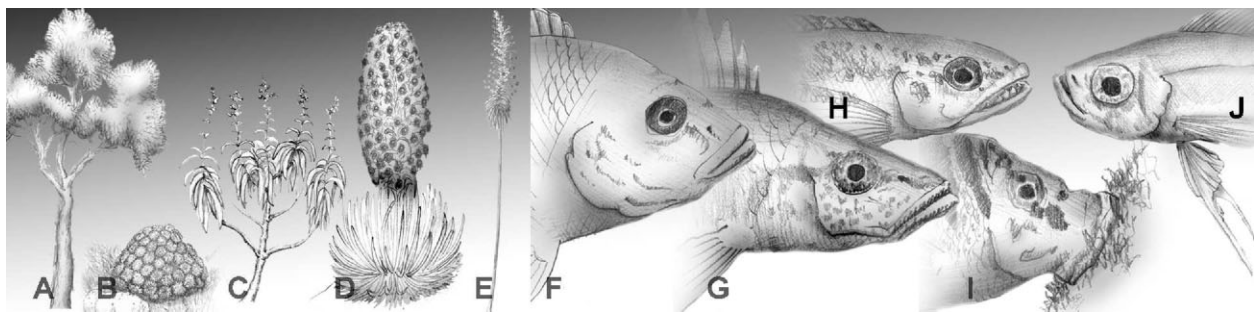
References to “ecological differences” in discussions of adaptive radiation allude to the idea that the species of an adaptive radiation should show high “disparity,” *i.e.*, a wide range in morphology, behavior, or ecological roles,<sup>(1,3,8,17–20)</sup> with the range in feeding strategies of the Rift Lake cichlids or the array of habits of the silverswords being prime examples (Fig. 2). Not all definitions emphasize disparity, but apparently no authors argue explicitly against it, the way some do against definitions based on diversity or speciation rate. Sander-son<sup>(15)</sup> does, however, balk at definitions based only on disparity, saying that “A clade of one species cannot show high character diversity – nor can a clade of two species,” and notes that “The only way this view [adaptive radiation as disparity] makes any sense is if there is some threshold amount of divergence required for any clade to be considered an adaptive radiation. Above that threshold (and hence over many orders of magnitude above it) is an adaptive radiation, but below it is not.” (p. 1652). Whether a definition is based solely or partially on disparity, ecological diversity is usually viewed as reflecting a fit between organismal form and function.

The fit between form and function can be called “adaptedness,” the notion that disparity is the result of adaptive divergence. Although it would seem implicit in the very name, only a few definitions of adaptive radiation actually involve adaptedness. Adaptedness in adaptive radiation studies is usually expressed as a statistical relationship between organismal attributes and environmental variables.<sup>(3,21–23)</sup> For example, Sabat *et al.*<sup>(24)</sup> studied renal traits in the context of diet in *Cinclodes*, the ovenbirds, whose species span high-salt marine and low-salt terrestrial diets. The authors found that various measures of the ability of

ovenbird kidneys to process salt were positively correlated with the proportion of marine organisms in the birds’ diets. Sabat *et al.* interpreted this pattern as congruent with their prediction that the diversification of the ovenbirds into an array of habitats should be reflected in adaptive differences in osmoregulatory function. As is the case for diversity, speciation rate, and disparity, there is no uniformity in how or even whether adaptiveness is to be included in studies of adaptive radiation.

Because there is no agreement regarding the definition of the term, it is impossible to tell what an author means when he or she says that a given clade represents an adaptive radiation. For example, there is no consensus regarding the importance of speciation rate in definitions of adaptive radiation. As a result, when biologists have wished to convey something about rapid speciation rate, they have needed such descriptors as “rapidly diverged” or “explosive” adaptive radiations (Table 1). When authors have wished to emphasize that the morphological diversity in their clade of interest is predicted by environmental variables, they have needed to append such descriptors as “adaptive radiation driven by ecology”. The host of qualifications of adaptive radiation (Table 1) indicates that the term is insufficient to communicate much of anything specific regarding speciation rate, species number, morphological diversity, or adaptedness.

As if it were not enough that the term is vague, many have found the “adaptive radiation *versus* everything else” dichotomy inadequate to catalogue all of the patterns that they would like to describe. Givnish<sup>(1)</sup> pinpointed “adaptive convergence” as the opposite of adaptive radiation, whereas others have identified “adaptive” and “non-adaptive” (or “fugitive”) radiations as extremes, with non-adaptive radiations being groups with many ecologically similar species that have diverged in allopatry under similar environmental



**Figure 2.** Paragons of adaptive radiation: Hawaiian silverswords and African Rift Lake cichlids. **A–E:** The silversword alliance spans a remarkable array of habits. The rainforest tree *Dubautia reticulata* grows more than 6 m tall (**A**), whereas *D. waialealae* is a highland bog cushion plant no taller than 50 cm (**B**). Other habits include the shrubby *D. microcephala* (**C**), the century-plant like *Argyroxiphium sandwicense*, whose white leaves on otherwise bare volcano summits are a Hawaiian icon (**D**), and the strange, unbranched “rosette tree” *Wilkesia gymnoxiphium* (**E**), which can grow to over 5 m tall. (**F–J**) The Rift Lake cichlids differ, among other things, in their feeding preferences. (**F**) Many, such as *Haplochromis*, gobble other fish, while members of *Didimochromis* (**G**) prefer shrimp. *Perissodus* (**H**) use recurved teeth to rip the scales from their lake fellows, whereas *Petrochromis* (**I**) rasp algae from rocks, and *Haplotaxodon* (**J**) seine plankton from the water column. Silverswords and cichlids have caught the attention of biologists, who have singled them out with the name adaptive radiation, but it is not clear how to draw the line between such clades and the rest of life, or even whether such comparisons between clades are valid.

**Table 1.** With the growth of quantitative tools for studying speciation rate, diversity, disparity, and adaptedness, scientists increasingly find it necessary to qualify “adaptive radiation” to be able to express the details of their clade of interest, as these phrases from the recent literature illustrate. A fully referenced version of this table is available in the supplementary material

Category of descriptor	Descriptive phrase	
Speciation rate	Explosive adaptive radiation	
	Fast adaptive radiation	
	Rapid adaptive radiation	
Diversity or disparity	Diverse adaptive radiation	
	Adaptive radiation driven by ecology	
Adaptiveness	Truly adaptive radiation	
	Extensive adaptive radiation	
Degree: large	Clear adaptive radiation	
	Considerable adaptive radiation	
	Extraordinary amount	
	Extreme adaptive radiation	
	Great adaptive radiation	
	Huge adaptive radiation	
	Large adaptive radiation	
	Large-scale adaptive radiation	
	Major adaptive radiation	
	Massive adaptive radiation	
	Substantial adaptive radiation	
	Successful adaptive radiation	
	Widest adaptive radiation	
	Degree: small	Limited adaptive radiation
		Little adaptive radiation
“Mini” adaptive radiation		
Minor adaptive radiation		
Modest adaptive radiation		
Clades that do not meet all the criteria of a favored definition	Incipient adaptive radiation	
	Initial phase of an adaptive radiation	
	Not yet an adaptive radiation	
	Young adaptive radiation	

conditions.<sup>(25–27)</sup> However, even the adaptive-nonadaptive radiation distinction does not encompass all possible phenomena. Various authors<sup>(16,20,28)</sup> have described the situation of a clade of high morphological disparity, as in many definitions of adaptive radiation, but with few instead of many species, such as Darwin’s finches or the Australian pygopodid lizards. Losos and Miles<sup>(20)</sup> have even suggested, presciently in our view, that it is impossible to compare groups as diverse as silverswords, cichlids, and finches because their biology is so divergent. However, when we assert that the cichlids are an adaptive radiation but the lungfishes are not, we are making exactly this sort of comparison. Losos and Miles suggested that assertions of adaptive radiation can only be made in cases in which one clade is significantly more disparate than its sister taxon, a major realignment of the concept that if followed would likely disqualify many adaptive radiations in the literature. These controversies and qualifications illustrate that, not only has no consensus emerged regarding what an

adaptive radiation is, but it is also not clear what the alternatives to adaptive radiation are.

## Why is there no consensus? Reification and the dark side of adaptive radiation

It is easy to say that the noonday sun is bright, but as daylight wanes, no threshold divides light from dark. In the same way, the variables that describe adaptive radiation are continuous, not categorical as distinctions of the adaptive-nonadaptive type might imply. Instead, definitions of adaptive radiation base themselves on arbitrary thresholds along smooth continua (Box 1). For example, phylogenetic trees describe a continuous arc from balanced, *i.e.*, divided into two clades of equal size, to highly imbalanced trees, in which a single species may be sister to the rest of the clade. Guyer and Slowinski<sup>(29)</sup> regarded trees that “had  $\geq 90\%$  of the taxa along the more diverse branch of the basal dichotomy” as potentially diagnostic of adaptive radiation. They go on to note that “This arbitrary cutoff was chosen because it (1) delimits a group of phylogenies in which most speciation has occurred along one basal branch and not its sister-taxon branch, and (2) provides expected cell frequencies of acceptable size for contingency table analyses.” (p. 258). The authors referred to this cutoff as arbitrary to highlight that nothing dictates that 90% is any more biologically significant than 91 or 89% or any other figure. Instead, the thresholds defining adaptive radiation may be placed anywhere. A further example of the dilemma of where to place thresholds is to ask how many species are enough for a clade to qualify as an adaptive radiation, with a glance at the literature showing that an adaptive radiation can be anything from a single species to the largest clade imaginable (Table 2). If definitions of adaptive radiation are based on arbitrary divisions of biological continua, then the term can only correspond to an arbitrary slice of nature, not to a biologically distinct phenomenon (Box 1).

The idea that adaptive radiation is simply part of a continuum is hardly new. Simpson,<sup>(8)</sup> routinely cited as the progenitor of the current conception of adaptive radiation, noted that “So far as adaptive radiation can be distinguished from progressive occupation of numerous zones, a phenomenon with which it intergrades, the distinction is that adaptive radiation strictly speaking refers to more or less simultaneous divergence of numerous lines all from much the same ancestral adaptive type into different, also diverging adaptive zones. Progressive occupation of such zones is not simultaneous and usually involves in any one period of time the change of only one or a few lines from one zone to another, with each transition involving a distinctly different ancestral type. Theoretically, at least, the whole of the diversity of life is explicable by these two not sharply distinct processes” (pp. 223–224). Similarly, Carlquist<sup>(19)</sup> deemed adaptive

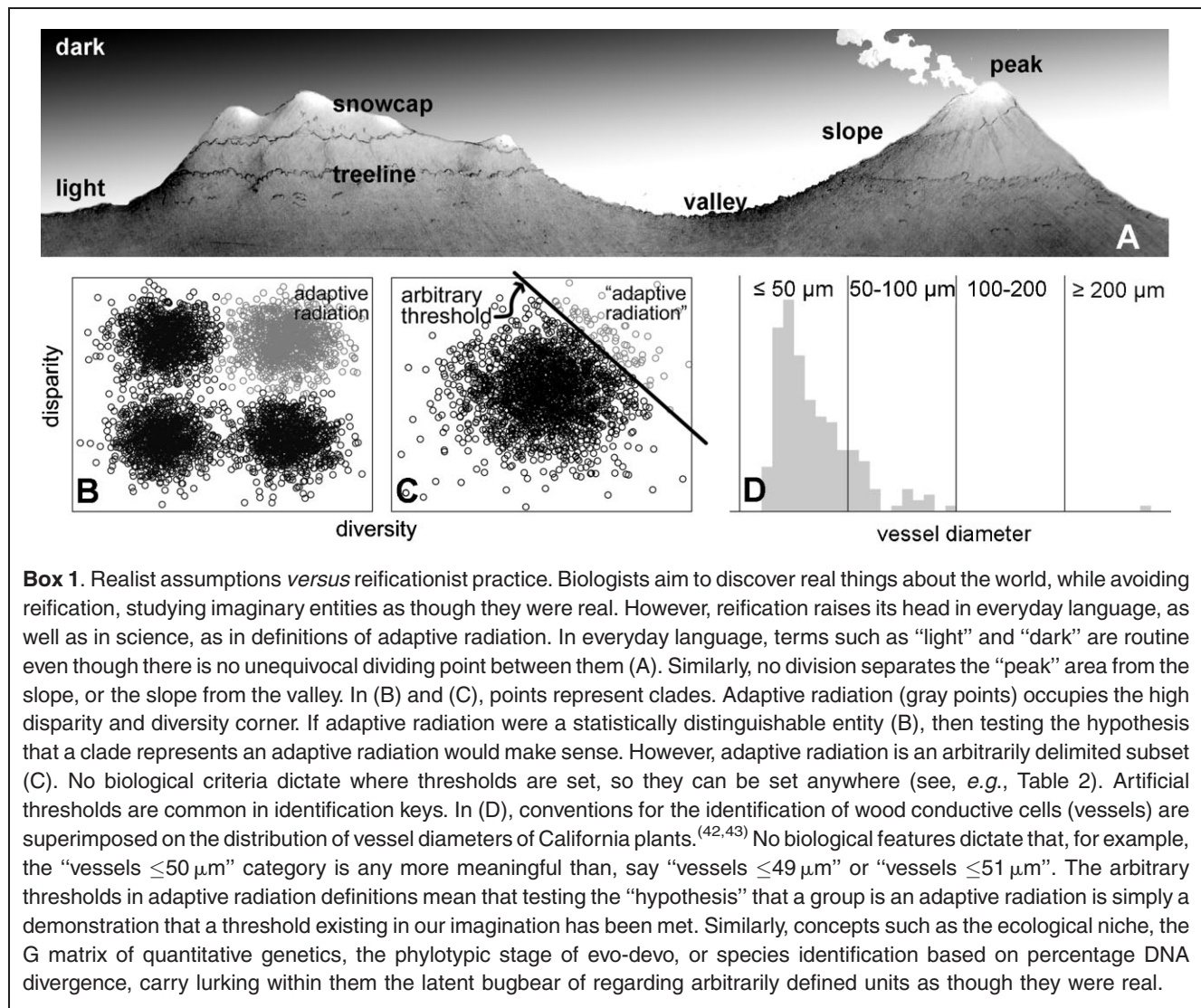


radiation a “flexible concept” for which “precision is virtually impossible;” as a result the concept should be used to “call attention to pertinent factors and results, not quantify them” (p. 116). The reaction of biologists in general, however, seems to be reflected by Gittenberger’s<sup>(12)</sup> statement that “...the epithets adaptive and non-adaptive are available and useful, emphasizing different aspects of the evolutionary process. Intermediate situations occur, but that should not prevent the use of different terms here.” (p. 136). We take issue with this last assertion.

Biologists generally aim for hypotheses that describe features of nature that exist independently of our imagination. However, the last 10 years have seen a surge in studies that violate this tenet in the form of “tests” of adaptive radiation, an approach that veers squarely into a treacherous fallacy.<sup>(3,11–14,23,24,30–37)</sup> For example, Roy *et al.*<sup>(38)</sup> tested the

“hypothesis of adaptive radiation” in four distantly related genera of fish from Lake Matano on Sulawesi. They found that a group of silversides in the lake met the definition of adaptive radiation devised by Schluter,<sup>(3)</sup> which includes the criterion of “rapid speciation.” Deciding what is “rapid” is akin to separating light from dark or the peak of a mountain from its slope (Box 1). Testing such arbitrary thresholds as though they were hypotheses embodies the reification fallacy, in which a concept that exists only in the mind is treated as having real existence in nature.<sup>(39–41)</sup>

Adaptive radiation studies are at risk of reification because of the way that they use statistical thresholds. Instead of using statistical techniques to discover and describe entities in nature, adaptive radiation studies use statistical thresholds to *define* what will be considered an adaptive radiation and what will not. For example, we can test the notion that humans



**Table 2.** Because the thresholds in definitions of adaptive radiation are arbitrary they can and are placed anywhere; e.g., no biological cutoff dictates how many species are necessary for a taxon to be considered an adaptive radiation, and everything from a single species to all of life have been discussed in the context of adaptive radiation. A fully referenced version of this table is available in the supplementary material

Taxon	Species
A highly sexually dimorphic woodpecker species	1
Trophic specialists within Cocos island finch	1
Cocos island <i>Wendilgarda</i> spider with numerous web building behaviors	1
<i>Polygonum arvense</i> , an herb with various forms	1
Glacial lake whitefish	2
Sticklebacks	2
Guadalupe Island <i>Deinandra</i> shrubs	3
African tree groundrels	11
Darwin's finches	14
Ichthyomyine rodents	14
Hawaiian silverswords	28
Pygopodid lizards	35
<i>Yucca</i> moths	30–40
Cats	37
Columbines	60–70
Marsupials	330
Elasmobranchs	~900
African cichlids	~1,000
Mammals	~4,000
Flowering plants	~350,000
Neopteran insects	~850,000
Metazoa	10+ million
All of life	3–30 million

should be diagnosably distinct in morphology from chimpanzees and other apes. Although the statistical methods involve the arbitrary choice of a significance level, we are assuming that our techniques will allow us to identify differences between humans and apes if they exist as diagnosable entities in nature (B in Box 1). However, in the case of arbitrary divisions of continuous variation, we first define a threshold value that distinguishes humans and apes. When we find that two entities are different, it is simply because our arbitrary threshold says so (C in Box 1). This fallacy can be clearly seen in the example of defining adaptive radiation as 90% clade imbalance, where the statistical threshold is not being used as a tool but as the definition itself.

When adaptive radiation is defined by an arbitrary threshold, it delimits an arbitrary category. Categories are human conceptions, and membership in them is based on possession of some key feature. For example, the category “red things” would include the dean's Ferrari, roses, macaws, and your dress. We invented the category red things and decided what would be the ticket for admission into the class. It is obvious in this example that the named objects have no relation to one another outside of our imagination. Language is filled with terms such as light, dark, which delimit discrete

categories where none exist in nature (Box 1), a cognitive bias that influences the way in which we generate hypotheses about the world.<sup>(44,45)</sup> Yet treating an arbitrary definition as though it were real negates the foundational aspiration of discovering the entities and phenomena that exist in nature. Because it leads to reification, instead of helping in the study of the evolution of diversity, disparity, speciation rate, and adaptedness, the term adaptive radiation is now hindering. Why, then, is the term still in use and where is it taking our field?

## Adaptive radiation and the life cycle of metaphors in science

On the one hand, we have characterized adaptive radiation as a key concept, one that has clearly been useful for biologists of all stripes (Fig. 1). On the other hand, we have argued that definitions of adaptive radiation are merely arbitrary divisions of biological continua that lead us into the pernicious fallacy of reification. Both views are correct. Adaptive radiation is, or at least has been, an extremely useful heuristic that has spurred much important research. But with the advent of novel techniques to quantify adaptive radiation variables, the term is beginning to show its limitations, and we predict that it will be abandoned for scientific use. To make these assessments, we turn to the life cycles of metaphors in science.

A metaphor is a device that evokes a system that we are already familiar with as a means of understanding a less familiar one by calling forth similarities that might be shared between them. Metaphors are integral to human thought<sup>(46)</sup> and evolutionary biology is no exception. Evolutionary thinking is guided by metaphors of “tinkering” and “trial and error,” the “struggle for existence,” “selection,” adaptive and epigenetic “landscapes,” genetic “information,” ecological “niches,” phylogenetic “trees,” molecular “clocks,” and a multitude of others.<sup>(47–51)</sup>

By grouping a range of phenomena under one expansive label, metaphors gather different research programs around a single topic, forging a powerful heuristic for further research.<sup>(50,52–54)</sup> This gathering of scientists under a single expansive label can be seen as the first in the three-stage life cycle of a scientific metaphor. As the first stage gains momentum, research shifts from qualitative to quantitative. The second stage is reached as it becomes clear that the label does not fit the newly gathered quantitative observations. As a result, the use of the metaphor becomes more and more vague. Different things may happen in the third and final stage. In the case of some metaphors, biologists winnow out the multitude of meanings, leaving a reference to a more or less specific feature or phenomenon. These metaphors are regarded as reflecting the real causal structure of the world. In other cases, the metaphor is found not to correspond to a

distinct phenomenon in nature and is replaced by direct study of the variables of interest.

“Gene” is a celebrated metaphor that exemplifies the life cycle stages and shows how the status of a metaphor can shift repeatedly over time. The term was coined in 1909 by Johannsen<sup>(55)</sup> to evoke the basis of the *generation* of new organisms. At the first stage, the gene represented a powerful heuristic that, among other things, helped to create the new research field of molecular biology and to reformulate old problems of heredity by separating them into what we now call development and genetics, establishing an entirely new set of methodological questions and solutions.<sup>(56)</sup> The gene metaphor was able to accomplish all this because scientists not only studied genes themselves but also took them for granted, using them as the basis for new theories spanning other aspects of biology from cell differentiation to organismal evolution. These programs received a boost with the elucidation of the structure of DNA in 1953, an event that along with a series of other major breakthroughs resulted in the gene being regarded as a real entity.<sup>(57,58)</sup> If our story were to end at 1953, then at the third stage we would conclude that the metaphorical gene had been substituted by the real causal structure of the world. However, a metaphor may be reinterpreted and the whole cycle begun anew. This is what has actually happened to the gene metaphor. Only a few years after the discovery of the structure of DNA, a new metaphor, this time the *genetic program*, sent the whole gene research program back to the first stage of the metaphor life cycle. The reinterpretation of gene continues to the present day and there is still no consensus on the “real” meaning of the term gene.<sup>(59,60)</sup>

The fate of adaptive radiation seems destined to be different from that of gene, although both metaphors have had similarly auspicious early stages. If a good metaphor unites scientists of diverse stripes at stage one, then adaptive radiation has done so *par excellence*. Harkening explosive bursts of energy, adaptive radiation ties together images of rapid divergence rate, increase in species number, and the filling of many ecological niches.<sup>(61)</sup> As a result, the term is in the conceptual toolbox of scientists working on every major group of organisms, at all levels of the phylogenetic hierarchy (Fig. 1) and has brought together a staggering array of research programs. For example, many authors agree that adaptive radiation is a rapid surge of speciation, but are interested in different aspects, such as simultaneous divergence,<sup>(8)</sup> exponential increase in species accumulation,<sup>(9)</sup> or episodic events of speciation.<sup>(3)</sup> This diversity translates into a very large adaptive radiation label under which a vast range of scientists have found room, just what would be expected of a compelling metaphor at stage one. Currently, adaptive radiation is at the second stage, as the controversies over definitions and the stretching of the term with qualifiers highlight the limitations of the term (Table 1).

At the third stage, metaphors may be winnowed until they reflect the causal structure of the world, or be abandoned as no longer useful. A current example of the latter may be the “landscape” metaphor, with authors calling for abandonment of the terms adaptive and epigenetic landscapes in favor of working with the relevant variables even if the results are complex and difficult to understand intuitively.<sup>(51,62)</sup> Although there is no consensus regarding the real meaning of gene, there is consensus on some salient physicochemical and conceptual characteristics, allowing biologists to manipulate genes and to construct new theories around them. Not even this sort of pragmatic consensus exists in the case of the adaptive radiation metaphor. Moreover, like the landscape metaphor, adaptive radiation cannot be winnowed to any core meaning, because there is no phenomenon in nature to which the term corresponds, simply arbitrary divisions of continua.

If we are interested in an evolutionary biology that corresponds with nature, then the destiny of adaptive radiation at the third stage would inevitably seem to be abandonment. Abandonment seems appropriate given that adaptive radiation studies divide the world into artificial slices and then reify these slices. If, moreover, forswearing adaptive radiation leads us to think about speciation rate, diversity, disparity, and other variables as continua instead of making unresolvable assertions about thresholds, then it would seem that there is everything to gain by moving beyond the term. These are the dilemmas of the second stage of scientific metaphors. Abandonment of a limited metaphor in favor of study of underlying causal processes is the promise of the third.

## Beyond adaptive radiation

The tools for studying adaptive radiation variables as continua are already at hand and have been growing in parallel with phylogenetic methods in general. To return to the example of phylogenetic tree shape, the argument from the point of view of adaptive radiation is that a clade that has undergone adaptive radiation should have significantly more species than its sister taxon, the usual approach being to specify an arbitrary cutoff at some degree of tree imbalance.<sup>(63)</sup> This approach produces two artificial classes, groups that qualify as adaptive radiations and those that do not. The challenge is then to explain the causes of adaptive radiation. However, the task of evolutionary biology is to explain the entire range of tree shapes, from highly symmetrical to maximally unbalanced, a task that is awkward or impossible from the adaptive radiation perspective. Happily, recent methods for exploring imbalance on continuous scales open the door to the study of the full range of imbalance and its causes.<sup>(64–69)</sup> For example, Holman<sup>(70)</sup> used an index of clade imbalance that varies continuously from 0 to 1<sup>(64,66)</sup> to assess the relationship between imbalance and the number of species found at a

given node. He found a positive relationship between the two variables and suggested that the relationship reflects the accumulation of differences in diversification rate between clades over time. Selecting an arbitrary threshold demarcating some of the clades that Holman studied as adaptive radiations would add nothing to his study, illustrating how current methods for studying phylogenetic tree shape are in no way benefited by classing clades as adaptive radiations or not.

Rates of speciation and molecular or morphological evolution are also more fruitfully studied as continua, and metrics for these have enjoyed spectacular growth.<sup>(71–75)</sup> For example, amounts of nucleotide substitutions, as reflected by phylogenetic branch lengths, are a major preoccupation for students of adaptive radiation.<sup>(3,11,31,33,76)</sup> Yet classing clades as adaptive radiations or not only makes study of the causes of branch length differences unwieldy. In a recent example, Smith and Donoghue<sup>(77)</sup> used carefully selected clades of plants that included both short-lived herbs and long-lived woody members to study the effects of generation time on nucleotide substitution rates. They found compelling evidence that short generation times are associated with higher rates of nucleotide substitutions. Adding tests of adaptive radiation to this study would no doubt find that some of the clades they examined qualify as adaptive radiations, but would in no way add to inferences of the causes of different substitution rates.

Similarly, without adaptive radiation, there is no reason to privilege high disparity clades as being inherently interesting. Instead, it is necessary to understand the entire range of disparity, from horseshoe crabs set in their ways to protean silverswords (Fig. 2).<sup>(12)</sup> Novel approaches for studying multivariate data in a phylogenetic context make the evolution of disparity accessible to study,<sup>(78)</sup> and render irrelevant the need to class clades as representing an adaptive radiation or not before proceeding to study the causes of ranges in disparity. Darwin's finches, a paradigm of adaptive radiation, are a prime example. Recent phylogenetic studies found that they are embedded within a clade that generally shows disparity in beak morphology comparable to that of the Galápagos finches. As a result, the Darwin's finch clade likely is not significantly more disparate or diverse than the rest of the "domed nest" finch clade to which it belongs,<sup>(79)</sup> and although they are the textbook example of adaptive radiation, would not qualify as one under many definitions.<sup>(15,80)</sup> Nonetheless, finding that Darwin's finches do not meet a given definition of adaptive radiation would not make them any less worthy of study, nor would it negate the important evolutionary inferences drawn over decades of illuminating work on the group. Although Darwin's finches are celebrated examples of adaptive radiation, the term no longer has anything to offer the study of the clade, whereas powerful and promising new phylogenetic methods do. We have argued that this progression is to be welcomed as the natural course of events in the life of a scientific metaphor.

## Conclusions and prospects

The metaphor of adaptive radiation has brought evolutionary biology to a point at which it is possible to imagine the field without the term. If the initial stage of a metaphor in science unites workers around the study of major themes, then adaptive radiation has fulfilled this charge admirably. However, the term now pales before novel techniques that quantify variables such as phylogenetic tree shape, speciation rate, and morphological disparity. The novel data generated by these techniques mean that dichotomies such as adaptive radiation *versus* everything else or "adaptive *versus* non-adaptive radiation" are inadequate to describe the ranges of diversity and disparity that are the salient features of life on earth. If we discard these needless dichotomies in favor of a full spectrum of continua, it becomes clear that the study of diversity and disparity requires a conscious effort to examine clades of all types, not just the most diverse and disparate ones.

Moreover, because adaptive radiation does not exist as a distinct phenomenon in nature, all of the research questions that invoke the term can be framed without it to no detriment whatsoever. For example, Gillespie<sup>(81)</sup> asked whether assemblages of spider ecomorphs in Hawaii differ in communities that are the products of adaptive radiation *versus* those that are made up of more distant relatives assembled *via* immigration. Adaptive radiation was simply shorthand for "the descendants of a common ancestor" and the question was whether communities made up of close relatives differed in their arrays of species ecological roles within communities as compared to communities made up of distantly related species. As in all adaptive radiation studies, in this example adaptive radiation had to be defined first before getting down to the real business of studying the variables of interest. As a result, our thinking loses nothing by eliminating the term.

Although we advocate abandoning a popular term and have criticized attempts to "test" definitions of adaptive radiation as falling victim to the reification fallacy, we also present a view of metaphors in science that shows the field moving exactly as it should be. The early stages in the life of the adaptive radiation metaphor have fulfilled their goal of generating research on the causes underlying patterns of diversity and disparity. From this vantage point, we can also see that evolutionary biology has far more chance of fulfilling this goal by exchanging a spent metaphor for the full diversity of evolutionary patterns and processes.

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