Metaphors as surrogate variables. The case of adaptive radiation

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We develop a new metaphor account where metaphors become surrogate variables for different but related phenomena. As we will argue, subrogation is the result of the interplay between the things inspired by the metaphor and the empirical dynamics that result from such inspiration. In particular, we focus on adaptive radiation, a major concept of evolutionary biology. Our study suggests that there is no distinct phenomenon, process, or pattern in nature than can be identified as adaptive radiation. What we have instead is a grouping variable that has surrogated different evolutionary phenomena into one expansive label. We believe this analysis of metaphors helps better understand the value of metaphors for science not only as a provider of epistemic and cognitive virtues but most importantly, as a crucial research tool that can both help and divert scientific experimentation.

1. Introduction.

The importance of metaphors in science is well documented. Ever since Black's seminal contribution (Black, 1962), the analysis of metaphors and their relation to scientific practice, theory construction, modeling, or inferential power has grown steadily (see for example, Ricoeur 1978, Ortony 1979, Hesse 1980, Keller 1995, Lakoff and Johnson 1999, Moser 2000, Maasen and Weingart 2000, Cat 2001, Kertész 2004, Kövecses 2005, Haser

2005, Walton 2005, Gibbs Jr 2008, Musolff and Zinken 2009). Generally, these studies have argued that the many uses of metaphors have to do with the numerous linguistic, epistemic, cognitive, and heuristic virtues that metaphors bring to scientific practice. These works analyze the ways in which metaphors inspire and direct both theory and experimentation, but by focusing exclusively on the level of speech, have overlooked that sometimes metaphors gain their virtues not because of their role as methodological and theoretical triggers, but by becoming the relevant research variables themselves.

In this paper we develop a novel metaphor framework where metaphors gain their experimental and epistemic value by becoming **surrogate variables** of natural phenomena. We borrow this term from scientific data collection, where single easy-to-measure variables are often used to diagnose difficult or impossible to measure ones. For example, "ecosystem health" is a complex state and for all practical purposes impossible to measure. However, water quality or the presence or absence of some “indicator” species or taxon are often taken as markers of the vast array of variables that make up variables such as ecosystem health or overall species diversity, and so are said to be surrogate variables for the whole system (Edwards et al. 1990, Lindenmayer et al. 2000, Sarkar et al. 2005, Heink and Kowarik 2010). Bearing this idea in mind, in the present account metaphors group and simplify under one expansive label a potentially vast array of different processes, entities, or causalities. In this grouping capacity, metaphors serve as surrogates for different but related phenomena, gaining in the process numerous virtues such as empirical, predictive, or explanatory power. As we will argue, subrogation is the result of the interplay between the things inspired by the metaphor and the empirical dynamics that result from such inspiration.

This way of conceptualizing metaphors adds to the prevailing views based on abstract virtues (rhetoric, epistemic, or cognitive) a material dimension that we believe better explains the use and success of some metaphors in scientific practice and proposes how abstract entities are eventually brought into alignment with natural phenomena. By adding this material dimension, our account departs from previous analyses in that our interest is not to account for the epistemic and cognitive virtues metaphors bring into science but to explain how metaphors are introduced, used, transformed, and often reified in the course of scientific practice. While the rhetorical, epistemic, and cognitive virtues associated with metaphors readily explain their theoretical and methodological value, we believe these virtues *alone* cannot explain satisfactorily how such an abstract element of speech can be so effective in experimentation, nor can it explain the empirical success of certain metaphors, how metaphor evoked concepts can become objects of nature or the reasons why, sometimes, metaphors become reified. In the context of this paper, we emphasize how metaphors not only help scientific research in virtue of the elements they import from colloquial language and other sources, but gain new meaning as they become more closely attached to scientific research. We believe this analysis of metaphors helps better understand the value of metaphors for science not only as a provider of epistemic and cognitive virtues but most importantly, as a crucial research tool that can both help and divert scientific experimentation.

To illustrate our thesis, we will analyze the case of adaptive radiation, a central concept in current evolutionary biology. We will argue that adaptive radiation is actually a very successful metaphor that owes its accomplishments to having become an umbrella variable that surrogates distinct phenomena such as speciation rate, phylogenetic tree shape, and morphological diversity. We will argue that adaptive radiation has to be sure become a popular concept due to its success in explaining a wide variety of phenomena, but that its explanatory success is the consequence of different phenomena being surrogated by the metaphor and not because of there being a particular phenomenon known as adaptive radiation in nature. In this sense, our account shares with previous analyses the idea that explanatory power does not necessarily entail truth (see for example Cartwright 1983, 1989, 2007, Baker 2003, or Hartmann, Hoefer and Bovens 2008).

Before we begin our exposition, some clarifications are in order. First, our account in no way presupposes that metaphors are only used as surrogate variables in scientific research. It is clear to us that metaphors in general gain their force from numerous theoretical, scientific, methodological, economic, political, and social factors (see for example Keller 2001, 2002). However, by focusing exclusively on meaning and language use, philosophical analyses have remained at the abstract level of theories, leaving unexamined how metaphors can sometimes be construed as objects and used in actual scientific practice. For example, in our case study, adaptive radiation was introduced not only as a means to think about evolutionary divergence but also a key research variable used as if the variable were a part of nature. Other examples include the metaphors of "information" in genetics (Griffiths 2001; Syed, Bölker and Gutmann 2008), "niche" in ecology (Griesemer 1992, Schoener 1986), or self-nonself discrimination in immunology (Tauber 1994, Löwy 1992) In all of these cases, metaphors play important roles in scientific research that, we believe, are not completely captured by traditional metaphor accounts, which tend to focus on language rather than metaphors as research objects.

While this is not a paper on the nature of explanation, we must briefly address this issue given that we will argue that one of the main reasons some metaphors become surrogate variables has to do with explanatory power and empirical adequacy. The nature of scientific explanation is a matter of much controversy in current philosophy of science (see for example Pitt 1988, Woodward 2003, Strevens 2009, Potochnik 2010). It is clear that there are different kinds of explanations and that many of them are used in different contexts in actual scientific practice. Evolutionary biology is a field true to the plural nature of explanation as scientists appeal to and understand different things when talking about what they consider explanatory. For example, an explanation could be causal (Fitzhugh 2006), mechanistic (Glor 2010) or nomological (Osborn 1902). Causes, laws, or mechanisms are intimately related to the data at hand and as a result it seems a good idea to simplify the discussion by endorsing Brigandt (2010) and Norton's (2003) notion of scientific explanation as material inference. In Brigandt's words, a scientific explanation is licensed because "the content of the concepts involved in the explanation is empirically adequate and the content of the explanans is appropriate to account for the explanandum" (Brigandt: 38; see pages 38-40 for details). While the idea is debatable, the intuition seems correct to characterize if not all, at least the kind of explanations one can normally find in discussions of adaptive radiation. In most papers, adaptive radiation is a function of a series of quantitative variables that serve as the material basis of most if not all explanations in the field. For example, these variables help explain what should be taken as an adaptive radiation or why there may be different kinds of adaptive radiation. In our account the quantitative variables are in fact the phenomena being surrogated by adaptive radiation. Each study of adaptive radiation that is seen to provide an empirically adequate explanation of an evolutionary phenomenon in nature then serves to entrench the metaphor further as a concrete entity.

We are aware that calling well-established scientific concepts such as the ecological niche or adaptive radiation *metaphors* is likely to raise numerous eyebrows. However, there are good reasons at least to consider the possibility that many frequently-invoked concepts may in fact be metaphors. In the case of adaptive radiation, biologists imagine explosions of evolutionary diversity, with many species originating suddenly and occupying different ways of life. This diversity from a single ancestor is reflected in the metaphorical invocation of radiation. However, as clear as the metaphorical intuition is, the scientific concept is riddled with conceptual and operational problems (see Olson and Arroyo-Santos 2009, Glor 2010, Losos and Mahler 2010, Givnish 1997). Several features of this literature make us interpret adaptive radiation as a reified metaphor. For example, there is no agreed upon definition of the term. While a lack of a consensus definition is not in itself a telling sign of reification, it is clear that the people using adaptive radiation can only agree on the metaphorical definition of the term. This lack of agreement leads to differences between studies as researchers focus on different aspects of the metaphor. On the view we present, this lack of consistency is a result of researchers picking and choosing different aspects of the many phenomena being surrogated by the notion of adaptive radiation. As a result, it can be shown that, contrary to what would be expected if adaptive radiation were a true phenomenon, more empirical research does not help to clarify the term but instead contributes to widen its fan of possible meanings.

The distinction between reified metaphors and natural phenomena is crucial for both science and the philosophy of science. That adaptive radiation has been very important to understanding and explaining numerous phenomena in evolutionary biology is beyond doubt. What we particularly want to discuss is that its numerous virtues are not the result of there being a natural phenomenon that can correctly be ascribed to adaptive radiation, but are the consequence of an evocative metaphor having surrogated many different phenomena. This distinction is of the utmost importance in science as confounding metaphors with natural objects can lead research completely astray. From a philosophical perspective, the distinction is also fundamental in the discussion of crucial topics such as realism, concept formation, inference, and explanation to name a few. Finally, the distinction is important because a major task of the philosophy of science is to analyze scientific activity critically and if possible, norm, warn, discuss, or explain what science is and the reasons it works.

This paper is organized as follows: in section 2 we develop our notion of metaphors as surrogate variables. We will show how metaphors can sometimes be construed as scientific objects. We do not suggest that this is a general rule of scientific metaphors, but we do argue that there are different kinds of metaphors, and that some of these kinds are more likely to become concretized than others. Next, in section 3 we will exemplify our claims with the example of adaptive radiation. We will briefly present the history of this concept and will end the exposition presenting some of its many characterizations. Finally, we will discuss how the term has acted as a great umbrella variable that has surrogated a panoply of distinct phenomena.

2. Metaphors as surrogate variables.

In this section we will explain how some metaphors can become surrogate variables. To do so, we have to introduce two ideas. First, that it is possible to divide metaphors into different kinds based on the ways they were first introduced to scientific practice. Metaphors enter scientific practice to serve distinct methodological, theoretical, or empirical roles, and based on such roles, they can be grouped into different kinds. While there may be different kinds of metaphors, here we will only present two with the purpose of discussing how some metaphors are more likely to become surrogate variables than others. Second, we defend that regardless of their kind, all metaphors change their meaning in the course of scientific research. This has to do mainly with empirical adequacy and the uses of metaphors as tools for scientific practice.

Based on the reasons metaphors are first introduced in scientific practice we can distinguish at least two kinds of metaphors. On the one hand we have **theory-constitutive metaphors**, meaning metaphors that arise in the context of theory construction. An example is Wright's adaptive landscape, which is used to represent the fitness of a population (see Kaplan 2008). The theory behind Wright's work is an abstract mathematical construction relating genotypes, phenotypes, and reproductive success called the shifting balance theory of evolution (Wright 1931). As has been documented (Ruse 1996, Kaplan 2008), this version of the theory had little success due in large part to its mathematical complexity that proved difficult for many biologists to understand. However, when Wright refurbished it with the metaphor of an adaptive landscape, it rapidly became one of the central tenets of evolutionary biology (see Wright 1932, Skipper 2004). On the other hand, **observation-conceived metaphors** are introduced as an initial description for a new phenomenon. For example, Wegener's continental drift was used to account for the conspicuous complementarity between the African and South American coastlines as well as the striking similarity in the fossil records from both areas (see Laudan 1983).

In both cases, metaphors play a major role in explanation but in different ways. Roughly speaking, theory-constitutive metaphors work *along* other theoretical elements whereas observation-conceived metaphors can sometimes be the sole initial explanatory element. For example, the adaptive landscape theory-constitutive metaphor is a very important element in Wright's theory that supports and complements other elements such as fitness, selection, or genetic drift but is of little help by itself. In contrast, in the case of observation-conceived metaphors, consider the early notions of the self-nonself metaphor in immunology (Tauber 1994), or the ecological niche (i.e. Griesemer 1992). In these cases, both metaphors were used in early explanations of certain phenomena even if they eventually lost part of their metaphorical content as these early explanations were substituted by larger theoretical bodies. For example, the metaphoric intuition of self-nonself discrimination in immunology served as the starting point to develop contemporary immunological theory as it became a means to imagine (or theorize, or propose hypotheses) how the immune system could respond to an apparently limitless array of antigens without damaging itself (see Tauber 1994, Löwy 1992). In time, the intuition was substituted by the numerous processes, entities, and mechanisms that account for our present understanding of the immune response.

The different uses of metaphors also show that their introduction to scientific practice has to do not so much with applying one linguistic framework onto another but to exploit the intuitions inspired by the ambiguity and polisemy of a metaphor that could be verbal or visual or take any form (see for example Hintikka 1994, or Ungerer 2000, or Forceville 2006). Regardless of its form, the important role of a metaphor has to do with the heuristic, epistemic, rhetorical, and cognitive virtues it brings to a nascent scientific project. These virtues help articulate an initial description, identify and evaluate the pros and cons of this preliminary description, generate pertinent questions, foresee potential problems, set a research agenda, and start constructing the basis of future theory (see for example Hesse 1980, Arbib and Hesse 1986, Keller 2002). If all of this is correct, then it is not surprising that some metaphors can become the cornerstone on which new research projects (or even new disciplines) are formulated.

Once metaphors enter the scientific arena, another important aspect of metaphors we want to emphasize is that they are very plastic, meaning that they can change their meaning in the course of scientific research (Fig. 1). This dynamism emerges because, as the metaphor is used to account for a new observation, or is applied in the context of a new theory, it becomes necessary to add the empirical elements that will assess the fit between the metaphor and the world. This means, for example, selecting a set of qualitative elements from the phenomenon under investigation in virtue of its relative coincidence with the metaphor or constructing a set of quantitative elements that will help measure certain aspects of nature suggested by the metaphor.

Figure 1.

In time, the dynamics resulting from the interaction of research and metaphor could produce different outcomes. For example, due to theoretical advances the metaphor could lose part of its metaphorical meaning and become part of a mathematical apparatus as in the case of the niche in ecology (Schoener 1986, Griesemer 1992), or could lose all of its metaphorical content and become a name as has happened to numerous biological entities such as chaperones, semaphorines, or helper cells, or the example of continental drift. Similarly, due to empirical adequacy the metaphor could change its meaning as the field changes its own research goals as has happened to the metaphor of information in genetics (Jablonka and Lamb 2005). While in the cases we have just mentioned there is a separation (loose if you will) between the metaphor and the world in the sense of the metaphor being recognized as such and different from the natural entity, there are cases where there is no clear distinction between metaphor and nature.

As the preliminary description is compared with the world and researchers learn more about the phenomena under investigation, the link between the metaphor as the material explanation of a part of nature and the characteristics of that part of nature become indistinguishable. The surrogating process is the result of experimental investigation that sometimes via empirical adequacy unintentionally imbues the metaphor with explanatory power, empirical success, and if there is a concurrent process of subrogation, with predictive power as well. This assignment of roles is not exclusive of metaphors, given that the roles can be assigned to other scientific concepts that lack referents in nature but that, like phlogiston or ether, did have explanatory and predictive power (i.e. Ladyman 2009). In all cases, the central notion is that scientists use a metaphor or concept without referent and unwittingly surrogate real processes, mechanisms, natural entities, or a combination of these. A ready way to think of the issue is to appeal to a kind of realism of causes (in the fashion of Cartwright 1983, 1989, 2007) in which the cause or "capacity" of nature is unintentionally linked to a concept, metaphorical or otherwise. This concept will become the phenomenon, entity, or natural process; in the parlance of Cartwright, the capacity will vouch the concept.

Once the agenda is set by the initial metaphor, it is immediately reinterpreted in terms of the scientific and experimental relations formed by the incorporation of new observations, feedback from related areas, theoretical underdetermination, new problems created the metaphor itself, incorporation of other research agendas, and so forth. In other words, the metaphor is an intuitive idea about something, and in the complex interplay of scientific research, different elements make their way in and out of the set of things covered by the metaphor in an attempt to clarify its meaning (Fig. 1). "Clarify" in this context refers to a function of a specific historical process where the general idea of the metaphor is subsumed into the set of philosophical, scientific, ontological, or social commitments of a particular time and place, a process that is not necessarily equivalent with moving the metaphor closer to what it actually stands for (i.e. the correct characterization of a process of nature or of an entity).

From the exposition above, it can be seen that metaphors becoming surrogate variables is the result of empirical adequacy and the *material* inferences drawn in the course of research. Given that the metaphor is (part of) the explanandum, the content of the explanans must be empirically adequate, meaning that the explanandum could be supported by different natural entities tied together by the material inference. This is what we mean when we say that the metaphor becomes a grouping variable that unites different entities, processes, or causes under one expansive label (Fig. 3). Also, because of the close link between material inferences and metaphors, observation-conceived metaphors seem likely to become concretized than others.

3. Adaptive radiation as a surrogate variable.

To illustrate the use of metaphors as surrogates, let us turn to adaptive radiation. Adaptive radiation was born a century ago when paleontologist Henry Fairfield Osborn coined the term to "express most clearly the idea of differentiation of habit in several directions from a primitive type" (Osborn 1902: 353). Osborn coined the term inspired by the branching diagrams constructed using the fossil record that depicted similarities between living and extinct species. With this terminology, he wanted to distinguish adaptive radiation from what is generically known as divergent evolution, the tendency for species descended from a common ancestor to differ increasingly with the passage of time. According to Osborn adaptive radiation was "more than divergence because it implies evolution in every direction from a central form" (Osborn 1910: 78; Fig. 2) based on the "well-known principle of zoological evolution that an isolated region, if large and sufficiently varied in its topography, soil, climate, and vegetation, will give rise to a diversified fauna according to the law of adaptive radiation from primitive and central types" (Osborn 1902: 355). Osborn considered that "This idea of radiation becomes a means of interpretation and a way of imagining the relations of extinct and living faunae (p. 354)".

Figure 2.

In short, adaptive radiation is an observation-conceived metaphor that grew out of the similarities implied by the fossil record. It was introduced to accomplish three main tasks: as a heuristic tool, as a term meant to clarify theoretical problems with the notion of divergence, and as a descriptor of what Osborn took as a law of nature. Over a hundred years later, adaptive radiation has fulfilled its roles admirably as it is now applied in the scientific literature hundreds of times a year to describe evolutionary patterns in all imaginable groups of organisms and at all levels of divergence, from single species to huge clades such as the mammals or even all of life (see Olson and Arroyo-Santos 2009).

After Osborn's introduction, adaptive radiation was reinterpreted under the growing influence of population genetics during the 1930s and 40s, and in the rise of the Modern Synthesis. Wright, to name one example, refurbished the concept to suit his adaptive landscape, introducing the idea that intergroup selection was the force behind adaptive radiation (Wright 1931, 1932, and Skipper 2004). The idea was that subpopulations of a species should be subject to different selective pressures resulting in divergent adaptations in the different populations. This interpretation meant changing the general tone of the metaphor from the problem of describing how new taxa arise from an original ancestor to explaining how selective pressures push populations to novel adaptive peaks representing different allele combinations, resulting in the adaptive radiation of organisms. To keep things in order we will call the introduction of Wright's adaptive landscape into the set of things being discussed, pondered upon, or manipulated within the context of the adaptive radiation metaphor **m1**.

Huxley further enriched the content of **m1** with the idea that Wright's intergroup selection worked better in combination with spatial isolation and helped create the idea that adaptive radiation (now **m2**) was one of the fundamental processes of evolution (Huxley 1942). As all of biology became intertwined in the paradigm imposed by the Modern Synthesis, Simpson reshaped **m2** in the 1950s to say that adaptive radiation (**m3**) is "more or less simultaneous divergence of numerous lines from much the same ancestral adaptive type into different, also diverging adaptive zones" (1953: 222).

While Simpson's description is entirely in line with Wright's account, he placed the emphasis of the concept on the adaptive nature of divergence between lineages. In doing so, he echoed the prevalent view of the Synthesis that evolutionary change is principally driven by adaptation. The array of organismal lifestyles ("adaptive zones") observed in the members of an adaptive radiation exist because they are favored by natural selection, and the imaginable lifestyles between them, say between dogs and cats, are empty because natural selection eliminates them (Simpson 1944, 1953). In the traditional Synthesis account, evolutionary radiation into novel adaptive zones is driven by "ecological opportunity," that is, that there are empty adaptive zones waiting to be occupied. Thus, while Wright and Huxley helped give adaptive radiation the population genetic basis demanded by the Synthesis, Simpson developed the adaptive aspect, also a crucial concern of the day.

The details of most uses of adaptive radiation after Simpson show little conceptual change with respect to the adaptation-driven and gene-centric view of the Modern Synthesis but do reveal an increasing preoccupation with quantification and the use of computer intensive tools. As we propose in section 2, this has to do with the incorporation of elements necessary to link the metaphor with the world. Observe that in the context of adaptive radiation, we find quantification of factors such as speciation rate, morphology, or the unequal distribution of species in evolutionary lineages. For example, Stanley (1979) dedicates a chapter to the quantification of speciation rate, with adaptive radiations being characterized by rapid bursts of speciation. Guyer and Slowinski (1993) draw on the techniques available for reconstructing phylogenies using computational algorithms to identify possible adaptive radiations, defined as groups with significantly more species than their most closely related lineage.

The efforts to quantify adaptive radiation have resulted in a huge literature that has bestowed important virtues to adaptive radiation but have not helped in clarifying what it is or the part of nature it refers to. For example, adaptive radiation finds a distinctive expression in the work of West-Eberhard (2003). Rather than viewing the source of adaptive evolutionary change as being selection acting on infinitesimal phenotype differences caused by micromutations, as in the Synthesis account, West-Eberhard sees the variation that is the raw material for adaptive evolution as deriving from the capacity for a single ontogenetic system to produce many phenotypes, which can be viable in the context of a very wide array of environmental or internal challenges. From her point of view, we find the rapid appearance of many species with different lifestyles as the result of the highly adaptive plastic changes that the dynamic ontogenetic systems of organisms make possible. These changes are stabilized through the generations by epigenetic and finally genetic factors, inverting the traditional genetic causality of the Synthesis (West-Eberhard 2003, Schwander and Leimar 2011). Likewise, Reid (2007) envisions adaptive radiation as being made possible not so much as by tiny incremental mutational changes being selected by adaptive processes but as being unleashed by major epigenetic events such as a novel symbiosis. These uses of the "adaptive radiation" would seem to betoken an overturning, or at least a significant extension, of the Modern Synthesis views and show how the term is still very open to reinterpretation.

Our brief historical account has three major goals in mind: 1) To show that adaptive radiation is what we have called an observation-conceived metaphor. Osborn used the metaphorical intuition to account for numerous observations of the relations between extinct and living fauna. 2) To stress the fact that after its introduction, adaptive radiation was reconceptualized to fit distinct theoretical views, but with all of them keeping the original intuition of numerous species "radiating" from an original ancestor. This diversity of views subsumed under the adaptive radiation label provided the metaphor with numerous epistemic and nonepistemic virtues. 3) To show that contemporary research has contributed to the empirical adequacy of the metaphor by quantifying aspects of nature inspired by the metaphor. Of course, this does not mean that they are measuring nonexistent objects, but rather, that they have turned the metaphor into a surrogate variable by involuntarily assigning to it certain aspects of nature.

4. The death of a metaphor and the birth of a concept.

In this section we will discuss whether the evolution of adaptive radiation is the natural result of a suggestive metaphor slowly zeroing in on the appropriate structures of the world or whether it evolves as a surrogate variable that continually includes and excludes aspects of interest to different researchers. We will begin by briefly commenting on some of the current definitions proposed for adaptive radiation and elaborate from there why we believe adaptive radiation to be a vast metaphor and not a natural phenomenon.

4.1 Are there adaptive radiations in nature?

In this section we show that all of the definitions devised for adaptive radiation involve treating arbitrary thresholds as though they were biological reality. For example, adaptive radiation is often defined as and distinguished from "normal" evolutionary divergence as episodes of very rapid species formation (Simpson 1953). However, "rapid" is a term open to interpretation. As a result, the term adaptive radiation does not suffice to express how rapidly species have diverged from one another so biologists wishing to denote rapid speciation rate use descriptors such as “rapidly diverged” or “explosive” adaptive radiations, in fact creating a set of new reinterpretations of the metaphor (**m4**) where rapid, whatever it is taken to mean, is the key element.

In a different conception, other biologists identify species number as a necessary characteristic, with adaptive radiations such as the mammals or the African Rift Lake cichlid fish being characterized by very large numbers of species (Simpson 1953, Sanderson 1998, Schluter 2000). Other biologists have singled out very small groups or even single species as adaptive radiations (Meerts et al. 1990). Like rapid, biologists do not agree on the number of species that are required to consider a group an adaptive radiation or not, turning species number into yet another set of metaphor-functions (**m5**) in their attempt to single out adaptive radiation from other evolutionary phenomena.

To complicate things even further, there is an **m6** that views adaptive radiation as a function of morphological, ethological, physiological, or ecological diversity. This is the idea that an adaptive radiation should show striking differences between species, such as the array of lifestyles of the mammals, which spans the marine, terrestrial, and aerial realms (Simpson 1953, Sanderson 1998, Schluter 2000). Biologists universally agree that examples such as the mammals are striking, but there is no apparent consensus on the degree of divergence between species that is necessary to qualify as an adaptive radiation, or even how to compare, say, morphological diversity between organisms as different as mammals, flowering plants, and fish (Losos and Miles 2002). Notice that, although the functions that we have mentioned so far are related to the radiation aspect of the metaphor, the adaptive side is equally open for reinterpretation especially because of the numerous problems with the concept of adaptation (see for example, Orzack and Sober 1994, Sterelny and Griffiths 1999, Godfrey-Smith 2001, Lewens 2002).

Today there is a plethora of distinct adaptive radiations differing in the relative importance they assign to speciation rate, species number, or morphological diversity, the very variables that can be quantified. As a result we have things such as explosive adaptive radiation, fast adaptive radiation, rapid adaptive radiation, diverse adaptive radiation, truly adaptive radiation, extensive adaptive radiation, clear adaptive radiation, considerable adaptive radiation, extraordinary amount of adaptive radiation and a long list of qualifications (see Olson and Arroyo-Santos, 2009, Table 1). Because there is no demarcation in nature between rapid divergence and slow, or morphologically diverse and uniform, these qualifications do nothing to improve our understanding of the nature of adaptive radiation and instead turn quantification into arbitrary descriptors showing contra common sense, that quantification alone is not enough to turn a powerful metaphor into a precise concept. There are many reasons for this but here we want to discuss two possibilities: 1) more work is needed to narrow down what counts as an adaptive radiation; or 2) the metaphor has been reified, and as a result any attempt to establish thresholds is simply setting an arbitrary line that will lead research further away from the real structures of the world and into the analysis of temporarily useful reified parameters.

4.2 More work is needed to narrow down what counts as adaptive radiation.

As said before, an ambiguous concept need not be a reified metaphor. It might well be a term in need of further research. For example, scientific concepts like proteins (Glas 1999), the electromagnetic field (Cat 2001), or the gene (even if its characterization is still debated, there is no doubt that DNA exists and that segments of it participate in important ways in numerous processes) once had a very open definition.

Bearing this in mind, many evolutionary biologists are well aware of the problem of labeling adaptive radiations as fast, explosive, or diverse. Some of them have actually tried to set objective settings to remedy this situation (for a review see Glor 2010, Losos 2010). For example, Guyer and Slowinski (1993) used the differences in numbers of species between sister groups, that is, the two evolutionary lineages that descend from a single most recent common ancestor in cladistic phylogeny reconstructions. Guyer and Slowinski´s definition identifies groups in which 90% or more of the descendants of a common ancestor are found in one of the two descendant lineages. These same authors acknowledged that the 90% threshold is arbitrary but did note that its use provides acceptable statistical properties. So what we have here is not an objective definition of adaptive radiation but an arbitrary characterization that favors a statistical value over an apparently subjective set of descriptors. However, because it is arbitrary, it is no improvement over definitions relying on labels such as rapid or slow.

The use of statistical thresholds in defining adaptive radiations highlights two fundamentally different espistemological positions. In the standard approach, statistical thresholds such as significance levels, which are ultimately arbitrary conventions, are used to discover or describe entities thought to exist in nature. For example, biologists might have used statistics to describe differences between human and neanderthal skull morphology (Bastir et al. 2007). These authors used admittedly artificial thresholds to describe entities, humans and neanderthals, which they believe actually correspond to true things of nature and not human imagination. Studies that define adaptive radiation quantitatively take an opposite epistemological position in that the arbitrary statistical threshold is the starting point. Rather than make assertions regarding entities thought to exist in nature, adaptive radiation definitions simply trace a line across a biological continuum and declare that, say, any point falling in the region delimited by 0.95 or less is not an adaptive radiation, whereas anything above it is. In these definitions, the arbitrary statistical threshold is not simply a tool for describing an entity of nature, it is the definition itself. This situation shows that mathematization while apparently assigning a specific and technical definition to a term, cannot solve problems of ambiguity, confusion, or misconception if the term is not fully understood before coupling it to a mathematical apparatus.

Definitions not setting arbitrary cutoffs usually describe the outcome of the metaphor but do not give an insight into what sets adaptive radiation apart from other evolutionary phenomena. For example, in a widely cited book on the subject, adaptive radiation is "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It involves the differentiation of a single ancestor into an array of species that inhabit a variety of environments and that differ in the morphological and physiological traits used to exploit those environments. The process includes both speciation and phenotypic adaptation to divergent environments” (Schluter 2000: 10-11). As can be seen, this definition includes Osborn’s intuition of an array of species diverging from a common ancestor, all of them making their living in different ways. However, there is a plethora of imaginable mechanisms, processes, or ways that could account for what Schluter defines as adaptive radiation. Therefore, it seems to us that selecting a set of particular mechanisms, processes, or descriptors involves creating a new interpretation of the metaphor. The obvious question is whether it will not be another arbitrary function into which scientists include what each believes to be the features that set adaptive radiation apart from related evolutionary concepts.

A rebuttal to what we have said could be saying that while there are important disagreements on things such as the specific mechanisms of adaptive radiation, there is a consensual that more work is needed. However, there is no consensus definition of adaptive radiation other than the intuition inspired by the metaphor. For example, Sanderson (1998: 1650-1651) says that “Minimally, modern views of adaptive radiation tend to consider three issues: lineage diversification (speciation and extinction), character (usually morphological) diversification and ecological diversification”. Three observations here: 1) these issues are at the heart of Osborn’s intuition of adaptive radiation being “more or less simultaneous divergence of numerous lines from much the same ancestral adaptive type.” 2) This is the very same set of quantifiable descriptors inspired by the metaphor and introduced to fit the theoretical concerns of Wright, Huxley, Simpson, and others. 3) Remember from the exposition above that these issues have been turned into arbitrary numerical thresholds the placement of which has produced strong disagreements between adaptive radiation specialists.

To summarize, there is no agreement on what adaptive radiation is. Attempts at clarifying adaptive radiation have imposed arbitrary quantitative cutoffs that nonetheless have not helped in reaching a consensus but instead have provoked the surge of a multitude of descriptors turning adaptive radiation into a terribly polisemic concept. Polisemy or even multiple referents are not necessarily marks of reification; adaptive radiation might well be a term in need of further research. This hardly seems the case given that some 100 years of research have suceeded only in widening the concept with each passing year rather than converging on a consensus. A concept lacking a core understanding other than the very metaphor that brought it about and that needs to be qualified to say something meaningful might well indicate that something is wrong.

4.3 Adaptive radiation as a surrogate variable.

Another option is to consider that there may well be no such thing as adaptive radiation. From this point of view, adaptive radiation is a slice of an evolutionary continuum. Osborn selected some features from the continuum and created an artificial subdivision that grouped certain groups with features he called adaptive radiation. Because of its enormous explanatory power this artificial subdivision became a concept deeply entrenched in evolutionary biology. The brief historical reconstruction presented in this paper suggests that there is no distinct phenomenon, process, or pattern in nature than can be identified as adaptive radiation. What we have instead is a grouping variable that has subsumed different evolutionary phenomena into one expansive label. These phenomena deal for example with divergence rates, morphological changes, or adaptation to new ecological niches (Fig. 3). Because until recently it was not possible to study these elements individually (for example because of lack of technology, mathematical models, or appropriate theories), the qualitative metaphor became a major tool for theory construction, interpretation of results, and the development of the very technology that allowed the quantification of variables. However, now that the techniques capable of quantifying the variables involved have been developed, what we are witnessing is a tension between the metaphor and the numerous individual variables it surrogates. This tension causes three distinct phenomena: study of individual variables under the guise of study of the umbrella concept, qualification of the metaphor, and reification of statistical thresholds.

Figure 3.

That the individual variables take precedence over the expansive metaphor can clearly be seen in interpretations m4, m5, and m6 where adaptive radiation is in fact defined by its individual variables. However, given that the individual variables are hidden behind the expansive label, once the metaphor becomes a key concept of its field, people working around it may not be aware that in fact what they are measuring or worrying about is another phenomenon and not the reified concept itself (e.g. Glor 2010).

The long history of different meanings for “adaptive radiation” means that in every study the author must define what they mean before using the term. For example, Gillespie (2004) examined communities of spiders that included species that were morphologically and ecologically very distinct from one another. She asked whether communities that were formed as a result of “adaptive radiation” differ in their arrays of spider lifestyles from those that do not, but given the vagueness of the term, what exactly is meant by “communities assembled by adaptive radiation” is not clear. In this case, “adaptive radiation” means “ecologically distinct close relatives that evolved their diversity in situ,” as opposed to communities made up of unrelated spiders that arrived piecemeal from different areas. In this way, different authors must explain their idiosyncratic definition of the term, and often include modifiers such as “fast,” “slow,” and “explosive” to describe a radiation. The universal need to define and modify the term upon each use would seem a clear illustration that the term, despite its success, is insufficient to specify a discrete phenomenon in nature.

Although there have always been voices warning about the misuse of what Carlquist (1974: 116) considered 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”, a rash of recent studies have begun to "test the hypothesis of adaptive radiation." In such studies, a biologist selects a group of species and asks whether or not the group represents an adaptive radiation. To accomplish this, the characteristics of the group are compared against the definition being favored (e.g. Claßen-Bockhoff et al. 2004, López-Fernández et al. 2005). As we argue above, all definitions of adaptive radiation are based on arbitrary thresholds of the fast vs. slow or diverse vs. depauperate type. Therefore, these studies show how the metaphor has ceased to be a heuristic tool and has come to be regarded as solidified reality.

4,4 Philosophy meets evolutionary biology

From a historical point of view, it is easy to discriminate between natural entities and reified concepts. All it takes is to trace back the history of a concept to learn that after a growing set of problems, a reified concept was discarded in favor of the “real” entity. However, discriminating between concepts when they are at the height of their popularity is another story. It doesn’t matter how much contradictory evidence is amassed because supporters of a reified concept can always say that more research is needed and that in due time the problems will be resolved. As a result, perhaps philosophy can offer a helping hand by promoting critical discussion around suspicious topics.

To show how, we propose four conditions that could help distinguish between natural entity and metaphor. These are: a) the people using a term can only agree on its metaphorical definition and not an empirical one. b) Inconsistencies are due to researchers focusing on different aspects of the metaphor. c) It can be shown that aspects in b are in fact distinct phenomena being surrogated by the notion of adaptive radiation. d) It can be shown that, contrary to what would be expected, more empirical research does not help to clarify the term but instead contributes to cloud its meaning further.

Based on our four conditions, we have shown how there are many characterizations of adaptive radiation. However, all they have in common is Osborn’s intuition that there should be a law of nature that accounted for the observation of rapid speciation processes (apparently) due to adaptation. Current research has not been able to zero in on the particular characteristics of adaptive radiation or to propose consensuscore examples. For example, Dawin’s finches, once the prime example of adaptive radiation would not qualify as such under certain accounts (see for example Pinto 2008 or Sanderson 1998). Furthermore, despite having developed numerous quantitative parameters, these have only provoked the explosion of different types of adaptive radiation. We believe this has been the case because the metaphor surrogates the distinct phenomena associated to those quantitative parameters (most notably, speciation rate, morphological diversity, and divergence).

5. Conclusion.

In this paper we have introduced a novel account of metaphors characterizing them as surrogate variables. Our motivation has been to complement previous analyses by adding a material dimension to the study of metaphors. While the rhetorical, epistemic, and cognitive virtues of metaphors readily explain their theoretical and methodological value, we believe these virtues *alone* cannot explain satisfactorily how such an abstract element of speech can be so effective in experimentation, nor can it explain the empirical success of certain metaphors, how metaphor evoked concepts can become objects of nature, or the reasons why, sometimes, metaphors become reified.

We have exemplified our scheme with an analysis of adaptive radiation, a key concept in modern evolutionary biology. The implications of our conclusion for biology suggest that perhaps what is needed is not to continue reinterpreting the expansive label but to notice that it provides a proxy for numerous variables that could be studied individually. While Osborn, Wright, Huxley, and Simpson were formulating their conceptualizations of adaptive radiation, few techniques were available to quantify variables such as the rate at which species diverged, the number of species in a related group, or their morphological diversity. Such quantifications could be made only for biological groups with excellent fossil records, a minimal proportion of taxa. However, the availability of molecular phylogenies over the last 20 years has led to the development of phylogenetic approaches to quantify aspects of groups such as their speciation rate, phylogenetic tree imbalance, and morphological diversity. It may just be that being able to examine adaptive radiation's constituent variables directly makes declaring groups as adaptive radiations or not irrelevant. Rather than focus on an ultimately arbitrary definition of adaptive radiation, perhaps it would be more informative to focus on the relevant variables as continua. Thus, instead of trying to parse the world into two classes, groups that are adaptive radiations and those that are not, biologists could focus on the entire range of species divergence rates, from the conspicuously fast to the very slow, the entire range of phylogenetic tree imbalance, and the entire range of morphological diversity. Surely the task of explaining these vast ranges would be more informative regarding the process of evolution than imposing an arbitrary and forever shifting metaphor onto the continuum of biological reality.

From a philosophical perspective we believe that this surrogate framework not only contributes to the important literature on scientific metaphors but could be used to better understand topics such as concept formation, explanation or inference. For one, it helps better understand how certain non-referential concepts, metaphoric or not, can be used in experimental research and have predictive power. It helps understand the dynamics that ultimately lead some metaphor-evoked concepts to become natural entities, or how some metaphors become reified. It helps better understand how explanatory power is independent of truth and therefore can provide important insights into current debates about scientific realism. Finally, it provides an excellent playground to discuss the nature of scientific inferences and their relation to empirical adequacy. In our account, the weight of material inferences is in part responsible for the reification of the adaptive radiation metaphor. It would be interesting to compare it to other scientific cases to learn more about the importance of this kind of explanation in science or to develop new frameworks that better account for scientific explanation.

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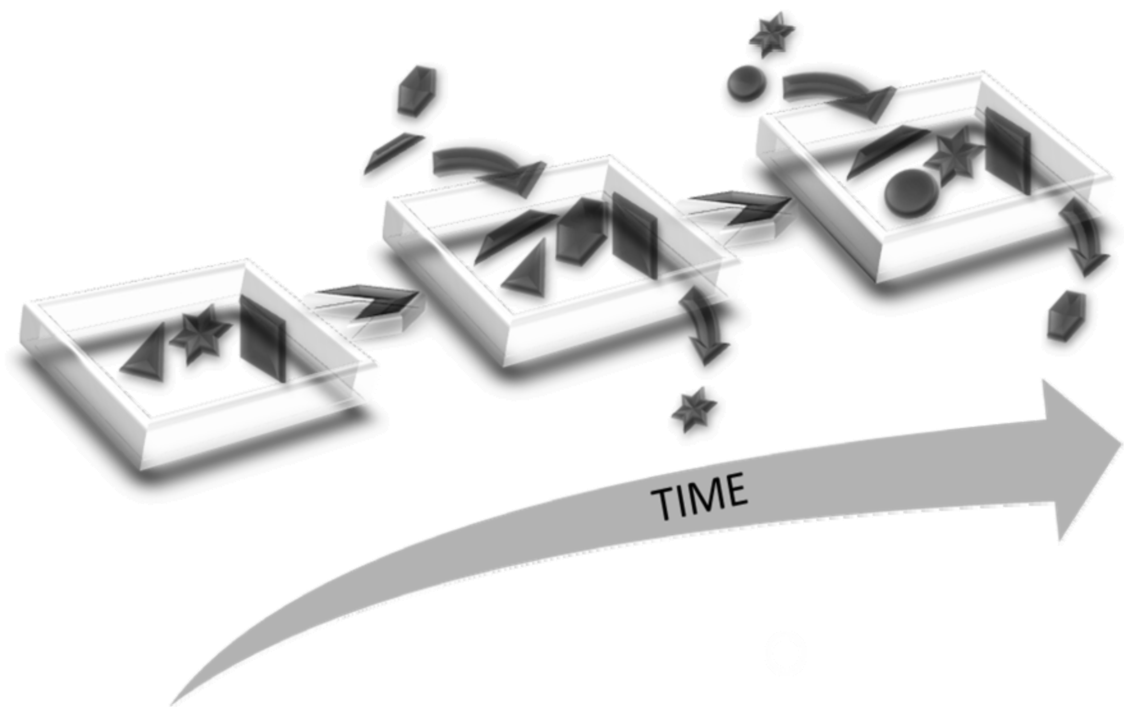

Fig. 1. The metaphor is a dynamic set that can incorporate and exclude different elements as needed. In the figure, the box represents adaptive radiation and the geometrical figures represent how entities and processes are added or discarded as the metaphor is reinterpreted in time. See text for further details.

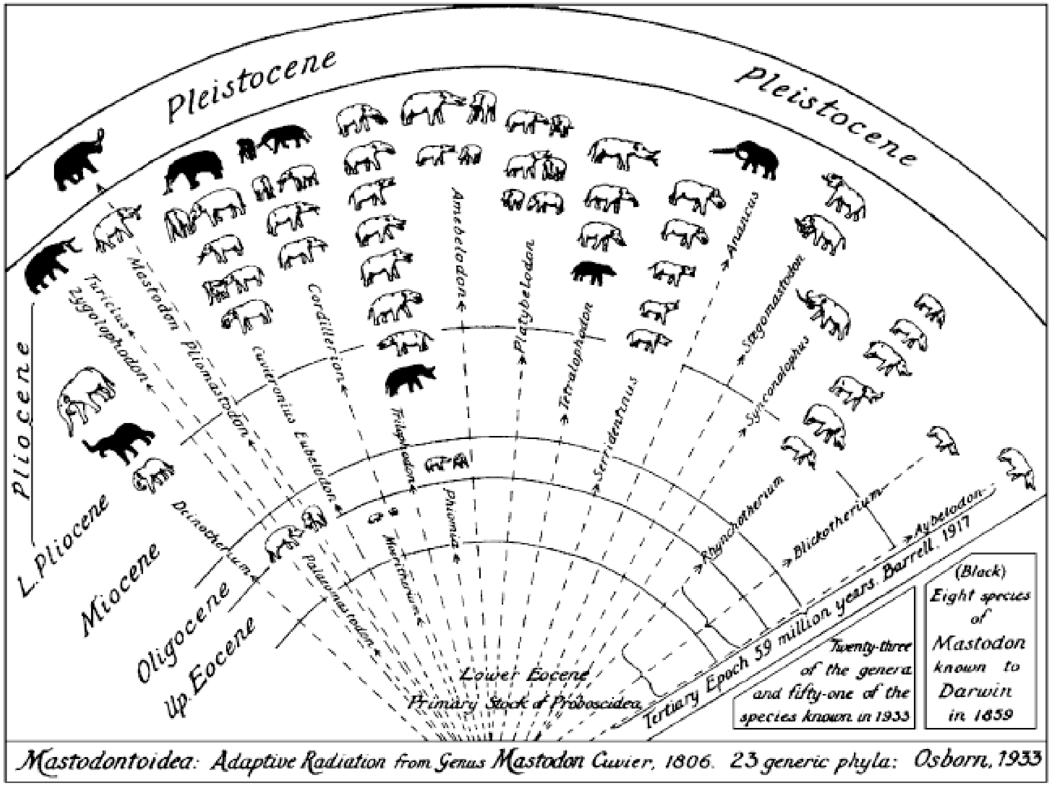

Figure 2. Osborn's adaptive radiation. Adaptive radiation was originally coined to reflect the idea of the evolution of many species that are very different from one another in size and shape from a single ancestral stock. Osborn underscored the "radiation" aspect of his metaphor by arraying the mammoths in this 1936 figure along lines radiating like the spokes of a wheel.

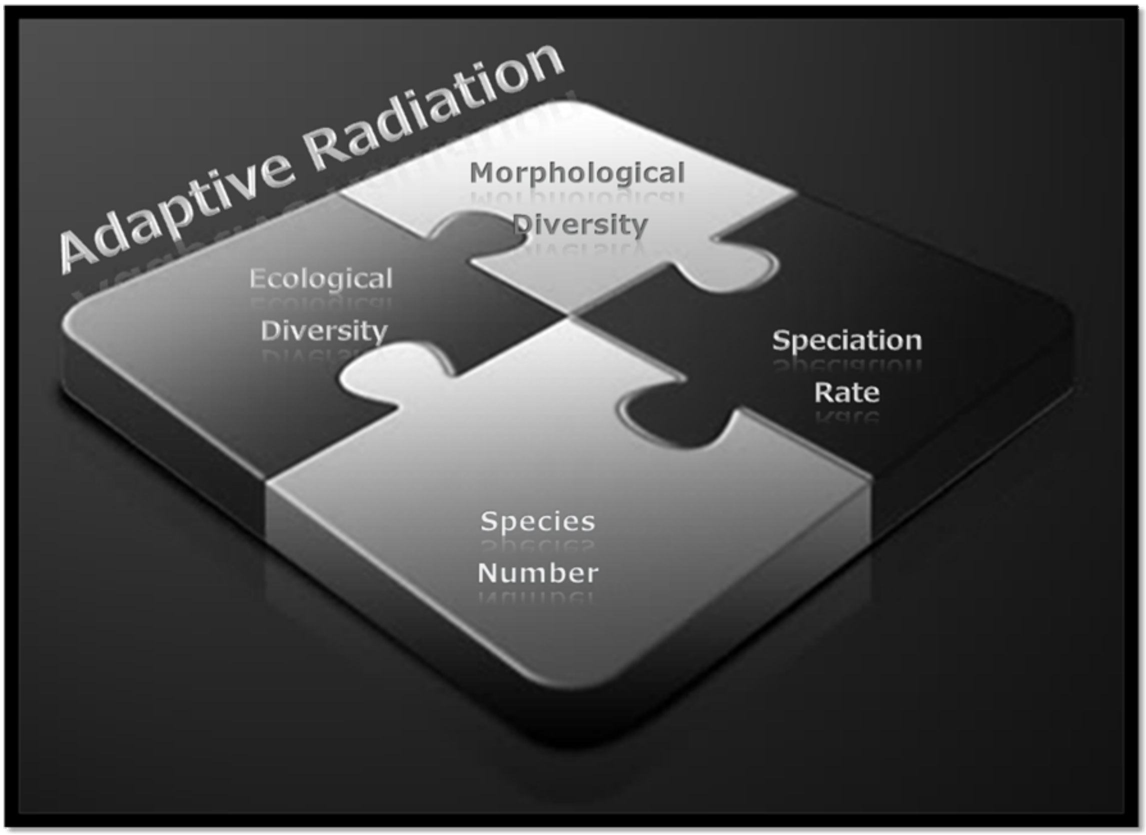

Figure 3. Adaptive radiation groups key evolutionary phenomena such as speciation rate, species number, or morphological diversity. This in part explains its theoretical success but shows that the *real* natural phenomena have to do with the individual variables grouped under the expansive label and not with adaptive radiation itself.