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Functional Versus Morphological Diversity in Macroevolution

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disparity, innovation, many-to-one mapping

Abstract

Studies of the evolution of phenotypic diversity have gained momentum among neontologists interested in the uneven distribution of diversity across the tree of life. Potential morphological diversity in a lineage is a function of the number of independent parameters required to describe the form, and innovations such as structural duplication and functional decoupling can enhance the potential for diversity in a given clade. The functional properties of organisms are determined by underlying parts, but any property that is determined by three or more parts expresses many-to-one mapping of form to function, in which many morphologies will have the same functional property. This ubiquitous feature of organismal design results in surfaces of morphological variation that are neutral with respect to the functional property, and enhances the potential for simultaneously optimizing two or more functions of the system.

INTRODUCTION

This review examines general principles and repeating themes in the evolution of complex functional systems, with a particular focus on intrinsic features of organismal design that influence diversity. There is an increasing interest in the patterns and causes of morphological diversity in the tree of life (Carroll 2001, Collar et al. 2005, Erwin 2007, Foote 1997, Gavrilets & Vose 2005, Harmon et al. 2003, Losos & Miles 2002, Losos et al. 1998, Lovette et al. 2002, Niklas 1986, 2004, Ricklefs 2006, Schaefer & Lauder 1996, Stadler et al. 2001, Vermeij 1973, Wagner et al. 2006, Warheit et al. 1999). This area has had a strong tradition in paleontology, but the rapid emergence of new phylogenies and some methodological advances have ushered in an era of phylogenetically informed comparative analyses of morphological diversity in living groups. Empirical studies of functional diversity are much less common (Collar & Wainwright 2006), in part because of the intense effort required to characterize the functional properties of the large number of taxa required for a comparative analysis, but simulations and theoretical analyses have augmented the harder-to-come-by empirical data on functional diversity (Alfaro et al. 2004, 2005; Gavrilets 1999; McGhee & McKinney 2000).

Of special concern is how innovation in design and the nature of the form-function relationship impact the evolution of diversity in functional systems. Not all evolutionary novelties are equally potent. Some, such as the feathery crest on the head of some birds, seem to have little effect on the ecological potential and success of the lineage in possession, whereas others, such as powered flight or endothermy, are major breakthroughs in functional design that drastically changed the ecology and evolution of the lineages in which they evolved. The history of life is characterized by the periodic introductions of novelties that have had significant effects on subsequent ecological and evolutionary diversity: multicellularity, genome duplications, body segmentation, flowers, jaws, etc. To the extent that innovations in design are an important causative agent in spurring bouts of morphological, functional, and ecological diversification, the study of innovation takes on great significance as we try to understand the uneven distribution of diversity across the tree of life. But, how exactly do innovations influence diversity and how do we go about testing hypotheses about their effects on macroevolution? These are issues I hope to get at in the following pages.

I begin by reviewing some general features of the relationship between performance traits and their underlying basis that are fundamental to understanding how this relationship evolves. I then consider several categories of innovation that can influence functional diversity. This leads to a discussion of intrinsic properties of the relationship between form and function that influence patterns of diversity, and I attempt to draw some general conclusions about how the relationship between performance and its underlying basis is likely to shape patterns of diversity. In the final section, I review a recently developed method for conducting comparisons of phenotypic diversity between phylogenetic groups while accounting for differences in time and shared history within the lineages.

PERFORMANCE, FUNCTION, AND MORPHOLOGY

It is generally accepted that organismal performance traits are a major target of natural selection (performance being the ability of individuals to do the tasks that fill their lives). Performance traits typically have a complex underlying basis in the size, shape, and various properties of component parts, and the interplay between performance and its underlying basis has revealed a number of interesting evolutionary dynamics. Throughout this review I refer to functional properties, by which I mean the emergent physiological and mechanical properties of specific organ systems. The mechanical advantage of a lever system is an example of a functional property: It is a predictable property of the system equal to the ratio of the input lever divided by the output lever. Organisms are full of functional properties. The study of these properties and their underlying mechanisms traditionally falls under the purview of disciplines such as physiology, biomechanics, and biochemistry. When I refer to functional diversity, I mean diversity in functional properties, as opposed to diversity in the underlying parts. The connection to performance is that functional properties underlie performance capacity. The maximum bite force that an individual can exert is partly a function of the mechanical advantage of the jaw muscle acting across the jaw joint. Thus, there is a basic hierarchy to organismal design that is a theme in this review: The details of the phenotype come together to determine functional properties and functional properties determine the performance capacity of the individual. Understanding exactly how functional properties are related to underlying design is necessary before we can contrast the evolutionary dynamics of form, function, and performance.

The dependence of performance on organismal design is most easily grasped when the performance trait has a simple mechanical basis in design (Wainwright 1988), and it becomes less clear when behavior mediates the impact of the underlying mechanical system on performance. Thus, though musculoskeletal design may determine the capacity for jump height, the animal must be motivated to ever make use of that capacity, so it is possible for the underlying basis of jump performance to be obscured by the complicating influence of motivation. It is also true that organisms may infrequently, or even never, exhibit peak performance capacity during their lives (Husak 2006, Husak & Fox 2006, Irschick et al. 2005). Further, the nature of the map of phenotype to performance may involve regions of parameter space where phenotypic variation does not influence the expectations for performance capacity (Alfaro et al. 2004, Koehl 1996). These and other factors can make it difficult or very complex to fully determine the basis of performance, and many performance traits are situation-dependent (Helmuth et al. 2005). However, performance capacity and functional properties are emergent properties of organismal construction, and cause and effect are fundamentally discoverable.

Hierarchical Nature of Performance

Performance has a natural hierarchical structure, with the most proximal measures being the most directly linked to particular systems and the highest-order traits involving the integration of multiple functional systems. Consider locomotion as an example. Force output from a single leg muscle can be estimated with remarkable accuracy from morphological measurements of the muscle and a little knowledge about its biochemistry (Powell et al. 1984). Sprint speed involves the coordination of mechanical output from many muscles and their gearing as they work across skeletal linkage systems (Vanhooydonck et al. 2006). The ability to escape from a predator may only partly depend on sprint speed, because it also depends on the ability to change direction quickly and to respond appropriately to the predator's movements (Irschick et al. 2005). The point is that muscle contraction force, sprint speed, and escape ability range continuously from functional properties of the muscle to whole-organism performance traits, and each is based on the design of underlying systems, but that the more proximal attributes, such as force and sprint speed, have a simpler basis because they involve fewer components of the integrated organism. Fitness itself is the ultimate performance trait, integrating across all performance properties and all levels of design. The hierarchical nature of performance has important implications for evolution.

Trade-Offs Are Fundamental to Adaptive Diversity

Organismal design involves trade-offs. One of the keys to understanding diversity in functional systems is to identify the trade-offs that are associated with the construction of individual systems. Mechanical and physiological mechanisms involve inherent trade-offs where modifications that improve performance in one aspect come at the cost of another property (Ghalambor et al. 2004, Toro et al. 2004, Vogel 1994, Wainwright & Richard 1995). An example of this can be seen in the mechanical advantage of a simple lever system. As the ratio of input lever to output lever increases, the force transmission of the system increases, but the amount of movement that is transmitted through the system decreases. Trade-offs like this one are constraints on evolution. One significant category of innovation is the type of qualitative design change that decouples two performance traits that are primitively linked to a trade-off.

INNOVATION AND DIVERSITY

Two categories of innovations can be recognized in terms of how they impact the evolutionary dynamics and diversity of functional systems: those that directly influence the potential for phenotypic variation and those that allow the lineage to move into new regions of the adaptive landscape where new variants are favored. Innovations in the first category change the potential morphospace of the body plan possessed by the lineage. Innovations in the second category represent breakthroughs in organismal performance that allow the lineage to move into a novel region of the adaptive landscape where a variety of new adaptive peaks can be reached. These two classes of innovations mirror the basic distinction in morphospace biology between the morphospace of the theoretically possible (Hickman 1993, Raup 1966) and the adaptive landscape that is produced by mapping fitness into the morphospace (Arnold 2003, McGhee 1999, Wright 1932).

I want to emphasize the distinction between species richness and other forms of diversity, such as morphological diversity, functional diversity, or ecological diversity. Here I am concerned with these latter forms of diversity. In addition to morphospace expansion, I illustrate that the nature of how morphology maps onto function can influence patterns of diversification in evolving lineages. Advancements in organismal design that affect this mapping have emerged as a new class of innovations that can impact phenotypic diversity. The science of doing comparative analyses of morphological and ecological diversity has lagged behind similar studies of lineage diversification rate, or species richness, and I review some recent methodological and conceptual progress on this front. Morphological and functional diversity are frequently measured as variance among the members of the group under consideration (Foote 1997) and, unless otherwise stated, this is what I mean when referring to diversity.

Expanding the Theoretical Morphospace

The potential morphospace occupied by a body plan is determined by the number of independent parameters that are required to define the morphospace (Niklas 2004, Raup 1966, Sanchez 2004, Vermeij 1973). In his classic work on the mollusk shell, Raup identified three parameters that generated a morphospace of all mollusk shells (Raup 1966). A novelty that increases the number of parameters required to describe the form increases the size of the potential morphospace and provides an opportunity for greater diversity. One conceptually simple novelty that results in this sort of increase in morphospace is a structural duplication or subdivision event that results in increases in the number of elements that make up the form, and thus increases the dimensionality of potential morphospace (Friel & Wainwright 1997, Schaefer & Lauder 1986).

A common anatomical form of duplication among metazoans is body segmentation, a phenomenon that typically involves replicated body regions each with the same basic plan. Segmentation illustrates the general ways in which duplication enhances diversity. Repeated body segments allow retention of a role in a primitive function in one or more segments, while other segments can become modified for novel functions. Arthropods offer a classic example of this pattern, in which the body is segmented into units that each possess axial structures and limb elements. Anterior body segments are modified for performance in sensory systems and jaws, and in more posterior segments for locomotor specialization. In decapod shrimps, some body segments are modified for walking, whereas other segments are specialized for burst locomotion, which is used during escape from predators. In arthropods, the duplication of body segments with the same suite of anatomical elements permits an expansion of the potential morphospace because each element in each segment becomes a new axis in morphospace. Some researchers have thought of the diversity of form among repeated elements as a form of complexity (McShea 1996). In practice, only a few case studies have explored the consequences of duplication or subdivision events for morphospace expansion and phenotypic diversity (Friel & Wainwright 1997; Schaefer & Lauder 1986, 1996; Wainwright & Turingan 1993). The idea here would be to test whether duplication events result in higher phenotypic diversity among lineages within that clade, as compared to a comparison clade—ideally the sister group—that lacks the duplication.

Redundancy creates the potential for different body segments to perform different functions, such that the specialization of a segment for, say, burst locomotion need not be constrained by the necessity for the same segment to maintain performance in a second function, such as walking behavior. This consequence of duplication events, known as functional decoupling, can enhance diversity because it more readily leads to body designs that exhibit higher overall performance capacities (Liem 1973, Wainwright & Turingan 1993). Thus, for example, when walking and burst swimming are performed by different body regions in shrimp, adaptation for higher performance is not constrained by the need for a single region to maintain both functions. Functional decoupling through redundancy in design appears to be a widespread and powerful way in which novelties become innovations that lead to increased diversity. This mechanism is well known in molecular evolution (Burmester et al. 2006, Chung et al. 2006, Lynch 2003, Ohno 1970, Spady et al. 2005), developmental biology (Carroll 2001, Hughes & Friedman 2005) and organismal functional design (Emerson 1988, Friel & Wainwright 1997, Lauder 1990, Schaefer & Lauder 1996).

The idea that a single anatomical system may be required to perform multiple functions has been viewed as a major constraint on evolutionary diversification, and conversely, the decoupling of such a constraint is seen as a major avenue to increasing diversity. In fact, it is a basic feature of organisms that body regions are involved in multiple functions, and the need to maintain functionality across the range of functions is likely to be an important factor in shaping adaptive evolution. Although structural duplication is one way to decouple functions, there are other routes. Gatesy & Middleton (1997) argued that the introduction of winged locomotion in birds released a constraint on the hindlimbs of theropods. Their proposal was that the theropod hindlimb had been morphologically constrained because this body region was the sole system used for locomotion. With the origin of forelimb-powered locomotion (flight), they argued that the bird hindlimb was free to become modified for a greater diversity of locomotor specializations. They showed evidence for increased diversity of the hindlimb in birds as compared to theropods (Gatesy & Middleton 1997, Middleton & Gatesy 2000). Similar arguments have been made by other researchers. The origin of a specialized condition of the pharyngeal jaw apparatus in cichlid fishes, by providing a second set of jaws that could specialize on prey processing functions, was hypothesized to result in increased diversity of the oral jaws, which are used in prey capture (Liem 1973, Liem & Osse 1975), and there has been some support for this idea (Hulsey et al. 2006).

Nature of the Form-Function Map

In recent years there has been mounting evidence of intrinsic design features that can relieve functional constraints on anatomical systems in the absence of duplication events. One general mechanism involves many-to-one mapping of morphology to function (Alfaro et al. 2004, 2005; Hulsey & Wainwright 2002; Wainwright et al.

2005). One inherent feature of a complex functional system is that multiple morphologies can have the same functional property. This occurs when the functional property depends on three or more underlying parameters and is contrasted with simple systems that are determined by one or two parameters. Many functions determined by only two parameters show many-to-one mapping (e.g., $y = a + b$). Consider the example of the mechanical advantage of a muscle acting across a joint. Mechanical advantage is the ratio of two distances: an input lever length and an output lever length. Once scale is removed, there is only a single combination of input lever length and output lever length that results in a particular value of mechanical advantage. This system exhibits one-to-one mapping of form to mechanical property. Now, consider instead the force exerted at the end of the outlever. This is a function of the mechanical advantage of the lever and a third parameter, the input force exerted by the muscle acting on the lever. Output force is equal to input force times the ratio of input lever to output lever. There are numerous combinations of the three parameters that all give the same value of output force. For example, mechanical advantage of 0.5 (input lever length/output lever length = 0.5/1) and input force of 8 give the same output force as a mechanical advantage of 1.0 (input lever/output lever = 1/1) and an input force of 4. In this case, there is a many-to-one mapping of musculo-skeletal design-to-force output of the system.

Many-to-one mapping of phenotype to functional property has been shown in many systems (Blob et al. 2006, Collar & Wainwright 2006, Guderley et al. 2006, Hulsey & Wainwright 2002, Lappin & Husak 2005, Marks & Lechowicz 2006, Stayton 2006, Toro et al. 2004). One well-explored example is suction index (SI) (**Figure 1**), the capacity of an individual fish to generate suction pressure during suction feeding. Suction index (SI) is based on the strength of a muscle and the morphology of the linkage system that transmits this force to the expanding mouth cavity during suction feeding. Because most biologically relevant functional properties have a basis in three or more elements, it can be expected that many-to-one mapping is a general feature of organismal design. Therefore, any macroevolutionary consequences of many-to-one mapping have the potential to be quite widespread.

The implications of many-to-one mapping of form to function for diversity are at least twofold. First, because many forms can have the same functional property, there are surfaces in morphospace that define mechanically neutral morphological variation (**Figure 2**). These regions of neutral change in morphology (or, more generally, in the parameters that determine the functional property) offer opportunities for lineages to explore regions in morphospace without altering the functional property of the mechanism. The simplest consequence of this is that there may be phenotypic variation among individuals in a population, or among species, that does not translate into diversity in the functional property. It is possible to see conservation of function in the presence of substantial morphological changes.

A second consequence involves the observation that most body parts serve multiple functions. Anatomical regions of the body almost always have multiple functional properties that are important to the organism and are potentially exposed to natural selection. Many-to-one mapping and the resulting regions of neutral morphological variation with respect to one functional property allow flexibility in design so that

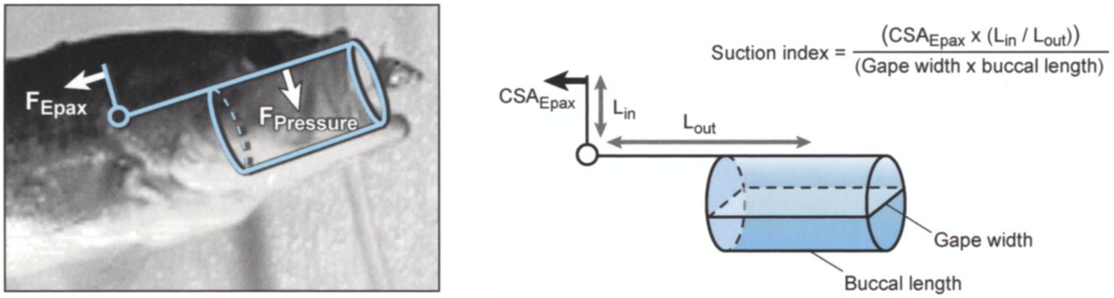

Figure 1

Model of suction feeding capacity in fishes that allows calculation of the capacity of an individual fish to generate suction as a function of several morphological features. The model treats the feeding mechanism as a lever system that transmits force and movement from the contracting epaxial muscles to the expanding buccal cavity (Carroll et al. 2004). It is assumed that the ability to generate a buccal pressure gradient is limited by the forces that the expansion muscles can generate and the ability of the skeletal elements to resist these forces. The expanding buccal cavity of centrarchids can be modeled as an expanding cylinder with pressure being distributed across its surface. The magnitude of the expansion force is equal to the magnitude of the buccal pressure multiplied by the projected area of the buccal cavity. This force exerts a torque on the neurocranium, directed ventrally at the buccal cavity. The force generated by the epaxial muscles (and matched by the ventral, sternohyoideus muscle) must be greater or equal to the resolved force of buccal pressure as it is transmitted through the lever system of the neurocranium. The magnitude of the pressure gradient that a fish can generate is therefore a function of the amount of force that the epaxial muscles can generate (proportional to physiological cross sectional area, PCSA), the moment arm of the epaxialis (L_{in}), the moment arm of the buccal cavity (L_{out}), and the projected area of the buccal cavity (buccal length × buccal width). Force generation of the epaxial muscles is based on force per unit of the cross-sectional area and PCSA and, by omitting the former from the equation, allows one to generate a suction index (SI) that involves the morphological parameters of the relationship, but does not make assumptions about how force per unit area of the muscle may vary among feeding events and across taxa. This model was tested by making measurements of peak suction pressure in 45 individual centrarchid fishes, ranging across five species, each ranging about 2.5-fold in body length. Morphological measurements were made from each specimen to parameterize the model, and the predictions were compared against realized performance. Suction index (SI) shows many-to-one mapping because many different combinations of the morphological parameters will have the same value of SI. That is, in terms of SI, many different-shaped fish skulls are functionally similar.

the structure can become modified for other functions while maintaining the original function.

Many-to-one mapping leads to several macroevolutionary expectations that have been explored in simulations and empirically in a few natural systems. First, many-to-one mapping can partially decouple the accumulation of morphological and mechanical diversity within clades. This pattern was found in simulations of the evolution of a four-parameter lever mechanism found in fish jaws, the 4-bar linkage, even when some constraints were placed on the evolution of the four skeletal elements from observed variance-covariance relationships (Alfaro et al. 2004, 2005). A weak positive relationship ($r = 0.5$) was found between the disparity of morphological traits

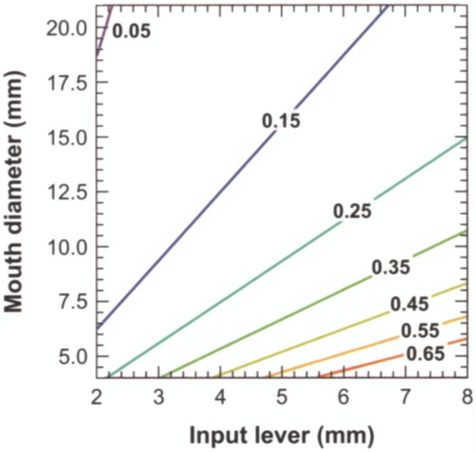

Figure 2

Plot of suction index (SI) in a two-dimensional region of morphospace defined by the input lever of the epaxial muscle and the diameter of the mouth. All other parameters in the SI model are held constant for this figure. The lines on the plot represent isoclines of constant value of SI, and indicate that many combinations of in-lever and mouth diameter result in the same value of SI. This many-to-one mapping is a general feature of complex systems: Any functional property determined by three or more parameters will show many-to-one mapping of morphology to the functional property.

(variance across tips) and the mechanical property of the 4-bar linkage after 1000 simulations on clades with 500 terminals (Alfaro et al. 2004). An empirical study of SI in centrarchid fishes found no relationship between variance among species in SI and variance in the parameters that make up SI across the three major clades in this group (Collar & Wainwright 2006). These studies consistently reveal the sobering pattern that morphological diversity may not predict functional diversity, even when the morphological parameters are being used to calculate the functional property. Indeed, if a weak or no correlation is the generally expected relationship between the diversity of functional properties and the diversity of the parameters used to calculate those properties, this is a major blow to research programs that try to interpret morphological diversity as being indicative of functional or ecological diversity based on the general assumption that different morphologies have different functional properties and result in different ecological patterns (Briggs et al. 1992, Valentine 1980). Studies of the evolution of functional diversity should measure functional properties and not rely upon the assumption that morphology can be used as a proxy for functional diversity.

A second link to macroevolution concerns expectations for convergent evolution. Using simulations of natural selection acting on a mechanical property of a complex lever system in the jaws of some fishes (the 4-bar linkage), Alfaro et al. (2004) showed that the morphology arrived at in response to selection depends on the starting morphology in the simulation, even when all cases result in the population reaching the same value of the mechanical property. Mechanical convergence only created morphological convergence when the starting forms were similar. Many-to-one mapping tends to amplify the contingency of evolution (Foote 1998) and results in different lineages taking different routes through morphospace, even if they are exposed to identical histories of selection.

One important property of organismal design is that body parts are almost always involved in determining multiple functional properties. This means that though selection is working to optimize many performance traits at once, the underlying basis for those traits often involves shared parts, and in some cases involves 100% overlap in parts. Although this connectedness is often seen as a major constraint on the evolution of design, one of the features of many-to-one mapping of form to function is that the surfaces of neutral variation with respect to one functional trait permit changes that alter other functional traits. In other words, the complexity of most organismal functional properties increases the capacity for optimizing multiple functions. Because of these neutral surfaces of change, there are pathways of change that need not necessarily involve trade-offs in function. Specific examples of this phenomenon are developed in recent papers that involve a combination of simulation and empirical data (Alfaro et al. 2004, 2005). The evolutionary flexibility that is provided by many-to-one mapping of form to function appears to be a major factor in facilitating phenotypic diversification.

Breakthroughs that Change the Adaptive Landscape

Although changes in body plan can alter the range of potential morphologies, it is also clear that some novelties have sufficiently radical consequences for the performance capacity of the organism such that they effectively open up whole new possible ways of life and can lead to subsequent diversification. Sometimes referred to as major innovations or key innovations, such an innovation is a breakthrough in design that moves the lineage into a new region of the adaptive landscape (Erwin 1992, Hunter 1998, Liem 1973, Vermeij 1995). There are many compelling examples (Bateman & DiMichelle 1994, Jernvall 1995, Jernvall et al. 1996, Norris 1996). With the origin of powered flight in birds, new feeding strategies, life history patterns, and opportunities for novel habitat use became possible, and the resulting radiation appears to be anchored on this design breakthrough. Similarly, the origin of jaws in vertebrates was followed by a successful radiation of highly predatory organisms. Note that in these examples, the innovations involve a significant enhancement in some aspect of the behavioral performance capacity of the organisms that opened up the exploitation of novel resources, such as new food types, new habitats, or new life-history patterns.

In recent years researchers have tended to focus on the implications of putative key innovations on lineage diversification rate (Bond & Opell 1998, Gianoli 2004, Hodges 1996, Sanderson & Donoghue 1996), and there has not been as much work done testing the impact of innovations on morphological, functional, or ecological diversity (Gatesy & Middleton 1997). This is in part owing to the difficulty and work involved in assembling data for a large number of taxa, and it can be anticipated that such studies will become more frequent in the future.

Both increases in the potential morphospace and breakthroughs in design only open up the potential for subsequent radiations; they do not make such radiations inevitable. There is an important role for stochastic processes and the appropriate ecological conditions of disruptive selection to realize the potential change in diversity. In this sense the innovations only set the stage for changes in diversity; they do not, by themselves, cause the change (Labandeira 1997, Wagner 2000). Changes in morphological diversification also need not be tied to changes in speciation rate, extinction rate, or net diversification rate (Ricklefs 2004, 2006).

COMPARATIVE ANALYSIS OF DIVERSITY

The discussions above suggest a research program in the history and biology of innovations. There are many questions that one might like to ask about a putative innovation and its consequences for diversity. Was the innovation followed by an increase in the diversity of the functional systems affected by the breakthrough or of other functional systems? Does the innovation result in a qualitative shift in some aspect of performance capacity or resource use? Given that the innovation is associated with an increase in diversity, what is the tempo of that change? Is there a period of relative stasis before the diversity is accelerated, or does the change happen coincident with the innovation? These questions are inherently historical, and all of them can be addressed with the use of a time-calibrated phylogeny of the group and its relatives as a basis for comparisons. Methods and concepts for conducting phylogenetically correct comparisons of morphological, functional, and ecological diversity (Foote 1996, Garland 1992, O'Meara et al. 2006) between lineages have lagged behind the development of methods for doing comparative studies of lineage diversification rate (Magallon & Sanderson 2001, Sanderson & Donoghue 1994, Slowinski & Guyer 1994). Important insights about the role of phylogenetic history in species diversity have resulted in the emergence in recent years of a focus on lineage diversification rate. But, just as diversification rate should be recognized as the phylogenetically corrected metric of species richness in a clade, similarly, rate of morphological evolution provides a phylogenetically corrected metric of trait diversity (Collar et al. 2005, Garland 1992, Martins 1994, O'Meara et al. 2006). Below I review an approach for comparing rates of morphological evolution (that is, morphological diversity) between two lineages.

Functional and Morphological Diversity

There are several widely used metrics of morphological diversity, but variance and range are the most widely used (reviewed by Ciampaglio et al. 2001, Erwin 2007, Foote 1997). Range is of interest because it reflects information about the farthest regions of morphospace that have been reached by members of the group in question (Pie & Weitz 2005). Range may be useful in addressing questions about which regions of morphospace have been occupied by a group and which have not (Stebbins 1951, Van Valkenburgh 1988). The multivariate measure of range is usually some version of an N-dimensional minimum polygon that encloses all individuals in the group. Although range is of particular interest in some case studies, the statistical properties of a range make doing careful quantitative comparisons between groups awkward. Also, in a Gausian distribution, range scales with sample size, which further complicates comparisons.

Variance of traits is the most widely used metric of morphological diversity (Foote 1997, McClain 2005, Roy & Foote 1997). Variance captures the dispersion of members of the group in morphospace, is not so susceptible to the effects of a few outliers, and does not scale with sample size so the metric is versatile and amenable to statistical tests. Variance also relates directly to the most commonly used model of character evolution, Brownian motion, and its derivatives so that the connection between this model of evolution and variance among evolving lineages is strong (Martins & Hansen 1997, O'Meara et al. 2006, Pagel 1999, Purvis 2004).

It is intuitive that morphological diversity among species is affected by their phylogenetic history. After all, species usually most resemble their closest relatives. But exactly how do we expect phylogeny to relate to morphological diversity, and how can we use this knowledge in framing comparative tests of morphological diversity? To get at these issues we first need a model of trait evolution. Perhaps the most straightforward model that is used is Brownian motion (Martins & Hansen 1997), the model used in calculating independent contrasts (Felsenstein 1985) and the estimation of ancestral states (Schluter et al. 1997). Under Brownian motion the potential for trait change occurs at some designated time interval, with the magnitude of the change being drawn from a normal distribution with a mean of zero and some variance. The variance of this distribution of potential trait change is referred to as the Brownian rate parameter, and the expected variance of the trait among lineages in a phylogeny is equal to the number of opportunities for trait change (proportional to time in the Brownian model) times this variance in the distribution of potential trait changes, or the Brownian rate parameter. The larger the rate parameter, the greater the expected variance among similar-aged lineages descending from a common ancestor. Thus, diversity among the lineages within a clade develops as a function of the time in the phylogeny, the amount of shared history between lineages, and the rate of evolution of the trait (Ackerly & Nyffeler 2004, Garland 1992, Gittleman et al. 1996, Mooers et al. 1999, O'Meara et al. 2006, Thomas et al. 2006). A key insight that emerges from this is that a phylogenetically corrected comparison of morphological diversity between two clades involves removing the confounding effects of time and shared history, and comparing the rate of evolution of the traits of interest (Garland 1992, O'Meara et al. 2006). To compare diversity in two clades after removing the effects of time and phylogeny, one can compare estimates of the Brownian rate parameter. The Brownian rate parameter can be estimated with average values for the phenotypic traits in each tip taxon, and a phylogeny can be estimated with branch lengths proportional to time.

As a simple illustration of this effect of time, consider two monophyletic groups of birds, one that shows considerable variation among species in bill morphology and the other that shows minimal differences among species (**Figure 3**). In each group, bill morphology has been diversifying since the time of the most recent common ancestor (MRCA). If the age of the MRCA of the diverse group is considerably older than the age of the MRCA in the low-diversity group (**Figure 3*a***), then time may be a

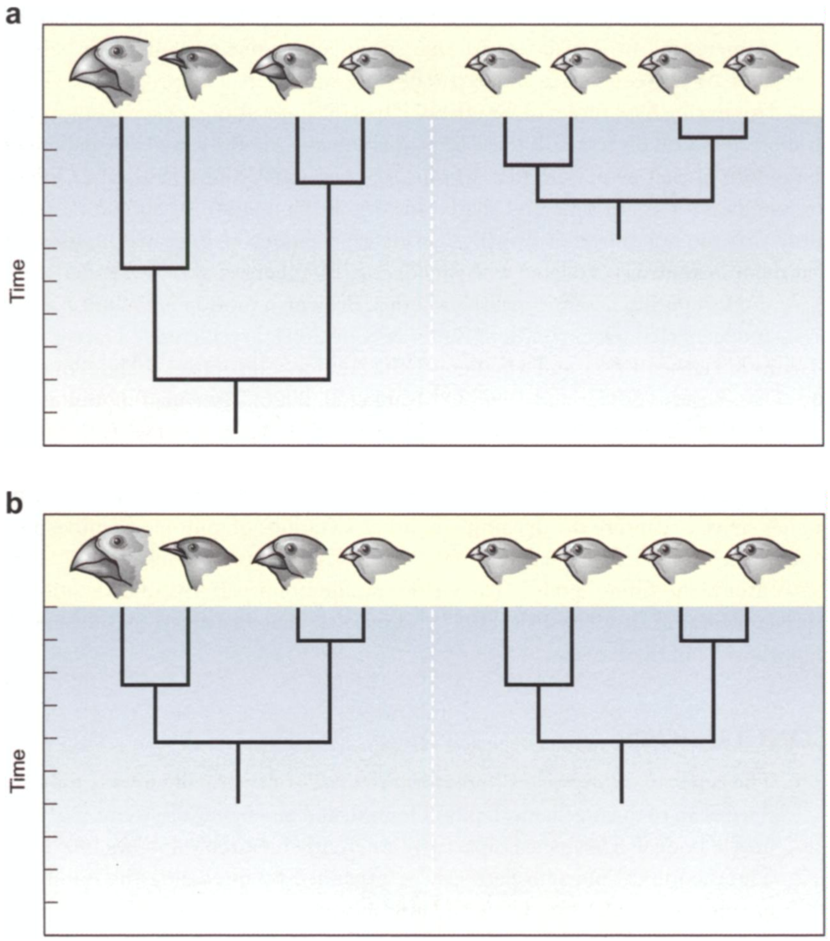

Figure 3

Diagrams illustrating the importance of time in the interpretation of differences in morphological diversity between two monophyletic groups of birds. (*a*) The high-diversity group is much older than the low-diversity group. In this case the difference in diversity between groups may be due to differences in the amount of time the two groups have had to diversify. (*b*) Here, the age of the two groups and the total time in the phylogenies are the same, suggesting that the rate of bill evolution in the high-diversity group would have been higher than in the low-diversity group. The approach described in this chapter is designed to separate the effects of time and rate of evolution on the observed diversity in a group of terminal taxa.

trivial explanation for the difference in diversity between groups. But, if the MRCAs are of similar age (**Figure 3*b***), or the age of the low-diversity group is actually older, then we would infer that the rate of evolution of bill morphology has been higher in the diverse group.

This framework is formalized in recently developed software that accepts as input a phylogeny with branch lengths in time, or relative time, and trait values for the tips of the phylogeny (Collar et al. 2005, O'Meara et al. 2006). The program, "Brownie," then estimates the Brownian rate parameter and allows one to compare it between two clades, or between a clade and its paraphyletic outgroup. This program is well designed for testing hypotheses of the effects of specific innovations, or synapomorphies, on morphological diversity. In these tests, it is actually the Brownian rate parameter, or the rate of trait evolution, that is compared between groups, thus removing the confounding affects of time and shared history. Preliminary tests should be run to verify that the exisiting trait distribution fits expectations of Brownian motion and that the trait value is correlated with phylogeny (Blomberg et al. 2003, Pagel 1997).

An important discussion concerns whether Brownian motion is the most appropriate model of character evolution (Butler & King 2004, Freckleton & Harvey 2006, Martins & Hansen 1997), and whether it is the best for comparative analyses of diversity (Diaz-Uriarte & Garland 1996, O'Meara et al. 2006). Brownian motion is well suited to this particular hypothesis-testing framework because it makes the fewest assumptions about constraints on trait evolution. However, it may not always capture the important ecological forces and processes that occur during radiations. Other models strive to capture the dynamics under expectations of multiple adaptive peaks superimposed upon Brownian motion (Butler & King 2004, Hansen 1997, Pagel 1997). But niche-filling models may yield quite different patterns of diversification (Harvey & Rambaut 2000, Price 1997), suggesting that Brownian motion may be inappropriate in these cases.

CONCLUSIONS

1. The capacity of organisms to perform the tasks of their daily lives is rooted in the design of the mechanical, physiological, and biochemical systems that make up the body. Performance capacity is inherently hierarchical in organization.
2. The theoretical morphospace can be expanded by increasing the number of parameters required to define the morphospace. This means that innovations that increase the number of parameters required to define the form can have the effect of increasing the potential diversity of lineages. Duplication and decoupling events are major mechanisms of morphospace expansion and can lead to increased diversity. They are documented to work at virtually all levels of organismal design.
3. Many-to-one mapping, in which many different morphological combinations have the same functional property, is an inherent property of all functions that are determined by three or more parameters. This ubiquitous feature of organismal design can encourage diversity by allowing morphological variation that is neutral with respect to the functional property. This flexibility in form allows parts of the body to accommodate multiple functions by adapting to one function through changes in form, while maintaining a second function by moving through regions of neutral morphological change.
4. Many-to-one mapping can lead to a disconnect between morphological diversity and functional diversity, a pattern that has been confirmed in several natural systems. This decoupling of diversity at adjacent levels of design poses a major

obstacle to attempts to infer ecological diversity from data sets on morphology, a program that has an especially rich history in paleontology.

5. In order to conduct phylogenetically correct comparisons of morphological or functional diversity one must separate the confounding affects of time, shared phylogenetic history, and rate of trait evolution, which combine to yield standing clade diversity. Methods for comparing rate of character evolution have recently been developed that require as input phylogenies with branch lengths proportional to time and trait values for taxa in the tree. These methods can be used to compare diversity in two clades, test for the effects of putative innovations on diversity, or study the tempo of evolution.

DISCLOSURE STATEMENT

The author is not aware of any biases that might be perceived as affecting the objectivity of this review.

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