Evo Edu Outreach (2008) 1:259–273
DOI 10.1007/s12052-008-0055-6

ORIGINAL SCIENTIFIC ARTICLE

Evolutionary Trends

T. Ryan Gregory

Abstract The occurrence, generality, and causes of large-scale evolutionary trends—directional changes over long periods of time—have been the subject of intensive study and debate in evolutionary science. Large-scale patterns in the history of life have also been of considerable interest to nonspecialists, although misinterpretations and misunderstandings of this important issue are common and can have significant implications for an overall understanding of evolution. This paper provides an overview of how trends are identified, categorized, and explained in evolutionary biology. Rather than reviewing any particular trend in detail, the intent is to provide a framework for understanding large-scale evolutionary patterns in general and to highlight the fact that both the patterns and their underlying causes are usually quite complex.

Keywords Body size · Complexity · Cope's Rule · Driven trend · Evolution · Extinction · Natural selection · Passive trend · Speciation

Introduction

The detection, characterization, and explanation of patterns represent major components of the scientific endeavor. However, those who seek to study patterns objectively must overcome several quirks of human psychology, including tendencies to identify patterns where there are none, to make assumptions regarding cause from the observation of a pattern alone, to extrapolate from individual cases to entire systems, and to focus on extremes rather than recognizing diversity. This is especially true in the study of historically contingent processes such as evolution, which spans nearly four billion years and encompasses the rise and disappearance of hundreds of millions, if not billions, of species and the struggles of an unimaginably large number of individual organisms.

This is not to say that no patterns exist in the history of life, only that the situation is often far more complex than is acknowledged. Notably, the most common portrayals of evolution in nonacademic settings include not just change, but directional, adaptive change—if not outright notions of "advancement"—and it is fair to say that such a view has in the past held sway within evolutionary biology as well. Evolutionary trends—which may be defined broadly as identifiable patterns in which the overall evolution of a trait occurs in a given direction within a group for a prolonged period of time[1] (Fig. 1)—are both real and important. Indeed, McKinney (1990) suggested that "the concept of 'trend' is arguably the single most important in the study of

T. R. Gregory (✉)
Department of Integrative Biology, University of Guelph,
Guelph, ON, Canada N1G 2W1
e-mail: rgregory@uoguelph.ca

---

[1] Some authors consider only consistent, directional change within lineages to constitute a trend, but a broader definition that allows for changes in average traits within entire clades is used in this article. This is in line with several more technical definitions of an evolutionary trend that have been presented previously, which include "a long-term directional change in a summary statistic for a clade, such as the mean" (McShea 2005) and "a directional character gradient through time in a well-defined monophyletic clade" (Gould 1990). According to McKinney (1990), "Trends are persistent statistical tendencies in some state variable(s) in an evolutionary time series. Such variables may be point estimates (e.g., mean, maximum) of a group (e.g., cladogenetic, concerning a number of species) or a single lineage (anagenetic, concerning a number of individuals in a species)." For a review of the terms "clade" and "monophyly", see Gregory (2008).

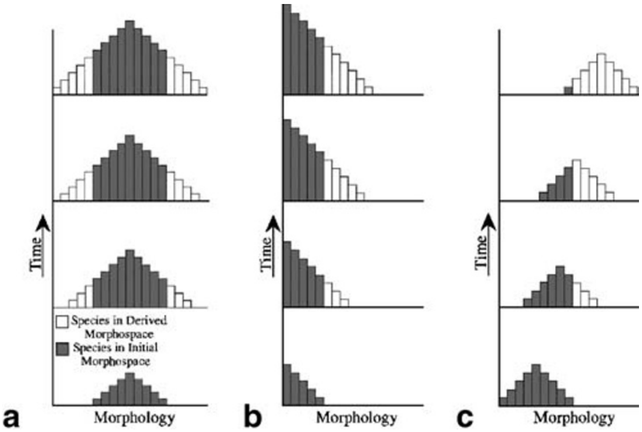

Fig. 1. Evolutionary trends represent directional changes in the average value of a given characteristic, such as body size (e.g., Alroy 1998) or some measure of complexity (e.g., number of cell types or differentiation of serially repeated limbs; Valentine et al. 1994; Adamowicz et al. 2008), among species and their descendants over prolonged periods of time. In this figure, the values of an undefined physical trait ("morphology") of older species are given in *gray*, and those of newer species are shown in *white*. In **a**, new species that differ from their ancestors in this morphological trait have appeared, but this has included both increases and decreases in the parameter in question in roughly equal measure, which means there has been no net change in the average and thus no trend with regard to this feature. In **b**, increases have occurred but decreases have not been possible, perhaps because of a physical limitation. In this case, there is an increase in the average of the trait in younger versus older species, but this is because of the fact that diversification was free to happen in only one direction. In **c**, there is a clear increase in the value of the trait in the whole distribution; in fact, nearly the entire initial distribution with lower values has been replaced over time. Figure from Wagner (1996), reproduced by permission of Blackwell

evolution," Alroy (2000) described their study as "one of the oldest and more intriguing topics in evolutionary biology," and Gould (2002) noted that "trends represent the primary phenomenon of evolution at higher levels and longer time scales." It is therefore critical that the nature, generality, underlying causes, and significance of trends be neither overlooked nor overstated.

This article provides a basic introduction to the way evolutionary trends are identified and explained in modern evolutionary biology. The general concepts reviewed in this article provide a framework for understanding large-scale patterns in evolutionary history. The most important message is that trends are real phenomena worthy of investigation, but that their properties and underlying causes are rarely simple.

Questions About Trends

Many broad trends have been postulated to characterize the history of life. For example, McShea (1998) listed eight potential large-scale trends, including overall directional changes in "entropy, energy intensiveness, evolutionary versatility, developmental depth, structural depth, adaptedness, size, and complexity." Of these, patterns of change involving increases in body size and morphological complexity are the most familiar, and it is not difficult to see why: it is obvious that, *on average*, organisms today are larger and more complex than they were in the distant past. In the beginning, all life was almost certainly small and relatively simple, whereas the largest and most complex species ever to have existed (as far as is known) are still alive today, having arrived on the scene very recently in Earth history. Because they have been discussed extensively in the scientific literature (see, e.g., Valentine et al. 1994; Gould 1996; McShea 1996; Kingsolver and Pfennig 2004; Hone and Benton 2005; Purvis and Orme 2005; Adamowicz et al. 2008) and because they are the most familiar, trends toward increases in body size and complexity will form the basis of most of the examples used in this paper. However, worthy as they are of detailed discussion in their own right, a comprehensive review of these trends falls outside the scope of this article.

Of course, one must interpret even the most familiar patterns with caution. An increase in the average value of a particular trait counts as a trend in the most basic sense, but averages and other summary statistics are not real entities, and biological systems are most often characterized by extensive variation. As such, a change in average by itself should not be overestimated in its importance (Gould 1988, 1996). Moreover, simple comparisons between the earliest versus a few of the most recent forms of life provide few insights regarding the possible trends that may pertain to life as a whole nor about the causes of any such trends that may exist. To gain a better grasp of a given trend, several key questions must be answered about it, the most important of which are outlined in the following sections.

Is There Really a Trend?

The most obvious question to ask first is whether a trend exists at all. This may seem straightforward, but the most reliable demonstration of a trend is one that includes detailed historical information that can be difficult to obtain. Comparisons of fossils and/or inferences drawn from phylogenetic analyses[2] are usually necessary to establish the existence of a trend, and these generally require considerable effort. As a result, there can be disagreement among researchers regarding the existence or generality of even the most widely studied trends such as

---

[2] Phylogenies, or evolutionary trees, provide information regarding the relationships among lineages (see Gregory 2008) and can be used—with due caution—to infer the characteristics of hypothetical ancestors for comparison with those of their modern descendants.

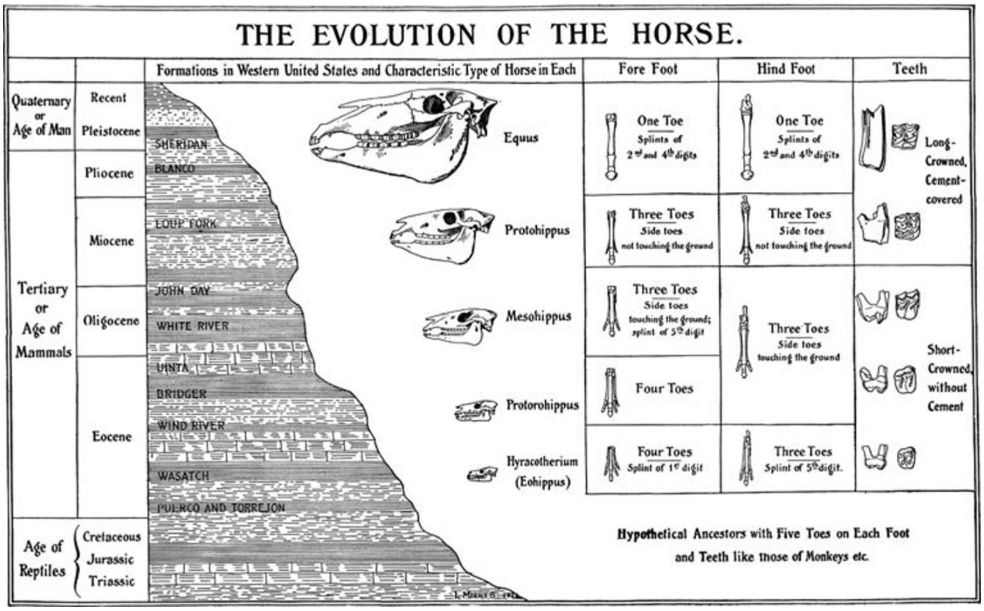

Fig. 2 A figure first printed in 1903 depicting the "classic" trends in horse evolution: increase in body size, reduction in number of toes, and increase in height of grinding teeth. A similar figure (although omitting body size) was drawn by O.C. Marsh for use in a lecture by T.H. Huxley in 1876. Representations of horse evolution in this linear manner can still be observed in many museums and textbooks, despite the fact that the history of this group and the trends that occurred in it are well-known to be far more complex (cf. MacFadden 1992). From Matthew (1903), also printed in Matthew (1926)

those involving increases in body size or complexity (e.g., Gould 1996, 1997; McShea 1996). In short, trends cannot be assumed to exist but must be demonstrated empirically, no matter how intuitive their occurrence may seem.

Local or Global?

When a trend is identified on the basis of reliable historical data, it is important to ask how universal it is or, conversely, to what taxonomic groups or time spans it is limited. That is to say, it is useful to determine whether the trend is "global" taxonomically (i.e., applies to a major group, up to and including all of life) or temporally (i.e., applies to the entire history of a group, up to and including the history of all life), or if it is only "local" in taxonomic or temporal scope.

As an example, it is often claimed that lineages in general tend to exhibit gradual increases in body size over time, an observation known as "Cope's Rule" after nineteenth century paleontologist E.D. Cope. This tendency is often taken as a global trend that applies to many lineages, if not to life at large. However, more detailed analyses of particular groups have shown it not to apply in some cases (e.g., Jablonski 1997) or to be local rather than global even in so-called classic examples of the trend.

In terms of the latter, one need look no further than horses, which had been thought since the late 1800s to provide an unambiguous demonstration of several evolutionary trends over their 55 million year history, including a progressive increase in body size as well as a reduction in the number of toes (modern horses walk on one toe) and adaptations of the teeth for grinding vegetation (Fig. 2; MacFadden 1992). However, more detailed analysis of horse fossils over the past 20 years has revealed that the first 35 million years of their evolution involved no significant change in body size at all and that the trend toward larger average size resulted mainly from an increase in the size of the largest horse as the diversity of the group expanded; reductions in size also occurred in some genera (Fig. 3; MacFadden 1986, 1992; Gould and MacFadden 2004). As MacFadden (2005) noted recently:

> Although the 55-My-old fossil horse sequence has been used as a classic example of Cope's Rule, this notion is now known to be incorrect. Rather than a linear progression toward larger body size, fossil horse macroevolution is characterized by two distinctly different phases. From 55 to 20 Ma [million years ago], primitive horses had estimated body sizes between ~10 and 50 kg. In contrast, from 20 Ma until the present, fossil horses were more diverse in their body sizes. Some clades became larger (like those that gave rise to *Equus* [modern horses and their relatives]), others remained relatively static in body size, and others became smaller over time. [See also MacFadden (1986, 1992)].

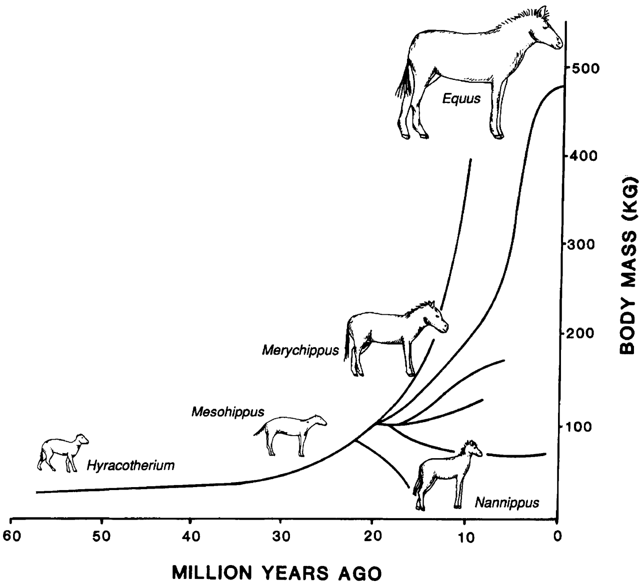

Fig. 3 Patterns of body size evolution in fossil horses from North America. For the first 30 million years of their history, there was relatively little change in body size, and the growth in average size over the past 25 million years reflects an expansion of diversity within the group as a whole rather than a progressive increase in every component lineage. In fact, several lineages of horses underwent reductions in body size over the same period. This shows how trends may be localized both temporally and taxonomically. From MacFadden (1992), reproduced by permission of Cambridge University Press

There evidently is a trend toward increased body size in horses, but it is localized to certain genera and time periods and reflects increasing diversity rather than a strong global tendency across all lineages. Merely comparing modern genera (*Equus*) with the earliest members of the group (*Hyracotherium*) may reveal an average increase in size, but this provides a greatly oversimplified view of a complex and interesting pattern. It also fails to indicate that had a different horse lineage, such as the dwarfed members of the genus *Nannippus*, been the sole survivor to the present instead of the familiar, large-bodied *Equus*—both of which went extinct in their original New World ranges in North America with migrant populations of *Equus* surviving in the Old World—then any such trend would hardly have been so apparent (Gould 1987).

Branching or No Branching?

Once its scope has been identified, the next key question about a trend is whether most of the directional change has occurred consistently within single lineages (anagenesis) or whether the trend has been generated by processes involving significant branching to form new daughter species (cladogenesis). Of course, it is possible—and perhaps quite likely—that both anagenetic and cladogenetic processes are at work in generating a given trend (e.g., Maurer et al. 1992). Nevertheless, any distinction that can be found is important because anagenetic trends, especially if repeated in multiple independent lineages, may be indicative of adaptive factors operating within populations that drive change in the observed direction, whereas cladogenetic trends can be explained by a variety of factors not involving population-level adaptation (Fig. 4; Gould 1990; McKinney 1990; see below). In addition, this may contribute to considerations regarding “global” versus “local” trends: a trend that occurs within only one or a few related species is by definition more local than one that appears only in comparisons across many species, although repeated anagenetic trends within multiple lineages may bespeak an especially strong global tendency.

What Accounts for the Trend? Dynamics, Causes, and Bases

A large-scale evolutionary trend is a pattern of directional change occurring over long periods of time. The detection of such a pattern does not, in itself, provide an explanation for it, and it is in the effort to account for observed trends that the situation becomes especially complex. After detecting and characterizing the trend (as in the first three questions above), one may investigate the reasons for the trend from perspectives focused on several levels of explanation; these are classified in this article into three distinct categories of increasing specificity (Table 1). Note that these are not technical terms or official jargon, they simply provide a useful means of organizing one’s thoughts regarding the multilevel influences that can generate evolutionary trends.

1. *Dynamics*. Digging down one level from the large-scale trend itself, one may ask about the patterns of change

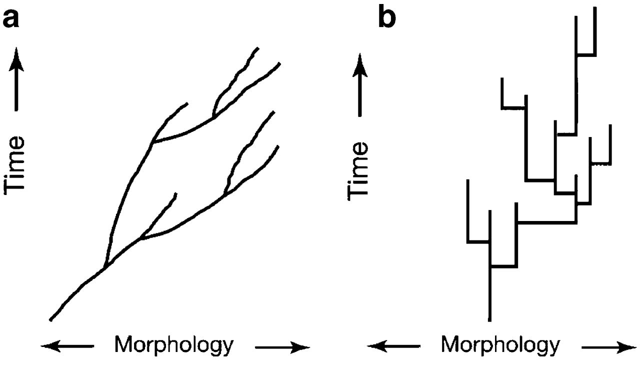

Fig. 4 Different patterns resulting from anagenetic versus cladogenetic trends. In **a**, most of the directional change occurs within species, and branching to form new species (speciation or cladogenesis) does not contribute to the occurrence of the trend. In **b**, which reflects a pattern of speciation known as “punctuated equilibria,” most morphological change occurs in association with speciation events, and the trend is said to be cladogenetic because change occurs primarily among species, not within them. Based on Gould (1990)

Table 1 Summary of the levels of explanation for large-scale evolutionary trends with hypothetical examples of each

Term	Definition	Hypothetical example
Trend	A pattern of large-scale change in a parameter in a given direction, especially in terms of the average across multiple lineages and long periods of time.	An observed pattern in which average body size increases within several major lineages of animals over millions of years.
Dynamic	The characteristics of changes among component lineages or at smaller time scales that underlie a large-scale trend. If the dynamics occur consistently in one direction, then the trend is driven, whereas if the dynamics vary, then the trend is passive.	A driven trend in which descendant species consistently have larger bodies on average than their ancestors, or a passive trend in which lineages begin at small size such that a bounded increase in variance results in an increase in average size.
Cause	The cause(s) of the dynamics that generate trends.	A driven trend caused by natural selection operating among individuals, or a passive trend resulting from a developmental constraint that limits change in one direction.
Basis	The specific underlying basis (or bases) for the cause(s) of trend dynamics.	Natural selection for larger body size on the basis of larger individuals being more effective predators or acquiring better territories relative to smaller individuals, or developmental constraints related to limitations on organ function at very small sizes.

that have occurred within component lineages and over shorter timescales. In particular, whether the internal dynamics of the larger trend have involved consistent change in all lineages or whether the trend represents the net outcome of a more complex internal dynamic (McShea 1994).

2. *Causes*. Proceeding a step farther, one may investigate the causes behind the internal dynamics that add up to a trend. For example, are these dynamics caused by natural selection or a nonadaptive constraint (see below)?
3. *Bases*. Finally, any particular cause (which results in dynamics that add up to a trend) must have a basis (or bases). For example, if the cause is determined to be natural selection operating among individuals in a population, one may ask what the basis is, i.e., what survival and/or reproductive advantage relative to alternatives is involved in generating nonrandom differences in success among individuals. This could be anything from enhancing prey capture to avoiding being eaten to attracting more mates or some combination of several such factors.

Not only do influences at each of these levels play a role in producing trends (and, therefore, remain important in explaining any given trend), but to further complicate the situation, it is possible that several factors are at play at each of these levels or that different ones apply at different times in the long-term history of a group (e.g., Trammer and Haim 1999). Fortunately, evolutionary biologists have developed a series of analytical methods for testing and understanding the dynamics underlying trends, the causes that generate them, and both adaptive and nonadaptive bases behind the causes.

Trend Dynamics: Driven Versus Passive Trends

Driven Versus Passive Trends: What They Are and Why it Matters

McShea (1994) defined two kinds of trend dynamics: driven and passive. In technical terms, driven trends are those in which the underlying dynamic is homogeneous, whereas passive trends result from dynamics that are at least locally heterogeneous. In simpler terms, the dynamics of driven trends occur primarily in one direction and apply to most component lineages, whereas passive trends are the net result of complex dynamics operating in different directions in different lineages or at different times (Fig. 5). Passive trends have been likened to the diffusion of particles from an area of high concentration to a more dispersed state (McShea 1994). At the level of individual particles, movement is

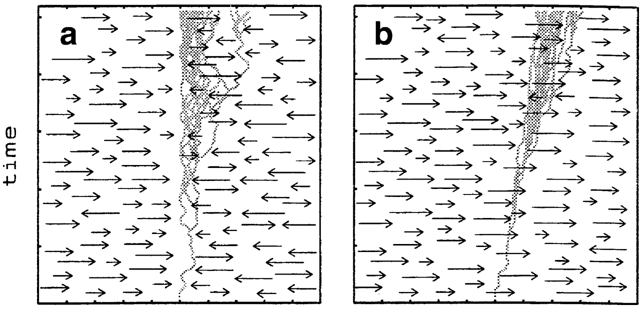

Fig. 5 The basis for classifying trends as passive or driven. According to McShea (1994), a trend is passive if the forces influencing change in lineages over time are heterogeneous (**a**), that is, if they occur in more than one direction. If the forces are homogeneous (i.e., they operate mostly in the same direction), then the trend is driven (**b**). Figure from McShea (1994), reproduced by permission of Blackwell

deterministic but the collection of particles as a whole does not exhibit any consistent directionality of movement. Passive evolutionary trends may represent increases in overall diversity among component lineages over time, but one in which expansion is limited to a single direction—for example, if ancestral species exhibit small bodies near the minimum possible size then diversity can only expand in the direction of larger maximum size (Fig. 6; Stanley 1973). Driven trends, by contrast, are analogous to particles moving together in one direction under the action of a shared force field, such as iron filings being drawn by a magnet.

Four cautions are warranted when it comes to a designation of trends as driven or passive. The first is simply that this terminology is widely but not universally accepted and that other options have been proposed.[3] The second is that "passive" should not be construed as implying randomness or that biologically important processes are not operating—in fact, passive trends are often underpinned by complex and interesting causal mechanisms (Alroy 2000; McShea 2000). The third is that large-scale trends may often consist of both driven and passive components, in some cases depending on the taxonomic and/or historical scale at which they are being observed (Fig. 7; McShea 1994, 2001; Trammer and Kaim 1999; Carroll 2001; Wang 2001; Hone and Benton 2005). The fourth is that "driven" versus "passive" does not automatically provide information regarding causation, as both can result from a variety of causes; moreover, some causes can generate either of the two dynamics.

Given these caveats regarding the way that driven versus passive trends can (or more properly, cannot) be interpreted, one may wonder why there has been so much interest among biologists in applying these designations to observed trends. A simple reason is that determining whether a trend is driven or passive can help to focus the inquiry regarding causes. For example, identifying a trend as driven may not automatically imply that it results from adaptive change, but it does highlight the need to investigate this possibility further. Discovering more complex dynamics while evaluating whether a trend is driven or passive may also help to direct further investigations, for example, by indicating which lineages follow the trend and which do not, with the differences allowing hypotheses to be formulated and tested regarding the causes of the dynamics.

Perhaps most importantly, the driven versus passive classification can have implications for how the evolutionary process is interpreted in the broad sense. As McShea (1994) noted, driven trends permit extrapolations from small-scale to large-scale and vice versa, whereas passive trends do not. For example, a trend caused by consistent patterns of change occurring within populations (microevolution) implies that large-scale evolutionary patterns (macroevolution) have been the result of small-scale processes amplified through deep time, whereas a trend resulting from higher-level processes above the species level requires an expanded, hierarchical view of macroevolution (see also Gould 2002). In addition, this has significant implications for the degree to which future patterns of evolution can be predicted. Raising the example of a presumed trend toward increased intelligence in the primate lineage, which is often assumed to imply that further increases in intellectual prowess can be expected in the human lineage over time, McShea (1994) noted that:

> If such a trend in primates exists and it is driven, that is, if the trend is a direct result of concerted forces acting on most lineages across the intelligence spectrum, then the inference is justified. But if it is passive, that is, forces act only on lineages at the low-intelligence end, then most lineages will have no increasing tendency. In that case, most primate species—especially those out on the right tail of the distribution like ours—would be just as likely to lose intelligence as to gain it in subsequent evolution (if they change at all).

Clearly, then, determining whether trends are driven or passive is an important aspect of their study. To this end, evolutionary biologists have developed several tests that can be applied to fossil data to address this question. In many cases these are used together, in part because no single test provides a conclusive designation on its own.

Test of the Minimum

If passive trends are most often the result of an increase in diversity within a group that is free to expand in only one direction, then one might expect this to involve only changes in the average and the maximum. As such, the simplest test that can be used involves an assessment of whether there has been a change not only in the mean or the maximum value within a group over time, but also in the

---

[3] Some authors have used the term "directed" in a manner similar to "driven" (e.g., McKinney 1990), and the term "active" has been used interchangeably with "driven" by others (e.g., McShea 1993; Trammer and Kaim 1999; Alroy 2000). On the other hand, Wagner (1996) defined "active" trends as ones in which there is replacement of ancestral morphologies with more derived ones over time (Fig. 1C), which is a broader category that includes McShea's (1994) driven trends as a subset (see also Finarelli 2007). At the same time, Wagner (1996) considered passive trends to be strictly those resulting from expansions of variance that can occur in only one direction (Fig. 6), which is more restrictive than McShea's (1994) definition. More recently, Alroy (2000) criticized the entire driven versus passive dichotomy as oversimplified, although McShea (2000) and Wang (2005) argued in favor of maintaining these terms. Debates about terminology and the concepts that it reflects are not uncommon when dealing with complex topics such as this. As McShea (2000) noted, "It has been said that most scientists would rather use another scientist's toothbrush than his terminology."

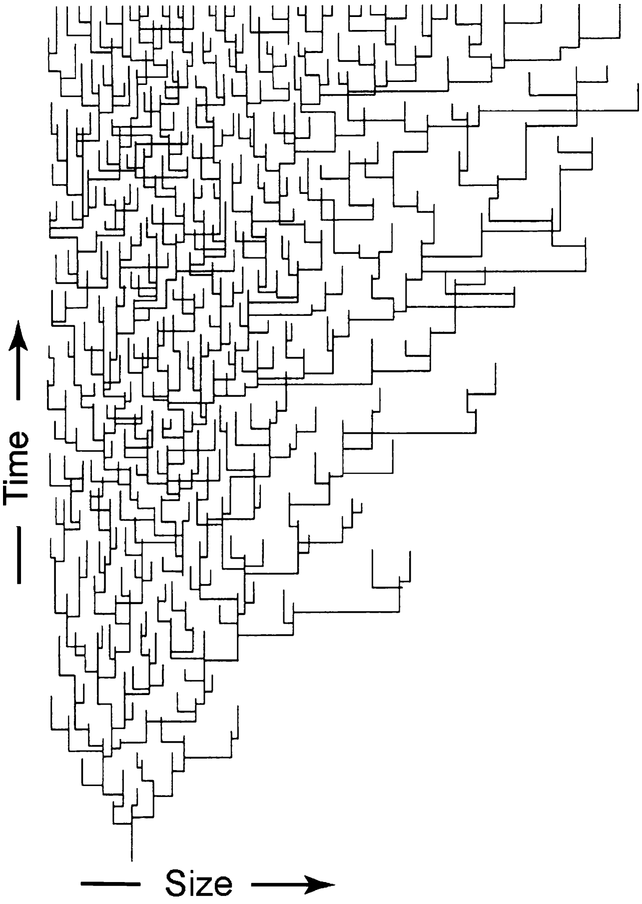

Fig. 6 A passive trend can result when the variance in some feature expands within a group of species over time after beginning at a low value close to a lower limit. In this hypothetical example, an ancestral species begins with a small body size and subsequent speciation events include both increases and decreases in size. However, there is a physical limit to how small species in this group can become, which means that the distribution is free to expand in only one direction, i.e., toward increases. Moreover, increases tend to be of a greater magnitude than decreases in this diagram, especially once species reach larger sizes. In this scenario, larger size does not need to be directly advantageous among species for the average to increase because this passive "diffusion" process alone can generate a large-scale trend. Figure from Stanley (1973), reproduced by permission of Blackwell

minimum (McShea 1998, 2000, 2001). If the minimum value for the trait increases along with the average and the maximum, then this is strongly supportive (but not conclusively demonstrative) of a driven trend (Fig. 8). If the minimum does not change, then this is suggestive of a passive trend, although it must be noted that some locally driven trends do not involve increases in the minimum (e.g., Alroy 1998). (In cases of decreasing trends, these criteria simply are reversed with the minimum changing and the test aimed at examining patterns of change versus stasis in the maximum.) Observations of averages, minima, and maxima have also been used to define much broader and more detailed categories of trend dynamics in some cases (e.g., Trammer and Kaim 1999).

Subclade and Skewness Tests

The second test of driven versus passive dynamics, known as the subclade test, involves comparisons of species from specific moments in time, rather than an examination of changes in minima over long periods. Therefore, an advantage (or perhaps a weakness; Alroy 2000) of this approach is that it does not require detailed historical information regarding relationships among species (only that they are part of the same subclade, i.e., subsamples of the overall group that are

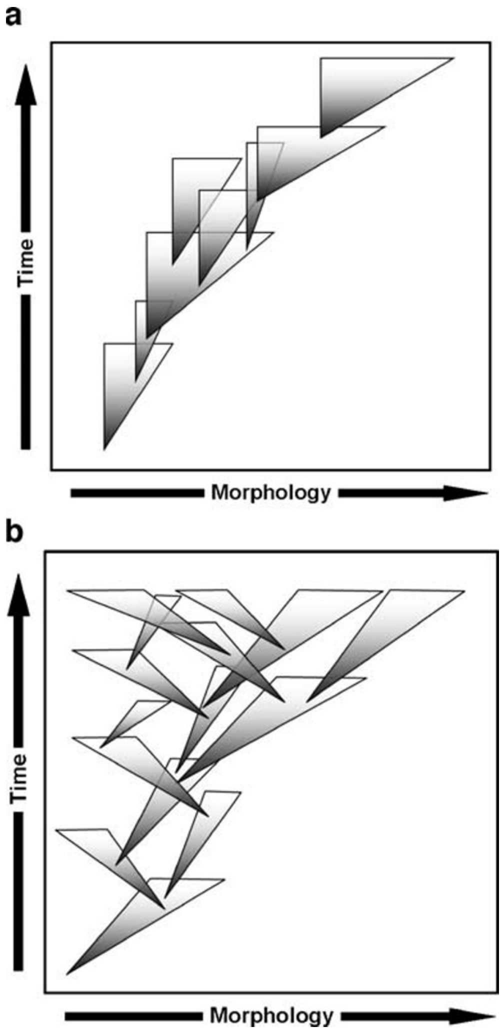

Fig. 7 Passive and active trends may occur simultaneously at different scales. In **a**, there is a driven trend at the global scale (note the increasing global minimum), although in each component lineage, the trend is passive (note that in each case variance increases but the minimum does not). In **b**, there is a passive trend at the global scale (because of an expansion in variance with a limit at the low end), even though within each component lineage the trend is driven (because the driven trends at local scales occur in both directions). Based on McShea (2001)

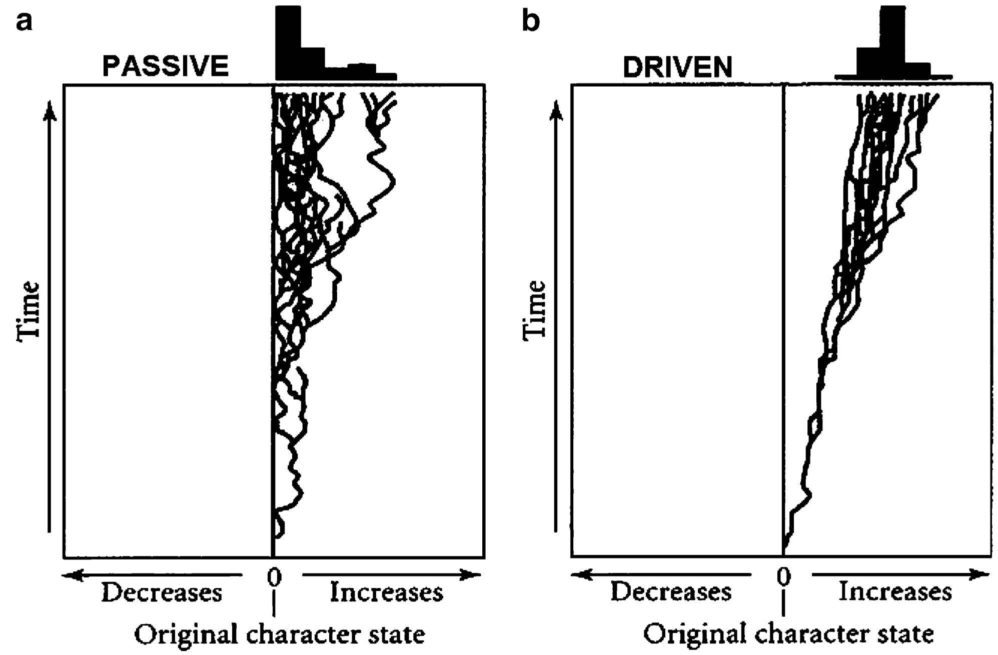

Fig. 8 The test of the minimum. This figure shows the results of computer simulations designed to illustrate passive versus driven trends as distinguished by the behavior of the minimum values in the distribution. In both cases, there is an increase in the mean value of a certain characteristic among species (e.g., body size); however, the mechanism generating this average increase differs greatly between passive and driven trends. In the passive trend (**a**), there is a lower bound to the parameter (e.g., a smallest possible body size) and the increase in the average results only from an expansion of the largest value—the minimum value in the distribution does not change and remains at or near the lower bound where it began. In a driven trend (**b**), the increase in the average results from a directional shift in the entire distribution in which both the maximum and the minimum values increase over time. Reprinted from McShea (1994) by permission of Blackwell

related to one another) (McShea 1994; Wang 2001). Both driven and passive dynamics may result in a distribution that is skewed in one direction, meaning that most species will exhibit values for a given trait at one end of the distribution with a decreasing number of species located along an extended tail at the other end of the distribution (Fig. 9). In a passive trend resulting from an expansion of variance that is bounded by an immovable minimum (a “left wall” in Fig. 9a), the overall distribution will be skewed, but a subsampling within clades that are not next to this wall would be expected

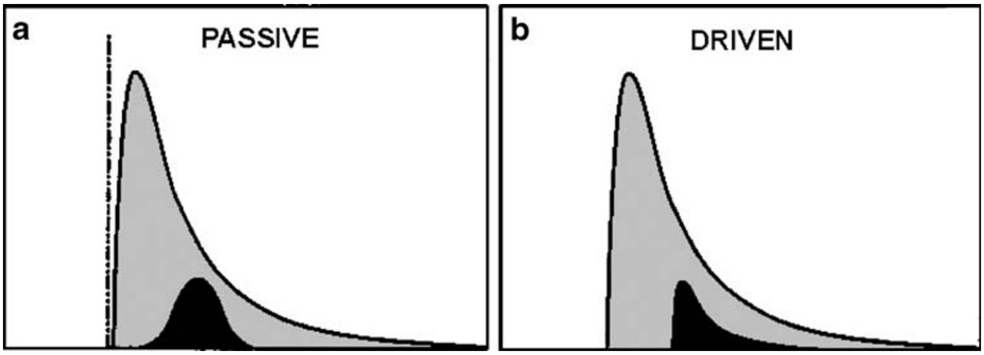

Fig. 9 The subclade test. Both passive and driven trends can result in a skewed distribution in which most species exhibit a trait near the low end and a smaller number of species display much higher values for the trait, resulting in a long “tail” of the distribution at the high end. (These distributions are right-skewed, but left-skewed distributions are also possible and the same principles apply). The subclade test involves examining groups of related species within the distribution and away from both the lower and upper ends. If the trend is passive and results from an increase in variance that is bounded at the low end (**a**), then groups falling within the distribution and away from this lower limit should not show a skewed distribution for the trait. On the other hand, if the trend is driven and there is some factor that drives increases in the trait (**b**), then groups not near the low or high end should nonetheless display a skewed distribution for the trait as well. Reprinted from McShea (1994) by permission of Blackwell

to exhibit a more normal (bell-shaped) distribution. On the other hand, if the skewness of the overall distribution results from a driven trend operating in each component lineage, then a subclade within the overall distribution should also be skewed because the same forces apply to most component lineages within the overall group. A similar method, known as the skewness test, incorporates a more detailed comparison of skewness among several subgroups within larger distributions and is designed to identify the relative proportions of driven versus passive dynamics in trends where both are at play (Wang 2001). Obviously, these tests are applicable only to situations in which the distribution for a particular trait is skewed, and even then the results may not be conclusive (Alroy 2000; McShea 2000).

Test of Ancestor–Descendant Pairings

The most powerful test of trend dynamics is one involving direct comparisons of large numbers of ancestor–descendant pairs (Fig. 10; McShea 1993; Alroy 2000; Wang 2005). Such comparisons provide a detailed view of the directionality of each change that took place and can deliver a convincing determination of whether trends have been driven or passive and whether this has changed at different times or at different scales. In particular, this test is capable of identifying whether there has been replacement of lineages with different properties (which could be because of chance) or consistent directional change within a majority of lineages (Fig. 11). In practice, it is rarely possible to identify actual ancestor–descendant pairs in the fossil record, and some alternatives have been developed that provide information as close to this ideal as can be obtained. The first involves comparisons of members of the same taxonomic group (e.g., species in the same genus) that appeared earlier versus later in the fossil record (e.g., Jablonski 1997; Alroy 2000). The second makes use of phylogenetic hypotheses to pair earlier taxa that are presumed to more closely resemble a common ancestor with those that arose later and are thought to be more derived. The relative age of taxa and ancestral morphological characteristics are established by reference to fossils (e.g., Hone et al. 2005; Adamowicz et al. 2008). In some cases, inferences about the characteristics of ancestors have been drawn using phylogenies alone with no reference to the fossil record, but this has been shown to be especially inaccurate in the presence of trends—which is precisely when it would be of the most interest (e.g., Oakley and Cunningham 2000; Webster and Purvis 2002).

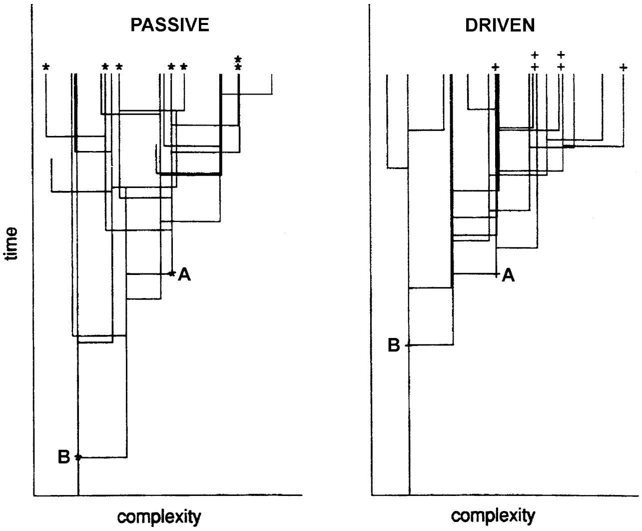

Fig. 10 The test of ancestor–descendant pairings. Comparisons of ancestors with their descendants can be used to distinguish passive versus driven trends (in this hypothetical example, of changes in average complexity), so long as an appropriate starting point is selected. For example, choosing species B, which is a distant ancestor starting at very low complexity, would not allow one to distinguish between passive or active trends, as in either case its descendants will very likely be more complex than it is. However, choosing species A, which is a more recent ancestor and is of intermediate complexity, allows an informative assessment of the direction of changes among its descendants. In a passive trend, the number of A's descendants (*asterisks*) that are more complex than A is roughly equal to the number of descendants that are less complex than A, but the average will still increase because there is a lower limit on complexity. In a driven trend, most of A's descendants (*crosses*) will be more complex than A. Figure from McShea (1993), reprinted by permission of Blackwell

Causes of Trends

Whether the dynamics underlying a particular trend are driven, passive, or some combination of both, they in turn call out for an explanation based on an identification of their underlying causes (and, at an even deeper level of resolution, the bases for those causes; Table 1). There are numerous processes capable of causing either driven or passive trends, which by and large are not mutually exclusive and may interact in interesting ways (Alroy 2000; Gould 2002). Some of these relate to processes operating within populations, or what can be considered standard neo-Darwinian evolution, and may involve either external factors (e.g., related to the environment in which organisms live) or internal ones (e.g., related to the development of organisms). Still others exert their influence only at higher levels, such as through sorting among species, and are, therefore, part of a broader, "macroevolutionary" view of evolution (e.g., Alroy 2000; Gould 2002). There is disagreement among evolutionary biologists as to whether population- or species-level processes predominate in the creation of most large-scale trends (Gould 1988, 2002; Maurer et al. 1992; Hallam 1998), but it is worth considering the various possible causes that have been proposed.

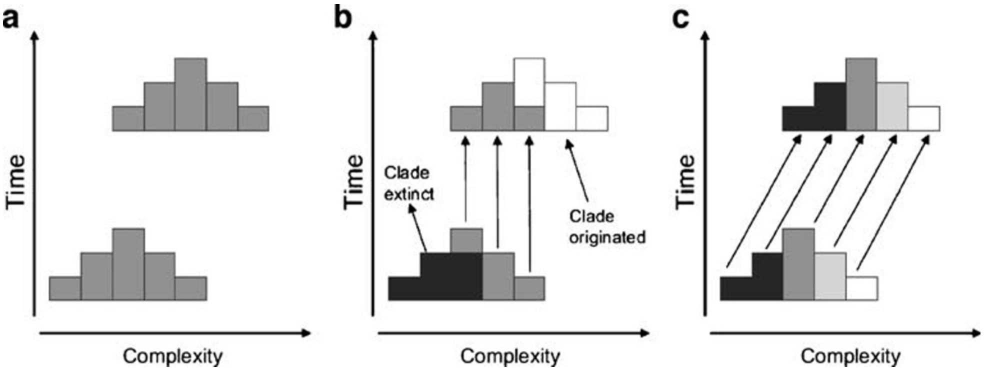

Fig. 11 An example of the importance of historical information in identifying the underlying dynamics of a trend. **a** Shows a clear trend toward increased complexity over time within a hypothetical group of organisms. In this case, the minimum has increased along with the maximum and the average. It is possible for this pattern to occur if less complex groups of related species ("clades") happen to go extinct and new lineages that originate happen to be more complex (**b**). By contrast, this could also result from a driven trend in which consistent increases in complexity occur within each component lineage (**c**). These two very different scenarios can only be distinguished by using comparisons of ancestors and descendants within lineages or by inferring ancestral characteristics from phylogenies. Figure from Adamowicz et al. (2008), reproduced by permission of the National Academy of Sciences of the USA. See Purvis and Orme (2005) for a similar discussion related to body size trends

Natural Selection and Constraints

The most intuitive explanation for why a majority of lineages in a group would evolve in a consistent direction (i.e., exhibit a driven trend) is that this change is adaptive—in other words, that it is the result of directional natural selection operating among individual organisms within populations of various species. On the other hand, the most obvious explanation for passive trends involving one-sided expansions in variance is some form of constraint, perhaps internal and nonadaptive in nature. However, as McShea (1994) noted, "the distinction between the passive and driven mechanisms is not necessarily that between selection and developmental constraints, nor even between internal and external factors." In fact, McShea (2005) has pointed out four combinations of dynamics and causes related to natural selection and constraints in evolutionary trends:

1. *Driven dynamic caused by natural selection*. This is the situation described above, in which standard neo-Darwinian natural selection engenders persistent, adaptive change at the population level which, over time, is extrapolated into larger-scale patterns. In terms of body size, for example, data from a range of species indicate that there is often a tendency for larger individuals to be at an advantage relative to smaller members of the population for many reasons (Fig. 12), such as better defense against predation, improved success as predators, increased success in competition for resources or mates, larger brain size, higher thermal tolerance, and longer lifespan (Kingsolver and Pfennig 2004; Hone and Benton 2005).
2. *Passive dynamic caused by natural selection*. It is important to note that the outcome of natural selection can be conservative as well as directional, meaning that some forms (known as purifying selection or stabilizing selection) may prevent changes in certain traits. In particular, if the morphology of organisms in a population is well suited to their environment, then any deviations from this could lead to lower fitness. If this limitation on change occurs primarily in one direction, for example if there is a lower boundary on complexity in which a reduction becomes maladaptive, then selection would prevent decreases in the minimum within a distribution such that any increase in diversity (which may, of course, represent adaptive change) would be in one direction and a passive trend would be the result. Thus, selection can be a cause of either driven or passive trends, depending on whether it is directional or stabilizing.
3. *Driven dynamic caused by constraints*. The development of organisms consists of a complex and interconnected series of programmed changes that can often be limited in flexibility. That is, some forms of mutation may be more likely to appear in the population than others, resulting in changes that occur consistently in only one direction—i.e., a driven trend. If this is based on internal constraints on the sorts of changes that are possible, then it would differ from the selective constraints described above. A driven trend may also result from a tendency for serially repeated or modular structures within organisms that begin similar to each other to become more different simply because there are more ways for such structures to differ than to be the same. Serially repeated limbs in arthropods, for

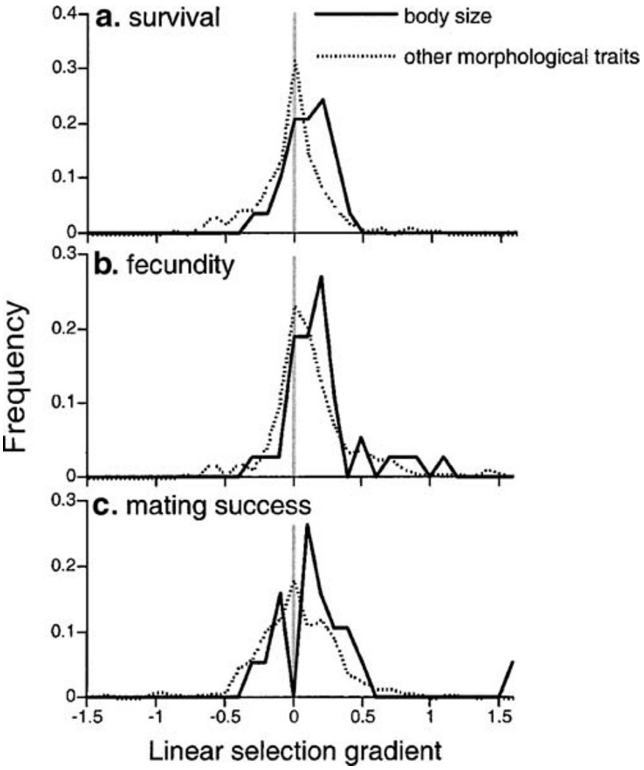

Fig. 12 Large body size appears to confer numerous advantages on organisms within populations. Based on an analysis of various vertebrates, invertebrates, and plants, Kingsolver and Pfennig (2004) reported that larger body size (*solid lines*) tends to be associated with positive selection gradients (i.e., greater success relative to smaller individuals) within populations as measured in terms of survival (**a**), number of offspring (fecundity) (**b**), and mating success (**c**). By contrast, other morphological traits (*dotted lines*) unrelated to body size tend to exhibit positive and negative selection gradients in roughly equal frequencies (i.e., overall they confer no significant advantage, nor a cost, on individuals with especially high or low values for the traits). The authors argue that there is consistent selection within populations for larger size and that this could translate into large-scale trends toward increased body size ("Cope's Rule") over evolutionary timescales. Figure from Kingsolver and Pfennig (2004), reproduced by permission of Blackwell

example, may be very similar to each other when they first evolve, such that any changes to the characteristics of their limbs will almost certainly involve divergence between them and, hence, greater limb complexity (McShea 2005).

4. *Passive dynamic caused by constraints*. Not all limitations to expanding variance are the result of natural selection. Some simply represent physical limits on the range of morphologies that are possible. For example, the minimum number of cells of which a living organism can be composed is one. If life began as single-celled, then expanding diversity could only involve increases in maximum cell number (see, e.g., Valentine et al. 1994).

Whether they relate to directional selection, selective constraints, or nonadaptive constraints (or some combination thereof), these causes often are assumed to operate at the level of organisms within populations. Their influence on large-scale trends would, therefore, involve extending these effects through long periods of time, which is consistent with the principles of neo-Darwinian theory. However, it has also been postulated that factors operating among species can generate trends at higher levels. It is interesting to note that many of these are recognizable as analogs of population-level processes.

Directional Speciation

In the same way that directional change within populations can result if offspring tend to differ from their parents more frequently in one direction than another, so species-level trends can derive from a tendency for new species to differ from their ancestors in a biased manner (Fig. 13a; Finarelli 2007). For example, it is possible that certain types of changes are inherently more likely than others to occur when new species arise, just as some kinds of mutations are more likely than others to appear in offspring. In this sense, Gould (1990, 2002) envisions the analog of "mutation pressure" at the species level as a cause of trends. A similar pattern may result from external causes, for example, if the niches available for new species to occupy (and adapt to) consistently differ in the same way relative to the niches occupied by existing species (Grant 1989).

It is also possible that once a change occurs in a new species, it cannot be undone. According to "Dollo's Law," many substantial changes during the course of evolution are irreversible. For example, it has been suggested that once lost, a complex feature cannot be regained as the probability of its reemergence is too slight. Possible exceptions to this principle have been noted (e.g., Collin and Cipriani 2003; Domes et al. 2007), but it remains the case that a tendency toward irreversibility would produce a trend resulting from directional speciation. Changes in a certain direction would create a "moving wall" under such a scenario, making further changes possible in only one direction. In another scenario proposed by Wagner (1996), reversals of evolution remain possible until a certain threshold has been crossed, at which point the lineage remains "trapped" and may continue to change only in one direction from that point on. This, too, could result in a large-scale trend (Fig. 13b).

Differential Speciation Rate

If larger-bodied individuals tend to leave more offspring than their smaller counterparts and if their offspring inherit their

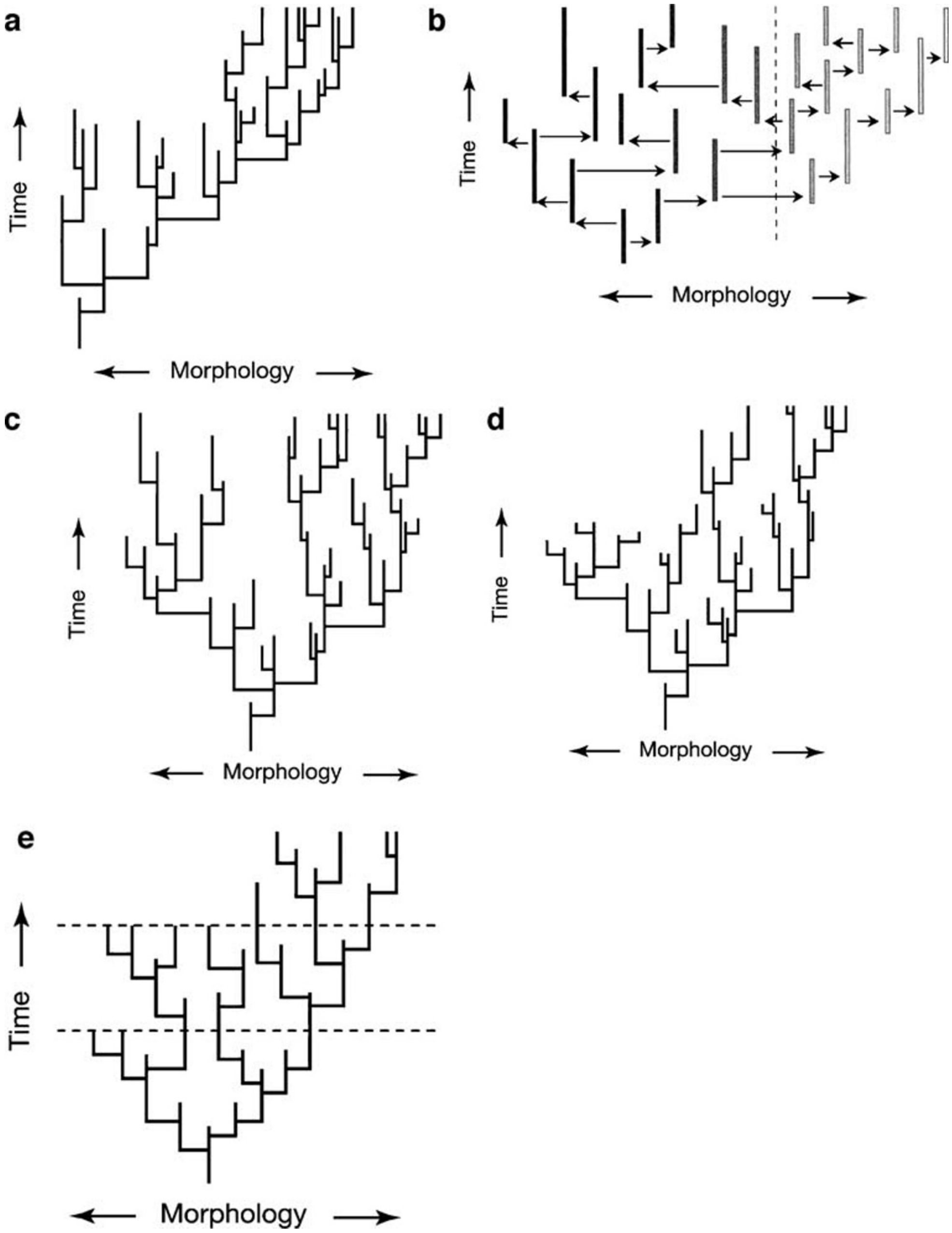

Fig. 13 Trends resulting from processes operating among species. In **a**, there is a bias whereby new species tend to differ from their ancestors in one direction (in this case, increase in some morphological parameter). It could be that that increases confer some advantage or simply that decreases are constrained or otherwise less likely (or both). The end result is a trend toward increase in the average value of the trait in the clade. In some cases, large-scale evolutionary changes in one direction (for example, the loss of a complex feature) are thought to be irreversible ("Dollo's Law"), which obviously would create a trend in one direction. However, even more limited forms of irreversibility may be sufficient to generate an overall directional pattern. For example, in **b**, increases and decreases are roughly equally likely up to a certain point, after which decreases become constrained. This can be thought of as creating a "trap" for lineages that pass a threshold representing a point of no return. This, too, will result in a trend toward an increased average value overall. Figure from Wagner (1996), reproduced by permission of Blackwell. In **c**, species with higher values of a particular morphological parameter tend to leave more descendant species than those with lower values of the parameter (i.e., more new branches split off those parts of the tree). Over time, this differential speciation results in the production of more species exhibiting higher values than lower ones, thereby generating a trend in which the average increases in the group as a whole. In (**d**), the rate of new species formation does not differ according to the morphological trait under consideration, but those with higher values for the trait tend to persist longer before going extinct (i.e., those branches of the tree are longer on the time axis). This results in a larger overall number of species with higher values for the trait, and once again generates a trend in which the average for the entire group increases over time. In **e**, new species exhibit both increases and decreases in the trait compared to their ancestors, but two mass extinction events have occurred (*dashed lines*) that affected groups with lower values much more than those with higher values. As a result of their greater rate of survival through mass extinctions, lineages with higher values for the trait are more common today than those with lower values such that that there has been an increase overall in the average value of the trait—and therefore a trend

parents' large size, then over time the average body size of the population will increase. A similar process may operate at the species level if the same basic requirements of differential reproduction and heritability are met. Thus, if species exhibiting a larger value for some characteristic tend to undergo speciation more often (i.e., to leave more daughter species) and these descendant species inherit this higher value from their ancestors, then a trend toward an increase in that characteristic can result (Fig. 13c; Gould 1990, 2002).

Differential Species Longevity

Like organisms, species produced through cladogenesis (branching of lineages) have a "birth" (speciation) and a "death" (extinction) in between which is a lifespan. As in the case of differential reproduction, differential longevity of species (i.e., longer duration before extinction based on particular characteristics) can generate large-scale trends over long time periods as species with this characteristic persist and become more abundant whereas those lacking it disappear more quickly (Fig. 13d).

Gould (1990) expressed concern that an extinction-driven trend may be hard to accept because the loss of species through extinction might be conceived as merely whittling down variation among species. However, he noted that the same objection was raised in the nineteenth century when natural selection was proposed as the creative force behind adaptive change. The answer, which has long been recognized, is that directional changes can continue to accumulate so long as new variation is generated at random around the distribution in each case after the elimination of some portion of the population. As Gould (1990) noted (and as can be observed in Fig. 13d):

> The classical Darwinian response works just as well at the level of species elimination within clades. Suppose that patterns of speciation are entirely random with respect to the direction of a trend… Differential extinction can move a cladal mode anywhere within the spectrum of variation among species. With a new mode at the old periphery, random speciation can reconstitute variation that moves into a previously unoccupied morphospace, and directional extinction can then continue to accentuate the trend.

Differential Survival Through Mass Extinctions

Because species within clades exist in small numbers compared to the number of organisms in populations, Gould (1990) argued that differential extinction will often be dominated more by chance (a species-level analog of genetic drift, as it were, which is stronger in small samples) rather than by species-level selection. Nowhere is this more apparent than in the case of mass extinctions: drastic and accelerated losses of biodiversity because of chance events (essentially species-level analogs of population bottlenecks).

Adaptive changes occurring within populations during "normal" conditions may have little bearing on whether a species survives a mass extinction event. Nevertheless, whether by chance or the possession of traits that are relevant for survival during such extraordinary circumstances, differential survival through mass extinction events does occur. This not only can halt trends that had been proceeding before the event, it also can generate trends of its own (Fig. 13e)—in fact, it is possible that trends generated during normal times can be reversed by those resulting from a mass extinction.

The Effect Hypothesis

Whereas some authors contend that large-scale trends are the end result of directional natural selection operating within species, others argue that differential speciation or extinction—perhaps even constituting a form of "species selection"—are more important. A third alternative was presented by Vrba (1980, 1983), which she dubbed the "effect hypothesis." Under this view, anagenetic change that may be adaptive within species can have incidental consequences for species diversification or extinction, thereby generating cladogenetic trends. In other words, large-scale trends can be nonadaptive side effects of small-scale, adaptive processes.

Species Hitchhiking

Organisms are integrated entities, and changes in one feature often engender correlated changes in other features. For this reason, it is possible that some trends, although they are well-supported by careful analysis, are merely spurious (Wagner 1996). That is to say, the trait showing a trend is merely correlated to another trait that is actually driving the trend. As an example, a driven trend toward increased body size will automatically bring with it many additional changes (e.g., longer generation time) that would exhibit trends along with body size. This process has been called "species hitchhiking," as an analogy to genetic hitchhiking in which a variant of a gene spreads in a population over many generations not because it confers an advantage itself but because it is linked to a different gene that does (Wagner 1996; Levinton 2001).

Why Don't Trends Continue Indefinitely?

With so many possible mechanisms for generating large-scale evolutionary trends, one may wonder why these do not occur more commonly or to an even greater extent than they do. Even in cases where there is evidence of a driven trend, this may not proceed to its theoretical maximum level (e.g., Adamowicz et al. 2008), and of course many lineages do not show evidence of the best-known trends such as increases in body size or complexity. This may seem particularly perplexing when the trend appears to be caused by natural selection acting consistently within populations. For example, why do so many species remain small if larger body size provides a clear advantage within many of them? There are several possible explanations for why trends may be limited in scope.

1. *Physical limits*. Organisms are subject to various physical limitations that can place a cap on the extent of change that is possible. For example, land-dwelling mammals are probably limited to a certain maximum size by the effects of gravity (which is lessened in water because of the effects of buoyancy) and insects may be limited to a maximum body size by their mostly passive respiratory systems.
2. *Genetic limits*. Consistent, directional change requires the continual addition of new variation (by mutation at the population level, by speciation at the species level). It is possible that, at some stage, the requisite mutations simply never occur and directional change slows or stops as a result.
3. *Ecological limits*. In addition to limitations inherent to individual organisms, there may be external limits imposed by the environment. By way of example, larger organisms require more energy intake, and it is possible that this becomes impossible to achieve beyond a certain size.
4. *Reaching an optimum*. In some cases, adaptive change may continue only to a certain point where an optimum is reached, beyond which any additional increase is less adaptive. Driven change in this case will occur only during the period before the point where this optimum is reached.
5. *Changing environments*. Driven trends caused by natural selection will continue only so long as the selective pressure exists. In a world of changing physical and biological environments, specific selective pressures that generate directional change are often only temporary.
6. *Organism-level trade-offs*. As noted previously, changes to one feature almost certainly instigate correlated changes in other features. In some cases, this is neutral or even positive, but in others it is negative. When changes in a particular feature begin to compromise the function of others, this may place a limit on further modification.
7. *Species-level trade-offs*. It is possible for directional changes occurring as a result of short-term, population-level processes to exert consequences for the species in the long term. For example, increases in body size may be favored within species (Kingsolver and Pfennig 2004), but larger animals tend to be less abundant and to have slower reproductive cycles, which can make them more prone to extinction (McKinney 1997; Hone and Benton 2005; Purvis and Orme 2005). Overall, then, there may be anagenetic increases within lineages creating a trend that is counteracted by the effects of differential species longevity. In North American canids, for example, there appears to have been a trend toward increased body size within lineages which then became more prone to extinction (Van Valkenburgh et al. 2004).
8. *Mass extinction*. Regardless of the trends that had been underway during normal times, the massive, mostly indiscriminate loss of biodiversity during mass extinctions may fundamentally change the distribution of species and halt, reset, or even reverse previous trends. For example, there appears to have been a trend toward increased body size among dinosaurs, but obviously this ceased when they disappeared during the Cretaceous–Tertiary (*K*/*T*) extinction event (Hone et al. 2005). Subsequently, a trend toward increased average body size began among mammals (Alroy 1998). In most early bird lineages, there was a trend toward increased body size before the *K*/*T* event, but only the lineage from which modern birds evolved, which had been undergoing a trend toward reduction in body size, survived this event (Hone et al. 2008).

Just as there are numerous complex and potentially interacting causes of trends, so too are there many reasons why trends may be limited in scope or duration.

Concluding remarks

The identification and explanation of large-scale patterns in the history of life represents an important but challenging component of evolutionary research. It is apparent that many different mechanisms can result in large-scale evolutionary trends with natural selection operating within populations representing only one of these. Both constraints and higher-level processes may be responsible for generating trends, which may be passive as well as driven and may be influenced by a number of factors. Many trends are localized either taxonomically or in time, and there is no evidence to support popular conceptions of evolution as an inexorable march in any direction, be it toward larger size, greater complexity, heightened intelligence, or any other trait. Rather, the processes and patterns of evolution are, like its products, intriguingly diverse.

Acknowledgements I thank Sarah Adamowicz and Niles Eldredge for helpful comments on an earlier draft of the paper. I also thank Sean, Makiko, and Julian of the Gregory/Kajimura family for their gracious hospitality in Japan while this paper was in preparation.

References

Adamowicz SJ, Purvis A, Wills MA. Increasing morphological complexity in multiple parallel lineages of the Crustacea. Proc Natl Acad Sci U S A 2008;105:4786–91.

Alroy J. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 1998;280:731–4.

Alroy J. Understanding the dynamics of trends within evolving lineages. Paleobiology 2000;26:319–29.

Carroll SB. Chance and necessity: the evolution of morphological complexity and diversity. Nature 2001;409:1102–9.

Collin R, Cipriani R. Dollo's law and the re-evolution of shell coiling. Proc R Soc Lond B 2003;270:2551–5.

Domes K, Norton RA, Maraun M, Scheu S. Reevolution of sexuality breaks Dollo's law. Proc Natl Acad Sci U S A 2007;104:7139–44.

Finarelli JA. Mechanisms behind active trends in body size evolution of the Canidae (Carnivora: Mammalia). Am Nat 2007;170:876–85.

Gould SJ. Life's little joke. Nat Hist 1987;96:16–25.

Gould SJ. Trends as changes in variance: a new slant on progress and directionality in evolution. J Paleontol 1988;62:319–29.

Gould SJ. Speciation and sorting as the source of evolutionary trends, or 'things are seldom what they seem'. In: McNamara KJ, editor. Evolutionary trends. Tucson, AZ: University of Arizona Press; 1990. p. 3–27.

Gould SJ. Full house. New York: Harmony Books; 1996.

Gould SJ. Cope's rule as psychological artefact. Nature 1997;385:199–200.

Gould SJ. The structure of evolutionary theory. Cambridge, MA: Harvard University Press; 2002.

Gould GC, MacFadden BJ. Gigantism, dwarfism, and Cope's rule: nothing in evolution makes sense without a phylogeny. Bull Am Mus Nat Hist 2004;285:219–37.

Grant V. The theory of speciational trends. Am Nat 1989;133:604–12.

Gregory TR. Understanding evolutionary trees. Evo Edu Outreach 2008;1:121–37.

Hallam A. Speciation patterns and trends in the fossil record. Geobios 1998;30:921–30.

Hone DWE, Benton MJ. The evolution of large size: how does Cope's rule work? Trends Ecol Evol 2005;20:4–6.

Hone DWE, Keesey M, Pisani D, Purvis A. Macroevolutionary trends in the Dinosauria: Cope's rule. J Evol Biol 2005;18:587–95.

Hone DWE, Dyke GJ, Haden M, Benton MJ. Body size evolution in Mesozoic birds. J Evol Biol 2008;21:618–24.

Jablonski D. Body size evolution in Cretaceous molluscs and the status of Cope's rule. Nature 1997;385:250–2.

Kingsolver JG, Pfennig DW. Individual-level selection as a cause of Cope's rule of phyletic size increase. Evolution 2004;58:1608–12.

Levinton JS. Genetics, paleontology, and macroevolution. 2nd ed. Cambridge, UK: Cambridge University Press; 2001.

MacFadden BJ. Fossil horses from "Eohippus" (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. Paleobiology 1986;12:355–69.

MacFadden BJ. Fossil horses. Cambridge, UK: Cambridge University Press; 1992.

MacFadden BJ. Fossil horses—evidence for evolution. Science 2005;307:1728–30.

Matthew WD. The evolution of the horse. Am Mus Nat Hist, Suppl. Am Mus J Guide Leaflet 1903;9:1–30.

Matthew WD. The evolution of the horse: a record and its interpretation. Q Rev Biol 1926;1:139–85.

Maurer BA, Brown JH, Rusler RD. The micro and macro in body size evolution. Evolution 1992;46:939–53.

McKinney ML. Classifying and analysing evolutionary trends. In: McNamara KJ, editor. Evolutionary trends. Tucson, AZ: University of Arizona Press; 1990. p. 28–58.

McKinney ML. Extinction vulnerability and selectivity: combining ecological and paleontological views. Ann Rev Ecolog Syst 1997;28:495–516.

McShea DW. Evolutionary change in the morphological complexity of the mammalian vertebral column. Evolution 1993;47:730–40.

McShea DW. Mechanisms of large-scale evolutionary trends. Evolution 1994;48:1747–63.

McShea DW. Metazoan complexity and evolution: is there a trend? Evolution 1996;50:477–92.

McShea DW. Possible largest-scale trends in organismal evolution: eight "live hypotheses". Ann Rev Ecolog Syst 1998;29:293–318.

McShea DW. Trends, tools, and terminology. Paleobiology 2000;26:330–3.

McShea DW. Evolutionary trends. In: Briggs DEG, Crowther PR, editors. Paleobiology II. Malden, MA: Blackwell Science; 2001. p. 206–11.

McShea DW. The evolution of complexity without natural selection, a possible large-scale trend of the fourth kind. Paleobiology 2005;31(Suppl.):146–56.

Oakley TH, Cunningham CW. Independent contrasts succeed where ancestor reconstruction fails in a known bacteriophage phylogeny. Evolution 2000;54:397–405.

Purvis A, Orme CDL. Evolutionary trends in body size. In: Carel J-C, Kelly PA, Christen Y, editors. Deciphering growth. Berlin: Springer; 2005. p. 1–18.

Stanley SM. An explanation for Cope's rule. Evolution 1973;27:1–26.

Trammer J, Kaim A. Active trends, passive trends, Cope's rule and temporal scaling: new categorization of cladogenetic changes in body size. Hist Biol 1999;13:113–25.

Valentine JW, Collins AG, Meyer CP. Morphological complexity increase in metazoans. Paleobiology 1994;20:131–42.

Van Valkenburgh B, Wang X, Damuth J. Cope's rule, hypercarnivory, and extinction in North American canids. Science 2004;306:101–4.

Vrba ES. Evolution, species and fossils: how does life evolve? S Afr J Sci 1980;76:61–84.

Vrba ES. Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. Science 1983;221:387–9.

Wagner PJ. Contrasting the underlying patterns of active trends in morphologic evolution. Evolution 1996;50:990–1007.

Wang SC. Quantifying passive and driven large-scale evolutionary trends. Evolution 2001;55:849–58.

Wang SC. Accounting for unequal variances in evolutionary trend mechanisms. Paleobiology 2005;31:191–8.

Webster AJ, Purvis A. Testing the accuracy of methods for reconstructing ancestral states of continuous characters. Proc R Soc Lond B 2002;269:143–9.

Online resources

Understanding Evolution. http://evolution.berkeley.edu/evosite/evo101/VIIDTrends.shtml