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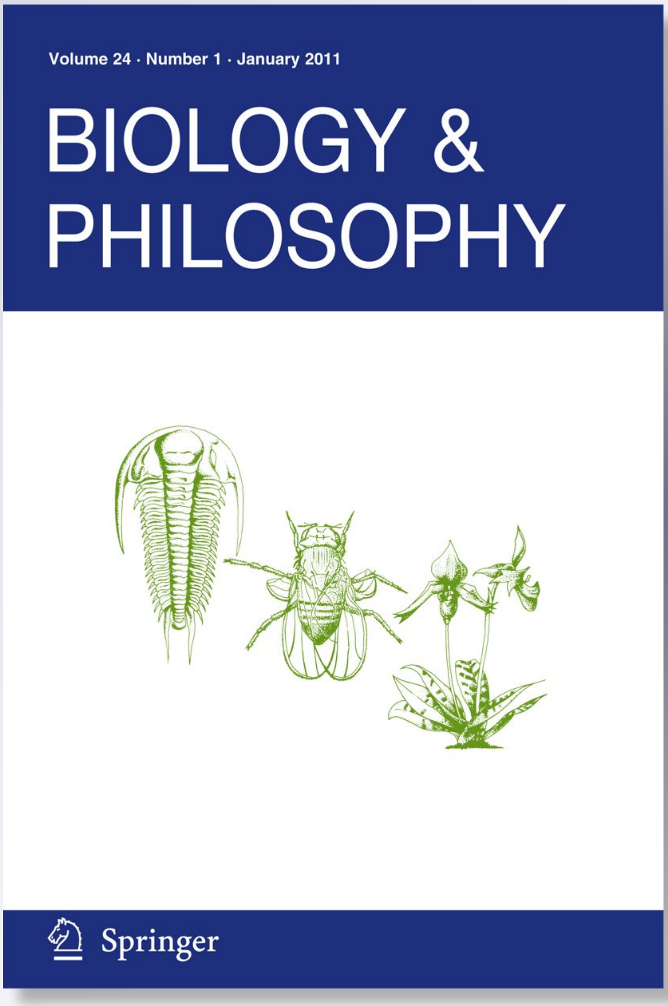

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BOOK REVIEW

Wandering drunks and general lawlessness in biology: does diversity and complexity tend to increase in evolutionary systems?

Daniel W. McShea and Robert N. Brandon: Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems, The University of Chicago Press, Chicago, London, 2010

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Abstract Does biology have general laws that apply to all levels of biological organisation, across all evolutionary time? In their book "Biology's first law: the tendency for diversity and complexity to increase in evolutionary systems" (2010), Daniel McShea and Robert Brandon propose that the most fundamental law of biology is that all levels of biological organisation have an underlying tendency to become more complex and diverse over time. A range of processes, most notably selection, can prevent the expression of this tendency, but they predict that, on average, we should see that lineages tend toward greater diversity and complexity, driven by fundamentally neutral processes. Their hypothesis can be summarised as "diversity is easy, stasis is hard". Here, I consider evidence for this "zero force evolutionary law". It provides a fair description of evolutionary change at the genomic level, but the predictions of the proposed law are not met for broad scale patterns in the evolution of the animal kingdom.

Keywords Evolution · Adaptation · Phylogeny · Genome · Molecular evolution · Drift · Biodiversity · ZFEL

Does biology have laws?

Laws fell out of fashion in biology. Nineteenth century naturalists seeking an overarching framework for natural history were comfortable describing observed patterns as "Laws". For example, Darwin's notebooks (1838) make mention of "Yarrell's law" (the parent from an older breed will have more influence on the

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offspring that the parent from a younger breed: see Liu et al. 2009) "Hunter's law of monstrosity" (large changes to morphology were produced at very early stages of embryo development: see Richards 1994) and "Herbert's law of idiosyncrasy" (hybrid sterility depends on "constitutional discrepancy": Herbert 1837). In the twentieth century, the use of the word "law" seemed to give way to the slightly less dogmatic "rule", such as Rensch's rule (that sexual size dimorphism increases with increasing body size in species where males are larger than females, but decreases with increasing body size in species where the female is the larger sex: e.g. Frydlova and Frynta 2010; Stuart-Fox 2009), Cope's rule (the tendency for the average body size of species to increase toward the poles: e.g. Hone et al. 2005; Monroe and Bokma 2010; Novak-Gottshall and Lanier 2008) and the island rule (large animal species tend to evolve smaller body size on islands, but smaller animals get larger: e.g. Bromham and Cardillo 2007; Lomolino 2005). More recently, the widespread acceptance that no rules in biology are without exception has lead to a reluctance to describe any generalities as rules or laws. Curiously, one of the best candidates for a biological law is, due to something of a historical accident, referred to as the Central Dogma rather than a law (Crick 1970; Maynard Smith 1990).

Perhaps we are now seeing a resurgence of interest in biological laws. Universal explanations for biological form and function have always been attractive, but with the increase in sophistication of analytical methods, and the availability of large biological databases, large-scale regularities can be investigated and described. For example, metabolic scaling has been suggested as a universal law that governs everything from the size of biomolecules to the structure of forest communities (West and Brown 2005). But these claims have been widely challenged by studies that show that the proposed universal constants are not, in fact, universal (e.g. Reich et al. 2006) and that predictions made using these general laws are not always confirmed by the data (e.g. Lanfear et al. 2007). In some cases, the apparent universality of scaling laws may be due to inappropriate statistical analyses that inflate the tightness of the relationship between biological variables, or due to taking such a wide view of the available data that the departures from the pattern are de-emphasized (Capellini et al. 2010; Nee et al. 2005; Lanfear et al. 2007). The devil, it seems, is in the detail.

Does the general lack of laws in the "soft science" of biology, as compared to the law-bound "hard sciences" of physics and chemistry, tell us about a fundamental difference in the sciences themselves, or a behavioural difference in the scientists (Colyvan and Ginzburg 2003; Sober 1997)? Do "hard scientists" seek universality and certainty, while "soft scientists" are happy with variation, exceptions and doubt? Or is the lack of laws in biology a demonstration of the importance of historicity in evolutionary processes (Beatty 1995; DesAutels 2010)? For example, the named laws most commonly taught to biology undergraduates—Mendel's law of independent segregation and the Hardy–Weinberg law—describe the expectation of random assortment of alleles in populations of diploid sexual organisms. Specifically, these laws apply to populations of organisms in which gametes are produced when pairs of chromosomes are randomly assorted into daughter cells under a "fair meiosis", then the gametes are randomly combined to make new diploid offspring. At a guess, then, these laws can only apply to genes in the nuclear genomes of perhaps 10% of species-level lineages that have these particular features of sexual reproduction. And, even for these particular genes in this subset of species, conditions of these laws are nearly always violated, by genetic linkage, migration, selection and mutation.

It is against this background of general lawlessness that Daniel McShea and Robert Brandon have made a bold claim to describe "Biology's First Law". In their book, subtitled "the tendency for diversity and complexity to increase in evolutionary systems", McShea and Brandon do not claim to have discovered anything new. Instead, they have formulated a biological law that they hope will provide a baseline expectation for the behaviour of evolving systems. The "Zero force evolutionary law", or ZFEL (the requested pronunciation of which is "zeff-el"), is given the following "general formulation":

> In any evolutionary system in which there is variation and heredity, there is a tendency for diversity and complexity to increase, one that is always present but may be opposed or augmented by natural selection, other forces, or constraints acting on diversity or complexity (p. 4).

By declaring this proposed universal tendency a "law", they hope to achieve two things. One is to bring about a change in perspective, by emphasizing that the baseline condition for evolving systems is increase in diversity and complexity, and that deviation from this (lack of change, loss of complexity) requires special explanation. Another is to bring about unification: by explicitly linking pattern and process across multiple levels of biological organisation, they aim to provide a single explanatory principle for evolutionary change that can apply to any level of organisation of any evolving system. To generate this unifying principle, they define "complexity" in a way that, they freely admit, may not sit comfortably with many people.

Complexity is defined, more or less, as the number of non-identical parts. This means that any process that introduces differences between parts increases complexity. An analogy used throughout the book to describe the action of the ZFEL is a picket fence decaying over time. When the fence is built, all the pickets are identical: same size, same shape, same colour. But over time, the pickets tend to diverge from each other: the shape of one is altered by termites, the colour of another is altered by bird droppings, the size of another modified by a wayward cricket ball. So over time, according to the ZFEL definition, the complexity of the fence increases: it is no longer a repeated series of identical parts, but a more diverse collection of non-identical parts. Under this definition, any biological processes that makes previously identical parts different from each other is subsumed under the ZFEL. For example, fluctuating asymmetry increases the complexity of an organism, because the left and right sides are no longer identical, so there are more non-identical parts to the organism (p. 72). The deleterious effect of radiation on the development of the vertebrae of mice is also presented as evidence for the tendency to increase in complexity through an increase in variance between parts (p. 74).

As the authors are at pains to stress, this definition of complexity will not please those who view complexity solely through the lens of adaptation, since this is a resolutely adaptation-free definition. In this sense, the argument presented here does not directly connect with much of the current literature on evolution of complexity. But this definition of complexity allows McShea and Brandon to do several things. Firstly, it allows them to define complexity in a way that is, at least in theory, able to be recognized, measured and compared. Secondly, it permits them to talk about the evolution of complexity by purely undirected processes, rather than being strictly tied to concepts of adaptation and utility. Thirdly, it allows them to construct a hierarchical view of complexity. By defining complexity as the number of non-identical parts, the authors can link diversity and complexity. The number of non-identical parts is diversity at one level, and complexity at the level above: a diversity of parts leads to a complex whole. An organism with greater diversity of cell types is more complex than an organism with fewer cell types. A community with more diverse species is more complex than one with fewer.

A neutral explanation of the evolution of complexity

The apparent increase in biological complexity over time has played an important role in many different frameworks for understanding the natural world. The idea of a *scala naturae* (Fig. 1) is repeated in many classification schemes (see Nee 2005), and can be seen reflected in the outline of many biology text books today (and many popular accounts of evolution), which tend to follow an ordered series beginning with the old and simple and ending with the recent and complex (see also Gould 1996). The increase in complexity over evolutionary time has been variously explained as a result of, amongst other things, an internal drive to perfection present in all beings (Lamarck 1809), adaptive responses that enables an increasing number of niches to be colonised and therefore a greater diversity of forms to evolve (Darwin 1872), stepwise transitions where previously independent units come together and reproduce as one (Maynard Smith and Szathmáry 1995), or a result of increase in informational capacity of genomes (Adami et al. 2000). In "Biology's First Law", McShea and Brandon argue that increase in complexity over time can and does arise from a wholly neutral process. Diversity and complexity increase over time because uniformity and simplicity must be actively maintained in the face of inevitable change.

The most useful aspect of this book is that it reasserts an important point that is sometimes lost in characterisations of the process of evolution: evolution is not all about selection and adaptation. You can get an awful lot of evolution happening, including increases in diversity and complexity, in the absence of selection. This is not a new idea. Darwin recognised that neutral processes could be responsible for the evolution of some traits, through the maintenance of polymorphic traits that had no impact on fitness, and the occasional chance fixation of neutral morphological variants:

> Variations neither useful nor injurious would not be affected by natural selection, and would be left either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions (Darwin 1872, p. 63).

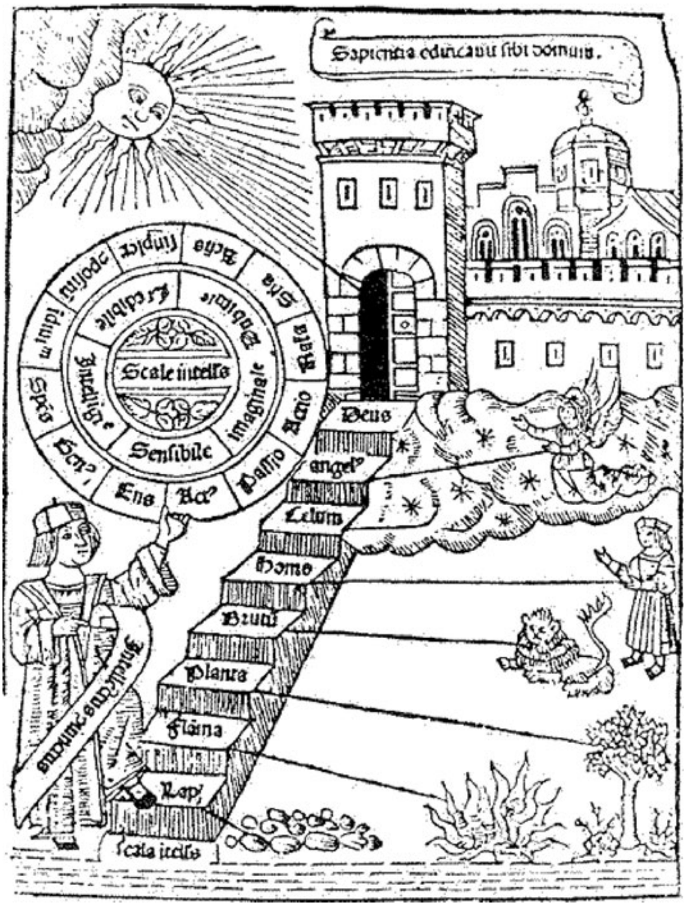

Fig. 1 The *scala naturae* (ladder of nature), or Great Chain of Being, has pervaded biological classification for hundreds of years. Here, the series is from inanimate matter (stones, fire), to plants, to animals, then humans, angels and with god at the top. But the idea of a natural scale of increasing complexity can also be found in many modern accounts of biological diversity, which typically begin with simpler organisms, such as bacteria, progress through algae, plants, invertebrate animals, vertebrates, mammals and, finally, humans

Neutral processes were brought to the fore by the study of molecular evolution (e.g. Kimura 1983). Though initially mischaracterised as “non-Darwinian evolution” (King and Jukes 1969), and rejected by some as a major force in evolution, the influence of neutral processes on molecular evolution is now a standard part of the explanatory toolkit of molecular evolution. Most studies of the patterns and causes of molecular evolution ask first whether a pattern could be explained by a neutral process before invoking a selective explanation. Neutral processes also play a role at much broader evolutionary scales. For example, the field of community ecology has been shaken up by the introduction of a neutral theory for explaining the species composition of a given area as a random sample from the regional species pool

(Hubbell 2001). In macroevolutionary studies of diversification, researchers typically test and reject a null model of differences in clade size arising by chance through random fluctuations in the origination and extinction of lineages.

But McShea and Brandon are making a different and somewhat bolder point. Their claim is not simply that it is possible for diversity and complexity to increase in the absence of selection, but that it is the expected outcome. Under this view, cases where diversity and complexity increase are the norm, and it is the cases where diversity and complexity do not increase that require explanation. In their words, "diversity is easy, stasis is hard" (p. 113). The authors echo some of the sentiments of Michael Lynch's (Lynch 2007) argument for the role of neutral processes in creating complex features of genome architecture (see Bromham 2009), and indeed McShea and Brandon pay homage to Lynch's work as a key stimulus for their work. But there are three important differences to Lynch's work. Firstly, McShea and Brandon do not restrict their discussion to the genetic level, but wish to construct a general law that works at all levels of biological organisation. Secondly, whereas Lynch resolutely frames his arguments in terms of the algebra of modern population genetics, McShea and Brandon offer an almost entirely verbal exposition of their thesis. Thirdly, where Lynch uses truckloads of data and analysis of the patterns and processes of genome change, McShea and Brandon make surprisingly light use of data or analysis in defence of their theory. This is surprising given the wealth of empirical studies that could be used to test their hypothesis.

Can the ZFEL be tested?

There are two broad problems with seeking corroborating evidence for the ZFEL. The first is that not all instances of increase in diversity and complexity are considered to be examples of the ZFEL in action. In particular, McShea and Brandon emphasise that the ZFEL does not apply in any cases where diversity and complexity are themselves promoted by selection. Only in cases where the evolutionary changes among lineages are independent of each other can the increase in diversity be counted as a result of the ZFEL.

Nonetheless, the ZFEL is said to be inherent in the Cambrian explosion of animal forms, whether driven by arms races, environmental change or ecological opportunity generated by extinction; the Ordivician radiation, whether driven by expansion into new ecospace or allopatric speciation driven by tectonic activity; the radiation of mammalian orders in the Tertiary, reportedly driven by key innovations in dental morphology; and the radiations of taxa following the massive extinctions in the Permian (p. 37). In each case, an "opportunity is exploited to some degree differently in each lineage. The result is divergence. And that is the ZFEL." (p. 38).

And yet the interpretation that an increase in complexity or diversity in each these lineages occurred independently of the others is not, as the authors acknowledge, the only interpretation of these evolutionary events. For example, the Cambrian explosion has been interpreted as an arms race, where the pace of change is accelerated by the need for each lineage to respond to other lineages' innovations, particularly in predation and defence (e.g. Bengston 2002), and the

Ordovician radiation has been interpreted as an example of ecological escalation, where each new species creates new niches for more species to colonize, creating a feedback loop that drives the evolution of diversity (e.g. Botting and Muir 2008). So it becomes difficult to tell when the evolution of diversity should be attributed to the ZFEL, and when it shouldn't.

The second problem with seeking corroborating evidence for the ZFEL is that it states that we should not be surprised if diversity and complexity increase, but that it is not inevitable. If constraints act on all systems, then all of them could potentially be prevented from increasing in complexity and diversity. The constraints that limit the evolution of diversity, or the forces that promote maintenance of systems against increasing variance among parts, are diverse and apparently without practical limit. For example, constraints that prevent the expression of the ZFEL include such diverse processes as DNA error correction, genetic linkage, fixation by drift, horizontal gene transfer, inbreeding, asexual reproduction, death and extinction (pp. 29–32). In short, the ZFEL allows every lineage to be like a coelacanth, remaining essentially unchanged for a hundred million years, if it is subject to "other forces". Since it is not obvious how to rule out possible constraints that may be acting to limit the evolution of complexity and diversity, it is not clear how to distinguish two possible explanations for cases in which diversity and complexity do not increase over time: either the ZFEL is false because the tendency to increase in diversity and complexity is not universal, or the ZFEL is true and constraints acting on those lineages to prevent the tendency from being expressed. So the ZFEL might not be true even if diversity and complexity do tend to increase, and it might be true even if they don't.

It does seem that the ZFEL in its pure form is difficult to disprove, because the tendency to increase in diversity and complexity is said to exist even if it is not manifest. However, the general formulation of the ZFEL is testable, because it states that we should see that complexity and diversity increase on average. Not every lineage will become more complex over time: a great many parasitic lineages, for example, become simpler through the loss of non-essential parts, and if we view this simplification as the results of selection for simplicity, then the interpretation is that the ZFEL is overcome in these cases by selection (though it's not clear if this interpretation also holds if the simplification of parasites is due to the undirected decay of parts that are not actively maintained by selection). But when we take a wide view we should see that diversity and complexity always show an average increase in evolving systems. Furthermore, the general increase in diversity and complexity should be evident at all levels of biological organization.

Increasing diversity at the genomic level

The best supporting evidence for the claim that biological diversity and complexity increase through neutral processes can be found in the DNA sequence of the genome. If you split a population of organisms into two separate subpopulations whose members can no longer interbreed, then those two subpopulations will begin with essentially identical genomes, but over time they will become progressively more different. This divergence may occur by selection, as each population discovers different responses to shared pressures or develops novel adaptations to differing environments. But the divergence will also occur in the absence of selection. Chance mutations can be inherited by members of one sub-population but not the other. Even if these mutations have no effect on fitness (and even if they have a slightly deleterious effect on fitness), they might increase in frequency in one subpopulation simply by chance, and eventually replace all other variants. In this way, the divided populations gradually and steadily acquire genetic differences.

The only brake on this process is negative selection: mutations that disrupt an essential function are less likely to be passed on to the next generation. In this way, selection can keep important sites in the genome in stasis. For example, the enzyme DNA polymerase plays a key role in replicating the genome, so a working copy of this protein is essential to all cellular life. The amino acid sequence of the active site of DNA polymerase has been maintained against change (more or less) for billions of years despite ongoing mutation occurring every generation (see Bromham 2000; Patel and Loeb 2000). A similar pattern can be seen in the Hox genes that influence the development of body plan in animals: a 60-amino acid sequence that forms an active site is conserved between disparate taxa, although the rest of the sequence has become entirely different (see Bromham 2011).

The tendency for genomes to become progressively more different from their relatives through mutation, drift and selection is so pervasive that it forms the basis of two important tools in evolutionary biology: molecular phylogenetics and molecular dating. Because change accumulates continuously, the more distantly related two species are, the more differences we expect to see between their genomes. Therefore, we can compare DNA sequences from different species to reconstruct patterns of relatedness, and also estimate approximate times since they last shared a common ancestor (Bromham and Penny 2003). Although the morphology of the coelacanths have been virtually in stasis for over a hundred million years, their genomes have continued to steadily diverge. The two species of coelacanth alive today are, apart from a difference in colour, essentially identical, but the differences between their genomes suggest they have been diverging for millions of years (see Bromham 2008). So, on average, the genomic level appears to broadly conform to the expectations of the ZFEL: there are forces that maintain stasis, but the general trend is for lineages to become steadily more different from each other.

But does it propagate to other levels of the biological hierarchy? This may be the case if, as genomes become more different from each other, populations become increasingly genetically distinct until they can no longer interbreed. There are several ways that increasing “complexity” at the genome level (defined for the ZFEL as accumulating differences) could lead to higher diversity at the species level. Greater rates of genomic change could increase the rate of speciation, either through neutral processes or selection. The accumulation of differences between genomes of different populations can lead to increasing hybrid incompatibility, as it becomes difficult to create a functioning offspring by combining genomes with too many differences between them (e.g. Orr and Turelli 2001). The accumulation of genetic differences may also generate standing variation that could provide fuel for adaptive divergence, or the raw material for selecting for reproductive isolating mechanisms. It is also possible that lineages with higher rates of genetic change are less vulnerable to extinction (e.g. Franklin and Frankham 1998) and therefore more diverse (see Lanfear et al. 2010 for discussion).

Gradual accumulation of heritable differences driving speciation was, in essence, Darwin's view of diversification. Darwin (1859) took pains to point out that it is often difficult to draw a line between races, varieties, sub-species and species, which in some cases formed a continuum of differences. He considered that the degree of divergence between lineages was the primary determinant of whether they would act as "good species" (to use the modern parlance), unable to interbreed: "the fertility of first crosses between species, and of the hybrids produced from them, is largely governed by their systematic affinity". Darwin stated that the formation of reproductive isolation was "not a special endowment", but "incidental on slowly acquired modifications".

In other words, the formation of species is contingent on the gradual accumulation of heritable differences rather than due to some special and demarcated process of speciation. This model of speciation has been controversial since Darwin's day (see Mallet 2008). It is clear that speciation does in many cases involve more than simply the continuous acquisition of small differences, and there are now many examples in the literature of the role of population subdivision, adaptation to different niches and selection for reproductive isolating mechanisms such as differential mate choice. However, there is also a growing body of evidence that Darwin's view of diversification is at least partially correct.

Analysis of genetic data has provided evidence that neutral processes of genomic change can, at least to some extent, drive the rate of diversification. There are two lines of evidence for this. Firstly, hybrid inviability increases with genetic distance in some taxa, for example, toads (Malone and Fontenot 2008), fishes (Bolnick and Near 2005), and fruit flies (Coyne and Orr 1989). Secondly, several studies have noted a significant association between rate of molecular evolution and species richness (Pagel et al. 2006; Webster et al. 2003), for example in plants (Barraclough and Savolainen 2001; Davies et al. 2004), and in birds and other reptiles (Eo and DeWoody 2010; Lanfear et al. 2010). If this association between species richness and molecular change arose because the process of speciation drove molecular evolution, then presumably it could not be considered evidence for the ZFEL. But a recent study of DNA sequence divergence in birds presented evidence that it is the mutation rate that is driving this relationship: bird families with a higher mutation rate have a tendency to be more species rich (Lanfear et al. 2010). This explanation is compatible with the ZFEL because it suggests that the inevitable processes of genomic change can propagate up the levels of biological hierarchy to contribute to diversity at higher levels. However, this effect does not appear to be universal: a similar analysis on mammalian genes revealed no association between rate of molecular change and species diversity (Goldie et al. 2011).

But even if complexity at the genetic level (here, the tendency for sequences to continuously become more different due to mutation and drift) can drive diversity at the species level (the separation of populations into separate species due to accumulation of genetic change), this mechanism appears to be frequently overridden by other processes. In many cases, the development of reproductive isolation is rapid and apparently driven by specific selection for divergence, rather than through the independent accumulation of differences in each lineage (whether by drift or selection).

For example, in African cichlids, the poster child of speciation studies, hybrid incompatibility increases with genetic distance (Stelkens et al. 2009). However, when different components of reproductive isolation are considered, they appear to have different patterns of acquisition over time: premating isolation (reduction in matings between members of different populations) accumulates rapidly then plateaus, whereas postmating isolation (reduction in the viability of hybrid progeny) increases steadily over time since divergence. This pattern is consistent with active selection for speciation by reproductive isolation, not simply a passive divergence. Indeed, the degree of genetic differentiation between diverging lineages can be highly variable across the genome, and evidence suggests a significant role for selection in driving genetic differences between populations (Nosil et al. 2009). So while the relationship between genetic change and diversification could be taken as evidence for the neutral processes of divergence described by ZFEL, the pattern may well be driven by selection in many (perhaps even most) cases. If subpopulations are under selection to become more different from each other, then the divergence is the active result of adaptation, not the neutral tendency to acquire differences described by the ZFEL.

Increase in biodiversity over time

At the molecular level, patterns of divergence are, by and large, consistent with the ZFEL, because genetic differences between lineages tend to accumulate continuously over time. There is also some evidence that this continuous genetic divergence can propagate to higher levels of biological organisation, because it has been shown that, for a range of lineages, the greater the rate of molecular change, the greater the diversity at the species level. But the ZFEL is not intended to describe only the genomic level of evolution. It requires that continuous increase in diversity and complexity should apply to all levels of the biological hierarchy. Diversity should, on average, increase at the species level, generating greater complexity at the level of the ecological community. In particular, we should see that the total amount of biodiversity increases over time, and that, on average, each ecological assemblage continues to accumulate ever more species.

Species diversity is a measurable quantity, even though it is difficult to estimate with precision. So one way to test the predictions of the ZFEL is to look at patterns of diversity over time. Figure 2 shows a famous representation of the diversity of marine animals over geological time (measured as the number of families identified for each period: Sepkoski 1981). Clearly, diversity does not steadily increase in all biological lineages, which wax and wane over time. For example, the diversity of trilobites (Fig. 3) rose in the Cambrian, declined from the Ordovician, and hit zero, alas, in the late Permian. Equally clearly, this graph suggests that there have been periods in the history of the earth when the amount of diversity not only failed to

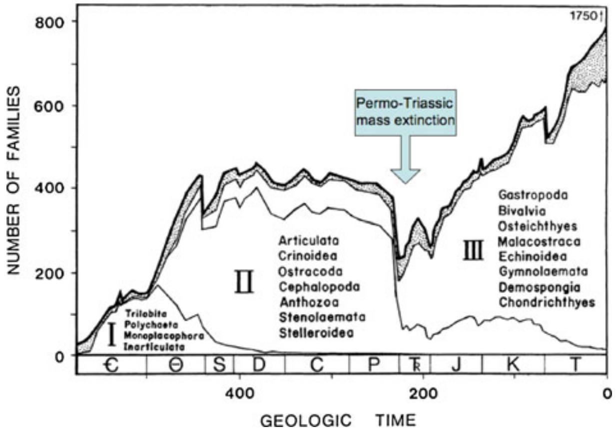

Fig. 2 One of the iconic graphs of number of known families of marine animals over the Phanerozoic period (from 543 million years ago, on the left, to the present, on the right) produced by palaeontologist Jack Sepkoski. This version is from Sepkoski (1981), though he refined and published several more versions. Sepkoski grouped the marine families into three faunas that differed in their patterns of diversity over time, marked here as I, II and III. Graphs like this one have been used to argue for an ongoing increase in net biodiversity over time, and also for the occurrence of a "big five" mass extinction events that reduced global biodiversity. The most dramatic of these is marked on this graph: estimates of the loss of taxa through extinction at the end of the Permian period vary from around 50% to over 90% of the standing diversity

Fig. 3 A fossil trilobite of the genus *Ceratarges* from the Devonian (about 360 million years old). This specimen is about 6 cm in length. Over 20,000 species of trilobite have been described, ranging in size from a millimetre to a quarter of a metre in length, and in age from early Cambrian (520 million years ago) to end Permian (250 million years ago). Photo credit: Woudloper, WikiCommons

increase, but underwent a dramatic reduction. The late Permian "mother of all mass extinctions" (Erwin 1993) is a good example (see Fig. 2). But it's the average picture that's important here, rather than the diversity of specific lineages or periods. And the data in Fig. 2 does indeed seem to suggest a trend toward increase in the diversity over time, at least of families of marine animals.

But analyses of the data underlying diversity curves such as the one presented in Fig. 2 show that the picture is not so straightforward after all. Figure 2 is based on absolute numbers of fossil families known from each period. If rates of preservation, discovery or identification are not even over all time periods, then the absolute numbers of described families will change over time, even if there is no change in diversity (Raup 1977). Reanalyses of the Sepkoski curve correcting for volume or area of rock outcrop (therefore opportunity for fossilization) results in flattening of the relationship between diversity and time leaving no signal of an increase of diversity over time (Peters and Foote 2001). It could be argued that this is an unfair correction, as area of rock outcrop might itself be related to biological diversity, through a species-area relationship. Adjusting the raw count of taxa per period to take account of sampling artefacts, independent of rock volume, also changes the shape of the curve, making it harder to support a hypothesis of ongoing increase in diversity over time (Smith 2001). It has even been suggested that the majority of the diversity curve is indistinguishable from a random walk in extinction and origination rates through time (Cornette and Lieberman 2004). While the jury is still out on the exact nature of the pattern in biodiversity over time, it seems fair to say that this data does not provide clear and unambiguous support for a tendency for diversity to increase over time, as predicted by the ZFEL.

Increase in morphological complexity over time

Even if the net number of species does not increase over time, it could still be argued that the average complexity of lineages has increased. At first glance, this appears self-evident, because the earliest appearing lineages tend to be the simplest: bacteria are simpler than eukaryotes, algae are simpler than “higher plants”, sponges are simpler than “higher animals”, and so on. Valentine et al. (1994) illustrated this increase in complexity over time in the animal kingdom by plotting the number of different cell types for a number of animal lineages against their age of first occurrence (Fig. 4a).

But, as McShea and Brandon point out, an upward trend in the maximum complexity does not, in itself, provide evidence for the ZFEL. The evolution of complexity could follow a “space-filling” trajectory. Gould (1996) described this as a “drunkard’s walk”, to illustrate how a random walk can end up with an apparently directional outcome. A drunk exits a pub and conducts a random stagger along the alleyway. Every time the drunk hits the pub wall on the left, they are repelled back into the alley, but if they reach the gutter on the right side of the alley they fall down and stop moving. So even though the movement of the drunk is undirected, they are pushed towards an inevitable outcome, eventually moving away from the pub and ending up in the gutter. Gould’s point is that there is a lower limit that cannot be crossed (the pub wall), so random movement will inevitably wander toward the upper bound (the gutter). If the evolution of life has taken a random walk in complexity, with increases or decreases equally likely, then it has started at low complexity (and cannot go lower), and while most lineages may wander back and forth or stay the same, it is inevitable that some lineages will wander toward an increase. The minimum cannot change, but the maximum will continue to increase, unless some upper limit is reached.

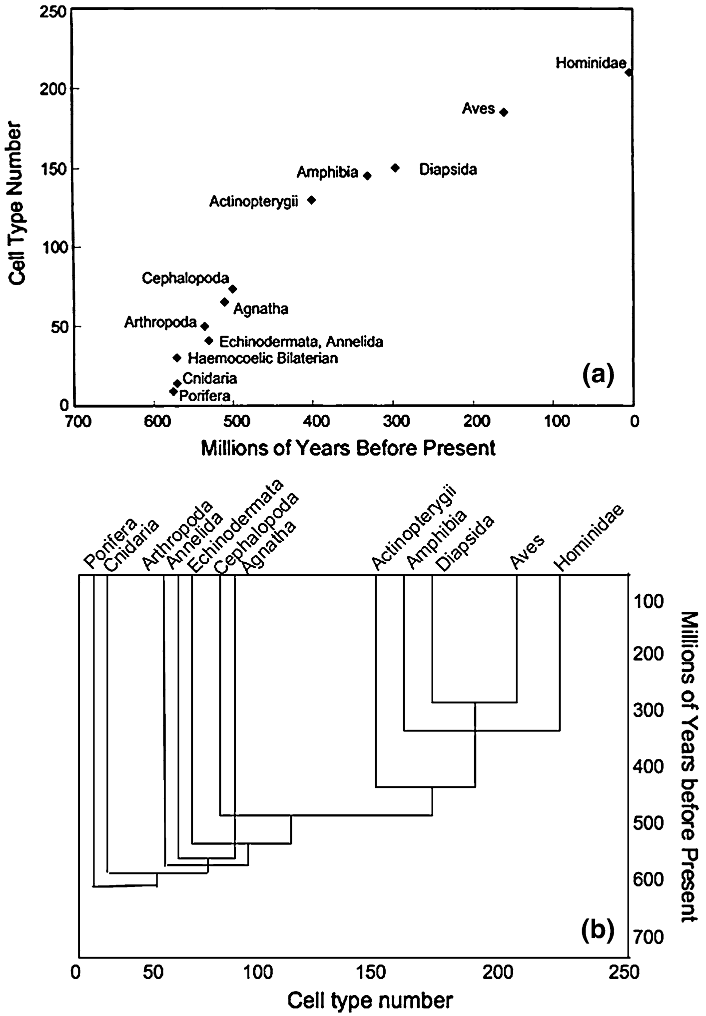

Fig. 4 Number of cell types in some modern animal taxa plotted against their earliest known occurrence in the fossil record from Valentine et al. (1994) (**a**). The same information is plotted as a phylogeny in **b**. The relationships between the taxa are not known with certainty, so the phylogeny is an approximate guide only

But a space-filling wander, where some lineages increase in complexity, some decrease, and others stay the same, is not what the ZFEL predicts. Instead, it makes the clear prediction that the average complexity of all lineages should increase. All lineages should have a tendency to move toward the right hand side of the graph, as depicted by McShea and Brandon (Fig. 5). The idea of a tendency to increasing complexity has rippled through evolutionary thinking, both professional and lay, since evolution was first discussed (see Gould 1996). In the terms defined by the ZFEL, this idea is testable: we can ask whether lineages increase in complexity over

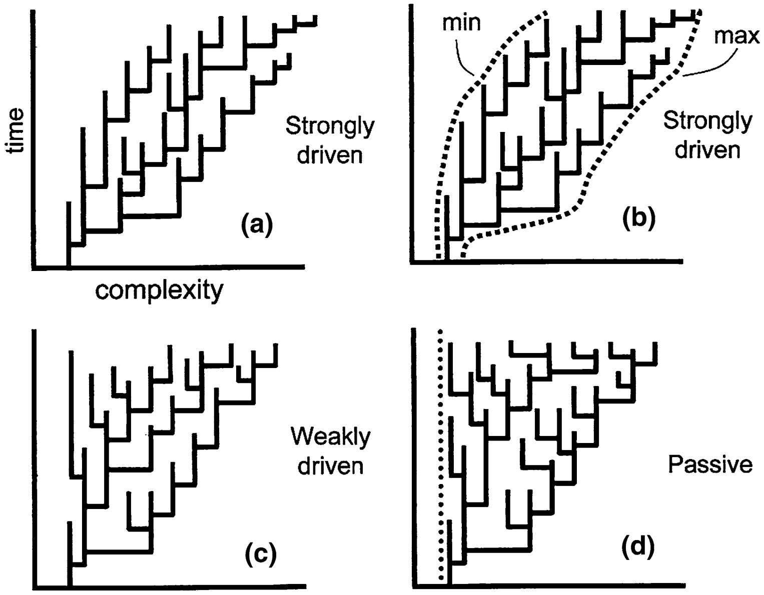

Fig. 5 Figure from McShea and Brandon (2010) gives a graphical presentation of the predictions for increase in diversity and complexity. The "strongly driven" trend (**a**) predicts that "the vast majority of changes among the lineages are increases", resulting in an increase in both the maximum and minimum complexity over time (**b**). A "weakly driven" trend results in an increase in the maximum, but not the minimum, complexity (**c**). In the "passive" case (**d**), there is no bias toward increases or decreases in complexity, but complexity cannot go below the initial minimum, so the maximum increases but the minimum stays the same. The ZFEL predicts a strongly driven trend, but the evidence does not support the predicted increase in the minimum (see p. 81 of McShea and Brandon 2010)

evolutionary time, by plotting some measure of the number of non-identical parts per organism against evolutionary time for lineages of descendents.

It may seem that Fig. 4a does exactly that. The earliest appearing animals, the sponges (Porifera) have fewer cell types that those that appear in the Cambrian (such as annelids and arthropods), which have fewer cell types than the fish that appear in the late Silurian, which have fewer cell types than birds, which appear in the Cretaceous. And the most complex animals, by number of cell types, are humans, which are a very, very recent arrival. But this is not a list of ancestors and descendants. The sponges whose cell numbers were counted for this graph are alive today, as are the jawless fish, the amphibians, the reptiles. Humans may be a recent addition to the evolutionary tree, but the lineage they descend from is as old as the lineage leading to the modern sponges. The sponges of today and the humans of today have had exactly the same amount evolutionary time to build their complexity, compared to that of their common ancestor. So, if all lineages have a tendency to increase in complexity, why are there not species on the sponge lineage with as many cell types as humans?

If we wish to trace the evolution of complexity over time, we need to do so in light of an evolutionary tree that maps lineages of descent. If we display the information from Fig. 4a as a phylogeny, a clear pattern emerges. The maximum complexity increases over time, but the minimum does not shift (Fig. 4b). It is not the rightward trend predicted by the ZFEL, but the space-filling diversification described by the Drunkard's Walk. If the ZFEL were true, then we should see that every lineage has a tendency to give rise to more complex descendents. Amongst the hundreds of thousands of bacterial lineages, we should see at least some that give rise to more complex kinds of organisms. The sponge lineages have had just as long to produce complex descendants as any other of the animal phyla, yet have remained resolutely simple. So instead of every lineage having a tendency to increase in diversity and complexity, it seems that complexity increases only occasionally in particular lineages.

If we start by trying to explain the evolution of a modern species on the right hand side of Fig. 4b (say, humans), then of course when we trace its history back to the root we will inevitably encounter a series of increases in complexity. But such an evolutionary path would not be typical. Most lineages are no more complex now than they were when their ancestors first arose. If we take a slice through the tree of animal life depicted in Fig. 4b, at any time we will find a range of complexities. A few lineages will have increased the upper bound, but most have not. There is no reason to believe that the animal kingdom is unusual in this sense. For example, the range of complexities and genome sizes of the single-celled prokaryotes is predicted to be no greater now than it has been for a billion or more years (Koonin 2009).

So taking a phylogenetic view of the evolution of complexity suggests a step-wise model of the evolution of complexity: early branching lineages remain, on the whole, less complex, because they have not evolved whatever invention made one or few descendant lineages more complex. We artificially create a sense of progress from simple to complex in the common habit of plotting the more complex and diverse members of a clade on the right hand side of a phylogeny (Omland et al. 2008). Think of any tree of mammals you have seen: probably the monotremes (platypuses and echidnas) were labelled on the far left of the tree, then the marsupials (kangaroos, koalas and so on), and the placentals (e.g. rats, bats, cows and humans) arrayed on the right hand side. Monotremes (5 species) and marsupials (334 species) may be less diverse than placentals (over 5,000 species), but it is hard to make an argument that they are less complex, whatever definition of complexity is being considered. For example, marsupials have, on average, larger genomes than placentals (Gregory 2005), and monotremes have complex features found in no other mammalian lineages, such as poisonous spurs and the ability to hunt by detecting electromagnetic radiation of their prey.

Likewise, phylogenies of green plants will tend to have mosses and liverworts on the left hand side, then gymnosperms, then flowering plants on the right. This left-to-right display of current diversity and, in some cases, complexity, gives a false sense of progress toward complexity. But this picture of a rightward march to complexity is changing in many groups. The animal phylogeny has been overhauled by the increasing use of molecular data to determine relationships. Animal phylogenies can no longer be plotted in a series from simple of the left to complex on the right. Instead, the new molecular trees scatter the more complex animals into groups with simpler animals.

In conclusion, the ZFEL makes a prediction that most lineages should show a rightward-trend from simpler ancestors to more complex descendants. But this pattern is true in only a minority of cases. We gain an inflated sense of the occurrence of a progression from simple to complex from our tendency to trace the history of atypically complex lineages to their inevitably simpler ancestors. Considering the evidence, McShea and Brandon state: “We conclude that what is currently know about the history of life offers little evidence for the ZFEL for complexity. A long-term increase in the mean has not been demonstrated… the ZFEL predicts a strong drive, but no such drive has been shown, and indeed the stable minimum… argues for the opposite, a weak drive or none at all” (p. 84).

Against the law

This book makes a valid and important point: the tendency to diversify is a common outcome of evolution, so that increase in diversity and complexity (as defined here) is not in itself surprising. Although the tendency to diverge is not a new idea, it is worth being reminded that we need not be surprised that things get more different over time even in the absence of selection for diversity. The authors' statement that “Diversity is easy, stasis is hard” is food for thought.

But claiming that a tendency toward diversification is a universal law of biology weakens this book considerably. Perhaps there is little harm in coming up with a snappy title and a claim for universality of a basic outcome of evolution. But by christening the tendency to divergence as a law, the authors are forced to jump through quite a lot of hoops to reject any cases where the tendency to diverge does not seem to be a general feature. For example, the Hardy–Weinberg law is rejected because it predicts no change in allele frequencies in the absence of selection, mutation or migration. The transient loss of variation as alleles become fixed in the population is also rejected by the bold claim that alleles cannot be discretely defined so therefore “population genetic theory is based on a fiction” (p. 105). In fact, much of the book is concerned with defending the ZFEL against examples where diversity and complexity do not increase. Since some of these defences are not particularly strong or convincing, the overall effect is to weaken the thesis.

The case for the ZFEL is also undermined by the data. A tendency to diverge and become more complex may well provide a general description of evolution at the genomic level (e.g. Lynch 2007). But McShea and Brandon fail to assemble convincing evidence that it is more generally true, and in particular that the ZFEL describes the behaviour of all levels of organisation of all evolutionary systems. To take the single, well-studied example of the animal kingdom, the ZFEL does not appear to be a good description of the evolution of diversity (for which there is currently no convincing evidence for an constant tendency to increase) or complexity (the upper bound has increased, but relatively few lineages show a trend from simple to complex).

Laws do not need to be without exception to be useful (Colyvan and Ginzburg 2003). And, as Maynard Smith (1990) acknowledged, “the fact that we expect our theories to have exceptions makes it hard to test them”. But surely a law does need to offer a useful guide for what to expect. It's not clear that the ZFEL does so. It is fair to say that we ought not to be surprised that diversity and complexity increase over time, and this prediction is indeed born out the general picture emerging from molecular evolution. But it is also clear that diversity and complexity very often do not increase over evolutionary time, and for such a wide and complex variety of reasons that the exceptions to the law seem unlikely to tell us anything interesting about the law itself. If McShea and Brandon's book had been called simply "the tendency for diversity and complexity to increase in evolutionary systems", with no mention of the L-word, it might have sold fewer copies, and been half the length, but might ultimately have convinced more people that an important general principle was being described.

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