

Phenotypic Evolution in Fossil Species: Pattern and Process

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Abstract

Since Darwin, scientists have looked to the fossil record with the hope of using it to document how the phenotypes of species change over substantial periods of time. How best to interpret this record has been controversial, but empirical and methodological advances have resolved at least two issues about pattern: (*a*) directional transformations are seldom sustained over geological timescales, and (*b*) net rates of morphological change in fossil species are usually quite slow. Considerable uncertainty remains, however, about the processes responsible for these patterns, but most fruitful explanations use the framework of adaptive landscapes to consider the role of natural selection and other processes. An additional, unresolved issue is the claim that most phenotypic change is associated with speciation. A variety of methods, using data from both fossil and extant species, have supported such a link, at least in some clades and traits, but its prevalence and underlying mechanism remain unresolved.

1. INTRODUCTION

Without the fossil record, we would have little or no knowledge of many major events in the history of life, including the timing of life's origins, the progressive alteration of the geosphere by the biosphere, and the diversification and extinction histories of major groups of organisms. When it comes to understanding evolutionary changes at the much finer scale of individual species, however, the fossil record has had a more mixed and controversial history. Darwin (1859) viewed the broad fossil record as consistent with the idea that species arise from other species and that they change over time. But, at the finer resolution needed to capture the transformation of species, he argued that the fossil record was woefully incomplete and that the lack of known fossil series exhibiting gradual morphological transformations was therefore no impediment to his theory of evolution by natural selection. Darwin's account of the limitations inherent to the fossil record remains mostly credible today (for a modern update, see Kidwell & Holland 2002), but some inadequacies he noted were a consequence of the then limited exploration of the stratigraphic record (Rupke 1983, Rudwick 1985). Sustained paleontological efforts over the past 150 years have vastly increased what we know about fossil organisms, and advances in geochronology, stratigraphy, and sedimentology have allowed the distribution of fossils to be placed in a much more rigorous temporal and environmental framework. In the present review, we consider what this accumulated knowledge tells us about the nature of evolutionary changes within fossil species over geologically relevant timescales. The focus throughout is on identifying the major patterns by which the phenotypes of species change over time, evaluating the microevolutionary mechanisms that have been proposed to account for these patterns, and considering the methods by which both goals are achieved.

For many years, paleontologists followed Darwin's lead in ascribing the absence of species-level transformations to incompleteness in the stratigraphic record. Paleontology was eventually integrated into the emerging modern synthesis, largely through G. G. Simpson's (1944, 1953) arguments that the population genetic processes of mutation, drift, gene flow, and selection were capable of producing the patterns of evolutionary change seen in the fossil record. Still, despite this integration of paleontology into mainstream evolutionary thought (Laporte 1983), studies documenting the transformation of individual species were rare. The conventional explanation for this paucity of species-level transformations—incompleteness of the record—was provocatively inverted by Eldredge and Gould (Eldredge 1971, Eldredge & Gould 1972). They argued that such transformations were seldom observed, not because of deficiencies in the geological record but because species usually do not change much once they are established. Large changes in morphology were suggested to occur when lineages split to form new species via allopatric speciation. This model of punctuated equilibrium was positioned as an alternative to what Eldredge and Gould saw as the traditional view of steady, accumulating change—so-called phyletic gradualism. This set of claims ignited a fierce and prolonged debate among paleontologists and evolutionary biologists about the dominance of different evolutionary patterns in the fossil record and what these patterns implied about the mechanisms that caused them (Gould & Eldredge 1977, Charlesworth et al. 1982, Gingerich 1985, Hoffman 1989, Erwin & Anstey 1995, Levinton 2001, Gould 2002).

It is difficult to overstate the influence of punctuated equilibrium, not only during the debates of the 1970s and 1980s but also in how paleontologists continue to view the evolution of species. This model motivated hundreds of studies, generated thousands of pages of rebuke and praise, and set many of the terms for the discussion about interpreting evolutionary changes in fossil species. Nevertheless, the present article is a review of evolutionary patterns and processes as expressed in the fossil record, not a review of punctuated equilibrium as an episode in the history of science (see instead Geary 2009, Princehouse 2009, Sepkoski 2009). As such, we exclude issues mostly of

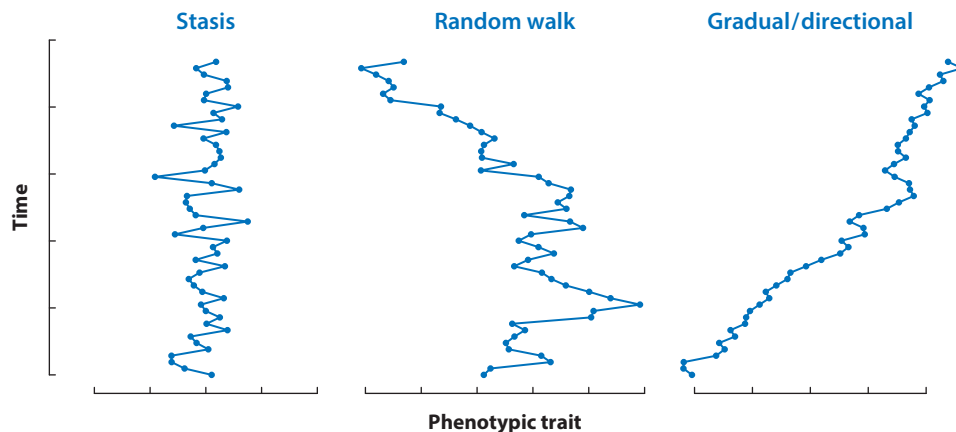


Figure 1

Simulated examples of trait evolution according to three different evolutionary modes: stasis, random walk, and gradualism. A random walk is a discrete-time model in which traits are equally likely to increase or decrease at each time step. Gradual (directional) evolution can be modeled as a biased version of a random walk in which trait increases are more probable than decreases (or vice versa). Stasis is modeled in different ways, but the salient feature of these models is that changes do not accumulate; instead, there is a stable long-term mean. Usually this behavior is caused by a tendency for evolutionary changes away from the mean to be followed disproportionately by changes that move the population back toward the mean.

historical interest, such as whether punctuated equilibrium fits comfortably within the modern synthesis or radically undermines it, whether this model should be construed as an extension of ideas by earlier thinkers such as Darwin or Simpson, and the degree to which proponents or detractors of punctuated equilibrium were influenced by philosophical commitments. Moreover, we defer on scientific issues that were sometimes linked to punctuated equilibrium but are peripheral to the focus of the present article, most prominently the roles of macromutation and species selection. Species selection, in particular, has seen a resurgence in popularity (e.g., Goldberg et al. 2010, Rabosky & McCune 2010), but it need not bear any relationship to punctuated equilibrium (McShea 2004, Jablonski 2008). These filters are surprisingly effective in restricting the present article to a manageable scope.

2. MODES AND MODELS OF TRAIT EVOLUTION

The term evolutionary mode comes from Simpson (1944), who used it to denote qualitatively different evolutionary patterns. The specific modes enumerated by Simpson were largely supplanted by two that arose from the punctuated equilibrium debates: stasis and gradualism (**Figure 1**). Initially, the identification of these modes was qualitative and impressionistic, which led to disagreements in which the same pattern was interpreted differently by different workers (e.g., Gould & Eldredge 1977 and references therein). In response, statistical tests were developed to help determine which interpretations of evolutionary mode were justified (Raup 1977, Raup & Crick 1981, Bookstein 1987). These approaches introduced a third mode into common usage, the random walk, which is a simple model in which trait changes at each interval of time are independent and equally likely to be in a positive or negative direction (**Figure 1**). The random walk was seen as intermediate between gradual change and stasis, and it was used as a null hypothesis in tests of evolutionary mode (Raup & Crick 1981, Bookstein 1987). Unfortunately, these null-hypothesis

tests turn out to have low statistical power, limiting their usefulness (Roopnarine et al. 1999, Sheets & Mitchell 2001b). Recent analyses usually rely instead on likelihood-based approaches that treat all candidate modes on an equal footing, with none given privileged null status (Hannisdal 2006, Hunt 2006). The advantage of this statistical approach is that once alternative modes are specified explicitly, the relative support each receives can be unambiguously compared (Hunt 2006), thus resolving the subjectivity that hobbled much of the early punctuated equilibrium debates.

2.1. Gradualism

Despite the advantages of this quantitative approach, the resulting statistically defined modes do not map seamlessly on to the initial discussions of stasis and gradual change. Statistical approaches today equate gradualism with directionality: a bias in the direction of change such that trait increases are more probable than decreases (or vice versa). This usage corresponds to how advocates of punctuated equilibrium saw gradualism, but to some others, the term merely implied the existence of populations of intermediate morphology between two related forms (Hoffman 1982, Gingerich 1985). Either view can be defended on historical grounds, but construing gradual to mean directional evolution has the advantage of turning gradualism into a specified and testable model (Hunt 2006, 2008b).

2.2. The Nature of Stasis

Similarly, stasis as modeled in statistical studies does not precisely match its description during the early phase of the punctuated equilibrium debates. These early contributions focused on magnitudes of change. Evolutionary changes were judged to be modest enough to qualify as stasis by comparison with various yardsticks, including geographic variation within defined species (Stanley & Yang 1987, Gould 2002), the conventional species limits used by taxonomists (Hoffman 1989), and two units of within-population standard deviation (Lande 1986). Regardless of the threshold, it was the amount of change, rather than the structure of that change, that defined stasis. As a result, stasis construed in this way is broader than any specific model; it encompasses any temporal pattern that produces modest evolutionary changes within species.

Numerical modeling forces specificity, however, and workers have devised a variety of explicit models for stasis (Roopnarine 2001, Sheets & Mitchell 2001b, Estes & Arnold 2007). Details differ, but all allow for some evolutionary change while incorporating mechanisms that ensure that evolutionary changes diverging away from the starting trait values are preferentially followed by changes moving back toward the long-term mean. Most commonly, statistical stasis is modeled as white noise—uncorrelated, Gaussian variation around a steady mean (Sheets & Mitchell 2001b, Hannisdal 2006, Hunt 2006)—but more complex options such as Ornstein–Uhlenbeck processes have also been used (Hansen 1997, Estes & Arnold 2007) (see **Figure 2** and the sidebar, *Stabilizing Selection on Generational and Geological Timescales*). With statistical approaches, it is the form of changes, not their magnitude, that defines stasis (Hunt 2008a). In principle, some parameter values of these stasis models can allow for substantial evolutionary variation within species, which would be inconsistent with the nonstatistical notions of stasis that emphasize small magnitudes of change.

In practice, the traditional and statistical notions of stasis will often coincide. Sampling error around trait means has the same analytical form as stasis, and when true evolutionary changes are modest, sampling noise will make the resulting sequence resemble stasis in the statistical sense (Hannisdal 2006, Hunt 2006). For example, of the 251 time series of trait values compiled by Hunt (2007), 73 offer strong evidence of stasis (Akaike weight >0.8). These examples of statistical stasis tend to exhibit only minor variation in trait values—on average, the evolutionary variance among

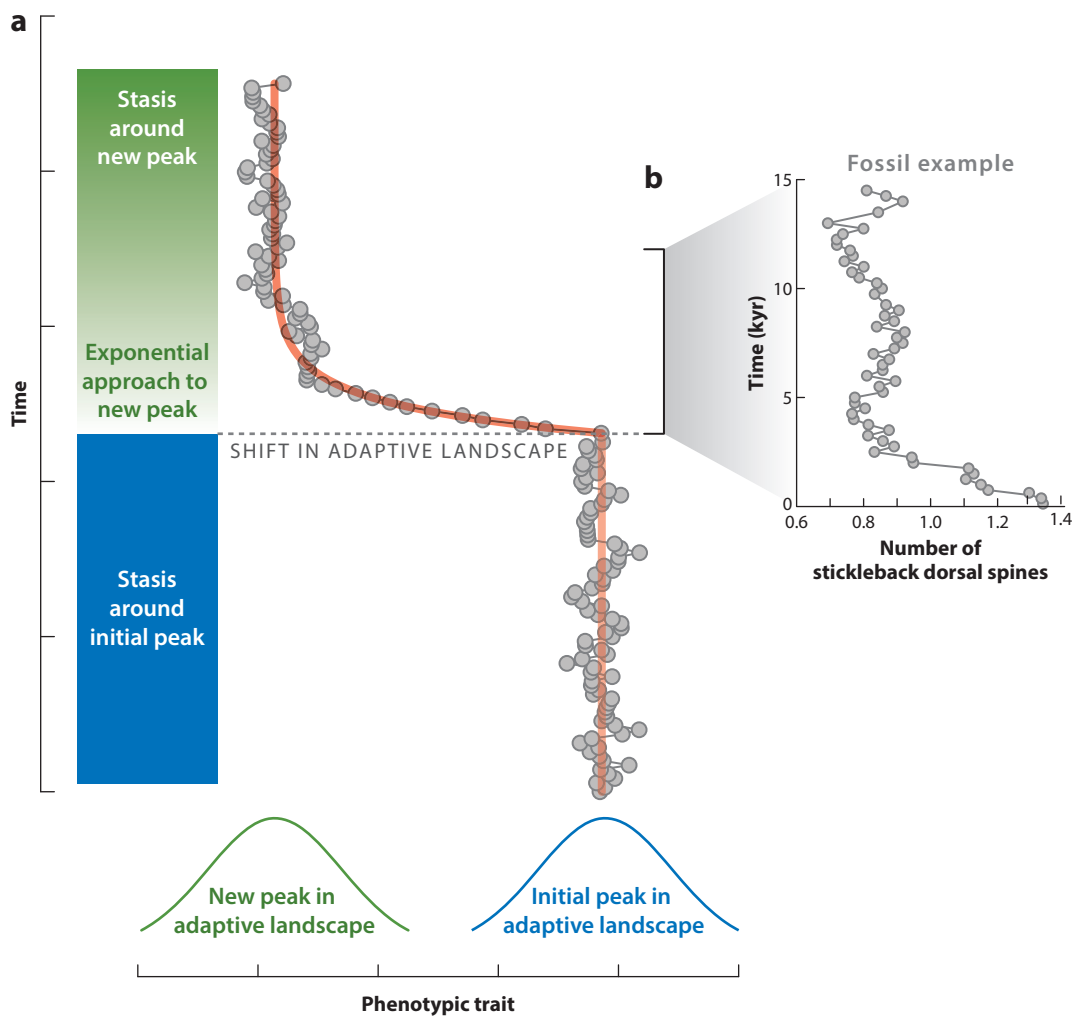


Figure 2

Evolution of a trait on a shifting adaptive landscape. (a) Simulated evolution of a trait that initially experiences stasis due to stabilizing selection around an adaptive optimum (blue). Suddenly, the adaptive landscape shifts so that the optimal trait value is lower (green). With this shift, the trait immediately starts an exponential approach to the new optimum, which steadily decelerates into stasis around the new peak on the adaptive landscape. The blue and green bell curves indicate how organismal fitness decreases away from optimal trait values, and the red curve shows the expectation (average) of this process. (b) An empirical example in which the fossil record captures the exponential approach to a new adaptive optimum in a lineage of stickleback fish in an ancient lake (Hunt et al. 2008).

temporally separated population means is less than 20% of the within-sample trait variance. In contrast, traits poorly accounted for by the stasis model (Akaike weight < 0.2 , $n = 109$) show much larger changes over time, on average seven times as large on the same scale ($t = 2.89$, $P = 0.005$).

2.3. Punctuations and Other Modes

The three models of stasis, random walks, and directional change are useful in exploring the relative frequency of different patterns in the fossil record, but they are by no means the only dynamics of

STABILIZING SELECTION ON GENERATIONAL AND GEOLOGICAL TIMESCALES

Stabilizing selection occurs when a population has a trait mean value close to the fitness optimum such that fitness decreases with increasingly extreme phenotypes. Fitness surfaces are often modeled as a Gaussian function with a standard deviation of ω ; for simplicity we assume that the fitness optimum occurs at a trait value of zero. Low values of ω translate to sharp decreases of fitness away from the optimum and correspondingly strong stabilizing selection. Populations evolving in the vicinity of a peak in the adaptive landscape evolve as an Ornstein–Uhlenbeck process, described as follows.

If a population's initial mean value, z_0 , is located some distance away from the optimum, the population exponentially approaches the peak in the landscape according to

$$E[z_t] = z_0 \exp \left[- \left(\frac{b^2 \sigma^2}{\omega^2 + \sigma^2} \right) t \right],$$

where b^2 and σ^2 are the trait's heritability and phenotypic variance, respectively, and t is the number of generations elapsed (Lande 1976, Estes & Arnold 2007) (**Figure 2a**). The variation around this expectation is a relatively complex function of these parameters (Estes & Arnold 2007) but becomes much simpler on paleontological timescales. When sampling resolution is coarse compared with the time it takes a population to ascend a peak, trait values will approximate statistical stasis as independent draws from a normal distribution with a mean equal to the trait optimum and a variance equal to $(\omega^2 + \sigma^2)/2N_e$, where N_e is the effective population size. This equilibrium variance represents the balance between drift-caused divergence and stabilizing selection pulling the population back toward the optimum. If stabilizing selection is absent, the resulting dynamic is instead that of a random walk with a step variance of $b^2 \sigma^2/N_e$ per generation (Lande 1976).

Stabilizing selection that is so weak as to be undetectable in extant populations can nevertheless exert a powerful effect on long-term trait evolution. Consider a trait from a large population ($N_e = 10^4$) with unit phenotypic variance and typical heritability ($b^2 = 0.4$) that experiences very weak selection ($\omega = 21.2$, equivalent to a fitness cost of 1% for individuals three standard deviations away from the optimum). Despite this weakness of selection, this scenario results in minimal long-term trait variation; the standard deviation among samples equals only about 15% of the within-sample standard deviation. By contrast, if selection is completely absent, evolution by genetic drift will typically change the trait value by more than six standard deviations over one million years, easily enough so that starting and ending populations will routinely be considered different nominal species.

interest. Other patterns were identified that implied heterogeneity in evolutionary mode within evolutionary sequences. Most prominent among these were suggestions of pulsed or punctuated change (Cisne et al. 1980, Chiba 1996), but a variety of other heterogeneous dynamics were also explored, including random walks with time-varying rate parameters (Bookstein 1987) and shifts from stasis to an unconstrained random walk (Malmgren et al. 1983), among others (Roopnarine 2001, Uyeda et al. 2011). It is straightforward to model these more complex scenarios by dividing a sequence into different segments with separate evolutionary dynamics in each segment (Hunt 2008b). The resulting models are more complex in that they require more parameters to specify, but their increased complexity can be accounted for appropriately using Bayesian or information criterion approaches.

Punctuations and other phenotypic changes within individual species have an ambiguous standing with respect to the predictions of punctuated equilibrium. Whereas examples of pulsed change within unbranched lineages were sometimes seen as consistent with punctuated

equilibrium (Gould 2002), they probably offer this model more challenge than support because they represent instances of significant phenotypic change that are not associated with lineage splitting. After all, the strong claim of punctuated equilibrium is that phenotypic changes are predominantly associated with the formation of new species, not the far less contentious claim that changes are episodic (Hoffman 1989). Evaluating whether changes are truly associated with lineage splitting turns out to be a more difficult problem, one that we return to below (Section 4.4).

3. ISSUES ABOUT PATTERN THAT ARE BASICALLY RESOLVED

3.1. Sustained Directional Change Is Rarely Observed in Fossil Sequences

In the aftermath of the punctuated equilibrium debates, several attempts were made to summarize what was known about the relative frequency of different modes of evolution within fossil lineages. These overviews came to remarkably divergent conclusions. Some suggested that gradual transformations of species were commonly represented (Gingerich 1985, Levinton 2001), whereas others saw stasis and punctuations as the norm (Gould & Eldredge 1977, Jackson & Cheetham 1999, Jablonski 2000, Gould 2002). Recent surveys that quantified the statistical support for different models—instead of relying on qualitative interpretations—have provided more support for stasis than for gradualism. Hunt (2007) found that only 5% of time series (13 of 251) were best accounted for by directional evolution. In a recent meta-analysis of an expanded set of cases (635 traits across 153 lineages), Hopkins & Lidgard (2012) found the exact same proportion, 5%, favored directionality. Moreover, this modest fraction must be an overestimate because paleontologists have disproportionately investigated traits and lineages with prior evidence of a trend (Stanley & Yang 1987, Gould 2002).

Darwin, among others, repeatedly emphasized the slow and incremental nature of evolution by natural selection (Bell 2010), but developments in the mathematical theory of phenotypic evolution have undermined gradualistic expectations in important ways. First, in response to a shift in circumstances, the expected evolutionary response is not constant, linear change but rather an exponential approach to the new optimal phenotype (Lande 1976, Arnold et al. 2001, Estes & Arnold 2007) (see **Figure 2** and the sidebar). Second, even when natural selection is quite weak, the time it takes to approach the new optimal phenotype is much shorter than typical paleontological resolutions (10^3 – 10^5 years). A fossil example of an adaptive reduction in armor development in a lineage of stickleback fish illustrates this point nicely (Bell et al. 2006, Hunt et al. 2008) (**Figure 2b**). Although selection was weak, with a difference in fitness between initial and final mean phenotypes estimated to be about 1% (Hunt et al. 2008), nearly all the adaptive evolution was completed in a few thousand years. If not for the exceptional resolution afforded by the yearly sedimentary layers in which these fish were found (Bell et al. 2006), this adaptive trajectory would have been undetected or would have manifested at a coarser scale as a single punctuation. Thus, although directional transformations are rarely captured in the fossil record, they are not necessarily rare. More likely, bouts of directional change are common but not sustained for long enough to be traced in the sedimentary record.

3.2. Net Rates of Change in Fossil Lineages Are Often Very Slow

Rates of phenotypic change are traditionally formulated as the change in morphology divided by elapsed time (Haldane 1949, Gingerich 2009), and rates computed in this fashion for fossil lineages are generally much slower than in living natural or experimental populations. However, these rates must be viewed with caution because they show a strong dependence on the length

of the interval over which they are observed: With longer and longer time windows, rates appear to be slower and slower (Gingerich 1983). There are a variety of reasons for this dependence, including evolutionary reversals, the effects of bounds or constraints, and observational difficulties surrounding very slow and very fast rates (Stanley 1985, Gingerich 1993, Sheets & Mitchell 2001a, Roopnarine 2003, Hunt 2012). The practical consequence is to complicate comparisons of rates measured over different interval durations, and thus it becomes difficult to say whether paleontological rates are meaningfully slower than those measured over generational timescales.

An alternative approach measures rates by using a model of a random walk or Brownian motion (Felsenstein 1985, Bookstein 1987, O'Meara et al. 2006, Ackerly 2009). Because this model more realistically captures evolutionary dynamics by allowing for reversals, this metric shows less temporal dependence than traditional rate metrics, although a weaker negative relationship remains in empirical compilations (Harmon et al. 2010, Hunt 2012). An additional advantage of this approach is that it can be benchmarked against the situation in which traits are unaffected by natural selection. The resulting equilibrium between mutation and neutral genetic drift produces a random walk with a rate that depends on the variance introduced each generation by mutation (Turelli et al. 1988, Lynch 1990), a quantity known within order-of-magnitude limits. When these rates are measured in fossil lineages, they are almost always too slow to be accounted for by trait neutrality (Hunt 2012), which implies that processes that restrain phenotypic divergence dominate more often than those that promote it.

4. ISSUES ABOUT PROCESS THAT ARE STILL OPEN

4.1. From Pattern to Process

For a variety of reasons, it will seldom be easy to infer the processes responsible for a particular pattern of trait evolution captured in the fossil record. The efficacies of drift and gene flow, for example, depend on effective population size and population structure, and these parameters are seldom knowable for extinct populations. Likewise, whereas the functional importance of certain traits can often be reasonably inferred in fossils, the history of selection coefficients that would be needed to make quantitative predictions cannot. Rare cases, such as the stickleback example described above, are sufficiently information rich and temporally resolved to permit specific microevolutionary explanations. But more often, any given low-resolution pattern in the fossil record will be consistent with a wide range of microevolutionary scenarios involving some combination of natural selection and other processes.

Given these limitations in inferring process for particular cases, one viable approach is to explore compilations of many examples and to assess whether the aggregate patterns are more consistent with some microevolutionary scenarios than with others (Estes & Arnold 2007, Uyeda et al. 2011). To varying degrees, different classes of mechanisms make different predictions about patterns in collective data and may imply differences among traits or lineages with different properties. In the following sections, we evaluate the microevolutionary mechanisms that have been suggested to account for long-term phenotypic evolution within species and consider further means by which they may be tested (summarized in **Table 1**).

4.2. Mechanisms of Within-Species Trends

Although they are not numerous, there are some good examples of sustained directional change within fossil species. Natural selection with consistent direction and magnitude can, in principle, produce such trends, but this is considered an unlikely scenario for at least two reasons. First, a

Table 1 Mechanisms hypothesized to account for gradual species-level trends and stasis

Pattern	Mechanism	Example references	Paleontological predictions
Species-level trends	Constant directional selection	Kingsolver & Pfennig 2004	
	Populations track adaptive peaks that track conditions that change directionally	Hunt & Roy 2006, Hunt et al. 2010	If driver can be identified, covariance between trait and driver changes can be tested. Plausible drivers should themselves trend only rarely on paleontological timescales.
	Long-term turnover of nearly cryptic species	Alizon et al. 2008, Hull & Norris 2009	Detailed morphometrics may be able to distinguish distinct morphs.
Stasis	Genetic constraints	Eldredge & Gould 1972, Hansen & Houle 2004	Stasis may be more common in traits, and combinations of traits, that are less variable.
	Stabilizing selection around a static peak in the adaptive landscape		The magnitude of morphological fluctuations should be modest and vary inversely with effective population size.
	Stabilizing selection around an adaptive peak that itself fluctuates around a steady mean	Estes & Arnold 2007, Balter et al. 2008, Secord et al. 2012	Analysis of trajectories of environmental and other drivers should match the relative frequencies of stasis, directional change, and other patterns.
	Gene flow in a subdivided species	Lieberman & Dudgeon 1996	Stasis should be more common in species with broad environmental and geographic ranges. Evolutionary change can be substantial at local scales but should cancel out across a species.

wealth of paleontological and biological observations suggests that conditions simply do not remain consistent enough to expect constant natural selection over long stretches of time (Siepielski et al. 2009, Bell 2010). Second, given a model of constant selection, one can compute the strength of selection required each generation to yield paleontological trends, and the resulting per-generation effects turn out to be unrealistically minuscule, implying only a few selective deaths per millions of individuals (Lande 1976). Moreover, as noted above, an exponential—not linear—response is expected when a population’s conditions shift or when it invades a new environment. Indeed, as noted by Gould (2002, p. 834), gradualism “represents a ‘weird’ result, not an anticipated and automatic macroevolutionary expression of natural selection.”

A more promising class of selective explanations for trends understands trait changes through the framework of phenotypic adaptive landscapes (Simpson 1944, Arnold et al. 2001). According to this view, populations are generally centered near optima in the landscape of trait values—i.e., combinations of traits that confer the locally highest fitness (see Hendry & Gonzalez 2008). Over time, optima shift when conditions change, and in response, populations either go extinct, if they cannot adapt quickly enough (Gomulkiewicz & Holt 1995, Bell & Gonzalez 2009, Gomulkiewicz & Houle 2009), or follow the peaks with a (geologically) short lag (Estes & Arnold 2007). Because populations ascend peaks quickly, it is the movement of the peaks as the landscape itself shifts that dominates changes over paleontologically relevant timescales. According to this explanation, long-term trends occur when those environmental or biotic factors that govern the position of the phenotypic optimum themselves trend consistently over time (Hansen 2012). Species-level trends are rare, so the reasoning goes, because these governing factors do not usually change in a directional manner over 10^5 – 10^6 years. This hypothesis has not been much explored empirically, but it does predict that geological proxies for conditions that are known to affect organismal

fitness (e.g., temperature) should seldom appear to be trended when sampled in a paleontologically realistic manner.

Recently, a different kind of mechanism was proposed to account for gradual trends. Alizon et al. (2008) created a model in which a morphospecies is composed of multiple, nearly cryptic species that compete along a resource axis. They showed that increasing the number of coevolving species slows down the rate of phenotypic change, so that it can be rather slower than the rate at which environmental conditions change. This model was proposed for planktonic microfossils, whose species commonly contain cryptic genetic diversity (Kucera & Darling 2002) and disproportionately experience long-term anagenetic trends (Hunt 2007). Indeed, shortly after this model was published, one classic example of gradual evolution in a planktonic foraminifera lineage (Malmgren et al. 1983) was reinterpreted as sequential replacement of previously unrecognized cryptic species, rather than the anagenetic transformation of a single lineage (Hull & Norris 2009). This scenario has the benefit of avoiding evolutionary transitions that are unrealistically protracted, but it does so by postulating equally slow ecological replacement. At present, it is not clear under what conditions geologically slow lineage replacement will be more plausible than geologically slow phenotypic change.

4.3. Mechanisms of Stasis

Punctuated equilibrium proponents emphasized that “stasis is data” (Gould & Eldredge 1977), and indeed it seems unlikely that, in the absence of a fossil record, the preponderance of stasis would have been predicted from microevolutionary theory alone. This does not mean, however, that stasis cannot be accounted for by the standard mechanisms of population genetics. In fact, we are faced with the opposite problem of an abundance of microevolutionary scenarios that can contribute to patterns that would be recognized in the fossil record as stasis, and the challenge is to ascertain their adequacy and relative importance.

4.3.1. Genetic constraints. Eldredge & Gould (1972) originally explained stasis as arising from the genetic cohesion of species, which would be disrupted only upon speciation. In this they followed the suggestions of Mayr and others, but this notion of genetic homeostasis has not fared well in the intervening years. It is inconsistent with the nearly universal success of artificial selection experiments in producing substantial trait change (Barton & Partridge 2000, but see Blows & Hoffmann 2005 for some exceptions) and with the numerous examples of substantial divergence in extant populations (Hendry & Kinnison 1999, Kinnison & Hendry 2001, Palumbi 2001). Indeed, Gould, in his latest work (2002, p. 880), downplayed constraint as a primary mechanism for stasis. It may be possible, however, to salvage a link between paleontological stasis and constraint with more sophisticated quantitative genetic approaches. Most continuous traits, when considered individually, harbor significant genetic variation, but much of that variation may be bound up in correlations with other characters (Hansen & Houle 2004). Natural selection acting on those other characters may limit the potential for a focal trait to change in response to changing selective conditions (Hansen 2012). Moreover, patterns of integration and modularity among traits can result in multivariate directions for which there is little additive genetic variance. As long as variance is not totally lacking, such constraints are not absolute, but very limited variance can slow down responses to natural selection to the extent that population extinction is more likely than successful adaptation (Gomulkiewicz & Houle 2009). Although these kinds of genetic constraints may impede the evolution of individual characters or character complexes, they may be less compelling in accounting for organismal stasis in which species show little change in all observable characters (Futuyma 2010).

4.3.2. Stabilizing natural selection. Stabilizing selection holds a strange place in the literature of stasis. This process is freely invoked by geneticists as a cause of stasis, but this judgment has been greeted skeptically by paleontologists (Hansen & Houle 2004). There are good, albeit indirect, reasons for suggesting that stabilizing selection is prevalent (Hansen & Houle 2004), and these are in accordance with the common biological intuition that populations are well adapted to their conditions and that fitness decreases in some fashion with increasingly extreme trait values. Excellent examples document exactly this pattern in natural populations (e.g., Benkman 2003, Rundle & Chenoweth 2011), but a broad survey of selection studies did not find stabilizing selection to be overly common (Kingsolver et al. 2001). Low statistical power is an important concern here: If stabilizing selection is routinely very weak in that fitness decreases only slightly at the typical limits of standing phenotypic variation (three or four standard deviations), then it is unlikely to be detected without extraordinarily large samples (Haller & Hendry 2014) (manipulations that extend the range of phenotypes can have more success; Garcia-Dorado & Gonzalez 1996, Cresswell 2000, Brooks et al. 2005). Very weak stabilizing selection will have only a trivial effect on evolutionary changes from one generation to the next, but it will severely limit divergence on much longer timescales (see the sidebar).

Evaluating the role of stabilizing selection is complicated by the fact that it is a component of several relevant scenarios. The simplest involves continual stabilizing selection around an invariant phenotypic optimum, and it is probably this version that has engendered so much paleontological skepticism (Lieberman & Dudgeon 1996, Prothero & Heaton 1996, Gould 2002). This resistance stems mostly from abundant geological and paleontological data that suggest that environmental and biotic parameters do not remain constant over time. Nevertheless, this scenario does make at least two testable predictions. Because divergence in this scenario is driven by genetic drift (Lande 1976), the potency of which varies inversely with effective population size, stasis fluctuations should be larger in smaller populations. Targeted comparisons between groups differing in population size (e.g., marine plankton versus benthos, narrow- versus wide-ranging species) could be used to test this scenario. The second prediction is that the fluctuations around stasis should be very small, unless population sizes are extremely low (indeed, observed divergences are often too large for this mechanism; Hansen 2012).

Next in complexity are models with an optimal phenotype that is not constant but rather fluctuates around a steady long-term mean. Again, populations follow such shifts with a short lag (or go extinct), and in doing so they experience combinations of directional selection (more so when the population is far from the optimum) and stabilizing selection (more so when they are close). Often this kind of dynamics is discussed as oscillating or fluctuating selection (Sheldon 1996, Siepielski et al. 2009, Bell 2010). Although the resulting pattern will resemble that of stabilizing selection around an invariant optimum, excursions from the optimum are caused by selection, not drift. As a result, they may be larger in magnitude, and they should bear no systematic relationship to population size. This may well be the scenario favored by many geneticists who cite stabilizing selection as a cause of stasis (Estes & Arnold 2007), and it is also compatible with paleontological suggestions of the same (Jackson & Cheetham 1999). This scenario can be consistent with a dynamic physical and biotic environment, as long as the fluctuations tend to be bounded rather than accumulating. Documenting the temporal trajectories of climate and other environmental variables offers an unexplored test of the mechanisms that drive long-term change in species (Table 1).

Although environments are in constant flux, several mechanisms may mute the evolutionary response to such changes. Most prominent among these is the tracking of individuals and populations to favored habitats or conditions (Eldredge 1989). When this occurs, shifts in conditions experienced by members of a species may be substantially less than indicated by geological proxies.

The dramatic distributional shifts in plant and animal species in response to glacial-interglacial cycles and other environmental changes (Davis et al. 2005, Smith & Betancourt 2006, Sandel et al. 2011) underscore the potential importance of this phenomenon. Phenotypic plasticity can also supplant genetic adaptation to environmental change in some circumstances, but it can facilitate adaptation under others (West-Eberhard 2005, Lande 2009). Finally, Sheldon (1996) suggested that taxa living in environments subject to dramatic fluctuations are filtered by extinction such that only tolerant and (morphologically) insensitive species are likely to persist, leading to widespread stasis in such environments.

4.3.3. Gene flow among populations. Lieberman & Dudgeon (1996) argued that the most important cause of stasis resides in the subdivided nature of many species. According to this view, semi-isolated populations adapt to local conditions, but because natural selection is unlikely to be uniform across different habitats and regions, local changes are homogenized by gene flow and net stasis prevails at the level of the species. This hypothesis has attracted some enthusiasm (Gould 2002, Eldredge et al. 2005), but it remains relatively unexplored by empirical or modeling analyses. Its paleontological basis is a study by Lieberman et al. (1994, 1995) that documented in two brachiopod species evolutionary changes that were substantial within habitats but averaged out when summed across habitats. If habitats represent constant and distinct selective environments—a rather strong condition—one expects to see stabilizing selection produce greater temporal differences between them rather than within them.

Modeling of subdivided populations supports the contention that gene flow usually reduces local adaptation (Garant et al. 2007, Räsänen & Hendry 2008). However, these results can be complex, and the dominant scale of adaptation in a subdivided species can range from local to global, depending on its parameters of selection, gene flow, and demography (Hanski et al. 2011). Nevertheless, two general points are worth emphasizing. First, although these models feature gene flow, they also include stabilizing selection, usually with adaptive optima that vary across local populations (Case & Taper 2000, Hendry et al. 2001, Hanski et al. 2011). Accordingly, this explanation for stasis may be thought of as less an alternative to stabilizing selection than an elaboration of stabilizing selection to include gene flow. Second, these population genetic models are used to understand adaptation in local populations, but Lieberman and Dudgeon's argument is more about how local evolutionary changes within populations may cancel out to produce stasis at the next higher level of organization, the species. Understanding the potential of gene flow and population structure to promote stasis will require coupling these models to realistic temporal and spatial variation in selective conditions and tracking the resultant phenotypic evolution at the level of populations and species. Additional paleontological examples beyond Lieberman et al. (1994, 1995) that decompose species trajectories into local or within-habitat components would also be invaluable (Table 1).

4.4. Speciation and Phenotypic Evolution

Thus far, our review has emphasized the dynamics of phenotypic evolution within fossil lineages. We now turn to one of the central claims of the original punctuated equilibrium model (Eldredge 1971, Eldredge & Gould 1972): that the process of speciation is itself coupled to morphological evolution. In general, the relationship between speciation and morphological change has proven far more difficult to study than within-lineage evolutionary dynamics. Whereas the mode of within-lineage evolution has been addressed in hundreds of independent fossil lineages (Hunt 2007, Hopkins & Lidgard 2012), few paleontological studies have directly tested whether speciation is itself associated with morphological change. As discussed below, several methods have now been

developed that enable researchers to test for speciation trait evolution (evolutionary change associated with speciation) by using time-calibrated phylogenetic trees of extant species only, without requiring data from fossil lineages (Pagel 1998, Bokma 2002). These approaches have contributed substantially to the literature linking speciation and phenotypic evolution, owing to the ease of obtaining both phylogenetic trees and character state data for living species. Many questions remain concerning the relative importance of speciation and gradual trait evolution within lineages, but it is increasingly clear that several distinct mechanisms can produce a coupling between speciation and trait change.

4.4.1. Empirical tests from phylogenies and fossils. The relationship between speciation and phenotypic evolution has been evaluated using several methodological frameworks. One approach involves high-resolution analysis of morphological change across individual speciation events in the fossil record (e.g., Gingerich 1976, Lazarus et al. 1995). This approach is sensitive to a range of assumptions about the completeness of stratigraphic and geographic sampling (Gingerich 1976), as well as the nature of species themselves (Levinton 2001). In short, the approach assumes that the fossil record accurately records the history of lineage splitting. This assumption would be invalid if morphologically cryptic species occur within the same stratigraphic section, or if putative speciation events actually record the immigration of a divergent lineage from a geographic region lacking a stratigraphic record.

A second approach involves phylogenetic tests of the variation in species' morphologies that can be explained by speciation (cladogenesis) relative to within-lineage change (anagenesis). Although this framework was pioneered on paleontological data (Cheetham 1986, 1987; Jackson & Cheetham 1994), the most widespread application has involved time-calibrated phylogenetic trees of extant species only. These methods (Pagel 1998; Bokma 2002, 2008; Ingram 2011), which do not require data from extinct species, test whether the variation in species' morphologies is best explained by the amount of time available for evolution or by the number of reconstructed speciation events on phylogenetic trees (**Figure 3**). A key advantage to this approach relative to single-lineage paleontological studies is that phylogenetic trees contain at least a partial record of the history of speciation, even if extinction sometimes obscures the true number of speciation events that have occurred (Bokma 2008). However, in the absence of paleontological data (Cheetham 1986, Hunt 2013), these approaches provide no direct information about the nature of morphological change through time, and inferences about speciation change rely solely on the correlation between numbers of reconstructed speciation events (nodes) in phylogenetic trees and magnitudes of trait change (Rabosky 2012).

Yet another approach involves directly testing the relationship between rates of phenotypic evolution and rates of species diversification. A number of paleontological and neontological studies have tested for temporally correlated shifts in rates of species diversification and morphological evolution (e.g., Foote 1993, Harmon et al. 2003), and several other studies have explored the possibility that evolutionary rates are coupled across clades (Adams et al. 2009, Rabosky & Adams 2012, Rabosky et al. 2013). However, if the data fail to meet the assumptions of the statistical model used for estimating evolutionary rates, spurious correlations between speciation and phenotypic evolution can readily arise (Rabosky & Adams 2012).

4.4.2. Alternative interpretive paradigms and mechanisms. The literature on speciation and phenotypic evolution is perhaps best viewed as a collection of disparate intellectual themes (Pennell et al. 2014). Unfortunately (in our view), these themes are often treated in isolation, leading to considerable confusion over the interpretation of patterns in the fossil record and phylogenies. The most prominent of these themes is punctuated equilibrium in its strict sense,

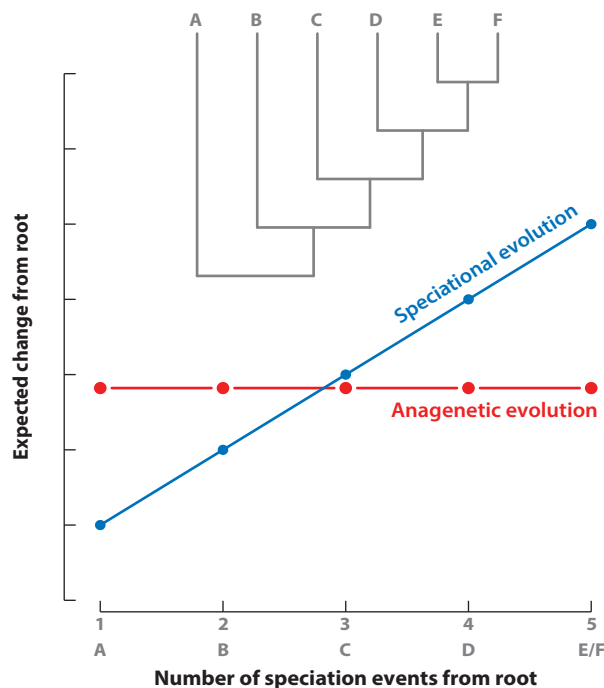


Figure 3

Distinguishing speciational (cladogenic) and gradual phenotypic evolution on a time-calibrated phylogenetic tree. The inset phylogeny represents an ideal molecular phylogeny of living species only, with branch lengths proportional to time. If evolutionary changes accrue only at speciation as predicted by punctuated equilibrium, the total amount of phenotypic change will be proportional to the number of splitting events, which increases from species A through species E/F (blue line). If evolution occurs gradually within lineages, all six species will differ from their common ancestor (the root) by the same amount, on average (red line). Expected change here represents the magnitude of absolute (or squared) divergence from the ancestral trait value. The concept illustrated here is fundamental to all phylogenetic tests of speciational trait evolution that do not incorporate paleontological data (e.g., Bokma 2002, Goldberg & Igic 2012).

whereby most phenotypic evolution is directly attributable to some aspect of the speciation process. A second major theme is adaptive radiation, whereby the tempo of both species diversification and phenotypic evolution changes concertedly through time in response to ecological opportunity (Schluter 2000, Losos & Mahler 2010). The adaptive radiation theme has its origins in Simpson's notion of rapid diversification during shifts to new adaptive zones (Simpson 1944) and currently enjoys great popularity in the context of recent work on the dynamics of species diversification and trait evolution during evolutionary radiations (Foote 1996, Schluter 2000, Harmon et al. 2003). A final major theme is the notion that evolutionary lability (Vermeij 1974, Wagner & Altenberg 1996)—the capacity to evolve novel phenotypic traits—can promote increased rates of species diversification (Adamowicz et al. 2008, Pigliucci 2008).

These themes encompass a range of conceptually distinct evolutionary mechanisms that may be difficult to separate given the nature of the methods and data available. Indeed, any pattern of speciational trait evolution is likely to be consistent with multiple candidate processes as well as several of the interpretative themes described above. For example, Stanley (1979) suggested that the existence of living fossils—clades with low species richness and slow rates of morphological change—provided compelling evidence for punctuated equilibrium. However, an alternative explanation for

this pattern is that clades with high rates of morphological evolution diversify more because they are better able to exploit novel ecological resources (Liem & Osse 1975, Rabosky 2012, Rabosky et al. 2013). In this latter scenario, there is no necessary coupling between the process of speciation and any particular quantity of phenotypic change; rather, lineages vary in the extent to which they explore evolutionary potentialities, and lineages that generate adaptive breakthroughs in form and function are more likely to diversify than those that do not (Lovette et al. 2002, Pigliucci 2008).

Indeed, the problem of identifying specific causal mechanisms is even more severe than this example would suggest. Consider a near-perfect paleontological demonstration of speciation trait change in a single lineage, in which we are able to unambiguously rule out immigration and other potential biases as the cause of the pattern. Such a pattern could result from Eldredge and Gould's allopatric model of speciation, or it could result from speciation attributable to divergent natural selection (ecological speciation; Nosil 2012). Alternatively, the pattern may have to do not with speciation per se but rather with postspeciation character displacement in ecological or reproductive traits (Schluter 2000, Pfennig & Pfennig 2013). Finally, the pattern would also be consistent with Futuyma's (1987, 2010) suggestion that speciation merely preserves morphological variation present in an otherwise ephemeral assemblage of geographically separated but conspecific populations (see also Rosenblum et al. 2012). We have much to learn about limits to inference from both paleontological and molecular phylogenetic data before we can claim to understand the relationship between speciation and phenotypic evolution. As a starting point, however, we believe there is great value in simply determining the extent to which species diversification and phenotypic evolution are coupled in the natural world. Once we understand the generality of the pattern, we can begin the more challenging process of decomposing it into specific causal mechanisms.

FUTURE ISSUES

1. The traditional evolutionary modes of stasis, random walks and directional (gradual) change describe patterns without recourse to causal drivers. Although existing methods can be modified to assess putative factors that drive trait evolution (Balter et al. 2008, Hunt et al. 2010, Secord et al. 2012), to what extent can plausible causal drivers be measured from the rock record, and to what extent can these drivers be associated with specific examples of morphological evolution?
2. Most existing methods are designed to operate on traits individually, but phenotypes are highly multivariate. Two recent studies (Hopkins & Lidgard 2012, Bookstein 2013) have presented simulations that show unexpected behavior when time series of inherently multivariate data are analyzed univariately. Although most models can be generalized to multiple dimensions, variation in mode across features and correlated evolution among traits present analytical and practical challenges.
3. Much has been written about the potential for species recognition to influence the inference of evolutionary patterns in the fossil record. One important improvement may be to adopt phylogenetic methods that permit terminal taxa to be ancestral to another taxon in the analysis, whether through stratocladistics (Fisher 1994, Marcot & Fox 2008) or other more model-based means. Such approaches allow for the possibility of greater change within a species-level lineage, thereby avoiding the charge that claims of elevated change at speciation are an artifact of how species are recognized in the fossil record.

4. Phenotype in fossils almost always refers to the preserved morphology of organisms. In principle, the concepts and methods described in this article could be extended without complication to nonmorphological attributes such as geochemical signatures or molecular markers, provided that such variables can be interpreted as properties of organisms (not just the environment) and can be localized to individual, species-level lineages.

DISCLOSURE STATEMENT

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Contents

Falling in Love with Waves <i>Hiroo Kanamori</i>	1
The Diversity of Large Earthquakes and Its Implications for Hazard Mitigation <i>Hiroo Kanamori</i>	7
Broadband Ocean-Bottom Seismology <i>Daisuke Suetsugu and Hajime Shiobara</i>	27
Extrasolar Cosmochemistry <i>M. Jura and E.D. Young</i>	45
Orbital Climate Cycles in the Fossil Record: From Semidiurnal to Million-Year Biotic Responses <i>Francisco J. Rodríguez-Tovar</i>	69
Heterogeneity and Anisotropy of Earth's Inner Core <i>Arwen Deuss</i>	103
Detrital Zircon U-Pb Geochronology Applied to Tectonics <i>George Gebrels</i>	127
How Did Early Earth Become Our Modern World? <i>Richard W. Carlson, Edward Garnero, T. Mark Harrison, Jie Li, Michael Manga, William F. McDonough, Sujoy Mukhopadhyay, Barbara Romanowicz, David Rubie, Quentin Williams, and Shijie Zhong</i>	151
The Stardust Mission: Analyzing Samples from the Edge of the Solar System <i>Don Brownlee</i>	179
Paleobiology of Herbivorous Dinosaurs <i>Paul M. Barrett</i>	207
Spin Transitions in Mantle Minerals <i>James Badro</i>	231
Mercury Isotopes in Earth and Environmental Sciences <i>Joel D. Blum, Laura S. Sherman, and Marcus W. Johnson</i>	249

Investigating Microbe-Mineral Interactions: Recent Advances in X-Ray and Electron Microscopy and Redox-Sensitive Methods <i>Jennyfer Miot, Karim Benzerara, and Andreas Kappler</i>	271
Mineralogy of the Martian Surface <i>Bethany L. Ehlmann and Christopher S. Edwards</i>	291
The Uses of Dynamic Earthquake Triggering <i>Emily E. Brodsky and Nicholas J. van der Elst</i>	317
Short-Lived Climate Pollution <i>R.T. Pierrehumbert</i>	341
Himalayan Metamorphism and Its Tectonic Implications <i>Matthew J. Kohn</i>	381
Phenotypic Evolution in Fossil Species: Pattern and Process <i>Gene Hunt and Daniel L. Rabosky</i>	421
Earth Abides Arsenic Biotransformations <i>Yong-Guan Zhu, Masafumi Yoshinaga, Fang-Jie Zhao, and Barry P. Rosen</i>	443
Hydrogeomorphic Effects of Explosive Volcanic Eruptions on Drainage Basins <i>Thomas C. Pierson and Jon J. Major</i>	469
Seafloor Geodesy <i>Roland Bürgmann and David Chadwell</i>	509
Particle Geophysics <i>Hiroyuki K.M. Tanaka</i>	535
Impact Origin of the Moon? <i>Erik Asphaug</i>	551
Evolution of Neogene Mammals in Eurasia: Environmental Forcing and Biotic Interactions <i>Mikael Fortelius, Jussi T. Eronen, Ferhat Kaya, Hui Tang, Pasquale Raia, and Kai Puolamäki</i>	579
Planetary Reorientation <i>Isamu Matsuyama, Francis Nimmo, and Jerry X. Mitrovica</i>	605
Thermal Maturation of Gas Shale Systems <i>Sylvain Bernard and Brian Horsfield</i>	635
Global Positioning System (GPS) and GPS-Acoustic Observations: Insight into Slip Along the Subduction Zones Around Japan <i>Takuya Nishimura, Mariko Sato, and Takeshi Sagiya</i>	653
On Dinosaur Growth <i>Gregory M. Erickson</i>	675

Diamond Formation: A Stable Isotope Perspective <i>Pierre Cartigny, Médéric Palot, Emilie Thomassot, and Jeff W. Harris</i>	699
Organosulfur Compounds: Molecular and Isotopic Evolution from Biota to Oil and Gas <i>Alon Amrani</i>	733

Indexes

Cumulative Index of Contributing Authors, Volumes 33–42	769
Cumulative Index of Article Titles, Volumes 33–42	774

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TABLE OF CONTENTS:

- *What Is Statistics?* Stephen E. Fienberg
- *A Systematic Statistical Approach to Evaluating Evidence from Observational Studies*, David Madigan, Paul E. Stang, Jesse A. Berlin, Martijn Schuemie, J. Marc Overhage, Marc A. Suchard, Bill Dumouchel, Abraham G. Hartzema, Patrick B. Ryan
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- *Brain Imaging Analysis*, F. DuBois Bowman
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- *Event History Analysis*, Niels Keiding
- *Statistical Evaluation of Forensic DNA Profile Evidence*, Christopher D. Steele, David J. Balding
- *Using League Table Rankings in Public Policy Formation: Statistical Issues*, Harvey Goldstein
- *Statistical Ecology*, Ruth King
- *Estimating the Number of Species in Microbial Diversity Studies*, John Bunge, Amy Willis, Fiona Walsh
- *Dynamic Treatment Regimes*, Bibhas Chakraborty, Susan A. Murphy
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