

The continuity of microevolution and macroevolution

ANDREW M. SIMONS

Department of Biology, College of Natural Sciences, Carleton University, Ottawa, Ont., Canada

Keywords:

adaptation;
bet-hedging strategy;
environmental variance;
evolutionary constraint;
geometric-mean fitness;
macroevolution;
mass extinction;
microevolution;
natural selection;
optimality.

Abstract

A persistent debate in evolutionary biology is one over the continuity of microevolution and macroevolution – whether macroevolutionary trends are governed by the principles of microevolution. The opposition of evolutionary trends over different time scales is taken as evidence that selection is uncoupled over these scales. I argue that the paradox inferred by trend opposition is eliminated by a hierarchical application of the ‘geometric-mean fitness’ principle, a principle that has been invoked only within the limited context of microevolution in response to environmental variance. This principle implies the elimination of well adapted genotypes – even those with the highest arithmetic mean fitness over a shorter time scale. Contingent on premises concerning the temporal structure of environmental variance, selectivity of extinction, and clade-level heritability, the evolutionary outcome of major environmental change may be viewed as identical in principle to the outcome of minor environmental fluctuations over the short-term. Trend reversals are thus recognized as a fundamental property of selection operating at any phylogenetic level that occur in response to event severities of any magnitude over all time scales. This ‘bet-hedging’ perspective differs from others in that a specified, single hierarchical selective process is proposed to explain observed hierarchical patterns of extinction.

Introduction

The continuity of selective processes over microevolutionary and macroevolutionary time continues to be a source of disagreement in evolutionary biology (Solé *et al.*, 1999; Erwin, 2000; Carroll, 2001; Plotnick & Sepkoski, 2001), one that Maynard Smith (1989) described as ‘unsatisfactory.’ In dispute is whether the effects of selection operating over microevolutionary time, or at the population level, account for observed trends over macroevolutionary time. That any particular evolutionary event can be explained by the neo-Darwinian synthetic theory (Charlesworth *et al.*, 1982) does not imply that the evolutionary consequences of rare events such as mass and minor extinctions will not tend

to oppose trends occurring between these events. A pattern of self-similarity of extinction at different temporal scales has been observed (Raup, 1986; Solé *et al.*, 1997; McKinney & Frederick, 1999; Plotnick & Sepkoski, 2001), fuelling further discussion of evolutionary mechanisms – beyond principles of microevolution – driving trends at different time scales (Solé *et al.*, 1999; Plotnick & Sepkoski, 2001). This is a debate, then, about the relevance of the process of natural selection operating at the ‘ecological moment’ (Gould, 1985) to the production of phenotypic trends over the long-term.

Resolution of the continuity issue is critical because if selection is discontinuous over different time scales, then palaeobiology and evolutionary genetics are not two approaches to the same evolutionary problems; they are only distantly related fields of study. Furthermore, disagreement over the relative importance of natural selection in determining trends over different time scales is eagerly distorted by anti-evolutionist groups to discredit both macroevolution as lacking a mechanism, and microevolution as being restricted to insignificant

Correspondence: Andrew M. Simons, Department of Biology, College of Natural Sciences, Carleton University, 1125 Colonel By Drive, Ottawa, Ont., Canada K1S 5B6.
Tel.: 613-520-2600; ext. 3869; fax: 613-520-3539;
e-mail: asimons@ccs.carleton.ca

phenotypic change. The fact that the debate has not been resolved means that a single perspective of selection consistent with both micro- and macroevolution is still needed. In this paper, I propose that no new theory is needed to attain this perspective; rather, it is attained through the broad application of an existing theory with a previously underappreciated significance.

Before making the argument for the continuous nature of selection, the rationale for views of discontinuity of selection operating over different time scales will be considered. The remainder of the paper presents a case for the applicability of the principles of bet-hedging theory, which are conventionally restricted to exceptional circumstances, to evolution in general. The relevance of the perspective will depend on premises about the interaction among patterns of environmental variance over different time scales, selectivity imposed by this environmental variance, and the heritability or phylogenetic nesting of traits. Support for the premises is found in the literature and provides reason to accept the argument in principle. The paper concludes with examples illustrating how the integration of bet-hedging ideas into evolutionary theory results in a self-consistent view of the way in which natural selection operates.

Views of discontinuity

The existence of the terms 'microevolution' and 'macroevolution' reflects the controversy (Eldredge & Gould, 1972; Stanley, 1975; Orzack, 1981; Charlesworth *et al.*, 1982; Maynard Smith, 1989; Gould & Eldredge, 1993; Van Valen, 1994; Bennett, 1997; Erwin, 2000; Carroll, 2001) over the unity of the process of natural selection operating at different time scales. Gould (1985), for example, contends that the process of selection is of a different nature at different time scales. His argument is based on the observation that what is seemingly an adaptive trend over one time scale is not consistent with trends over another. For this reason, Gould stated that the synthetic theory, at least as portrayed by Mayr, is 'effectively dead' (Gould, 1980; but see Gould, 1985); adaptation over a few generations is insignificant because major evolutionary trends are not established by processes circumscribed by the modern synthesis (Gould, 1985). Even if population genetic theory can explain patterns observed in the fossil record (Charlesworth *et al.*, 1982), it does not address the problem of why the fossil record should reveal trends contrary to those observed over microevolutionary time. Implicit in the disagreement is that the outcome of selection is qualitatively different when acting at different levels, but the relationship between these outcomes has remained indistinct.

Palaeobiologists have developed a variety of explanations for trends on different scales, most treating the opposition of trends as reflecting a fundamental discontinuity of processes acting across these scales. For

example, Jablonski (1997) argues that, whereas body size is an important fitness correlate in microevolution, Cope's rule – a trend of increasing body size through time – plays a 'weak or unpredictable role' in macroevolution. To explain such contrasting trends, a qualitative difference between processes operating during the mass extinctions and during background times is proposed (Jablonski, 1986). Under this view, mass extinctions are not caused merely by an intensification of background selection: an alternation of macroevolutionary regimes would explain opposing trends in survival, and survival over the longer term would depend on the 'chance occurrence' of traits allowing survival under both regimes (Jablonski, 1986).

Raup (1986) sees mass extinctions as one extreme on the continuum of environmental variance, but envisions a dichotomy between 'destructive' and 'constructive' forces operating over different time scales. He argues that, in order to be constructive, an environmental event must occur often enough to be within the 'experience' of the organism (Raup, 1986); hence, extinction is a nonconstructive evolutionary force (Raup, 1986). Similarly, in a theory to account for evolution above the species level, Stanley (1975) proposes that higher level processes are necessary to explain evolutionary trends, and that natural selection provides 'little more than the raw material and fine adjustment of large-scale evolution' (Stanley, 1975).

Rather than an alternation between two processes, Gould (1985) proposes a three-tiered model of evolution to account for the 'paradox' implied by the uncorrelated evolutionary trends across time scales. Evolution at the three tiers (ecological moments, normal geological time, and periodic mass extinctions) is governed by distinct processes with independent 'rules and principles' (Gould, 1985). Gould (1985) asserts 'We will all, I trust, at least allow that creatures cannot prepare for catastrophes of such spacing and that their adaptive struggles at the first tier can therefore, at the very best, only produce exaptations for later debacles.' Thus, for Gould (1985), trends over normal geological time are autonomous, and the accumulation of adaptations occurring at the first tier are 'reversed, undone, and overridden'. Bennett (1997), with the intention of 'linking evolution with ecology' which, in his view had been decoupled by Darwin, adds a fourth tier to Gould's three. He envisions different processes acting concurrently over four time scales to account for observed trends within each, and calls this view the 'postmodern evolutionary synthesis' (Bennett, 1997, p. 184). Bennett outlines the relevance of individual lifespans to his arguments (Bennett, 1997, p. 176): diurnal and seasonal changes, unlike fluctuations over longer time scales, are predictable and thus may form an organism's 'environmental background' (Bennett, 1997).

We could continue to accept the addition of discrete tiers as higher-resolution data permit, but a four-tiered process of evolution, while explaining more of the data

than a three-tiered model (but perhaps not as much as would a five-tiered model), still falls short of reconciliation. The construction of the concept of a tier is merely a deferral of a description of the way in which natural selection operates which should be comprehensive enough to subsume any number of tiers. Jablonski (1986) proposes that '...a complete theory of evolution must incorporate the different sets of selective and random processes that characterize the background and mass extinction regimes'.

The debate has produced empirical study of temporal patterns of radiation and extinction. These studies suggest that variance might increase with the inclusion of longer time scales, resulting in fractal or self-similar patterns through time (Steele, 1985; Raup, 1986; Pimm & Redfean, 1988; Ariño & Pimm, 1995; Bengtsson *et al.*, 1997; Solé *et al.*, 1997), possibly driven by a hierarchy of physical causes. Raup (1986) called attention to the apparent self-similarity between plots of species survivorship on the scale of about 38 My when compared with survivorship on the family level over about 300 My. Hierarchical and fractal views of evolution have advanced our understanding of patterns of extinction, but have solved neither the question of the continuity of selective processes at different scales nor the nature of processes underlying observed patterns (Solé *et al.*, 1999; Carroll, 2001; Plotnick & Sepkoski, 2001). Furthermore, these views of evolution are perceived to preclude extrapolation from microevolutionary processes to macroevolutionary patterns (Solé *et al.*, 1999; Erwin, 2000; Jablonski, 2000).

A prominent but controversial hypothesized mechanism that would explain the uncoupling of micro from macroevolutionary processes (Solé *et al.*, 1999) is self-organized criticality (SOC): complex behaviour exemplified by evolution may be reducible to intrinsic and relatively simple rules. However, SOC does not provide a mechanism at the biological level, and explains evolutionary pattern based on 'a synergy between natural selection and self-organizing processes' (Solé *et al.*, 1999). The SOC view has been widely challenged (Jablonski, 2000; Plotnick & Sepkoski, 2001). A contrasting macroevolutionary 'multifractal' model (Plotnick & Sepkoski, 2001) has been proposed that emphasizes context-dependent disparities in the reaction of biological systems to abiotic and biotic driving mechanisms.

There remains little consensus on the mechanisms driving observed patterns at different scales (Carroll, 2001). Two different kinds of explanation for hierarchical patterns have emerged: first, as in the case of views based on alternation of regimes at a fixed number of tiers as well as hierarchical views, a hierarchy of diverse processes corresponds to a hierarchy of pattern. Secondly, as in the case of SOC, simple rules lead to hierarchical pattern. I will argue that the key to understanding micro- and macroevolution as continuous lies in a third possibility; a single process that is itself hierarchical produces hierarchical

evolutionary pattern. Although the perspective does not require an adoption of new theory, it requires the application of existing theory in a novel manner. The proposed perspective relies only on established biological principles, accepts trend reversals as a universal property of evolution, and expects the emergence of self-similar patterns of extinction.

A bet-hedging perspective of evolution

The following argument posits bet-hedging theory as a foundation for a general model of evolution. It is important to note at the outset that so-called 'bet hedging' is not an expected outcome of the perspective; rather, bet-hedging theory is the framework on which the evolutionary model is based. Reasons for the restriction of bet-hedging theory to microevolutionary applications has never been addressed. After briefly reviewing the concept of bet hedging and causes of misunderstanding on the topic, I will argue that a bet-hedging perspective, although sparsely applied even at the population level, is equally applicable to evolution at all levels of biological organization. A unified view of evolution follows directly from the logical argument, but is more or less important depending on the extent to which several premises hold. A case for the tentative support for these premises is made, but it is clear that further empirical study is required. Nonetheless, because the perspective relies only on extrapolation of established theory yet accommodates patterns that are otherwise unexplained, it must be considered for its parsimony.

What is bet hedging, again?

Environments may vary unpredictably across generations, and a trait that contributes to a high relative fitness in one generation might be inappropriate in another. Under environmental variance, genotypes that perform best in the 'average' environment will not necessarily be represented by the highest number of descendants (Gillespie, 1973, 1974). Because fitness is determined by a multiplicative process, the geometric mean (the n th root of the product of n values) is the appropriate measure of fitness under environmental unpredictability across generations (Dempster, 1955; Gillespie, 1977). The geometric mean is strongly influenced by low values, and selection acts to reduce the variance in fitness over generations even if this entails the 'sacrifice' of expected fitness within any given generation. Lewontin & Cohen (1969) presented a formal argument showing the absurdity of the use of the arithmetic mean fitness under environmental variability: even when expected fitness approaches infinity, the probability of extinction in a variable environment may rise to one (Lewontin & Cohen, 1969). 'Bet-hedging' (Slatkin, 1974) traits are defined as those that reduce the expected within-generation fitness yet confer a higher geometric mean

fitness (Seger & Brockmann, 1987; Philippi & Seger, 1989).

The evolution of a bet hedging strategy within a population occurs through the elimination of variants not exhibiting the strategy, even if these variants have the highest expected fitness in an average environment. As an example, consider the evolution of flowering time in a herb inhabiting a northern temperate region. *Lobelia inflata* (Campanulaceae) is a monocarpic perennial: it may live several seasons as a frost-hardy rosette until it enters the reproductive mode by producing a flowering stalk (i.e. it 'bolts'). Individuals may reach an appropriate size to bolt at any time during the growing season (Simons & Johnston, 2000). Once it commits to bolting, an individual becomes vulnerable to frost, and must reproduce within the confines imposed by a seasonal environment. Bolting only initiates reproduction: considerable time is required for stem elongation, flower development to anthesis, and seed set. However, at the time the bolting 'decision' must be made, the quality of the remaining growing season is unpredictable: although photoperiod indicates the time of year, effective season

lengths are variable among years. An individual incurs little risk by bolting early in a growing season and should have ample time for successful reproduction, whereas the risk of reproductive failure increases with later bolting dates. Under circumstances of environmental unpredictability, a conservative bet-hedging bolting strategy is expected to evolve in which bolting is restricted to occur prior to a particular final 'safe' date in the season although, in an average season, bolting after this date would maximize expected fitness.

Bolting behaviour of *L. inflata* is used here as a model to demonstrate the dynamics of the evolution of a bet-hedging trait (Fig. 1). Determining what measure of environmental variance is relevant to organisms is difficult. Tree growth-ring variation offers a biocentric and synoptic measure of environmental variance at a resolution that conveniently corresponds to the lifespan of annual plants (or univoltine insects), and is available over time scales relevant to the evolution of bet hedging (tree-ring data from D'Arrigo & Jacoby, 1993; based on sample of 27 white spruce, *Picea glauca*, Ogilvie Mountains, Yukon Territory). A conservative bet-hedging

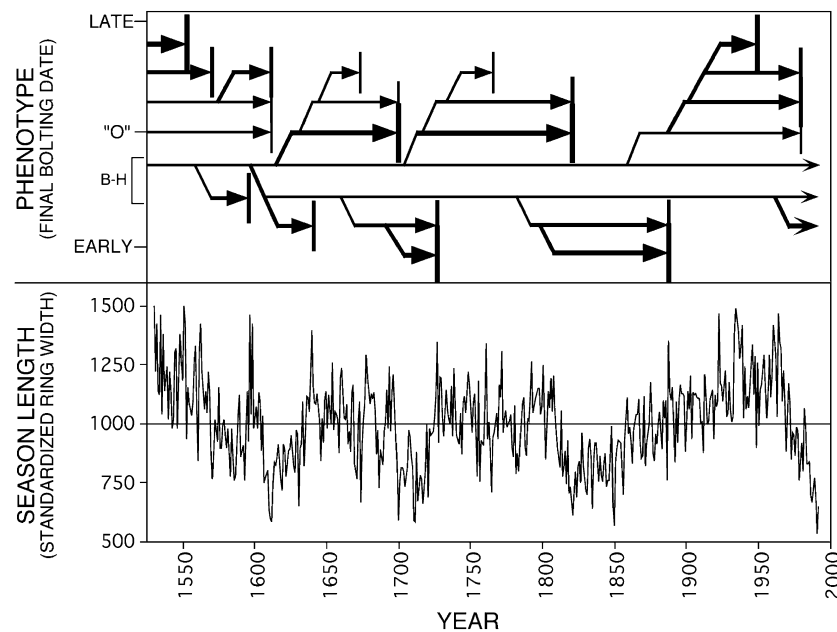


Fig. 1 How a conservative bet-hedging strategy evolves (upper panel) within a population in response to environmental unpredictability (lower panel). The bet-hedging phenotype chosen for discussion is the timing of the onset of reproduction (bolting) in a monocarpic perennial herb (see text). Environmental variance is measured here using dendroclimatological methods (data from D'Arrigo & Jacoby, 1993). Phenotype on the y-axis ranges from short-year (early final bolting) to long-year (late final bolting) specialists. Line thickness represents arithmetic-mean fitness of the phenotype relative to other strategies over the duration of the line, and barred arrowheads depict the selective elimination of the lineage. More severe environmental events are depicted as exerting stronger selection against maladapted phenotypes. Assuming nonzero heritability, selection tends to eliminate related individuals, but the more severe the event, the more inclusive the group of relatives eliminated. The phenotype 'O' (for 'optimal') has the highest arithmetic-mean fitness over extended periods of time, as well as over the entire 463 years included in this study, and performs best under average conditions (corresponding to mean standardized ring width = 1000). However, this 'optimal' phenotype may be represented by fewer descendants – in this case, zero – than is a bet-hedging (B-H) phenotype. Although a conservative bet-hedging strategy is not associated with the highest relative fitness under average conditions, it persists because it is associated with reduced variance in fitness, and has maximized geometric-mean fitness.

strategy evolves over many generations of environmental variance despite its lower relative fitness under average conditions (Fig. 1). Nevertheless, as a bet-hedging strategy evolves, selection favours an early final bolting date during periods of shorter effective seasons (early bolters have high relative mean fitness), and favours later final bolting dates during periods of longer seasons (late bolters have high relative mean fitness). Furthermore, the evolution of late bolting over the time scale of a few generations of long seasons is an adaptive trend over that time scale. If random variation in season length continues over a time scale of many generations, however, bet-hedging genotypes would have the highest geometric-mean fitness over that time scale. Selection for bet hedging, then, is necessarily attained through the continual reversal of adaptive trends over some shorter time scale.

The 'sacrifice' fallacy

Despite the attention paid to bet hedging (Seger & Brockmann, 1987; Philippi & Seger, 1989; Hopper, 1999), misunderstanding endures. This confusion is over how selection for bet hedging can be reconciled with selection more generally. The geometric mean principle is implicitly assumed to be a special case of the way in which natural selection works but is the general case and applies to all microevolutionary situations, even the implausible situation of complete constancy of environmental conditions through time (Roff, 1992, pp. 41–42). In this latter situation, the arithmetic and geometric means happen to be equivalent but, under temporally variable environments, calculating the arithmetic mean fitness over several generations might yield an inappropriate fitness estimate. What has not been acknowledged is that, notwithstanding its status as a defining concept of bet hedging, the notion of a 'sacrifice' of expected fitness for geometric mean fitness is deceptive. There is no detrimental effect of maximizing the geometric mean fitness and, hence, no tradeoff between the mean and variance in fitness exists; the assumption that expected or within-generation fitness is maximized by natural selection is simply wrong. Therefore, the idea of bet hedging is a conceptual 'spandrel' (*sensu* Gould & Lewontin, 1979); it exists only because it has been defined.

Although the idea of a tradeoff between the mean and variance of fitness is faulty, the concept of bet hedging should not be discarded. Bet hedging theory says something general and true about the way natural selection operates but then, through the misguided tradeoff idea, specifies a smaller set of circumstances to which it should be applied. The idea of a tradeoff between the mean and variance of fitness has persisted because it reconciles the more accessible view of selection, wherein organisms are selected towards an optimal state for a given environment, with the more accurate view, wherein organisms

are selected towards an optimal state given a series of different environments.

A hierarchical selective process

Selection for the geometric mean is the general case in microevolution even if bet-hedging strategies, as they are defined, do not result. One consequence of selection for the geometric mean is the reversal of adaptive trends: the elimination of phenotypes that are well adapted to a narrow array of environments occurring during a few generations. If we accept that the geometric mean principle is the general case over short time scales (and applies also to constant conditions), we can ask whether reversals in adaptive trends over microevolutionary and macroevolutionary time scales are a manifestation of a single hierarchical selective process. The answer to this question will be explored first by addressing why bet-hedging principles have traditionally been restricted to short time scales and second, if there is no theoretical justification for the restriction of bet-hedging, by asking whether components essential to a unified hierarchical selective process are present. If all components are present, the observation of trend reversals across time scales is not a valid basis for views of discontinuity.

Traditional bet-hedging strategies are maintained through a history of fluctuating selection. Bet-hedging models reflect this variability and are constructed on the basis of a prescribed level of variance characterizing only recent environments. Although not made explicit, this is tacitly justified by a vague appreciation for the diminishing relevance of environments in the distant past; the genetic 'memory' (Levins, 1968, pp. 90–91) of an anomalous event in the distant past will no longer contribute to the maintenance of a contemporary bet-hedging strategy as new mutations and recombination occur and are acted upon by current selection pressures. No genetically based risk-averse strategy for a past anomalous event could persist at the population level indefinitely. A current anomalous environmental event outside the range of recent historical variance might thus cause the extinction of the population. In this sense, adaptation – to conditions at the 'ecological moment' that proved to be transient over a longer time scale – is overridden by this anomalous event.

The elimination of the population may appear to impose a legitimate boundary on the bet-hedging model of selection depicted in Fig. 1. Rather than a limit to the evolution of bet hedging, this population extinction event may be considered as a starting point for the argument for a hierarchical extrapolation of the geometric-mean principle. The line of reasoning relies on the tentative acceptance of several premises, the support for which will be discussed later.

Assume that environments vary through time, and the severity of an event is inversely proportional to its probability of occurrence. Assume also that at least some

of these events are selective to some extent (for which the general term 'selectivity' is used): the differential survival of organisms is nonrandom with respect to phenotype. Furthermore, assume that there is a heritable basis of the phenotypic variation at the level at which differential survival occurs; that is, the resemblance among those eliminated is attributable, at least in part, to common origins (for which the term 'phylogenetic nesting' is used).

Under the above assumptions, differential survival can be found at some level of biological organization for a selective event of any magnitude. Now, of all proposed long-term evolutionary trends, one that is beyond reasonable doubt is one of increasing structural hierarchy (McShea, 2001) or 'the number of levels of nesting of parts within wholes' (McShea, 1998). Therefore, characters that are variable only at a more fundamental phylogenetic level – order or family, for example – are more deeply embedded or nested than are traits that are variable at the genus, species or population level. (Diagnostic traits at a particular taxonomic level are variable among groups at that level, but do not vary

among taxonomic levels nested within the group.) The more severe an extinction event, the more inclusive the set of affected taxa, and deeper the nested level upon which selection operates. Traits that are more deeply nested in structural hierarchy are those that have persisted through longer time scales and through events of more catastrophic proportions than have more superficial traits. Whereas 'normal' environmental variation among generations is sufficient to maintain traditional bet-hedging strategies within populations, major changes are rarer, and genetic 'memory' for such events could be maintained only at deeper phylogenetic levels. Therefore, deeply embedded bet-hedging strategies could be persistent even if no genetically based risk-averse strategy persists at the population level.

We may now recognize how the bet-hedging perspective of evolution is continuous across scales. The evolution of a bet-hedging strategy within a population as illustrated in Fig. 1, with a change of axes (Fig. 2), is equally a representation of selection over any time scale (x -axis) of a phenotype at an appropriate clade level (y -axis, upper panel), and in response to environmental

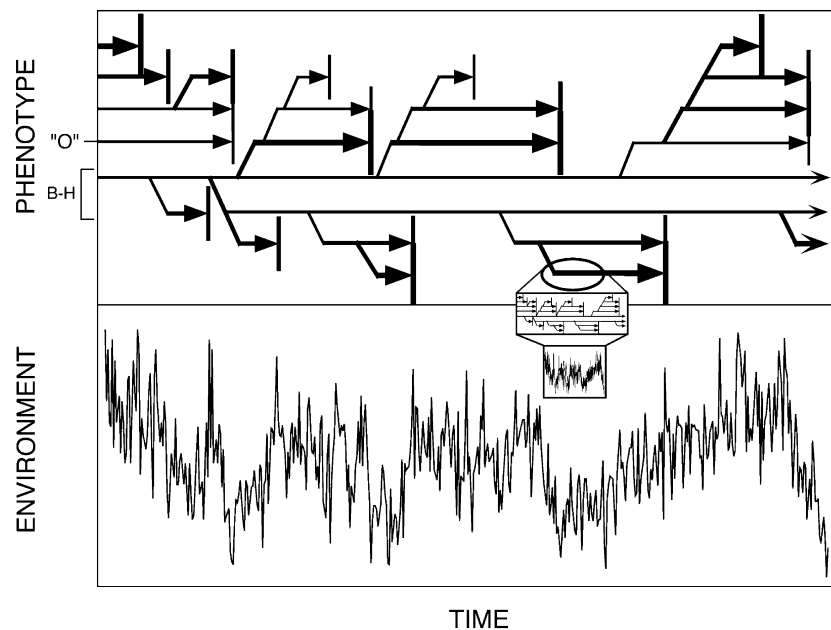


Fig. 2 Evolution in response to environmental variance, showing the continuity of evolutionary process occurring at different phylogenetic levels and over different time scales. Phenotypic change (y -axis) may represent divergence at any clade level over a corresponding time scale (x -axis). The inset is a high-resolution depiction of evolution over a shorter time scale than that of the main figure, which itself could be an inset to an even larger figure. Reversals in evolutionary trends resulting from events of any magnitude are in principle identical to reversals in adaptive trends occurring within populations during selection for traits that maximize geometric-mean fitness. Line thickness represents arithmetic-mean fitness of the phenotype relative to other strategies over the duration of the line, and barred arrowheads depict the selective elimination of the lineage. More catastrophic events are shown to exert stronger selection, and selection tends to eliminate individuals that are similar through descent; the more severe the event, the more inclusive the group eliminated. The phenotype 'O' (for 'optimal') has the highest arithmetic-mean fitness over extended periods of time, and performs best under average conditions (corresponding to the mean environment). However, this 'optimal' phenotype is not necessarily represented by the greatest number of descendants over the longer term. Instead, although a conservative bet-hedging strategy is not associated with the highest relative fitness under average conditions, it persists because it is associated with reduced variance in fitness, and has maximized geometric-mean fitness.

events of any magnitude (y -axis, lower panel). For example, if bifurcations on the y -axis represent population differentiation or speciation over a longer time scale, the inset would represent the self-similar evolutionary process occurring within these populations in response to finer-scale environmental variation as described in Fig. 1. Although a major extinction event might extinguish entire genera and would thus override trends evolving over the shorter time scale, this event is in principle identical to the elimination of adaptations that maximized arithmetic-mean fitness in the process of selection for bet hedging at the population level.

There are two classes of bet-hedging traits: diversification and conservative (Seger & Brockmann, 1987; Philippi & Seger, 1989). A diversification strategy is characterized by the production of a diversity of phenotypes, thereby reducing temporal variance in fitness and the chance of complete failure. A conservative strategy – flowering behaviour in *L. inflata* – was used as an example because extrapolation to longer time scales is more straightforward for conservative than for diversification traits. The mechanisms underlying the generation of individual-level diversification strategies, such as polymorphism in seed germination behaviour (Cohen, 1966), are poorly known (Cooper & Kaplan, 1982; Simons & Johnston, 1997). Although some clades seem to be characterized by consistently high rates of speciation and extinction (Anstey, 1978; Jablonski, 1986; Dennis *et al.*, 1995) – suggestive of clade-level diversification – it is unknown whether mechanisms exist at the clade level that would allow diversification bet hedging to evolve. In contrast, conservative traits at the clade level may be individual-level traits. Thus, although long-term diversification is possible, this paper focuses on the more compelling cases of the existence of long-term conservative strategies.

The validity of the geometric mean principle, and thus a bet-hedging perspective, is independent of whether bet hedging traits, as strictly defined, result: there may or may not be a discrepancy between the arithmetic and geometric mean fitnesses associated with a trait at any structural level. However, if an extinction event is selective, selection is nonrandom with respect to a phylogenetically nested trait, and the event overrides adaptive trends, the trait associated with survival has maximized the geometric mean fitness 'at the expense of' the mean fitness of its bearers. Ever since its origination, this trait has been consistently associated with survival in the lineage. This is equally true for all traits, whether they originated recently and are variable at the within-population level or whether they have endured through millions of years, as in the case of a trait of deeper structural nestedness. A bet-hedging perspective posits that whether the trait – either now or ever during its history – maximizes arithmetic-mean fitness is immaterial except in its transient effect on geometric-mean fitness.

This argument holds that, at least in principle, the restriction of bet hedging theory to short time scales is not justified. Our population that was extinguished because none of its members were equipped to survive an event outside 'normal' variation can be seen as a trend reversal, but also as selection for geometric-mean fitness at a deeper phylogenetic level. The maximization of the geometric-mean fitness is thus an inevitable outcome of variable selection to the extent that the underlying premises hold.

Empirical and theoretical support

The bet-hedging perspective posits that bet-hedging traits may occur at any level of structural nestedness, and evolve through trend reversals driven by major selective events of low frequency set in a background of more minor selective events of higher frequency. The general relevance of the geometric-mean principle to evolution thus depends on the temporal structure of environmental variance, selectivity of environmental events and the phylogenetic nesting – or heritability – of traits under selection. Support for these underlying premises will now be examined.

The nature of environmental variance

The hierarchical application of bet-hedging theory requires that environmental variance include a wide array of event magnitudes – possibly a continuum spanning the spectrum from minor fluctuations occurring over short time scales (seconds or hours) to rare events leading to mass extinction. A second requirement is that event magnitudes be inversely related to their frequency of occurrence.

Time-series models in ecology and evolution that are built by assigning simple properties – such as a fixed variance – to environmental 'noise' have proven to be inadequate (Halley, 1996). Recent theoretical and empirical studies have advanced our understanding of the structure of temporal environmental variance (Ariño & Pimm, 1995; Halley, 1996; Bengtsson *et al.*, 1997; Cyr, 1997; Solé *et al.*, 1997; McKinney & Frederick, 1999; Solé *et al.*, 1999; Plotnick & Sepkoski, 2001). Based on records of sea-level changes and temperature from the deep ocean, Steele (1985) showed that environmental variation in marine environments increases continually with longer time series over timescales from hours to millennia. The implication is that environmental events that are disproportionately influential occur at a relatively low frequency. This general pattern of variance is known as $1/f$ -noise (Halley, 1996).

$1/f$ -noise can be further broken down into qualities or 'colours' of variance, depending on the relative duration of influence of events of different frequencies. Through analogy with spectral analyses of visible light, white noise is so named because it is influenced equally by all

frequencies. Each event is independent, and thus white noise contains no temporal correlation. Just as red light contains an abundance of low frequency radiation, a 'reddened' temporal spectrum (Steele, 1985) is a pattern of environmental variance that is disproportionately influenced by components of low frequency. The strength of temporal correlations depends on the relative frequencies of events of different magnitudes, or the different 'spectral density' profiles of $1/f$ -noise. Accordingly, there are different shades of 'redness.' A spectral analysis describes the shade by measuring contributions of all frequencies present in a time series, and takes the form $S(f) \propto f^{-\beta}$. Each frequency, f , present in a time series contributes to the spectrum where the spectrum is defined as $1/f$ -noise only for $0 < \beta < 2$. A characteristic of $1/f$ -noise spectra is that they are scale-independent, and thus constitute fractal objects in time (Halley, 1996; Solé *et al.*, 1999).

Recent empirical evidence points to ever-increasing environmental variance through time (Pimm & Redfearn, 1988; Ariño & Pimm, 1995; Bengtsson *et al.*, 1997; Solé *et al.*, 1997), corroborating Steele's (1985) earlier findings. Pimm & Redfearn (1988) found strong evidence that, for terrestrial systems, population densities through time are characterized by $1/f$ -noise, possibly as a result of forcing by the reddened spectrum of environmental variables. Ariño & Pimm (1995) estimated the Hurst exponent – a measure of the degree of redness inherent to a time series – for 115 populations of 57 species of birds, mammals, plants, insects, diatoms, and fish for which appropriate data were available. They found the mean exponent to be consistent with 'pink' noise – the degree of redness falling about half way along the continuum of $1/f$ -noises (Ariño & Pimm, 1995).

The applicability of the conclusions of Ariño & Pimm (1995) to longer time scales is supported by the finding that foraminifera species with low variance in abundance persist through a greater number of geological stages in the fossil record (McKinney & Frederick, 1999). Furthermore, the reddened pattern of increased variance through time has also been detected at geological time scales (Solé *et al.*, 1997; McKinney & Frederick, 1999). Consequently, the reddened, or $1/f$ -noise approach has become widely accepted as the most appropriate null model (Halley, 1996) for the structure of environmental variance, and supports the potential importance of the geometric mean principle over long time scales.

Mass extinctions are sometimes regarded as qualitatively distinct from other selective events. In the history of life on this planet, five mass extinctions are recognized along with a variable number of minor extinctions (see, for example, Raup, 1986; Benton, 1995). The minor extinctions, in turn, are set in a 'background' of even more minor extinctions. Variation in the severity of the five mass extinctions (Raup, 1986; Kitchell, 1990; Benton, 1995), and among the minor extinctions is pronounced (Benton, 1995), which Stigler (1987) used to

demonstrate that discontinuity of mass and background extinctions cannot be concluded. Evidence from extinction records of 2316 families of marine animals over Phanerozoic time (last 600 My) suggests that variation of extinction intensity over the 79 geological stages conforms to a Poisson distribution (Fig. 1 in Raup, 1986). Furthermore, when data permit study of extinction events at a high temporal resolution, mass extinction events have been shown to be better explained as periods of faunal turnover spanning several time intervals (Ausch *et al.*, 1994). Mass extinctions may be caused not by a single factor, but by the temporal clustering in geological time of several minor disturbances (Hoffman, 1989), or by interactions among several factors (Jablonski & Sepkoski, 1996; Bennett, 1997) operating over different time scales (Plotnick & Sepkoski, 2001).

Kitchell (1990) argues that background and mass extinctions cannot be distinguished, and Van Valen (1994) suspects that mass extinctions may be considered the extreme of a continuum of environmental variance. Raup (1986) states that 'although names may imply that qualitatively different processes are operating, this may not be the case'. Temporal environmental variance, then, may be viewed as a fundamental influence on evolution from common minor fluctuations within generations (Simons & Roff, 1994, 1996), to less common but more severe perturbations among generations (Gibbs & Grant, 1987; Seger & Brockmann, 1987; Philippi & Seger, 1989), to extremely uncommon but catastrophic events (Benton, 1995).

By accepting a range of single physical causes, cumulative effects of coincidental physical causes (Hoffman, 1989), and the context-dependence of their effects on biota (Plotnick & Sepkoski, 2001), event severities occurring on a continuum of possibilities is a more plausible view than is the concept of a fixed number of possible magnitudes. Because pink $1/f$ -noise results from a random assemblage of events acting at different time scales, it should be considered an appropriate model of environmental variance not only for empirical reasons, but for theoretical reasons as well (Halley, 1996). Although the evolution of longer-term bet hedging requires the event magnitudes be inversely related to their frequency of occurrence, it does not rely on a particular pattern of environmental variance. Pink $1/f$ -noise is one example of a structure of temporal environmental variance that would permit the evolution of long-term bet hedging.

The structure of environmental variance provides compelling reason to consider a hierarchical application of the geometric mean principle. However, the bet-hedging perspective's importance depends also on differential survival being correlated with phenotype (selectivity), and on the existence of heritable variation for traits under selection at any clade level (phylogenetic nesting). Although selectivity in extinction was documented as early as the nineteenth century (Markov &

Naimark, 1994), evidence for both selectivity and phylogenetic nesting is now increasing rapidly with the recent growth of macroecology (Gaston & Blackburn, 1999).

Selectivity

Selectivity, or correlation between phenotype and fitness, has been established for a range of extinction events. McKinney (1997), in a comprehensive review of the empirical literature on selectivity, concludes that extinction vulnerability is 'rarely random', and that there is considerable consistency of traits influencing differential survival across temporal scales. He compiles data on over 20 traits, 15 of which are individual-level traits that have been associated with patterns of selectivity over both ecological and geological time scales (McKinney, 1997). The following accounts of selectivity of extinction are chosen for their variety; the list is not intended to be exhaustive.

Survival of obligate autotrophic planktonic diatoms through the global darkness of the end-Cretaceous mass extinction was considered to be an 'enigma' until Kitchell *et al.* (1986) were able to attribute survival of the autotrophs to a resting spore stage that had evolved in response to local environments of low light during background times. Similarly, terrestrial plant survival in the Northern hemisphere during the Cretaceous-Tertiary event was selective, and was dependent on the ability to enter a dormant stage through deciduousness, a perennating organ, or a seed bank (Spicer, 1989).

Three traits have been specified as conferring extinction-resistance on mollusks during late-Cretaceous background times: planktotrophic larval development, species richness, and species-level broad geographical range (Jablonski, 1986). Extinction is selective both during background and mass extinctions and, although Jablonski (1986) sees selectivity during mass extinctions as often 'indifferent' to adaptations accumulated during background times, some continuity exists (Jablonski, 1995). Jablonski (1995) cites two examples: mollusks showed exceptionally low extinction during the Pleistocene climate changes, which may have resulted from the previous elimination of vulnerable forms during the Pliocene (Jablonski, 1995); and the bivalve order Pholadomyoidea suffered extensive extinction during the end-Permian event but was not vulnerable to the conditions of the end-Triassic. In fact, less than 35% of marine bivalve genera survived the end-Triassic event, and extinctions were nonrandom with respect to feeding habit (McRoberts, 2001).

The differential extinction of specialized taxa is common, and has been referred to as 'one of the most important rules of macroevolution' (Markov & Naimark, 1994). The evolution of specialization is inferred by the relative complexity of characters (Anstey, 1978). Among other taxa, selectivity with respect to character complexity

has been observed in bryozoans (Anstey, 1978; Gorjunova *et al.*, 1997). Anstey (1978), using 398 specimens of 123 Palaeozoic genera of bryozoans, measured selection on character complexity based on 150 binomial character states. Phenotypically complex taxa were associated with higher overall relative extinction rates. Interestingly, extinction of complex taxa is attributable almost exclusively to mass extinction events; simple taxa experienced high relative survival during mass extinctions (Anstey, 1978).

Although study of selectivity is most common for single events, changing relationships between phenotype and fitness have also been documented. The feeding habit of bivalves (infaunal vs. epifaunal) is associated with differential survival through the end-Triassic extinction, and is most likely attributable to the reduction of primary productivity (McRoberts & Newton, 1995). Survival of echinoids through the end-Cretaceous event, although selective (Smith & Jeffery, 1998; Eble, 2000), is independent of infaunal or epifaunal habit (Smith & Jeffery, 1998); rather, variation in feeding strategy among both deposit-feeding (penicillate tube feet, suctorial tube feet, or no tube feet) and lantern-feeding (omnivore or herbivore) sea urchins accounts for differential survival (Smith & Jeffery, 1998). Also, the selective extinction of a number of cold-stenothermic species, including the gastropod *Homalopoma emulum*, from the Mediterranean was likely affected by cyclic homothermic phases during interglacial periods of the Upper Pleistocene (DiGeronimo & LaPerna, 1997).

The Foraminifera are particularly well suited to the study of changing patterns of selectivity because three major extinction episodes have been recognized (Banerjee & Boyajian, 1996). Two extinction events – the late Cenomanian and upper Eocene – showed selectivity on Foraminifera test composition: whereas agglutinated tests are associated with significantly higher extinction during the late Cenomanian event, calcareous genera suffered significantly higher extinction during the upper Eocene (Banerjee & Boyajian, 1996). Moreover, selectivity against agglutinated tests during the late Cenomanian was a reversal of background trends, whereas selectivity during the upper Eocene was an amplification of background patterns of selectivity. Both test types experienced elevated extinction during the Maastrichtian event (Banerjee & Boyajian, 1996).

Selection may thus operate over a wide range of events (Stanley, 1984; Jablonski, 1986; Raup, 1986; Gould, 1989; Kitchell, 1990; Van Valen, 1994; McKinney, 1997; Russell *et al.*, 1998), and a consensus on the relative importance of nonrandom extinction at deeper clade levels to evolution will become more certain as more studies become available. Van Valen (1994) argues that conclusions about selectivity are influenced by the focal time scale of the observer, and that even extreme catastrophes are selective at some level. Raup (1986) affirms, 'Most extinction episodes are biologically selective, and further analysis of

the victims and survivors offers the greatest chance of deducing the proximal causes of extinction'.

Phylogenetic nesting

If traits associated with extinction vulnerability are nonrandomly distributed among taxa, patterns of selectivity may be explained by phylogenetic nesting of traits (McKinney, 1995). Just as resemblance among relatives within populations implies nonzero heritability, phylogenetic nesting of a trait at a deeper clade level implies the presence of heritable variation for the trait at that clade level (Jablonski, 1987; Williams, 1992; Van Valen, 1994). Heritable variation may thus occur at any clade level (Williams, 1992) regardless of whether the trait is an emergent property at that level (Van Valen, 1994).

Of the three traits that conferred extinction-resistance to mollusks during background times (Jablonski, 1986, above), only broad geographical range is associated with diminished extinction proneness during the late-Cretaceous mass extinction; selectivity occurred only at deeper phylogenetic levels than it did during the preceding background extinctions (Jablonski, 1986). The resting spore stage, to which Kitchell *et al.* (1986) ascribed survival of autotrophic diatoms, is an example of a phylogenetically nested trait restricted to the centric diatoms (Kitchell, 1990). Rates of extinction of sea urchins through the end-Cretaceous event (Smith & Jeffery, 1998) varied significantly among higher taxonomic groups.

Nonrandom extinction vulnerability may be ascribed to phylogeny within a diversity of taxa including birds and mammals (Russell *et al.*, 1998) and plants, echinoids, and fossil mollusks (McKinney, 1997). Whereas phylogenetic nesting of clade-level variation is most readily studied for extinction events, it has also been argued that threatened status, and presumably extinction risk, of modern bird species is phylogenetically nested within families (Bennett & Owens, 1997). A history of environmental disturbance may account for present day differences in vulnerability: survival through an event would be high if the biota entering the event represent a 'filtered' subsample of survivors through earlier, similar events (Balmford, 1996). Coope (1995), on the subject of insects' capacity to avoid climatic extremes, compares selectivity to a hurdle race; 'any species that could leap the first gate could similarly leap the rest'.

In summary, extinction events of any magnitude are neither entirely random nor selective; differential survival, both over longer and shorter time scales, is attributable to individual-level traits (Ward & Signor, 1983; Kitchell, 1990; McKinney, 1997) that tend to be phylogenetically nested (Ward & Signor, 1983; McKinney, 1995, 1997; Russell *et al.*, 1998). A 'reddened' spectrum of selective events acting on phylogenetically nested traits means that the geometric mean principle may be

extrapolated to long-term evolution. Survivors of reversals in trends established at any clade level may be bet hedgers in precisely the same way as are traditional bet hedgers; they have 'sacrificed' arithmetic mean for geometric mean fitness.

Implications

The predominant view of discontinuity of microevolution and macroevolution is based on observations of trend reversals that effectively negate the effects of selection that have accumulated over short time scales. Attempts at explaining discontinuous patterns of evolution have taken two paths. The first is that a hierarchy of processes at different tiers result in a hierarchy of pattern. The second is that simple rules can lead to hierarchical pattern. I have argued for a third possibility: that discontinuity of pattern is not evidence of discontinuity of process; it is a fundamental result of a single process. This process is based on a principle of accepted general importance in microevolution – the geometric-mean principle – that is itself hierarchical. I have further argued that all necessary components are in place for the general application of the geometric-mean principle.

The principal contribution of the perspective is that it specifies how trend reversals at any phylogenetic level can be understood within an accepted theoretical framework, and without recourse to mechanisms other than natural selection. An implication of the geometric mean perspective is that there should be no expectation of optimality for traits of extant organisms under present conditions or over short time scales. A specific prediction is that a trait's optimality over the short-term should be inversely related to its level of structural nestedness. This is because the probability of encountering ever more anomalous events increases through time, and more deeply nested traits have been associated with survival over greater time scales. Therefore, deeply nested traits are most likely to be adequate under any circumstance even if not the most appropriate under any circumstance.

The perspective exposes the close relationship and possible ambiguity between optimality and phylogenetic constraint. Adaptation may be constrained by various factors (Williams, 1992, pp. 72–88) including phylogenetic history. The precise relationship between the ideas of optimality and phylogenetic constraint is elusive. Stearns's (1982) description of organisms as being 'a mosaic of relatively new adaptations embedded in a framework of relatively old constraints' concurs well with the proposed perspective; Stearns adds that the selective mechanisms underlying constraints deserves attention (Stearns, 1982). If a fundamental characteristic of environments is that they are variable, the optimal trait, even locally, should be considered to be that which maximizes the geometric mean fitness. Global constraints, however, may have been produced by variable selection and should, by the same criteria, be considered potentially

optimal because there is no single correct time scale for assessing fitness. Thus, an implication of the bet-hedging perspective is that a single trait that is a constraint on optimality at one time scale might concurrently be optimal over a longer time scale.

Providing convincing evidence of a long-term bet-hedging strategy would require detailed knowledge of selection on the trait over different time scales. This has proven difficult even for traditional bet hedging within populations (Hopper, 1999). Nonetheless, that selection, whether constant or variable, maximizes geometric-mean fitness is accepted because it is a necessary outcome of the fact that reproductive success associated with a trait is inherently multiplicative over generations. Therefore, the following examples are not meant as evidence of bet hedging at deep phylogenetic levels; they are meant only to demonstrate how our expectation of evolutionary results would be altered, and how cases of apparent discontinuity would be readily accepted, through the adoption of the bet-hedging perspective.

The resting spore stage of diatoms, to which survival through the end-Cretaceous mass extinction is attributed (Kitchell *et al.*, 1986), provides a convenient illustration of the perspective by underscoring the confusion between optimality and constraint. Although recently evolved families are not spore forming – instead forming a resting cell – (Simonsen, 1979), older groups retain the primitive character, for which Kitchell (1990) provides two possible explanations. One explanation is adaptive, the other based on constraint: ‘...unfavourable environmental conditions may be sufficiently frequent...that many phytoplankton have retained the primitive life history strategy’ or ‘spore formation may be genetically linked to other indispensable aspects of cell metabolism...’. The same trait may thus be regarded as an adaptation to environmental variance over the longer term, or as a genetic constraint on adaptation over the short-term. Similarly, in the field of animal behaviour, suboptimal behaviour under short-term environmental variability has been explained by ‘coarse behaviour rules’ that are optimal over longer time scales (Bookstaber & Langsam, 1985). A potential example of perhaps the most extreme phylogenetically nested conservative trait is a ubiquitous property of the secondary structure of protein that is considered suboptimal under present conditions, but was probably appropriate in the prebiotic environment (Mróz & Latajka, 1997).

The global bet-hedging view of evolution should not be reduced to the expectation of generalist strategies, although long-term trends away from specialization may result through the maximization of geometric-mean fitness. Some traits conferring high relative extinction risk may be interpreted as enhancing specialization (McKinney, 1997); traits such as temperature specialization (Stanley, 1984), diet specialization, symbiosis, and complex morphology. Results of Anstey’s (1978) analyses (see Selectivity, above) are particularly suggestive of

short-term selection for specialization countered by long-term selection for generalist strategies. Character complexity can arguably be interpreted as degree of adaptive specialization in this group (Anstey, 1978). Between mass extinctions simple, unspecialized forms were outperformed by complex genera, but their long-term fitness is greater once mass extinctions are accounted for.

Anstey’s (1978) findings, however, cannot be taken as evidence that selection acts against specialization over the long-term. Explanation of patterns is dependent on time scale and such patterns reflect a diversity of causes; the decline of a clade may or may not be accompanied by a concurrent reduction in morphological complexity (Ward & Signor, 1983; Foote, 1993). As Foote (1993) notes, no single pattern of evolution of generalist strategies exists among trilobites. One exceptional trilobite lineage of the five studied shows little morphological variation through its history, suggesting that it is a ‘morphologically conservative group’ (Foote, 1993). This conserved clade is the sole survivor through the post-Devonian decline (Foote, 1993). Conversely, clades might repeatedly evolve traits inappropriate for events over a longer time scale if ‘genetic memory’ decays. The evolution of keeled from unkeeled planktonic foraminifera has occurred at least 16 times (Norris, 1991), but the unkeeled species invariably survive the mass extinctions to once again found new species of keeled species (Norris, 1991).

The process of evolutionary change, from changes in allele frequency to extinction events, is a constant interplay between the inevitable adaptation to environmental parameters if they are constant at one temporal scale, and the elimination of those forms which have specialized to these constant environments if it turns out that the constancy is itself transitory, and the parameters prove to be unreliable on any larger scale. The ‘plus ça change’ model (Sheldon, 1996), for example, predicts that persistent lineages that have evolved in fluctuating environments will show little evolutionary response to their variable environment, whereas organisms inhabiting more stable environments will show wide fluctuations in morphology if exposed to relatively small environmental shifts. Key characters (Van Valen, 1971) or innovations (Hunter, 1998) are ‘key’ in hindsight; they have allowed the use of some aspect of the environment in a novel manner. However, if the environmental parameter proves transient over a longer time scale, the character that allows its exploitation is not considered key, and may contribute to the ‘phylogenetic load’ of the lineage (in a manner analogous to population-level genetic load). Whereas most definitions of key innovations (Hunter, 1998) describe the adaptive result of selection, Van Valen’s (1971) statement that a key character ‘...makes a taxon more or less committed to a way of life...’ clearly reflects the selective process itself. True plant extinctions during the end-Cretaceous event seem to be the result of ‘the loss of specific environments

to which a particular group or groups have become irreversibly specialized' (Spicer, 1989).

It has been assumed that if similar processes operate over all time scales, long- and short-term trends should not be in opposition. Many experts in the study of macroevolution, because of reversals in phenotypic trends observed in the fossil record, believe microevolution and macroevolution to be 'decoupled' (Stanley, 1975); that selection is characterized by alternating regimes (Jablonski, 1986) and operates constructively or destructively (Raup, 1986) depending on the time scale or 'tier' (Gould, 1985; Bennett, 1997), and believe the opposite trends across tiers to be a 'paradox' (Gould, 1985) resolved only by accepting a hierarchical structure (Vrba, 1980, 1983; Vrba & Eldredge, 1984) of autonomous processes operating over these tiers (Gould, 1985). However, a fundamental property of evolutionary trends is that they are continually being 'reversed' from the viewpoint of any unit of selection. Extinction is a 'fundamental cause' of evolution (Van Valen, 1994) whether selection acts in similar or opposite directions during different events, just as intergenerational fluctuations select for bet hedging.

Conclusions

This paper investigates the repercussions of a point that has previously been acknowledged yet has been ignored: that selection for a bet-hedging strategy is not a special case of the way in which natural selection operates. I have argued that the principles of bet-hedging theory should be considered as relevant not only to a broad range of microevolutionary studies, but may also be applied hierarchically to macroevolutionary time scales and to all phylogenetic levels. Integral to this perspective is the treatment of environmental variance as a potentially continuous variable, spanning minor fluctuations to catastrophic events, where event frequency and severity are inversely related. Recent empirical and theoretical studies suggesting the prevalence of 'reddened' or '1/f' temporal spectra thus offer support to the proposed perspective. More deeply embedded traits are shared at deeper phylogenetic levels. Reddened selective extinction that is nonrandom with respect to traits shared at any phylogenetic level thus results in organisms composed of structurally nested traits that have persisted through all environmental events occurring over the time period since the origin of the trait. The most recently evolved traits are most likely – and ancient, deeply embedded traits least likely – to be optimal over short time scales.

Gould (1980) predicts a new, unified theory that is 'rooted in a hierarchical view of nature...It will possess a common body of causes and constraints, but will recognize that they work in characteristically different ways upon the material of different levels...' I argue that no new theory is necessary. A depiction of evolution based on environmental unpredictability and trend reversals

occurring concurrently at all levels of biotic organization offers a self-consistent and parsimonious perspective on short- and long-term evolution, one that should be acceptable to both palaeobiologists and population geneticists. In this view, mass extinctions, 'so utterly beyond the power of organisms to anticipate' (Gould, 1984) comfortably take the extreme position opposite the selective elimination of allelic variants on the continuum of perturbations, none of which is anticipated: adaptation, although judged from the present, is always a relic of the past. Claims of qualitative differences in the process of natural selection depending on the severity of selection events become unnecessary and therefore should bid a tierful goodbye.

Acknowledgments

I thank M.O. Johnston for helpful criticism throughout the preparation of this manuscript. I also thank G.A.C. Bell, A.R. Fisher, B.K. Hall, M.W. Hart, J.A. Hutchings, M.O. Johnston, S. Kalisz, P. Li, I.A. McLaren, T. Philippi, D.A. Roff, D.E. Ruzzante, M.K. Trzcinski, D.B. Wake, E. Zouros and four anonymous referees for comments on this manuscript or earlier drafts. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) grants to M.O. Johnston and A.M. Simons.

References

- Anstey, R.L. 1978. Taxonomic survivorship and morphologic complexity in Paleozoic bryozoan genera. *Paleobiology* **4**: 407–418.
- Ariño, A. & Pimm, S.L. 1995. On the nature of population extremes. *Evol. Ecol.* **9**: 429–443.
- Ausich, W.I., Kammer, T.W. & Baumiller, T.K. 1994. Demise of the middle Paleozoic crinoid fauna: a single extinction event or rapid faunal turnover? *Paleobiology* **20**: 345–361.
- Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. *Trends Ecol. Evol.* **11**: 193–196.
- Banerjee, A. & Boyajian, G. 1996. Changing biologic selectivity of extinction in the Foraminifera over the past 150 m.y. *Geology* **24**: 607–610.
- Bengtsson, J., Baillie, S.R. & Lawton, J. 1997. Community variability increases with time. *Oikos* **78**: 249–256.
- Bennett, K.D. 1997. *Evolution and ecology: the pace of life*. Cambridge University Press, Cambridge, UK.
- Bennett, P.M. & Owens, I.P.F. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. Lond B* **264**: 401–408.
- Benton, M.J. 1995. Diversification and extinction in the history of life. *Science* **268**: 52–58.
- Bookstaber, R. & Langsam, J. 1985. On the optimality of coarse behavior rules. *J. Theoret. Biol.* **116**: 161–193.
- Carroll, S.B. 2001. The big picture. *Nature* **409**: 669.
- Charlesworth, B., Lande, R. & Slatkin, M. 1982. A neo-Darwinian commentary on macroevolution. *Evolution* **36**: 474–498.

- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* **12**: 119–129.
- Coope, G.R. 1995. Insect faunas in ice age environments: why so little extinction? In: *Extinction Rates* (J.H. Lawton & R.M. May, eds), pp. 55–74. Oxford University Press, New York.
- Cooper, W.S. & Kaplan, R.H. 1982. Adaptive 'coin-flipping': a decision-theoretic examination of natural selection for random individual variation. *J. Theoret. Biol.* **94**: 135–151.
- Cyr, H. 1997. Does inter-annual variability in population density increase with time? *Oikos* **79**: 549–558.
- D'Arrigo, R. & Jacoby, G.C. 1993. Secular trends in high northern latitude temperature reconstructions based on tree rings. *Climate Change* **25**: 163–177. Data archived at the World Data Center for Paleoclimatology, Boulder, CO, USA.
- Dempster, E.R. 1955. Maintenance of genetic heterogeneity. *Cold Spring Harb. Symp. Quant. Biol.* **20**: 25–32.
- Dennis, R.L.H., Shreeve, T.G. & Williams, W.R. 1995. Taxonomic differentiation in species richness gradients among European butterflies (Papilionoidea, Hesperioidea): contribution of macroevolutionary dynamics. *Ecography* **18**: 27–40.
- DiGeronimo, I. & LaPerna, R. 1997. *Homalopoma emulum* (Seguenza, 1876), a bathyal cold stenothermic gastropod in the Mediterranean Pleistocene. *Geobios* **30**: 215–233.
- Eble, G.J. 2000. Contrasting evolutionary flexibility in sister groups: disparity and diversity in Mesozoic atelostomate echinoids. *Paleobiology* **26**: 56–79.
- Eldredge, N. & Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: *Models in paleobiology* (T.J.M. Schopf, ed.), pp. 82–115. Freeman, Cooper & Co., San Francisco, CA.
- Erwin, D.H. 2000. Macroevolution is more than repeated rounds of microevolution. *Evol. Dev.* **2**: 78–84.
- Footo, M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19**: 185–204.
- Gaston, K.J. & Blackburn, T.M. 1999. A critique for macroecology. *Oikos* **84**: 353–368.
- Gibbs, H.L. & Grant, P.R. 1987. Oscillating selection on Darwin's finches. *Nature* **327**: 511–513.
- Gillespie, J.H. 1973. Polymorphism in random environments. *Theoret. Popul. Biol.* **4**: 193–195.
- Gillespie, J.H. 1974. Natural selection for within-generation variance in offspring number. *Genetics* **76**: 601–606.
- Gillespie, J.H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. *The Am. Naturalist* **111**: 1010–1014.
- Gorjunova, R.V., Markov, A.V. & Naimark, E.B. 1997. Phases of the evolution of bryozoans of the order Rhabdomesida. *Paleontologicheskii Zhurnal* **4**: 27–34.
- Gould, S.J. 1980. Is a new and general theory of evolution emerging? *Paleobiology* **6**: 119–130.
- Gould, S.J. 1984. The cosmic dance of Siva. *Natural History* **93**: 14–19.
- Gould, S.J. 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* **11**: 2–12.
- Gould, S.J. 1989. *Wonderful Life: The Burgess Shale and the Nature of History*. W.W. Norton & Company, New York.
- Gould, S.J. & Eldredge, N. 1993. Punctuated equilibrium comes of age. *Nature* **366**: 223–227.
- Gould, S.J. & Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* **205**: 581–598.
- Halley, J.M. 1996. Ecology, evolution and $1/f$ -noise. *Trends Ecol. Evol.* **11**: 33–37.
- Hoffman, A. 1989. What, if anything, are mass extinctions? *Philos. Trans. R. Soc., Lond. B* **325**: 253–261.
- Hopper, K.R. 1999. Risk-spreading and bet-hedging in insect population biology. *Annu. Rev. Entomol.* **44**: 535–560.
- Hunter, J.P. 1998. Key innovations and the ecology of macroevolution. *Trends Ecol. Evol.* **13**: 31–36.
- Jablonski, D. 1986. Background and mass extinctions: the alteration of macroevolutionary regimes. *Science* **231**: 129–133.
- Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* **238**: 360–363.
- Jablonski, D. 1995. Extinctions in the fossil record. In: *Extinction Rates* (J.H. Lawton & R.M. May, eds), pp. 25–44. Oxford University Press, New York.
- Jablonski, D. 1997. Body-size evolution in Cretaceous mollusks and the status of Cope's rule. *Nature* **385**: 250–252.
- Jablonski, D. 2000. Micro- and Macroevolution: scale and hierarchy in evolutionary biology and paleobiology. *Paleobiology* **26** (Suppl.): 15–52.
- Jablonski, D. & Sepkoski, Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* **77**: 1367–1378.
- Kitchell, J.A. 1990. Biological selectivity of extinction. *Lecture Notes Earth Sci.* **30**: 31–43.
- Kitchell, J.A., Clark, D.L. & Gombos, A.M. 1986. Biological selectivity of extinction: a link between background and mass extinction. *Palaaios* **1**: 504–511.
- Levins, R. 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, NJ.
- Lewontin, R.C. & Cohen, D. 1969. On population growth in a randomly varying environment. *Proc. Natl. Acad. Sci., U S A* **62**: 1056–1060.
- Markov, A.V. & Naimark, E.B. 1994. Selective extinction of specialized taxa and its role in the evolution of biota. *Zhurnal Obshchei Biologii* **55**: 673–683.
- Maynard Smith, J. 1989. The causes of extinction. *Philos. Trans. R. Soc. Lond. B* **325**: 241–252.
- McKinney, M.L. 1995. Extinction selectivity among lower taxa: gradational patterns and rarefaction error in extinction estimates. *Paleobiology* **21**: 300–313.
- McKinney, M.L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**: 495–516.
- McKinney, M.L. & Frederick, D.L. 1999. Species-time curves and population extremes: ecological patterns in the fossil record. *Evol. Ecol. Res.* **1**: 641–650.
- McRoberts, C.A. 2001. Triassic bivalves and the initial marine Mesozoic revolution: a role for predators? *Geology* **29**: 359–362.
- McRoberts, C.A. & Newton, C.R. 1995. Selective extinction among end-Triassic European bivalves. *Geology* **23**: 102–104.
- McShea, D.W. 1998. Possible largest-scale trends in organismal evolution: eight 'live hypotheses'. *Annu. Rev. Ecol. Syst.* **29**: 293–318.
- McShea, D.W. 2001. The minor transitions in hierarchical evolution and the question of a directional bias. *J. Evol. Biol.* **14**: 502–518.
- Mróz, I. & Latajka, Z. 1997. Direction of protein biosynthesis as a reflection of the prebiotic environment. *J. Theoret. Biol.* **189**: 151–158.
- Norris, R.D. 1991. Biased extinction and evolutionary trends. *Paleobiology* **17**: 388–399.

- Orzack, S.H. 1981. The modern synthesis is partly Wright. *Paleobiology* **7**: 128–134.
- Philippi, T. & Seger, J. 1989. Hedging one's evolutionary bets, revisited. *Trends Ecol. Evol.* **4**: 41–44.
- Pimm, S.L. & Redfearn, A. 1988. The variability of population densities. *Nature* **334**: 613–614.
- Plotnick, R.E. & Sepkoski Jr J.J. 2001. A multiplicative multifractal model for originations and extinctions. *Paleobiology* **27**: 126–139.
- Raup, D.M. 1986. Biological extinction in Earth history. *Science* **231**: 1528–1533.
- Roff, D.A. 1992. *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, New York.
- Russell, G.J., Brooks, T.M., McKinney, M.M. & Anderson, C.G. 1998. Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biol.* **12**: 1365–1376.
- Seger, J. & Brockmann, J. 1987. What is bet-hedging? *Oxf. Surv. Evol. Biol.* **4**: 182–211.
- Sheldon, P.R. 1996. Plus ça change—a model for stasis and evolution in different environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* **127**: 209–227.
- Simons, A.M. & Johnston, M.O. 1997. Developmental instability as a bet-hedging strategy. *Oikos* **80**: 401–406.
- Simons, A.M. & Johnston, M.O. 2000. Plasticity and the genetics of reproductive behaviour in the monocarpic perennial, *Lobelia inflata* (Indian tobacco). *Heredity* **85**: 356–365.
- Simons, A.M. & Roff, D.A. 1994. The effect of environmental variability on the heritabilities of traits of a field cricket. *Evolution* **48**: 1637–1649.
- Simons, A.M. & Roff, D.A. 1996. The effect of a variable environment on the genetic correlation structure in a field cricket. *Evolution* **50**: 267–275.
- Simonsen, R. 1979. The diatom system: ideas on phylogeny. *Bacillaria* **2**: 9–71.
- Slatkin, M. 1974. Hedging one's evolutionary bets. *Nature* **250**: 704–705.
- Smith, A.B. & Jeffery, C.H. 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous period. *Nature* **392**: 69–71.
- Solé, R.V., Manrubia, S.C., Benton, M. & Bak, P. 1997. Self-similarity of extinction statistics in the fossil record. *Nature* **388**: 764–767.
- Solé, R.V., Manrubia, S.C., Benton, M., Kauffman, S. & Bak, P. 1999. Criticality and scaling in evolutionary ecology. *Trends Ecol. Evol.* **14**: 156–160.
- Spicer, R.A. 1989. Plants at the Cretaceous–Tertiary boundary. *Philosoph Trans. R. Soc. Lond. B* **325**: 291–305.
- Stanley, S.M. 1975. A theory of evolution above the species level. *Proc. Natl. Acad. Sci.* **72**: 646–650.
- Stanley, S.M. 1984. Mass extinctions in the ocean. *Scientific American* **250**(June): 46–54.
- Stearns, S.C. 1982. The role of development in the evolution of life histories. In: *Evolution and Development* (J.T. Bonner, ed.), pp. 237–258. Springer-Verlag, Berlin.
- Steele, J.H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* **313**: 355–358.
- Stigler, S.M. 1987. Testing hypotheses or fitting models? Another look at mass extinctions In: *Neutral Models in Biology* (M. Nitecki & A. Hoffman, eds), pp. 147–159. Oxford University Press, New York.
- Van Valen, L.M. 1971. Adaptive zones and the orders of mammals. *Evolution* **25**: 420–428.
- Van Valen, L.M. 1994. Concepts and the nature of selection by extinction: is generalization possible? In: *The Mass-Extinction Debates: How Science Works in a Crisis* (W. Glen, ed.), pp. 200–216. Stanford University Press, Stanford.
- Vrba, E.S. 1980. Evolution, species and fossils: how does life evolve? *S. Afr. J. Sci.* **76**: 61–84.
- Vrba, E.S. 1983. Macroevolutionary trends: new perspectives on the roles of adaptation and incidental effect. *Science* **221**: 387–389.
- Vrba, E.S. & Eldredge, N. 1984. Individuals, hierarchies and processes: towards a more complete evolutionary theory. *Paleobiology* **10**: 146–171.
- Ward, P.D. & Signor, III P.W. 1983. Evolutionary tempo in Jurassic and Cretaceous ammonites. *Paleobiology* **9**: 183–198.
- Williams, G.C. 1992. *Natural Selection: Domains, Levels, and Challenges*. Oxford University Press, New York.

Received 10 December 2001; accepted 20 March 2002