










REVIEW ARTICLE

The many ways toward punctuated evolution

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Abstract: Punctuated equilibria is a theory of evolution that suggests that species go through periods of stability followed by sudden changes in phenotype. This theory has been debated for decades in evolutionary biology, but recent findings of stasis and punctuated change in evolutionary systems such as tumour dynamics, viral evolution, and artificial evolution have attracted attention from a broad range of researchers. There is a risk of interpreting punctuated change from a phenomenological, or even metaphorical, standpoint and thus opening the possibility of repeating similar debates that have occurred in the past. How to translate the lessons from evolutionary models of the fossil record to explain punctuated changes in other biological scales remains an open question. To minimize confusion, we recommend that

the step-like pattern seen in many evolutionary systems be referred to as *punctuated evolution* rather than punctuated equilibria, which is the theory generally linked with the similar pattern in the fossil record. Punctuated evolution is a complex pattern resulting from the interaction of both external and internal eco-evolutionary feedback. The interplay between these evolutionary drivers can help explain the history of life and the whole spectrum of evolutionary dynamics, including diversification, cyclic changes, and stability.

Key words: adaptive landscape, frequency-dependent selection, hierarchy, punctuated equilibria, punctuated evolution, spatio-temporal dynamics.

PUNCTUATED equilibria (PE) is a theory of evolution proposed by Eldredge & Gould (1972) that suggests that species undergo periods of stasis (no significant change) followed by punctuated changes (rapid phenotypic changes). Despite being widely discussed and studied for the past 50 years, PE remains a controversial and often poorly understood concept. Some researchers have criticized PE as being 'anti-Darwinian', while others see it as a natural extension of well-established evolutionary theories, such as modes of evolution (Hunt 2006) and the pattern of change in fossil lineages (Simpson 1944). While many scientists agree that the alternating pattern of stasis and punctuated changes is real, there is debate over the applicability of PE (Charlesworth *et al.* 1982; Hancock *et al.* 2021).

In response to such criticism, Eldredge and Gould's initial idea of PE has evolved over time, along with criticisms of the theory and its implied assumptions (Pennell

et al. 2014). Rather than rethinking PE, our perspective focuses on a much broader issue that has always been central to PE and a cornerstone of evolutionary biology: how complexity emerges by means of punctuated evolutionary dynamics from the interplay between internal and external processes (Chevin *et al.* 2022; Duran-Nebreda *et al.* 2024). The assumptions underlying evolutionary models, which may introduce significant biases, are central to this question. Different models of morphological evolution are used to fit trajectories in the fossil record. However, statistical fits might result in ambiguous predictions for difficult scenarios, such as when examining externally forced transitions such as stasis to punctuation (Hunt *et al.* 2015), or how models obstruct the development of a robust theoretical framework (Hunt 2012). More parsimonious approaches should make punctuated change, as well as other complex trends, easier to detect.

Evolution is driven by the inherent complexity of biology, such as the length of the genome, the shape of fitness landscapes (Newman *et al.* 1985), and developmental constraints (Eldredge & Gould 1972; Müller & Newman 2003), which now are often referred to as developmental biases (O'Brien & Lala 2023). In addition, many mechanisms can direct evolution through a global pattern that routinely alternates among evolutionary modes (Hopkins & Lidgard 2012). Recent work in developmental biology has identified mechanisms of tissue morphogenesis that may underlie abrupt morphological transitions during evolution (Müller & Newman 2003; Casanova & Konkel 2020). This has led to increased consideration of mechanisms of phylogenetic change that are non-gradual in the field of evolutionary developmental biology. One such mechanism is frequency-dependent selection (FDS) (Heino *et al.* 1998), which could account for both stasis and divergence (Melián *et al.* 2010). There have been few attempts, however, to incorporate these mechanisms into models of morphological evolution.

We examine the many forms of punctuated evolution, including phenotypic evolution, tumour dynamics and viral evolution, and their drivers, such as the features of fitness landscapes or geophysical processes, to show how the interplay between multi-scale processes produces complex evolutionary trends. Moreover, we present a series of models used in the literature to explain the diversity of evolutionary modes (e.g. Brownian motion, stasis, and directional evolution) in phenotypic traits. Combinations of these models can also be used to explain more complex trajectories, such as the pattern of punctuated change, when integrating the effects of both external and internal factors. Evidence of multi-scale evolutionary dynamics as well as simple though rich theoretical models of morphological evolution renders a unified framework possible, not only in the study of diverse lineages in the fossil record but also in a multitude of evolutionary systems displaying punctuated changes.

A WALK ON THE FITNESS LANDSCAPE

In the 50 years since the initial PE proposal, punctuated change in the fossil record has often been explained via infrequent speciation events caused by external changes in the environment (Vrba 1985), which interrupt periods of long-term stability. Alternative explanations have been offered for stasis (Lewin 1986; Chevin 2013) and rapid speciation (Dobzhansky 1982; Mayr 1999), but given that these theories overlap in their processes, it is difficult to confirm one theory over another based on empirical evidence.

Many theories of PE invoke the concept of fitness landscapes (see Fig. 1), also called 'adaptive landscapes', after

Wright (1932). Adaptive landscapes account for the aggregated effect of many alleles with minor contributions to phenotypic traits. In the adaptive-landscape metaphor, evolution is a population's excursion through genotypic space (Kauffman & Levin 1987), where mutation creates new genotypic variants that are subject to natural selection. Through mutation, populations explore their genetic surroundings and gradually 'optimize' their genotypes to climb the highest fitness peaks accessible to them. Conversely, stasis is associated with populations unable to find better solutions. In theory, fitness landscapes would help predict how populations change over time (Svensson & Calsbeek 2012).

In the past, the landscape was portrayed as a two-dimensional surface that was easy to relate to our everyday lives, such as how topographical features look on a map. Figure 1A shows a typical adaptive landscape, in which the 'peaks' and 'valleys' represent groups of genotypes with high fitness and low fitness, respectively. Non-additive genetic interactions, or epistasis (Cordell 2002), would make the landscape surface more 'rugged', containing more complex features (Kauffman 1993). The magnitude and quantity of peaks and valleys determine how evolution works. Gradual evolution is likely to happen when populations can find consistent gains in fitness without getting stuck on local optima by climbing infrequent and wide peaks. On the other hand, populations stuck on local optima will have to diffuse through valleys of low fitness to reach a peak of higher fitness. In a typical rugged landscape, peaks and valleys will lead to evolutionary trajectories that are mostly stable but that can change quickly as well (Newman *et al.* 1985).

An additional layer of complexity in the fitness landscape is given by genotype–phenotype mapping (GP) (Schuster & Fontana 1999; De Visser & Krug 2014; Ahnert 2017). The GP map must take into account multiple genotypes underlying a given phenotype (i.e. neutrality; Kimura 1983) and the fact that the genotype space is large and multidimensional (Maynard Smith 1970). Neutrality and multidimensionality of the GP map reveal how the 2D surface metaphor is a major hindrance: real fitness landscapes are characterized by abrupt discontinuities (Gavrilets 2018) (signifying lethal and deleterious mutations, see Fig. 1B), and the average distance between distant regions is small as the result of multidimensionality (Greenbury *et al.* 2022). This introduces the contemporary notion of 'networked landscapes' (see Fig. 1E) in which each node represents a distinct phenotype and is characterized by a fitness value, and edges between nodes denote paths of increasing fitness. Vastly different genotypes can be aggregated into a single phenotype node, driven by the ubiquity of compensatory mutations in RNA (Schuster & Fontana 1999) and protein structures (Greenbury *et al.* 2022). Another recent advancement is the

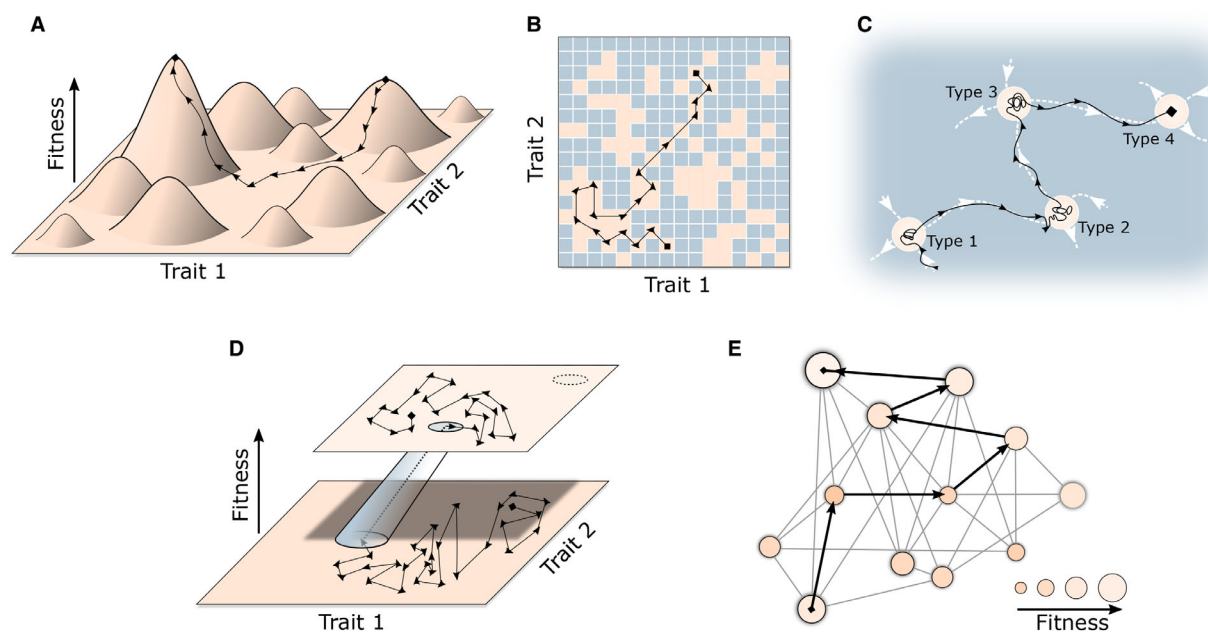


FIG. 1. Features of adaptive landscapes associated with punctuated equilibria. In all panels, adaptive walks (black arrows) represent evolutionary trajectories displaying stasis and punctuated change. A, in a two-dimensional picture of a rugged adaptive landscape, the peaks and valleys show well-adapted and poorly adapted phenotypes, respectively. B, populations evolve in holey landscapes where clusters of highly fit genotypes spread across genotypic space (blue squares), ignoring differences in fitness and treating all other genotypes as holes (light squares); adapted from Gavrilets (2018). C, saddles (circles) induce stasis as well as rapid changes in adaptation. D, punctuated evolution on a saddle-dominated adaptive landscape, where planar shapes represent different genotype classes; ‘ramp’ tubes indicate available transitions (discontinuous line) to higher fitness classes; in the neutral network, solid lines show the order of genotypes from the same class during the stasis phase; adapted from Bakhtin *et al.* (2021). E, landscape network with nodes representing phenotypes and grey edges representing possible differences between genotypes; the fitness of the corresponding genotype varies with node size; from the source phenotype (bottom), an adaptive walk (set of black arrows between nodes) leads to the target phenotype (top).

conception of large genotype spaces as dynamical systems characterized by saddle points (Fig. 1C, D). Following paths of increasing fitness, populations slow down while approaching the saddle points (appearing as stasis), accelerating their pace as they move farther away (Bakhtin *et al.* 2021).

THE MODES OF MORPHOLOGICAL EVOLUTION

In the fossil record, PE is explained differently depending on whether morphological evolution is related to speciation or phylogenetic trends. Eldredge & Gould (1972) linked bursts of evolutionary change to lineage splitting, whereas others explored when PE appeared within-lineage patterns unrelated to speciation. Because of the limited sampling of speciation events, the best PE tests employ clades rather than individual lineages (Gould 2002). Since extinct species can be identified only by their morphology, PE might be difficult to detect when punctuated changes do not correspond with lineage splitting

(Hunt 2010). The presence of cryptic species, which do not register as phenotypic divergences, means that lineage splits might occur covertly within periods of apparent stasis (Wagner 2002). On the other hand the quick, and more importantly persistent, phenotypic divergence can hardly be accomplished without speciation.

Figure 2 illustrates three examples of trait evolution over time that, according to statistical likelihood analysis, correspond to the three canonical modes of evolution: directional evolution, stasis, and random walk (Hunt 2010). Directional evolution corresponds to the pattern of gradual change predicted by Darwin (Fig. 2B). Stasis, originally intended to cover all non-directional evolutionary trends, is currently used to describe patterns of trait change with little fluctuation around an average value (Fig. 2A). Under a random walk (Fig. 2C), all changes are independent of one another, and both gains and losses have the same chance of happening. Unlike directional evolution, the random walk has no inherent direction, yet it results in growing diversity over time.

Directional evolution, stasis, and random walks are homogeneous modes given that their rules do not change

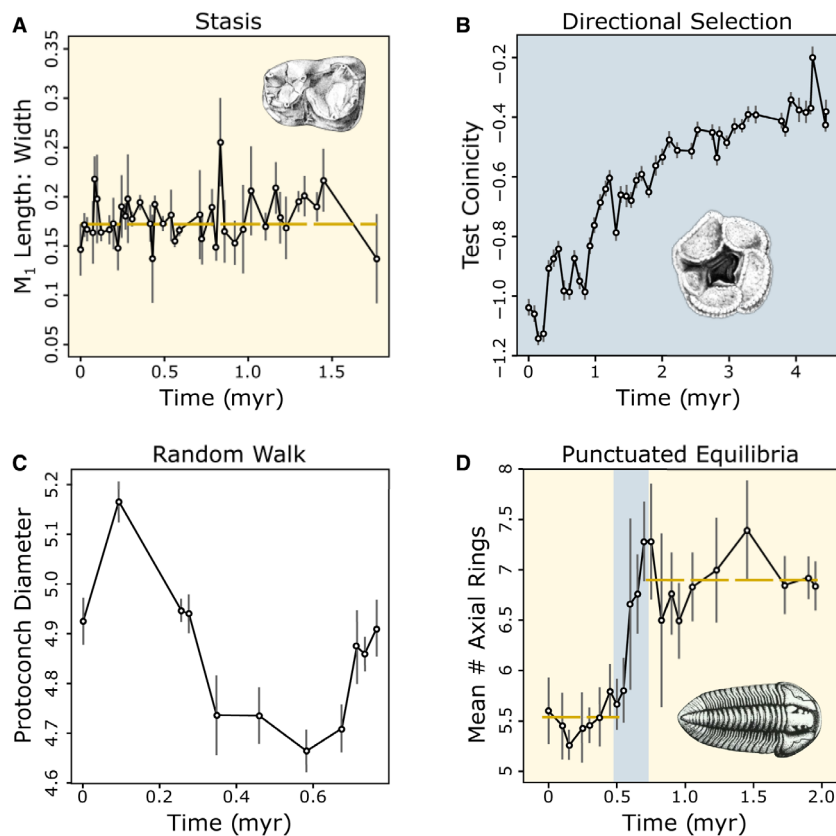


FIG. 2. Examples of trait evolution in fossil lineages which fit different forms of morphological evolution. A, stasis in the length-to-width ratio of the lower first molar of the mammal *Cantius* (Clyde & Gingerich 1994). B, directional change in test shape from the planktonic foraminifera *Contusotruncana* (Kucera & Malmgren 1998). C, a random walk in protoconch diameter from the benthic foraminifera *Discocyclina* (Fermont 1982). D, punctuated change in the evolution of the number of axial rings in the pygidium (posterior body region) of a trilobite lineage in the genus *Flexicalymene* (Cisne *et al.* 1980). The whole trajectory may be broken down into three separate evolutionary stages: stasis (ochre), fast directional change (light blue), and stasis again (ochre), with each mode specified as an explicit statistical model and fitted to data using maximum likelihood (see text). Dashed lines show the average trait values for the stages of stasis. In all panels, each point represents a sample mean, and error bars indicate 1 standard error. Time is in millions of years elapsed from the start of the sequence; adapted from Hunt (2010).

over time (see [Models of trait evolution](#), below). PE, on the other hand, loosens the premise of homogeneity and follows a three-stage model in which evolution passes through stasis, quick directional change, and stasis again. These complex, multi-stage trajectories are more difficult to define than the modes outlined above, but statistical methods have been developed to account for the increased number of parameters (Landis *et al.* 2013; Hunt *et al.* 2015). Figure 2D, for example, shows an example where a multi-stage model outperforms homogeneous modes. A multi-stage model with a single punctuated change occurring at the ninth sample best fits the evolution of the number of axial rings in the posterior body region of a trilobite lineage. A broad meta-study of 251 cases indicated that just 5% of examples investigated supported directed evolution, with the other 95% divided about evenly between stasis and random walk

(Hunt 2010). These data support one of the primary tenets of PE, that is, gradual change is uncommon in the fossil record. When integrated with other populations of the same species from various geographical regions, the random walk in a single population frequently results in the overall cancellation of the random trend in the species as a whole. As a result, random walks may also represent a pattern of general stasis (Lieberman *et al.* 1995).

Models of trait evolution

Several statistical models have been developed to detect evolutionary modes in the fossil record (Raup & Crick 1981; Gingerich 1993; Roopnarine 2001). The Ornstein–Uhlenbeck (OU) process (Doob 1942), a probabilistic model with friction or biological restrictions

instead of free motion, encompasses the three main modes of evolution: Brownian motion (also known as random walk), stasis, and directional evolution.

The OU process has four parameters: initial $z(0)$ and optimal θ trait values, selection strength α , and an intensity of fluctuations σ_s^2 that captures the strength of mutations. The dynamics of the OU process can be described as follows:

$$dz(t) = \alpha(\theta - z(t))dt + \sigma_s dW(t) \quad (1)$$

where the term $dW(t)$ is a random, independent variable that is normally distributed (Gardiner 1985), with mean 0 and variance dt , which is scaled by σ_s . The first term, $\alpha(\theta - z(t))dt$, defines the selection force under the assumption of simple linearity. This force is proportional to the distance between the present trait value and the optimal value of the trait $\theta - z(t)$; in other words, there will be a strong pull whenever the phenotype deviates significantly from the optimal. The selection force, however, disappears when $\alpha = 0$, transforming the process into a typical Brownian model (BM): $dz(t) = \sigma_s dW(t)$, which depicts the evolution of traits under genetic drift (see Fig. 2C). Alternatively, if the phenotype is already optimal, selection will have no impact. Using the full OU model, for instance, we may simulate stasis by placing the initial condition $z(0)$ near the optimal trait value, θ . In contrast to stability, directional evolution is characterized by continual change. Directional evolution can be described with a similar equation without any specific optima: $dz(t) = \mu_s dt + \sigma_s dW(t)$, where μ_s is the average per-generation step (Hunt 2012). According to Hunt (2007), directional evolution is rarely found on palaeontological time scales, perhaps because episodes of directional change are often too short to be resolved in the fossil record (see Fig. 2B).

The mode of evolution significantly affects its tempo. Table 1 shows that each mode has a distinctive rate metric (Hunt 2012).

The OU process can also be used to explain more complex sequences (Hunt *et al.* 2015), including those containing punctuated changes, which can occur when a population invades an area that is distinct from its ancestral habitat or when the environment changes abruptly. These quick shifts may be included into a multi-stage OU

process by changing the model parameters. We can divide the evolutionary sequence, for instance, into various regimes that do not overlap and represent each of them with a different stochastic process (Hunt 2006). Figure 2D depicts an evolutionary trajectory with two phases associated with differing optimal trait values and mutation strengths. In this case, the species lineage abruptly transitions from a stasis regime centred on an optimal trait value, θ_1 , to a separate stasis regime centred on a second optimal value, θ_2 (Hansen 1997).

PUNCTUATED EQUILIBRIA IN THE FOSSIL RECORD

The pattern of punctuated equilibria consists of two features in need of explanation: (1) relatively fast phenotypic transition between relatively stable phenotypic states; and (2) the existence of stasis itself. Many empirical observations show that phenotypic evolution can proceed very fast, but on longer time scales it is constrained (Uyeda *et al.* 2011). The palaeontological observations show that in order to explain both features of punctuated equilibria (stasis and potential for the fast change) we need to understand species as large and heterogenous hierarchically organized spatial entities interacting with similarly a complex multiscale Earth system (Spiridonov & Eldredge 2024).

The fossil record shows that despite diverging in different regions, lineages retain enough similarities to be considered the same species over long periods of time (Lieberman *et al.* 1995; Lieberman & Dudgeon 1996). This approach treats populations, not species, as evolving in ecosystems, yielding multiple locally contingent pathways of change (Vrba 1993; Eldredge *et al.* 2005). This view situates each species within an ensemble of fitness landscapes across actual geographical space and that are connected by the dispersal of individuals. Species stasis occurs via gene flow as the result of interpopulation movement of organisms. Speciation interrupts this regional homogenization by protecting newly diverged states from re-absorption into a greater lineage (Futuyma 1987; Gould 2001). Moreover, the high resolution fossil record of index taxa such as graptolites confirms the importance of such a mechanism by showing many examples of so called 'iterative speciation', where physical perturbations geographically fragment morphologically and ecologically conservative, long existing 'stem lineages', thus producing repeated although short-lived, and sometimes ephemeral, species radiations (Crampton *et al.* 2020; Whittingham *et al.* 2020). The duration of synchronization of evolutionary innovation depends on population structures and rates of species dispersal. On a global scale, the so-called Geo-Red Queen (GRQ) mechanism has been offered for

TABLE 1. Statistical values for the different evolutionary modes (from Hunt 2012).

Mode	Mean change	Variance	Rate metric
BM	0	$\sigma_s^2 t$	σ_s^2
Stasis	$\theta - z(0)$	σ_s^2	σ_s^2
Directional	μ_s^2	$\sigma_s^2 t$	μ_s^2

the global synchronization of biota and the onset of global scale diversity-dependent evolution of marine animal genera. GRQ states that plate tectonics and the climate-mediated dispersal of taxa effectively synchronizes biospheres at scales greater than 40 million years, thereby enabling stasis of diversity of taxa at scales of eras and eons (Spiridonov & Lovejoy 2022, 2023). The spatial extent and the heterogeneity of biotic systems, as well as the nature of geodynamics, result in patterns of divergence and stabilization at many spatial and temporal scales. The different relevance of endogenous and exogenous drivers is not merely epistemological. Rather, these factors have different relative ontological importance at varying biological scales.

Fine-scale studies of the fossil record often show simultaneous taxonomic, ecological, and phenotypic turnovers in many unrelated lineages, which suggests a significant role for external destabilization in generating the pattern of punctuated change (Vrba 1985, 1993; Ivany *et al.* 2009; Brett 2012; Eldredge 2003). On the other hand, we should not see the matter of explaining punctuated equilibria in terms of either/or when regarding internal factors of population dynamics of evolutionary individuals vs external forcing and spatial structures of environments. Biological systems, in the wider sense, are structured by multiplicative interactions between environments and their internal states (Levins & Lewontin 1985). This results in a wide, multifractal range variability, which can be detected in the dynamics of abundance of individuals inside species lineages as well as higher-level taxic dynamics of originations and extinctions (Plotnick & Sepkoski 2001; Spiridonov *et al.* 2016, 2017). The hierarchical change in climate states induces strong control on the abundances of whole clades. Depending on the environmental preferences, populations can explode in abundance, but also transition into so-called mass rarity states (Hull *et al.* 2015; Spiridonov *et al.* 2017).

Sometimes climatic variability induces the patterns of anti-dominance. Take, for example, the case of the, presumably astronomically forced, late Silurian Šilalè Event (422 Ma), which lasted a million years. During that period, cold climate conditions resulted in expansion of clear-water-loving benthic faunas (reef builders and brachiopods) and almost complete collapse of pelagic vertebrate (conodont) populations, an abundance that was two to three orders of magnitude lower than in neighbouring time intervals (Spiridonov *et al.* 2020). Without a doubt, this systemic change in abundance should influence the modes and rates of evolution. The decrease in abundance by order of magnitudes should increase the role of drift, isolation, and therefore the rate of local adaptation as well as the persistence of locally adapted phenotypes. On the other hand, the expansion of a population after prolonged environmental stress, with little

competition on the expansion front, should increase the role of spatial segregation, spatial sorting, increase in evolvability, and fixation of new and rare phenotypes, that also can result in fast evolution, crossing of barriers and the expansion of phenotypically diverging lineages (Yablokov 1986; Shine *et al.* 2011; Spiridonov *et al.* 2015; Lehman & Miikkulainen 2015). Therefore, the Earth system, which can drive whole biotas through the phase space of abundances, helps the comprehensive exploration of parameter spaces of evolutionary processes. It could be parsimoniously suggested that some of these combinations can break the integration of evolving populations and, as a result of density-dependent non-linearities of population dynamics, drive the punctuated pattern of change.

MORPHOLOGICAL EVOLUTION AND FREQUENCY-DEPENDENT SELECTION

In evolutionary biology, distinct schools of thought tend to support external or internal causes for different components of punctuated evolution (Eldredge & Gould 1972; Gould & Eldredge 1977; Newman *et al.* 1985; Estes & Arnold 2007), often based on historical data and experience with a particular model system. Seasonal cycles in allelic frequency or adaptability to climatic change are good examples of external biotic and abiotic variables influencing natural selection regimes. On the other hand, evolutionary dynamics may be driven internally from within the ecosystem by eco-evolutionary feedback that is dependent on the phenotypic and genotypic composition of the population; that is, they can be frequency dependent. Frequency-dependent selection (FDS) is an umbrella term that encompasses a wide range of biological processes in which selection relies on trait frequency (Ayala & Campbell 1974; Heino *et al.* 1998). This term includes, for example, different types of sexual selection (Lande 1980), deformable landscapes (Bajić *et al.* 2018), sociality (Newberry & Plotkin 2022), self-incompatibility in plants (Wright 1939; Castric & Vekemans 2004), crypsis (Nosil *et al.* 2018), and polymorphisms under host-pathogen interactions (Piertney & Oliver 2006). It has been suggested that FDS contributes to trait diversification (Melián *et al.* 2010), maintenance of diversity (Fitzpatrick *et al.* 2007; Kurbalija Novičić *et al.* 2020), cyclic changes in trait distributions (Calsbeek *et al.* 2010), as well as evolutionary stasis (Eldredge *et al.* 2005; Svensson 2019). Therefore, FDS cannot be reduced to a unique role in evolution or mode of evolutionary dynamics (Brisson 2018).

We can combine directional selection and positive FDS into a theoretical model (Vidiella *et al.* 2022) of morphological-trait evolution using a reduced number of

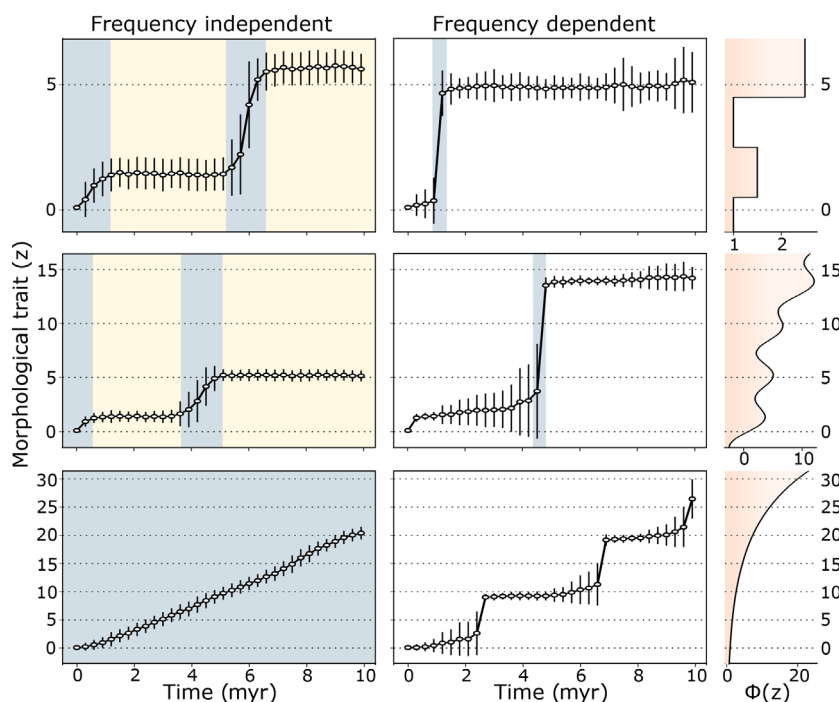


FIG. 3. Morphological evolution under frequency-dependent selection. We show the predicted evolutionary dynamics as a function of the fitness (Φ) landscape (from top to bottom: holey, rugged, and infinite ramp) and under frequency-independent (left column, $J = 0$) and (positive) frequency-dependent (right column, $J = 1.2$) selection (see text). Except when there are no constraints on phenotypic variation (bottom-left panel), the mean trait follows the pattern of punctuated equilibria. Despite the fact punctuated evolution displays essentially comparable behaviour in all cases, frequency-dependent selection leads to a pattern of stasis in the average trait marked by growing trait variance (see error bars on the frequency-dependent plots) that is not seen when evolution is frequency independent (see error bars on the left column plots). Population size has been fixed to $N = 1000$ individuals in all scenarios.

external parameters (for a description of the model, see [Modelling morphological evolution under frequency-dependent selection](#), below). Figure 3 shows predicted patterns of morphological evolution within a species lineage for different landscape topologies and under different degrees of FDS and constant population size. For instance, holey (top row) and rugged (middle row) landscapes induce abrupt changes in morphological evolution. When the fitness of a phenotype does not depend on the frequencies of other phenotypes in the population (left column), every punctuated change in the trait mirrors the topology of the underlying landscape (blue regions), and the population settles in a peak depending on the mutation-selection balance (see the top and middle-left panels). Here, trait variance is roughly constant (yellow regions) and can be anticipated based on the underlying evolutionary mode (Hunt 2012). Consequently, the pattern of PE is not expected when morphological evolution takes place in a landscape without local peaks (e.g. a section of a single-peak fitness landscape (Poelwijk *et al.* 2007); bottom-left panel). Because there are no developmental constraints (biases) inhibiting natural

selection, the fossil record follows a gradual trend (Gould 1981), as shown in artificial-selection experiments (Bolstad *et al.* 2015).

Figure 3 suggests how punctuated evolution could be facilitated by a tension between directional and positive FDS; a pattern of stabilizing selection alternates with rapid directional selection. A common view proposes that directional selection homogenizes the population when there is a limited number of accessible phenotypes. Diversification here is driven by directional selection taking place in an unbounded phenotypic space, whereas positive FDS homogenizes the population toward the most common phenotype. This endogenous process can contribute to the pattern of punctuated change, which can be identified experimentally in the connection between the average and variance of phenotypic traits. When morphological changes in a population are influenced by its own evolution (unshaded regions), a scaling of variance with mean trait is predicted (De Menezes & Barabási 2004), which is not observed when punctuated changes are externally induced or they are associated with fitness landscape features (blue regions).

Modelling morphological evolution under frequency-dependent selection

The unpredictability that arises under exogenous factors, such as the specific placement of the punctuation stage and variable rate of change, hinders the empirical testing of morphological models. When trying to explain evolutionary trends, we prefer hypotheses that are as simple as possible and have a small number of unknown or complicated parameters. Potentially significant parameters, such as finite population sizes, are, on the other hand, sometimes disregarded (for example, differential-equation models assume that populations are effectively very large or even infinite) or assigned to estimations subject to empirical errors. By extending models to endogenous factors, we can further investigate how complex evolutionary dynamics arise from eco-evolutionary feedback (Blanco *et al.* 2021) and without disregarding the role of external features. In a simple model (Vidiella *et al.* 2022) of morphological evolution within a species lineage, the probability $\Pi(z)$ of inheriting a (continuous) phenotypic trait $z \in \mathbb{R}$ is the interaction of two selection factors:

$$\Pi(z) \sim \Phi(z) \times s(\rho_z) \quad (2)$$

where $\Phi(z)$ is the fitness of the trait z or phenotype-fitness map, $s(\rho_z)$ is a frequency-dependent selection coefficient, $\rho_z = n_z/N$ is the frequency of the trait in the population, n_z is the density of the trait, and N is the (constant) population size. The simplest model of directional evolution ($\Phi(z) = e^{\beta z}$) assumes that fitness increases exponentially with increasing trait values and β is the strength of directional selection (Lande 1983). Frequency-dependent selection can be modelled with a nonlinear relationship, $s(\rho_z) = \rho_z J$, where J measures the degree of FDS. This equation includes the common scenarios of negative ($J < 0$), positive ($J > 0$) FDS, and frequency-independent selection ($J = 0$).

The model reproduces a broad range of evolutionary patterns, including random walk, gradual change, stasis, and punctuated change. A step-like pattern of morphological evolution can be induced by positive FDS and also follows from the features of the underlying phenotype-fitness map (see Fig. 3). In the case of a smooth landscape and directional selection, this model predicts that the minimal size $\Delta z = z_1 - z_0$ of adaptive steps is defined by the ratio between selection strength and the degree of positive FDS:

$$\Delta z \geq \frac{J-1}{\beta} \log(N) \quad (3)$$

where z_1 is the mean trait after the step, and z_0 is the mean trait before the step. Experiments tracking adaptive changes in an expanding bacteriophage $\phi 6$ population support the

link between the magnitude of an adaptation step and the logarithmic population size (Burch & Chao 1999).

PUNCTUATED EVOLUTION BEYOND THE FOSSIL RECORD

As PE gained popularity, researchers in fields other than palaeobiology started investigating punctuated evolution. Recent work suggests that punctuated change is a widespread pattern in many evolutionary systems across scales (see Table 2). There is, however, a risk of using PE from a phenomenological, or even metaphorical standpoint and thus opening the possibility of repeating similar debates that have occurred in the past.

Evidence for punctuated change has been reported at different temporal and spatial biological scales (see Fig. 4). Scales here refer to different levels of ecological or genealogical organization, ranging from the smallest unit to the largest (e.g. from cells to ecosystems in the economic hierarchy of life), which are arranged in a nested, interrelated structure (Jablonski 2000). Processes at any given scale can affect other scales through ecological and evolutionary feedback (Svensson 2018, 2019; Govaert *et al.* 2019), leading to reciprocal and often nonlinear interactions. For example, changes in a population's genetic composition can alter its interactions with the environment (Bajić *et al.* 2018), promoting changes in both the population and the environment. Although the processes and methods involved are very different (Lion 2018), the fact that many systems exhibit step-like evolution invites us to find unifying insights. However, any direct mapping of existing theories and models is likely to be imperfect.

For example, punctuated dynamics in ecosystems might relate to large-scale episodes of reorganization in ecological networks of interactions between species (Fig. 4 top layer), possibly caused by major climatic shifts and extinction (Blanco *et al.* 2021). This is a far cry from the experimental evidence of punctuated phenotypic changes (Fig. 4 third layer) encountered in artificial evolution over the years (Elena *et al.* 1996). The models involved in each case might be completely different, and the integration of biological processes acting at different scales remains an open challenge (Svensson 2018). However, the prospect of disentangling ecological complexity and eco-evolutionary feedback using the fossil record is certainly promising. In a pioneering study by Blanco *et al.* (2021), exceptional temporal resolution in the fossil specimens was required, as well as ample redundant samplings, something that is rarely available. Yet, this approach provides a road map to incorporate population-level phenomena into our understanding of complex evolutionary sequences from the deep past.

TABLE 2. Examples of observed punctuated change in genealogical, social and ecological hierarchies, summarizing the accepted drivers of stasis and change, as well as empirical and theoretical evidence.

Scale	Topics	Drivers of		Evidence	
		Stasis	Change	Theoretical	Empirical
Gene regulatory networks	Artificial evolution	Local optima	Adaptation	Burke <i>et al.</i> (2004)	Grozinger & Goñi-Moreno (2023)
Cells	Oncology	Neutrality	Adaptation	Aguirre <i>et al.</i> (2018); Gavrillets (2018)	Guo <i>et al.</i> (2022)
	Virology	Local optima	Mutations	Kauffman & Levin (1987); Kauffman (1993)	Elena <i>et al.</i> (1996); Burch & Chao (1999)
	Microbiology	Dynamics	Saddle-node bifurcation	Bakhtin <i>et al.</i> (2021); Liaghat <i>et al.</i> (2024)	
	Oncology		Change in evolutionary rate	Dietrich (2003)	Baca <i>et al.</i> (2013); Graham & Sottoriva (2017); Heasley <i>et al.</i> (2021)
Individuals	Behavioural sciences	Costs to adaptation	Fitness evaluation	Parker & Larochelle (2000)	Parker (2002)
Populations, demes & avatars	Linguistics	Interoperability, Frequency-dependent selection	Change in evolutionary rate	Valverde & Solé (2015)	Heggarty <i>et al.</i> (2023)
	Ethology	Frequency-dependent selection	Sexual selection	Nöbel <i>et al.</i> (2023)	Lachlan <i>et al.</i> (2018); McEntee <i>et al.</i> (2021)
Species-lineage	Morphology	Local optima	New environment	Gillespie (1996); Hunt (2006); Cooper <i>et al.</i> (2016)	Hunt (2007, 2012); Hunt <i>et al.</i> (2015)
		Local optima Local optima	Isolation Climatic drivers and biological interactions	Eldredge & Gould (1972) Spiridonov <i>et al.</i> (2015)	Gould & Eldredge (1977) Spiridonov <i>et al.</i> (2015)
Populations, demes & avatars	Sociology	Conformity	Transparency	Vidiella <i>et al.</i> (2022)	True <i>et al.</i> (2019); Carrignon <i>et al.</i> (2023)
Polities	Archaeology, anthropology	Technological barriers	State competition	Turchin & Gavrillets (2021)	Turchin <i>et al.</i> (2015)
	Technological barriers	Climatic drivers		Axtell <i>et al.</i> (2002); Scheffer <i>et al.</i> (2021)	Chapman <i>et al.</i> (2019); Daumantas <i>et al.</i> (2020); Goder-Goldberger <i>et al.</i> (2020); Kennett <i>et al.</i> (2022)
Ecology	Palaeoecology	Resilience	Climatic drivers		Blanco <i>et al.</i> (2021)
		Generalist–specialist trade-off	Exogenous stressors	Vrba (1993)	Gómez Cano <i>et al.</i> (2013)
	Ecology	Regimes	Exogenous stressors	Scheffer <i>et al.</i> (2001); Foley <i>et al.</i> (2003)	Claussen <i>et al.</i> (1999); deMenocal <i>et al.</i> (2000)

To determine the biological significance of population-level phenomena, we need: (1) reliable indicators of FDS over long time scales; (2) improved estimates of the ecological context of species; and (3) mechanistic models of evolution. Better indicators of FDS are necessary, given that it is difficult to estimate FDS using current methods due to

the dynamic nature of the fitness landscape (Bajic *et al.* 2018). Ecological drivers of punctuated change (Blanco *et al.* 2021) are undervalued by phenomenological models that do not take into account the nonlinear interactions among different types of selection. By establishing an explicit relationship between FDS and mechanistic models

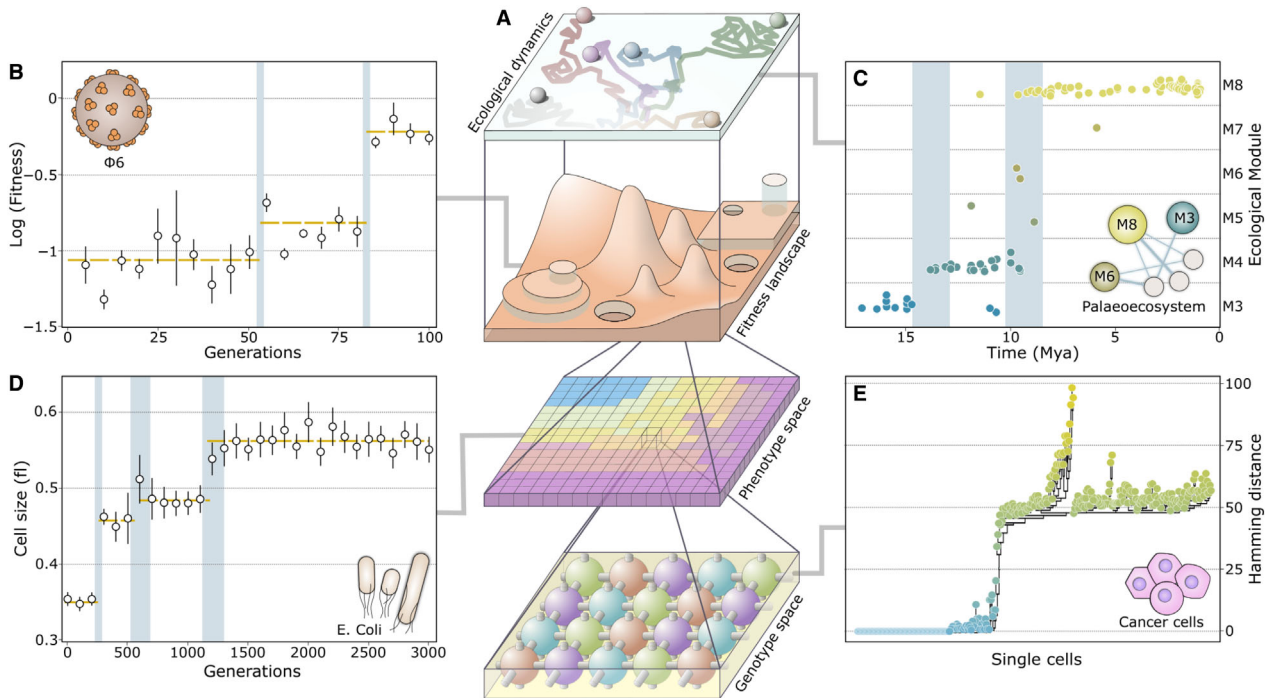


FIG. 4. The pattern of punctuated change across biological scales. A, the empirical patterns of punctuated change across biological scales: ecological population dynamics (top layer), fitness landscapes (second layer), phenotype space (third layer), and genotype space (bottom layer); genotype is represented as a high dimensional network of connected sequences if they are reachable through mutation; this space is embedded in the phenotype space, where multiple genotypes give rise to the same phenotype as a result of neutrality and compensatory mutations (Schuster & Fontana 1999; Greenbury *et al.* 2022) (here represented with different colours); the fitness of each unique phenotype and its accessibility through the genotype space produce the fitness landscape, shown here as a simple 2D surface with rugged features (continuous and discrete); finally, various lineages can coexist on a given fitness landscape, establishing an ecological layer where population densities and interactions can be taken into account. B–E, for each scale, we show examples of punctuated evolutionary dynamics (see main text): B, punctuated pattern of fitness change in the RNA virus $\phi 6$ due to rugged landscapes (Burch & Chao 1999); C, evolution of ecosystem organization in different modules during the Miocene, as described by Blanco *et al.* (2021); D, evolution of *E. coli* cell size in a long-term evolutionary experiment by Elena *et al.* (1996); E, clonal evolution in hepatocellular carcinoma progression (Guo *et al.* 2022).

of evolution, we can obtain more accurate estimations of the rate of change (Pagel *et al.* 2006).

PE has faced serious criticism over the years from those who have equated it with the idea of ‘hopeful monsters’; organisms that are recipients of extreme mutations that have the potential to establish new lineages. While evolutionary biologists have seemingly reached a consensus downplaying the historical relevance of these ‘monsters’ as an explanation of the pattern of PE (Dietrich 2003), the recent study of punctuated change in cancer has given new life to these ideas. For example, it has been proposed that punctuated changes taking place in some carcinomas involve massive reorganization events of genetic material and the generation of new clonal lineages (Fig. 4 bottom layer), a process which shows both punctuated and gradual features (Guo *et al.* 2022). Far from isolated work, there is a growing interest on whether tumour progression follows gradual or punctuated change (Baca *et al.* 2013; Graham &

Sottoriva 2017; DeGregori 2018; Turajlic *et al.* 2019), a question with outstanding implications for human health. Outside cancer biology, phylogenomic research has revealed a wealth of mechanisms driving sweeping changes in genome size (Leitch *et al.* 2007) and organization (Heasley *et al.* 2021), including segmental duplications in human evolution (Jiang *et al.* 2007), gene transfer between mitochondria and nucleus (Adams *et al.* 2002), transposable element-driven innovation that occurred during plant domestication (Palmer *et al.* 2012), and massive genomic rearrangements in clitellates (Vargas-Chávez *et al.* 2024; Lewin *et al.* 2024).

While these avenues of evidence suggest that patterns of punctuated change might be pervasive across scales, PE proponents have been largely reluctant to connect trait evidence collected from the fossil record and microevolutionary processes (Erwin 2000). This is mainly due to the fact that morphological and genotypic evolution can be

uncorrelated (Wayne & O'Brien 1986), in other words, sequence-based analysis of evolution can appear completely gradual while phenotypes, fitness or populations change abruptly (Ocaña-Pallarès *et al.* 2022). This is evidently shown in viral evolution (Volz *et al.* 2013), a domain with enormous societal impact and in which research has shown both gradual and punctuated patterns in genotypic (Wolf *et al.* 2006; Cobey & Koelle 2008) and fitness evolution (Fig. 4 second layer). COVID-19 evolution, for instance, has been shown to be punctuated (Nielsen *et al.* 2023), an aspect that must be incorporated into effective policy making and healthcare strategies. Causal explanations for punctuated viral evolution range from the ruggedness of the underlying fitness landscape (Burch & Chao 1999; Nielsen *et al.* 2023), environmental changes relating to seasonality (Wolf *et al.* 2006), migration-driven radiation (Nichol *et al.* 1993), as well as intrinsic factors such as host–pathogen interactions (Cobey & Koelle 2008) (antigenic evolution and immunity, which are frequency-dependent).

CONCLUSION

Evolution, be it of ideas, artefacts or organisms, is inherently messy and complex (Basalla 1988). Punctuated equilibria was disregarded as a byproduct, with detractors advocating for a focus on its individual components such as stasis and speciation. This is rooted in the view that a single model cannot accurately depict evolutionary pathways and that it is preferable to employ multiple models to address different evolutionary stages. However, this view does not completely remove the possibility of a unified framework to punctuated evolution but rather highlights the limitations of current models in predicting complex evolutionary paths.

In the history of evolutionary biology, there has been a trend toward developing more-complex models of evolution that can account for multiple mechanisms; witness the Wright vs Fisher debate (Svensson & Calsbeek 2012). Theoretical advances have been organized around two schools of thought (quantitative genetics and adaptive dynamics; Waxman & Gavrilets 2005) that make different assumptions and naturally emphasize the use of different tools. The fragmentation of the theoretical environment did not address the issues surrounding the PE debate and may have further exacerbated them. *Ad hoc* changes to stochastic processes, such as altering the local optima in an Ornstein–Uhlenbeck model, can fit the pattern of PE in the fossil record. In this manner, punctuated evolution is modelled as a forced, unparsimonious change in an otherwise gradual process. This approach is more of an after-the-fact fit than a prediction; hence, its results are inherently restricted in their applicability. To

fully reconstruct the history of life, we will need a mechanistic understanding of how different evolutionary processes interact (Doebeli *et al.* 2017) as well as improved estimations of its multiple drivers (Pennell *et al.* 2014), including the ecological contexts in which populations have evolved. Current theoretical and empirical research shows that when both internal and external variables are present, evolution may exhibit diversification, cyclical variations, and stability. Even in the absence of discontinuities or other fitness landscape traits, simple evolutionary models can recapitulate a wide range of complex evolutionary trajectories (Vidiella *et al.* 2022).

The pattern of stasis in punctuated evolutionary sequences suggests, implicitly or explicitly, that there are limitations to divergence. The constraints (biases) on change could be of different kinds and reside at different levels, from canalization of development, to self-stabilizing spatial population structures, to the lack of adaptive variation. Therefore, the origins of punctuated change depend on constraint-breaking processes, which could be endogenous or exogenous with respect to evolving systems (Duran-Nebreda *et al.* 2024). For example, host switch or expansion to non-immune populations in viral dynamics, transition to unstable climate regimes increasing chances of isolate formation at supra-specific level, or conversely stable climates which enable the population growth and the dominance of competitive intraspecific interactions, and consequently the explosive accumulation of culture, as in the case of humans (O'Brien *et al.* 2024). Although the proximal mechanisms would differ in each of these systems, they could nonetheless display common dynamical features, which have the potential to be captured by structurally identical mathematical laws.

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