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Trends in Ecology & Evolution

Opinion

On the multiscale dynamics of punctuated evolution

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For five decades, paleontologists, paleobiologists, and ecologists have investigated patterns of punctuated equilibria in biology. Here, we step outside those fields and summarize recent advances in the theory of and evidence for punctuated equilibria, gathered from contemporary observations in geology, molecular biology, genetics, anthropology, and sociotechnology. Taken in the aggregate, these observations lead to a more general theory that we refer to as punctuated evolution. The quality of recent datasets is beginning to illustrate the mechanics of punctuated evolution in a way that can be modeled across a vast range of phenomena, from mass extinctions hundreds of millions of years ago to the possible future ahead in the Anthropocene. We expect the study of punctuated evolution to be applicable beyond biological scenarios.

Highlights

Evolutionary processes span multiple hierarchical levels, with nested causality.

Punctuated evolutionary changes occur unevenly as a result of environmental conditions and multiscale feedback across hierarchical levels.

Slow evolution among interconnected units (e.g., molecules and organisms) can trigger abrupt changes at higher organizational levels (e.g., species and ecosystems).

Punctuated evolution is evident in biological and cultural evolution, abrupt extinctions, biodiversity crashes, evolution of the pathogens, and technological change.

Understanding punctuated evolution aids in developing more effective strategies for the conservation of biodiversity in the face of significant anthropogenic impacts.

Evolution as a punctuated process

Over 50 years ago, the theory of **punctuated equilibria** (see Glossary) was introduced to explain speciation in the fossil record [1]. That theory, later made singular (i.e., punctuated equilibrium), holds that throughout most of their existence, species undergo little morphological change, especially when averaged across populations of those species. Abrupt evolutionary change can be the result of both endogenous and exogenous events, with abrupt change at one scale emerging from gradual change at another. Although it was developed to explain apparent gaps in the fossil record, punctuated equilibria facilitate a broader rethinking of evolution across scales, from genes to biomolecules, cells, organisms, technologies, and cultures [2].

Numerous complex biological systems display extraordinary stability over long periods of time, punctuated by brief bursts of change [3]. We refer to this broader process as **punctuated evolution**. As with punctuated equilibria, punctuated evolution is a macroevolutionary event, where selection occurs at the level of a population, as opposed to a microevolutionary event, where selection occurs at the level of individual genes over short periods of time. As we will see in the following section, macroevolution is anything but simply repeated rounds of microevolution [4]. Punctuated evolution involves multilevel feedback, bridging endogenous and exogenous causality across evolutionary scales. For the Anthropocene [5], we consider how developing a better understanding of punctuated evolution can lead to both the conservation of biodiversity and the forecasting of punctuations that could dramatically affect cultural evolution.

A macroevolutionary phenomenon

The simplest example of punctuated evolution—but certainly not the only one—is an external event such as a volcanic eruption or meteoritic impact. At the end of the Permian period, about 250 million years ago, for example, large-scale volcanism in the 6 million km^2 igneous Siberian Traps region of Russia liberated massive concentrations of CO_2, SO_2, and other gases [6–8].

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This led to global warming, a reduction in ocean oxygen, and terrestrial acidification, [9], which, in turn, triggered 2 million years of extinctions—the 'Great Dying'—and eliminated about 95% of all species [10] (Figure 1). Similarly, the Chicxulub meteoritic impact north of the Yucatán Peninsula 66 million years ago released 25 trillion metric tons of debris, created waves hundreds of meters high across the Gulf of Mexico [11], and acidified the seas and oceans. This cascaded into ecological collapse and the extinction of 75% of plants and animals, including all nonavian dinosaurs. It also opened habitats for the rapid emergence of mammals [12].

Punctuated evolution can also be driven by gradual changes in climate. The **turnover pulse hypothesis** [13] predicts that climatic shifts affect macroevolutionary change by way of modifications in the ranges and abundance of populations across multiple lineages [14]. The late Silurian Šilale Event of 422 million years ago was caused primarily by **Milankovitch cycles** that yielded cold conditions and led to the dramatic decline in nektonic (free-swimming) organisms, global reorganization of paleo-communities, and the expansion of new clades leading into the Devonian period around 419 million years ago [15]. The collapse of the abundance of pelagic vertebrates (conodont), which was by two to three orders of magnitude, lasted for hundreds of thousands of years [15]. Millions of years later, during the Early to Middle Pleistocene climatic

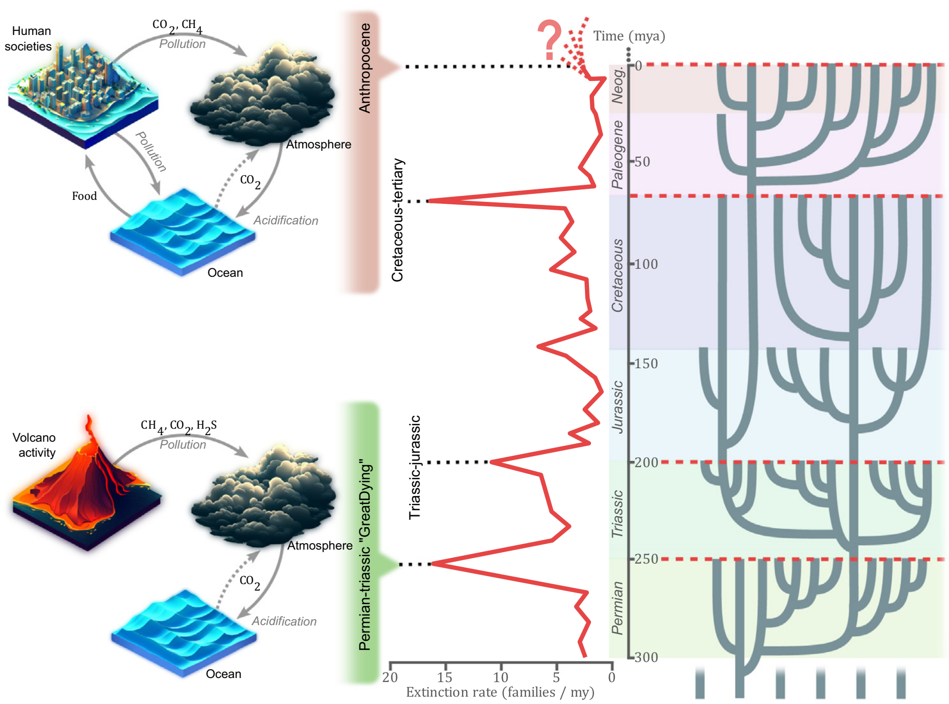

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Figure 1. Large and rapid CO_2 emissions overwhelm the oceans, causing mass extinctions of marine life. In both the Permian and the Anthropocene, rapid carbon expulsion has been documented. This is within the timescale of fast-feedback processes, which include interactions among atmospheric dust, the ocean surface's dynamics, water vapor, cloud formation, and the biosphere. These processes happen too quickly for the ocean to be able to absorb and control changes in carbon. As a result, the greenhouse effect causes carbon to build up in the atmosphere and results in rapid global warming. The surface waters grow more saturated and acidic as atmospheric CO_2 concentrations rise, posing a serious threat to marine ecosystems and their delicate balance of life. In accordance with the turnover pulse hypothesis [13], such large carbon emissions can result in a rapid diversification of life following a substantial loss of biodiversity. Abbreviations: my, million years; mya, million years ago.

transition (740 000 years ago) and its 100 000-year glacial–interglacial Milankovitch cycles, the lineage leading to *Homo sapiens* experienced a hundredfold drop in population size that lasted for over 100 000 years [16].

Cascading effects

These paleontological examples reveal the vulnerability of the Earth's complex and interconnected ecosystems to causal interactions [17]. Ecosystems are dynamic and prone to **nonlinear responses** [18]. Competition, collaboration, and **victim–exploiter dynamics** are density-dependent interactions with nonlinear population effects, such as abrupt changes in the ecosystem's composition [19]. The cascade of effects can be delayed, however, as shown by recent computational models applied to fossil evidence [20,21]. During the Permian–Triassic mass extinction, for example, the decline in taxon richness (the number of taxa) occurred over 60 000 years before the subsequent collapse of the marine ecosystem's stability. Although delayed in effect, the biodiversity crash set the stage for a later catastrophic collapse of the ecosystem [20].

At a broader scale of aggregation, the fossil record shows right-skewed, **fat-tailed distributions** of the sizes of extinctions since the Cambrian period, some 500 million years ago [22]. Such distributions in the magnitude of events are expected under the extreme value theory, where large events represent much of the geomorphological and evolutionary change. As a means of explaining fat-tailed distributions, complexity theory maintains that complex adaptive behaviors can be self-organized properties of interactive systems. This approach focuses on the connectivity and heterogeneity among discrete, interacting agents, each with its own individual threshold for change [23].

Many cascade models, which yield abrupt, system-wide avalanches of change among the interacting elements, apply a binary threshold to each individual agent [24]. This exposes such models to criticism, especially if each agent represents a 'species' that immediately becomes extinct when a threshold fraction of its 'neighboring' species in the ecosystem becomes extinct. From the perspective of the individual organism, this extinction would be a catastrophic, external event, not the internal change claimed by such models.

Nevertheless, decades ago, these simple models demonstrated how an interconnected system can become poised for a major cascade [24]. **Network topology** determines the susceptibility of biota to external shocks, which cause random primary extinctions as opposed to secondary extinctions that result from perturbation of the network. In this view, external versus internal causation depends on the scale. Across scales from organisms to plate tectonics, the **Geo-Red Queen** (GRQ) mechanism refers to the global synchronization of biota and the onset of the diversity-dependent evolution of marine animal genera at a global scale [25]. Under the GRQ mechanism, plate tectonics drive the climate-mediated dispersal of taxa and synchronization of the biosphere at scales greater than 40 million years. In mixing biota globally, geodispersal is a process of self-stabilizing macroevolution. A similar mechanism, on the scale of local adaptation limited by cross-populational dispersal, was proposed to explain the morphological stasis of single-species lineages [26]. Hence, in terms of the richness of taxa or in morphology, both stasis and punctuated evolution are driven by spatiotemporal connections across a wide range of temporal and spatial scales.

Multiscale feedback

Ecological mechanisms for punctuated evolution include seasonality, migration-driven radiation, and host–pathogen interactions. Some are microevolutionary and others macroevolutionary [4], although there is debate over the roles played by each [27,28]. The two modes and accompanying tempos are ontologically and hierarchically separate phenomena [29].

Glossary

Coevolutionary feedback: the reciprocal interaction between a population and its environment, which could be a population from another species.

Ecosystem engineers: species that modulate flows of energy and matter through their environments, creating new habitats or modifying existing ones to suit their needs.

Epigenetics: the study of how behaviors and the environment can cause changes that affect the way genes work. Unlike genetic changes, epigenetic changes are reversible and do not change a DNA sequence.

Fat-tailed distribution: a broad term for highly right-skewed distributions, where the smallest events are typically the most frequent and the largest events, which are the rarest, still occur more often than under a Gaussian (normal) distribution.

Fitness landscape: a metaphor used to describe the possible mutational trajectories that lineages take as they evolve from genotypes that lie in regions of low fitness to regions of higher fitness.

Geo-Red Queen hypothesis: this predicts the synchronization of biota by means of geodispersal of the constituent taxa as a result, say, of plate tectonics and climate change, which results in a density-dependent diversity dynamic that stabilizes evolution.

Milankovitch cycles: periodic changes in the orbital characteristics of a planet that control how much sunlight is received in different seasons and latitudes, thus affecting its climate and habitability over time scales ranging from tens of thousands to several millions of years.

Network topology: the physical and logical arrangement of nodes and connections in a network.

Nonlinear response: changes in an output that do not change in direct proportion to changes in the inputs; a linear relationship creates a straight line when plotted on a graph, whereas a nonlinear relationship creates a curve.

Punctuated equilibria: a macroevolutionary pattern in which species exhibit little morphological change between periods of rapid speciation due to geographic isolation.

Punctuated evolution: a dynamical pattern in a complex system that alternates between stability and rapid bursts of change as a result of multiscale feedback.

Punctuated evolution crosses multiple orders of magnitude in a nested, hierarchical fashion. Extinctions create evolutionary space for new expansions through drift, isolation, local adaptation, and the persistence of locally adapted phenotypes [30]. The expansion of a population after prolonged environmental stress, with little competition on the expansion front, should increase the role of spatial segregation, which increases the ability to adopt quickly to new environments [31], and the fixation of new and rare phenotypes [32]. This can also accelerate the tempo of evolution, the crossing of fitness barriers [33], and the expansion of phenotypically diverging lineages [30].

As a scale-dependent spectrum, an evolving hierarchical system encompasses more than the binary distinction between microevolution and macroevolution or between internal and external causality [4]. Although each hierarchical level differs from the others in patterns of its style, frequency, and causal modes of change, these levels can interact in all modes. Links between scales within the hierarchy include phenotypic plasticity and **epigenetics**, in which an organism's genetic instructions are translated during development to adapt to recent environmental information, potentially as part of a burst of evolutionary change within the larger population.

Species' interactions, reciprocal adaptations, and **coevolutionary feedback** loops can create both stability and bursts of adaptation across different evolutionary scales [24]. One example is the punctuated evolution of carcinomas, which involves massive reorganization events of genetic material and the generation of new clonal lineages [34]. Other examples include segmental duplications in human evolution [35], horizontal gene transfer in eukaryotes [36], and transposable element-driven innovation during the domestication of plants [37]. In host–parasite interactions, the hosts evolve defense mechanisms, whereas parasites develop counteradaptations to evade the host's defenses, leading to rapid adaptations in both populations in an evolutionary 'arms race' [38]. These interactions generate hierarchical selection pressures that facilitate the evolution of novel traits and adaptations. Within ecological systems, coevolutionary feedback loops are potent agents of accelerated evolution: organisms can influence their local environments through ecological or cultural changes that lead to periods of stability punctuated by bursts of adaptation [39]. Through these operations, **ecosystem engineers** actively maintain stable ecological structures, resulting in internal adaptations.

Fitness landscapes

Punctuated evolution resembles **slow–fast dynamics**, where certain components within a system change at different rates and the system's dynamics are driven by the dependence on frequency [40], heterogeneous networks [33], and the spatial structure [41]. Eldredge and Gould [1] proposed that ephemeral local adaptations contribute to long-term trends only when 'fixed' by speciation as a threshold-like event. Within lineages of closely related organisms, stability often prevails, as they adopt similar adaptive strategies. Distinct lineages, however, occupy separate adaptive peaks on the **fitness landscape** (Figure 2). Organisms 'climb' these peaks via genetic and epigenetic adaptations but remain stable in their vicinity when there is nowhere locally left to climb [33]. Occasionally, through mutations or a sudden environmental change, organisms find themselves in a valley where genetic adaptation can increase in both tempo and mode, leading them to climb a different fitness peak. The fitness landscape model helps explain the distribution of the sizes of extinctions since the Cambrian period [22], with sudden jumps potentially arising from significant alterations or from gradual changes in the environment [42].

The network structure underlying fitness landscapes affects how evolution navigates from one peak to the next [43]. Evolutionary stability and phenotypic robustness emerge from highly redundant genotypic networks [44], allowing small mutations to lead to various outcomes, ranging from neutral (or no) changes to substantial phenotypic jumps [33]. This can involve even the genome's

Slow–fast dynamics: nonlinear dynamic systems in which two or more variables are governed by very different time scales.
Turnover pulse hypothesis: this predicts that major environmental changes can result in rapid extinction and high turnover of new species across multiple lineages, in contrast to with the Geo-Red Queen hypothesis.
Victim–exploiter dynamics: an interplay between two species where one species benefits at the cost of another. The exploiter profits from strengthening their interaction, whereas the victim profits from weakening it.

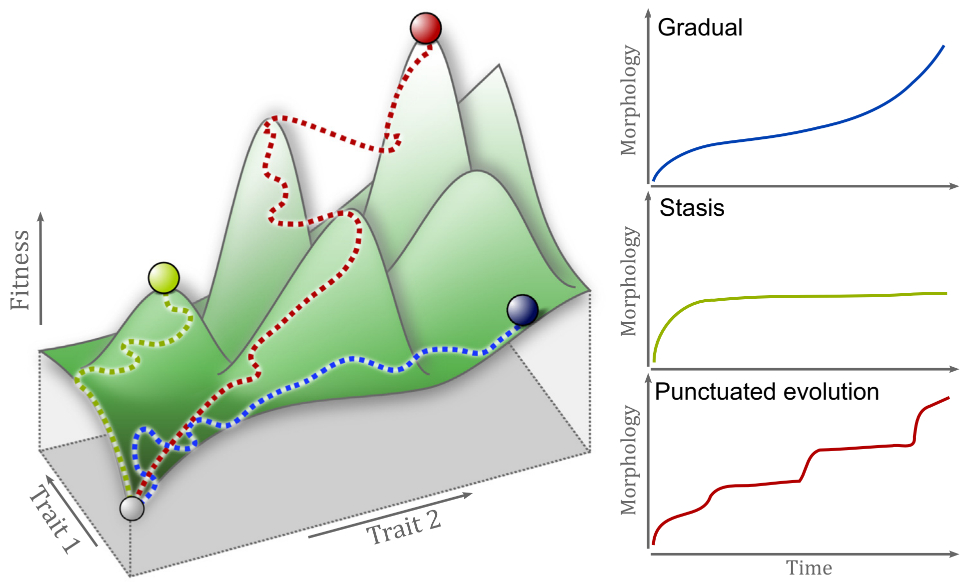

Figure 2. Three agents take adaptive walks on a fitness landscape, starting at the same point. Sewell Wright introduced the metaphor of a fitness landscape to describe the possible mutational trajectories (gradual, stasis, and punctuated) that lineages take (evolve) from genotypes that lie in regions of low fitness to regions of higher fitness. The landscape also contains valleys, which correspond to designs that yield negative fitness. There might be any number of pathways that the agents can take as they move about the landscape, a process that Kauffman *et al.* [89] referred to as an 'adaptive walk.' The model shown here is highly simplified in that it assumes a static landscape, which is rarely the case. Rather, the actions of other agents are constantly affecting the landscape, creating what Kauffman referred to as a 'dynamic fitness landscape' [90].

size and organization [45]. The balance between external influences and stochastic events underlies how and why evolutionary novelties occur [46].

Punctuated evolution and humanity

Decades before punctuated evolution was proposed in paleontology, it was known that human knowledge, from prehistoric technologies to modern science, has witnessed periods of relative stasis punctuated by bursts of exponential increases [3,47]. Frequently discussed prehistoric examples include stone tools, art, clothing, fire, farming, and weapons, whereas more intriguing possibilities include kinship systems [48] and languages [49]. For humans, as opposed to other culture-bearing animals, culture is cumulative [50], meaning that culturally transmitted modifications, if beneficial, are progressively accumulated over time. Possible drivers of cumulative cultural evolution include an increase in the effective population size [51], neurochemical and cognitive evolution [52], climate change [53], migration into new environments [54], and key technological innovations [55–57]. Punctuated evolution can be detected through extended phylogenetic analyses of cultural artifacts (Box 1).

Cognitive theories for punctuated technological and/or social change in *H. sapiens*, such as art, fire, stone tools, and group cooperation, are pertinent not only to the situation 50 000 years ago, when anatomically modern humans first arrived in Europe, but also well before then. Between 300 000 and 50 000 years ago, for example, the human brain changed in shape, connectivity, and hormonal balance [58]. A key change occurred in the neocortex of modern humans compared with Neanderthals (*Homo neanderthalensis)*, which interacted and interbred with modern humans in western Europe [59]. This difference could have originated in a single amino acid change in the production of a certain protein (transketolase-like 1) in the basal radial glia, where

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Box 1. Revealing the punctuated evolution of culture and technology through phylogenetic analysis

Darwin famously argued that human language evolved through variation, selection, and inheritance, similar to organismal evolution. In *The Descent of Man* [94], he noted that 'the formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel.' This concept has influenced contemporary ideas of the evolution of language, highlighting similarities and differences across languages and their adaptations over time. The phylogenetic approach to cultural evolution is not limited to languages or human culture for which there is an accessible genotype. Homology can be reconstructed from similarity in a morphological trait, a perspective with a long tradition in the biological domain before the advent of genetic information. Although the mapping between genetic and cultural evolution is not perfect, we can identify similar principles governing both: (i) the presence of variation, regardless of its source; (ii) the ability of variants to be transmitted; and (iii) the sorting of variants in subsequent generations, primarily through selection, drift, and psychological processes such as mate identification.

Tëmkin and Eldredge used these approaches to reconstruct the phylogeny of cornets [55], showing vertical transmission as a dominant mechanism, although horizontal influence was much more prevalent than in many biological systems (Figure IA). The phylogenetic study of cornets demonstrates a surge in innovative designs around 1900, a process resembling biological speciation, which might be used as a proxy for the concept of species in cultural domains. Cultural evolution exhibits lateral transfer, which means that multiple innovations can result from the merging of pre-existing components, and this should be considered when conducting phylogenetic analyses of artifacts. Valverde and Solé [56] used network analysis to define a similarity metric that can be used to reconstruct the phylogeny of programming languages, which represent the evolution of the syntactic and semantic rules used by human developers to write software or computer instructions. They found that branches of programming languages have changed at different rates over time, revealing a macroevolutionary pattern of punctuated evolution in information technology (Figure IB). The unbalanced tree structure reflects the emergence of major innovations that are difficult to detect using conventional methods, and it provides strong evidence for punctuated evolution in this technological domain.

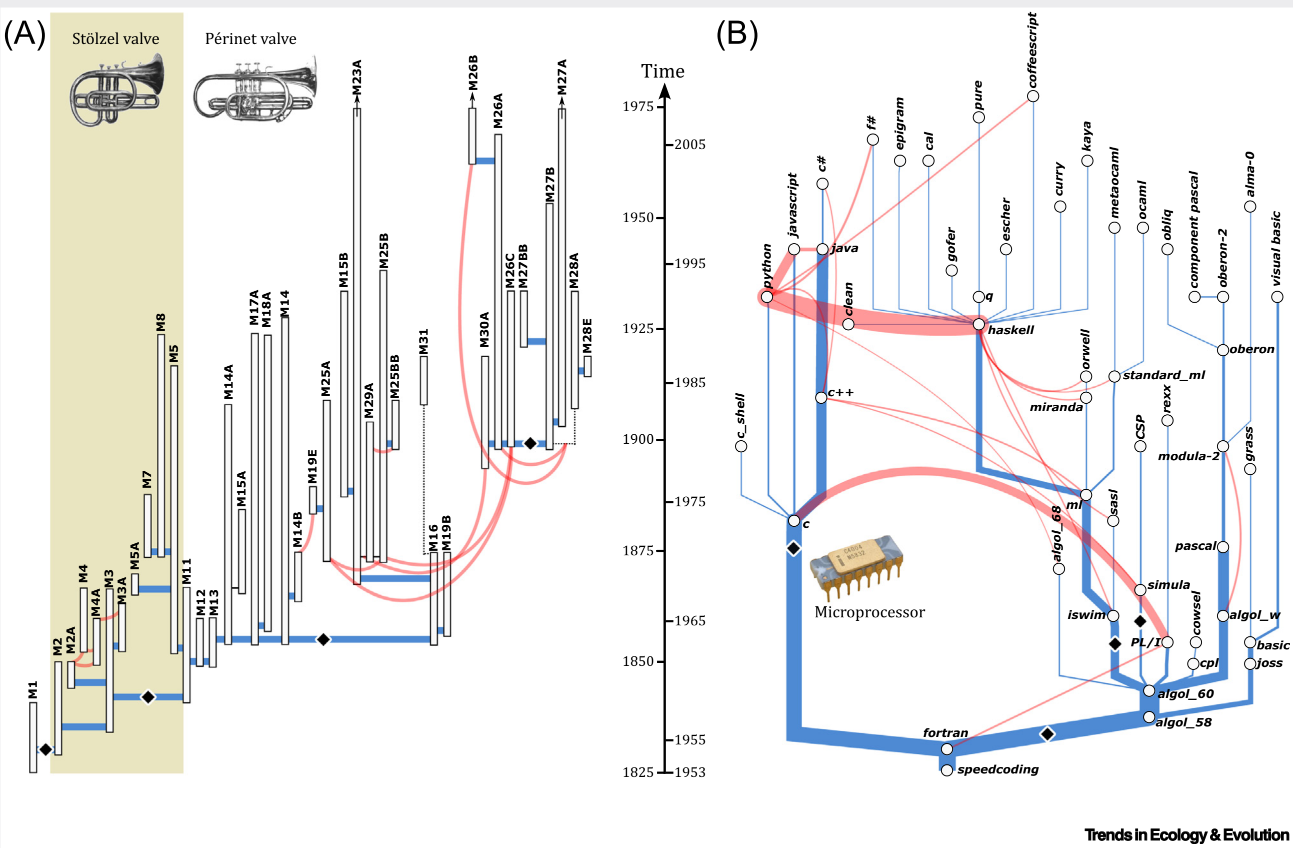

Figure I. Phylogenies of cornets and programming languages. (A) The evolution of cornet designs from 1825 onwards is depicted in a figure adapted from Tëmkin and Eldredge [55]. Vertical lines represent different 'cultural species', covering the design lifespan, while horizontal lines represent vertical transfer between them. The phylogeny is reconstructed using morphological traits, revealing two major epochs, shown as the shaded area on the left and the unshaded area on the right, which represent the Stölzel and Périnet valve systems, respectively, as well as key innovations such as the number of valves, a second valve slide shift, the exit position of the bell, and modification of the shape. (B) A reconstructed tree of programming languages based on Fortran (one of the first general-purpose languages developed by IBM in the 1950s for scientific computing and engineering applications) depicts the macroevolution of software. The vertical axis represents the release time. The tree shows bursts of radiation-like events, and some languages (Algol 60 or C) have been found to produce more offspring than others as a result of the introduction of key technological innovations such as the microprocessor. Adapted from Valverde and Solé [56]. Abbreviation: M, distinct morphologies.

the neocortex is generated [60]. As the neocortex facilitates social learning, modern human cognition and its cultural achievements might have followed this single amino acid change.

In the frequently debated demographic model, the number of social learners in a population determines the probability that any one learner will exceed the level of the most skilled or knowledgeable expert in the population. For any given set of learning parameters [61], cumulative cultural evolution occurs above a threshold effective population size, which is a punctuated change in cultural evolution that does not require cognitive evolution. In archaeologist Michael Rosenberg's view, 'new cultural systems always come about through a punctuational episode' [62]. The archaeological record contains a myriad of examples of punctuated change [2], including the 'Upper Paleolithic Revolution' [63], which was a period of seemingly sudden explosion of additions to the European material record some 45 000–40 000 years ago (Figure 3). Another example is the Neolithic 'revolution' [49], which began about 12 000 years ago and led to rapid selection for numerous genes, including lactase persistence [64] and resistance to zoonotic diseases [65] in certain Neolithic populations. In general, the Neolithic saw humans, animals, and plants coevolve as shapers not only of each other but of the natural environment [66], and they did it rapidly.

Recently, more ephemeral but no less inherited aspects of prehistoric culture have revealed traces of their punctuated evolution [3]. For example, the coevolution of kinship and language has been demonstrated through multiple lines of evidence (e.g., linguistic, archaeological, isotopic, and ancient DNA) for patrilineal kinship among Bantu-speaking pastoralists who migrated into sub-Saharan Africa about 2000 years ago [67], and early European Neolithic farmers several millennia before that. About 10 000 years ago, in the Epipaleolithic of the Levant, there was no clear signature of a kinship system other than a flexible or possibly matricentric system up until perhaps 8000 years ago [48]. At that point, Europe was colonized by patrilineal and patrilocal farming populations with a similar language, crop cultivation and livestock practices, timber houses, and burial practices. Subsequent migrations from the Black Sea region around 5000 years ago furthered this punctuated change in kinship systems [68].

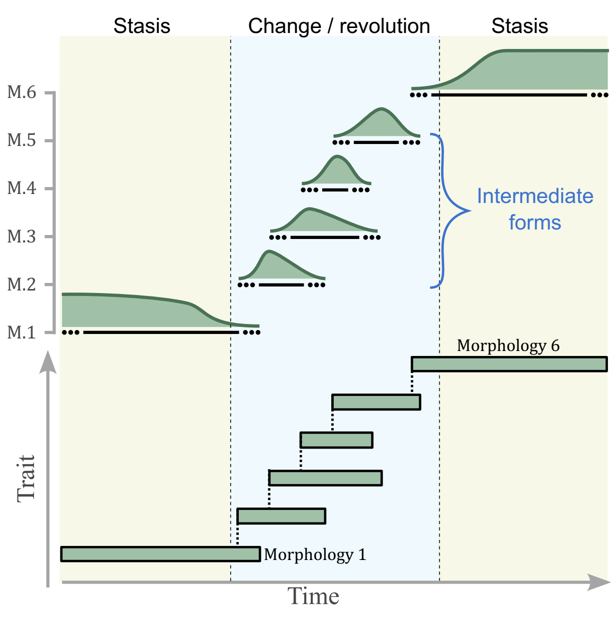

Figure 3. Archaeological phases and the Upper Paleolithic transition. Around 45 000 years ago, an important turning point in Eurasia's archaeological record signaled the end of the Middle Paleolithic and the beginning of the Upper Paleolithic. This period displayed a great diversity of artifacts, spanning many intermediate forms, and an unprecedented rise in personal adornments (e.g., the making of marine shell beads) in less than 10 000 years (shown by the blue region). Researchers used Bayesian modeling to estimate the timeframe of the cultural transitions between distinct morphologies. Based on [91]. Abbreviation: m, morphology.

From the perspective of scaling laws, punctuated changes in human social organization and technology can be viewed as faster components of larger, slower geoecological systems [66]. For example, increases in atmospheric carbon dioxide and methane around 8000 years ago were anthropogenic [5], brought on by clearing forests, livestock-based pastoralism, and crop irrigation [66]. On multiple continents, agriculture was the foundation for inherited wealth and property [48], the subsequent rise of complex sociopolitical hierarchies [69], and ultimately the appearance of cities and states [70,71]. Human cultural evolution has witnessed punctuated evolution in the technologies of communication and computation [72], sociopolitical organization [69], the exchange of specialized products [73], and food production [49], to name just a few.

These changes from early farming villages to cities to artificial intelligence took place over several millennia, but in geological time, this is a mere blink of an eye. Occurring even more quickly is the turnover in biota that has occurred during the Anthropocene, a pattern that is distinctly different from those seen in the fossil record [21]. Multiscale feedback among physical, natural, and social systems characterizes the Anthropocene, resulting in a pattern of punctuated evolution in behavior (Figure 4). In the physical world, the increase in greenhouse gases results in abrupt cascades in climate change through positive feedback such as the collapse of ice sheets. In the cultural realm, the slow, linear increase in human levels of concern is likely to cause a nonlinear change in behavior, such as electricity generation and electric transport, as a result of the inherent feedback in economies of scale.

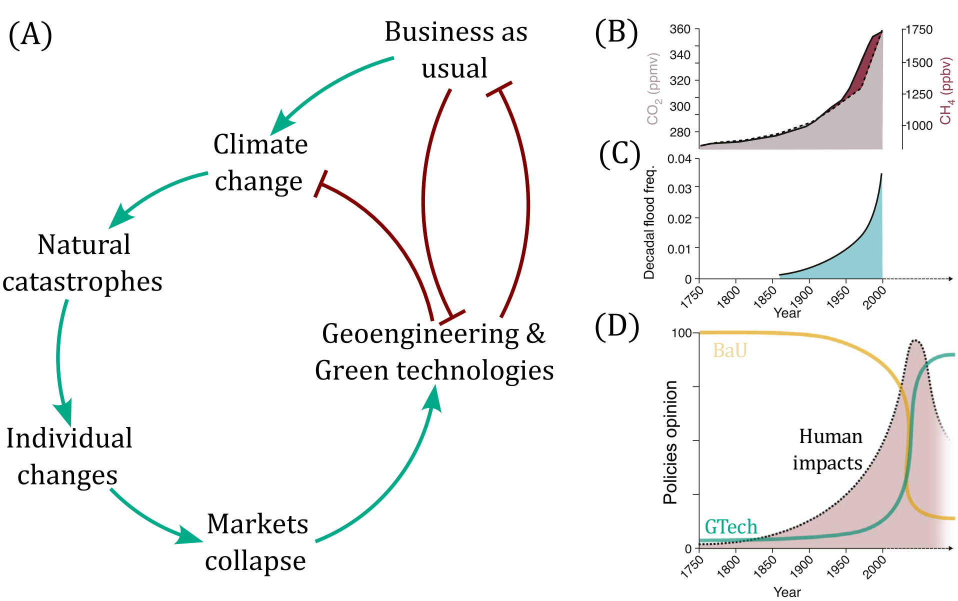

Figure 4. Rapid shifts in society and economy in the face of human-caused climate change. (A) Schematic representation of the impacts of business as usual on climate change that pose hazards to human societies and could ultimately alter the entire economic system. (B) Exponential CO_2 and CH_4 emissions up to the year 2000. (C) The likelihood of flooding is also rising exponentially. (D) Human impacts on ecosystems caused by greenhouse gas emissions, habitat devastation, pollution, and the like will continue to increase until humans alter their behavior. As a result of the multiscale feedback that maintains policies in a state of stasis (business as usual), the expected response to climatic threats is a rapid shift (e.g., promoting green technologies), while external drivers press for a change to survive. Panels (B) and (C) were adapted from [92] and Panel (D) is adapted from [93]. Abbreviations: BaU, business as usual; GTech, green technologies; ppbv, parts per billion volume; ppmv, parts per million volume.

Concluding remarks

Inspired by the punctuated equilibria model of half a century ago [1], punctuated evolution can be observed across biological, paleontological, and cultural systems at scales of magnitude ranging from the GRQ to neurons to organisms, species, and human cultures and organizations. Can punctuated evolution offer anything pertinent to modern social challenges? We think there is much to learn, be it from population pressure and social collapse [74], the devastating effects of European diseases on indigenous New World populations [75], endemic violence in prestate societies [76], agropastoral innovations [67], biological and cultural development [77], hereditary inequality [78], and private ownership of goods and property [79]. Anthropogenically driven extinctions are dramatically different in terms of their tempo from previous catastrophic extinctions [21], but the results are the same. Instead of meteoritic hits or volcanic explosions, events such as land clearance, urbanization, and the construction of roads and canals have quickly led to the loss of suitable animal habitats [80].

These events have fostered a dramatic increase in global CO_2 emissions, leading to a significant rise in sea level, a decrease in crops' productivity, acidification of the oceans [81], and the loss of biodiversity [82]. For comparison, human-related emissions of CO_2 were 160 times higher in 2011 than they were in 1850 [83], which is a punctuated change at both the geological and biological scales. This kind of disruption makes it difficult for many species to respond [84], which has profound effects on speciation [85]. Humans, however, are different in that they can, under some circumstances, migrate in response to climate change [86] and potentially change the Earth's systems through geoengineering. Ironically, the proposed geoengineering strategy for releasing aerosols into the stratosphere is similar to how volcanic eruptions caused prior extinctions [82].

Geoengineering, however, risks setting off a potential domino effect of uncertain effects on regional climatic and hydrological patterns [82]. It is unclear how humans will collectively and heterogeneously adopt such innovations. In the punctuated evolution pattern, we can expect feedback and accelerated responses to long-term shifts. For example, temperature increases of 0.5°C per decade will lead to more extreme weather events, coastal flooding, hurricane damage, and rising insurance rates. Coastal residents could perceive a pressing need to sell their homes, influencing their neighbors and causing house prices to drop abruptly.

These diverse, multiscale examples of punctuated evolution share the multiplicative effects of either rarity or abundance on the networks of the interactors (slow–fast interaction). The scale of perturbation, either external or internal, in space and time (amplitude and duration) determines if a single evolutionary lineage or whole assemblages (biotas or regional cultures) will experience change. The punctuation is related to changes in the dominant modes of interaction transferred in an interaction network. Severe conditions can lead to population loss, causing disconnection, modularization, and rapid spatial differentiation. Conversely, if the system transitions to an extremely abundant state, the density of the new interactors could also have destabilizing effects on the ecosystem by diluting the interactions with other components [87].

The study of multiscalar feedback, influenced by abundance and connectivity, offers a promising way to identify the causes of stasis and punctuation (see Outstanding questions). We suggest that such work should become a punctuated event itself because the clock is ticking. A recent report [88] suggested that if the growing global energy demand continues to be met with fossil fuels, CO_2 emissions by 2100 will reach 75 billion tons per year and atmospheric CO_2 will be above 800 parts per million, higher than at any point in the last 50 million years. This trend threatens our own extinction; the difference is that, unlike any species before us, we can see it coming and respond—if we choose to do so.

Outstanding questions

How is punctuated evolution reflected in the genomes of species that have undergone rapid bursts of change? Are there specific genomic signatures associated with periods of rapid adaptation and diversification?

What roles do developmental biases play in shaping the patterns of punctuated evolution?

How does the ecological context influence the occurrence and timing of punctuated evolution? Are periods of rapid change linked to particular ecological opportunities or disruptions?

How do the temporal and spatial scales at which punctuated evolution operates vary across different species and ecosystems? Do different taxa or environments exhibit distinct patterns of punctuated evolution? Can we predict when periods of punctuated change might occur in specific lineages or ecosystems? Are there any recurring features or triggers that precede these events?

What role has punctuated evolution played in human evolution with respect to things such as the development of specific cognitive, behavioral, or physiological traits?

How can our understanding of punctuated evolution aid in the development of strategies that are more effective for the conservation of biodiversity in the face of significant anthropogenic impacts?

Acknowledgments

We thank Andrea Stephens, Christopher Carleton, and the two anonymous reviewers for their many helpful comments on the initial manuscript. S.V. is supported by the grant PID2020-117822GB-I00, funded by the Ministerio de Ciencia, Innovación y Universidades (MICIU)/Agencia Estatal de Investigación (AEI)/10.13039/501100011033. B.V. and S.V. are supported through the 2020–2021 Biodiversa and Water JPI joint call under the BiodivRestore European Research Area Networks (ERA-NET) Cofund (grant application No. 101003777) project MPA4Sustainability, with the funding organizations: Innovation Fund Denmark (IFD), Agence Nationale de la Recherche (ANR), Fundação para a Ciência e a Tecnologia (FCT), the Swedish Environmental Protection Agency (SEPA), and grant PCI2022-132936 funded by MICIU/AEI/10.13039/501100011033 and by the European Union NextGenerationEU/PRTR. S.D.-N. is supported by the Beatriu de Pinós postdoctoral program from the Office of the General Secretary of Research and Universities and the Ministry of Research and Universities (2019 BP 00206), and the support of the Marie Sklodowska-Curie COFUND (BP3 contract No. 801370) of the H2020 program. We acknowledge the support of the network Proyecto Intramural Especial (PIE)-202120E047-Conexiones-Life.

Declaration of interests

The authors have no interests to declare.

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