ESSAY

Biodiversity, resilience and the stability of evolutionary systems[OK?]

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Various macro-evolutionary phenomena, such as long-term stability punctuated by bursts of evolution, are difficult to explain via the micro-evolutionary process of weak selection acting steadily on individual mutations. In contrast, bursts of change are expected if evolutionary systems are complex and balanced, with occasional disruption of balance. Such disruption represents the collapse of resilience, akin to the snapping of an elastic band. It can be driven by external factors, or by self-propagating feedback loops internal to a system. Thus, evolutionary resilience could help explain how evolution generates broader patterns of biodiversity. We outline evidence and tests for this hypothesis, which emphasizes the processes balancing evolution, as urged fifty years ago in ecological genetics and via modern results in a range of complex systems.

The processes of natural selection, mutation, recombination, gene flow, and genetic drift drive micro-evolution, and their short-term effects are highly measurable [1]. In contrast, ascertaining the extent to which these processes explain broad macro-evolutionary patterns of biodiversity across long timescales remains a significant challenge in biology [2-4]. In many population genetic models, evolution proceeds at a fairly constant pace due to weak natural selection acting on individual mutations, leading to gradual evolution and an interconnected series of evolutionary forms [5]. However, it is difficult for such a steady microevolutionary process to explain at least three fundamental macro-evolutionary phenomena, and thus some general biodiversity patterns (Figure 1).

First, phylogenetic analyses, modeling of comparative data and the fossil record have documented extended periods of little or no net change, that are only occasionally punctuated by bursts of evolution [3, 4-7], consistent with Simpson's model of adaptive zones [AU worth explaining?] [8]. Second, speciation can result in discrete species pairs separated by a paucity of intermediates, rather than an interconnected series [1,5]. This implies changes so rapid that they are difficult to catch in the act, and that leave limited trace of intermediates (similar arguments apply to other discrete units of biological diversity, such as ecotypes or morphs). Third, the rate of evolution is often inversely related to the time-scale it is measured at (i.e., rapid rates over short time-periods, and slow rates over long ones)[9], inconsistent with a constant evolutionary direction. Here we consider a simple explanation for these and other punctuated patterns: a collapse of 'evolutionary resilience' that causes a previously stable and balanced system to suddenly evolve rapidly, as the tension between opposing evolutionary [OK?] forces shifts or is released. We develop this hypothesis below, giving credit to its historical underpinnings, and describe tests of its predictions.

Defining resilience, balance, and feedback

Resilience is the capacity of a system to resist or recover from disturbance [10]. It is a key concept in life, science and engineering. Indeed, resilience principles apply whether one is considering a food web, a social media network, a banking system, an asthma attack, a disease outbreak, climate change or an evolutionary shift [10]. In ecology, the concept was introduced by Crawford Stanley Holling in 1973 [11] and has since been applied extensively to study the stability of ecosystems and the services they offer. The core idea is that a balance of opposing or fluctuating processes — and feedback loops among them — generates resilience. Here, we thus use the term 'balance' to refer generally to cases where different processes oppose one another and give concrete examples below. By feedback we specifically mean cases where a change in a dynamic variable '*x'* affects '*y*', which feeds back to affect '*x'*, and so on. When feedbacks are negative, they can resist directional change and stabilize systems. An example is a stable predator–prey cycle, where increased predator number decreases prey abundance, which in turn reduces predator number, which increases prey abundance, which allows predators to once again increase in number, and so on. In contrast, positive feedback can drive self-propagating directional change.

Elasticity and the collapse of resilience

Although the concept of resilience in evolutionary biology is less emphasized than in ecology[OK?], evolutionary systems can also resist or recover from perturbations, thus exhibiting resilience. A useful metaphor here is that of an elastic band. Even if a force pulls the band to elongate it, the band usually retracts back to (near) its original length when the opposing force is released or resolved (Figure 1). For example, divergent selection might generate an allele frequency difference between populations — the band elongates — which is then reset by migration and gene flow — the band returns to its original length [1]. Thus, marked net evolution only occurs if the band 'snaps' such that resilience collapses altogether. In our example of selection–migration balance, this could occur via a perturbation external to the system, such as a geographic event that blocks gene flow or a rare extreme climate event than imposes strong natural selection [12]. In addition, the band may snap if feedback loops that are internal to a system become self-propagating in a set direction and run out of control [10]. For example, maladaptation might reduce population size, leading to greater maladaptation, which further reduces population size, potentially propagating to drive local extinction [1].

Ecological genetics and the balance school

Although ideas about balance in evolution have a long history, their emphasis emerged approximately fifty years ago in ecological genetics [13]. This field studies genetics in natural populations and focuses on traits involved in interactions between and within species, and between an organism and its environment. The British school of ecological geneticists, catalyzed by Edmund Brisco Ford and including Philip Sheppard, Cyril Clarke, Arthur Cain and Bernard Kettlewell, made seminal contributions. Collectively, these researchers worked extensively on variation within and among populations of moths, butterflies and snails. Their work solidified the concept of polymorphism and balancing selection, with variation maintained by heterozygote advantage and microhabitat variation. In both cases, a balance of selective advantages and disadvantages maintains variation [13]. The field also emphasized that a balance between selection and recombination can shape evolution and might even cause linked blocks of genes to evolve into a single non-recombining ‘supergene’ [14]. Thus, ideas about balance in evolution are not new. Moreover, a connection between balance and macro-evolutionary stasis was made by Douglas Futuytma in a 2010 article emphasizing the ephemeral nature of evolutionary divergence [15]. Nonetheless, a renaissance in the study of these topics could be warranted based on recent findings.

Generality across taxa

Evidence that evolutionary systems are balanced is accumulating in organisms ranging from microbes to plants and animals. For example, differentiation between morphs of butterflies, sunflowers or stick insects is balanced between divergent selection and recombination between genes controlling adaptive traits [16-18]. This balance is occasionally disrupted by large-scale mutations, such as chromosomal inversions, that suppress recombination to form supergenes and allow greater differentiation. Across the landscape, population differentiation in many organisms evolves under a balance between selection and migration [1]. Here, major effect mutations in single genes, as observed for body armor in stickleback fish [19-20], might tip this balance more strongly in the favor of selection to promote greater differentiation. A number of other balancing processes mediate variation across time and space, including negative frequency-dependent selection, heterozygote advantage, and life history trade-offs, as exemplified in stickleback, dragonflies[OK?], bacteria, snails, guppies, cichlids, stick insects and wild sheep [1, 4, 21-26]. Despite the taxonomic diversity noted above, we focous on one example of evolutionary balance, specifically the evolution of cryptic color and color-pattern morphs in *Timema* stick-insects (Figure 2).

In *Timema* stick insects, which feed on plants, differentiation between morphs is balanced between divergent selection and recombination affecting genes that control body [OK?] color [18, 27-28]. This balance is occasionally disrupted by large-scale mutations, such as mega-base size deletions and chromosomal inversions [18, 27], that suppress recombination between color genes. Likewise, population differentiation in morph frequencies across the landscape evolves under a balance between selection and migration [29, 30], and a jump in differentiation was documented when a geographic event blocked migration [31]. A number of other balancing processes mediate variation across time and space, including negative frequency-dependent selection [25], heterozygote advantage [25, 27] and trade-offs in crypsis versus thermoregulation [25]. Immigration itself has balanced effects, causing both a demographic influx of individuals but also introducing locally maladapted color-pattern alleles that reduce population size by attracting bird predators [32, 33]. The predatory effects then extend beyond *Timema*, because birds eat or scare away other arthropods to have community-level consequences. Additionally, speciation and genome-wide differentiation involve a balance between reproductive isolation and homogenizing gene flow [34]. Finally, although the mechanism of balance is less clear, niche evolution via host-plant shifts usually occurs between related plant families, only occasionally punctuated by major shifts between conifer and flowering plant divisions [35]. Thus, balance is evident at many levels in this system, and when broken is followed by marked evolution.

Balanced processes such as those described above can, in principle, involve feedback loops, although evidence for these[OK?] scarce [1, 36]. For example, adaptive divergence might reduce effective gene flow, which increases adaptive divergence, which further reduces gene flow, and so on. Likewise, adaptation might increase population size, which increases the efficacy of selection, which increases adaptation, and so on. Conversely, as noted previously, maladaptation might reduce population size, leading to greater maladaptation and so on. Such interactions and feedback are the hallmarks of complex systems [10]. Thus, evolutionary resilience may be informed by general principles emerging from the study of a range of complex systems.

Dynamics of complex systems

Complex systems are widespread across the physical, life and social sciences [10, 37]. They can be conceptualized and studied as networks of nodes with different degrees of connectivity between nodes. Examples in biology are food webs among interacting species, meta-populations comprising sub-populations connected by migration or gene expression networks. Decades of work have revealed the striking finding that general principles govern the dynamics of a wide range of complex systems.

For example, the resilience of a system can be mediated by its connectivity (or, conversely, modularity) [10, 37]. In a well-connected system, local disturbance of individual nodes is countered by input from neighbouring nodes, buffering the system against local change. A biological example is where individual sub-populations (i.e., nodes) in a well-connected meta-population are buffered against extinction by immigration. Thus, pronounced change in well-connected systems may not occur until the entire system hits a threshold or ‘tipping point’ — where the elastic band snaps (or shoots off in a new direction) — generating a shift to an alternative, system-wide state. In contrast, poorly connected systems allow gradual node-by-node change, because change of individual nodes is not buffered by input from other nodes. Highly connected systems are thus robust to local perturbation, but prone to system-wide change. Such a trade-off between local and system-wide resilience has been shown to apply theoretically to adaptation and speciation, although data are again scarce [38, 39]. These principles facilitate the development of a framework for hypothesis-testing concerning evolutionary resilience.

Predictions and a research program

Highly balanced and resilient evolutionary systems are predicted to exhibit the following characteristics (Figure 3): first, if one perturbs a trait value (e.g., increases body size) or allele frequency, the system should either rapidly return to its original state or shift to a markedly altered state, depending on whether or not the perturbation stretches the metaphorical elastic band to the point that it snaps; second, similar predictions apply if one perturbs evolutionary process directly. For example, selection can be manipulated by increasing population density or by excluding predators, migration can be altered with geographic manipulations, and recombination or mutation could be manipulated using gene-editing techniques; third, feedback loops can be tested for by manipulating the variables involved and testing for reciprocal effects between them; fourth, alterations to the connectivity of a system should affect whether responses are gradual or sudden and system wide.

The measurements and approaches noted above focus on micro-evolutionary processes. These would ideally be connected to macro-evolutionary patterns, such as the bounded fluctuations at moderate time-scales and occasional bursts of evolution at longer time-scales documented when modeling body size evolution in mammals, squamates, and birds [6, 7]. Ideally, this would be done via parameterizing models with information on micro-evolutionary process to generate macro-evolutionary predictions. Such an approach has shown that evolution at long time-scales is much too slow to be explained by random drift alone [40, 41], and has tested the role of mutation in shaping macroevolutionary patterns [42, 43]. Further such work linking process and pattern is warranted and might help test the role of resilience in evolution across time-scales.

Conclusion

Resilient evolutionary systems are predicted to be characterized by bursts of evolution when the balance of standard microevolutionary processes is disrupted. This view of evolution has at least two broad scientific and societal implications. First, it provides a potential link between micro- and macro-evolution. Beyond its obvious scientific importance, this could help alleviate the common criticism of anti-evolutionists that Darwin's theory cannot account for evolutionary jumps and a paucity of transitional (i.e., intermediate) forms in extant taxa and the fossil record. Second, complex and balanced systems can be difficult to understand via the sum of their individual parts [10, 36-37]. This is because feedback and resilience in such systems generates non-linear and emergent properties. For example, many traits are affected by numerous genes, as exemplified by human diseases [44]. In such cases, polygenic selection and interactions between genes can cause evolutionary dynamics to be non-linear and to depart from those predicted by the additive effects of individual genes [45-48], with genome-wide consequences. Thus, network and system-based approaches, rather than pure reductionism, may be required to predict complex evolutionary phenomena, such as the emergence of pathogens and genome-wide evolution.

Only further work will reveal whether the ideas presented here are largely correct. Nonetheless, we predict that the inherently polygenic and multi-faceted nature of evolution makes balance and resilience important for understanding evolutionary dynamics. In turn, understanding such dynamics can help inform the question of how patterns of biodiversity emerge [15].

Acknowledgements

We thank T. Reimchen for years of discussion that influenced the development of the ideas presented here, and C. Sommer-Trembo for comments on previous versions of the manuscript. The work was funded by a grant from the European Research Council (EE-Dynamics 770826, https://erc.europa.eu/) to PN, from NSF (DEB-1638997) and the USDA-NIFA program (2015-67013-23289) to JLF, and from the NSF (DEB 1844941) to ZG. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

All authors conceived the project and contributed to writing. Competing interests. The authors declare no competing interests.

Figure 1. Variation in evolutionary dynamics and macro-evolutionary patterns. (A) Evolutionary patterns, including continuous evolution through time, episodic burst of evolution through time, time-independent evolutionary rate, and time-dependent evolutionary rate. For the latter two, 'Time step' refers to the time interval (i.e., window) for which rate is measured. Insets show the actual dynamics through time, and larger panel the evolutionary rate at different time steps. (B) A simple illustration of evolutionary resilience. Divergent selection (DS) causes allele frequencies to change, i.e., elongates the elastic band. Migration from a divergent population then resets allele frequencies to the balanced state, i.e., the elastic band retracts. (C) A balanced evolutionary system. Arrows denote causal effects. Plus signs (+) indicate a positive effect and minus signs (-) a negative one. Some processes can have either positive or negative effects. N_e is effective population size (increased population size reduces drift and increases the efficacy of selection), m_e is effective migration rate (generally reduces adaptation), u is mutation (effects depend on the fitness consequence of specific mutations) and s is selection (if it fluctuates in time or space it can reduce the frequency of an allele that would be advantageous in a different time or place).

Figure 2. An empirical case study in balance and resilience from *Timema* stick insects. (A) Multi-locus genotypes evolve under a balance between selection and recombination. Differentiation increases when large-scale mutations affect color genes and suppress recombination. (B) Populations evolve under a balance between selection and gene flow. Differentiation increases when migration is blocked by geographic events or via local extinction of a host (populations on different hosts are depicted by blue and orange circles. (C) Meta-populations experience dual and opposing effects of immigration, which causes a demographic influx of individuals but also introduces maladaptive color-pattern alleles that reduce population size by attracting predators. There is also evidence for an eco-evolutionary feedback where maladaptation reduces population size which further decreases adaptation and so on, potentially spiraling to cause local extinction of sub-populations. (D) Bi-modality in the speciation process. Early stages of divergence between co-occurring populations are characterized by low genome-wide differentiation (F_{ST}) and modest reproductive isolation (depicted here as mating between populations). Late stages are characterized by high genome-wide differentiation (F_{ST})

and strong or complete reproductive isolation (depicted here as mating isolation via chemical cues). Intermediate stages are not readily observed such that they may be passed through rarely and quickly, via a disruption of evolutionary balance (here illustrated by a geographic event that blocks migration). DS is divergent selection, r is recombination, u is mutation, m_e is effective migration rate, N_e is effective population size, NFDS is negative frequency-dependent selection, Het refers to heterozygote advantage, and RI is reproductive isolation.

Figure 3. Empirical tests concerning evolutionary resilience and balanced systems. (A) Perturbation of evolutionary process, here depicted as divergent selection (DS), creates a measurable response. (B) Tests for feedback loops. (C) Effects of connectivity. Circles are sub-populations in a meta-population and arrows indicate connectivity via migration. (D) Modeling of evolution to generate macro-evolutionary predictions concerning trait evolution, lineage-through-time plots, and phylogenetic patterns. Abbreviations: s is selection, r is recombination, u is mutation, m is migration rate, and N_e is effective population size. See main text for further details.

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