The Role of Disequilibrium in Evolutionary Discovery

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Abstract

During certain evolutionary scenarios, such as genetic sweeps and range expansions, the driving lineages either have increased competitiveness or experience an absence of competition, which results in a higher tolerance of deleterious mutations. We have named this phenomenon, during which individuals are more likely to explore their fitness landscape, "adaptive momentum". We present evidence for adaptive momentum and discuss some of its implications for evolutionary science. *This document summarizes work that we are preparing for publication.*

Conceptual foundation Adaptive momentum describes how a reduction in selection experienced by some part of a population during *all* selective sweeps and range expansions(Miller et al., 2020) can alter evolutionary dynamics. Research has already shown that reduced selection strength results in increased exploration and a greater likelihood to discover beneficial mutations(Jain et al., 2011; Peischl et al., 2013). Adaptive momentum describes periods that start when a stable population shifts into disequilibrium and end when the population reaches a new equilibrium. We call the period of disequilibrium, the "momentum window." While adaptive momentum increases the likelihood of genetic discoveries, it does not guarantee them. If the population reaches equilibrium before making a new discovery (as in Fig. 1 (a-c)), the momentum is lost, and diversity will decline. However, if the population does make a new discovery before it equilibrates (as in Fig. 1 (d-f)), a new subset of advantaged individuals emerges and extends the momentum window. When adaptive momentum results in a series of discoveries in quick succession, we call the series of discoveries a cascade.

Methods In a fitness landscape, any pair of peaks separated by a valley will have four measurable quantities: the stochastic tunneling time T_{st} (Alili et al., 2005; Yi, 2010; Artime et al., 2018), the neutral drift time T_{nd}, the fixation time T_f (Kimura and Ohta, 1969), and the observed tunneling time T_{obs}. Fig. 2 provides definitions for these quantities. To illustrate adaptive momentum, we use a simple 1-dimensional saw tooth fitness function defined as an infinite
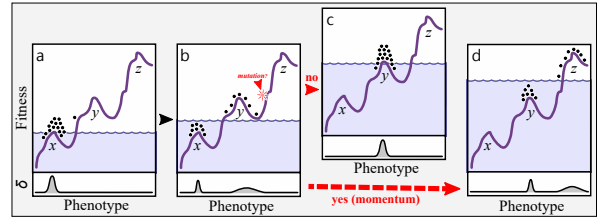

Figure 1: Two scenarios, (a-c) and (d-f), of populations evolving on a simple fitness function. In each panel, the fitness function is shown, with dots representing the current phenotypes in the evolving population. The blue "water line" represents the average population fitness. At the bottom of each panel, a line shows phenotype density. Arrows indicate the temporal progression between panels. In a through c, panel (a) shows a population fixed on peak x, with average population fitness near that peak. At a later time, after the discovery of peak y, panel (b) shows a genetic sweep in progress, with the population shifting towards the higher fitness peak. Individuals near peak y have higher fitness and thus experience reduced purifying selection, leading to increased diversity. In panel (c), the sweep has ended, and as a result of an increased average fitness, purifying selection has tightened the distribution of phenotypes around peak y. In d through f, panel (d) shows a population in an identical state to panel (a). However, in panel (e), mutations around peak y happened to reach the base of peak z. Rather than fixing to peak y (as in panel c), a peak shift to z results in panel (f). From panel (f), the population may fix to peak z, or continue making new genetic discoveries to even higher peaks.

number of repeating peaks where the fitness delta between each peak is the same (i.e., the function has no diminishing returns).

Results In Fig. 3 shows the main results supporting adaptive momentum. In (a), at small population sizes, T_{st} is a good predictor of T_{obs}, because individual mutations fix faster than they can be discovered. At large population sizes, there is a disassociation between T_{st} and T_{obs}, $T_{obs} > T_{st}$, that illustrates the emergence of clonal interference. At middling population sizes, in particular where T_f is close to but below T_{st}, we see that $T_{obs} < T_{st}$ because adaptive momentum makes it more likely for additional valleys to be crossed, but not so much that it results in significant clonal interference.
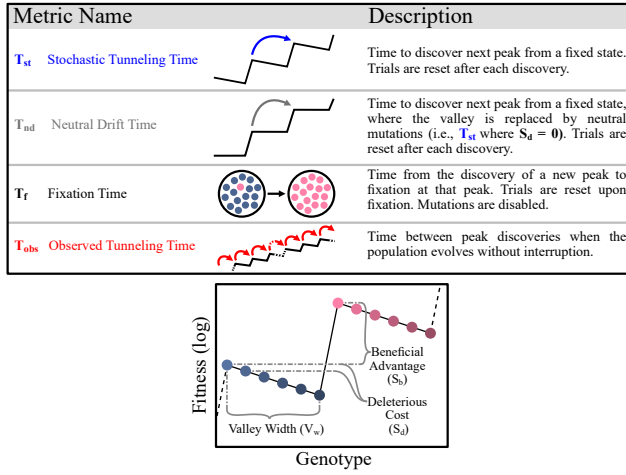
Figure 2: Descriptions of metrics used in the main figure. The figure below shows the saw tooth fitness function used in Fig. 3.

Figure 3: Panel (a) displays the relationship between population size and the average times measured for stochastic tunneling (T_{st}) in blue, neutral drift (T_{nd}) in gray, fixation (T_f) in black, and the observed crossing time (T_{obs}) in red, using the saw tooth fitness function. Panels (b) through (d) show distributions of times between discoveries (using bins with log size) corresponding to the labeled population sizes in panel (a), using the same color keys. Panels (e) through (g) show a subset of valley crossings observed while recording T_{obs} for (b) through (d), respectively, where black and red indicate the maximum and average fitness. Inserts have been added to panels (e) and (f) to show details.

Fig. 3 (a) includes labeled population sizes (b-d); the distributions of times between discoveries for T_{st}, and T_{obs}, as well as the average of T_{nd}, and T_f, are shown in the corresponding panels, also labeled (b-d). In the regions with accelerated rates of "observed stochastic tunneling" (c), where $T_{obs} < T_{st}$), the T_{obs} distribution is bi-modal: one mode is correlated with T_d (crosses from a fixed state) while the other mode contains values less than T_f (crosses during an open momentum window). Note that the T_{st} distribution is uni-modal, indicating the equilibrium tunneling dynamics *do not* predict the disequilibrium tunneling dynamics; adaptive momentum cannot occur without disequilibrium.

Finally, Fig. 3 (e-g) shows the typical observed behavior for each labeled population (b-d). In these plots, the black solid line shows the highest fitness individual in the population, and the red dashed line shows the average. At low population sizes (e), the system rarely makes discoveries and rapidly fixes each before the next. At large population sizes (g), discoveries are common, and the population is in perpetual disequilibrium, causing significant clonal interference. At middle population sizes (f), we see that adaptive momentum results in cascades punctuated by periods of status (punctuated equilibrium). The inset in panel (f), shows how the momentum window is kept open by each new discovery, and closes when a new discovery is not made.

Discussion While the system we have designed is ideal for demonstrating adaptive momentum, it is not biologically plausible because it lacks features such as gene interactions, multiple mutations in a single offspring, and diminishing returns in the fitness function. Still, the simulation does not have any properties that could not be found in a naturally occurring instance of evolution, and additional complexities would obfuscate the effects of adaptive momentum. That being said, future investigations should consider how more realistic conditions interact with adaptive momentum.
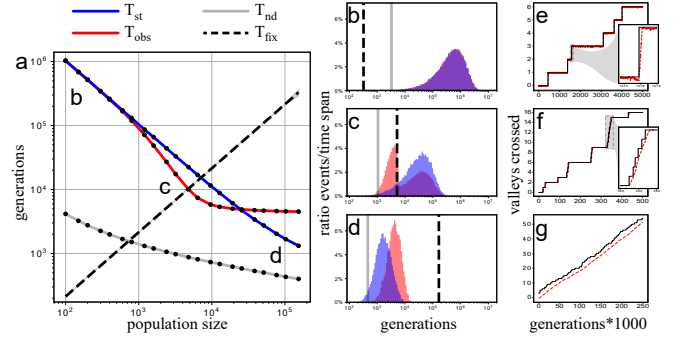
Adaptive Momentum and shifting balance theory (SBT, Wright (1982)) are two concepts that explain how shifts in selection strength can create alternating periods of stasis and rapid change in evolutionary processes. SBT explains how isolated subpopulations experiencing reduced selection are more likely to cross fitness valleys, while adaptive momentum describes how the strength of selection shifts during transient events, such as range expansions or genetic sweeps. Others have argued that SBT should be expanded to include range expansions (Johnson, 2008). We support this extension. Moreover, we view range expansion as a special case of a genetic sweep (where the 'wild type' has zero fitness), and so we further propose that SBT should also include genetic sweeps, making it a far more reasonable hypothesis for explaining the variable rates of evolution observed in punctuated equilibrium. We suggest that the integration of adaptive momentum into SBT provides a more comprehensive explanation for evolutionary patterns in natural systems.

Conclusions In this study, we have introduced and defined the adaptive momentum and its impact on rates of adaptation, particularly during periods of genetic sweeps and range expansions. We have demonstrated that adaptive momentum can lead to the discovery of beneficial mutations and the possibility of cascades of discoveries, providing a novel explanation for punctuated equilibrium.

Thus, adaptive momentum reveals a more dynamic and complex view of the evolutionary process. Moreover, we have emphasized that adaptive momentum is a ubiquitous phenomenon that occurs in all evolving systems. We propose that this idea should be integrated as a fundamental concept in evolutionary theory.

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