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Darwinian evolution as a dynamical principle

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Darwinian evolution (DE)—biology's powerful process of adaptation—is remarkably different from other known dynamical processes. It is antithermodynamic, driving away from equilibrium; it has persisted for 3.5 billion years; and its target, fitness, can seem like "Just So" stories. For insights, we make a computational model. In the Darwinian Evolution Machine (DEM) model, resource-driven duplication and competition operate inside a cycle of search/compete/choose. We find the following: 1) DE requires multiorganism coexistence for its long-term persistence and ability to cross fitness valleys. 2) DE is driven by resource dynamics, like booms and busts, not just by mutational change. And, 3) fitness ratcheting requires a mechanistic separation between variation and selection steps, perhaps explaining biology's use of separate polymers, DNA and proteins.

Darwinian evolution | survival of the fittest | competitive exclusion | driven nonequilibrium

Darwinian Evolution (DE) is the unrelenting drive for biological adaptation on earth. Also referred to here as Survival of the Fittest (SOF), DE is among the most resourceful, innovative, and powerful drivers in the earth's balances of energy, matter, water, and food. Ever since the work of Charles Darwin and Herbert Spencer in the 1860's (1, 2), SOF has been invoked in narratives about biological adaptations, such as the shapes of the beaks of Darwin's finches, the color patterning on the wings of England's peppered moths (3, 4), and many others (5, 6). Its operational basics are well known: Genes encode proteins encode traits; variations are explored by mutational change; organisms compete for finite resources; and natural selection retains those genes/proteins that give the species greater fitness for its environment.

But as a matter of basic principle, DE is not fully understood. What is the force? Why is there any force at all? What has sustained its extraordinary persistence since life began 3.5 billion years ago? SOF resembles variational principles in physics, wherein a system explores its degrees of freedom and tends toward those states that are maxima or minima of some mathematical function, but it has its differences. Variational principles are central to physics: balls roll downhill toward states of minimum gravitational potential energy; gas molecules diffuse, tending toward states of maximum entropy. Living systems do not drive toward equilibrium. Rather, they tend toward adaptation, selfishness, and intricacy, powered by persistent inflows, in a process that has not died for billions of years. The driver of evolution is not the Second Law of Thermodynamics and is not a tendency toward equilibrium (7–9). Fitnesses in biology are unlike energies in physics. While material equilibria are tendencies toward endstates, fitnesses are tendencies across uncountably many different molecules, mechanisms of action, and degrees of freedom, toward opportunistic advantages across uncountably many environmental situations. Here, we frame these questions in terms of evolution as a machine-like cycle.

Evolution as a Cyclic Machine

We look at Darwinian Evolution as a machine; Fig. 1. We define the Darwinian Evolution Machine (DEM) as the biosphere-wide process that undergoes cycles of local actions, powered by local environments. Fig. 1 column (*a*) shows the starting point of the operating cycle, namely a wild-type (WT) population (status quo) at time *t*. The operating cycle has these steps:

- The driver is external resources out of equilibrium. The persistent intake of resources drives the autocatalytic process of moms making moms*. Evolution is a machine insofar as it undergoes repetitive cycles of operation, driven by a nonequilibrium (NEQ) input of resources from the environment.

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*"Mom" is our shorthand for a collection of related mutants, or a specific phenotype, made more quantitative below, resembling what Manfred Eigen called a quasispecies (10, 11).

Significance

Biological matter undergoes evolutionary change through Survival of the Fittest. Darwinian evolution (DE) is remarkably different from the dynamics of dead matter: It is self-serving, adaptive to its environment, and innovative. It has tended away from equilibrium—not toward it—persisting for the 3.5 billion years of life on earth. We develop a mechanistic model of how replication, mutations, and natural selection, driven by resources out of equilibrium, explain these features. Since life is often defined as matter that obeys Darwinian evolution, mechanistic models such as this may also help to understand the origins of life.

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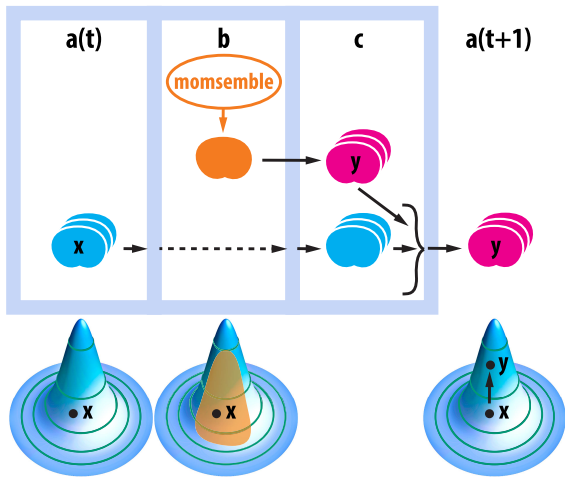[2]To whom correspondence may be addressed. Email: dill@laufercenter.org.

Fig. 1.   The Darwinian Evolution Machine. (*Top*) (*A*) A reference (wild type) population of organisms produces functional devices *X* at time *t*. (*B*) Searching the momsemble by mutation produces device *Y*. (*C*) *X* and *Y* compete for finite resources. (*D*) The winner *Y* produces more population, and that population now replaces the old reference at *t* + 1. (*Bottom*) The corresponding climbing of the fitness landscape in the competition of *X* with *Y*, produced by the momsemble search (shaded area).

- Mutational search. Column (*b*) indicates a search over a space that we call a momsemble of all possible mutations in sequence-function polymers (proteins, DNA and RNA, and their corresponding phenotypes). Unlike equilibrium statmech, these are searches over molecular structures and functions, not over coordinates, velocities, and conformations. The mutant sequence encodes a mutant function, but at the stage of column (*b*), these are hypothetical, not yet realized by growth into a corresponding population.
- Growth and competition for finite resources.   Column (*c*) shows the competition of the mutant vs. WT populations for resources.
- Natural selection and updated status quo. Column (*a*) at time *t* + 1 indicates that winners now become the status quo at the next time step, and they now acquire the greater resources befitting their new status. The resultant climbing of fitness can be regarded as a Feynman ratchet, a device in which undirected inputs, which act randomly forward or backward, drive a directed output action, like in a ratchet[†]. Such a process has been called kinetic asymmetry in molecular machines (13–15). By converting the growth rates of individual cells to populations of their progeny, growth-rate advantages at the cell level convert to larger populations and larger utilizations of resources, which propagate into the next generation.
- Division of labor: Variance (*b*) is distinct from selection (*c*). Fig. 1 (*Bottom*) shows a fitness landscape. Panel (*b*) shows the momsemble as a cloud of options around *X*, which are (mutationally possible) proposed future populations. A specific mutant *Y* is one point in this cloud. The step from (*b*) to (*c*) entails the realization of functions by growing up a population *Y*, competing it with *X*, and selecting *X* or *Y*. Fitness ratcheting would be impossible without this functional separation of variation from selection (Section I).

Theory of the DEM

The heart of the DEM is "moms making more moms" in competition for resources. Let A_n be the number of individuals (moms) of "type" n. These individuals take in resources r_j from the environment at a total rate[‡] $U_{nj}(A_n, \{r_i\}_i)$ and turn them into internally stored intermediates P_{nj}. We assume no interactions between the types of moms other than indirectly through their drawdown of resources[§]. Second, we suppose that reproduction rates depend only on the internal levels P_{nj}—a single mom of type n has a reproduction rate of the form $R_n(\{P_{nj}/A_n\}_j)$. Since each individual acts independently, the total rate of new moms of type n that are made is $R_n(\{P_{nj}/A_n\}_j)A_n$. These internal intermediates grow and decay according to $\dot{P}_{nj} = g_{nj} - D_{nj}P_{nj}$, where g_{nj} is the production rate and D_{nj} is the decay rate of the intermediates. At steady state, we have $P_{nj} \propto g_{nj}$. Since reproduction rates (use of the P_{nj}) are usually much slower than eating rates (production of the P_{nj}), $g_{nj} \propto U_{nj}(A_n, \{r_i\}_i)$. The total amount of an intermediate is proportional to the eating rate that produces that intermediate.

The full dynamics of duplications of N moms and depletion of M resources is given by

$$\frac{dr_j}{dt} = \alpha_j(t) - d_j r_j - \sum_{n=1}^{N} U_{nj}(A_n, \{r_i\}_i),$$
$$\frac{dA_n}{dt} = R_n\left(\left\{\frac{U_{nj}(A_n, \{r_k\}_k)}{A_n}\right\}_j\right)A_n - D_n A_n, \qquad [1]$$

where $\alpha_j(t)$ is the rate at which the environment supplies resource j. In the case of only a single resource, which we will focus on below, we have

$$\frac{dr}{dt} = \alpha(t) - d_r r - \sum_{n=1}^{N} U_n(A_n, r),$$
$$\frac{dA_n}{dt} = R_n\left(\frac{U_n(A_n, r)}{A_n}\right)A_n - D_n A_n, \qquad [2]$$

Before taking the next step in our analysis, we note that the competition Eqs. **1** and **2** are similar to consumer-resource models of population genetics (popgen) or ecology, such as of Volterra (16), Fisher (17), MacArthur (18, 19), and later Tilman (20). Popgen models treat the dynamics of the reproduction of multiple moms that compete against each other for resources. These models entail asserting different simplifications of the functional forms of U_n and R_n. In popgen models of the Fisher type as formulated by, e.g., Crow and Kimura (21), R_n and D_n are taken to be constants. In the Tilman model, R_n is a function of the resources only, $R_n = R_n(f_n(r))$, because the eating rate is assumed to be linear in A_n, $U_n(A_n, r) = f_n(r)A_n$.

We describe in *Coexistence Helps to Avoid Extinctions* below how the linearity approximation is too simple for the principles of interest here. For now, we note that to advance beyond the linearity approximation, we assert here a saturating form of the eating conversion rate $U_n(A_n, r)$. To illustrate the need for it, consider the Tilman model. If A_n is increased while r is held constant, then the resource drawdown rate $U_n(A_n, r) = f_n(r)A_n$

[†]Brownian ratchets are examples of Feynman ratchets when the input is thermal energy (12). But here, the randomness is from sequence mutations.

[‡]We use the simplified notation $f(\{r_j\}_j) = f(r_1, r_2, \dots)$.

[§]Of course, in any particular application of the model, there can be additional interactions. One example is sexual reproduction, which causes type n to have offspring of type $m \neq n$.
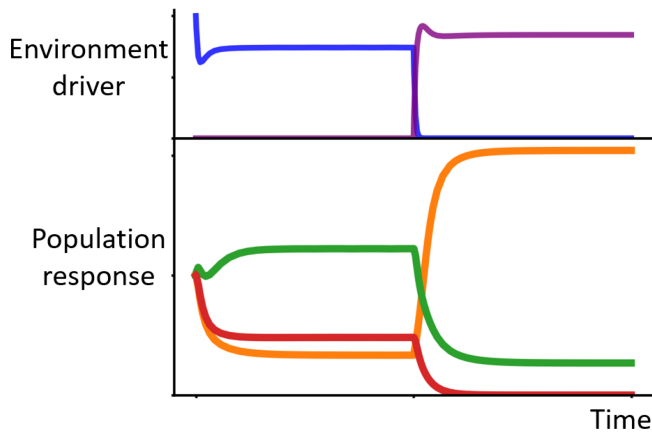
Fig. 2. How environments drive relative populations. (*Left*) Coexistence of three moms (orange, green, and red) on a single resource (blue, NEQ supplied by the environment). (*Right*) Switching to the purple resource drives a change in populations; now orange moms take over from green, and red dies out.

Fig. 3. Before, orange and green moms share the food. After, orange gets it all. (*Left*) During the boom, orange and green share the resource. (*Middle*) In the bust, green dies, freeing up its resources. (*Right*) In the next boom, orange gets all of the resources.

will diverge. Biochemical processes have speed limits, often given by the Michaelis–Menten function, because molecular processes of binding entail sites that can fill up. Similarly, if the amount of food is held constant, no matter how many individuals are added, the rate at which it is eaten will eventually saturate. The same is true for keeping A_n constant while increasing r. If both A_n and r are increased, however, then the eating could increase indefinitely[¶]. A function that satisfies all of these conditions is $U_n(A_n, r) = (k_n A_n r)/(B_n + c_n r + A_n)$, as proposed elsewhere in refs. 22–24. If we let $R_n(x) = q_n x$ and we consider just two competitors for simplicity, we find that there exists a stable coexistence steady-state with both moms present (*SI Appendix*).

What the Machine Perspective Tells Us about Evolution

In the sections below, we reason with the DEM equations above and the machine cycle shown in Fig. 1 about the questions raised in the introduction. On the one hand, our premises are simply the well-known basics of mutation, selection, and the dynamics of winning resources through competitions. On the other hand, this machine formulation gives new quantitative insights into the role of environmental dynamics (how unruly and fluctuating resources drive evolution); the role of search and sample (to achieve innovation, to cross fitness valleys, and to sustain persistence of the biosphere); and the power of converting individual growth rates to population sizes.

A. Adapting to Environments by Changing Mom Populations. Environments can be unruly, unstable, and undependable, even rapidly and sharply so, such as in resource booms and busts. The DEM has some memory of its history of food availability through its relative mom populations. Fig. 2 shows how an environment switching from "blue food" to "purple food" drives a transition from a coexistence of mostly green moms, with some red and orange ones, to mostly orange moms, where red has gone extinct. This environmental transition from blue to purple food drives a rebalancing of populations toward moms that can best utilize the new food and away from moms that cannot[#]. It's just a simple
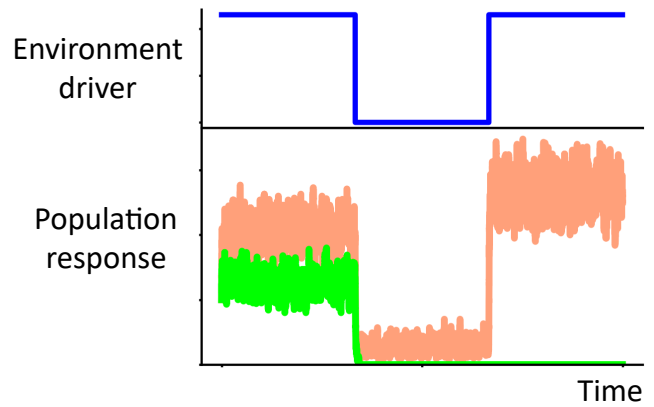
computational example of how the DEM description captures the essential feature of Darwinian adaptation to environments.

B. Changing Environments Drive Resource Reallocations. Fig. 3 is a DEM calculation showing a boom-bust cycle of resources driving a change in moms and reallocated resources. Our term boom and bust is simply a surrogate to represent the many different kinds of ways that environments can change, either in regular or more capricious irregular ways, through small fluctuations or huge disruptions. Before the bust (*Left*), orange and green moms coexist, both feeding from the same supply of resources (blue). Then, the bust kills off the green mom, now freeing up the resource supply that green previously commanded. In the next boom (*Right*), those resources are now available to the orange mom, in addition to the resource allocation she would naturally receive from the next environmental boom. In short, "orange eats green's lunch." We refer to this reallocation as a turn of the fitness ratchet because it is part of a unidirectional cycle: Busts flush out unfit moms (green), freeing up more resources, which are taken up by the more fit moms (orange). The cycle recenters the momsemble around the new dominant moms at each step, moving away from moms that are diminished or extinct. During a bust, the unfit moms that struggled to survive during the boom are cleared away, leaving all of the resources for the more fit moms.

Here is a note on modeling extinction—deterministic vs. stochastic. On the one hand, we have expressed the DEM dynamics as deterministic ODEs. In practice, ODEs cannot properly treat extinction: Continuum dynamics allows populations of moms to become infinitesimal, less than a single individual, but still not zero. This is unphysical. Only stochastic simulations (Fig. 3) or a manual extinction cutoff (Fig. 4) can properly capture the complete irreversibility when the last mom dies (*SI Appendix*).

C. Coexistence Helps to Avoid Extinctions. A common view of Darwinian evolution, as often embodied in population genetics and ecology models, is that Winners-Take-All (WTA). That is, even the smallest advantage of one mom and her lineage ultimately wins out, driving all the other competing moms to extinction. Called competitive exclusion[‖], or Gause's Law (27), this is

[¶]For simplicity here, we neglect spatial heterogeneities, but the model is readily generalized.

[#]The result in Fig. 2 is quite general. If we were to instead make the constants k_n in the eating rates a function of the environment, we would get the same result, since changing

parameters with the environment is mathematically the same as treating the resource after the environmental change as a new resource (*SI Appendix*).

[‖]In the Tilman model, competitive exclusion is also known as the R^* rule (25, 26).
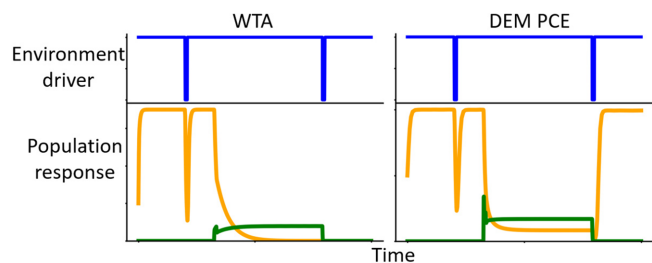
Fig. 4. Winner-takes-all dynamics is more susceptible to extinction than coexistence dynamics. (*Left*) WTA models are "brittle" to supply chain disruptions. The lone winner after the first bust (green) dies out after the second bust. (*Right*) In the DEM, orange doesn't fully die out in the first bust, so it rises up again after the second bust.

"one of the central themes of research ecology" (28). Competitive exclusion is the idea that n species cannot coexist unless there are at least n distinct resources available. It says that the number of species that can coexist is limited by the number of resources available. In the case of one resource, a single winner takes all.

However, competitive exclusion does not always hold in reality. Biology has many examples of peaceful coexistence (PCE). One is the paradox of the plankton, in which "it is possible for a number of species to coexist... all competing for the same sorts of materials" (29). Different explanations have been given for apparent violations of the competitive exclusion idea (30–35). Systems may not reach steady state or may have more complex interactions, such as cooperative couplings between moms (36). An important class of models that encompass both WTA and PCE in different situations are those such as in the present work, in which mathematically the function U_n is nonlinear and saturating as a function of resources or populations (37–40). Such nonlinearity could arise from various mechanisms (41–43): predators interfering with each other (24); or that moms cannot become infinitely dense or produce offspring infinitely fast. Our purposes here do not require specifying a particular mechanism. What is essential here, however, for explaining key features of evolutionary dynamics, is that U_n saturates.

Fig. 4 compares models: those allowing peaceful coexistence versus those that are only winner-takes-all. It shows an environmental resource that undergoes booms (blue line, high value) and busts (low value). This figure illustrates two points. First, the left side shows how a WTA competition of two moms on a single resource leads to an extinction. The orange mom can survive busts. Orange begets a green mom during a boom. The green mom is good enough to win and "take all" during that boom. However, the second bust kills green, so neither green nor orange survives. The WTA mechanism is brittle: The risk of total extinction is high in an oscillating environment, because not all mutants that win during boom times can survive every bust (*SI Appendix* for details). Even though WTA leads to good fitness in today's boom, it may die out in tomorrow's bust.

Second, Fig. 4, *Right* shows how the peacefully coexisting community of the DEM model is more resistant to extinction, able to survive both busts. The saturating form of $U_n(A_n, r)$ in our DEM model admits additional solutions to the dynamics, beyond just winner-takes-all steady states. As before, orange can survive all the busts, and a mutation raises up the green. This time, green does not take all. Orange still remains "lurking in the bushes"— i.e., having a small population—because the DEM allows for the coexistence steady state. The second bust kills green, but now the orange lurkers rise up again because they weren't fully killed off by green. The DEM is more robust to extinctions caused by a short-term beneficial, but long-term unfit, mutation. This is

consistent with the well-known importance of biodiversity for ecosystem robustness.

In a WTA-model world, where every niche has exactly one mom filling it, an extinction event leaves the niche unfilled. If this niche is vital to the ecosystem (part of a resource recycling chain, say), leaving it vacant could collapse other dependent populations. In contrast in a PCE-model world, the "lurkers" can pick up the burden of carrying the community. There are other solutions to this problem too, such as species coexisting on multiple resources and overlapping in niche.

D. How Davids Beat Goliaths: The Power of Fitness Ratcheting.
One way that Darwinian evolution differs from physical flows is in their dominant components. In physics, such as a river flow, the average velocity is roughly the speed of the dominant population, say from the middle of the river. But in DE, it's the fitness that ultimately drives dominance. It's sometimes the "Davids," not the "Goliaths," that matter most. Adaptation raises up "more fit" sequences no matter how far they are from the average. A phenotype can come to dominate a population by starting in a single individual. It's because in DE cellular rates convert to populations, and rate differences are inside the "moms making moms" autocat loop. The type of signal amplification that happens in the DEM is very different from simple amplification. An amplifier makes a whole signal louder, both the quiet and the loud parts. In the DEM, only the "best" signal is amplified (i.e., "most fit"), even if that signal is very weak. To use a metaphor, the DEM takes in all the noise in a crowded room and picks out only the conversation most important to you.

How does evolution leverage small advantages? Consider a mom A eating a resource and growing exponentially (ignore for the moment its death rate and resource considerations), $dA/dt \sim k_A A r$. It develops a fairly large population. Now, imagine that it mutates one individual of type B, growing at $dB/dt \sim k_B B r$. Initially, while the total amount of B is much less than the total amount of A, the fraction of B in the population goes as $B/(A + B) \approx B/A \sim \exp(\Delta k r t)$, where $\Delta k = k_B - k_A$. Unsurprisingly, the mutant mom will grow in population fraction if it grows faster than the existing mom. The exponential leveraging of different growth rates leading to dominance in the population is the essence of the DEM's unique amplification—after all, biology's principle is survival of the fittest, not survival of the most numerous—and thus applies to populations that start out small, at the level of a single cell.

The simple qualitative argument above is deterministic, and it only holds exactly when we can model the populations as growing exponentially. We can more precisely account for all of the details using a stochastic model. We follow Kimura (44), who calculated the probability of fixation of an allele given that it starts with a population fraction p and has a constant selective advantage s. We apply his argument to a system of N total moms that starts with one mutant mom so that $p = 1/N$. Kimura's treatment gives the fixation probability u as

$$u = \frac{1 - e^{-2s}}{1 - e^{-2Ns}}. \quad [3]$$

By "a constant selective advantage s," we mean that the average change in the fraction of mutant moms per generation, which equals dp/dt times the generation time, goes as $sp(1 - p)$. In the DEM, we can calculate dp/dt using $p = A_n / \sum_m A_m$ and the DEM ODEs to find $s(\Delta k)$ and subsequently $u(\Delta k)$, the probability for one mutant individual with a growth advantage of Δk to eventually fix in the population—that is, to be the
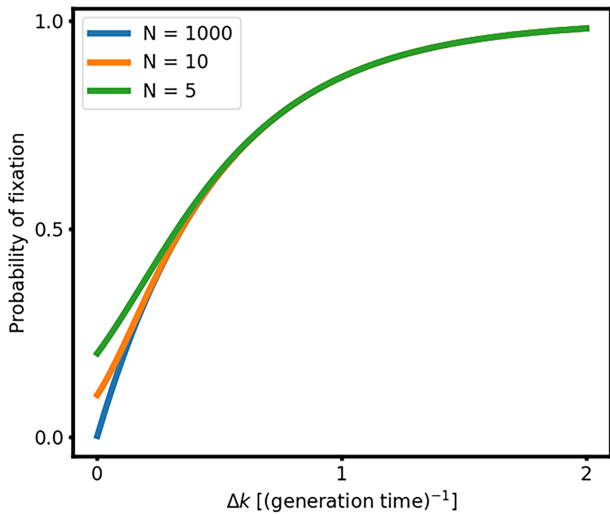
Fig. 5. Even small advantages in growth rate Δk lead to high fixation probabilities. Sometimes advantageous mutants do not survive (*Lower Left*), but if a mutant is able to make even one or two more of itself per generation than the current wild type, then its odds of fixation approach unity (*Upper Right*).

Fig. 6. The DEM is able to traverse fitness valleys. Species *A* (orange) competes with species *B*, which has three strains: an initial WT (green), a poor mutant strain (blue), and a much better mutant (red). Green cannot mutate to red directly—it mutates to blue which can mutate to red. The ability of *B* to traverse the poor (fitness valley) blue state is because orange, green, and blue can coexist until the better red mom mutation appears.

winner-taking-all**. However, in general, in the DEM, s will depend on the total number of moms N, which changes with time. To use Eq. **3**, s must be constant. To demonstrate the leveraging of Δk in amplifying small advantages in the DEM, we will take a special case. In the case†† where two moms A and B are at carrying capacity, i.e., with $N = A + B$ constant, but A and B are still able to change their population fraction during each generation of time δt, it was found in ref. 46 that $s = \Delta k \delta t$. If we scale time so that $\delta t = 1$, the probability of fixation of a beneficial mutation that starts as one mom is

$$u = \frac{1 - e^{-2\Delta k}}{1 - e^{-2N\Delta k}}. \qquad [4]$$

This probability is plotted as a function of the rate difference Δk for various values of N in Fig. 5. It shows that even very small selective advantages (differences Δk) lead to appreciable differences in fixation.

E. Innovation by Incremental Opportunism. A key concept of Darwinian evolution is that biology achieves adaptations, even complex ones, through incremental random changes and opportunistic selection among those variations. Many adaptations seem clever and intricate, with many components working together with precision, like a watch. Examples are eyes, lightweight wings on birds, molecular motors, blood clotting systems, chemotaxis, and glycolysis and photosynthesis systems. Counterarguments to incremental opportunism are that complexity seems so unlikely in the absence of purposeful design, that blind watchmakers cannot make watches (47, 48), and that reaching such high fitness peaks would require crossing fitness valleys. An example is the eye: To evolve an eye, opponents say, would require first creating half an
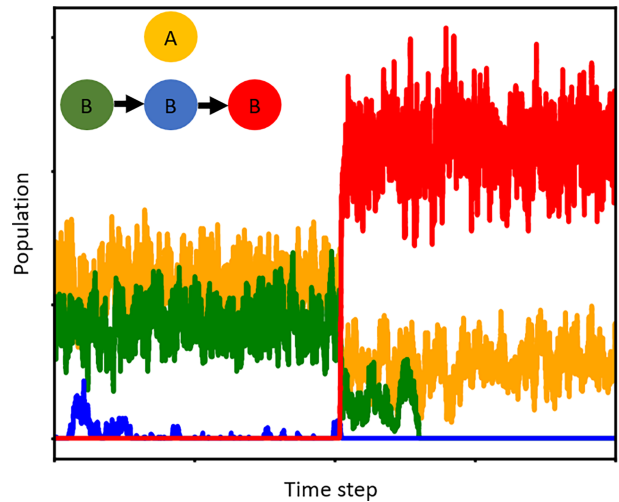
eye, which is costly and would have no value. An organism that is in a local minimum of fitness would be less fit—and therefore less stable—than the wild-type organism that is already the dominant population.

In response, we first note that incremental random opportunistic strategies are well known to succeed in complex situations, such as high-dimensional spaces—in protein folding (49, 50) and in explore-and-exploit computer algorithms (51–54), such as Metropolis Monte Carlo (55, 56). Second, we note that there is a connection between complexity and functionality (57, 58). Third, the biosphere search of functional options is massively parallelized among organisms and species.

F. How the DEM Crosses Fitness Valleys. Fourth, an important part of diversity generation boils down to the difference between winner-takes-all (WTA) and peaceful coexistence (PCE). In PCE, many organisms exist in low population. Such rare organisms can readily experience a rise in their populations, either driven by a change in environment (Figs. 2 and 3) or by a mutational change in the organism (Fig 6). In the latter case, the orange mom (species *A*) is initially better than the green mom (species *B*). The green mom can mutate into the blue variant (by which we mean have blue offspring), which is worse than the original wild type of species *B*, but the blue variant can mutate into the red variant which is much better than any of the other moms. There is a fitness valley, the blue mom, between the current wild type and the true fitness maximum. Because of peaceful coexistence in the DEM model, the blue strain "lurks in the weeds" and is eventually able to mutate out the red one, which replaces the green one as the wild type of species *B*.

G. The NEQ Input Powers the Climbing of Fitness Hills. Fig. 7 illustrates the difference between a nondriven tendency of materials relaxing toward equilibria (*Left*) vs. a driven tendency of evolution toward opportunistic adaptation (*Right*). In the former, there is a cost (free energy) of climbing over barriers. In the latter, there are kinetic costs too, but some costs are paid by the nonequilibrium drivers, by the large numbers of moms in parallel,

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** In a stochastic competition with fixed competitors, one mom will always win out in the end because of "random extinctions," as argued directly by Cole (45) and by Kimura (44, 46) as a consequence of his fixation probability.

†† Here, we note that Kimura and Crow use the common reproduction term $k_A A$, where the resource is presumed to be its constant steady-state value, while we have been using the ecology-type term $k_A A r(t)$. The units of k now change accordingly. The model of Kimura and Crow is an approximation to our competition equations where the resource is taken to always be at steady state and the total number of moms is constant at carrying capacity.
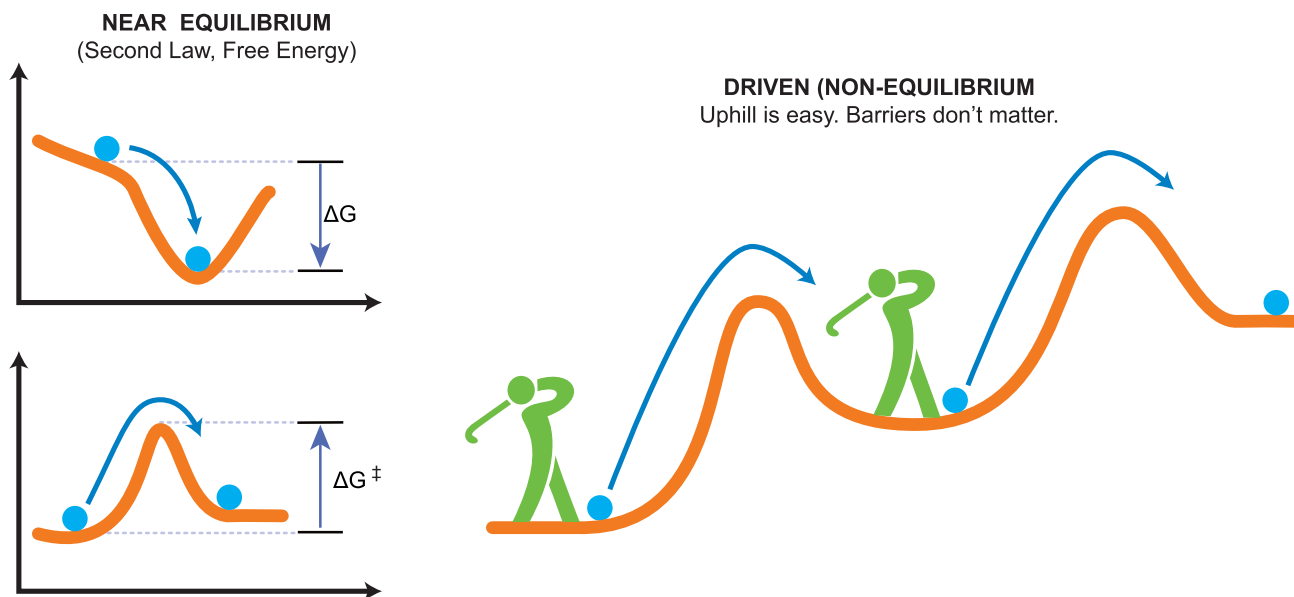
Fig. 7. **Nonequilibrium dynamics can be very different from those of near-equilibria**. (*Left*) Near equilibrium: (*Top*) processes flow downhill in free energy and (*Bottom*) crossing kinetic barriers entail rare events. (*Right*) A driven learning machine like the DEM is like having many golfers driving balls uphill.

and by the coexistence of lurkers. We use the metaphor of golfers on a mountainside to express how fitness valleys are crossed. Because evolution entails a driven nonequilibrium system with persistent resource availability, it is much like aimless golfers located broadly across the landscape driving golf balls uphill and downhill. The ratcheting upward on a fitness landscape happens only because those points are selected for after the fact, not targeted a priori. Since the DEM is not winner-takes-all, there are many such golfers sampling the space simultaneously. There's power in numbers.

H. The Drive to Persist. Persistence in evolution—that is, the ability to self-sustain over time—is different from persistent stability in an equilibrium thermodynamic system. The former entails sustaining nonequilibrium fluxes, driven by nonequilibrium inputs. It is dynamic, not static (7). But evolution's persistence goes beyond just being a driven system. Evolution is also adaptive—that is, persistent even in the face of capricious unruly ever-changing environments. This adaptability of the DEM comes from two key features: i) Autocatalysis, of moms making moms, giving an exponential growth regime because $dA/dt \propto A$; and ii) Variance, which samples rate coefficients $k = k(s, r)$ that depend both on phenotype and environmental resources. It is the intrinsic sloppiness of copying that further protects the DEM from extinction. Because the rate $k(s, r)$ depends on sequence, and because in the DEM model there is peaceful coexistence among many different sequences, the death of any one sequence or lineage or species is not sufficient to extinguish the full Darwinian Evolution Machine; Fig. 4. Extinction can be avoided by innovations that arise in coexisting variants.

I. Why Variation Must Be Functionally Distinct from Selection. In all fitness ratchets, such as computational Monte Carlo (55), the propose step is distinct from the accept step. The propose step must be as unbiased as possible and sample the space of options as uniformly and completely as possible, without prejudgment about where successes will be found. The bias and judgment are localized in the acceptance step, which selects for improved fitness. Without this separation, fitness ratchets

cannot tell uphill from downhill[‡‡]. Without the separation of the propose step from the accept step, a machine could not discriminate a good status quo with a poor mutation from a poor status quo with a good mutation. Evolution would have no sense of fitness direction without a way to distinguish the status quo from a proposed future.

J. Speculation: Why There Are Two Polymers, DNA and Proteins. Today's biology uses both informational and functional polymers, DNA and proteins. The need for two different polymers can be rationalized by the essential requirement for functional distinction between variation (*b*) and selection (*c*) in Fig. 1. Biology implements the biased/unbiased separation by using different polymer types[§§]. DNA and RNA are informational while proteins are functional. Here is a sensible explanation for this. Biases reside in proteins by virtue of the sequence-to-function relationships of foldable polymers, or correspondingly by bias in phenotype expression during development (48, 60–63). Information is unbiased in DNA because these are stiff rod-like chain molecules by virtue of their double-strandedness and high persistence lengths. No matter what a DNA sequence is, DNA's conformation is relatively independent of the sequence. In contrast, proteins have structure–function relationships because they can fold into different shapes. Biology separates unbiased search and proposal from biased function and acceptance by these different physical properties of biomolecules.

Conclusions

We have sought insights into dynamical features of Darwinian evolution. Here are three. First, we find the importance of coexistence, rather than winner-takes-all, for evolution's power of innovation, ability to cross fitness valleys, and resilience against extinction to the vagaries of the environment. Second, we find

[‡‡]Imagine no panel (*b*) step, with mutations simply acting on *X* directly. Mutations would simply drive random steps up and down on the fitness landscape, never ratcheting up on average.

[§§]In a sense, the story of the origin of life can be interpreted as the story of how nature discovered a physical realization of these two properties and coupled them together (59).

that environment histories are as important as fitness landscapes of mutations for understanding biological adaptations. Third, a dynamic mechanism that climbs fitness landscapes must have a division of labor, like propose and accept in Monte Carlo computer algorithms: unbiased search coupled with biased functional evaluation. Biology has performed this separation by using different polymer types—DNA for information and proteins for function.

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