Evolution in leaps: The punctuated accumulation and loss of cultural innovations

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Archaeological accounts of cultural change reveal a fundamental conflict: Some suggest that change is gradual, accelerating over time, whereas others indicate that it is punctuated, with long periods of stasis interspersed by sudden gains or losses of multiple traits. Existing models of cultural evolution, inspired by models of genetic evolution, lend support to the former and do not generate trajectories that include large-scale punctuated change. We propose a simple model that can give rise to both exponential and punctuated patterns of gain and loss of cultural traits. In it, cultural innovation comprises several realistic interdependent processes that occur at different rates. The model also takes into account two properties intrinsic to cultural evolution: the differential distribution of traits among social groups and the impact of environmental change. In our model, a population may be subdivided into groups with different cultural repertoires leading to increased susceptibility to cultural loss, whereas environmental change may lead to rapid loss of traits that are not useful in a new environment. Taken together, our results suggest the usefulness of a concept of an effective cultural population size.

toolkit | cultural accumulation | creativity | social stratification | fluctuating environment

The breadth and diversity of cultural traits and their rates of accumulation have received a great deal of scholarly attention. Scientific knowledge in many fields appears to accumulate exponentially (1, 2). However, although the number of tool types in the archaeological record also seems to fit this pattern of exponential increase broadly (3), the number of tools and other cultural traits does not increase steadily and monotonically over time. Depending on the timescale studied, change in tool repertoire may appear punctuated and stepwise. Long, seemingly static, periods are interspersed between "cultural explosions," periods of sudden cultural accumulation (3–13). Further, in some populations, there is evidence that whole suites of cultural traits, such as the ability to make tools, clothing, and fire (14–16), may be lost, defying the general trend of cultural accumulation over time (4, 7, 8).

Reasons for the sudden changes in hominid material culture in the archaeological record continue to be debated; they could be related to demographic factors (17), rapid cognitive change (18–21), relatively sudden changes in hand morphology (22, 23), or dramatic climatic shifts (10, 24–28). Further, intermediate-scale environmental change or migration to a new environment also could affect the accumulation and loss of traits that are primarily useful in specific environments (29–33). In addition, the relationship between the number of cultural traits in a population and population size has been debated (4, 14, 29, 34–41); this relationship also might depend on the social learning strategies of the population (42, 43). Further, there could be a feedback process between the number of tools in a population and the population size: A larger population might be able to invent and retain more tools, but certain innovations also might support a larger population (44, 45). Finally, the distribution of traits in the population (as a result, for example, of social stratification) might affect both stochastic and environmentally mediated cultural losses.

Several models of the dynamics of cultural evolution explicitly incorporate appearance, transmission, and in some cases disappearance of cultural traits (14, 35, 40, 45–53). Sudden dramatic changes in cognition, morphology, or climate are not invoked in these models as a precursor to cultural change; instead, cultural change derives from endogenous properties of the models.

Most models of cultural evolution focus on the dynamics of the transmission of cultural traits (40, 50, 51), often omitting the details of the creative processes underlying the origin of these traits (e.g., refs. 14, 35, and 54). The source of cultural traits is represented as a random process occurring at a constant rate, analogous to a genetic mutation rate (40, 46, 48, 50, 51, 55). This representation has proven useful but differs from realistic human innovation (56). For example, a particular genetic mutation occurs independently of previous mutations, whereas a cultural trait's likelihood of invention could depend on the configuration or frequency of existing traits. For example, the invention of a snaring method enabling new kinds of game hunting may lead to the invention of specialized tools for processing this novel food source. This dependence is one sense in which culture is fundamentally cumulative. A second intriguing difference is the cost of failed attempts at adaptation; although deleterious mutations are costly to the organism, the invention of a useless tool typically would not have long-lasting effects: it simply would be discarded and forgotten. A few models do not assume a constant

Significance

The archaeological record suggests that cultural traits, as manifested in the tool repertoire, can accumulate exponentially, that technology can appear in bursts after long periods of stasis, and that dramatic cultural losses can occur. We introduce a model that accounts for this range of observations by considering a multifaceted creative process of innovation, accounting for the possibility that certain traits facilitate the invention of related traits. Further, we determine that differential distribution of tool-related knowledge, typically ignored in models, can dramatically affect the dynamics of cultural evolution, suggesting the concept of an effective cultural population size. Finally, we demonstrate that a fluctuating environment can lead to large-scale cultural losses and select for generalist tools that are useful in multiple conditions.

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rate of creative invention: as the existing repertoire becomes larger, they allow an increase (47, 57) or decrease (e.g., ref. 54) in the invention rate, or more subtle dependencies among particular traits (49, 52); other models allow cultural traits to influence the dynamics of cultural transmission and homophily (58–63).

Large-scale cultural loss has been observed in human populations; however, most existing models lack a mechanism to account for this process. Many represent cultural loss as a Poisson process (47, 49, 51, 52, 57), but, as with cultural accumulation, this assumption of a constant rate may be an oversimplification. In reality, factors such as population size (taken into account in some of these models) and environmental change (7) likely affect the rate and nature of cultural loss. Finally, existing models also implicitly assume a uniform distribution of knowledge in the population. This assumption is unrealistic in human populations, where some knowledge may be concentrated in specific subgroups, such as medicine-women and -men who know the uses and risks of medicinal plants. We suggest that a concept of effective cultural population size as a cultural analog to effective population size in genetics could be highly useful in this context. Notably, Shennan (35) and Premo (64) have suggested the use of an effective population size in the context of cultural evolution for different reasons, stemming from the details of the transmission process or from the geographical substructure of the population.

Existing models of cultural evolution cannot reproduce many features of archaeological and anthropological observations of cultural accumulation in hominids. Few models show an exponential increase in the number of cultural traits (47, 49, 57) or large-scale cultural losses (14, 45, 46), and we are unaware of any that reproduce a pattern of cultural accumulation with punctuated bursts of innovation separated by periods of relative stasis (although ref. 45 suggests the possibility of bistability: a sudden shift between two levels of cultural diversity).

We suggest that the assumption that all cultural traits originate via a single process cannot generate an accurate representation of human cultural accumulation. Indeed, researchers in fields such as psychology and cognitive science often divide creativity into multiple types or processes, such as everyday and genius-level creativity (65–67, see also ref. 57). Other categorizations reflect properties of the underlying cognitive processes (68, 69). Both approaches suggest that some creative events are rare and somewhat unpredictable and others are more everyday occurrences that depend on the current environment and preexisting knowledge in a population.

The Model

We propose a model of cultural evolution that explicitly incorporates a number of pathways that give rise to innovations. The model allows the stepwise accumulation of cultural traits as well as other dynamics, depending on parameter values. We take into account insights from recent theoretical and empirical work on cognitive processes that might underlie creativity (57, 70), ideas from developmental psychology and cognitive science (68–71), and a detailed view of how technological innovations develop (influenced by refs. 72–74). Our model also is inspired by the long-standing debate regarding punctuation versus gradualism in related fields (6, 8, 75–79).

We conducted computer simulations of a population of N individuals, which remains constant during the simulation for simplicity although the accumulation of cultural traits realistically might influence population size in some situations. At each time step, which can be viewed as a single generation but also could refer to an arbitrary timespan, each of the processes described below occurs with a certain probability. We will refer to the entities whose dynamics are followed as "tools" (80). Our model incorporates four pathways that give rise to novel tools. We use the size of a population's tool repertoire as a proxy for its cultural complexity (14, 81). Groundbreaking novel innovations can arise via the first pathway, termed "lucky leap innovation" (Fig. 1). These innovations can occur as a result of a lucky coincidence or an unusually far-reaching analogy in an individual's mind. This process is independent of the current state of cultural diversity and, like genetic mutation, is described by a rate parameter, denoted P_{lucky}, defined per individual, giving rise to a Poisson process with an exponential distribution of waiting times between occurrences. Tools that arise via this process are depicted along the horizontal main axis in Fig. 1 and are referred to henceforth as "main-axis tools."

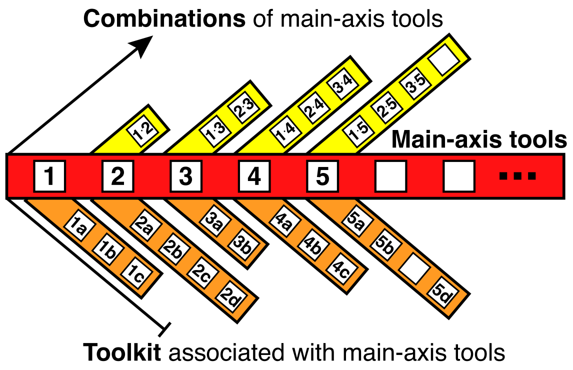

Fig. 1. Schematic representation of the state of tool knowledge in a population. By a stochastic process of lucky leaps, novel tools are added to the tool repertoire, indicated along the main horizontal axis of the figure (red). A main-axis tool can facilitate the invention of a number of other tools: tools that are part of a toolkit made useful by the new main-axis tool or tools that are invented by functional analogy to the main-axis tool. These two processes are grouped under the "toolkit" label (orange). Alternatively, new main-axis tools can generate new tools by combining with existing tools to make novel and useful combinations (yellow). Useful tools need not be accumulated in a certain order: here, the population tested tool "5d" before "5c."

Once a new main-axis tool appears, it may bring about new necessities, prompting creative innovations to address them. For example, the invention of a fishing net could further facilitate other related tools that are made useful by the existence of this new tool, e.g., a weight to sink the net; we call this second pathway of inventions, in which a main-axis tool creates the cultural niche for associated toolkit tools, "toolkit innovation." A third pathway of tool invention is by direct analogy to the main-axis tool in question: For example, once fishing nets are invented, similar nets soon may be designed to catch animals on land. The two tools do not necessarily share a common context of use; instead they share a common functional principle. In our model, each main-axis innovation can be associated with between 1 and 20 toolkit and direct analogy tools (Fig. 1). Both toolkit and direct analogy innovations are inspired by a single main-axis tool and do not depend on comparisons with the rest of the tool repertoire, and the number of possible toolkit and analogy tools associated with a given main-axis tool does not depend on the number of tools in the population; thus, these two processes have similar effects on tool accumulation, and we do not model them separately. Henceforth, the term "toolkit innovation" refers to both processes and occurs with probability $P_{toolkit}$, which typically is greater than P_{lucky} by at least one order of magnitude in our simulations, reflecting a plausible relationship between these processes. Finally, a main-axis tool also may prompt novel technology through its combination with existing tools to generate an "innovative combination," which occurs with probability $P_{combine}$ per individual. In our model, only some of the possible combinations of tools are useful (each combination with probability $P_{combUseful}$) and are retained following their invention; the rest are lost from the population immediately after their emergence. The model was implemented in two modes: In one, only single main-axis tools can combine with one another, and in the other a main-axis tool may combine with previously constructed combinations as well as with other main-axis tools. For simplicity, a combination tool in our model is always regarded as associated only with the tool that was invented last among the tools that it combines. In Fig. 1, for example, the tool composed of main-axis tools 2 and 5 is associated with the latter and would be lost if main-axis tool 5 were lost but not if main-axis tool 2 were lost; further details are given in *SI Appendix, SI1: Extended Model Description*. A scenario in which each combination tool is associated with both of its constituents is explored in *SI Appendix, SI6: Loss of Combinations Following Loss of Their Constituents*. In *SI Appendix, SI7: Groundbreaking Combinations as an Additional Source of Main Axis Tools*, we explore a scenario in which a combination tool may, with a certain probability, turn out to be groundbreaking and thus become a main-axis tool with an associated toolkit and combination tools.

Tools may be lost in several ways that represent realistic cultural forces. First, a main-axis tool may be lost immediately following its invention because of drift, although such loss is rare. The likelihood of this occurrence, 1 − s, is related to a tool's usefulness, determined by the selection coefficient *s* associated with each tool upon its invention (*SI Appendix, SI1: Extended Model Description*). Second, tools of all types can be lost stochastically because of drift even after having been widespread in the population. This loss is less likely to happen to tools that are used by many individuals; it occurs with probability $P_{SpontLoss}/N_{Tool}$, where N_{Tool} is the number of individuals that know the tool (*SI Appendix, SI1: Extended Model Description*). Last, tools might be useful only in particular environments and be lost quickly in environments in which they are useless (31–33). The environmental state (representing different climatic conditions, for example) changes with probability P_{switch} per time step, which typically is low. Each tool is useful in the environment in which it was invented and in each subsequent environment with probability $P_{envUseful}$; thus $P_{envUseful}$ represents a measure of the degree of similarity between environmental states. At every time step, each tool that is not useful in the current environment is lost with probability $P_{EnvLoss}/N_{Tool}$. Importantly, when a main-axis tool is lost from the population via either of these processes, its associated tools—both toolkit and combination tools—are immediately lost with it.

Finally, social subdivision of cultural knowledge may occur in a population. For example, a population may contain a small subgroup with specialized knowledge, such as shamans or medicine-men and -women, with ramifications for both the accumulation and loss of cultural diversity (e.g., ref. 82). We simulated two types of populations. The first is not subdivided: All individuals share the same tool repertoire. The second is divided into two social groups, thus affecting N_{Tool}: One of the two social groups, comprising a fraction C_{elite} of the population, knows the full tool repertoire; the rest of the population knows only half of the tool repertoire. These groups are not separated spatially but rather by societal roles so that knowledge in one subdivision (e.g., shamans) is different from that in the population as a whole.

Results

Lucky Leaps Only. When tools are added only along the main axis and are not lost, the mean accumulation of tools is linear (see analytical derivation in *SI Appendix, SI2: Analytical Predictions*). This plot appears punctuated and stepwise (Fig. 2*A*, *Left Inset*), but not in the way that the empirical data appear punctuated

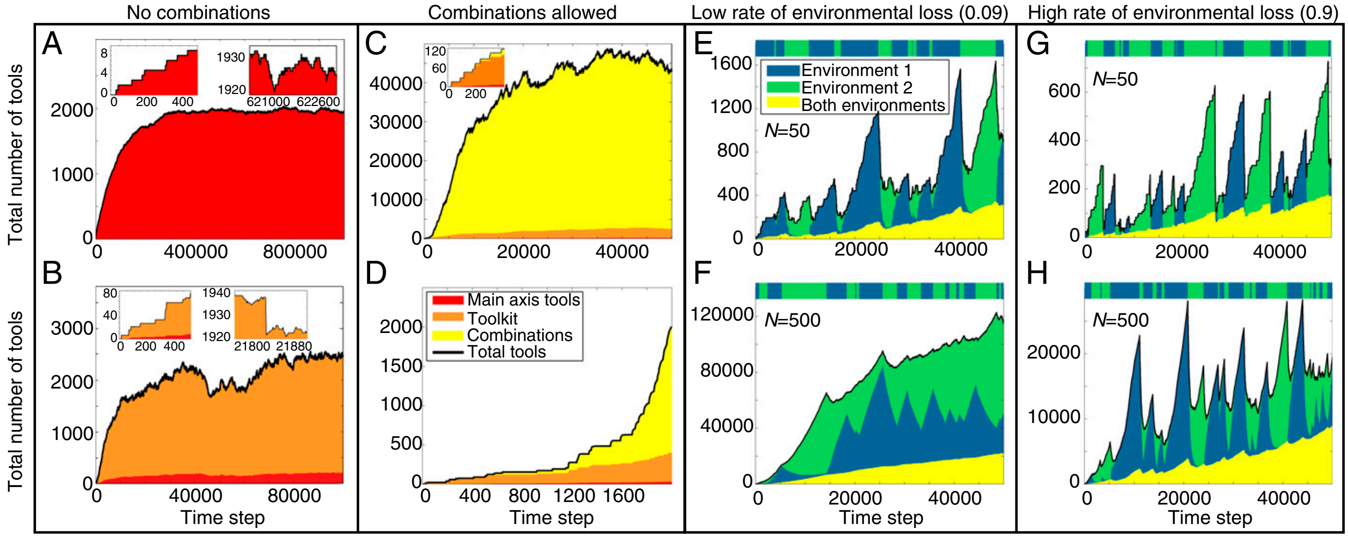

Fig. 2. Simulated cultural evolution in constant (*A*–*D*) and alternating (*E*–*H*) environments. The black line indicates the total number of tools, and a stacked histogram shows the types of tools at each time step. (*A*–*D*) Main-axis (red), toolkit (orange), and combination (yellow) tools; (*E*–*H*) tools that are useful only in environment 1 (blue), only in environment 2 (green), or in both environments (yellow). Each graph depicts a single simulation run. (*A*) The lucky leap innovation process is the only source of new tools. (*Left Inset*) The first 500 time steps, during which no loss occurred. (*Right Inset*) The dynamics of tool invention and loss when the number of tools is near steady state. (*B*) Here, main-axis tools have an associated toolkit (mean size 10.5 tools); $P_{toolkit} = 0.5$ per tool. (*Left Inset*) Early tool accumulation. (*Right Inset*) The dynamics near the steady state. In *A* and *B*, $P_{SpontLoss} = 0.001$ per tool. (*C*) Here, main-axis tools can combine both with one another and with existing combinations. Toolkit tools initially outnumber combinations (*Inset*), but combinations quickly dominate the tool repertoire. $P_{SpontLoss} = 0.01$, $P_{toolkit} = 0.5$, $P_{combine} = 0.5$, $P_{combUseful} = 0.2$. (*D*) Main-axis tools can combine both with one another and with existing combinations; $P_{SpontLoss} = 0$, $P_{toolkit} = 1$, $P_{combine} = 1$. There is exponential increase in the tool repertoire size, dominated by combination tools. In *A*–*D*, $N = 100$, $P_{lucky} = 0.002$ per individual. (*E*–*H*) Alternating environments. The bar at the top of each graph indicates the environmental state (green/blue) at each time step. Population size is 50 in *E* and *G* and is 500 in *F* and *H*; the probability of loss of tools that are not useful in the current environment is low (0.09) in *E* and *F* and high (0.9) in *G* and *H*. Additional parameters are $P_{lucky} = 0.001$, $P_{SpontLoss} = 0$, $P_{toolkit} = 0.05$, $P_{combine} = 0.05$, $P_{switch} = 0.001$, $P_{envUseful} = 0.1$. The *y* axes differ in all panels, and comparisons between panels should reflect relative changes and not the absolute number of tools. Full parameter lists for Figs. 2 and 3 can be found in *SI Appendix*, Table S1.

(3–5): Each step in the left inset of Fig. 2*A* represents the addition of a single innovation.

In simulations with stochastic cultural loss, the number of main-axis tools in a population approaches equilibrium (Fig. 2*A* and *SI Appendix*, *SI2: Analytical Predictions*); several existing models showed similar results (35, 40, 47, 48, 50, 51, 53). For given rates of lucky leaps and stochastic losses, this equilibrium, which depends on population size, *N*, is characteristic of the population and can be regarded as its cultural carrying capacity. [Here, "carrying capacity" differs in meaning from its use in the literature of human demography (e.g., ref. 83)].

Lucky Leap and Toolkit Innovation. In simulations with toolkit innovation, patterns occur that have been reported in the archaeological record, namely periods of stasis interspersed with bursts of rapid change (Fig. 2*B*, *Left Inset* and *SI Appendix*, *SI2: Analytical Predictions* and Figs. S4.1–S4.3). With stochastic tool loss, we again observe that the number of tools in the population approaches a cultural carrying capacity, dependent on *N* (*SI Appendix*, *SI2: Analytical Predictions*, *SI3: Analytical Simulations*, and *SI4: Extended Results*). The trajectory of the tool repertoire is strongly affected by both the number of time steps in the simulation and the interplay of the various parameters (*SI Appendix*, *SI4: Extended Results* and *SI5: Sensitivity of the Model to Parameter Values*).

Strikingly, most cultural losses are small, resulting from the loss of individual toolkit tools, but occasionally the size of the tool repertoire drops sharply, reflecting the loss of a main-axis tool together with the tools that are associated with it (Fig. 2*B*, *Right Inset*). The rates of recovery following these occurrences differ: Recovery from the loss of a main-axis tool requires a rare occurrence, whereas a tool lost from a toolkit is likely to be reinvented swiftly because the specific context in which it is useful still exists in the population.

Lucky Leap Innovation and Innovative Tool Combination. Polynomial or exponential growth of the number of tools accumulated by a population has been reported from analysis of empirical data (1–3). The two schemes of innovative combination described earlier lead, respectively, to these two patterns (*SI Appendix*, *SI2: Analytical Predictions* and *SI4: Extended Results*). This growth consists of bursts of change interspersed by static periods, as seen before; however, when innovative combinations occur, every additional main-axis tool can lead to larger increases in the tool repertoire, because the number of possible combinations associated with a main-axis tool depends critically on the number of previously existing tools (Fig. 2*C* and *SI Appendix*, *SI1: Extended Model Description*, *SI3: Analytical Simulations*, *SI4: Extended Results*, and Fig. S4.1*D*). Accordingly, the loss of a main-axis tool that arose at a later time step can lead to a greater drop in the size of the tool repertoire. This decrease is in contrast with reductions in the repertoire size associated with the loss of whole toolkits, because a toolkit's size is independent of the repertoire size. The differential magnitude of loss that is associated with the loss of a main-axis tool depends on the scheme by which combination tools are associated with main-axis tools: The increase in the magnitude of loss does not occur when every combination tool is associated with its constituent tools (*SI Appendix*, *SI6: Loss of Combinations Following Loss of Their Constituents*).

An additional invention pathway in which a main-axis tool can be the result of a combination of existing tools is explored in *SI Appendix*, *SI7: Groundbreaking Combinations as an Additional Source of Main Axis Tools*. This pathway is somewhat similar to Schiffer's cascade model, in which a set of interacting artifacts can spur a burst of invention as people attempt to improve on them (84–86). In our model, this pathway creates a positive feedback loop in which combinations give rise to main-axis tools, which in turn increase the number of possible combinations. In some parameter regimes this process leads to the accumulation of tools at a rate greater than that described by a simple exponential. In some cases it also leads to a transition, as the tool repertoire grows, from a punctuated trajectory of tool accumulation to a smooth trajectory.

All Three Processes: Lucky Leap Innovation, Toolkit Innovation, and Innovative Combination. Combining the three creative processes leads to punctuated accumulation of tools triggered by each occurrence of a lucky leap. The size of the toolkit associated with each main-axis tool is independent of the momentary repertoire size, but the number of potential innovative combinations associated with each main-axis tool increases with repertoire size. Accordingly, toolkit tools dominate the repertoire in earlier stages of cultural accumulation and combination tools dominate at later stages (Fig. 2*C* and *Inset*).

This pattern is not observed under all parameter regimes; if toolkit and combination tools appear at very low rates, near the rate of lucky leaps, many of the potentially useful niches for these two types of tools might remain unfilled, and toolkit and combination tools might accumulate at similar rates. In general, different rates for the toolkit innovation and innovative combination processes can give rise to a range of curves between the one that describes the main-axis tools alone (Fig. 2*A*) and the one describing the case in which the toolkit and combination axes are populated almost immediately (Fig. 2*D* and *SI Appendix*, *SI2: Analytical Predictions* and *SI3: Analytical Simulations*).

In addition to their effect on the shape of the curve that describes change in the repertoire size, the relative rates of the creative processes dramatically affect the extent to which this curve is punctuated (*SI Appendix*, *SI5: Sensitivity of the Model to Parameter Values* and Figs. S5.1–S5.4). Additionally, whether the accumulation of tools appears smooth or stepwise can depend on the total number of time steps observed (compare Fig. 2 *A–C* with their respective *Insets*).

For a wide range of parameter combinations, stochastic loss of tools alongside all three creative processes leads the repertoire size to reach a steady state that reflects the population's cultural carrying capacity, dependent on its size and the rates of loss and invention (*SI Appendix*, *SI2: Analytical Predictions*, *SI3: Analytical Simulations*, and *SI5: Sensitivity of the Model to Parameter Values*).

Environmental Shifts. A shift in environmental conditions may bring about loss of tools that are not useful in the new environment. Because the parameter that determines the rate at which this loss happens, $P_{EnvLoss}$, may be quite high, and because this loss process could act on many tools at once, sudden and dramatic decreases in the number of tools may follow an environmental change, even in large populations. The pattern of tool loss as a result of environmental change thus may appear less dependent on the size of a population than stochastic loss through drift, demonstrated in Fig. 2 *E–H*. When $P_{EnvLoss}$ is high, nearly all tools that are useful in a single environment are lost following each environmental shift, for both small and large population sizes (Fig. 2 *G* and *H*, respectively). In larger populations, many new tools that are useful in the new environment are invented by the time that all non-useful tools are lost (Fig. 2*H*). In small populations, however, a sharper decrease in the overall number of tools occurs following an environmental change (Fig. 2*G*). Importantly, if $P_{EnvLoss}$ is small, the qualitative differences between populations of different sizes are greater (Fig. 2 *E* and *F*): In a large population, not all tools that lose usefulness are lost following environmental change, and the overall relative change in tool repertoire size is small, whereas in a smaller (but otherwise similar) population, losses are large relative to the number of tools in the population, and these losses are quite sudden.

The rate of environmental change affects both the type of tools that accumulate in a population and the severity of a cultural

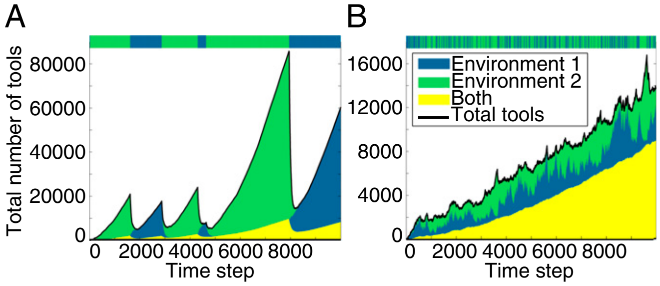

Fig. 3. Simulated cultural evolution with lucky leap, toolkit, and combination processes as well as environmentally mediated loss of tools. The environment switches between two possible states. In *A* the rate of environmental change is 0.0001 per generation, and in *B* it is 0.01 per generation; other parameters are the same. (*A*) When the environment changes infrequently, each change can initiate a large crash in the number of tools. (*B*) When the environment changes frequently, tools that are useful in both environments accumulate over time. Note that the *y* axes differ in *A* and *B*. Additional parameters are $N = 100$, $P_{lucky} = 0.002$, $P_{SpontLoss} = 0$, $P_{toolkit} = 0.05$, $P_{combine} = 0.05$, $P_{envUseful} = 0.1$, $P_{EnvLoss} = 0.1$.

loss event. If the environment changes very rarely, a population's tool repertoire can become highly specialized to the environment; then a rare environmental switch can lead to a precipitous drop in the number of tools (Fig. 3). In contrast, if environmental changes occur frequently, the population mainly accumulates tools that are useful in multiple environments. Each environmental change thus is less disastrous for these cultural generalists because a higher percentage of their tools are retained after an environmental switch (Fig. 3).

Population Subdivision and Unequal Distribution of Tools. Cultural population structure, in the sense that different subpopulations possess knowledge about different subsets of the tool repertoire, can lead to very different trajectories of cultural accumulation. Fig. 4 graphs the mean number of tools near equilibrium for various population sizes in unstructured populations (black curve). This number is compared with the mean number of tools in 100-individual populations divided into two subgroups, with the knowledge of half of the tools concentrated in one subgroup (the cultural elite) and the rest of the tools known by all individuals in the population (red curve). The red points are simulation results for different sizes of this cultural elite subgroup. The number of tools at equilibrium in each structured population is similar to the number of tools in a smaller unstructured population, suggesting that the notion of cultural effective population size (N_{CE}) is useful in such cases. Thus, for example, the tool repertoire in a structured population of 100 individuals in which 10% of individuals know the full tool repertoire and the rest of the population knows only 50% of the tools is similar to the tool repertoire in an unstructured population of less than 75 individuals. To demonstrate the potential effect of the unequal distribution of knowledge among subgroups, we simulated a population divided into two subgroups, in which the cultural elite subgroup consists of 10% of the population and a different fraction of the overall tools is known only to this subgroup (blue curve). As one might expect, the distribution of knowledge has a dramatic effect on the population tool repertoire. Near the extreme of the simple knowledge distribution studied here (the leftmost section of the blue graph in Fig. 4), we find a population of 100 individuals carrying a tool repertoire that is smaller than that of a 50-individual unstructured population.

Note that all three graphs are nearly overlapping, demonstrating that, under our assumptions about substructure and knowledge distribution in the population, a simple linear term relates N_{CE} to N to a reasonable approximation. This relationship is not necessarily the case in general: There are multiple possible population structures and many possible distributions of knowledge among subgroups in the population, and the overall dependency pattern of tool repertoire size on population size is itself nonlinear.

Discussion

We have constructed a model that takes into account realistic aspects of the processes that produce cultural innovations. The model leads to trajectories of cultural evolution that appear qualitatively similar to those found in the archaeological and historical record on different time scales. We provide a plausible explanation for several seemingly conflicting observations that have been the source of much recent debate. In the evolutionary history of humans, these observations include evidence for exponential increases in culture (1–3); for bursts of cultural accumulation and rapid cultural change together with long periods of little observed change in the material culture (4, 11, 14, 21, 34, 35, 53, 87); and for dramatic losses of cultural diversity (8, 14–16). These observations cannot be explained by the mutation rate analogy, and the latter two have not been observed even in existing models that treat the innovative process more elaborately (e.g., refs. 47, 49, and 52).

Creativity in humans is not a single process, as noted in studies of cognitive science and psychology (57, 65, 68, 69). Further, numerous population-level factors, such as population size, environmental change, stochastic cultural losses, and population subdivision, also can affect the origin and spread of cultural traits. Here, we propose a modeling framework capable of accounting for all these processes. We include three types of creativity: one in which independent large creative leaps can occur (main-axis

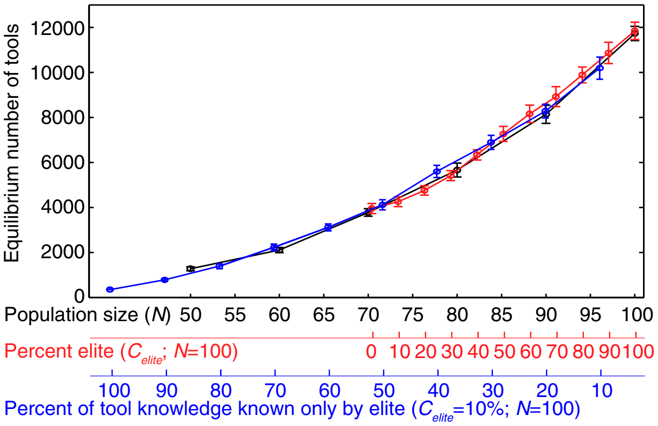

Fig. 4. Effects of population size, population subdivision, and distribution of knowledge among subgroups on tool repertoire of a population at equilibrium. After 100,000 time steps of each simulation, the equilibrium is estimated by averaging the number of tools in the last 10,000 time steps. Each point is a mean of this estimated equilibrium for 20 runs with the same parameter values; error bars bound two SEs. The plot has three *x* axes corresponding to the points of the same color. These axes have been scaled to illustrate the effect of population subdivision on effective cultural population size: The effect of changes in population subdivision is similar to the effect of changes in absolute population size. The black points represent the equilibrium number of tools for nonsubdivided populations of varying sizes (N). The red points represent the equilibrium number of tools for populations ($N = 100$) with varying subdivision sizes, where C_{elite} is the percent of the population with knowledge of the entire tool repertoire and the remainder of the population knows only 50% of the tools. The blue points represent the equilibrium number of tools for a subdivided population ($C_{elite} = 0.1$, $N = 100$) in which a certain proportion, indicated along the blue axis, of the overall tool repertoire is known only to the cultural elite and the rest is known to all individuals.

tools), another in which tools are created as part of a toolkit of tools that are made useful by a main-axis tool (or by functional analogy to that main-axis tool), and a third in which existing tools can be combined to make new tools. Of course, these three are not an exhaustive list of human innovation processes, but this framework represents a step forward in characterizing creativity as a multifaceted process. In addition, we consider populations that are subdivided into groups with different subsets of cultural knowledge, and we include processes of both stochastic and environmentally mediated cultural loss. By combining analytical derivations with a separate exploration of each of the various processes in our model and by simulating cultural evolution under a range of parameter regimes, we were able to tease apart the effects of each process and pinpoint which processes, or combination of processes, account for each observation in the range of outputs produced by our model.

We find that the process of innovation of tools via lucky leaps, with or without the invention of tools that are part of a toolkit, leads to a mean linear increase in tool repertoire size. For any given simulated population, however, tools accumulate in a stepwise trajectory whose step sizes—sudden increases in the tool repertoire—are determined by the size of the toolkit associated with each main-axis invention.

A similar stepwise trajectory, with bursts of change and periods of relative stasis, is seen when the innovative process includes invention through the combination of previously invented tools. This scenario differs from the previous one in that the magnitude of these bursts depends on the existing tool repertoire at the time of their occurrence, giving rise to a mean rate of cultural accumulation that may be polynomial or exponential depending on the details of the innovative combination process. For simplicity and tractability, we set limitations on which tools may combine with others, but in reality these limitations may not exist, further accelerating cultural accumulation.

Importantly, we find that the relative rates of the different innovation processes set not only the timescale of cultural change but also the form of the curve that describes this change. The clear trends described above are produced when invention of associated toolkit and combination tools is rapid compared with the lucky leap innovation process, a condition we view as realistic. However, in a scenario that includes all three processes, reduction in the rates of toolkit and combination tool invention leads to smoother curves, with fewer sudden bursts and with less stasis in the periods between lucky leaps (*SI Appendix, SI5: Sensitivity of the Model to Parameter Values*). Further reduction affects the overall trend and could even produce a nearly linear curve. Intermediate curves, ranging from linear to exponential, may be produced depending on the relative rates of the three invention processes.

Our framework also accommodates a number of loss processes. One is the loss of tools following their invention, when they are still rare, because of stochasticity or to a low adaptive value associated with the tool. Stochastic interindividual transmission, which accounts for such loss, is not modeled explicitly. Instead, we use mean rates of loss and fixation (justified in refs. 49 and 52) (*SI Appendix, SI1: Extended Model Description*); this type of loss can be viewed as analogous to a decrease in the rates of the various innovation processes.

The second type of loss is the result of stochastic drift of tools that previously had reached their equilibrium frequency. In line with refs. 49 and 52, which model tool transmission explicitly, this loss may happen to every tool, with a probability inversely proportional to the number of individuals that know it. In most scenarios, this loss leads to the overall repertoire size reaching a steady state at a level that is dependent on the population size, the loss rate, and the invention rate, i.e., the population's cultural carrying capacity (*SI Appendix, SI2: Analytical Predictions*). Importantly, in our framework, stochastic loss of a main-axis tool brings about the immediate loss of all its associated toolkit and combination tools. Apart from affecting the value at which the repertoire size stabilizes, this process leads to sudden losses of suites of tools because of endogenous features of the model and without the need to invoke external factors such as changes in environment or population size. Such punctuation has been regarded as characteristic of cultural evolution (3–5).

Third, tools can be lost in our framework following an environmental change that renders some of the tools useless, which may provide an alternative explanation for empirical observations of sudden cultural losses. The rate of environmental change and number of possible environments affect the trajectory of cultural evolution; for example, a low rate of environmental switching would lead to a major decrease in the repertoire size when change does occur, whereas frequent switching selects for tools that are useful in multiple environments and leads to modest decreases following each switch. Finally, environmental loss appears to be much less dependent on population size than the other loss processes: A tool that is useless in a new environment may be lost regardless of the number of individuals that know it; hence, if loss of tools occurs primarily as a result of environmental change, large cultural losses should be observed in populations of all sizes; however, if cultural losses seem strongly tied to population size, stochastic loss might be the dominant process. We have explored a simple representation of environmental change; our model can be used to explore additional scenarios, such as a series of nonrecurrent environmental changes such that each new environment has never been encountered before, potentially representing the changes experienced by a population during migration.

Finally, our model includes the realistic possibilities that knowledge is not evenly distributed among individuals and that some knowledge may be concentrated in a subgroup, such as medicine-men and -women. We explore a simple scenario in which a subset of knowledge is concentrated in a single elite subgroup, and we vary both the fraction of the population in the subgroup and the percentage of knowledge confined to it. Changes to either of these parameters can mimic changes in the overall population size of an unstructured population, demonstrating the utility of an effective cultural population size (Fig. 4). This scenario is simple, and further exploration is necessary to understand the effect of interactions between these parameters, including different knowledge distributions and more complex population structures.

Our results suggest that whether the cultural trajectory appears smooth or punctuated may depend critically on the studied scales of space and time. In empirical data, these scales are likely to be confounded with archaeological, anthropological, and evolutionary processes, lending importance to such questions as what was the rate of migration between populations? What was their population structure? What is the correct timescale to study cultural accumulation? To what extent is each population a separate experiment of cultural development?

Different relative rates of the various processes in our model can lead to qualitatively different trajectories. Thus, seemingly contradictory observations of trajectories of cultural evolution can be reconciled within our framework. Notably, our model offers a parsimonious explanation for the puzzling observation that cultural evolution on a long timescale consists of long periods of little change separated by short periods in which bursts of rapid change take place.

There are two alternate explanations of the punctuation. The first, suggested directly by our model, is that the periods of little change are waiting times between occurrences of large leaps, and each of these rare occurrences brings about rapid change in the form of the invention of functionally related tools, functionally analogous tools, or innovative combinations. Alternatively (e.g., refs. 18–20, 22–27, and 45), these are stretches of time in which the population is at steady state in its cultural evolution. Bursts of cultural change are hypothesized to occur following a change in one or more of the parameters that determine the cultural carrying capacity (the size of the tool repertoire at equilibrium). Such changes may involve the environment, population size, cognitive ability that determines the rates of tool invention, or cultural or genetic change that affects the rate of transmission and hence the rate of tool loss. In addition, a shift to a new equilibrium level may result from changes in the structure of the subgroups in the population or in the norms regarding the distribution of knowledge among subgroups without requiring change in the overall population size. A framework such as ours helps make these alternatives explicit and can generate predictions regarding what empirical evidence might support one explanation over others.

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1. Lehman HC (1947) The exponential increase of man's cultural output. *Soc Forces* 25(4): 281–290.
2. Darmstaedter L, Du Bois-Reymond R (1904) *4000 Jahre Pionier-Arbeit in den Exakten Wissenschaften* (JA Stargardt, Berlin).German.
3. Isaac GL (1972) Chronology and the tempo of cultural change during the Pleistocene. *Calibration of Hominoid Evolution*, eds Bishop WW, Miller JA (Scottish Academic, Edinburgh), pp 381–430.
4. Kuhn SL (2012) Emergent patterns of creativity and innovation in early technologies. *Origins of Human Innovation and Creativity* ed Scott Elias (Elsevier, Amsterdam), pp 69–88.
5. Kuhn SL (2013) Cultural transmission, institutional continuity and the persistence of the Mousterian. *Dynamics of Learning in Neanderthals and Modern Humans* eds Akazawa T, Nishiaki Y, Aoki K (Springer, Tokyo), pp 105–113.
6. Mokyr J (1990) Punctuated equilibria and technological progress. *Am Econ Rev* 80(2): 350–354.
7. Dow GK, Reed CG (2011) Stagnation and innovation before agriculture. *J Econ Behav Organ* 77(3):339–350.
8. Aiyar S, Dalgaard C-J, Moav O (2008) Technological progress and regress in pre-industrial times. *J Econ Growth* 13(2):125–144.
9. Bar-Yosef O (2002) The Upper Paleolithic revolution. *Annu Rev Anthropol* 31:363–393.
10. Clark JL (2011) The evolution of human culture during the later Pleistocene: Using fauna to test models on the emergence and nature of "modern" human behavior. *J Anthropol Archaeol* 30(3):273–291.
11. Jones TL, Klar K, eds (2010) *California Prehistory: Colonization, Culture, and Complexity* (AltaMira Press, Lanham, MD).
12. Brumm A, Moore MW (2005) Symbolic revolutions and the Australian archaeological record. *Camb Archaeol J* 15(2):157–175.
13. d'Errico F, Stringer CB (2011) Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philos Trans R Soc Lond B Biol Sci* 366(1567):1060–1069.
14. Henrich J (2004) Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses: The Tasmanian case. *Am Antiq* 69(2):197–214.
15. Hill KR, et al. (2011) Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* 331(6022):1286–1289.
16. Russo L (2004) *The Forgotten Revolution* (Springer Science and Business Media, New York).
17. Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324(5932):1298–1301.
18. Ambrose SH (2001) Paleolithic technology and human evolution. *Science* 291(5509): 1748–1753.
19. Mithen SJ (1996) *The Prehistory of the Mind: A Search for the Origins of Art, Religion and Science* (Thames & Hudson, London).
20. Klein RG (2000) Archeology and the evolution of human behavior. *Evolutionary Anthropology: Issues News and Reviews* 9(1):17–36.
21. Klein RG (2008) Out of Africa and the evolution of human behavior. *Evolutionary Anthropology: Issues News and Reviews* 17(6):267–281.
22. Marzke MW (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102(1):91–110.
23. Niewoehner WA (2001) Behavioral inferences from the Skhul/Qafzeh early modern human hand remains. *Proc Natl Acad Sci USA* 98(6):2979–2984.
24. deMenocal PB (1995) Plio-Pleistocene African climate. *Science* 270(5233):53–59.
25. Brain CK (1981) The evolution of man in Africa: Was it a consequence of Cainozoic cooling. *Transactions of the Geological Society of South Africa* 84:1–19.
26. Bar-Yosef O (1995) The role of climate in the interpretation of human movements and cultural transformations in western Asia. *Paleoclimate and Evolution with Emphasis on Human Origins*, eds. Vrba ES, Denton GH, Partridge TC, Burckle LH (Yale Univ Press, New Haven, CT), pp 507–523.
27. Vrba ES (1995) *Paleoclimate and Evolution, with Emphasis on Human Origins* (Yale Univ Press, New Haven, CT).
28. Buchanan B, O'Brien MJ, Collard M (2015) Drivers of technological richness in prehistoric Texas: An archaeological test of the population size and environmental risk hypotheses. *Archaeol Anthropol Sci*, 10.1007/s12520-015-0245-4.
29. Collard M, Kemery M, Banks S (2005) Causes of toolkit variation among hunter-gatherers: A test of four competing hypotheses. *Canadian Journal of Archaeology* 29(1):1–19.
30. Collard M, Buchanan B, O'Brien MJ (2013) Population size as an explanation for patterns in the paleolithic archaeological record: More caution is needed. *Curr Anthropol* 54(S8):S388–S396.
31. Boyd R, Richerson PJ (1985) *Culture and the Evolutionary Process* (Chicago Univ Press, Chicago).
32. Rogers AR (1988) Does biology constrain culture? *Am Anthropol* 90(4):819–831.
33. Richerson PJ, Boyd R (2008) *Not by Genes Alone: How Culture Transformed Human Evolution* (Univ of Chicago Press, Chicago).
34. Kline MA, Boyd R (2010) Population size predicts technological complexity in Oceania. *Proc Biol Sci* 277(1693):2559–2564.
35. Shennan S (2001) Demography and cultural innovation: A model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal* 11(1):5–16.
36. Collard M, Buchanan B, O'Brien MJ, Scholnick J (2013) Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunter-gatherers. *Philos Trans R Soc Lond B Biol Sci* 368(1630):20120412.
37. Read D (2006) Tasmanian knowledge and skill: Maladaptive imitation or adequate technology? *Am Antiq* 71(1):164–184.
38. Henrich J (2006) Understanding cultural evolutionary models: A reply to Read's critique. *Am Antiq* 71(4):771–782.
39. Read D (2012) *Population Size Does Not Predict Artifact Complexity: Analysis of Data from Tasmania, Arctic Hunter-Gatherers, and Oceania Fishing Groups* (UCLA Center for Human Complex Systems, Los Angeles).
40. Kempe M, Lycett SJ, Mesoudi A (2014) From cultural traditions to cumulative culture: Parameterizing the differences between human and nonhuman culture. *J Theor Biol* 359:29–36.
41. Zilhão J, et al. (2010) Symbolic use of marine shells and mineral pigments by Iberian Neandertals. *Proc Natl Acad Sci USA* 107(3):1023–1028.
42. Bentley RA, O'Brien MJ (2011) The selectivity of social learning and the tempo of cultural evolution. *J Evol Psychol (Bp)* 9(2):125–141.
43. Vaesen K (2012) Cumulative cultural evolution and demography. *PLoS One* 7(7): e40989.
44. Coleman DA, Schofield R (1988) *The State of Population Theory: Forward from Malthus* (Basil Blackwell, Oxford).
45. Aoki K (2014) Modeling abrupt cultural regime shifts during the Paleolithic and Stone Age. *Theor Popul Biol* 100C:6–12.
46. Aoki K, Lehmann L, Feldman MW (2011) Rates of cultural change and patterns of cultural accumulation in stochastic models of social transmission. *Theor Popul Biol* 79(4):192–202.
47. Enquist M, Ghirlanda S, Jarrick A, Wachtmeister C-A (2008) Why does human culture increase exponentially? *Theor Popul Biol* 74(1):46–55.
48. Enquist M, Ghirlanda S (2007) Evolution of social learning does not explain the origin of human cumulative culture. *J Theor Biol* 246(1):129–135.
49. Enquist M, Ghirlanda S, Eriksson K (2011) Modelling the evolution and diversity of cumulative culture. *Philos Trans R Soc Lond B Biol Sci* 366(1563):412–423.
50. Strimling P, Sjöstrand J, Enquist M, Eriksson K (2009) Accumulation of independent cultural traits. *Theor Popul Biol* 76(2):77–83.
51. Lehmann L, Aoki K, Feldman MW (2011) On the number of independent cultural traits carried by individuals and populations. *Philos Trans R Soc Lond B Biol Sci* 366(1563):424–435.
52. Lewis HM, Laland KN (2012) Transmission fidelity is the key to the build-up of cumulative culture. *Philos Trans R Soc Lond B Biol Sci* 367(1599):2171–2180.
53. Mesoudi A (2011) Variable cultural acquisition costs constrain cumulative cultural evolution. *PLoS One* 6(3):e18239.
54. Fogarty L, Wakano JY, Feldman MW, Aoki K (2015) Factors limiting the number of independent cultural traits that can be maintained in a population. *The Replacement of Neanderthals by Modern Humans*, ed Terashima H (Springer, Tokyo).
55. Cavalli-Sforza L, Feldman MW (1981) *Cultural Transmission and Evolution* (Princeton Univ Press, Princeton, NJ).
56. Mesoudi A, Whiten A, Laland KN (2006) Towards a unified science of cultural evolution. *Behav Brain Sci* 29(4):329–347, discussion 347–383.
57. Fogarty L, Creanza N, Feldman MW (2015) Cultural evolutionary perspectives on creativity and human innovation. *Trends Ecol Evol*, in press.
58. Ihara Y, Feldman MW (2004) Cultural niche construction and the evolution of small family size. *Theor Popul Biol* 65(1):105–111.
59. Creanza N, Fogarty L, Feldman MW (2012) Models of cultural niche construction with selection and assortative mating. *PLoS One* 7(8):e42744.
60. Creanza N, Fogarty L, Feldman MW (2013) Exploring cultural niche construction from the Paleolithic to modern hunter-gatherers. *Dynamics of Learning in Neanderthals and Modern Humans*, eds Akazawa T, Nishiaki Y, Aoki K (Springer, Tokyo) Vol. 1, pp 211–228.
61. Fogarty L, Creanza N, Feldman MW (2013) The role of cultural transmission in human demographic change: An age-structured model. *Theor Popul Biol* 88:68–77.
62. Rendell L, Fogarty L, Laland KN (2011) Runaway cultural niche construction. *Philos Trans R Soc Lond B Biol Sci* 366(1566):823–835.
63. Flynn EG, Laland KN, Kendal RL, Kendal JR (2013) Target article with commentaries: Developmental niche construction. *Dev Sci* 16(2):296–313.
64. Premo LS (2015) Mobility and cultural diversity in central-place foragers: Implications for the emergence of modern human behavior. *Learning Strategies and Cultural Evolution During the Palaeolithic*, eds Aoki K, Mesoudi A (Springer, Tokyo), pp 45–65.

65. Merrotsy P (2013) A note on big-C Creativity and little-c creativity. *Creat Res J* 25(January 2015):474–476.
66. Madjar N, Greenberg E, Chen Z (2011) Factors for radical creativity, incremental creativity, and routine, noncreative performance. *J Appl Psychol* 96(4):730–743.
67. Stein MI (1987) Creativity research at the crossroads: A 1985 perspective. *Frontiers of Creativity Research: Beyond Basics*, ed Isaksen SC (Bearly, Buffalo, NY), pp. 417–427.
68. Dietrich A (2004) The cognitive neuroscience of creativity. *Psychon Bull Rev* 11(6): 1011–1026.
69. Boden MA (1990) *The Creative Mind: Myths and Mechanisms* (Routledge, London).
70. Kolodny O, Edelman S, Lotem A (2015) Evolved to adapt: A computational approach to animal innovation and creativity. *Curr Zool* 61:350–367.
71. Kahrs BA, Jung WP, Lockman JJ (2013) Motor origins of tool use. *Child Dev* 84(3): 810–816.
72. Christensen CM (1997) *The Innovator's Dilemma: When New Technologies Cause Great Firms to Fail* (Harvard Business School Press, Cambridge, MA).
73. Kuhn TS (1962) *The Structure of Scientific Revolutions* (The Univ of Chicago Press, Chicago).
74. Youn H, Strumsky D, Bettencourt LMA, Lobo J (2015) Invention as a combinatorial process: Evidence from US patents. *J R Soc Interface* 12(106):20150272.
75. Bak P, Sneppen K (1993) Punctuated equilibrium and criticality in a simple model of evolution. *Phys Rev Lett* 71(24):4083–4086.
76. Newman CM, Cohen JE, Kipnis C (1985) Neo-Darwinian evolution implies punctuated equilibria. *Nature* 315(6018):400–401.
77. Gould SJ, Eldredge N (1977) Punctuated equilibria: The tempo and mode of evolution reconsidered. *Paleobiology* 3(2):115–151.
78. Gersick C (1991) Revolutionary change theories: A multilevel exploration of the punctuated equilibrium paradigm. *Acad Manage Rev* 16(1):10–36.
79. Wollin A (1999) Punctuated equilibrium: Reconciling theory of revolutionary and incremental change. *Syst Res Behav Sci* 16(4):359.
80. O'Brien MJ, Lyman RL, Mesoudi A, VanPool TL (2010) Cultural traits as units of analysis. *Philos Trans R Soc Lond B Biol Sci* 365(1559):3797–3806.
81. Oswalt WH (1976) *An Anthropological Analysis of Food-Getting Technology* (Wiley, New York).
82. Mokyr J (2015) Economics. Intellectuals and the rise of the modern economy. *Science* 349(6244):141–142.
83. Seidl I, Tisdell CA (1999) Carrying capacity reconsidered: From Malthus' population theory to cultural carrying capacity. *Ecol Econ* 31(3):395–408.
84. Schiffer MB (1996) Some relationships between behavioral and evolutionary archaeologies. *Am Antiq* 61(4):643–662.
85. Schiffer MB (2005) The devil is in the details: The cascade model of invention processes. *Am Antiq* 70(3):485–502.
86. O'Brien MJ, Bentley RA (2011) Stimulated variation and cascades: Two processes in the evolution of complex technological systems. *J Archaeol Method Theory* 18(4): 309–335.
87. Sharon G, Alperson-Afil N, Goren-Inbar N (2011) Cultural conservatism and variability in the Acheulian sequence of Gesher Benot Ya'aqov. *J Hum Evol* 60(4):387–397.