Eusociality and other improbable evolutionary outcomes can be accelerated by trait hitchhiking in boom-bust feedback loops

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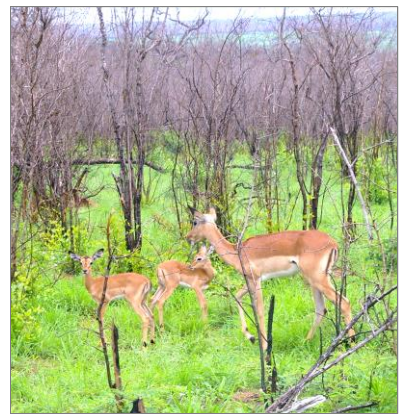
Here I analyze the brush-fire cycle behind the brushy frontier of a grassland, seeking evolutionary feedback loops for large grazing animals and their hominin predators. The burn scar's new grass is an empty niche for grass-specialized herbivores, which evolved from mixed feeders only in the early Pleistocene. The frontier subpopulation of grazers that discovers the auxiliary grassland quickly multiplies, creating a secondary boom among predators. Following this boom, a bust occurs several decades later when the brush returns; it squeezes both offshoot populations back into their core grasslands population. For both prey and predators, such a feedback loop can shift the core's gene frequencies toward those of the brush explorers. Any brush-relevant allele could benefit from this amplifying feedback loop, so long as its phenotypes concentrate near where empty niches can open up in the brush; with hitchhiking, improved survival is unnecessary. Cooperative nurseries in the brush's shade should concentrate the alleles favoring eusociality, enabling their amplification.

It is important to analyze evolution's fast tracks because they can occasionally pre-empt the more familiar slow tracks. The traditional Darwinian approach looks to some immediate usefulness that allows differential survival to slowly operate on current variations in a trait.

Here I am instead looking for a self-sustaining process in the habitat, then asking if it could affect a trait in the manner that a catalyst increases chemical reaction rates. A desirable feature of such a process would be amplifying feedback, where some fraction or function of the output feeds back to become part of the input during the next time step, as in the compounding of interest.

I earlier illustrated (1) how feedback could operate on a broad front during an ice-age cycle. A more useful case to analyze is the boom and bust that follows a brush fire; they recur far more often than climate change. In a month, the burn scar becomes an auxiliary grassland (Fig. 1) supporting a population boom for large grazing animals and their dependent predators such as *Homo erectus*. The bust comes decades later when returning brush squeezes the boom time population out of the burn scar; then, many end up in the parent population, the setup for feedback. Here I explore the boom-and-feedback process and show how it can enable trait hitchhiking in evolution.

This analysis of the brush-fire feedback loop demonstrates an exception to the usual way an adaptation is shaped by natural selection. Boom-and-bust feedback loops can allow an unrelated trait to repeatedly hitchhike; it need not be useful to be repeatedly amplified. It was only when grazer booms began 2.4 mya (2) that hitchhiking became available to amplify *Homo* traits such as eusociality and behavioral versatility.



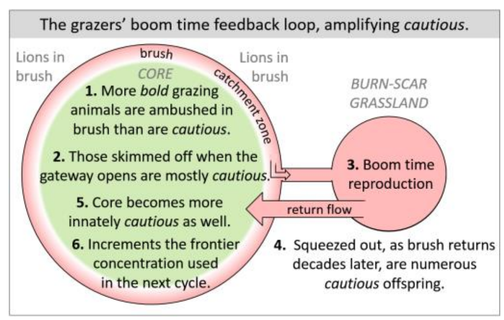


Fig. 1. Antelope and the new grass in Kruger National Park, two months after a brush fire. Credit: Navashni Govender, fire ecology manager, South African National Parks.

Fig. 2. The grazers' brush-fire version of the selective boom time feedback loop. Cautious grazers from the frontier (many of the bold were eaten earlier) discover the burn scar and experience a population boom. Later, their mostly *cautious* descendants are squeezed out as the brush returns, making the core and its frontier more *cautious*.

Conditions for the boom in the feedback loop

The mile-high savannas of East Africa and South Africa have a particularly high rate of lightning strikes. Many brush fires result and, in the dry season, a large area can burn. Soon, grass sprouts (Fig. 1). If the burn scar has a path connecting to inhabited grassland, grazing animals from the brush frontier subpopulation will move in, followed by their predators.

This offshoot grazer population quickly doubles and re-doubles to fill the empty niche, all based on the grazer genes at the brush frontier. They may differ from those of the core population, making gene flow non-random (3).

To illustrate, consider the heritable cautious-to-bold spectrum for exploratory behaviors. In the period before a lightning strike, the lions and leopards hiding in the brush would preferentially reduce the frontier numbers of the bold grazers, and so the innately cautious ones would get more of the population boom when the corridor to the empty niche (Fig. 2.2) suddenly opens up via one of the "dead end" paths.

In subsequent decades, as returning brush gradually replaces the temporary grass, their offspring are squeezed out of the burn scar (Fig. 2.4). If they join the parent population, they make both its grasslands core and brush frontier (Fig. 2.6) more innately cautious.

The cycle repeats because lightning strikes keep iterating the loop. Lightning may also cause grass fires but grasses recover so quickly that grazing resources are little affected. The leaf-eating browser populations may be somewhat reduced by a brush fire; populations of mixed-feeders such as modern elephant and impala need not experience a decades-long change in overall food resources.

Thus there is no boom-time population with a feedback loop except for brush fires near grasslands inhabited by grass-specialized herbivores–and their predators. Minor climate fluctuations can enhance the amplification process: droughts beforehand or stronger winds make for a larger burn scar, a bigger population boom, and thus more return flow into the core decades later.

Quickly shifting gene frequencies

Most genes come in only one fixed version but some have slightly different versions called alleles, produced earlier by mutations. The allele varieties in play help generate, for example, the 15% spread in human brain size within a generation.

Gene frequency refers to the relative proportion of alleles in the gene's population. Here, *concentrating* an allele refers to making it relatively more common in the catchment zone and *amplification* to the entire process that increases an allele's numbers in the core, thus shifting the allele proportion there. Altering allele proportions, often in multiple genes, is the route to an adaptation, such as making the population more innately cautious.

Even without feedback, differential survival shifts the frontier gene frequencies, relative to the core, but mixing is slow to shift the core when, say, the frontier subpopulation is only 5% of the total. However, feedback's consolidation of a nonstandard offshoot population back into a parent population quickly shifts its gene frequencies in the manner of Sewall Wright's shifting balance theory (4).

The sequence repeats with the next lightning strike, perhaps somewhere else along the brushy border. How many complete episodes does it take to triple the core's numbers of a frontier-relevant allele?

Only five (Fig. 3). Were the contrasts between core and frontier not so exaggerated, it might be 50 repeats instead but that is still a short time by the continuous-mixing standard.

Selective survival on the frontier may provide the skewed setup, but the rapid tripling comes from filling the empty niche with the frontier's gene frequencies and the later consolidation of this biased offshoot population into the larger parent population to create feedback.

Amplifying *cautious* is but one example of a trait that can be enhanced by this feedback mechanism.

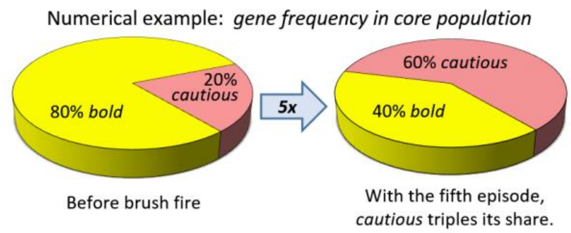


Fig. 3. Core population gene frequencies, before and after five boom-and-bust feedback episodes using a burn scar that is one-fourth the size of the core grassland (here I fix the frontier at 80% *cautious* to emphasize the larger effect of sheer numbers). After the squeeze by returning brush, the core becomes 32% *cautious*, then 41%, 49%, 55%, and 60%. Tripling in five episodes depends on the core starting at 20% *cautious*. If it starts at 50%, the five episodes advance the core from 50% to 71% *cautious*. Such a simple model using relative population sizes is possible because the desideratum, gene frequency, is itself a ratio, because an overfull core is handled by carrying capacity in an unchanged way, and because I assume no selective survival changes during amplification.

The Darwinian process and state-dependent fecundity

For the gradual quality improvement that we associate with natural selection, I earlier identified six essential conditions for a full-fledged Darwinian process, which I formulated in more general terms to cover non-genetic examples such as competing cerebral codes (5,6,7):

1. There must be a pattern involved (such as the ordering of a DNA string) that stores the heritable information;
2. The pattern must be copied somehow; indeed, that which is semi-reliably copied may help to define the pattern, as in genes. This copying requirement is likely to restrict patterns to one-dimensional ones.
3. Variant patterns must arise occasionally (alleles from mutations and copying errors).
4. The pattern and its variant must compete with one another for occupation of a limited work space (much as bluegrass and crabgrass compete for space in a back yard).
5. The copying competition between variants is biased by a multifaceted environment (for grass: soil moisture, rate of cropping by grazers, nutrient availability). This condition is Darwin's natural selection.
6. A variant pattern is more likely to arise from the more successful of the current patterns, simply because the successful are more numerous as a target for mutation-making. This is Darwin's

inheritance principle, promoting continuing improvement in the trait's fit to the phenotype's environment.

Boom-and-bust feedback loops seem not to require modification of these "six essentials." This is because natural selection operates both by selective survival (mostly via deaths of the immature) and by changes in fecundity (as when double ovulation creates dizygotic twins when food quality improves). While no change in live births per mother is postulated here, the temporary boom time allows more surplus-to-requirements infants to grow up to reproduce themselves.

Boom-time amplification is consistent with a generation-skipping definition of fecundity. Counting *grandchildren per grandmother* rather than *children per mother* can allow for environmental influences that are state-dependent, such as a boom time that temporarily reduces immature mortality. Fecundity already encompasses environmental influences, as when some drinking-water sources promote a high rate of spontaneous abortion: sometimes more than half drop out (8) before the heartbeat begins six weeks after conception in humans; there is a 10-15% "miscarriage" rate thereafter.

Evolutionary hitchhiking through a feedback loop

The basic components of the burn scar feedback loop are

- a prey species that can experience a boom in the empty niche because of unused resources,
- a catchment area for wicking off into this empty niche,
- an allele concentration mechanism (natural selection or hitchhiker concentration) in the catchment, and
- a migration path from the boom territory back to the core population during the bust phase.

For the prey species, what concentrates in the catchment area might be *cautious* or a habitat preference. Or nothing. But unless the prey can experience a boom time in the empty niche (which leaves out browsers and mixed-feeders), there is little shift in the core's allele ratios for either prey or their predators.

However, unlike Fig. 3 with its fixed 80:20 allele ratio in the catchment, an increment in the core usually means some increase in the catchment zone, the traditional setup for an exponential rise. I have de-emphasized it here to better illuminate those aspects of amplifying feedback that require both a concentrating mechanism and a boom.

Hitchhiking traits in the predator species depend on all of the above but their concentration mechanism may go beyond selective survival in the catchment to include traits such as food preference and shade-seeking. Hitchhiking alleles prosper not by their own usefulness but because their phenotype got a free ride to a boom by hanging out in the burn scar's catchment zone.

It would be a mistake to view this boom-time feedback process as simply amplifying the effects of antecedent selective survival. In considering how the ragged brush border could have affected one of the predators of grazing animals, *Homo erectus*, I will use examples that do not involve differential survival, yet produce the same amplification via fecundity and survivorship (9).

In the example from grazing animals, selective survival was what made the peripheral population in the brush different from the core in the grassland. Yet if the affected individuals simply tended to have longer dwell times in the catchment zone for amplification, it will suffice. Around the loop, there need not be a filter via selective survival, which is merely one way that relevant alleles can be concentrated in the catchment zone.

Most obviously, the brush fire loop should amplify frontier habitat preference in the core population (Fig. 3.5). But it also amplifies any trait that co-locates in the brush, provided it has a concentration gradient between the core and the catchment.

Eusociality and the opportunity zones for allele amplification

Eusociality, where some individuals reduce their own lifetime reproductive potential to raise the offspring of others, underlies the most elaborate forms of social organization. Breast feeding someone else's infant serves to suppress ovulation, depressing fertility for the wet nurse. Eusociality is rarely seen in evolutionary lineages (N=19), with an odd distribution through the Animal Kingdom (10); there are only two examples among mammals and one is the *Homo* lineage.

Might eusocial alleles concentrate in the brush and be amplified in the core by the boom-and-return loop for grazing animals' predators? In addition to the tendency of many animals to stay out of the midday sun, the bodies of human infants and children demand protection from heat stroke because they have a lot of surface area for their volume. They can quickly overheat on hot days when they are not being held against a large heat sink having additional area for evaporative cooling. In cooperative nurseries, infants may outnumber wet nurses and cannot all be held simultaneously, making shade more necessary for infant survival. The shade serves to concentrate eusocial genes in the catchment zone for the burn scar's population boom for the predator species.

The repeated booms could keep shifting the overall population toward eusociality, even without selective survival judging its usefulness. Recall that the frontier's selective survival is slow to alter the genetic makeup of the core by continuous mixing because of the numerical disproportion. The feedback loop inverts this, spreading brush frontier genes and culture into the core based merely on who was in the right place (the catchment zone) at the right time (when the empty niche opened up). Many catchment-zone alleles, not merely my examples, could be amplified if a concentration gradient is maintained between core and the catchment zone.

A similar loop for amplifying antibiotic resistance

One can see the feedback loop components more generally in this hypothetical example of a loop through a bed-sore abscess serving to accelerate the development of antibiotic resistance in the systemic circulation:

- a central population of a gene that mixes (e.g., a pathogen in the bloodstream; most variants are sensitive to antibiotics, some are resistant);
- a selective mortality (the sluggish arterial circulation to an abscess allows more time for antibodies and antibiotics to act on susceptible pathogens, thus concentrating resistant variants before arriving at the abscess);
- a population boom for this biased population in early stages of the abscess; if it repeats daily, even a small boom may suffice;
- feedback from leakage of the abscess population back into the core (the venous circulation from the abscess unkinks when a bed sore is repositioned or a hot compress is applied, releasing some of the biased boom-time population into the general circulation, increasing antibiotic resistance there, along with whatever escaped antibodies);
- repeat when the vein kinks again, pumping up the resistant pathogens in circulation.

Discussion

The feedback loop provides more than the evolutionary overdrive that one might expect from my earlier analogy to catalysts. It better resembles a free ride up an escalator, where a habitat preference for its intake position enables this exception to the familiar process of shaping an adaptation by selective survival. Trait hitchhiking joins such free ride examples as Darwin's conversion of function (11) and the head start provided by an existing adaptation, from which an elaborate secondary use may develop that itself has no history of natural selection (12).

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