Survival of the Systems

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Abstract

Since Darwin, individuals and more recently genes have been the focus of evolutionary thinking. The idea that selection operates on non-reproducing, higher-level systems including ecosystems or societies has met with scepticism. But research emphasising that natural selection can be based solely on differential persistence invites reconsideration of their evolution. Self-perpetuating feedback cycles involving biotic as well as abiotic components are critical to determining persistence. Evolution of autocatalytic networks of molecules is well studied, but the principles hold for any ‘self-perpetuating’ system. Ecosystem examples include coral reefs, rainforests and savannahs. Societal examples include agricultural systems, dominant belief systems and economies. Persistence-based selection of feedbacks can help us understand how ecological and societal systems survive or fail in a changing world.

Evolution based on persistence

In times of pervasive global change it is important to ask: Why do some ecological, social or social-ecological systems dominate the world today? Why not others? Plausibly the winners we see have out-persisted other systems. But how does that work? And can we view it as an evolutionary process?

The founders of ecology and biogeochemistry thought so. Tansley [1] argued that there is “a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest”. Hutchinson [2] postulated that systems with self-correcting mechanisms tend to persist longer, and disruptive elements tend to get filtered out by causing their own extinction. Subsequent researchers argued “the criterion for selection is survival of the system” [3] and that ecosystems have become more stable over time through undergoing a winnowing series of “limited catastrophes” [4]. Archaeologists and anthropologists advanced comparable ideas involving differential persistence of cultural groups [5, 6], with state formation occurring through a sequence of “experiments”, which often fail but sometimes achieve a persistent configuration [7].

Evolutionary theory, however, has struggled to accommodate such explanations. It generally refuses to recognise **ecosystem evolution** (see Glossary) [3, 4, 8], because that involves systems of unrelated species that do not faithfully replicate as a whole – despite having some limited heritability [9]. Whilst **cultural evolution** is widely recognised [5, 10-13], and often involves only distantly related humans, most theory focuses on lower levels of selection than whole societies or cultures – because the latter do not faithfully replicate as a whole. But if both social systems and ecosystems have **irreducible properties** at the system-level, then (how) can those properties evolve?

Recent theory [14-21] highlights that natural selection does not require replication and instead can be based on variation in persistence alone. The basic idea of **persistence-based selection** is straightforward: Some systems tend to spread through space at the expense of others and persist longer over time than others, and thus come to dominate the world. Persistence in turns increases the chances of acquiring further persistence-enhancing traits – providing a potential mechanism of adaptation [17]. Variation could be amongst a population of non-interacting, non-reproducing systems, e.g. a hypothetical population of planetary-scale biospheres [17, 19, 21], or amongst *interacting* populations of non-reproducing systems [18, 20, 21] – re-opening the tantalising possibility of whole social and/or ecological system evolution.

Feedback cycles as units of persistence-based selection

Building on recent [18, 19, 22, 23] and earlier [2, 24] work, we argue that biotic feedback cycles – closed loops of causal interactions involving life – are key units of persistence-based selection. Box 1 and Table 1 relate this to existing theory.

Feedback loops have irreducible properties that cannot be exhibited by any of their individual components in isolation [24] – including the overall sign and strength ('gain') of the feedback. Abiotic systems subject to an external supply of free-energy develop structures – such as waves, galaxy spiral arms, convection cells, or snow crystals – which rely on unstable modes of motion which grow exponentially because of self-amplifying (positive) feedbacks [25]. A stationary state emerges when the free energy dissipated around these structures balances the external supply.

This provides a starting point to think about the development of complex ecological and social systems. Hypercycles [26] and other **autocatalytic networks** of molecules [27], are widely recognised as irreducible self-amplifying phenomena [28] integral to the origin of life. Autocatalytic networks can grow in complexity, as well as size, by acquiring more self-perpetuating feedback cycles [29].

However, biological systems – in contrast to abiotic ones – have the capacity to transfer context-dependent information through time or space by mechanisms including heritability and signalling, which generally involve information-carrying molecules. These uniquely biological traits provide the foundation for evolution by learning and adaptation [24, 30], including **replication-based selection**.

Feedback cycles in ecosystems [31] and social systems generally involve multiple, genetically-unrelated components, either fulfilling different functions within a cycle, or representing diversity amongst the performers of a given function. We argue that their irreducible, higher-level properties may be subject to selection based purely on differential spread and persistence – with these measures of relative system performance providing an analogue to conventional ‘fitness’ (Table 1). There are several proposed mechanisms through which such persistence-based selection could occur (Table 1) (see ‘Finding stability’). When combined with lower-level replication-based selection the result may be a form of type ‘2’ **multi-level selection** [28] (Box 1, Table 1).

We define the corresponding (ecological or social) system as comprised of multiple feedback cycles that contribute to its identity (i.e. what is maintained through time and space for it to be considered the same system) [32]. A system’s spatial boundaries may be set by physical constraints (e.g. island area) or by the extent of spatial influence of its components, their relationships, and resultant feedbacks, bounding against other systems. We define creation as when a new system identity arises, and destruction (or collapse) as when identity is lost [32]. Persistence (lifetime) can be measured as the intervening interval. Box 1 addresses the critical issue of how feedback information is transmitted through time.

For ongoing selection to occur (at the system-level) there must be a source of variation: Evolution at lower levels can give rise to changes in information at the system level [28], particularly when a new interaction or variant of an existing interaction gives rise to a new feedback cycle or a new variant of an existing feedback. Box 2 considers inter-system dispersal as a further source of variation.

Feedback cycles can be built from the **by-products** of traits that are naturally selected at lower (e.g. individual, gene) levels [33]. This reduces the problem of invoking altruism to close feedback cycles – as in that case, natural selection can favour components that disrupt or break the cycles. It differentiates this review from extensive work on the evolution of altruism by multi-level selection [28].

Feedback cycles can be continually regenerated by different organisms performing the same metabolic function with the same by-products, e.g. members of a **microbial guild** [18]. This provides continuity of information over time (Box 1) in the same gene complexes encoding particular metabolisms, regardless of the organisms carrying them [34] – as well as in the persistence of the feedback cycle structure [35] – adding for societies behavioural or symbolic **inheritance systems** [36].

Types of self-perpetuating feedback

Several key types of self-perpetuating feedback can form a basis for persistence-based selection.

Resource acquisition and recycling

Resource recycling (Fig. 1a,b) is self-perpetuating in that it decouples productivity and population size from being wholly limited by external supply fluxes of material resources, which may be meagre [21]. This benefits all members of a recycling loop. Recycling is irreducible in that it requires multiple, different, usually unrelated components, in both ecosystems and social-ecological systems.

Resource-recycling microbial ecosystems built on ‘waste’ by-products robustly emerge in evolutionary simulations [23, 35, 37-39], and in experiments [40], and can evolve into altruistic recycling [41]. Nutrient cycle assembly can be helped by ‘waste’ consumption by one microbial guild enhancing its production by another, which increases the resulting free energy yield [42]. In plant-decomposer models, natural selection for improved individual resource competition can increase system-level cycling over time [43]. Even if there is an evolutionary cost to closing a recycling loop (altruism), this can be overcome by positive fitness feedbacks within cellular clusters [41], or by recycling systems spreading at the expense of non-recycling ones, because they support denser populations [38] (Box 2). Real-world examples of recycling therefore abound. The Amazon rainforest maintains stunning productivity through highly effective nutrient recycling on otherwise very nutrient-poor highly weathered soils [44] and by recycling its own rainfall [45]. Global recycling ratios of essential elements range from ~10 for sulphur to >1000 for phosphorus [46].

An input of free energy is required to power a recycling loop (Fig. 1a), which usually comes from autotrophic members of the loop (e.g. plants). Some members may also enhance the input of the material resource(s) being recycled. For example, nitrogen fixers produce a costly, leaky public good – available nitrogen – enjoyed by other members of the ecosystem. Hence as nitrogen fixers become more common and increase available nitrogen levels, negative feedback regulates their abundance [47]. Nitrogen fixation in turn fuels a nitrogen cycle which contains diverse components and is a candidate unit of persistence-based selection [18, 19].

Other resource-acquisition strategies have a more favourable cost-benefit for the acquirers. In coral reef ecosystems, sponges filter-feed on coral mucous and dissolved organic matter from the water column and convert it to particulate organic matter, also shedding their cells, providing a resource for other ecosystem members. The resulting **sponge loop** is an integral part of the self-perpetuating recycling coral reef system that involves many unrelated functional groups and helps support a large population of sponges [48]. Other resource-acquisition and recycling strategies have evolved into tight symbioses. Some involve multiple, unrelated resource acquirers, making conventional evolutionary explanations problematic – for example, both cyanobacteria and eukaryotic algae in symbiosis with a fungus within one lichen [49].

Over geologic time, more productive resource acquisition and recycling systems have displaced less productive ones [50]. In the progressive colonisation of the land, microbial mats, lichens and non-vascular plants, have largely been displaced by vascular plant-dominated ecosystems that are more effective at acquiring and recycling nutrients [51]. Larger plants also transpire more, supporting more rainfall and hence larger plants [52]. Subsequently, angiosperm ecosystems with a resource-recycling plant-fungal relationship, have displaced gymnosperm ecosystems with a resource-acquisition plant-fungal relationship, in many areas [53].

Human agricultural systems, with 6-10 independent regional origins during the Holocene, represent hugely successful resource acquisition and recycling systems (Fig. 1b), which have spread across the world and persisted for thousands of years, accumulating countless improvements. They capture solar energy and via human and animal labour transform it into consumable calories more efficiently than previous systems dependent on wild plants. The domesticators were consequently also domesticated. More settled households could better monitor plant growth and protect plants from predation by other animals or other people. They also accumulated waste which could be recycled to infields at very low cost with high rewards to plant productivity. Where readily domesticated animals were available, recycling of animal manure added to a highly productive, self-perpetuating system [54]. The addition of charcoal and other organic matter to Amazonian soils, creating ‘terra preta’ and other ‘anthropogenic dark earths’ [55], helped the recycling of water and nutrients and plausibly boosted the success of communities using this technology [56]. Efficient water use and recycling through diverse capture, storage and irrigation systems has also been integral to the persistence of many ancient and modern societies [57].

In early agrarian societies, resource extraction began with the use of natural islands of fertility. **Landesque capital** [58] captures the idea that by investing in productivity-improving technologies (e.g. pre-Colombian use of guano as fertiliser, terracing) the population a landscape can support increases, in a self-perpetuating cycle. Whilst this can be interpreted as due to a family’s or a society’s investment in its own success, the exceedingly long duration of soil enrichments by mobile herders in African savannahs [59], provide an example of ecological legacy that is broadly dispersed to many organisms and societies. The system of pastoralism may even have locally delayed the demise of the “Green Sahara” well beyond what would be predicted from orbital-driven climate change [60]. Conversely, where land-use change degrades the environment, self-perpetuating feedbacks working in the opposite direction can bring about the collapse of social-ecological systems – for example in the Dust Bowl across the American Great Plains during the 1930s [61, 62].

Local environmental alteration

Material resources are not always the limiting factor for system productivity and spread. Sometimes environmental conditions such as temperature or pH are limiting and feedbacks alter these conditions in a manner that is self-perpetuating. In principle, such environmental alteration might derive from a single species, but in practice examples of successful artificial ecosystem selection for environmental properties [63, 64] appear to involve multiple species [64, 65] affecting the same environmental variable to differing degrees and sometimes in opposing directions.

Evolutionary simulations show that microbial ecosystems whose diverse metabolic by-products collectively improve aspects of their environment which are limiting to the growth of their constituents, have denser populations than ecosystems that degrade their environment [66]. Hence under conditions of selectively neutral genetic dispersal (Box 2) environment-improving ecosystems tend to spread and persist at the expense of environment-degrading ones [66]. Diverse real-world ecosystem engineers [67] often alter their environment in a manner that enhances their persistence. For example, different *Sphagnum* moss species contribute to acidifying and waterlogging the soil, thus perpetuating the peat bog ecosystem by preventing trees from establishing [68]. Forests of diverse tree species, in contrast, typically modify their micro-climate in a manner that enhances tree growth [69]. Reintroducing ecosystem engineers and promoting such positive feedbacks can be key to successful ecosystem restoration [70].

Humans also often improve their local environments in self-perpetuating ways. This started with fire as a technology that warms up humans in cold conditions, detoxifies food, improves caloric intake, and provides protection from predators [71]. Later the construction of buildings created a regulated micro-environment for humans (and often their domesticated livestock), which both persisted across generations and enhanced the persistence of their inhabitants.

Disturbance enhancement

Feedback between the biological members of a system and a disturbance factor that benefits that system over others can be self-perpetuating (Fig. 1c).

Grasslands promote fire and herbivory, in self-perpetuating feedbacks that displace forests. This has enabled grasslands to cover a third of the Earth’s productive land surface in just the last ~35 million years. Anti-flammability is a more plausible individual-level adaptation hence promoting flammability is argued to be a systems-level property [72]. Transplant experiments have shown that fire, rather than climate, limits the distribution of trees in the African savannah [73]. Together, fire and herbivores tend to remove trees and suppress their regeneration – forming a potentially lethal combination for woody plants [74].

Early human social groups using fire in hunting facilitated the transition of forest to grassland and savannah. This may have positively fed back on the hunters by supporting a greater food source. In Australia, small-scale Aboriginal hunting fires buffered the landscape against large-scale fires started by lightning strikes, thus maintaining greater mammal diversity [75]. The later domestication of livestock was also self-perpetuating; domesticated herbivores got rid of trees, thus tending to maintain a pasture state in which they thrived. The introduction of fire and domesticated herbivores to New Zealand illustrates self-perpetuation of the pasture state [76].

In cultural evolution, grasslands inhabited by horse-riding nomads are seen as a source region for military technological innovation and warfare [10] – where war is an extreme disturbance factor for societies. The resulting conflicts are argued to have selected for altruistic **ultra-social** traits (particularly self-sacrifice as part of an army), and through the assimilation of cultural traits of the victors, to the emergence of increased agrarian state complexity. If this complexity – resulting in resources that could be plundered – in turn led to more aggressive, war-waging behaviour, then a self-perpetuating feedback loop would be closed. Agrarian societies, by supporting a transition to grasslands and domesticating horses, may have closed a further feedback loop. For example, European settlers introduced horses to Native American communities, who then rapidly assimilated them into trade networks, hunting practices, and resistance against the invaders (e.g. the Comanche). The independent origin of this feedback, recognised in earlier Eurasian contexts [10], supports it being a potential unit of persistence-based selection.

Feedbacks involving diversification and specialisation

Self-perpetuating systems typically support diversification and specialisation within them, producing further feedback [35, 39] (Fig. 2). This is abundantly clear in societies. Productive systems based on plant and animal domestication may produce surpluses which can be concentrated in a small social segment which in turn may sponsor specialists to provide this elite with socially valuable goods. In places where cattle were domesticated, oxen could be used to extend farming well beyond the infields, providing new sources of revenue for their owners [77]. Resulting feedbacks may, ultimately, help explain the typically greater wealth concentration, technological innovation, and specialization in late prehistoric Eurasian societies than among late prehispanic societies in the Americas [78].

The intensification of labour in agriculture was incentivised at the household level and increased production at the social system level. Investment of labour into the landscape and taxation in turn provided ways of gathering and privatizing common pool resources. This began to subsume agroecosystems within larger food systems and economic systems. Further diversification and specialisation is seen in more productive social systems [79], where cycling can take new material and non-material forms – classically described by Durkheim as the shift from **mechanical solidarity** to **organic solidarity** [80].

In ecology, the most intensive resource-recycling systems, including coral reefs and the Amazon rainforest, are also the most spectacularly biodiverse, plausibly because effective recycling both requires a diversity of functional roles and supports increased diversity within those roles. The resulting **functional redundancy** [18], gives ecosystems robustness against extinctions and resilience to perturbations. Increased species diversity can increase net primary production and reduce the risk of exotic species invasion, thanks to inter-species niche complementarity and facilitative interactions that increase resource extraction and use, and make them available to the rest of the community via recycling [81, 82].

Finding stability

What constrains the spread of self-amplifying (positive) feedbacks and gives rise to stability? Individual feedbacks can be bounded by their own limited strength, by other constraints kicking in, or in biological systems by driving themselves past optimal conditions for their perpetrators and into a regime of self-stabilising (negative) feedback. More complex systems can find stable configurations through trial-and-error 'experiments' [1-4, 7]. Ashby [83] first demonstrated an abiotic mechanism for such **sequential selection** [21], whereby a system that left prescribed tolerable bounds randomly rewired its connections, repeatedly, until a stable configuration was found within tolerable bounds, which by definition tended to persist. Collapse and random rewiring destroy memory and hence the potential for evolution. However, in biological systems more incremental reconfiguration can find stability whilst retaining information through time (e.g. in the gene pool or in written records). Whilst sequential selection applies to repeated trials of one system over time,

stability-based sorting [22, 84] considers populations of interacting systems that differ in their stability properties – with the most stable coming to predominate.

In ecology, selection based on stability is recognised across a range of scales [21, 84]. Selective extinction at the species level has long been recognised [85]. In the construction of food webs [86], the steady arrival of species at a given location – thanks to natural selection favouring dispersal [87] – can add to an incumbent community or destabilise it, driving other species to extinction – but once a stable configuration is found it (by definition) persists. Recent models extend this to show how life-environment coupled systems can find stable configurations [21]. Fossil data shows stable ecological configurations prior to the End Permian mass extinction, 'random rewiring' in the aftermath, then the emergence of new stable ecological configurations [88].

Sequential selection of stable social systems is seen in the history of state formation in Madagascar, Mesopotamia and the US Southeast [7]. In the northern Pueblo region of the US Southwest there were at least four successive attempts to achieve stable socio-political formations, each ending in pulses of violence, marked declines in wealth inequality, and local and regional disaggregation [89, 90]. Each time high proportions of the population and their cultural repertoire survived. Finally, around AD 1300 relatively stable socio-political formations emerged, only to be disrupted two centuries later by the invading Spanish. Similar patterns are visible in the persistence of foraging systems across the ice age to Holocene transition in the Levant [91], and in early Holocene farming societies of southwest Central Europe [92]. They may be especially prominent among societies developing novel forms of subsistence and social organization.

Social systems contain endogenously generated practices and institutions, such as law enforcement, democracy and organised religions that promote internal stability and persistence. Whilst some are portrayed as deliberately constructed stabilising mechanisms [93], others were presumably chanced upon, but then enhanced their own persistence. Ritual can play a key role in social-ecological system regulation. For example, the ritual sacrifice of pigs among the Maring tribe of Papua New Guinea helps restore a sustainable ratio of pigs to humans, provides food, and prevents land degradation [94].

The endogenous generation of new feedbacks (e.g. by random mutation or cultural innovation) and subsequent sequential selection of persistence-enhancing ones, provides a plausible mechanism to accumulate system-level complexity, as well as stability [17-19]. However, it is too slow to account for rapid, recent cultural evolution [12] – plausibly because it lacks a mechanism for recombination of beneficial innovations occurring in different systems (Box 2).

Concluding remarks

A ‘survival of the systems’ perspective can help us understand the changing predominance of ecological, social and social-ecological systems, including those driving and responding to contemporary global change.

The ideas discussed need to be formalised and tested (see Outstanding Questions). Existing theories of feedbacks and multi-level selection could be combined. Resulting theory could be tested in the lab by sequentially assembling microbial microcosms from sequenced representatives of functional guilds, and e.g. examining the relative persistence of non-recycling and recycling systems in isolation [95], then allowing them to interact through limited mixing to see which predominates. If persistence-based selection supports system-scale evolution, then cases of convergent system evolution would be expected. For example, savannah ecosystems found in South America, Africa, India and Australia all have a similar functional structure even though the species involved differ [74]. Statistical patterns in ancient and contemporary ecosystems could also provide a test of the persistence of particular ecosystem configurations – noting the remarkable similarity of reconstructed Cambrian food webs and present ones [96]. Differential persistence as a mechanism of replacing cultural norms with more persistent ones, already has empirical support in that its timescale fits early cultural evolution [6]. System-level persistence-based selection may also explain the existence of **archaeological cultures** (or “traditions”) – for example, Pueblo societies comprised of several ethnolinguistic groups [97]. Such cultures link disparate populations, built on exchanges of people, goods, and ways of life that provide mechanisms for recombination and accumulation of technologies and practices.

The industrial revolution was propelled by self-perpetuating feedbacks between new technologies, capitalism and an expanding labour force [98]. It continues to spread around the world, as banks finance and governments subsidise resource-extraction industries, which repay them with capital and contented voters. For some, the **technosphere** has co-opted humans to perpetuate itself [99]. But powering it with fossil fuel burning cannot persist – the resource is finite and the externalities are cumulatively toxic [100]. If achieving long-term sustainability requires fundamental changes, ranging from sustainable energy and increased material recycling to different governance structures [101], these can be viewed as alternative systems to the currently predominant one. The salient questions then become: Under what conditions can such alternative systems spread at the expense of the incumbent one(s)? Must the currently predominant system fail (to persist) before another can replace it? Or can we find ways to promote collective human persistence without going through such a crude and potentially brutal selection mechanism?

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Box 1: Relationship to existing theory

Parallels and distinctions between proposed mechanisms of ‘survival of the systems’ and replication-based natural selection (Table 1) centre on the nature of information transmission over time (usually called “inheritance”) and the type of selection.

Information transmission: Particulate inheritance plays a key role in replication-based selection because it prevents variation in fitness being diluted at each generation (as would occur under blending inheritance) [102]. Feedback cycle properties arise from the combined relations of components – here often both biotic and abiotic – making information transmission more complex. Information regarding the response of a biotic variable (e.g. grass) to another biotic variable (e.g. herbivores), or an abiotic one (e.g. fire), can be encoded in a recognised [36] (e.g. genetic) inheritance system. But if such links in feedback cycles are “re-produced” by unrelated organisms performing the same function [18] (i.e. breaking parent-offspring inheritance), one must look harder for continuity of information, e.g. to a common gene complex encoding a particular response [34], or a reference text in the cultural case. In general, a complex interplay between such physical structures and their environmental context serves to interpret the structures and confer on them a functional role. Information regarding the response of an abiotic variable to a biotic one (or another abiotic one) is not encoded, yet it may be conserved e.g. because it is governed by thermodynamics. Thus at least some pertinent information transmission resides in the persistence of feedback cycle structures. Conceivably, variation in particulate heritability may be subject to selection based on its impact on system performance [103]. Niche construction theory (NCT) recognises persistent niche states as derived from genetic information within the biological entities that create them, but it does not treat whole niche-population feedback loops as units of selection.

Types of selection: Natural selection in cases of overlapping generations combines elements of replication-based and persistence-based selection, which can be partitioned using the Price equation [104]. Hence purely persistence-based selection can be formalised this way. Recursive application of the Price equation can distinguish multiple levels of selection, showing that selection at one level becomes a source of variation at the level above [28]. Multi-level selection type '2' recognises distinct (irreducible or "emergent") properties at the higher-level that are subject to selection [28]. However, it retains an emphasis on discrete replication, whereas we focus on purely persistence-based selection at the higher-level: Different systems comprised of different feedback cycles differ in their propensity to spread. Shared physical boundary conditions on Earth constrain the spread of ecosystems and social-ecological systems. Hence different systems with different feedback properties interact ("compete") and some may out-persist others.

Box 2: Dispersal mechanisms

Dispersal (horizontal transfer) of individuals, norms and innovations and resultant recombination of successful components coming from different ‘parent’ systems provides a potential source of variation in feedback cycles, which may then be subject to persistence-based selection.

Genetic dispersal. Dispersal of members of genetically-related populations of an ecosystem or social system, is usually naturally selected because dispersal, even to an equally populated habitat, reduces the likelihood of competing with relatives [87]. Under neutral dispersal, members of larger groups will tend to spread at the expense of members of smaller ones. Hence models show that systems with self-perpetuating feedbacks that enable them to support larger populations tend to spread their components at the expense of systems that lack such feedbacks [38, 66]. Humans also sometimes undertake ‘selective migration’ [13], involving the use of knowledge and foresight on the part of the migrators – who usually seek to move to wealthier, safer and more just societies.

Cultural dispersal. In social systems innovations that are not tied to genetics can be horizontally transferred. Imitation provides one mechanism for the spread of group-beneficial norms and the recombination of different group-beneficial norms arising in different populations [12]. However, it relies on fairly faithful imitation, which has been questioned [105]. Selective (biased) imitation of the best-performing strategy – ‘selective transmission’ – can overwhelm the eroding effect of inaccurate imitation, if population density is sufficiently high [106]. In principle, cultural dispersal can enable social systems to evolve much faster than ecosystems. The spread of literacy, ever-better means of transportation, and ever-faster means of communication have plausibly increased the importance of cultural evolution based on ‘borrowing’ (recombination) relative to slower group extinction mechanisms [12].

System dispersal. In microbial ecology system-level dispersal can occur through community coalescence [107]. Members of microbial communities produce extracellular compounds that bind the entire community together (e.g. in a microbial mat) and thus facilitate coherent dispersal. Thus, whilst system components may be genetically unrelated there may still be some ‘heritability’ of the whole. A social equivalent of system dispersal is when cultural groups going to colonise new lands take a whole system of skills, domesticated plants and animals, and their language with them. The European colonization of the New World was undertaken by competing national entities, but the diseases, plants, and animals introduced by any one of these entities enhanced the disruption of Native polities that facilitated the success of all the colonisers.

Outstanding questions

- How should persistence-based selection of feedback cycles be mathematically formalized and modelled? The sign and strength of feedback cycles can be quantified by ‘gain’ factors. Selective and non-selective effects can be partitioned – at multiple levels – using the Price equation, but it relies on counting objects, whereas feedback cycles are patterns of relations, not objects.
- What are the relative influences of system-level persistence-based selection and lower-level replication-based selection where both are occurring? Empirical test cases where the levels and types of selection are in conflict may be the most revealing, if not the most common.
- Can persistence-based selection generate increasing complexity? Learning through a series of trials over time is inherently slower than learning through trials over time and space (i.e. replication-based selection) but should still be able to accumulate adaptations.
- Can persistence-based selection explain apparent convergent evolution of ecosystems? Recognizably similar ecosystem structures – e.g. savannahs, coral reefs and forests – are found assembled out of different species on different continents. The feedbacks involved appear conserved, whereas the component species performing specific functions in the feedback loops appear to be substitutable.
- Can archaeological cultures be explained as persistence-enhancing systems? Their spatial extent is large, and they sometimes contain several ethnolinguistic groups, making explanations based on cultural group selection problematic.
- Can a system persistence perspective help guide ecosystem-scale conservation efforts? Some ecosystem configurations may be destined not to persist, as local-to-

global change pressures can tip them into alternative states leading to irreversible species loss. Looking across ecosystems to identify variation in their persistence-enhancing properties could provide a novel way to target ecosystem-scale protection efforts.

Glossary

Archaeological culture: a recurring assemblage of artefacts, architectural styles and combined subsistence, settlement, and organizational practices, from a specific time and place that represent the material culture of a particular past human society, e.g. “Anasazi” and/or “Puebloan”, “Hopewell”, or “Weeden Island”.

Autocatalytic network: a network of entities (usually chemical), the creation of each of which can be catalysed by other members of the network, such that the whole network can catalyse its own production.

By-product: a consequence of a phenotype selected for other reasons, for example, environmental changes due to excreted metabolic waste products. By-products can subsequently become selected for, e.g., if they form the basis of a closed recycling loop.

Cultural evolution: change in cultural information over time – that is information capable of affecting individuals’ behaviour that is socially transmitted from other members of their species.

Ecosystem evolution: change in organisation over time here argued due to persistence-based selection operating on variation in irreducible ecosystem-level properties.

Functional redundancy: many species performing the same metabolic function.

Inheritance systems: genetic, epigenetic, behavioural, and cultural means of faithfully transmitting information through time.

Irreducible properties: properties that cannot be assigned to any of the components of a system in isolation because they depend on the relations between components – for example, the self-amplifying or self-damping properties of feedback cycles.

Landesque capital: capital goods which replace land (e.g. fertiliser, irrigation, pest control), increasing yield without replacing labour (as distinct from laboresque capital goods which replace labour, e.g. tractors).

Mechanical solidarity: social cohesion coming from homogeneity of individuals, their values, and beliefs – people feel connected through similar work, education, religious training, and lifestyle.

Microbial guild: a group of microbial species that perform the same metabolic biogeochemical transformation (a guild more generally is a group of species that exploit the same resource).

Multi-level selection: Selection operating simultaneously on multiple levels of biological organisation. In type '1' the higher-level properties subject to selection are simple aggregates of lower-level properties. In type '2' – pertinent here – irreducible higher-level properties are subject to selection.

Organic solidarity: social cohesion based on the interdependence between people that arises from complementary specialisation of work. For example, farmers make food that feeds factory workers that make tractors that help farmers make food.

Persistence-based selection: differential persistence of non-reproducing entities, which exhibit variation, results in increasing frequencies of persistence-promoting properties among survivors.

Replication-based selection: heritable variation in phenotypic traits among members of a reproducing population results in increasing frequencies of descendant-producing properties amongst the descendant population.

Sequential selection: repetitions of a system over time alone enable it to acquire stabilising mechanisms because fragile systems are fleeting whereas stable configurations tend to persist.

Stability-based sorting: differential persistence of interacting, non-reproducing systems, which exhibit variation in their steady states, with those exhibiting more stable steady states coming to dominate.

Sponge loop: the hypothesis that sponges on coral reefs absorb large quantities of dissolved organic carbon released by seaweeds and corals and return it to the reef as particles in the form of living and dead cells, or other cellular debris.

Technosphere: that part of the Earth system that is made or modified by humans.

Ultra-social: the ability to co-operate with huge numbers of genetically unrelated individuals.

Table 1. Relating mechanisms of survival of the systems discussed herein to other forms of selection

Property subject to selection	**Example**	**Mechanism**	**Selection acts upon entities within an interacting population?**	**Negative selection removes pre-existing properties?**	**Interaction between selection and variation produces novel adaptations at the level under selection?**	**References**
Heritable variation causing differential survival and reproduction	Natural selection of individuals	Organism-level survival and/or reproduction	Yes	Yes	Yes	[28]
	Multi-level selection ‘type 1’	Group fitness equates to total fitness of constituent individuals	Yes	Yes	No (but knock-on effect on organism-level adaptation)	
	Multi-level selection ‘type 2’	Group fitness irreducible to individual-level properties	Yes	Yes	Yes	
Propensity for non-reproducing systems to spread across space	Feedbacks upon relative spread of distinct systems	Differential spread and/or encroachment based on distinct environmental boundary conditions	Yes	Yes	No? (but knock-on effect on organism-level adaptation)	[8] This study
Propensity for non-reproducing systems to persist through time	“It’s-the-song-not-the-singers” (ITSNTS)	Feedback cycles interact with biota in a way that affects their persistence & “recruit” biological species to perform steps	No	Yes	No? (but co-evolutionary adaptations in individual genomes)	[18, 19]
	Generalized stability-based sorting	Properties promoting static physical stability inherently promote persistence	No	Yes	No	[22, 84]
	Sequential selection for dynamic stability (cybernetics, biogeochemistry)	Reconfigurations when the system-state exceeds certain bounds tend to remove unstable configurations and promote stable ones	No	Yes	Yes, provided no re-set permanently undermines the process (e.g. runaway climatic feedbacks)	[21, 83] This study

Figure captions

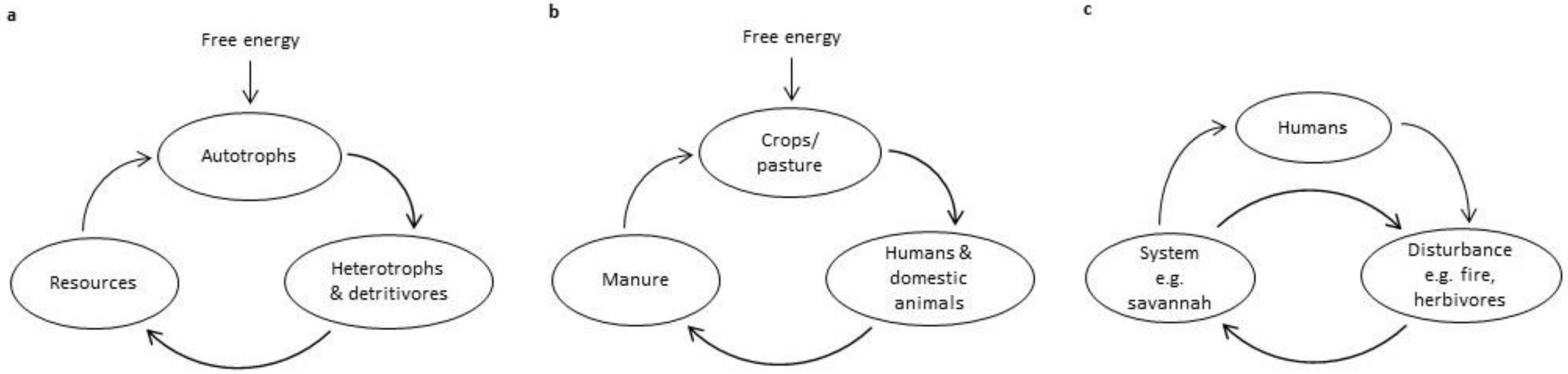

Fig. 1. Self-perpetuating (positive feedback) cycles. (a) Ecological resource recycling powered by free energy input. (b) Example of manuring in human agricultural systems. (c) Positive feedback between a system and disturbance factor(s): Example of savannah, fire and herbivores, further augmented by humans promoting fires and domestic animal grazing.

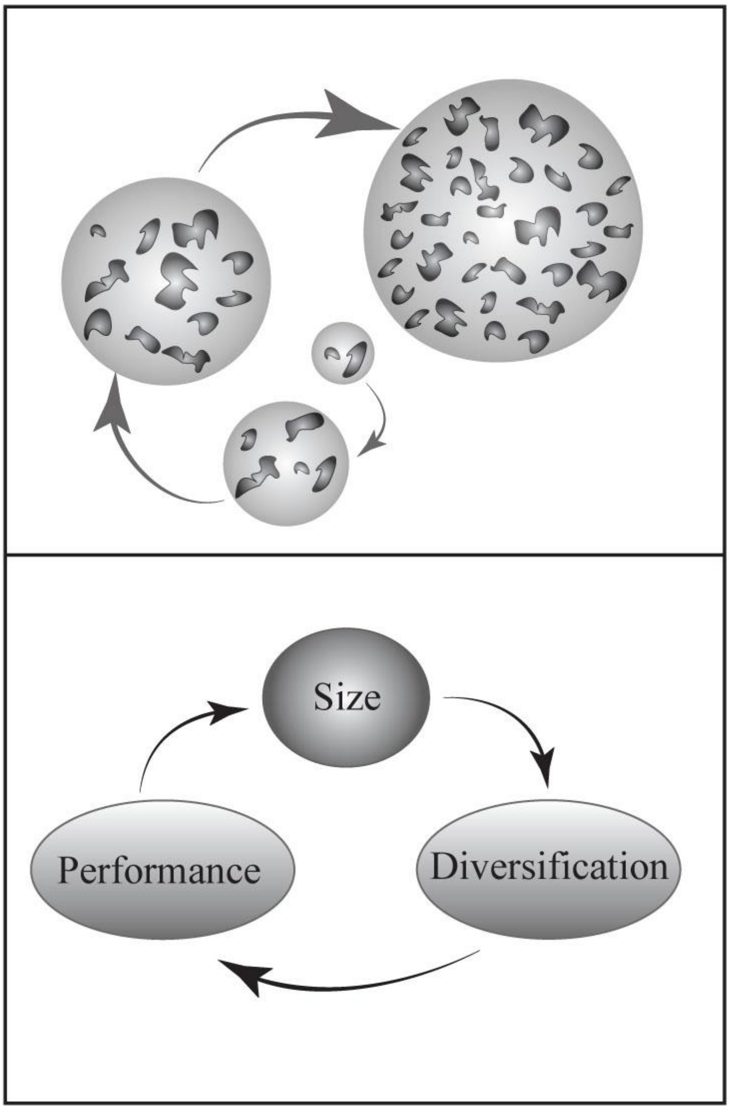

Fig. 2. How self-promoting cycles support diversification. Increased size allows diversification which can improve performance thus promoting further growth of the system.