Trends in
Ecology & Evolution

CellPress

Opinion

Feedbacks in ecology and evolution

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Ecology and evolutionary biology have focused on how organisms fit the environment. Less attention has been given to the idea that organisms can also modify their environment, and that these modifications can feed back to the organism, thus providing a key factor for their persistence and evolution. There are at least three independent lines of evidence emphasizing these biological feedback processes at different scales: niche construction (population scale); alternative biome states (community scale); and the Gaia hypothesis (planetary scale). These feedback processes make us rethink traditional concepts like niche and adaptation. We argue that organism–environment feedbacks must become a regular part of ecological thinking, especially now that the Earth is quickly changing.

Highlights

Organisms can modify their environment and these modifications can feed back to the organism, generating emergent properties with evolutionary consequences.

These feedback processes are common in ecological systems; they occur at different levels of organization (e.g., population, community, global) and can cascade across scales.

Considering feedback processes make us rethink traditional ecological concepts such as environmental niche, adaptation, and succession.

Feedback processes are key to understanding both the past (evolutionary history) and the future of the Earth system.

Homage to Richard Lewontin (1929–2021)

> '*Just as there can be no organism without an environment, so there can be no environment without an organism*' Lewontin 2000

Organisms modify their environment

Early ecologists can be divided between those with an ecosystem approach [1] and those with a population approach [2]. Population ecology has been the mainstream ecology for many years, in part because of the dominant idea that natural selection operates at population scale (i.e., some individuals do better than others in each environment and so are favored by natural selection). This organism-centered approach is well rooted in the major advances in biology during the nineteenth and early twentieth centuries (Darwinian evolution and Mendelian inheritance). Subsequently, much ecological research has been focused on how individuals within and between populations respond to environmental variability in terrestrial (soils and climate) and aquatic environments. In this framework, competition is a key ecological process sorting species along environmental gradients, and feedbacks are considered mainly among organisms (e.g., predator-prey cycles, mutualisms).

However, there is increasing evidence that organisms can also modify their environment, and these modifications can feed back to the organism and generate **emergent properties** (see Glossary) with evolutionary consequences [3–7]. The idea of feedback processes between organism and the environment has been around for a long time [8,9], especially in aquatic systems [10,11] and at the planetary scale [4,7,12], but also for terrestrial ecosystems at population and community scales [3,5]. Yet these processes are still poorly recognized in mainstream ecology and evolutionary biology (including textbooks). For instance, the individualistic (Gleasonian) concept of communities, which has been dominant for many researchers, considers that communities are basically the sum of species. The concept of ecological niche is typically assumed as a static state defined by the environment, which can be filled by organisms or remain empty. Classic succession theory proposes that early successional plants change their environment, making it less suitable for themselves but facilitating later successional species (Clements' facilitation), thus preventing the existence of open stable and disturbance-maintained vegetation that is common in many

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landscapes [6]. These examples clash with evidence of organisms modifying the environment for their own benefit.

The rise of global environmental problems is currently enhancing the importance of **positive feedbacks** especially at the planetary scale (e.g., the forest albedo [13]). However, both positive and **negative feedbacks** between organism and the environment are important for understanding the dynamics of our ecosystems. Positive feedbacks amplify changes and destabilize the state, whereas negative feedbacks tend to reduce fluctuations and keep the system within a particular state. There are at least three independent lines of evidence of feedbacks between organism and the environment acting at different scales (Figure 1): **niche construction** (population scale); **alternative biome states (ABS)** (community scale); and the Gaia hypothesis (global scale). Most of these processes have been independently studied by different groups and disciplines; they are, however, not integrated in a unified framework. We suggest that incorporating feedback thinking and understanding how feedbacks may operate at different scales may help in opening our minds to key processes contributing to the dynamics and resilience of our biosphere.

Population scale feedbacks: niche construction

The idea that interaction between populations and environment can be both cause and effect of evolutionary processes was suggested long ago by Lewontin [8,9]; niche construction is a clear example of this process [5,14]. The collective consequences of niche construction accumulate over generations and affect the evolution of populations (eco-evolutionary feedbacks). Typical examples of niche construction include beavers that build dams to generate their own habitat [15], trees that produce litter with chemical properties that benefit their growth (plant–soil feedbacks [16]), and flammable plants that generate fire regimes favoring their own persistence [17,18]. These are iconic examples, but there are many others. For instance, most plants produce root exudates that inhibit harmful microbes and promote the growth of mycorrhiza which in turn nourish the plant; and most legumes increase soil nitrogen (thanks to rhizobia) for their own benefit. We can even view plants as creating their own drought, as without plants, their soil would be moister (at local scale). There are also examples in the microbial world, where bacteria become dependent on their own modifications of their chemical environment [19]. Humans also construct their niches and have been doing so for a long time [20].

Under this framework, species niche and evolutionary processes cannot be estimated based on abiotic factors alone, and competition and facilitation are but two among several major mechanisms explaining their realized niche. Evolution is not viewed as an adaptation to fit the environment, but as a feedback process of the organism and the environment. That is, organisms do not adapt to a pre-existing environment (available niche), they construct their environment and then both 'coevolve'. A higher level of fitness is the result of this coevolution [9].

Community scale feedbacks: alternative biome states

In a seminal article Richard Lewontin asked, 'Can there be more than one stable community composition in a given habitat?' [21]. The answer is yes. In fact, one of the most striking examples of feedbacks in ecology is the occurrence of mosaics of **open biomes** and **closed biomes** in the same climate and bedrock type (ABS [6,22,23]). The existence of these mosaics has long been known [24] and is well recognized among theoretical ecologists [11,25]. However, because the maintenance of each component of the mosaic by feedback clashes with the traditional 'bottom-up' determinism of plant communities [26], ABS has largely been ignored until recently by field and experimental ecologists [6,27–29]. The two contrasting systems, open and closed biomes, are maintained during long periods by different stabilizing (negative) feedback processes

Glossary

Alternative biome states (ABS): it is a special case of the alternative stable states theory applied to terrestrial biomes. It refers to the occurrence of open and closed biomes in the same environmental conditions (climate, bedrock type). These biomes are stable and persist over generations (maintained by negative feedback processes); a change in the disturbance regime can trigger positive feedbacks and a biome switch.

Closed biomes: closed-canopy biomes are forests, that is, tree-dominated ecosystems in which the density and leaf area is high enough to exclude shade-intolerant plants in the understory. They typically have higher plant biomass than open biomes.

Emergent properties: properties and behaviors of a system as a whole that its parts do not have on their own; they emerge thanks to the interactions among parts. For instance, in biology, each level of organization has properties which emerge at that level. That is, organisms are not just a group of organs, and ecosystems are not just a group of species; they need to be bound together by specific interactions to emerge as such. Thus, diversity and stability of an ecosystem are emergent properties as are the life and behavior of an organism.

Negative (stabilizing) feedback: a feedback process where a stimulus (e.g., disturbance) causes a reaction in the opposite direction so that the state of the system is maintained. Negative feedbacks promote stability (e.g., homeostasis) and ensure the maintenance of a steady, stable state. For instance, forest tree shade inhibits grasses and fire and maintains the forests after a small disturbance; or open-canopy environments enhance flammable plants and fire that inhibit forest tree colonization. Negative feedbacks are also common at the global scale, where atmospheric characteristics are maintaining the biosphere.

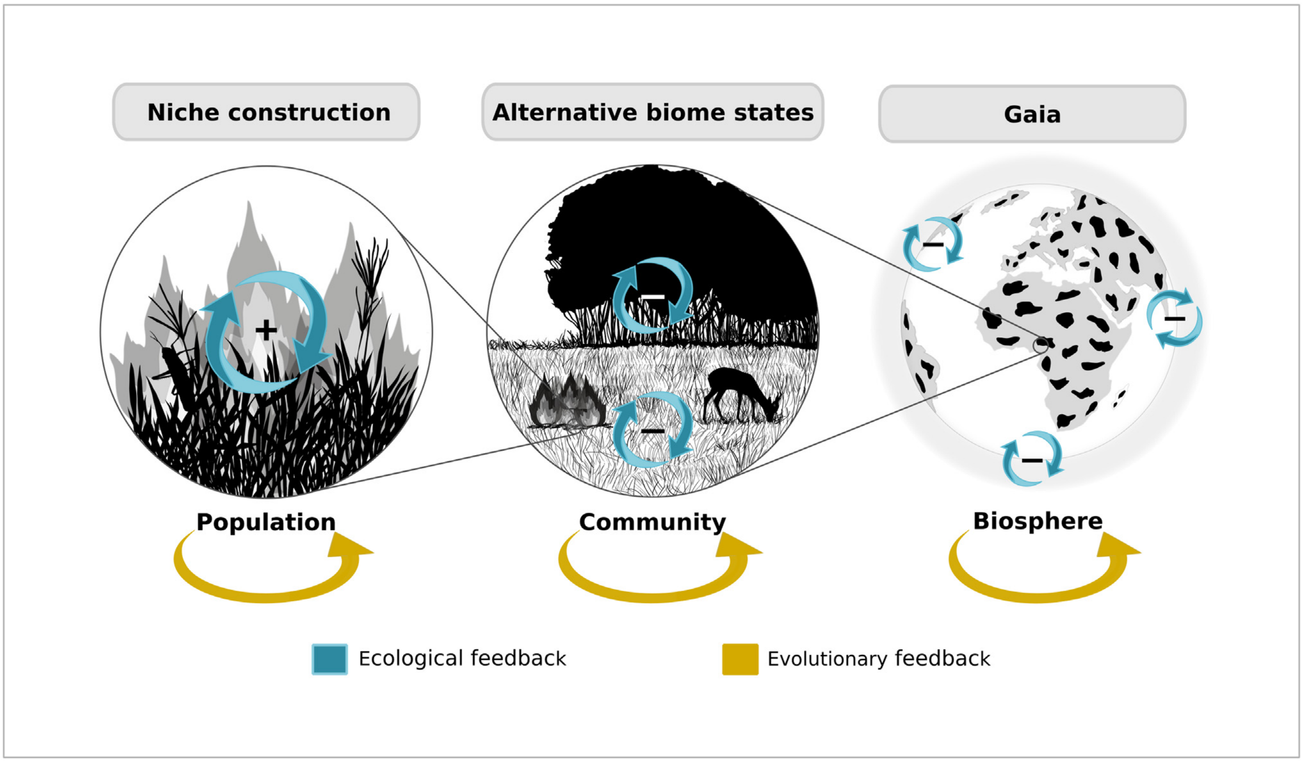
Niche construction: the process whereby organisms modify their own environment (their niche) for their own benefit, and thus, in turn, modify the selective pressure to which they are exposed. The term 'ecosystem engineering' is often used when the evolutionary consequences are not considered.

(for a review, see [6]). Forests create shady conditions diverging from the macroclimate in having higher humidity, lower temperatures, and lower wind speeds; this microclimate limits the occurrence of fires and enhances tree growth that further shades the system [30–32]. By contrast, open biomes are subject to lower humidity, higher temperatures, higher windspeeds, and sufficient light to grow a dense layer of highly flammable, or palatable, grasses and shrubs [6,22,27,30]. Thus, frequent fires and/or large herbivores limit forest trees, maintain these open biomes, and enable a dominance of shade-intolerant graminoids or flammable shrubs [33]. A strong reduction of these drivers (e.g., long fire-free interval during moist years, or herbivore exclusion or extinction) allows the colonization of forest trees that shade the environment (favoring forest trees; positive feedback) with the consequent switch to a closed biome [6,34]. Similarly, in a closed biome, a change in the drivers (e.g., a high-intensity fire driven by extreme weather conditions) can open the canopy, increasing flammable grasses and fire, thus switching to an open biome [6,35]. The two negative feedbacks stabilize either a closed or an open biome in a given climate (bistability) and can remain as such for millennia [34]. There are also examples of bistability of other biomes (reviewed in [6]), as well as examples of tri- or multistability [23].

While classic succession theory (driven by facilitation and competition) suggests that communities change as species modify their environment, making it more favorable for later successional species (ecological succession as self-destruction mechanism [8]), the ABS perspective is that species modify their environment, making it more favorable for their own continued occupancy,

Open biomes: open-canopy biomes are those dominated by light-demanding shade-intolerant plants; tree density and leaf area is low enough (or null) to allow abundant shade-intolerant species. Typical examples are grasslands, savannas, open woodlands, and shrublands. Open biomes in moist environments are typically maintained by negative feedbacks driven by plant consumers (fire, large herbivores).

Positive (amplifying) feedback: a feedback process where a stimulus (e.g., disturbance) causes a reaction in the same direction and thus it amplifies the stimulus. Thus, it moves the system away from equilibrium; it generates instability, and when strong enough, it causes state shifts. It may require an external force to initiate it. Niche construction and the forest-albedo feedbacks are examples of positive feedback between the organism and the environment. Disruptions of negative feedbacks may generate positive feedbacks until a new state is reached.



Trends in Ecology & Evolution

Figure 1. Examples of eco-evolutionary feedbacks at different organizational levels: niche construction (population; for example, flammability), alternative biome states (community; forests and savannas), and Gaia (biosphere). The signs of the feedbacks (blue arrows) indicate the most common type of feedback for each example. Evolutionary feedbacks represent the evolutionary processes at different scales (from selection at the microevolutionary scale to the acquisition of key macroevolutionary innovations). Details are provided in the main text and in Box 2. Illustration by DharmaBeren Studio (www.dharmaberen.com).

and thus enhancing resilience. States can persist for millennia if the feedback persists, in contrast to successional theory where open habitats are temporary (early successional).

Given the different light and disturbance regimes in each alternative biome, plants in open and closed biomes have evolved dramatically different traits related to fire, herbivore resistance, and shade tolerance. These include differences in the degrees of insulation of buds [36,37], the prevalence of resprouting [38], the thickness of the bark [39], the abundance of defenses (e.g., spines [40,41]), and a suite of physiologically divergent traits related to shade tolerance [30,31]. The net effect is a pronounced taxonomic and functional divergence of closed and open biomes [42–44], suggesting that these contrasted biomes provide different ecological and evolutionary frameworks. The importance of these different biomes is also conspicuous for fauna, as it provides a contrasting habitat for a myriad of animals with divergent requirements.

Global scale feedbacks: Gaia revisited

Space research in the 1960s paved the way for the development of the Gaia hypothesis by James Lovelock [7,12] which proposed the Earth as an evolving system. This hypothesis was heavily criticized, especially by population ecologists, because the biosphere cannot be a unit of selection [45,46], and thus, the hypothesis was often dismissed as a teleological concept. There have been debates on the appropriateness of this theory with defenders and detractors (see [46–50]). However, the basic ideas of this hypothesis (global self-regulation with evolutionary implications) are now well accepted by Earth system scientists, although still with limited recognition by ecologists working at smaller scales. By Gaia we refer to understanding the Earth as a global system with feedbacks that stabilize the planetary environment to certain states, and with state changes in geological time [51–53]. The central premise is that the biosphere has a major effect on the atmosphere and thus produces ecological and evolutionary feedbacks that sustain life. While feedbacks of organisms to the environment were neglected in the classic models of theoretical ecology, Lovelock's 'Daisyworld' model showed the contrasting predictions when those feedbacks are included (Box 1).

Perhaps the clearest example of global feedbacks is the maintenance of an oxygen-rich atmosphere on our planet, as free O_2 is a by-product of life (photosynthesis). The origin of photosynthesis

Box 1. Simulating feedbacks: the Daisyworld

The Lotka–Volterra system is perhaps the most studied model in ecology and has attracted theoretical ecologists for the past 100 years. This model is based on the interaction between organisms (predators, preys), without any feedbacks with the environment; thus, it falls short in responding to global warming. An alternative model is the Daisyworld, a simple dynamic model that includes population dynamics, natural selection, and feedbacks with the environment [7,47,69,70]. It was first introduced to demonstrate emergent properties of the Gaia hypothesis, but the model has since been treated as a mathematical model in its own right among Earth system scientists; it is little known among ecologists. In its simplest version, the model is composed of two daisy species (black daisies and white daisies) living in a simulated planet. Black daisies are cold-tolerant, and because of their color, their spread reduces albedo and warms the planet; by contrast, white daisies are hot-tolerant and their spread increases albedo and cools the planet. Thus, if the two species are common, they generate a negative feedback in such a way that if it gets colder, black daises are favored and warm the environment, and then white daises are favored and cool the environment. This generates a stable equilibrium where temperature is maintained within a narrow interval. However, if the environment becomes very hot (by an external force), white daises start to die back and the regulation system collapses.

Daisyworld provides an example on how traits at population level (cold vs. warm tolerance) can scale up and have consequences at large scale. More elaborate versions include disturbance, a more diverse community of daisies (with different colors), additional trophic levels, and daisies that adapt to changing temperatures (for a review, see [69]). This kind of model provides a way for understanding the reciprocal dependence of organisms on the environment and the environment on the organisms; it also shows the sensitivity of ecological processes to nonlinear changes. Daisyworld is a valuable teaching resource for raising awareness of feedbacks in a globally changing world.

Box 2. Feedbacks across scales

The three mentioned feedback processes acting at different levels of organization are not necessarily independent; some population-scale feedback processes may cascade to communities and ecosystems, and to larger (regional-to-global) scales. Similarly, atmospheric changes affecting the biosphere may affect processes at community (assembly) and population level (selection). However, many of these links across scales have been poorly studied. Ecological spillovers of the effect of organisms on the environment, from population to communities and ecosystems, and with evolutionary consequences, have been explored under the umbrella of the 'extended phenotypes' and 'community genetics' [71]. Thus, feedbacks between organism and the environment are likely to be a unifying process in ecology and evolution that needs further development.

An example of the links across scales is the case of plant flammability. Some plants increase their recruitment after a fire (postfire gaps generate recruitment opportunities [72]) and so benefit from being burnt. In such conditions, there is an evolutionary force for the population toward increasing flammability [18], which in turn, changes the fire regime for their benefit (niche construction). This increase in fire activity also has effects on the whole community. That is, fire, by opening the vegetation, favors light-demanding fire-adapted plants against shade-tolerant fire-sensitive forest species. This maintains open biome states and the associated communities of plants and animals. Thus, a population-level benefit of flammability may alter the community and therefore expand the proportion of the landscape dominated by open biomes that are frequently burnt or grazed, thereby making further changes in albedo [73] and to the scale of biogeochemical cycling [63].

Many plants can construct their environment by providing shade or by regulating soil fertility – which can result in feedbacks that influence plant evolution, competitive ability, and community structure [16,74,75]. For instance, plants may possess root traits that modify soil resources in favor of their own survival while deterring other species, and thus contribute to maintaining biome stability [76]. The different micro-environments driven by different genotypes have different cascading effects on interacting species [71]. Examples also include invasive species that modify their own environment with consequences for plant and soil communities [77]. At the geological scale, there is evidence of an evolutionary feedback between the increasing intensification of rock weathering by plants, the type of mycorrhiza, and the long-term carbon cycle [57]. However, research programs addressing cross-scale issues are scarce.

(cyanobacteria) made drastic atmospheric changes in the early history of the biosphere; this included the reduction of atmospheric CO_2 and generation of O_2 that paved the way to the evolution of aerobic biodiversity (including eukaryotic cells and multicellularity). This process was greatly boosted with the colonization of land by plants that significantly increased the amount of Earth photosynthesis, and then by the evolution of leaves, woody vegetation, and lignin [4]. Oxygen levels dropped later probably enhanced by the fire activity in an oxygen-rich world [54,55]. All this led to different states of O_2 concentration across Earth history [53,56] with important implications for plant and animal evolution.

Another key example of global feedback is the maintenance of the CO_2 concentration in Earth's atmosphere. Through geological history, atmospheric CO_2 has been drawn down by the chemical weathering that occurs in the rhizosphere [57], especially from the fresh weatherable minerals after mountain uplifts (the carbonate–silicate cycle). There is evidence that the rate of reduction of CO_2 was attenuated in the Miocene by negative feedbacks: the low CO_2 level attained at that time limited the growth of trees (C starvation), and forests were replaced by grasslands that exert a lower weathering effect on rocks [58]. The spread of grasses was favored by the seasonal Miocene climate, the increase of flammable C_4 grasses (more efficient in C fixation), and the consequent increase in fire activity that further limited trees [59–61] while releasing CO_2 back to the atmosphere. All these factors contributed to stabilizing the atmospheric CO_2 concentration and temperature [58,62]. It also stabilized grasslands and savannas across large areas [59,60] with likely consequences for the evolution of the associated biota and for global biogeochemical cycles [63].

Living organisms caused O_2, CO_2, and temperature to remain within certain limits through geological history, and this range of conditions created the appropriate niche for the evolution of biodiversity. Lifeless planets lack oxygen and have very high concentrations of CO_2 in their atmosphere. These are key examples; there are other elements and factors that also feed back with organisms at the global scale [4,7,54]. Overall, there is growing evidence that the biosphere and the atmosphere 'coevolved' during their geological history.

There are also global scale feedbacks at the human time scale resulting from anthropogenic modifications to the Earth system. For instance, the northward expansion of evergreen forest into areas currently occupied by tundra (due to global warming) reduces the albedo (from white snow to dark forests) and amplifies anthropogenic warming [13] which can feed back by further reducing snow and enhancing forest colonization. The opposite feedback (increasing albedo) may have occurred with the loss of polar forests of the Mesozoic and early Cenozoic. Increasingly, global feedbacks are seen as key to understanding both the history and the future of our planet.

Implications of feedback thinking

The three scales of processes mentioned previously are not necessarily independent and their coupling across scales shapes the biosphere (Box 1 and Figure 1). The existence of feedbacks producing emergent properties and evolutionary interactions requires a revision of classical paradigms [28,29,49]. For instance, the idea of evolution as a process of adaptation to fit a pre-existing environment needs to be replaced by a 'coevolutionary' species-environment approach. An implication is that the concept of species niche, and niche occupancy, is less relevant than traditionally thought. Feedbacks also provide an alternative framework for understanding spatial and temporal patterns of vegetation that differ from those based on gradual changes (e.g., gradient analysis and succession) and suggest that multistability and abrupt transitions in a given environment are common [6]; this also has implications for species' niche modeling [29].

Incorporating feedbacks into ecological thinking requires novel approaches. For instance, in running pot experiments, we are trained to consider fast growth as indicative of superior performance. Under the feedback framework we may need to test whether a species modifies its soil and whether these modifications affect the growth of the next generation. At community level, correlative methods remain popular for exploring the environmental context of a species or assemblage, although they do not prove causation. The problem is well known for soils where different tree species alter the chemistry of the soil beneath them over their life span [64]. Yet correlative models (e.g., niche models) are still widely used to establish causal relationships between topsoil nutrient variables and the plant species or communities they are supposed to determine.

Ecological feedbacks also have consequences for biodiversity conservation and management. Will converting a landscape to forest, for example, create more humid climates because of the high transpiration rates of trees [65]? Or will such conversions just lower the water tables and dry up rivers as shown by catchment experiments [66–68]? Major and expensive decisions on afforestation are being made on the expected atmospheric feedbacks of such land cover changes. The challenge of quantifying and testing large-scale predictions of ecological feedbacks is still flimsy despite the significant costs and potential benefits for society.

Concluding remarks

There is a bulk of evidence suggesting that feedbacks between organisms and the environment acting at different organizational levels have been key in the evolutionary history of the biosphere. They are also likely to be so in the future as we are modifying plant cover and atmospheric composition of the Earth. Earth is in transition to a new and warmer state due to anthropogenic forcing, and feedback thinking may help us understand the process. Feedbacks provide persistence mechanisms for the systems in question [49] and suggest that there are thresholds from where feedbacks can be disrupted to generate abrupt (nonlinear) changes. Yet there are still many questions about when, where, and how biological feedback processes occur and how

Outstanding questions

How much can organisms alter their environment? For instance, what is the relative contribution of plants and geology to soil fertility?

Under what conditions are feedback processes (between organism and the environment) key to explaining ecological and evolutionary patterns? For example, when does niche construction explains evolutionary patterns? Under what conditions are negative feedbacks key to explaining the distribution of ecosystems? To what extend does climate change modify the importance of feedbacks?

How do characteristics at one scale (e.g., the flammability of the community) affect the evolutionary process at the population scale (e.g., the evolution of flammability of a component species)? And vice versa: can an evolutionary process at the population scale alter properties at larger scales? For example, can the evolution of greater flammability in a population alter the fire regime of a community?

Can we estimate the relative contribution of a species to the maintenance of negative feedbacks in a community? What is the impact of the feedback on their fitness?

What are the implications of feedback thinking for current ecological theory?

What are the implications of feedback thinking for dealing with current environmental problems such as invasive species, afforestation, and other land-use changes?

we can detect them (see Outstanding questions). Feedback thinking may also help to bridge population, community, and planetary ecology (Figure 1) and become a unifying framework for ecology and evolution. What is clear, however, is that the simple cause–effect thinking that has served us so well in the past is no longer adequate. We need to acknowledge the importance of feedbacks in ecology, know when to use feedback ideas, and recognize the diverse scales at which they operate.

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Declaration of interests

The authors declare no conflict of interest.

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