INTEGRATING ECOLOGICAL FEEDBACKS ACROSS SCALES AND LEVELS OF ORGANIZATION

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Number of words: Abstract = 214, Main text = 8110

3 figures, 2 boxes and 2 tables

Acknowledgments: This work was supported by a doctoral fellowship from the chaire Modélisation Mathématique et Biodiversité of VEOLIA-Ecole Polytechnique-MNHN to B.P. We declare that we have no conflict of interest. We thank the three reviewers for their comments that improved the manuscript. We also thank the Mathieu Pélissié and Claire Jacquet for discussions.

Author's contribution: All authors contributed to the presented ideas. B.P wrote the paper with significant input from all authors.

ABSTRACT

In ecosystems, species interact in various ways with other species, and with their local environment. In addition, ecosystems are coupled in space by diverse types of flows. From these links connecting different ecological entities can emerge circular pathways of indirect effects: feedback loops. This contributes to creating a nested set of ecological feedbacks operating at different organizational levels as well as spatial and temporal scales in ecological systems: organisms modifying and being affected by their local abiotic environment, demographic and behavioral feedbacks within populations and communities, and spatial feedbacks occurring at the landscape scale. Here, we review how ecological feedbacks vary in space and time, and discuss the emergent properties they generate such as species coexistence or the spatial heterogeneity and stability of ecological systems. With the aim of identifying similarities across scales, we identify the abiotic and biotic modulators that can change the sign and strength of feedback loops and show that these feedbacks can interact in space or time. Our review shows that despite acting at different scales and emerging from different processes, feedbacks generate similar macroscopic properties of ecological systems across levels of organization. Ultimately, our contribution emphasizes the need to integrate such feedbacks to improve our understanding of their joint effects on the dynamics, patterns, and stability of ecological systems.

Keywords: Feedback loops, temporal and spatial scales, level of organization, emergent properties, self-organization, ecosystem patterns, species coexistence, stability, ecosystem

functioning, niche construction

INTRODUCTION

The discovery of art caves depicting species interactions (*e.g.*, Viereck and Rudner, 1957), or more recently, narratives and paintings about self-organized patterns in ecosystems (Walsh et al., 2023) illustrate that human curiosity toward patterns and interdependencies in nature has been a long-standing interest. In the last century, the development of cybernetics (*i.e.*, the study of regulation and dynamics of interconnected systems; Wiener, 1948; Maruyama, 1963) has led feedbacks to become increasingly studied. In a set of connected entities, a feedback loop corresponds to a circular path of dependencies. This means that a focal entity modulates its own dynamics by changing other entities composing the system, which, in turn, affect its variations. Examples involve social norms that regulate people's behaviors in complex societies (Fehr and Fischbacher, 2004), or nitrogen-fixing plants that increase the local availability of nitrogen on which they grow (Menge and Hedin, 2009). The feedback concept now infuses all complex systems including climatology (Rial et al., 2004; Kemp et al., 2022), history (Downey et al., 2016; Centeno et al., 2023), political and economic sciences (Casillas and Kammen, 2010; Leonard et al., 2021), and ecology (DeAngelis et al., 1986).

In ecology, the adoption of a system's approach to quantifying indirect effects began with the early development of ecosystem ecology (Margalef, 1963; Hannon, 1973; Patten and Odum, 1981), which was built using a complex system approach, with compartments (biotic and abiotic) mapped into a network of flows of resources and energy (Lindeman, 1942; Odum, 1968; O'Neill et al., 1987). Since then, feedbacks have been used across all levels of organization from individuals interacting with their environment (Cuddington et al., 2009), communities (Zelnik et al., 2022), ecosystems (Veldhuis et al., 2018), including at larger spatial scale (Phillips, 2016) to explain how emergent macroscopic properties of complex adaptive systems could derive from the interdependency of smaller entities (Levin, 1998). Incorporating such feedbacks often leads to interdisciplinary outcomes. For instance, in the context of ongoing global changes, knowledge of feedbacks is central to understanding how ecosystems participate in the global carbon balance, and ultimately whether ecosystems will amplify or dampen climate change in a warmer world (Field et al., 2007; Heimann and Reichstein, 2008). More practically, the mechanistic understanding of feedbacks has been crucial to design effective restoration programs for degraded ecosystems such as coastal areas or shallow lakes (Suding et al., 2004; Byers et al., 2006; Silliman et al., 2015).

Hitherto, despite the development of feedback-based studies at different levels of organization in ecology, we lack an integrative understanding of their global implications. Indeed, because feedbacks are observed at different scales, they may generate similar emergent properties and principles across levels of organization (see Table 1 for examples). A unified framework of feedbacks going from organisms to the landscape extent could help to better understand the pervasiveness of feedbacks, how they contribute to the organization of ecological systems by linking scales and levels of organization, and how they determine the response of ecological systems to different type of disturbances. Indeed, feedbacks are key mechanisms of the regulation of ecological systems and contribute to their stability properties. Feedbacks are thus involved in the response of ecosystems to disturbances and more broadly to human-induced global changes.

With this contribution, we emphasize that ecological feedback loops connecting entities (from organisms to ecosystems) give rise to emergent properties across scales. For this purpose, we first give a general definition that includes a set of properties characterizing each ecological feedback. Then, we present how feedbacks vary across space and time, and show that, while acting at different scales, they interact in both space and time. We also show that these feedback loops generate emergent properties that impact the patterns of coexistence, functioning, stability, and heterogeneity of ecological systems. We give examples where a better knowledge of feedbacks has helped to build conservation and restoration measures (Table 2). Finally, after acknowledging mechanisms that modulate the strength and sign of these loops, we propose open avenues for studying ecological feedbacks.

PROPERTIES OF FEEDBACK LOOPS

System and ecological entities

Let us consider a system composed of a set of entities interacting with each other. In ecology, these entities can represent individuals, or a species interacting with its local environment (abiotic or biotic), but also higher levels of organization such as complete ecosystems connected by flows of resources, organisms , and information across landscapes. Each entity acts on others through both direct and indirect pathways, creating a network of dependencies (Hutchinson 1948). Feedbacks emerge when an entity modulates, through these different paths, the direction and speed of its own dynamic. A feedback loop is therefore defined relative to a response variable measured on the focal entity such as body temperature, population abundance, or carbon or nutrients stocks in ecosystems.

Feedbacks emerge from links between entities

Feedbacks emerge when there is a circular path of directed links (Fig. 1). In the simplest context, a feedback loop appears when two entities are bidirectionally connected. Here, because the feedback is made up of two steps, goes to another entity and then back to the focal entity, the feedback is said to be of length two. In consumer-resource systems, the consumer generates negative feedback on its own demography because it is continuously lowering its resource availability (Fig. 1). At higher spatial scales, bidirectional flows of resources connecting forests and streams (*e.g.*, through aquatic insect emergence and plant litter subsidies) generate spatial feedbacks across the landscape (Leroux and Loreau, 2012; Baruch et al., 2021). Yet, in more complex settings, feedbacks can involve far more than two links. For instance, in intransitive competitive communities, long loops can emerge because there is no best competitor (rock-paper-scissors game; see Fig. 1): all species beat some competitors and are weaker than some others (Kerr et al., 2002; Allesina and Levine, 2011). Together, this entails that for a set of connected entities, the interdependency of entities can result not only from direct links but also from the many emerging feedback loops of varying length. Importantly, the definition of the feedback loop, and the quantification of its length, depends on the defined system, and in particular on the nature of its entities. Demographic regulation, for instance, corresponds to a negative feedback between individuals of a given population, directly (*e.g.*, interference competition) or indirectly (*e.g.*, through a resource in exploitative competition). If one wants to consider only the population level, or to ignore the resource dynamics, then the underlying feedback could be represented in a phenomenological way (as in the logistic growth) and the feedback would be of length one (of the population on itself). Hence, the way the system is defined and its scale impose a "perceptual bias" (*sensu* Levin, 1992) on the feedback identified and their lengths (see also O'Neill et al., 1987). Here we base our definition on a mechanistic representation of feedbacks, with a minimal length of two.

Strength, sign, and dynamical properties

Feedbacks are characterized by their length, but also their strength and sign. On one side, positive feedbacks emerge when the circular path benefits the focal species (*e.g.*, plants attracts pollinators, while pollinators feed on nectar in a mutually beneficial interaction; Fig. 1). Such positive loops are destabilizing because they can self-reinforce over time (Maruyama, 1963; DeAngelis et al., 1986), potentially leading to a runaway growth ("orgy of mutual benefaction", May, 1981) and/or alternative stable states and tipping point dynamics in ecosystems (Scheffer and Carpenter, 2003). On the contrary, negative feedbacks, for instance generated by consumptive interactions, tend to be regulation forces that limit exploding dynamics (see Emergent properties from feedback loops section).

The quantification of the feedback strength and sign relies on a multiplicative network approach derived from the input–output theory in economy (Hannon, 1973). In a network of connected entities, the strength and sign of a loop is given by the product of all signed weights of the links forming the loop. Then, positive feedbacks can emerge from negative interactions when the loop contains an even number of negative interactions (see Fig. 1). For instance, in a two-species competitive community, each species competes with the other, therefore limiting the negative effect that it experiences from its competitor (positive feedback on each species). Accessing the feedback sign alone provides information about whether the system will be stable or not. Notably, qualitative loop analysis can be used to infer the stability of a system from the sign of links between entities (May, 1973a; Levins, 1974). Moreover, the feedback strength depends on the cumulation of the link weights along the feedback loop. The weight of a link can correspond to interaction strengths for food-webs or plant-pollinator networks (*i.e.*, the effect that a species has on the growth of another for instance obtained by the partial derivative of the per capita growth rate with respect to the density of another species, typically summarized in the Jacobian matrix; see Ramesh and Hall, 2023 or Zelnik et al., 2022 for the generic framework), or to material flows between populations, communities or ecosystems in a spatial context. Many methods have been proposed to quantify the weight of links (as reviewed in Wootton and Emmerson, 2005). In practice, direct interactions are often difficult to measure due to possible influence of indirect effects (Lawlor, 1979; Paine, 1992), timescale, functional response, and context dependencies (Berlow et al., 1999; Wootton and Emmerson, 2005). Yet, assuming all link weights are known, the strength of a loop corresponds to the product of the weights of links involved in the loop. Interestingly, when using feedbacks within an ecological network (*i.e.*, the different links of the feedback loop correspond to ecological interactions), a general pattern seems to emerge. Ecological interactions are known to be heterogeneous in strength, with ecological communities typically having few strong and many weak interactions (McCann et al., 1998; Wootton and Emmerson, 2005). Therefore, as a loop becomes longer it will likely contain weak interactions so that the product of links will become weaker. This leads to a predicted pattern, where longer loops are expected to be weaker, that is often observed in nature (Neutel et al., 2002, 2007; Lever et al., 2023). Moreover, because each link connecting entities has a unit (*e.g.*, consumption rate in food-webs in mass.m^{-2}.year^{-1}, or interaction strength in interaction networks in year^{-1}; De Ruiter et al., 1995). This implies that two feedbacks of different lengths have different dimensions, making them impossible to be compared (Ulanowicz, 2004). To avoid this dimensionality issue, studies have proposed to define direct interactions relatively to self-links (*e.g.*, corresponding to regulation mechanisms) by dividing interaction strengths by self-links, thereby making each link non-dimensional (Neutel and Thorne, 2014; Zelnik et al., 2022). Since its first application on ecosystem flows (Hannon, 1973), this network approach has been applied in a wide variety of contexts, including the integration and interdependence of species within communities (Zelnik et al., 2022) or the evolution of species in mutualistic networks (Guimarães et al., 2017). To summarize, quantifying feedback strength and sign allows comparing different loops and understanding whether a given loop will self-amplify or counteract the effects of a perturbation. However, this is not sufficient if one wants for instance to quantify the contribution of a given loop on the transient dynamics following a perturbation (*e.g.*, how much a given feedback loop increases or decreases the effect of a disturbance and the recovery time). Therefore, a complementary approach has been proposed, which we detail in Box 1.

Timescales are the essence

Feedbacks are characterized by the focal entity on which it acts (*e.g.*, an organism , an ecosystem), as well as a timescale. Each process and entity has a characteristic timescale: decomposition is faster in freshwater compared to terrestrial ecosystems (Gounand et al., 2020), and a given feedback duration will be perceived differently by species that have very different generation times (*e.g.*, a phytoplankton vs a tree species if considering primary producers; Steele and Henderson, 1994). For a feedback loop, the timescale corresponds to the sum of all durations of processes involved in the loop. It therefore always generates a time lag between the cause and its effect (Higashi and Patten, 1989). In the case of nutrient recycling feedback on plants for instance, the delay is due to decomposition and nutrient release by decomposers (McClaugherty et al., 1984). Comparing the generation timescale of the focal entity and the one of the feedback is critical to determine how the loop may impact the focal entity. If the timescale of the feedback loop is high compared to the one of the entity, its effect may generate slow-fast dynamics and induce cycles (Daufresne and Hedin, 2005; Pastor and Durkee Walker, 2006; Barraquand et al., 2017) or long transients (Hastings, 2010; Hastings et al., 2018; Miller and Allesina, 2023). When the feedback has a very long timescale compared to the entity of interest, the feedback loop may impact the system but via long-term legacy effects (Albertson et al., 2022). Let us illustrate this point by considering phytoplankton. Phytoplankton participates in capturing carbon and regulating the climate, which ultimately conditions its own environment, but the timescale at which this feedback operates makes it irrelevant to investigate phytoplankton life-cycle. However, in the long term, the feedback between plankton and the climate has been shown to strongly shape the dynamics of planktonic assemblages (Gibbs et al., 2006; Slater et al., 2022). Hence, depending on the timescale defined by the entity of interest (here cell versus assemblage), the same feedback may matter or not, depending on the temporal scale one looks at. On the contrary, the timescale of the feedback can be smaller than the one of the entity, in which case it is important for the focal entity: in forest-savanna systems for instance, the fire-mediated feedback loop, which determines the canopy cover and the strategies of plants, occurs at a smaller timescale compared to the life-span of trees, and determines the bistable dynamics in the system (Pausas and Bond, 2020).

Framing feedbacks in terms of timescales has received a lot of attention in the context of climatic mitigation measures such as carbon sequestration to understand when will carbon sequestrated in biomass or the ocean be remineralized (*i.e.*, return to the atmosphere, Table 2; Boyd et al., 2019; Friggens et al., 2020). Also, this strongly matters when comparing the timescales of ecological and evolutionary processes (see Govaert et al., 2019; Fronhofer et al., 2023 for dedicated reviews on this topic).

FEEDBACKS ACROSS LEVELS OF ORGANIZATION

Organisms interact with its abiotic environment but is itself embedded in a community, while populations, communities and ecosystems are part of a landscape and interconnected through flows of individuals, information and resources. The feedback concept can be applied at any of these levels of organization. Here, we identify three types of feedbacks depending on the level they act on: feedbacks from organisms interacting with their abiotic environment, demographic and behavioral feedbacks in populations and communities and spatial feedbacks at landscape scale (Fig. 2, Table 1).

Feedbacks between organisms and their abiotic environment

From the observation that organisms interact with their abiotic environment, Tansley defined the concept of ″ecosystem″ encapsulating both species and their environment (Tansley, 1935). Later, Lewontin suggested thinking of the environment as a third helix of the DNA because the environment constrains the evolution of organisms and is in turn modified by organisms (Lewontin, 2000, see also Patten, 1982). Though we do not focus on eco-evolutionary feedbacks here, this metaphor illustrates the importance of interactions between organisms and their environment.

Organism-environment interactions can involve modifications of the physical habitat and landforms that feed back on the focal species' growth, survival, or abundance (*i.e.*, biogeomorphic feedback; Temmink et al., 2022). Examples include intertidal sea-grass meadows that stabilize the sediments (soil accretion) and change the hydrodynamic system via their rooting and shooting systems (Bouma et al., 2013; Maxwell et al., 2017), or coastal plants that capture sediments transported by wind and help maintain dunes that limit the erosion by waves and sand resuspension (Zarnetske et al., 2012). All these mechanisms foster plant survival by buffering against the physical stress induced by anoxic conditions, or waves and wind erosion (Silliman et al., 2015; Maxwell et al., 2017), and therefore have been used as knowledge to guide restoration of coastal areas (Table 2). These engineering species “modify their own niche and/or each other's niches” (*sensu* Odling-Smee et al., 1996), a wide phenomenon called niche construction. Such habitat modifications in turn affect the ecology of other species, thereby creating new feedback loops. For instance, seagrass recruitment provides shelter from predation to meso-grazers that graze on seagrass epiphytes and invasive algae, which benefits seagrasses (Maxwell et al., 2017). Hence, niche construction encapsulates both biotic and abiotic changes (see next section for biotic niche construction; Odling-Smee et al., 1996, 2013).

Organism-environment interactions often involve the modulation of local resource availability. On one side, consumers deplete their resources, which generates a negative feedback loop: increased consumption leads to lower resource availability (negative niche construction). Such a loop can switch from negative to positive for engineering or facilitating species (positive niche construction; Kylafis and Loreau, 2008). In intertidal systems, sea-grass meadows or mussel-beds increase organic deposition, availability of oxygen and nutrients, either by trapping them in their rooting system for sea-grass (Maxwell et al., 2017) or by ammonium excretion in mussel beds Pfister, 2007. Ultimately, it positively affects their growth. Similarly, facilitation by nurse species in stressed ecosystems (arid, salted mashed, alpine) enhances local availability of resources (through the increase in water infiltration, organic matter and by limiting evaporation; Filazzola and Lortie, 2014)), which enhances seedling recruitment. Feedbacks bounding species and the availability of resources are also observed at the ecosystem-level. Each species is involved in a recycling-mediated feedback loop, where organic matter is recycled and in return positively or negatively affects each trophic level through a bottom-up cascade (Loreau, 2010). These loops between the ecology of species and their ever-changing local environment set the theater for evolution to play (Lewontin, 1978; Odling-Smee et al., 1996; Phillips, 2016).

Population and community-level feedbacks

Individuals do not simply interact with their abiotic environment, they also eat, compete or cooperate with each other. These interactions generate demographic and behavioral feedbacks within and between populations of the same or different species (Fig. 2, central panel).

Within populations, demography is modulated by the balance between growth and regulation. Contrary to intrinsic population growth , that acts by definition positively on population demography, regulation from density-dependent mechanisms such as intraspecific competition for resources slows down population growth (*e.g.*, due to stronger intraspecific competition or to the accumulation of specialized enemies), thereby acting as a negative loop (see also Table 2 human-induced demographic regulation of harvested systems). Negative density-dependent mechanisms regulate population growth, however, conspecific density-dependence mechanisms such as cooperation can also positively affect population growth (Gil et al., 2019). For example, group defense in meerkats reduces the individual risk of being eaten by predators. Another example comes from the collective foraging of coral-reef fishes that increases their foraging rate when they have more conspecific in their neighborhood (Gil et al., 2020). At low density, these social or sexual interactions between individuals generate positive feedback between population demography and growth rate (positive density-dependence). By contrast, as the population grows, density-dependent negative feedbacks overcome positive ones. Such an interplay of positive and negative feedback loops at the population level leads to Allee effects (Allee, 1931, Box 2), where the population can collapse under a defined threshold (minimum viable population) as it becomes insufficient to sustain the cooperation level required for population persistence (see also Kylafis and Loreau, 2008; Koffel et al., 2021).

Species are also embedded in a complex web of diverse interactions with other species. The intertwinement of interaction in networks such as in plants-pollinators, and food-webs illustrate this ‘entangled bank of species’ (Darwin, 1876), describing the diversity and complexity of interspecific interactions. In a network, direct interactions between pairs of species are well pictured. Direct interactions also generate a multitude of less visible indirect loops that create strong interdependence of species (Ulanowicz, 2004). Because positive and negative interactions such as competition, mutualism, exploitation coexist in communities (Fontaine et al., 2011; Pocock et al., 2012), these loops vary in sign, strength and length. Consequently, when a species enters a community, by interacting with other species it modulates the emergent feedbacks that any species in the community experiences (Arnoldi et al., 2022). Recently, Zelnik et al (2022) proposed the term “interaction horizon” to describe the maximal length of indirect pathways connecting species that significantly contribute to the community patterns and dynamics. In particular, using the network approach to decompose the direct and indirect effects of perturbations (Box 1), they found that indirect paths increase in importance when species interact more strongly together, that is, when species assemblages are more integrated (*i.e.*, interdependent).

Spatial feedbacks coupling ecosystems

Feedbacks can also emerge in space when species, individuals or material flows are exchanged at the landscape extent (Fig. 2). Such feedbacks have been addressed in all theoretical frameworks of spatial ecology (metapopulations, metacommunities and metaecosystems) and will be discussed hereafter. Considering metapopulations (*i.e.*, sets of local populations linked by the dispersal of individuals), spatial feedbacks can emerge from the dispersal of individuals through local patches, and thus affect the general state of the metapopulation (*e.g.*, total abundance or occupancy). For instance, the "spatial rescue" effect relies on the idea of a positive feedback between population abundance and spatial flows of organisms. Specifically, migration from locally abundant populations increases the size of small populations and therefore decreases their risk of extinction (Brown and Kodric-Brown, 1977). In turn, the number of individuals dispersing from these small populations increases (positive density-dependent dispersal, *e.g.*, Fonseca and Hart, 1996, for an empirical example) and can rescue other populations, thereby increasing the metapopulation occupancy (Hanski and Gyllenberg, 1993). Further, spatial flows of individuals link local and spatial feedbacks in various ways. If local feedbacks are dominated by intraspecific competition, a common expectation is that the dispersal of individuals will balance competitive constraints among patches (Fretwell and Lucas, 1969). If, on the other hand, the establishment of local populations is constrained by local positive feedbacks (*e.g.* local Allee effects), the effectiveness of dispersal at the landscape scale is reduced. For instance, local Allee effects constrain the range expansion of the gypsy moth, an invasive species in North America (Tobin et al., 2007). Finally, from an evolutionary point of view, spatial heterogeneity in the local states of patches is expected to select for lower dispersal levels and weaker spatial feedbacks (Hastings, 1983; Parvinen et al., 2020). Similarly, in metacommunities (*i.e.*, sets of local species assemblages linked by dispersal), spatial feedbacks emerge from the dispersal of species through the different local assemblages. For instance, when competition among species dominates in metacommunities, low dispersal leads to high local competition and competitive exclusion, so that species are sorted differently in different patches depending on local environmental conditions ("species sorting"; Leibold et al., 2004). When dispersal is high, spatial feedbacks homogenize local communities making competition happen at the scale of the metacommunity and may lead to competitive exclusion at this level (Mouquet and Loreau, 2003). While most metacommunity works assume undirected dispersal (diffusion), dispersal can also be context-dependent (*i.e.*, when it depends on the presence of resources, competitors, predators and mutualists,Cote et al., 2013; Fronhofer et al., 2015; Trekels and Vanschoenwinkel, 2019). Spatial flows of species are then directly coupled to locally dominant feedbacks. In addition to flows of species, resources or information connect ecosystems in space and can also generate spatial feedbacks (meta-ecosystems; Polis et al., 1997; Loreau et al., 2003; Massol et al., 2011; Gounand et al., 2018a). An interesting example comes from oceanic salmon that migrate upstream for reproduction. By doing so, salmons produce carcasses that foster biofilm growth (Rüegg et al., 2011), and serve as resources for freshwater insects. In turn, salmon juveniles feed on these insects, which positively increase their growth and survival (Giannico and Hinch, 2007). A recent synthesis on spatial flows of resources shows that their magnitude can be as high as the local ecosystem fluxes in some ecotones (*e.g.*, freshwater-terrestrial; Gounand et al., 2018b), suggesting that the spatial feedbacks generated by resource flows can be as important as local feedbacks within ecosystems. These flows of species and resources generate negative and positive spatial feedbacks through other ecosystems (Montagano et al., 2018). Resource flows between ecosystems can relax local limitations in nutrients or carbon in each local ecosystem, therefore generating a mutually beneficial spatial loop (Pichon et al., 2023). However, spatial feedbacks can also be negative, when dispersing individuals carry parasites or diseases that decrease the demography of local populations (anti-rescue effect; Harding and McNamara, 2002) or when subsidy flows correspond to low-quality resources ((Kelly et al., 2014); see Modulators of feedback properties).

EMERGENT PROPERTIES FROM FEEDBACK LOOPS

We next review the effects of positive and negative feedback loops on species coexistence, the functioning, stability and emergent spatial patterns of ecological systems.

Feedbacks have contrasting effects on species coexistence

Positive feedbacks can have positive effects on species coexistence. In drylands, the facilitation-driven positive feedbacks between nutrients and water in soil and some facilitating species create a favorable environment for their growth but also sustain some species that would not be able to persist without facilitation (Filazzola and Lortie, 2014; Bulleri et al., 2016). This heterospecific positive density-dependence acts on mortality: higher density of the facilitating species decreases the mortality of other species. In theoretical models, this mechanism fosters species coexistence (Gross, 2008; Gil et al., 2019, see also Aubier, 2020 for similar results between conspecifics).

Such positive effects on coexistence are however not systematic. Because of the cost associated with facilitating another species that also competes for resources and space (Schöb et al., 2014), the species benefiting from facilitation may eventually out-compete the facilitating species when environmental conditions allow its persistence alone and decrease coexistence (Koffel et al., 2021). When the positive density-dependence acts on conspecific growth rates, it can also reinforce the competitive hierarchy thereby decreasing coexistence (*i.e.*, reducing further the growth rate of least competitive species that already have a lower abundance compared to best-competing species; Wang et al., 1999). Similar effects can be observed with nutrient recycling that can promote the dominance of a single plant when it increases the loss of the nutrient that limits their competitor growth (Daufresne and Hedin, 2005), or the dominance of a mobile consumer connecting ecosystems by foraging: if the consumer forage in the ecosystem that is fertilized by its competitors, it benefits from the positive recycling feedback and can exclude other mobile consumers (Peller et al., 2021). Positive feedbacks may also generate priority effects when species pre-empt or modify available niches, ultimately limiting further invasions (Drake, 1991; Fukami, 2015). Such priority effects may be reinforced over evolutionary timescales when early-arriving species adapt to local conditions and radiate available niches ("monopolization hypothesis", De Meester et al., 2002; Leibold et al., 2022). These mechanisms may explain the patterns of dominance and low species diversity in some ecosystems such as peatlands, boreal forests, or coastal mangroves (Zobel et al., 2023). For instance, in bog areas where the pH is low, a moss species (Sphagnum) can colonize and modulate the local conditions by increasing acidity in its neighborhood and limiting decomposition (Clymo, 1984), which promotes its ecosystem dominance. By contrast, in areas where pH is higher, the community is more diverse and composed of grasses, forbes, and sedges (Laine et al., 2021). Similarly, in the context of biotic invasion, an invader experiencing a positive feedback while invading a resident species will enter a community and replace the resident species (*i.e.*, invasional meltdown; ‘Arnoldi et al., 2022). By contrast, when positive feedbacks are more frequent between native plant species than between invasive ones, they offer a mechanism of resistance against invasions (Yin et al., 2022).

Links between negative feedbacks and species coexistence have a long history in ecology. Classical theory suggests that coexistence is enhanced when intraspecific negative feedbacks are stronger than interspecific competition (*e.g.*, when species have large niche differences; Levins, 1966). The later work of Janzen and Connell (Janzen 1970, Connell, 1971) suggested that the accumulation of pathogens near adult trees inhibiting the survival and recruitment of their juveniles would favor coexistence (a mechanism known as negative-conspecific density-dependence or self-regulation). Since then, there has been accumulated evidence of the positive effect of negative density-dependence on coexistence using both experiments (Klironomos, 2002; Mangan et al., 2010; Teste et al., 2017), regional observations (Johnson et al., 2012; LaManna et al., 2017), and theory on plant-soil feedbacks (Bever et al., 1997; Loeuille and Leibold, 2014; Eppinga et al., 2018). This is corroborated by the negative relationship between the species abundances in plant communities and the strength of the negative feedback loop with the soil: least abundant species are the ones involved in the stronger negative feedbacks with the soil (Mangan et al., 2010; Johnson et al., 2012).

While we simplified the explanation above by splitting positive and negative feedback loops, in communities, feedbacks of different signs are generally intertwined. In addition, given that their signs can change along environmental gradients and timescales (see Modulators of feedback properties section; Box 2), understanding how each loop relates to species coexistence can be tricky. In this regard, recent developments of niche theory explicitly link the feedbacks emerging from organism-environment interactions (both biotic or abiotic environment), the niche of each species and species coexistence (see Koffel et al., 2021 for details on the mathematical framework). Another possible way of unveiling the links between different feedback loops and the patterns of species coexistence is to acknowledge the scale at which each feedback loop acts (see Zobel et al., 2023). At the scale of an individual, or a patch of vegetation, species-level positive feedbacks driven by facilitation may promote species coexistence by enhancing environmental conditions and expanding the niche of other species (Bulleri et al., 2016; Koffel et al., 2021). Yet, when this positive niche construction scales-up to be dominant at the ecosystem level, it promotes the dominance of a single species (*e.g.*, due to priority effects or monopolization). Over timescales, niche construction may shift to ecosystem-level negative feedbacks that limit such cases of dominance, by accumulating resources that promote competition-driven coexistence mechanisms (Box 2). Therefore, in many ecosystems the maintenance of a high number of species may tie in the balance of feedbacks having various signs and acting at different scales. We argue for the development of a theory investigating how feedbacks acting at different scales modulate species coexistence.

The central role of organism-abiotic resource feedbacks on ecosystem functioning and development

Feedbacks are key to understanding how ecosystems and landscapes function. At the root of many ecosystems lies a positive feedback loop between plants, performing photosynthesis, and decomposers that close the recycling loop of matter, a loop that can also be accelerated by herbivores (Mazancourt et al., 1998). Depending on whether decomposers are limited by either carbon or nutrients, plants and decomposers compete for nutrients or become mutualists, respectively (Daufresne and Loreau, 2001). In the latter case, plants and decomposers benefit from the by-product of the other (decomposers decompose litter produced by plants and make nutrients available again for plants) making an autocatalytic loop (*sensu* Veldhuis et al., 2018; Fig. 3). As long as this self-reinforcing loop is fed with energy (*i.e.*, light for photosynthesis), resource competition leads to the selection of species with the highest resource-use intensity (lowest R^* according to resource competition theory, Tilman, 1982) within plants and decomposers, and consequently increases biomass and energy production while minimizing resource losses (Loreau, 1998; see also Box 2). Taken together, this simple system shows that feedbacks can generate auto-catalytic processes that determine the development and functioning of the ecosystem (Odum, 1988; Ulanowicz, 2009; Lenton et al., 2021). Interestingly, such ecosystem principles can be extended to the landscape extent, where subsidy flows can connect ecosystems with different functioning (Harvey et al., 2023). Freshwater or benthic ecosystems tend to have a net heterotrophic functioning (respiration $>$ primary production; Gounand et al., 2018b, 2020), while terrestrial and pelagic ecosystems have on average a net autotrophic functioning but transfer less efficiently energy to the higher-trophic levels (Shurin et al., 2006), making them carbon sources at the landscape scale (Fig. 3). In addition, these ecosystems correspond to communities with different carbon, nitrogen and phosphorous needs (Elser et al., 2000). Hence, when looking at terrestrial-freshwater or benthic-pelagic ecotones, it appears a spatial analogy of the plant-decomposer relationship: when nutrients and detritus are spatially exchanged and meet the local needs of communities within each ecosystem (*i.e.*, the exported by-products of an ecosystem bring the resource limiting the other). In that case, a positive feedback loop can emerge at the landscape scale, fostering the landscape-scale production and maximizing the use of nutrients and carbon between ecosystems (Pichon et al., 2023; see also Modulators section). Taken together, we notice similar autogenic development of ecological systems driven by autocatalytic loops at different spatial scales.

Feedbacks properties determine ecosystem stability and fragility

Feedbacks are also intrinsically linked to the stability of ecological systems. While positive feedbacks can maintain an ecosystem in a high biomass state, they can also promote its fragility. Indeed, the strong positive interdependencies of entities can serve as a medium to amplify and propagate perturbations across the whole system. In multiple ecosystems such as lakes, coral-reefs, and drylands, where strong positive feedbacks are observed, under some conditions, small perturbations can lead to a sudden change in ecosystem state (so-called "catastrophic shifts "; Scheffer, 2009; Kéfi et al., 2016). Similar alternative ecosystem states have also been described at the population and community levels (Table 1; Fig. 3). Priority effects from positive feedbacks discussed in the coexistence section can generate alternative community states depending on the order of assembly in the community ("historical contingency"; Case, 1990; Fukami and Nakajima, 2011). Importantly, the stability of communities is impacted differently when feedbacks are species-specific (*i.e.*, depends on the species identity, such as a pollinator specialized on one plant) or aggregated (*i.e.*, which does not depend on the species identity; *sensu* Karatayev et al., 2023). With aggregated feedbacks all species experience the same Allee effect, and therefore a single perturbation can drive the collapse of the community simultaneously (Lever et al., 2014; Karatayev et al., 2023). With positive species-specific feedbacks, each species experiences a specific Allee threshold, which thereby does not necessarily cause cascades of extinctions in the community (Aguadé-Gorgorió et al., 2023). For example in plant-pollinator communities, because specialist species experience stronger positive feedbacks, they are more vulnerable to perturbations than generalist species (Saavedra et al., 2013). Because some traits of interacting partners can be lost over evolutionary timescales (*e.g.* loss of genes to produce arginine in leaf-cutter ants), positive interdependencies between species can be strengthened (*e.g.*, ants rely on fungus for arginine; Ellers et al., 2012). In some cases, such high specialization to a partner can lead to population collapse due to an evolutionary trap (Singer and Parmesan, 2018) or evolutionary 'cul-de-sac' at longer timescales (Perez-Lamarque et al., 2022). Related impacts of positive dependencies can be drawn for spatial systems. In this case, the spatial dependencies emerge from species dispersal or spatial flows of resources. When such flows are important, a small local perturbation can spread in space through a traveling wave changing the state of the connected populations (Keitt et al., 2001; Villa Martín et al., 2015; Saade et al., 2023), or leading to alternative ecosystem states (Gounand et al., 2014; Fig. 3). To summarize, mutual benefits create dependencies and integration of entities, thereby fostering their joint persistence or possible collapse. In other words, interdependency can beget fragility (Vespignani, 2010; Centeno et al., 2015; Brummitt et al., 2015).

Conversely, negative feedbacks have been related to homeostasis, or regulation (Odum, 1969; Wiener, 1948). Negative feedbacks stabilize ecological systems, avoiding infinite growth, either by mediating a return of the system to its equilibrium after a perturbation (*i.e.*, resilience), or by constraining dynamics in cycles (*i.e.*, avoiding runaway). Cycles are observed when long-delayed negative loops overcome shorter ones (Barraquand et al., 2017; Lever et al., 2023), as exemplified by the slow-fast dynamics of shallow lakes where the interaction between a slow loop with phosphorus and a fast loop with turbidity induces primary producer cycles between macrophytes and microalgae (van Nes and Scheffer, 2007). Theory also suggests that cycles emerge when the time delay of negative feedbacks is long compared to focal entity timescale (*e.g.*, long delayed demographic regulation compared to slow population' growth; (May, 1973b). In such cases, the system is destabilized because growth and negative regulation feedbacks are out-of-phase (Ramesh and Hall, 2023; Yang et al., 2023). These delayed feedbacks can be promoted by legacy effects that can persist for years (Hastings et al., 2007; Albertson et al., 2022). For example, drought legacy effects were shown to switch plant-soil feedbacks of two grassland species from positive to more negative (and potentially destabilizing) feedbacks (Kaisermann et al., 2017). In this experiment, drought led to turnovers in soil fungal communities, which may explain the change in feedback sign, although the precise mechanism and the impact of the change in feedback sign on the stability of the system were not elucidated (see De Vries et al., 2023 and references therein for further discussion on the topic).

Because ecological systems host both positive and negative interaction types, loops of opposite signs are intertwined. Theoretical studies investigating the impact of this diversity of interactions in communities showed that inclusion of negative interactions in mutualistic communities can stabilize them (*i.e.*, generates negative loops; Mougi and Kondoh, 2014; Coyte et al., 2015). This is also corroborated in a simple plant-pollination-herbivore module, where coexistence is favored by the mutualistic part (positive feedback) while stability is favored by the herbivory (negative feedback) so that overall maintenance requires a specific balance between the two interactions (Yacine and Loeuille, 2022).

Feedback loops induce spatial heterogeneity

Lastly, feedbacks can generate emergent spatial patterns (self-organization; Fig. 3; Rietkerk and van de Koppel, 2008). Different patterns can be distinguished depending on the type of feedback that has generated them (scale-dependent or density-dependent). On the one hand, local feedbacks between species and their abiotic resources generate self-organized patterns and have been observed across a wide range of biological systems (Rietkerk and van de Koppel, 2008; Kondo and Miura, 2010), including drylands (Rietkerk, 2004; Kéfi et al., 2007), planktonic communities (Okubo, 1980), salt marsh communities (Zhao et al., 2021), and mussel beds (Liu et al., 2014). When seeing these ecosystems from the sky, one may see a two-phase mosaic with species aggregated in space separated by open areas. This spatial heterogeneity results from two antagonistic forces acting at different spatial scales: a short-range facilitation (*e.g.*, by plants or mussels) and a long-range competition due to the redistribution of nutrients or water in space. The balance between the two determines the sign and the strength of the feedback, as well as the type of pattern observed. In particular, when competition is high, these patterns show a regular shape (Turing-like; Klausmeier, 1999; Rietkerk and van de Koppel, 2008), while they have more irregular structures, characterized by a scale-free patch size distribution (*i.e.*, power-law) when facilitation dominates the system (Kéfi et al., 2007; Scanlon et al., 2007). Importantly, the emergent feedback from the balance of interactions in space is somehow similar to the temporal balance of feedback loops found to trigger oscillations in shallow lakes (van Nes and Scheffer, 2007): both spatial patterns and oscillatory dynamics emerge when there are differences in scale (space or time) between loops of contrasting signs.

On the other hand, biogeomorphic feedbacks in intertidal ecosystems described previously generate another type of self-organized pattern, referred to as phase separation (see Liu et al., 2016 for review). Contrary to Turing patterns, they involve a density-dependent aggregation and are found across a wide range of systems (Ge and Liu, 2021; Siteur et al., 2023). In seagrass meadows for example, because seagrass patches favor the accumulation of sediments, it limits grazing by waterfowl during low tide as they cannot feed on dense seagrass patches elevated above the water and thereby graze on the water-logged hollows (Van Der Heide et al., 2012). Grazing pressure is therefore determined by the spatial distribution of the seagrass, which in turn is controlled by grazing (via consumption). Ultimately, this feedback between grazing/foraging behavior and seagrass density generates emergent spatial patterns (Ge and Liu, 2021). These types of patterns differ from the Turing ones as the mean patch-size coarse-grain over time and their patch-size distribution is best described by a log-normal distribution (Siteur et al., 2023).

Spatial heterogeneity can also emerge from single negative or positive feedbacks. Because mobile consumers such as predators actively track hotspots of resources, they can produce heterogeneity in the spatial distribution of their prey by feeding preferentially on some areas rather than on others (Barraquand and Murrell, 2013). In addition, by spending more time in these areas, they excrete more nutrients locally, which can positively feed back on their growth (Anderson et al., 2010; McLoughlin et al., 2016). For example, nutrient-rich guano deposited by birds on islands has been shown to leach to neighboring marine ecosystems, boost fish growth, and positively affect sea-bird demography in return (Graham et al., 2018; McInturf et al., 2019). Hence, localized animal wastes generate nutrient hotspots and spatial heterogeneity (Monk and Schmitz, 2022; Ferraro et al., 2022; Johnson-Bice et al., 2023). Interestingly, the interaction between this positive recycling loop and a negative one acting at lower scale can erase spatial heterogeneity. In the example of bird guano, islands where birds deposit large amounts of nutrients can also be invaded by coconut trees that benefit from the bird nutrient enrichment. By consuming the nutrients locally, and inhibiting the deposition of guano because seabirds prefer to roost on non-invasive trees, these invasive trees limit the emergence of heterogeneity (Young et al., 2010; Table 2). By being antagonists and acting at different scales, feedback loops therefore may cancel each other.

MODULATORS OF FEEDBACK PROPERTIES

Physical constraints can switch the sign of feedbacks

Physical constraints are a strong modulator of feedbacks across spatial scales: in arid ecosystems, local slopes determine how water is redistributed in space and acts in fine on the scale of interspecific competition. Higher slopes lead to change from spot to stripe patterns due to water flowing downhill between each stripe; this structures competition in space: competition is stronger in the direction of the slope compared to orthogonally to the slope (Klausmeier, 1999; Deblauwe et al., 2011). Similarly, because of gravity, the structure of ecosystems (*e.g.*, convex versus concave profiles; Lindeman, 1942) changes the strength of spatial feedbacks through ecosystems. Watersheds or streams receive more resource flows than grasslands or forests (Gounand et al., 2018b), which modulates trophic cascades (Leroux and Loreau, 2008) and how many subsidies are exported back. In addition, in alpine, arid, or salt marshes ecosystems, the sign of the feedback among plants can change with the level of stress ("stress-gradient hypothesis"; (Callaway et al., 2002; Maestre et al., 2009)). In particular, what is generally being observed across ecosystems, is that stress promotes positive facilitation-driven feedbacks (McCluney et al., 2012; He et al., 2013; Piccardi et al., 2019).

Species traits can change the sign and strength of feedback loops

Stoichiometry of organisms (*i.e.*, elemental composition) modulates the recycling-mediated feedback loops at different spatial scales. At the ecosystem-level, when plants get richer in carbon due to nitrogen depletion for instance or predation risk (Hawlena and Schmitz, 2010), their detritus have a higher C:N ratio due to more recalcitrant carbon structures (*e.g.*, lignin), which slows down the decomposition process (Cherif and Loreau, 2013; Hawlena et al., 2012) and reduces the strength of nutrient cycling. In a meta-ecosystem context, we previously stressed that spatial positive feedbacks can emerge through ecosystems (see Emergent properties from feedback loops section), but the stoichiometry of spatial flows may also exacerbate local stoichiometric mismatches between consumers and their resources (*e.g.*, decomposers and detritus). This happens when a large magnitude of nutrient-poor terrestrial litter falls into lakes or streams (Kelly et al., 2014), and leads to reduced secondary production, eutrophication, or hypoxia (Subalusky et al., 2015; Dutton et al., 2018). In this case, terrestrial and aquatic ecosystems are involved in a negative feedback loop: terrestrial ecosystems benefit from nutrient-rich spatial subsidies, while stoichiometric mismatch impairs freshwater functioning (Pichon et al., 2023). Trait variation can largely constrain the sign and intensity of these feedbacks. In arid ecosystems, whether plants are involved in positive (facilitation) or negative (exploitation) niche construction with the soil depends on their position on the slow-fast functional gradient: contrary to slow facilitating species, fast exploitative ones exhibit high density tissues and leaf-dry mass adapted to the conditions beneath canopies (Liancourt et al., 2005; Butterfield and Briggs, 2011). As a consequence, variation in species traits can change the emergent patterns in ecosystems such as intertidal areas where the stiffness and the density of plant shoots have been shown to modulate the flow velocity, the sedimentation rates, and ultimately, the scale-dependent feedback (Zarnetske et al., 2012; Bouma et al., 2013; Schwarz et al., 2015 in coastal areas and Box 2).

Last, we want to emphasize species with uncooperative strategies (cheaters), and their cascading effect on the stability of communities. Cheating is a phenomenon in cooperative systems where some species have evolved an uncooperative strategy by benefiting from an interaction without paying the associated cost (*e.g.*, Klironomos, 2003; Genini et al., 2010). While there are constraints upon cheating (Perez-Lamarque et al., 2020), when a cheater enters the community, it exercises a negative effect on its mutualistic partners, consequently switching some mutually beneficial feedbacks to negative ones. Such changes of the emergent biotic feedbacks ultimately affect the stability of communities (*e.g.*, Mougi and Kondoh, 2012; Coyte et al., 2015). Duchenne et al. (2023) recently suggested that when cheaters emerge among pollinators, they reduce the community-level positive feedback between mutualistic species, which negatively impacts community persistence.

TOP-DOWN AND BOTTOM-UP VIEWS OF FEEDBACK' REGULATION

We reviewed existing knowledge on the tight bounds between entities and macroscopic systems' behavior in complex adaptive systems. A question remains, however: how are feedbacks modulating the system? Feedbacks between entities contribute to the dynamics, patterns and stability of the whole system (see "Emergent properties" section). In this regard, the system can be constrained by the feedbacks between lower-level entities (*i.e.*, feedbacks as bottom-up regulating forces). At the same time, the system's organization may reciprocally impose structural or stability constraints on the interacting entities (*i.e.*, the system is a top-down regulating force). To illustrate this top-down view of systems' functioning, let us consider the non-random organization of mutualistic networks and food-webs. Nestedness is often observed in mutualistic networks, with specialist species interacting more with a subset of the more generalist species (Bascompte et al., 2003). This non-random structure has been shown to reduce interspecific competition among mutualistic partners (Bastolla et al., 2009), widen the conditions of coexistence (Rohr et al., 2014), and ultimately promote the stability of mutualistic communities (Thebault and Fontaine, 2010). In the same vein, in food webs, studies have sought to explain food-chain lengths or the skewed distribution of interaction strengths towards a dominance of weak links in food webs (De Ruiter et al., 1995; Wootton and Emmerson, 2005): longer food-chains are less stable (Pimm and Lawton, 1977) and weak links promote food-webs stability (Yodzis, 1981; McCann et al., 1998; Neutel et al., 2002; Rooney et al., 2006). Notably, such system's non-random organization may explain why empirical networks include remarkably few feedback loops (Albergante et al., 2014; Domínguez-García et al., 2014; Johnson and Jones, 2017). Hence, under such "systemic selection" (*sensu* Borrelli et al., 2015), the macroscopic properties of a system (*e.g.*, stability, robustness or coherence) constrain the links connecting species, the strength of interactions, and ultimately the emergent feedbacks in the community.

CONCLUSION

Since the early cybernetic interest in positive and negative feedbacks, ecological studies have scaled-up from organism level to the whole landscape to understand how feedback loops could generate diverse, emergent properties. Throughout our contribution, we emphasize, from locally interacting species to spatially connected ecosystems, the ubiquity of feedbacks interacting across space and time and levels of organization, and their importance in generating macroscopic patterns, such as species diversity, emergent spatial patterns or the functioning and stability of ecological systems. Furthermore, properties such as species traits, or physical constraints modulate the strength and sign of feedback loops, and ultimately the pattern they generate across scales.

All the research reviewed suggests that knowledge about ecological feedbacks is essential to improve our fundamental understanding of the interdependence of ecological systems across scales and levels of organization. Given their contribution to the functioning and stability of ecological systems, acknowledging the links connecting species and ecosystems (*i.e.*, ecological interdependencies) could help improve the design of effective conservation and restoration measures that integrate local and spatial dependencies.

BOX 1: QUANTIFYING THE DYNAMICAL EFFECT OF A FEEDBACK LOOP

Let us consider the recycling loop that links herbivores and decomposers as an illustration (Fig. below). Herbivores feed soil decomposers through their carcasses and excretions. Microbes and fungi decompose organic matter, making nutrients available again for plants to grow and indirectly benefiting herbivores that feed on plants. Quantifying the strength of this recycling loop is not sufficient in itself to understand how the feedback loop modulates the transient response of herbivores (or any other compartment) to a perturbation such as nutrient enrichment. To do so, one can compare how herbivores deviate from its equilibrium following nutrient enrichment, as well as their recovery dynamics with and without the feedback loop. For the system in the Figure of Box 1, it can be done by replacing the link between decomposers and the nutrient compartments with a controlled inflow of nitrogen, corresponding to the flow at equilibrium when the loop is closed (*i.e.*, breaking the recycling loop). Then, comparing the system with and without the feedback loop allows us to understand how the feedback loop contributes to transiently increasing or decreasing the perturbation even if the long-term equilibrium in the two situations might be the same. This method has been for instance applied to quantify the impact of the feedback emerging from nutrient recycling on the asymptotic stability of food web (Quévreux et al., 2021).

Box 2: feedbacks across temporal scales (1/2)

Ecological feedbacks do not only vary in space, but also in time, along the development of populations, communities or ecosystems. At the population level, positive feedback loops can dominate at small populations, while negative feedbacks (*e.g.*, resource competition) seem inevitable at high population levels. Starting at low levels, Allee effects will constrain the development of the population, as too few individuals are present for cooperation or group defense to be effective. This creates a minimum viable population. If, however, the population manages to pass this threshold, the positive feedback will act to favor population growth, eventually leading to a state where individuals are abundant and resources are scarce. Competition for resources then creates a dominant negative feedback. When reaching a demographic threshold, there is therefore a switch in the sign of the dominant feedback loop that individuals experience: from positive feedbacks to negative ones. Such changes in the sign of dominant feedbacks can also happen along ontogenies. This is for instance the case of some shrubs in drylands: adult shrubs facilitate the establishment of juveniles, while juveniles compete with adults for the availability of water and nutrients (Miriti, 2006). When juveniles grow, adult plants no longer facilitate their recruitment but compete for the resource availability, therefore changing the sign of the dominant feedbacks from positive to negative. From a community point of view Yin et al. (2022) highlight how local feedbacks can vary in time within communities, along succession. The authors show that facilitative interactions are globally as frequent as competitive interactions in New Jersey grasslands over fifty years. They also reveal that facilitation among species dominates at the early stages of their settlement (colonization probability and general occurrence probability), while it is less common at later stages (survival of species in the patch and the growth of their population). This leads to a succession of dominant feedbacks (from positive to negative) that is akin to the one proposed above within populations (Allee effects).

BOX 2: FEEDBACKS ACROSS TEMPORAL SCALES (2/2)

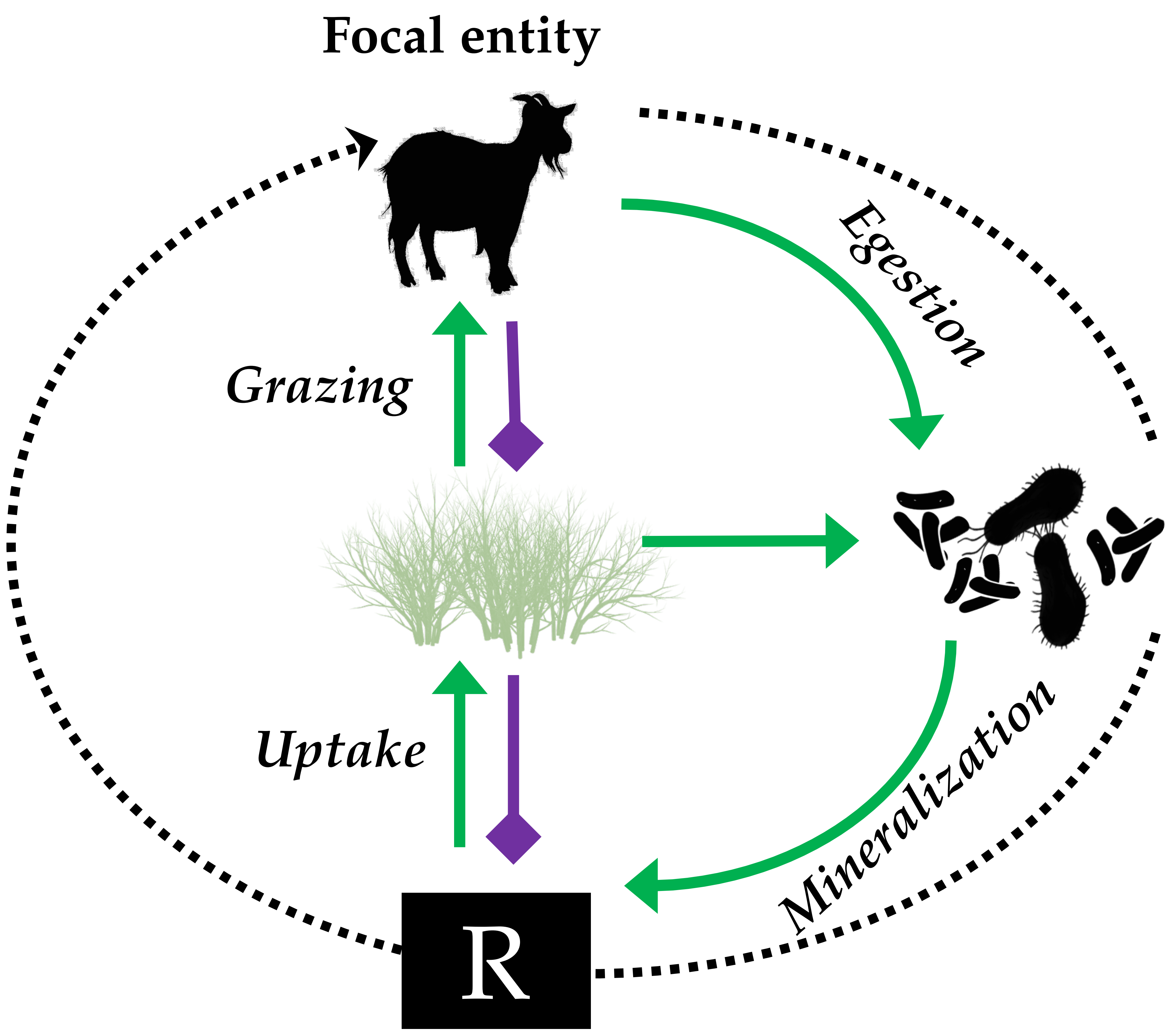
At the ecosystem level, temporal succession of feedbacks along successional stages have also been discussed. In their seminal work, Odum and Margalef suggested that ecosystem development would lead to increasing dominance of negative feedbacks regulating ecosystem functions and increasing its stability to external perturbations (Margalef, 1963; Odum, 1969). While the argument was mostly verbal at the time, there is now evidence of such changes along successional times. In nitrogen-poor ecosystems, facilitation dominates at early-successional stages because some nitrogen-fixing plants increase the availability of nitrogen, which positively affects their growth capacities (positive feedbacks with soil). As succession goes, higher availability of nitrogen drives phosphorus limitation and competitive exclusion of early nitrogen-fixing species by late-colonizing ones eventually leading to dominant negative feedbacks during the late stages (Menge and Hedin, 2009; Koffel et al., 2021). Finally, this succession from positive to negative feedbacks can also be observed in the context of species invasion. For instance, the "enemy release hypothesis" suggests that invasive species may escape pathogens at initial stages, therefore leading to positive (or weakly negative) feedback with the soil at initial stages. However, the accumulation of pathogens in later stages contribute to stronger negative feedbacks (Klironomos, 2002; Diez et al., 2010). Importantly, because feedbacks change over successional stages, they can scale up to produce self-organized patterns at different times. This is the case in intertidal systems, where fast colonizer plants do not self-organize in patches because they produce many seedlings that rapidly occupy most of the landscape and stabilize existing wetland channels (Schwarz et al., 2018). Later colonizing plants, on the other hand, are characterized by a higher lateral expansion which leads to stronger biogeomorphic feedbacks and the emergence of new vegetation-induced channels.

Figure Box 1: Understanding a feedback loop using two complementary approaches. The feedback strength is obtained by multiplying the weight of the links along the circular path (here, egestion, mineralization, uptake, and grazing processes; left panel). The feedback strength estimates whether a loop will self-amplify (when positive) or limit (when negative) the effects of a perturbation. This also allows to compare the strength of different loops in a system. As a complementary approach, to understand how this feedback modulates the transient dynamics of the focal entity (here the herbivore) following a perturbation (here nutrient enrichment), one needs to control for the loop, and compare the dynamics of recovery and the distance to equilibrium with the feedback and when controlling for it (right panel). "R" stands for resources.

Complementary approaches to quantify feedbacks

Network approach
for feedback strength

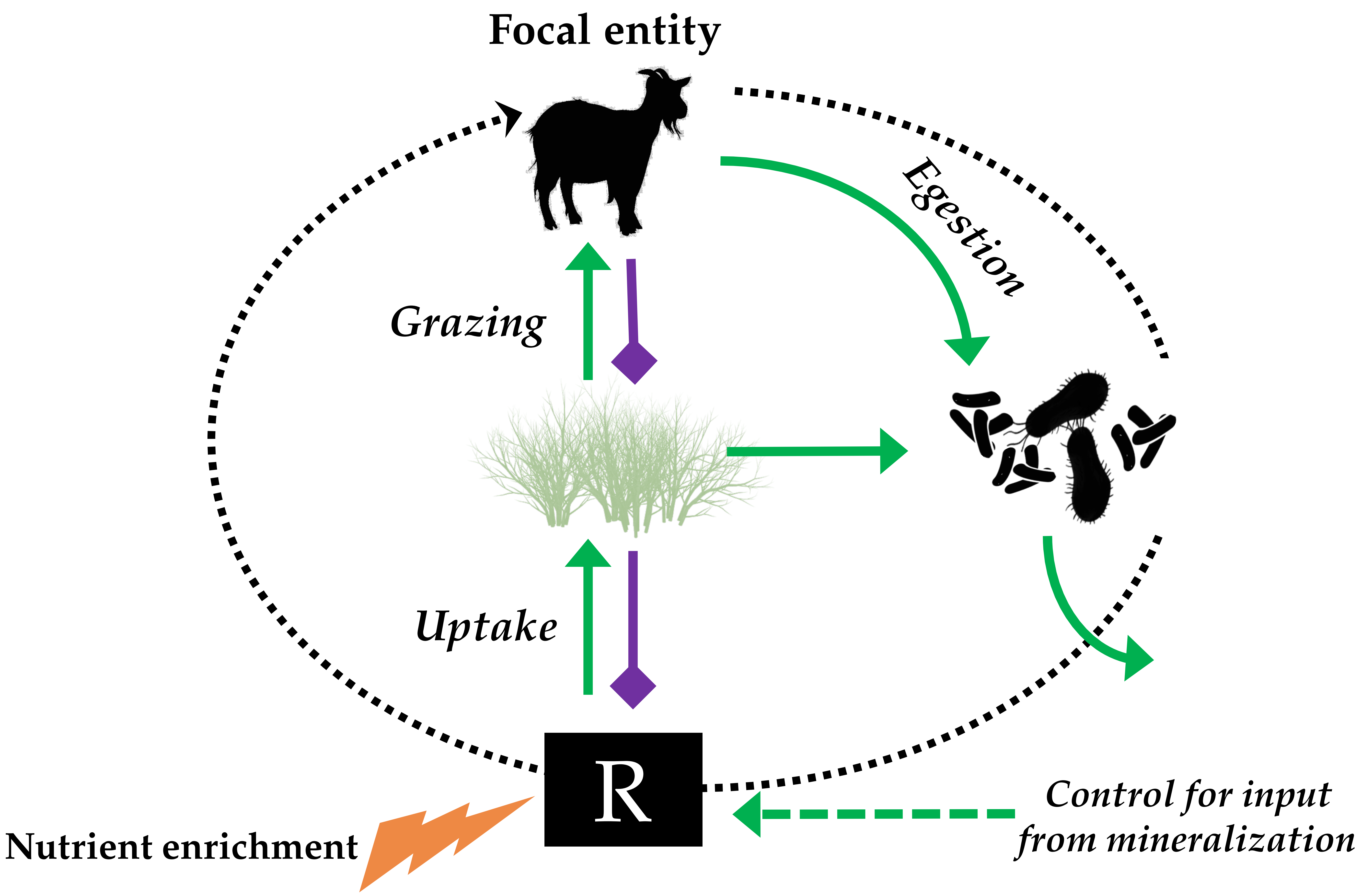
Hannon 1973, Neutel et al., 2002



Feedback strength = Egestion * Mineralization * Uptake * Grazing

Loop-control approach
for feedback dynamical property

Quévreux et al., 2021, Theis et al. 2021



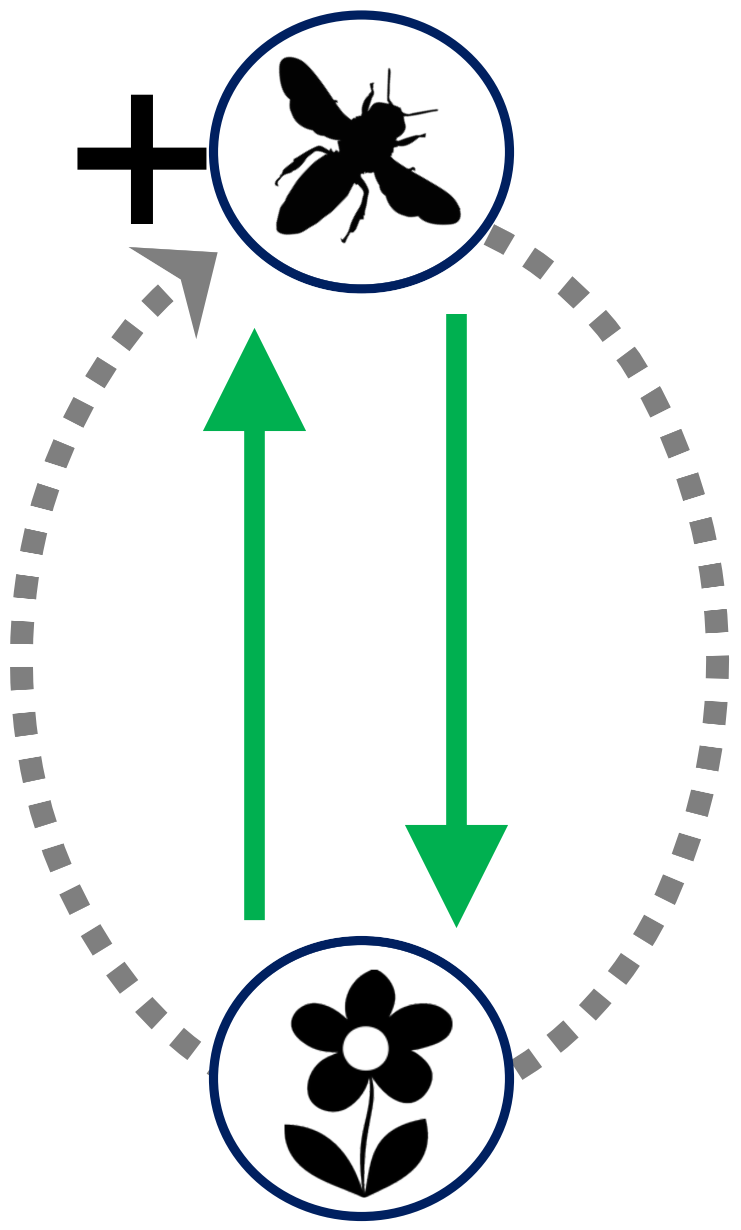
Feedback dynamical effect = difference in transient dynamics between control and full loop

Figure 1: The length and sign of the feedback loop. Feedbacks can emerge when two species interact through mutualism (positive feedback) or between a species and its resource (negative feedback). Some feedback loops have longer lengths such as in intransitive competitive networks, where the feedback sign is determined by the number of negative links involved in the loop. “R” stands for resources.

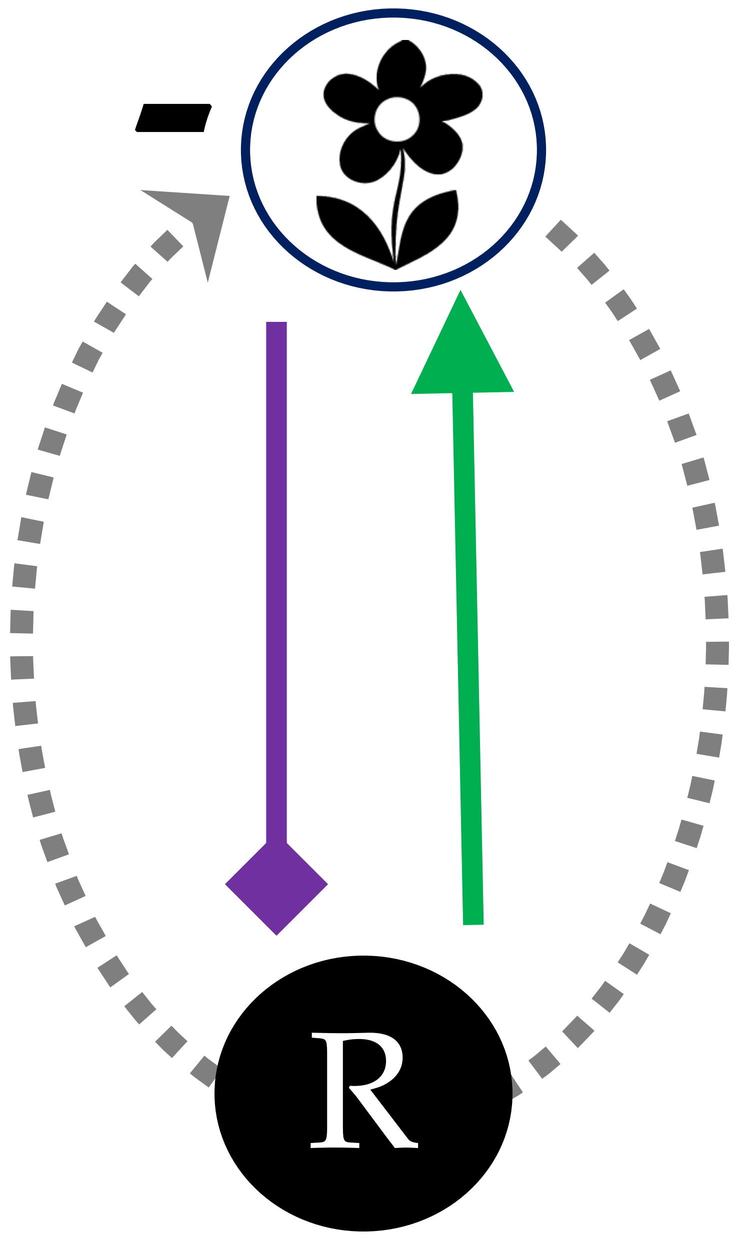
Feedback length & sign

Feedbacks of length 2

Facilitation positive loop

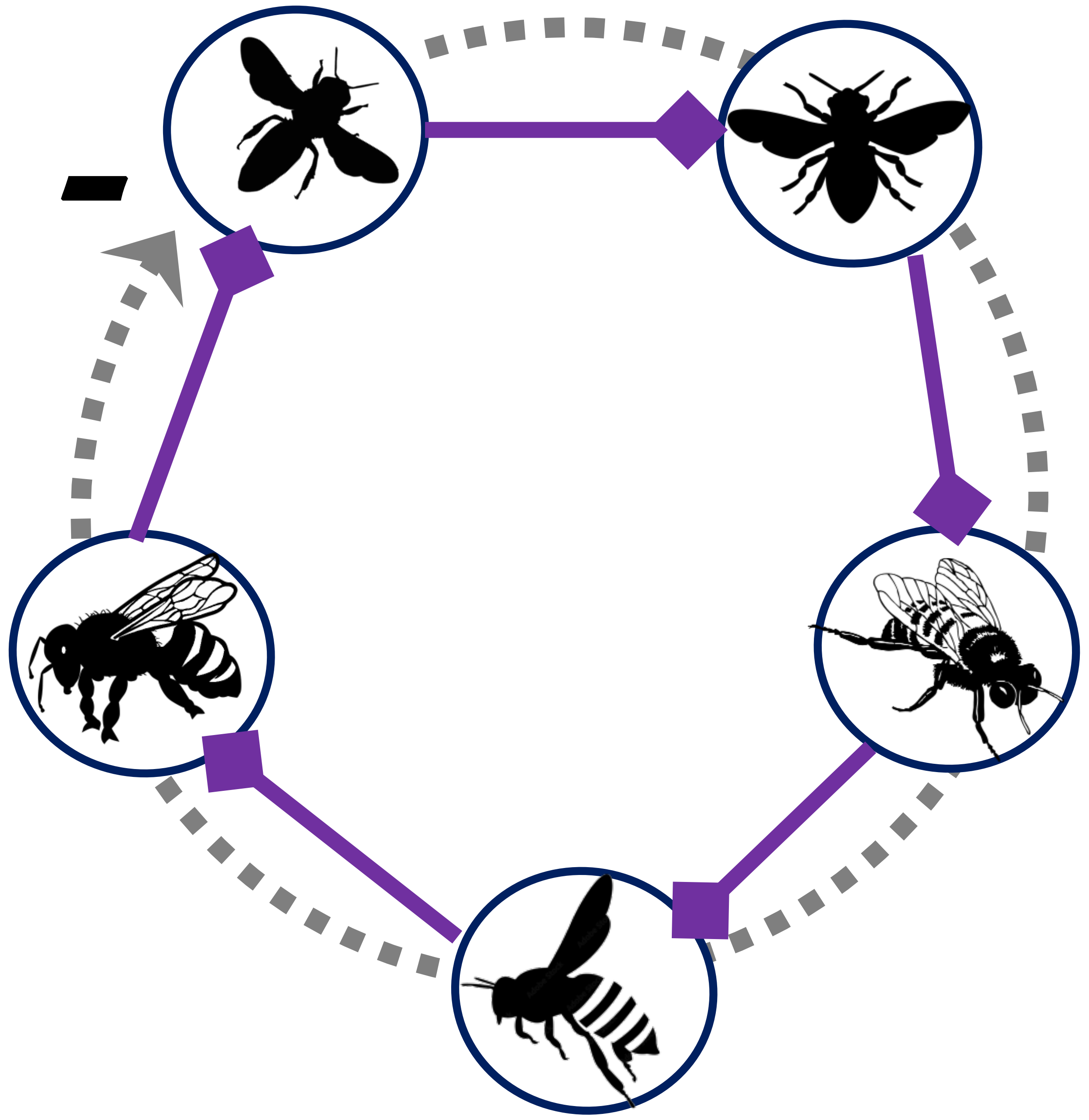


Consumption negative loop

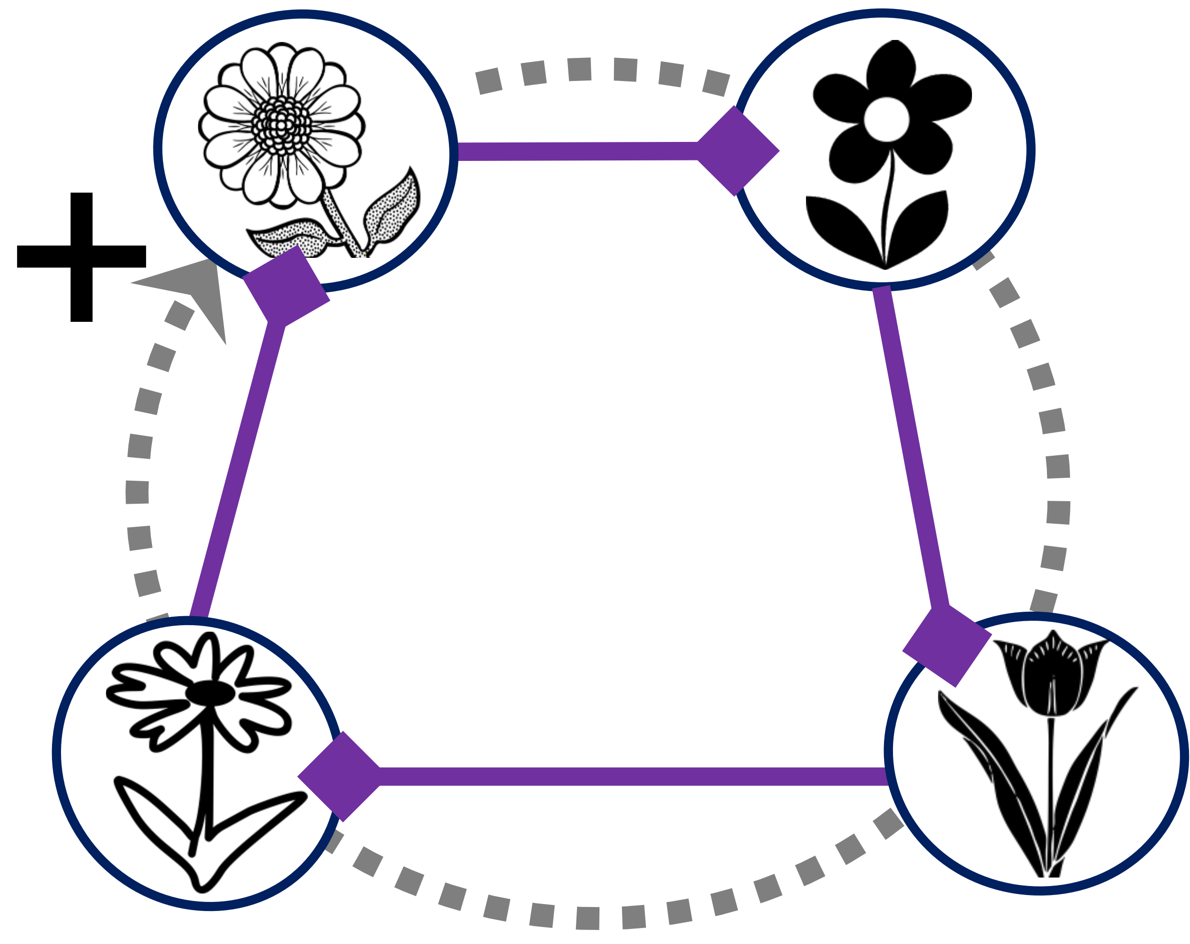


Longer feedbacks and feedback signs

Negative intransive loop



Positive intransive loop



→ Positive link

◆ Negative link

⋯> Feedback loop

Figure 2: Ecological feedbacks across spatial scales. At the scale of an individual or a species, interactions with the local abiotic environment generate feedback with resource availability or landforms (biogeomorphic feedbacks), but also more generally through niche construction processes (*e.g.*, habitat creation or modification). At the population or community level, the individual or species may also be involved in demographic or behavioral feedbacks emerging from competition, facilitation, and density-dependent behavior. Last, at the landscape scale, populations, communities and ecosystems exchange individuals, resources and information, which generates spatial feedbacks linking local and landscape scale dynamics. For detailed examples not represented in this figure (*e.g.*, behavioral feedbacks or dispersal spatial feedback) see Table 1. "R" stands for resources.


Feedbacks across spatial scales
Local organisms-abiotic feedbacks
+
Plant- soil water feedback
Biogeomorphic feedback
+
Community-scale biotic feedbacks
Consumption feedback
-
Competition feedback
+
Facilitation feedback
+
+
R
Recycling feedback
Spatial feedbacks
Resource spatial flow feedback
+/-
terrestrial ecosystem
aquatic ecosystem

Figure 3: Mapping the emergent properties from feedback loops. The position of each emergent property corresponds to a level of organization (from individual to ecosystem) and a spatial scale (local or spatial). See Table 1 for examples for each emergent property and the associated references.

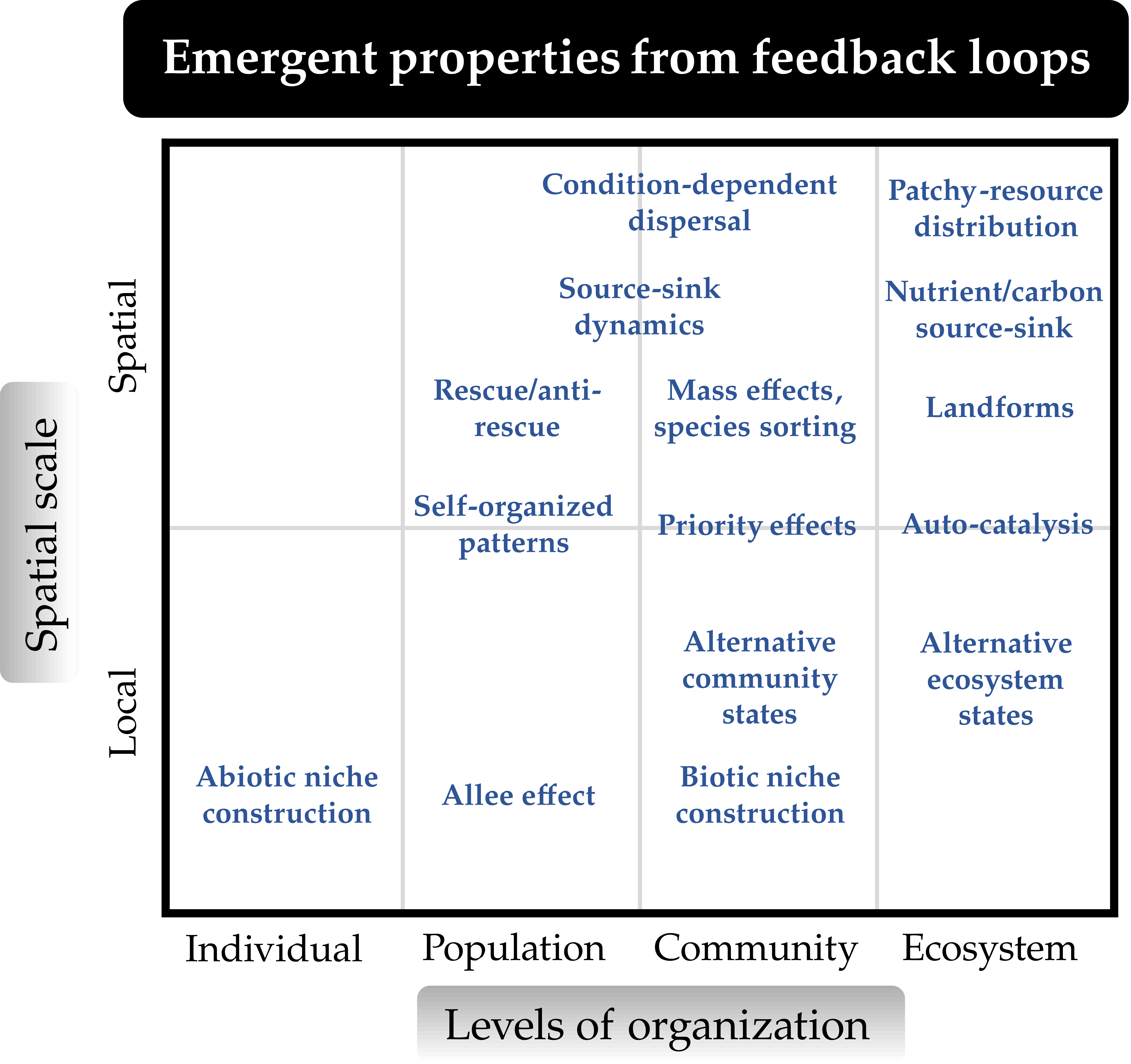

Emergent properties from feedback loops
Spatial scale
Spatial
Local
Levels of organization
Individual
Population
Community
Ecosystem
Condition-dependent dispersal
Patchy-resource distribution
Source-sink dynamics
Nutrient/carbon source-sink
Rescue/anti-rescue
Mass effects, species sorting
Landforms
Self-organized patterns
Priority effects
Auto-catalysis
Alternative community states
Alternative ecosystem states
Abiotic niche construction
Allee effect
Biotic niche construction

Table 1: Examples of the different types of feedbacks and their associated emergent properties

Table 1: Examples of the different types of feedbacks and their associated emergent properties

Type of feedback		Example	Emergent property
Species-environment feedbacks	**Biogeomorphic**	Sea-grass meadows stabilize sediments and change hydrodynamic regime [1]	Alternative stable states [2] Landscape formation [3-4]
	Involving resources	Plant facilitation increases the availability of nutrients, water, and limits water evaporation, which positively affect their growth and maintenance in drylands [5]	Alternative stable states [5-7] Self-organized patterns [6,7]
Population and community-level feedbacks	**Behavioural feedbacks**	Fish populations in coral reefs display density-dependent foraging rates [8]	Alternative stable states [8, 9]
		High predation risk areas generate nutrient hotspot through decomposition of carcasses and nutrient excretion, which fosters plant growth and the patch quality for herbivore consumption [10-13]	Patchy distribution of resources [10-13]
	Demographic feedbacks	Positive feedback between plants and pollinators [14]	Alternative stable states [14]
		Negative feedbacks between predators and preys [15]	Long transients, cycles [15,16]
Spatial feedbacks	**Feedbacks driven by dispersal**	Dispersing individuals can experience density-dependent dispersal emerging from interspecific competition [17] or patch-dependent colonization rate [18] (*e.g.* which depends on the patch quality) creating a feedback between local and spatial dynamics	Alternative stable states [19] Spatial heterogeneity and source-sink dynamics [18,20] Positive spatial feedbacks (rescue) or negative spatial feedbacks (anti-rescue) [19]
	Feedbacks driven by resource flows	Seabirds excrete guano that positive affect their growth through a cascading effect on coral reefs and fish [21, 22]	Source-sink dynamics of carbon and nutrients [23] Spatial auto-catalytic loop on functioning [24] Emergent colimitation of resources [25]
		Bidirectional exchanges of resources between ecosystems (*e.g.*, at terrestrial-aquatic ecotone) [25-27]	Alternative stable states [28] Diffusion-induced instabilities [29,30]

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Table 2: Examples of how feedback knowledge can help for conservation, restoration and mitigation measures across scales

Table 2: Examples of how feedback knowledge can help for conservation, restoration and mitigation measures across scales

	Description	**Consequence**
Ecosystem restoration	Increasing the success of dryland restorations through higher seeding (fostering positive feedback from facilitation) and weed control (limiting competition on seedlings)	Higher establishment success of plants [1] More carbon sequestration and services provided by plants [2]
	Maximizing the restoration success of coastal ecosystems by planting propagules in clustered patches and adding clams (interspecific facilitation) to promote positive feedbacks during establishment	Higher survivorship, biomass and expansion of propagules [3-5] Landscape formation, carbon capture and storage [6]
	Managing the demography of harvested species to regulate population demography and maintain high catch or yield	Fisheries assessment and management control can, in theory, maintain fisheries at a maximal sustainable yield either by increasing the catch when population demography is high (*i.e.,* more negative feedbacks) or by adopting rebuilding plans for overfished species (promoting positive feedbacks) [7]
Conservation	Limiting the spread of invasive species such as island rats or foxes preying on seabirds, or coconut trees replacing birds' nesting habitats to maintain the positive recycling feedback loop from bird guano	Nitrogen depletion in soils that changes the stoichiometry of plants and the community composition [8,9] Disrupts the positive feedback mediated by guano that increased sea-bird demography, fostered island vegetation and coral-reefs' functioning [10,11]
	Protecting the spatial feedbacks between adjacent ecosystems such as at the forest/stream ecotone	Forest subsidies can cascade from organic matter to top consumers in streams (fish), where it fosters fish growth and food-web functioning [12]. Disruption of such coupling may lead to nutrient loading and stream eutrophication [13]
	Protecting specific marine areas by excluding fishing pressure to promote restoration of adjacent areas through spatial rescue (positive spillover via dispersal from the marine protected area)	Designing effective marine protected areas contribute to preserve larval sources, areas connectivity, and fish population abundances [14]
Climatic mitigation	Understanding the feedback loop involved in decomposition process (from organic carbon to carbon release in the atmosphere) to design efficient carbon sequestration measures	Mechanisms such as predation risk [15,16] and priming effect [17-19] can accelerate the loop of carbon decomposition and lead to more carbon loss and in shorter timescales
	Understanding animal-driven recycling loops involving nutrient and carbon cycles to design climatic mitigation measures and species conservation	Trophic downgrading of large animals breaks nutrient and carbon recycling loops and lead to reduced nitrogen and carbon cycles, higher soil-respiration rates, lower ecosystem functioning, and can ultimately switch ecosystems from carbon sink to source [20-24]

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