

# Facultative mutualisms: A double-edged sword for foundation species in the face of global change

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## Abstract

Ecosystems worldwide depend on habitat-forming foundation species that engage in facultative mutualisms. Global change, however, is causing rapid declines of foundation species-structured ecosystems, often typified by sudden collapse. Although disruption of obligate mutualisms involving foundation species is known to precipitate collapse (e.g. coral bleaching), how facultative mutualisms (i.e. context-dependent, non-binding reciprocal interactions) affect ecosystem resilience is uncertain. Here, we synthesize recent advancements, and combine this with model analyses supported by real-world examples, to propose that facultative mutualisms may pose a double-edged sword for foundation species. We suggest that by amplifying self-facilitative feedbacks by foundation species, facultative mutualisms can increase foundation species resistance to global change stressors. Simultaneously, however, mutualism-dependency can generate or exacerbate bistability, implying a potential for sudden collapse when the mutualism's buffering capacity is exceeded, while recovery requires conditions to improve beyond the initial collapse point (hysteresis). Thus, our work emphasizes the importance of acknowledging facultative mutualisms for conservation and restoration of foundation species-structured ecosystems, but highlights the potential risk of relying on mutualisms in the face of global change. We argue that significant caveats remain regarding the determination of these feedbacks, and suggest empirical manipulation across stress gradients as a way forward to identify related nonlinear responses.

## Introduction

Since the Industrial Revolution humans have been altering environmental conditions at an unprecedented pace and scale (Kareiva *et al.* 2007; Steffen *et al.* 2018). Human-induced global warming (Costanza *et al.* 1997; IPCC 2014) together with other impacts such as pollution, biotic invasions, overharvesting, and land-use changes have triggered the sixth mass extinction of plants and animals (Cardinale *et al.* 2012). Biodiversity loss can be a direct consequence of such impacts, but can also arise from loss of organisms that are disproportionately important to ecosystem functions and structure (Bruno *et al.* 2003; Angelini *et al.* 2011; Estes *et al.* 2011). Particularly the loss of foundation species (Dayton 1972) – also known as autogenic ecosystem engineers (*sensu* Jones *et al.* 1997) – can elicit dramatic shifts in biodiversity and ecosystem functioning (Ellison *et al.* 2005; Angelini *et al.* 2015; van der Zee *et al.* 2016; Borst *et al.* 2018; Bulleri *et al.* 2018). Such spatially dominant habitat-forming organisms – including trees, wetland plants and reef-building corals and bivalves – create complex 3-dimensional biogenic structures that modulate the availability of critical resources and ameliorate physical stressors (Ellison *et al.* 2005; Altieri *et al.* 2007; Hoegh-Guldberg *et al.* 2007; Donadi *et al.* 2013). Because many species are dependent on the presence of foundation species, disturbances that cause their decline often impact whole habitats to the extent that entire ecosystems and their associated communities collapse (Stachowicz 2001; Bruno *et al.* 2003; Angelini *et al.* 2011).

Although the foundation species concept typically considers a single dominant species or a limited number of co-occurring species in the same functional guild (e.g. as often occurs in forests, coral reefs and macroalgae beds), many foundation species engage in obligate or facultative mutualisms (Stachowicz 2001; Hay *et al.* 2004; Angelini *et al.* 2016; de Fouw *et al.* 2016). Obligate mutualisms, such as the association between fungi and phototrophs in lichens or the partnership between endosymbiotic zooxanthellae and corals, are by definition vital to both species irrespective of environmental conditions (Hoeksema & Bruna 2000; Kiers *et al.* 2010; Bronstein 2015). Facultative mutualisms, by contrast, are not vital to the organisms involved but can extend the natural environmental range limits of one or both organisms, thereby causing a species' realized niche to exceed its fundamental niche (Bertness & Callaway 1994; Stachowicz 2001; Bruno *et al.* 2003; Afkhami *et al.* 2014; Bronstein 2015; Crotty & Bertness 2015). Mounting evidence suggests that facultative mutualisms commonly influence biodiversity and ecosystem structure, as many organisms are directly involved in networks of such beneficial interactions (Stachowicz 2001; Hay *et al.* 2004; Kiers *et al.* 2010; Silknetter *et al.* 2020; Valdez *et al.* 2020).

In this paper, we synthesize recent advancements to suggest that facultative mutualisms can strongly affect ecosystem stability and resilience when the interaction involves a foundation species. It's already well known that positive interactions in general, including mutualisms, support positive (also known as 'exacerbating') feedback mechanisms that, if strong enough, generate ecosystem thresholds or 'tipping points' in environmental conditions beyond which ecosystems shift to alternative stable states (Kéfi *et al.* 2016; Maxwell *et al.* 2017). However, while studies have mostly focused on a single feedback mechanism (e.g. the foundation species facilitating itself), many ecosystems are characterized by multiple, potentially interacting feedbacks (Maxwell *et al.* 2017; van de Leemput *et al.* 2018). Here, we propose that facultative mutualisms and the feedbacks they initiate can increase foundation species' resistance to global change stressors, but simultaneously predispose foundation species to abrupt collapse. To test this hypothesis, we build a conceptual framework that considers (1) how habitat modification by foundation species can lead to self-facilitation via a positive feedback and consequently affect ecosystem resilience, and (2) how mutualisms generate another positive feedback that may interact with the first feedback. Finally, we present examples (Fig. 1; Table S1), and discuss implications and future challenges.

## Foundation species and self-facilitative feedbacks

Foundation species modify the physical environment through their formation of complex physical structures that alter water and/or air flow, mediate nutrient cycling, and trap debris and detritus (Dayton 1972; Jones *et al.* 1994; Stachowicz 2001; Angelini *et al.* 2011). Although the typically positive consequences of such habitat modification for other community members has been the conceptual focus of many studies, foundation species also commonly improve living conditions for themselves and their conspecifics through the same mechanisms (Fig. 2 a-d) (e.g. van de Koppel *et al.* 2005; Hirota *et al.* 2011; Scheffer *et al.* 2012; Maxwell *et al.* 2017). Often, such self-facilitation is generated via positive density-dependence (Bertness & Callaway 1994; Bruno *et al.* 2003) yielding a positive feedback, in which habitat quality improves with the density and/or patch-size of the foundation species. Importantly, the strength and relevance of such self-facilitation depends on environmental conditions. Changes made to an already suitable habitat via self-facilitation will yield little overall improvement in living conditions. By contrast, self-facilitation can be essential to a foundation species' survival, growth and reproduction in hostile conditions, by alleviating physical or biotic stress and thereby extending the foundation species' own realized niche (Bruno *et al.* 2003; Crotty *et al.* 2018). Examples of ecosystems where foundation species benefit from positive density-dependence include tropical forest and desert vegetation that mediate water availability by creating a humid microclimate to stimulate plant growth (Rietkerk *et al.* 2004; Hirota *et al.* 2011); coral and shellfish reefs that facilitate settlement of additional coral and shellfish recruits by providing hard structures (Schulte *et al.* 2009); and seagrasses, salt marsh plants, and mangroves that enhance their own growth by stabilizing sediments, and trapping suspended particles to locally enhance nutrient availability (Balke *et al.* 2011; Zemp *et al.* 2017) (see Table S1 for further examples).

Many ecosystems structured by foundation species have been rapidly declining, with losses often characterized by sudden collapse and low restoration success rates of degraded habitats (Ellison *et al.* 2005; Hoegh-Guldberg

*et al.* 2007; Maxwell *et al.* 2017). A growing body of theoretical and empirical studies suggests that collapses are a consequence of the existence of feedbacks often derived from strong self-facilitation (van de Koppel *et al.* 1997; Nyström *et al.* 2000; Scheffer *et al.* 2001). Ecosystems with such feedbacks typically respond in a nonlinear fashion to environmental change whereby the feedbacks buffer increasing external stress to support the foundation species' persistence until a stress threshold is exceeded, at which point the foundation species experiences mass mortality. Moreover, if the feedback is sufficiently strong, it can cause alternative stable states (bistability); a condition where, depending on the initial state, either a foundation species-structured or an alternative state are stable under the same environmental conditions (Fig. 2a-d) (Scheffer *et al.* 2001). An important consequence is that recovery is very difficult once the foundation species' abundance drops below the critical threshold required to induce the level of habitat modification needed to initiate and sustain new growth (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; Balke *et al.* 2011).

In recent decades, there has been a surge of theoretical work on how feedbacks may lead to sudden ecosystem collapse and ecosystem bistability, as well as models and indicators to detect nearness to collapse (e.g. Scheffer *et al.* 2001; Dakos *et al.* 2015). Yet, both the protection and restoration of foundation species-dominated ecosystems remain extremely difficult, suggesting that density-dependent positive feedbacks have yet to be systematically integrated into ecosystem management designs and that certain fundamental mechanisms supporting foundation species performance are overlooked (Bruno *et al.* 2003; Silliman *et al.* 2015). Contemporary studies have largely focused on a single feedback, often self-facilitation, as the central mechanism underpinning non-linear ecosystem responses and bistability (van de Leemput *et al.* 2016; Maxwell *et al.* 2017). In reality, however, foundation species-dominated systems are often governed by multiple feedbacks, which may theoretically interact to alter nonlinear responses to environmental change (van de Leemput *et al.* 2016; Maxwell *et al.* 2017).

### **Foundation species, self-facilitative and mutualistic feedbacks: a theoretical framework**

Mutualisms, by their very nature of providing reciprocal benefits, generate a positive feedback in which each partner stimulates the growth or survival of the other, thereby indirectly facilitating itself (Kiers *et al.* 2010; Bronstein 2015). Because facultative mutualisms typically vary in strength with environmental conditions (Bronstein 1994; Hoeksema & Bruna 2000; Stachowicz 2001; Bronstein 2015), such interactions may invoke nonlinear responses of partnering species to environmental change, similar to the self-facilitation by foundation species discussed above (Dakos & Bascompte 2014; Lever *et al.* 2014; de Fouw *et al.* 2016; Maxwell *et al.* 2017; de Fouw *et al.* 2018). Indeed, theoretical work suggests that strong mutualistic interactions in plant-pollinator networks can cause bi-stability due to thresholds in environmental conditions, beyond which these mutualistic networks collapse (Goh 1979; Dean 1983; Dakos & Bascompte 2014; Lever *et al.* 2014).

When a foundation species that, on the one hand, facilitates itself also engages in a mutualism, an inherent consequence is that the growth or survival of the foundation species is now mediated by two feedback mechanisms, not one (Maxwell *et al.* 2017; de Fouw *et al.* 2018). As the two feedbacks are both positive in nature, they may act in concert to facilitate the foundation species, potentially amplifying nonlinear ecosystem responses to global change (Fig. 2e-f). However, the two feedbacks may alleviate the same or different stressors, generating a context-dependence that could strongly affect the foundation species' vulnerability to global change.

To explore how the self-facilitative and mutualistic feedbacks may interactively affect the resilience of foundation species-structured ecosystems, we used a minimal mathematical model to investigate three scenarios: (1) the foundation species generates a single, self-facilitative feedback that mitigates an environmental stressor; (2) the foundation species also engages in a facultative mutualism that mitigates a second environmental stressor; or (3) the foundation species also engages in a mutualism that acts on *the same* environmental stressor as the self-facilitative feedback. Note that we define 'stressor' as any external environmental force that can reduce the health of the foundation species (*sensu* Stachowicz 2001).

The model consists of a system of two differential equations (de Fouw *et al.* 2018). The change in foundation

species biomass or population size ( $FS$ ) over time is described by the following differential equation:

$$\frac{dFS}{dt} = gfs \bullet \left(1 - \frac{FS}{Kfs}\right) \bullet FS - mfs \bullet fS1 \bullet FS - mfs \bullet fS2 \bullet FS \quad (eq.1)$$

where  $gfs$  is the maximum relative growth rate,  $Kfs$  is the carrying capacity,  $mfs$  is the maximum relative mortality, and  $fS1$  and  $fS2$  are functions controlling the mortality due to stressor 1 and 2, respectively.

Following de Fouw *et al.* (2018) we assume simple linear growth of the mutualist population size ( $M$ ) that is facilitated by the foundation species:

$$\frac{dM}{dt} = gm \bullet \frac{FS}{Hfs1 + FS} \bullet \left(1 - \frac{M}{Km}\right) - mm \bullet M \quad (eq.2)$$

with  $gm$  as the maximum growth rate,  $Hfs1$  as the half saturation constant for the positive effect of  $FS$  on  $M$ ,  $Km$  as the carrying capacity of  $M$ , and  $mm$  as the relative mortality constant of  $M$ .

Function  $fS1$  is described as follows:

$$fS1 = S1_{max} \bullet \frac{Hfs2}{Hfs2 + FS} \bullet fM1 \quad (eq.3)$$

where  $S1_{max}$  is the maximum stress level from stressor 1,  $Hfs2$  is the half rate constant for reducing the stressor by the foundation species, and  $fM1$  is a function controlling the effect of the mutualist on stressor 1.

Function  $fM1$  is described as:

$$fM1 = \frac{Hm1}{Hm1 + M} \quad \text{if mutualist } M \text{ is present} \quad (eq. 4.1)$$

$$fM1 = 1 \quad \text{if mutualist } M \text{ is absent} \quad (eq. 4.2)$$

in which  $Hm1$  is the half-saturation constant for the effect of the mutualist on reducing stressor 1.

Finally, function  $fS2$  is described as:

$$fS2 = S2_{max} \bullet fM2 \quad (eq.5)$$

where  $S2_{max}$  is the maximum stress level from stressor 2, and  $fM2$  is the function controlling the mutualist's effect on stressor 1:

$$fM2 = \frac{Hm2}{Hm2 + M} \quad \text{if mutualist } M \text{ is present} \quad (eq. 6.1)$$

$$fM2 = 1 \quad \text{if mutualist } M \text{ is absent} \quad (eq. 6.2)$$

in which  $Hm2$  is the half-saturation constant for the reducing effect of the mutualist on stressor 2. Default model parameter settings are presented in Table 1.

In each scenario, we used bifurcation analyses to evaluate the stability of the equilibria of the model at varying settings of stressors 1 and 2, and as a means of generally exploring how gradients in both stressors affect ecosystem resilience. For each analysis, either stressor 1 or 2 was increased in small steps, after which

the model was run to stabilize to its equilibrium. This analysis was then performed backwards, such that each stressor was decreased in small steps. Finally, the two analyses were combined to construct bifurcation plots demonstrating how the foundation species' population size varies across gradients in stressor 1 and 2 under each of the three scenarios. We determined unstable equilibria making a quasi-steady state assumption and plotting equilibria for different values of the control parameters in GRIND for MATLAB.

## Model results

Similar to earlier studies of self-facilitation (Scheffer *et al.* 2001; Scheffer & Carpenter 2003; van der Heide *et al.* 2007), the model first predicts that self-facilitation by the foundation species causes nonlinear behavior and bistability across the environmental stress gradient (Fig. 3a). Second, when a mutualism that mitigates a second stressor is added, the foundation species' overall health is enhanced (i.e. its net growth:mortality ratio is higher), allowing it to reach a higher maximum population size, and to occur across a broader range of both stressors (Fig. 3b-c). However, nonlinearity also increases, such that bi-stability emerges for stressor 2, and the range of bi-stability increases for stressor 1. Third and finally, when the self-facilitative and mutualistic feedbacks mitigate the same environmental stressor, they together amplify the buffering capacity for stressor 1, but also greatly enhance the bi-stability range (Fig. 3a,c).

Although theoretical, this exercise yields several notable insights. First, foundation species can, by engaging in a mutualism, significantly expand their environmental range limit for a stressor (Afkhani *et al.* 2014). Interestingly, this 'niche-broadening' may be achieved even if the mutualism does not directly mitigate the stressor itself, but instead stimulates the foundation species by alleviating a second stressor. In addition to increasing ecosystem resistance to stress, the mutualism extends the range of hysteresis, amplifying nonlinear system responses to environmental stress. Consequently, environmental conditions may have to be improved over a much larger range to achieve natural recovery to a stable alternate state compared to systems whose behavior is not mediated by a mutualism. Finally, in binding both species to a common fate under conditions where the mutualism is essential for persistence, mutualistic interactions can increase the foundation species' vulnerability to perturbations that affect the mutualist.

## Examples from real ecosystems

Foundation species in marine, aquatic and terrestrial ecosystems often engage in mutualistic interactions (Fig. 1; Table S1) (Stachowicz 2001; Hay *et al.* 2004). For example, the vast majority of terrestrial plants engage in mycorrhizal or plant-pollinator interactions (Smith & Read 1997; Potts *et al.* 2010), submerged marine and freshwater macrophytes provide shelter to grazers of algae that compete with the plants for light and nutrients (e.g. Scheffer 1999; Peterson & Heck Jr 2001; Valentine & Duffy 2007), *Sphagnum* mosses harbor methanotrophic and nitrogen-fixing bacteria that increase CO<sub>2</sub> and nitrogen availability to the plant (Raghoebarsing *et al.* 2006; Larmola *et al.* 2014), and sponges growing on the solid substrate provided by mangrove roots increase nutrient availability for the trees (Ellison *et al.* 1996). Here, we discuss four relatively well-studied examples (Fig. 1) in more detail to illustrate how both self-facilitative and mutualistic feedbacks can affect ecosystem stability, and how global change may affect these interactions.

### Arid ecosystems

In arid systems, grasses and shrubs often modify soil conditions to their own benefit (Rietkerk *et al.* 2004; Kefi *et al.* 2007; Rietkerk & van de Koppel 2008; Angelini *et al.* 2011). Following scenario 1, patches of grasses and shrubs enhance water availability by increasing infiltration with their root system, while simultaneously lowering evaporation through shading with increasing density and patch size (Klausmeier 1999; Hille Ris Lambers *et al.* 2001; Rietkerk *et al.* 2002).

In many cases, these foundational plants engage in mutualistic interactions with mycorrhizal endophytes that benefit from the plants by receiving carbohydrates (Smith & Read 1997). In return, these fungal mutualists can increase the productivity, biomass and environmental range limits of the plants that adopt them by alleviating multiple stressors, including nutrient deficiency, salinity, and temperature stress (Millar & Bennett 2016). In dry environments, plants can particularly benefit from mycorrhizae as they increase their tolerance

to drought by increasing both water and nutrient uptake potential (Márquez *et al.* 2007; Afkhami *et al.* 2014; Peay 2016; Bahadur *et al.* 2019). Such mitigation of drought and nutrient stress by both self-facilitation and mutualism is similar to scenario 3, where the mutualist mitigates the same stressor (or two interrelated stressors in this case) as the foundation species (Fig. 3).

Although mycorrhizae can mitigate abiotic stressors, excessive stress in the form of anthropogenic nutrient input or extreme drought can reduce the plants' carbon allocation to the mycorrhizae (Millar & Bennett 2016). Reciprocally, mycorrhizal partners have been found to adopt resource-hoarding strategies under enhanced nutrient availability (Kiers *et al.* 2010). A potential consequence of such a weakening in mutualism strength is that the plants' resistance to drought also decreases (Márquez *et al.* 2007; Afkhami *et al.* 2014; Brunner *et al.* 2015; Peay 2016). Such a loss of drought resilience may increase the potential for arid grassland and shrubland ecosystems to degrade and collapse in the face of warming-induced decreases in precipitation.

### Tropical forests

Trees are the dominant habitat-structuring organisms of forests (Ellison *et al.* 2005). Following scenario 1, trees in tropical regions modify the environment to their own benefit by outcompeting grasses that would otherwise facilitate wildfires that in turn promote open savannas or grasslands (Hirota *et al.* 2011). Moreover, in particularly large and/or dense forest patches, trees can generate a vegetation-climate feedback in which the trees via evapotranspiration maintain a moist micro-climate that stimulates rainfall, thereby stabilizing tree-dominance and preventing grassland encroachment (Lewis 2006; Hirota *et al.* 2011; Lindenmayer *et al.* 2016; Zemp *et al.* 2017).

Similar to arid ecosystems, tropical trees also commonly engage in endophytic mutualisms that, following scenario 3 in the model, can increase tree tolerance to drought and wildfires (Brunner *et al.* 2015). Simultaneously, many tropical tree species engage in mutualisms that act on a second stressor – i.e. following scenario 2 – as they depend on pollinators and seed dispersers for their reproduction (Janzen & Martin 1982; Rodriguez-Cabal *et al.* 2007; Peres *et al.* 2016). Extirpation of monkeys, birds, bats, and other vital seed-dispersers and pollinators, however, weaken the strength of these plant-animal mutualisms in many areas. In the Amazon, for instance, overhunting has severely reduced populations of seed-dispersing vertebrates, causing “empty forests” (Redford 1992). Consequently, seed dispersal becomes depressed, reducing tree recruitment and causing forest canopies to become more open (Peres *et al.* 2016). This can in turn weaken the tree-micro-climate feedback that mitigates the first stressor (drought), thus increasing the risk of forest collapse, particularly in many tropical regions where global warming is altering precipitation regimes.

### Salt marshes

Salt-tolerant marsh grasses are important foundation species along temperate and subtropical coastlines. By progressively baffling currents and waves with increasing shoot density and patch size, marsh grasses stabilize and elevate the sediment bed and increase nutrient availability (van de Koppel *et al.* 2005; Temmerman *et al.* 2007; Bouma *et al.* 2009). Following scenario 1, these self-facilitative feedbacks have been found to increase ecosystem resistance to small-scale disturbances, but also increase the potential for bistability and collapse following intense, large-scale disturbances like winter storms (van de Koppel *et al.* 2005; van Belzen *et al.* 2017).

Along the US Atlantic and Gulf coasts, ribbed mussels (*Geukensia demissa*) aggregate in the mud around cordgrass stems, where they profit from stable settlement substrate and canopy shading (Altieri *et al.* 2007; Borst *et al.* 2018). In return, as mussels filter phytoplankton and clay particles from the water column, they deposit nutrient-rich pseudofeces, stimulating cordgrass growth and survival (Bertness 1984; Borst *et al.* 2018). This mussel fertilization acts in concert with cordgrass particle trapping to alleviate nutrient limitation, following our model scenario 3.

In addition to enhancing nutrient availability, mussels can also enhance soil moisture and decrease salinity stress during hot dry spells, increasing cordgrass survival by 5-25 times (Angelini *et al.* 2016). During drought,

the mutualism therefore buffers a second stressor in ways similar to scenario 2. Recent work, however, suggests that intense or repetitive droughts may ultimately exceed the mutualism's buffering capacity (Derksen-Hooijberg *et al.* 2019). Should these extreme events increase in both severity and frequency as predicted, the salinity-buffering mechanism will be under intensifying pressure, increasing the likelihood of salt marsh collapse (Angelini *et al.* 2016; Derksen-Hooijberg *et al.* 2019).

### Seagrass meadows

Seagrasses are habitat-forming, flowering plants in shallow coastal areas worldwide (Larkum *et al.* 2006). Similar to salt marsh plants, dense and large seagrass meadows reduce hydrodynamic energy and trap suspended particles, while their root mats prevent sediment resuspension, increasing light penetration (Koch 2001; van der Heide *et al.* 2007; Hansen & Reidenbach 2012; Christianen *et al.* 2013). Following scenario 1, these habitat modifications increase seagrass growth and survival, but also increase the potential for bistability (van der Heide *et al.* 2007; Maxwell *et al.* 2017).

Although sediment trapping and stabilization stimulate seagrass growth, they also cause a negative feedback as organic matter from the water column accumulates in the sediment, and its anaerobic decomposition involving sulfate-reducing bacteria has the potential to produce toxic-levels of sulfides (van der Heide *et al.* 2012; de Fouw *et al.* 2016; Maxwell *et al.* 2017; de Fouw *et al.* 2018). Although seagrasses stimulate sulfide oxidation by releasing oxygen from their roots, sulfide production can outpace oxygen release under warmer conditions, resulting in sulfide accumulation and seagrass mortality (de Fouw *et al.* 2016; de Fouw *et al.* 2018). Following model scenario 2, over 90% of seagrasses growing in subtropical to tropical conditions, and over 50% in temperate areas, are associated with lucinid bivalve mutualists that have endosymbiotic sulfide-oxidizing bacteria in their gills (van der Heide *et al.* 2012). In this pervasive facultative mutualism, the lucinid-bacteria consortium profits from both the sulfide and released oxygen and, in consuming and oxidizing sulfide, alleviates sulfide toxicity stress experienced by seagrass (van der Heide *et al.* 2012).

Drought, however, was recently shown to disrupt this mutualism in West African intertidal seagrass meadows. On the mudflats of Banc d'Arguin, a drought in 2011 initiated seagrass degradation, decreasing oxygen release from the roots, and causing the mutualism to collapse. This, in turn, spiked sediment sulfide levels, amplifying seagrass die-off and causing landscape-scale degradation (de Fouw *et al.* 2016; de Fouw *et al.* 2018). These results illustrate that extreme conditions, such as drought or excessive eutrophication (Maxwell *et al.* 2017), may exceed the buffering capacity of this mutualism, thus triggering its breakdown and seagrass mass-mortality. After such collapse, recovery may only be possible once sediment organic matter and sulfide levels have been dramatically reduced (de Fouw *et al.* 2018).

### Perspectives

Collectively, our findings highlight that foundation species often facilitate both themselves and associated community members through density- or patch size-dependent alterations of abiotic conditions, and that they commonly engage in facultative mutualistic interactions that initiate additional feedbacks. Our model simulations, supported by empirical observations from four different types of ecosystems, suggest that the self-facilitative feedback can be amplified by the mutualistic feedback, increasing the potential for nonlinear ecosystem responses and bistability in the face of global change stressors (Fig. 3a). Specifically, our modelling results suggest that when the self-facilitative and mutualistic feedbacks operate on the same environmental stressor, ecosystem resistance to stress can be particularly high, but, consequently, also the range of hysteresis and thus the risk of catastrophic collapse. Our real-world examples highlight the relevance of these findings as they indicate that this may occur when i) drought resistance is bolstered by both desert plants and their endophytes (Márquez *et al.* 2007; Peay 2016), and ii) nutrient-enhancement is sustained both by salt marsh grasses and ribbed mussels (Bertness 1984). Although this 'amplification effect' is less dramatic when the self-facilitating and mutualistic feedbacks operate on different stressors, their simultaneous functioning can have important consequences for ecosystem resilience, as bistability may now be generated along two (instead of one) stress gradients (Fig. 3a-b). In our real-world examples, these dynamics appear to occur in tropical forest where trees engineer the micro-climate to support their own persistence, and simultaneously benefit

from a seed-dispersing mutualist feedback.

These central findings build upon a number of prior studies demonstrating that mutualists can broaden species' environmental tolerance ranges (e.g. Kiers *et al.* 2010; Afkhami *et al.* 2014). However, our work further suggests that when facultative mutualistic interactions involve foundation species, they increase both their resistance to gradual changes or sudden perturbations, and their propensity to exhibit nonlinear ecosystem responses to global change pressures (Fig. 4). Thus, consideration of both self-facilitating and mutualism-generated feedbacks is likely to be essential for predicting the stress thresholds beyond which foundation species and their associated communities and ecosystem functions will collapse, as well as the level of environmental stress mitigation that must be achieved to trigger natural recovery.

More broadly, the results of our modelling and literature review emphasize the importance of acknowledging and quantifying how multiple feedbacks interact to drive ecosystem dynamics. Recent work from coral reefs and seagrass meadows have similarly highlighted that foundation species can be involved in multiple feedbacks that collectively influence nonlinear responses (see Maxwell *et al.* 2017; van de Leemput *et al.* 2018). Moreover, the strength of such feedbacks and their level of interaction are likely highly context-dependent (Maxwell *et al.* 2017); an area of study that requires far more research. Specifically, for ecosystems shaped by foundation species, it is important to identify those that are simultaneously engaged in self-facilitating and facultative mutualistic feedbacks. Clearly, although our real-world examples highlight only four ecosystems, there are many more of ecosystems with foundation species where both feedback types can occur and interact (see Table S1).

A vital next step is to resolve the relative strength of the self-facilitating and facultative mutualistic feedbacks in modulating the dynamics of foundation species-dominated ecosystems. A first approach could be to construct a more system-specific simulation model to assess the potential for non-linear behavior and bistability in response to increasing global stressors. A second possibility is to correlatively investigate the response of such ecosystems when they are undergoing a sudden perturbation. Recent examples were presented by de Fouw *et al.* (2016) and Angelini *et al.* (2016) where intertidal seagrass meadows with lucinid bivalves and salt marshes with ribbed mussels partly collapsed due to droughts. Although they do not provide definitive proof for bistability, new statistical techniques such as potential analysis may yield important clues regarding the importance of feedbacks in driving ecosystem dynamics (Hirota *et al.* 2011; Scheffer *et al.* 2012; Dakos *et al.* 2015; de Fouw *et al.* 2016).

The ultimate step is then to experimentally manipulate both the self-facilitating and mutualistic feedback across relevant stress gradients to identify nonlinear responses and alternative stable states. To our knowledge, such elaborate experiments, which basically represent an empirical version of our model simulations, have not yet been conducted with foundation species and their mutualists. However, different part of such an experiment have been carried out across a range of different ecosystem types. For instance, Afkhami *et al.* (2014) manipulated endophyte-mutualisms across a range of environmental conditions to empirically demonstrate mutualism-mediated broadening of environmental tolerance to drought in plants. In addition, Angelini *et al.* (2016), experimentally demonstrated mutualism-mediated drought resistance in US salt marshes during a heat spell. Neither study, however, simultaneously manipulated the strength of the self-facilitating feedback (e.g. by manipulating plant density or patch size). Experiments in which both the foundation species and the mutualist were manipulated have been carried out with seagrasses and lucinids (van der Heide *et al.* 2012), and with cordgrass and ribbed mussels (Borst *et al.* 2018). In these cases, however, the environmental conditions were not manipulated. Moreover, none of the above experimental studies focused on identifying nonlinear responses or bistability across stress gradients such as presented in our model analyses, emphasizing that understanding these systems through experimental manipulation is currently an important caveat.

### Potential management implications

From a conservation standpoint, it is of primary importance to identify whether foundation species generate self-facilitative feedbacks, mutualistic feedbacks, or both, and to measure their strength. If feedbacks are indeed important, our work suggests that, ideally, managers and regulators should aim to maintain stress



levels well below the point where these feedbacks become vital for foundation species persistence (i.e.  $<0.3$  in our model; see Fig. 3). Obviously, this may be infeasible, especially when a stressor is initiated by global rather than local processes, such as droughts or heat waves. In such cases, however, it may be possible to reduce local stressors for the purpose of increasing foundation species' capacity to persist under increasing global stress. Specifically, as suggested by our model and earlier work (Scheffer *et al.* 2015; He & Silliman 2019), when self-facilitating and mutualistic feedbacks both buffer against the same global stressor (i.e. stressor 1), mitigation of a second local stressor that is not affected by the feedbacks (see Fig. 3C, scenario 3) can be highly effective in enabling the ecosystem to persist in a foundation species-dominated state. The underlying reason for this is that the maximum net growth of the foundation species increases linearly with a reduction of stressor 2, which in turn increases both self-facilitation and mutualism feedback strength and thus the foundation species' capacity to buffer stressor 1. Furthermore, when one of these feedbacks instead buffers a local stressor, the response of the foundation species to local improvements, and therefore also its ability to withstand and mitigate the global stressor, becomes non-linear.

Even when local stressors are mitigated via proactive management or regulation, continued global environmental change may ultimately cause foundation species to become fully reliant on their facultative mutualistic partners. Under such circumstances, further escalation of the global stress or sudden perturbations, such as extreme storms or consumer outbreaks, may ultimately exceed the buffering capacity of the self-facilitating and/or mutualistic feedbacks, causing foundation species collapse. Once degraded, density- and patch size-dependent self-facilitative feedbacks cause establishment thresholds that stifle the natural recovery of the foundation species; dynamics that become exacerbated due to the absence of mutualists that can help improve environmental conditions and the foundation species' health (Angelini & Silliman 2012; Angelini *et al.* 2016). Consequently, environmental conditions need to be improved much more than the level of stress that provoked the collapse to initiate natural, or unassisted, recovery (hysteresis) under such circumstances (Fig. 4).

In the context of restoration or habitat creation efforts, our findings suggest that harnessing self-facilitation and mutualisms can enhance the success of such interventions to regain foundation species and their ecological benefits (Gagnon *et al.* 2020; Valdez *et al.* 2020). Indeed, recent experimental work in salt marshes highlights that including self-facilitation into restoration designs by clumping cordgrass transplants rather than planting them in dispersed arrays can double restoration yields (Silliman *et al.* 2015). Moreover, integrating mutualisms into restoration by co-transplantation of cordgrass and mussels can enhance success by a similar margin (Borst *et al.* 2018). At the same time, however, it is important to realize that such reliance on self-facilitation and mutualisms comes at the cost of increased threshold behavior, which decreases predictability and may unintentionally set systems up for sudden collapse in the long run.

## Conclusions

It is clear that the biodiversity and functioning of many terrestrial, freshwater and marine benthic ecosystems hinges on habitat-forming foundation species (Angelini *et al.* 2011; Borst *et al.* 2018; Ellison 2019). Such spatially dominant habitat-forming organisms (e.g. trees, terrestrial shrubs and grasses, marine and freshwater macrophytes, bivalve and coral reefs) create complex biogenic structures that ameliorate physical stress and modulate resource availability. Although it is widely appreciated that associated species often benefit from such habitat modification, foundation species also facilitate their own growth through these same mechanisms. Although such self-facilitative and mutualistic feedbacks can act as a buffer against increasing stress from global change, theory and observations suggest that when they are disrupted, foundation species can experience rapid mortality, resulting in persistent collapse of the ecosystem they support.

This study highlights that many foundation species engage in facultative mutualisms that, by providing reciprocal benefits, generate a second positive feedback that may act on the same or a different stressor as the self-facilitating feedback. Overall, our model and case studies suggest that such mutualisms, which are pervasive in natural systems, pose a double-edged sword in the face of global change. Specifically, mutualisms help protect and restore foundation species-structured ecosystems in times of rapid, global environmental change, but reliance on self-facilitative and mutualistic feedbacks may come at the inherent cost of increased

threshold behavior, increasing the potential for bistability and sudden, persistent collapse.

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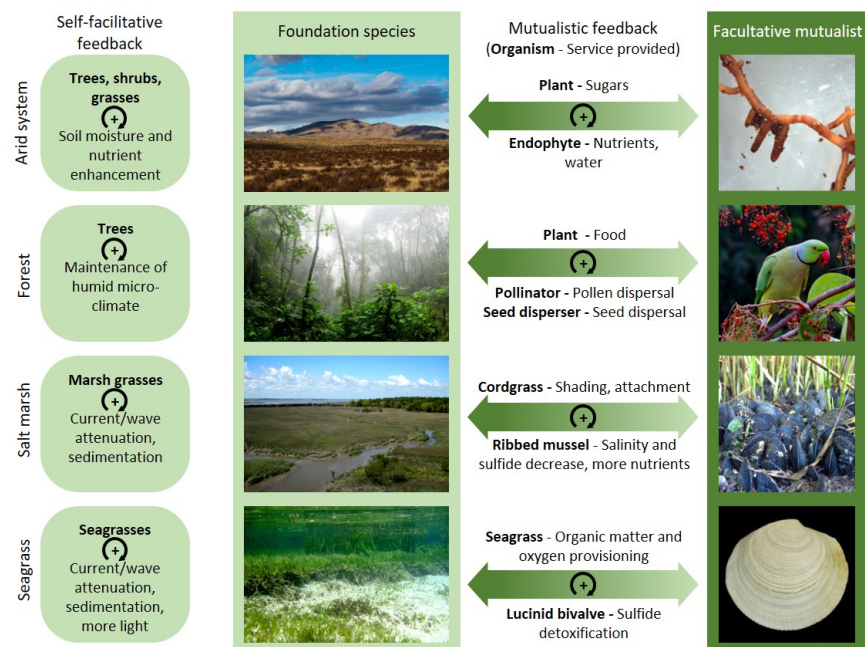
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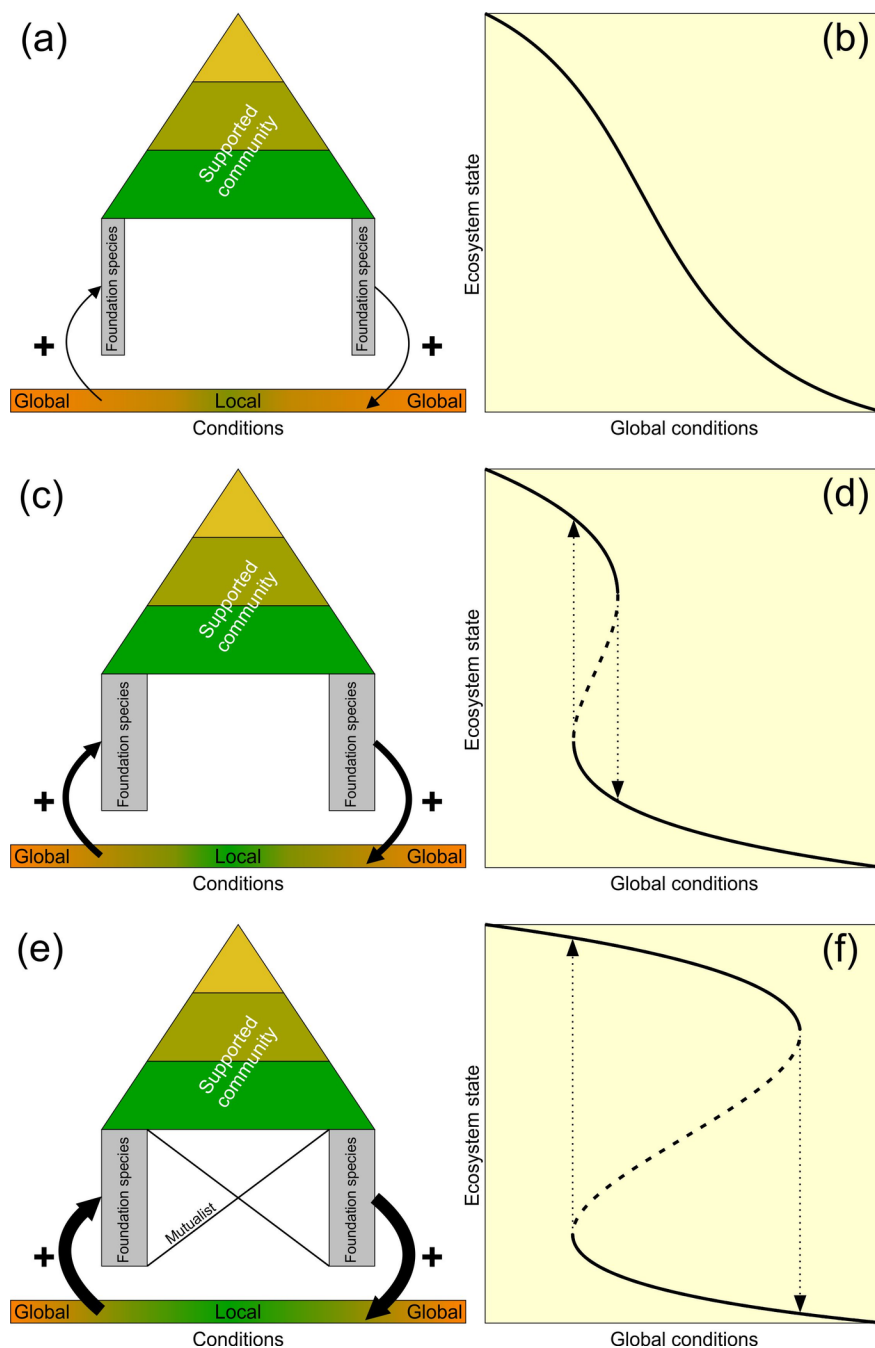
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## Figures

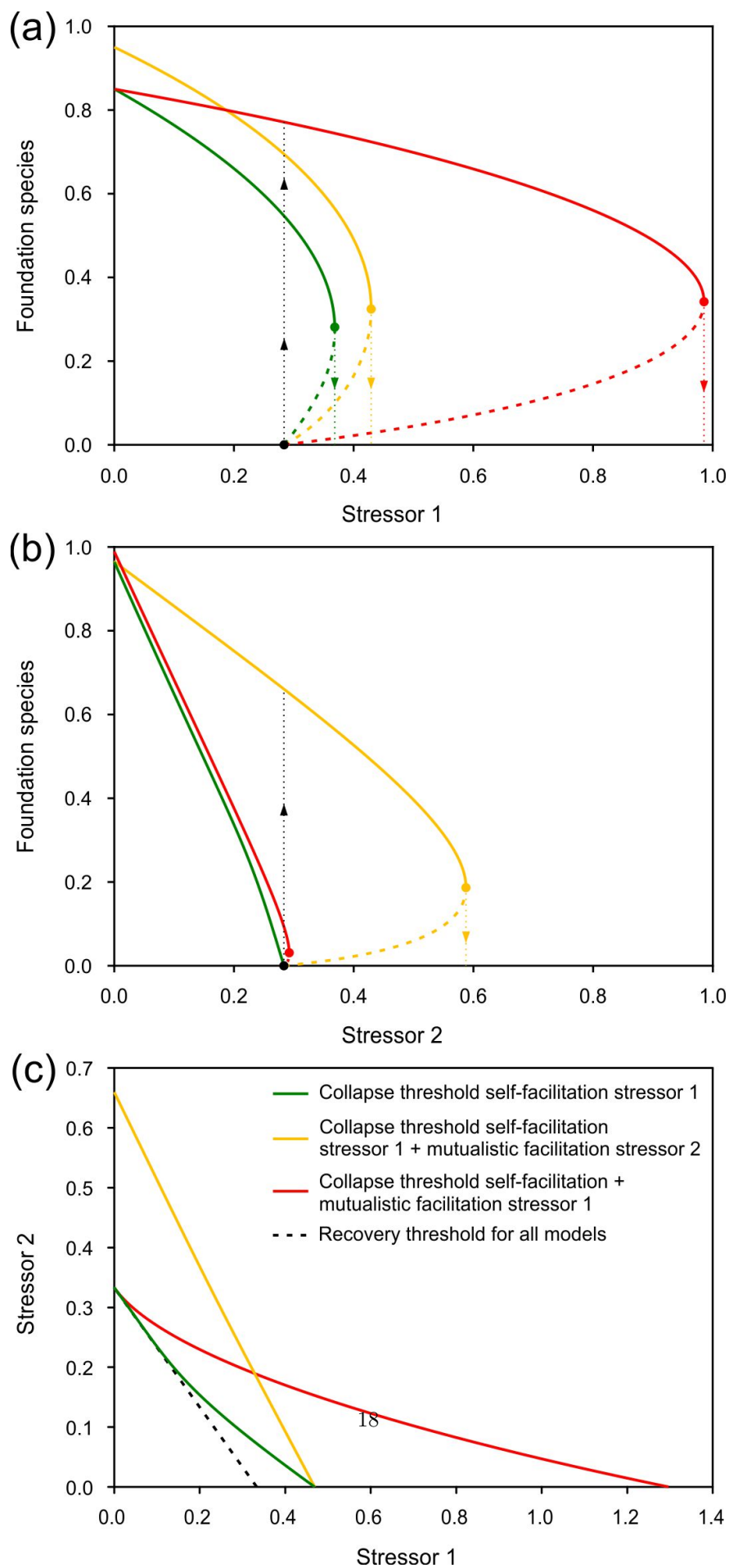


**Figure 1.** Four examples of ecosystems shaped by foundation species, their facultative mutualists, and the positive feedbacks generated.

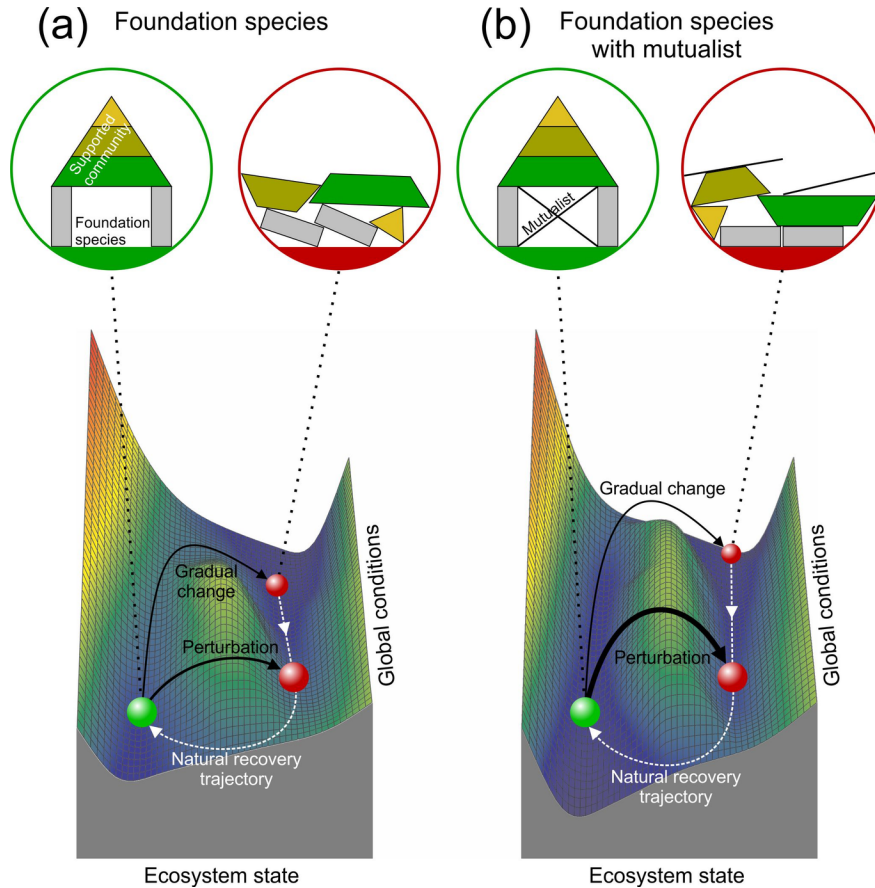




**Figure 2.** Self-facilitative and mutualistic feedbacks stimulate foundation species and their associated community. Low foundation species population size generates relatively a weak self-facilitative feedback and local environmental modification (a), yielding a slightly nonlinear ecosystem response to changing global, ecosystem-level conditions (b). Higher population size generates a stronger feedback (c), thereby increasing the nonlinearity of the ecosystem's response to change and enhancing the potential for bistability (d). When the foundation species engages in a mutualism, both feedbacks act together to amplify environmental modifications (e), and the nonlinearity of the ecosystem's response to changing global conditions (f).



**Figure 3.** Bifurcation analyses of a minimal model of foundation species with mutualisms. The self-facilitative feedback acts on stressor 1, generating bistability (green; scenario 1). The mutualism increases this bistability range, particularly when it also acts on stressor 1 (red; scenario 3), but even when mitigating stressor 2 (yellow; scenario 2) (a, c). When mitigating stressor 2, the mutualist also introduces bistability for this variable (b, c).



**Figure 4.** Stability landscape of ecosystems shaped by foundation species without (a) and with mutualists (b). Ecosystem A is controlled by a self-facilitative feedback, and hence a relatively small change in global conditions (or perturbation) is sufficient to cause the healthy (green) system to collapse (red). Contrastingly, as ecosystem B is controlled by self-facilitative and mutualistic feedbacks that amplify each other, a more severe change in global conditions (or perturbation) is required for a collapse. If collapsed due to gradual changes, recovery requires conditions to be improved beyond the point of collapse, a pathway that is much longer for ecosystem B.

**Table 1.** Variables and default parameter settings of the conceptual model.

	Default	Description
Variables		
$FS$	-	Foundation species population size
$M$	-	Mutualist population size
Parameters		
$gfs$	0.1	Maximum relative growth rate of the foundation species

	Default	Description
$Kfs$	1	Carrying capacity of the foundation species
$mfs$	0.3	Maximum relative mortality of the foundation species
$gm$	0.1	Maximum growth rate of the mutualist
$Hfs1$	0.3	Half saturation constant for the positive effect of $FS$ on $M$
$Km$	1	Carrying capacity of the mutualist
$mm$	0.05	Relative mortality constant of the mutualist
$S1_{max}$	0.05	Maximum stress level from stressor 1
$Hfs2$	0.3	Half rate constant for the reducing effect of $FS$ on stressor 1
$Hm1$	0.3	Half rate constant for the reducing effect of $M$ on stressor 1
$S2_{max}$	0.05	Maximum stress level from stressor 2
$Hm2$	0.3	Half rate constant for the reducing effect of $M$ on stressor 2

**Table S1.** Examples of terrestrial, freshwater and marine ecosystems structured by foundation species that generate a self-facilitating feedback and can engage in a facultative mutualistic feedback.

	Ecosystem	Foundation species	Facultative mutualist	Self-facilitating feedback	Mutualistic feedback	Key references
<i>Terrestrial</i>	(semi-)Arid systems	Trees, shrubs, grasses	Fungal endophytes	Plants enhance soil moisture with increasing density and patch size	Plants provide sugars; endophytes provide water and nutrients	Smith and Read (1997); Afkhami <i>et al.</i> (2014); Peay (2016)
	Temperate arid systems	Shrubs	Shrubs	Plants enhance soil moisture and soil nutrients with increasing density and patch size	Shrub mutualists provide shelter; further improve soil nutrient availability	Rietkerk <i>et al.</i> (2004); Tirado <i>et al.</i> (2015)
	Tropical forests	Trees	Ants	Dense tree canopy maintains humid microclimate	Acacia trees provide shelter and food; ants provide pollination, seed dispersal and defense against herbivores	Janzen (1966); Speight <i>et al.</i> (1999); Hirota <i>et al.</i> (2011); Zemp <i>et al.</i> (2017)

	<b>Ecosystem</b>	<b>Foundation species</b>	<b>Facultative mutualist</b>	<b>Self-facilitating feedback</b>	<b>Mutualistic feedback</b>	<b>Key references</b>
<i>Freshwater</i>	Tropical forests	Trees	Pollinators and seed dispersers	Dense tree canopy maintains humid microclimate	Trees provide food and shelter; dispersers provide pollination and seed dispersal	Hirota <i>et al.</i> (2011); Peres <i>et al.</i> (2016); Zemp <i>et al.</i> (2017)
	Temperature montane forests	Trees	Seed dispersers	Tree canopies retain warm air, reduce wind stress, reduce evaporative loss of soil moisture and stabilize soils with increasing tree island size	Birds cache seeds near trees to facilitate the formation of tree islands that feedback to enhance tree island size and resilience	Malanson <i>et al.</i> (2007); Rodriguez-Cabal <i>et al.</i> (2007); Pyatt <i>et al.</i> (2016)
	Sphagnum peat bogs	Sphagnum mosses	Methanotrophic bacteria; N <sub>2</sub> -fixing bacteria	Sphagnum mosses create wetland conditions above groundwater level by retaining and acidifying rainwater	Sphagnum mosses provide habitat in hyaline cells; bacteria oxidize CH <sub>4</sub> to CO <sub>2</sub> that mosses use for photosynthesis, fix N <sub>2</sub> to alleviate N-limitation	Raghoebarsing <i>et al.</i> (2006); Larmola <i>et al.</i> (2014)
	Helophyte swamps	Phragmites australis	Endophytic mycorrhizae	Dense Phragmites stands exclude grazing by water fowl	Plants provide sugars; endophytes provide water and nutrients	Oliveira <i>et al.</i> (2001); Ernst <i>et al.</i> (2003); Reijers <i>et al.</i> (2019)

	<b>Ecosystem</b>	<b>Foundation species</b>	<b>Facultative mutualist</b>	<b>Self-facilitating feedback</b>	<b>Mutualistic feedback</b>	<b>Key references</b>
<i>Marine</i>	Riparian forests	Trees	Fish	Dense forests attenuate flow, trap and stabilize sediment during inundation	Trees provide fruits as food; fish provide seed dispersal	Horn (1997); Horn <i>et al.</i> (2011); Silknetter <i>et al.</i> (2020)
	Shallow lakes	Submerged freshwater macrophytes	Mesograzers	Submerged macrophytes attenuate hydrodynamics, trap sediment and improve light conditions	Submerged macrophytes provide predation shelter; mesograzers consume epiphytic algae growing on plant leaves	Scheffer (1999)
	Seagrass meadows	Seagrasses	Mesograzers	Dense seagrasses attenuate hydrodynamics, trap sediment and improve light conditions	Seagrasses provide predation shelter; mesograzers consume epiphytic algae growing on plant leaves	Valentine and Duffy (2007); Maxwell <i>et al.</i> (2017)
	Tropical seagrass meadows	Seagrasses	Coraline algae	Dense seagrasses attenuate hydrodynamics, trap sediment and improve light conditions	Seagrasses protect the algae from removal by currents and waves; spiny coralline algae structures protect seagrass from grazing.	Maxwell <i>et al.</i> (2017); Leemans <i>et al.</i> (2020)

Ecosystem	Foundation species	Facultative mutualist	Self-facilitating feedback	Mutualistic feedback	Key references
Warm temperate to tropical seagrass meadows	Seagrasses	Lucinid bivalves	Dense seagrasses attenuate hydrodynamics, trap sediment and improve light conditions	Seagrasses provides organic matter for sulfide production and oxygen for sulfide oxidation; lucinids detoxify sulfides	van der Heide <i>et al.</i> (2012); de Fouw <i>et al.</i> (2016); de Fouw <i>et al.</i> (2018)
Salt marshes	Marsh grasses	Ribbed mussels	Marsh grasses attenuate hydrodynamics, trap sediment with increasing density and patch size	Grasses provide shading and attachment; mussels lower salinity and sulfides, increase nutrients	Temmerman <i>et al.</i> (2007); Angelini <i>et al.</i> (2016); Derksen-Hooijberg <i>et al.</i> (2019)
Mangrove forests	Mangrove trees	Sponges	Mangroves attenuate hydrodynamics and trap sediments	Mangroves provide habitat, with roots as attachment substrate; sponges increase nutrient availability	Ellison <i>et al.</i> (1996); Huxham <i>et al.</i> (2010)
Coral reefs	Hard corals	Herbivores	Corals form reefs that attenuate hydrodynamics, and serve as for attachment for recruits	Coral provide predation shelter; herbivores lower competition from macroalgae	van de Leemput <i>et al.</i> (2016)