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MECHANISMS AND CONSEQUENCES OF FACILITATION IN PLANT COMMUNITIES
When can positive interactions cause alternative stable states in ecosystems?

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Summary

1. After a period of heavy emphasis on negative interactions, such as predation and competition, the past two decades have seen an explosion of literature on the role of positive interactions in ecological communities. Such positive interactions can take many forms. One possibility is that amelioration of environmental stress by plants or sessile animals enhances growth, reproduction and survival of others, but many more intricate patterns exist.

2. Importantly such positive interactions may contribute to creating a positive feedback. For instance, biomass can lead to improved environmental conditions causing better growth and therefore leading to more biomass. A positive feedback is a necessary (but not sufficient) condition for the emergence of alternative stable states at the community scale. However, the literature on positive interactions in plant and animal communities rarely addresses this connection.

3. Here, we address this gap, asking the question of when positive interactions may lead to alternative stable states, and hence set the stage for catastrophic transitions at tipping points in ecosystems. We argue that, although there are a number of now classical examples in the literature for which positive interactions are clearly the main actors of positive feedback loops, more empirical and theoretical research scaling up from the individual-level interactions to the community and the ecosystem scale processes is needed to further understand under which conditions positive interactions can trigger positive feedback loops, and thereby alternative stable states.

Key-words: alternative stable state, bistability, critical transition, facilitation, hysteresis, multi-stability, negative feedback loop, positive feedback loop, resilience, tipping point

Introduction

Ecological communities and ecosystems respond to external changes and perturbations in different ways. Some ecosystems respond in a smooth, gradual manner to gradual changes in environmental conditions (e.g. climate change; Fig. 1a,b). Others remain practically inert until a threshold in external conditions is passed, at which point the ecosystem may respond abruptly (Fig. 1c) or suddenly switch from one state to another, a phenomenon referred to as 'catastrophic shift' (Rietkerk *et al.* 1996; Scheffer 2009; Fig. 1d). These sudden shifts can involve dramatic ecological and economic consequences, including losses or gains of species, habitats and ecosystem services. One of the best-studied ecosystem shifts is the switch from clear to turbid water in shallow lakes as a result of increased nutrient loading causing algal bloom, loss of animal diversity and poor water quality (Scheffer *et al.* 1993). Another classic example is the desertification of drylands that can switch to predominantly bare conditions when losing their perennial vegetation because of climatic variations, human activities and often the combination of both (Noy-Meir 1975; Schlesinger *et al.* 1990). Desertification results in a reduction of the biological potential of the land to support wild herbivores, livestock, agricultural crops and ultimately human populations (Reynolds *et al.* 2007).

Catastrophic shift behaviour typically occurs in systems that have alternative stable states, meaning that, for the

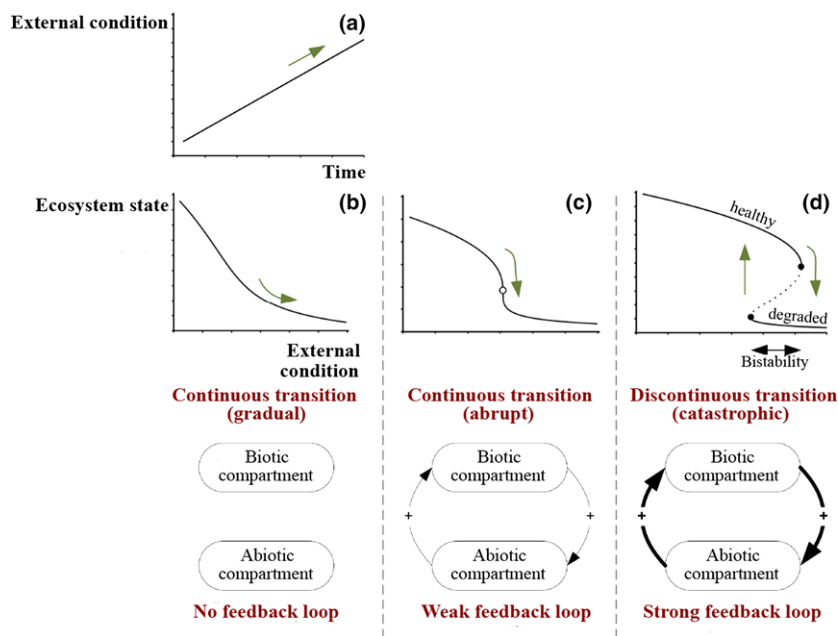*Correspondence author. E-mail: sonia.kefi@univ-montp2.fr

Fig. 1. Types of ecosystem responses to external changes. (a) Let us imagine an external condition which gradually varies in time (e.g. rainfall). (b–d) Three types of ecosystem responses to the changes in external condition depending on the strength of the positive feedback loop between the biotic (e.g. vegetation) and abiotic (local water availability) compartments as typically predicted from simple ecosystem models (e.g. May 1977; Kéfi *et al.* 2013). The ecosystem state may correspond to, for example, vegetation cover. Without positive feedback (b), the ecosystem state responds gradually to the gradual change in external condition. When there is a weak positive feedback loop (c), the ecosystem response becomes abrupt and less predictable. When the feedback loop is strong (d), the ecosystem state hardly changes until a threshold in external condition is reached, at which point a small change in external condition leads to an abrupt shift of the ecosystem from its present state to a contrasting one (e.g. from a green to a desert state). Once the shift happened, going back to the previous ecosystem state requires the external condition to decrease to lower values than the values at which the shift occurred. This behaviour (referred to as hysteresis) is due to the fact that two alternative states of the ecosystem (healthy and degraded) coexist for a range of environmental conditions (bistability).

same level of a given external condition, the system can be in more than one stable state (e.g. clear vs. turbid water in shallow lakes; perennial vegetation vs. annual herbaceous plants or bare soil in drylands). As hinted by simple mathematical models of ecosystems (e.g. Noy-Meir 1975; May 1977; Rietkerk *et al.* 1996; Scheffer 2009), a positive feedback is a necessary (but not sufficient) condition for systems to have alternative stable states. As discussed later in this paper, a positive feedback is typically composed of a succession of links (between species as well as between species and their abiotic environment), whose product should be positive for the feedback to be positive. In many classical examples of alternative stable states, some of those links composing the feedback loop involve positive interactions between organisms. This may lead to the hasty conclusion that positive interactions can lead to alternative stable states, but what do we actually know about the contributions of positive interactions to catastrophic shifts? Here, we explore the question of to what extent positive interactions, by contributing to the establishment of positive feedbacks, can lead to alternative stable states and thereby catastrophic shifts in ecological communities and ecosystems.

Positive interactions occur when one organism makes the physical or biotic environment more favourable for another of the same or a different species, either directly

(e.g. reduction of abiotic stress or increased resource acquisition) or indirectly (e.g. by suppressing a competitor) (Wilson & Agnew 1992; Bertness & Callaway 1994; Holmgren, Scheffer & Huston 1997; Bruno, Stachowicz & Bertness 2003; Callaway 2007; Soliveres, Smit & Maestre 2015). Many direct positive interactions involve an improvement of the physical environment (e.g. reducing thermal, water, or nutrient stress, protection from wind or waves). If these positive interactions end up benefiting the same species (or group of species, e.g. functional group) as the one performing it, the positive interaction gives rise to a positive feedback (Wilson & Agnew 1992). For example, in drylands, where water is often the most limiting resource, some vegetation can modify the local environment in such a way that water infiltration is higher and soil water evaporation rates lower in vegetated than in non-vegetated patches, leading to water concentration in vegetated patches (Schlesinger *et al.* 1990). In such a case, vegetation modifies the abiotic environment in a way that is beneficial for itself, creating a positive feedback: the better the vegetation growth, the higher the vegetation cover or biomass, and the more water available for plants to grow. Conversely, when vegetation is lost, the soil loses the physical protection it had from the vegetation cover, which leads to soil erosion and crust formation, which further impede water infiltration and enhance runoff

(Schlesinger *et al.* 1990). This creates hostile conditions for plant establishment. This positive feedback loop, which can work both ways ('more vegetation, better growth conditions' or 'less vegetation, worse growth conditions'), could be responsible for the often catastrophic aspect of desertification (Fig. 1d; Schlesinger *et al.* 1990; Rietkerk *et al.* 1996; Holmgren & Scheffer 2001).

Because they can be important contributors of positive feedback loops, examining the potential role of positive interactions is particularly interesting. However, the link between positive interactions at the individual level and positive feedback loops at ecosystem scales (thereby leading to alternative stable states and catastrophic shifts) is not straightforward, neither from a theoretical, nor from an empirical point of view. Here, we first briefly review the relations between catastrophic shifts, alternative stable states and positive feedback loops before reflecting on what we know about the link between positive interactions and catastrophic shifts using illustrative examples from both terrestrial and aquatic ecosystems.

Catastrophic shifts in ecosystems and alternative stable states

A sudden ecosystem response to a gradual change, combined with difficulties in reversing the shift once it happened (as illustrated in Fig. 1d), has often been considered a hallmark of multiple stable states (Scheffer 2009; Petraitis 2013). Abrupt ecosystem responses can also occur for other reasons than catastrophic shifts (e.g. Fig. 1c), an obvious one being an abrupt change in environmental conditions. In the presence of alternative stable states, however, an abrupt ecosystem response can reflect an ecosystem transition from one of its stable states to another. Typically, a change in external conditions (e.g. increasing nutrient loading in shallow lakes or herbivore pressure in drylands) may push the ecosystem towards a threshold (or 'tipping point'), at which point a small change in external condition leads to an abrupt shift of the ecosystem from its present state to a contrasting one (i.e. Fig. 1d).

Since its introduction to ecology in the early 70s (Lewontin 1969; Holling 1973; Sutherland 1974; May 1977), the concept of alternative stable states has attracted much attention, in particular because of its important implications for ecosystem management and conservation. Different types of mathematical models have demonstrated the potential of populations, communities and ecosystems to exhibit alternative stable states, for instance in single-species exploitation models (e.g. Noy-Meir 1975), in two-dimensional consumer-resource models (e.g. May 1977), in food webs and in size- or stage-structured models (e.g. Chase 1999; de Roos & Persson 2002) and in community assembly models (e.g. Law & Morton 1993).

Although the theory of alternative stable states is well understood, whether multiple stable states actually occur in nature has been hotly debated, in part because of the difficulty of demonstrating their existence in nature but also because of the lack of clear guidelines regarding what needs to be checked for in the field and in experiments to clearly demonstrate the existence of alternative stable states (Schröder, Persson & de Roos 2005; Petraitis 2013). Digging into the details of the published literature, an extensive survey by Schröder, Persson & de Roos (2005) stressed that although there is ample evidence that ecological systems can exhibit alternative stable states, their existence should not be considered as the rule. Even when observational data may show signs of alternative stable states, demonstrating their existence unequivocally in an ecosystem requires using experimental approaches, which are often expensive, time consuming and not always possible at meaningful spatial and temporal scales (Schröder, Persson & de Roos 2005; Petraitis 2013; but see e.g. Carpenter *et al.* 2011; Sirota *et al.* 2013).

Alternative stable states and positive feedback loops

Mathematical models highlighted early on the importance of positive feedback loops for alternative stable states (e.g. Holling 1973; Noy-Meir 1975; May 1977). More precisely, mathematical models show that alternative stable ecosystem states are possible if there are positive feedbacks which are strong enough (Fig. 1b–d). The general idea is that positive feedbacks amplify small deviations which can destabilize the system globally, whereas negative feedbacks counteract deviations and stabilize the system locally (DeAngelis, Post & Travis 1986).

Let us look into how positive feedback loops function in one of the most studied and best understood cases of alternative stable states in nature: the case of shallow lakes (Scheffer *et al.* 1993). In shallow lakes, the whole feedback loop is thought to involve submerged vegetation and water clarity. Submerged vegetation increases water clarity, allowing light to reach deeper in the water column, which in turn favours submerged plants that tend to be strongly limited by light in shallow lakes (Fig. 2a). We can intuitively understand how this positive feedback loop between vegetation and water clarity can re-inforce an ecosystem state with clear water and abundant submerged vegetation. This same feedback can also work the other way around once it has been disrupted (e.g. by water becoming turbid because of external nutrient loading), thereby driving the ecosystem away from a clear water state to an alternative state with turbid water and no submerged vegetation (Fig. 2b). This example is a simplified version of the story where a positive interaction (i.e. submerged plants facilitating other submerged plants) is directly linked to a positive feedback loop (through increased water clarity).

Positive feedback loops and positive interactions

In reality, the relationship between submerged vegetation and water clarity in shallow lakes involves a large variety
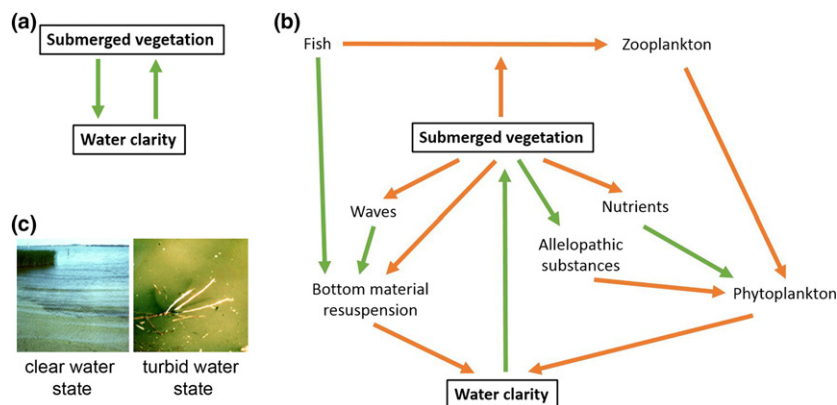
Fig. 2. Positive feedback loops and positive interactions. (a) Main feedback loop thought to be responsible for alternative stable states in shallow lakes. (b) Details of the interactions between the components of the system. Orange: negative effects (source decreases target). Green: positive effects (source increases target). A feedback loop is a series of interactions that goes from one component of the system back to itself. The sign of a given loop can be obtained by multiplying the signs along the way. In this way, it can be seen that both the clear and the turbid states are self-reinforcing, and diagram b can thereby be summarize as diagram a. Note that a positive feedback loop can be obtained by the combinations of negative interactions only, as long as there are an even number of negative interactions along the loop. Adapted from Scheffer *et al.* (1993). (c) Pictures of a shallow lake in the clear water state (left) and in the turbid water state (right) (Pictures: M. Scheffer).

of mechanisms and ecological interactions that link biotic and abiotic compartments in both positive and negative ways (orange and green arrows on Fig. 2c): submerged vegetation stabilizes the substrate with its root system and decreases water velocity and sediment re-suspension, favouring water clarity (James & Barko 1990); plants provide refuge to zooplankton against their fish predators (Hosper 1989); and vegetation suppresses phytoplankton growth because of nutrient competition (van Donk *et al.* 1990) and the production of allelopathic substances (Scheffer *et al.* 1993). Altogether, this network of direct and indirect interactions includes several feedback loops, that is there are several possible paths leaving and coming back to the vegetation 'box'. This network of interactions between the different components of the system makes the generalization of the link between positive interactions and feedback loops not straightforward.

Looking more in detail at the net effects of all these interactions, it is clear that all the loops leaving and coming back to the 'vegetation box' have a net positive effect, independently of the path followed (the sign of the net effect is obtained by multiplying the signs of the composing arrows along the way). For example, an increase in submerged vegetation would lead to more nutrient uptake by the vegetation, so have a negative impact upon nutrients (−), which would increase competition with phytoplankton, thereby leading to less phytoplankton (−), which would result in improved water clarity (+), which would further improve the growth of submerged plants (+). The whole path constitutes a net positive feedback loop (−*−*+*+). Although there are different loops involved in the diagram that may have different weights and relative importance, the two states of 'clear water and abundant submerged vegetation' on the one hand, and of 'turbid water and absent submerged vegetation' on the

other hand are clearly self-reinforcing in this example. In other words, independently of the route chosen in this very particular case, Fig. 2c can always be summarized into Fig. 2a.

What is the contribution of positive interactions to these positive feedback loops? It is noteworthy that the illustrative shallow lake diagram (Fig. 2c) includes several positive interactions:

1. Submerged plants stabilize the substrate through their roots and decrease the water velocity nearby. This reduces sediment re-suspension and improves light penetration for the photosynthesis of other submerged plants.
2. Plants uptake nutrients, reducing the nutrient loading in the water column that would be available for floating algae. This increases water clarity and thereby light for other submerged plants.
3. Plants create a shelter for zooplankton from their fish predators. Since zooplankton predates on floating algae, this also reduces water turbidity and increases the light for other submerged plants.

These positive interactions are components of the feedback loops previously discussed. They may constitute a feedback loop (i) or be only part of a more complex loop (ii). In case (i), the results of the theoretical models previously mentioned are directly applicable: the stronger the positive interaction (e.g. the ability of plants to stabilize the substrate), the stronger the positive feedback loop and the higher the chance of the system having alternative stable states and therefore of experiencing catastrophic shifts in response to perturbations. In case (ii), that is when a positive interaction is part of a complex loop, the link between positive interaction and positive feedback loop depends on the sign and intensity of the other interactions involved in the loop. In particular, the sign of the loop

crucially depends on the number of negative interactions involved (an even number is required for the feedback loop to be positive).

In addition, because several loops may link the biotic and abiotic compartments, the overall net effect at the ecosystem scale depends on the relative strength of all the feedback loops, in particular if loops of opposing directions (different signs) co-occur. At this point, it is important to emphasize again that the existence of positive feedbacks is not a sufficient condition for alternative stable states; it is rather the sign and intensity of the net effect of all the positive and negative feedbacks which matter.

Beyond shallow lakes

We 'dissected' the well-known shallow lake example to illustrate how positive interactions in ecological communities can generate strong positive feedbacks that affect ecosystem dynamics. There are numerous examples from different types of ecosystems, which hint at a link between positive interactions, positive feedbacks and possible ecosystem shifts between alternative stable states (see Table 1 for some examples and Suding, Gross & Houseman 2004; Scheffer 2009 for more extensive reviews).

POSITIVE INTERACTIONS AND SELF-ORGANIZED PATTERNING

Positive interactions are well-known to play an important role under harsh environmental conditions where some individuals (e.g. nurse plants) create favourable microenvironments for others by buffering abiotic stress, improving resource acquisition and protecting from predators (Holmgren, Scheffer & Huston 1997; Callaway 2007). When these individuals are sessile, their positive effects only occur very close to them and the positive effects have a spatial component which leads to spatial clustering of individuals. At the same time, because resources are limited in harsh environments, clusters compete among each other for resources, leading to a 'scale-dependent feedback' of local facilitation and competition father away (Rietkerk & van de Koppel 2008).

Scale-dependent feedbacks allow the coexistence, in space, of two alternative states: dense patches with high biomass coexisting with patches of low plant biomass or bare ground. In drylands, this leads to the typical patchiness of vegetation cover, with patches of perennial plants (shrubs, trees, perennial herbaceous plants) growing in a matrix of annual herbaceous plants or bare soil (Fig. 3a; Holmgren & Scheffer 2001). Vegetation patches of different sizes and shapes have been observed in arid and semi-arid ecosystems throughout the world, such as irregular patterns in Mediterranean ecosystems (Fig 3a; Kéfi *et al.* 2007a), or regular stripes ('tiger bush'), labyrinths, spots ('leopard bush') and gaps in the vegetation cover of other arid ecosystems (Rietkerk & van de Koppel 2008). Other examples of ecosystems with local positive interactions show striking spatial patterning, such as regular bands of mussel beds perpendicular to the flow of the water (Fig. 3b; van de Koppel *et al.* 2005b), self-organized plant patterns in saltmarshes (van de Koppel *et al.* 2005a), diatom patterns on tidal flats (Weerman *et al.* 2012), hummock-hollow patterns in peatlands (Fig. 3c,d; Eppinga *et al.* 2009) and fog-driven vegetation patterns in temperate forest (Stanton, Armesto & Hedin 2014). Mathematical models suggest that scale-dependent feedbacks, in addition to leading to spatial patterning, also lead to system-scale alternative stable states and possible catastrophic shifts at the ecosystem scale (e.g. van de Koppel *et al.* 2005a,b; Eppinga *et al.* 2009; Kéfi *et al.* 2010), meaning that increasing stress can lead to large scale collapse of these patterned ecosystems.

POSITIVE INTERACTIONS AND ECOLOGICAL RESTORATION

Long-term observations have made clear that simply recovering the historical disturbance level or abiotic conditions that shifted an ecosystem to a degraded condition is not enough to restore the previous ecosystem state (Suding, Gross & Houseman 2004). Indeed, in the degraded state, feedbacks between components of the ecosystem act as stabilizing mechanisms, making the ecosystem resilient to restoration efforts. Knowledge about the feedback loops at play can be extremely relevant to restoration by providing the keys to engineer transitions between alternative stable states (Westoby, Walker & Noy-Meir 1989). For example, in shallow lakes, reducing nutrient inputs into the lakes proved to be insufficient to restore a clear water condition. Understanding the underlying ecological mechanisms suggested that drastically reducing the abundance of benthic fishes was the most effective way of disrupting the positive feedbacks that maintained the turbid state. This biomanipulation approach has been widely used to clear up European shallow lakes in countries such as Denmark and the Netherlands (Søndergaard *et al.* 2007).

Much work has been done on trying to take advantage of some species' ability to perform positive interactions to disrupt the feedbacks in place in degraded systems, and thereby enhance their restoration (Suding, Gross & Houseman 2004; Byers *et al.* 2006). For example, reforestation programs in degraded semi-arid ecosystems, such as the Mediterranean ones, have long recognized the benefits of using key nurse plant species to restore original shrublands and forests (Gómez-Aparicio 2009). Understanding under which conditions these facilitative effects are indeed main contributors of dominant positive feedback loops is critical for successful long-term ecological restoration. Field evidence indicates that nurse facilitation is not always successful or persistent. Although it is well-established that facilitative interactions become increasingly important in stressful environments (Callaway 2007; He, Bertness & Altieri 2013), plant–plant interactions are context dependent and can shift to neutral or negative ones with

Table 1. Examples of facilitative mechanisms and alternative stable states in a variety of ecosystems

Alternative stable states	Ecosystem	Reinforcing mechanism	Example of reference
Submerged plant – clear water state	Shallow lake	Aquatic plants improve water clarity	Scheffer *et al.* (1993)
Phytoplankton – turbid water state			
Stoneworts (charophytes) - pondweeds (submerged macrophytes)	Shallow lake	Stoneworts favour carbon depletion, suppressing pondweeds and creating better light conditions for themselves	Hargeby *et al.* (1994)
Green algae - cyanobacteria	Shallow lake	Cyanobacteria favour shade which stabilizes their dominance	Scheffer *et al.* (1997)
Free-floating plants - submerged vegetation (macrophytes)	Temperate ponds, ditches and tropical lakes	Floating plants favour dark, anoxic conditions. Submerged vegetation decreases nutrient availability for floating plants.	Scheffer *et al.* (2003)
Coral - algae (no actual proof of alternative stable states, just a suggestion)	Coral reefs	Nutrient loading and disappearance of herbivorous fish favour algae. Algae prevent coral recruitment and have a low palatability.	Knowlton (1992)
Kelp - urchin and crustose coralline algae (urchin barren state)	Temperate rocky reefs	Kelp foliage and waves keep sea urchins out, thereby decreasing kelp grazing by urchins. Crustose coralline algae (CCA) facilitate the recruitment of sea urchins which enhances urchin grazing and prevents CCA being overgrown by macroalgae.	Baskett & Salomon (2010)
Vegetated - bare soil	Drylands	Vegetation improves water retention locally (by increasing albedo, transpiring).	Schlesinger *et al.* (1990)
High vegetation cover - low vegetation cover	Sahel-Sahara, amazon	Vegetation promotes precipitations at a regional scale.	Brovkin *et al.* (1998)
High diatom cover, high silt content, low erosion - erosion state (low diatom and silt content)	Intertidal mudflats	Benthic diatoms decrease sediment erosion by secreting extracellular polymeric substances, which increases their growth.	van de Koppel *et al.* (2001), Weerman *et al.* (2012)
Saltmarsh vegetation, thick sediment layer - saltmarsh collapse, vegetation lost	Saltmarshes	Saltmarsh plants increase clay deposition, prevent erosion by waves and decrease salt stress for other plants, which favour plant growth.	Bertness & Hacker (1994), van de Koppel *et al.* (2005a)
Vascular plants - no vascular plants	Boreal peatlands	Shrubs colonize moss hummocks and facilitate further tree establishment by ameliorating abiotic stress (e.g. cooling air in summer, lower soil water logging).	Eppinga *et al.* (2009), Holmgren *et al.* (2015)

ontogeny or with changes in environmental conditions (Holmgren, Scheffer & Huston 1997). Under very severe abiotic stress (Maestre & Cortina 2004; Butterfield *et al.* 2010) or herbivore pressure (Smit *et al.* 2007), plant–plant interactions can become negative. The loss of net facilitative interactions under extreme levels of environmental stress could occur either if nurses reach a limit in their capacity to improve the microenvironment or because the positive effects do not compensate the unavoidable costs of sharing resources between neighbouring individuals (Michalet *et al.* 2006; Holmgren *et al.* 2012). Indeed, meta-analysis of the published literature (Holmgren *et al.* 2012) and assessments of restoration experiments indicate that nurse plant effects depend on their morphological traits and the overall environmental conditions (Padilla & Pugnaire 2006; Gómez-Aparicio 2009). Further understanding these processes can help improve restoration programs, taking advantage of positive interaction's potential to dis-
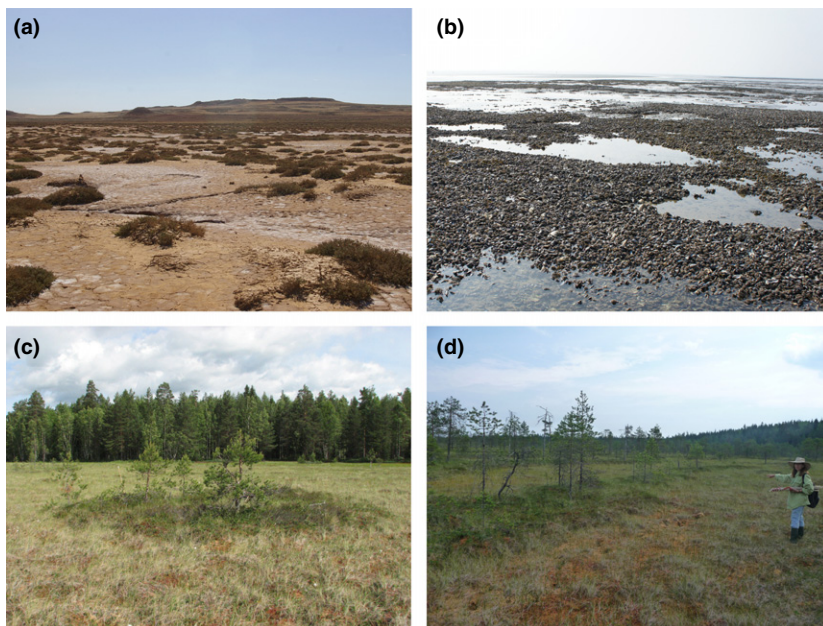
Fig. 3. Spatial patterns due to facilitative interactions in (a) drylands (El Planeron, Belchite, Northeast of Spain; Picture: S. Kéfi), (b) mussel beds on intertidal flats (Dutch Wadden Sea; Picture: Jim van Belzen) and c–d) boreal peatbogs in Finland (C: circular hummocks, D: long stripes; Pictures: M. Holmgren).

rupt feedbacks in place and favour restoration of the ecosystem to the desired state.

POSITIVE INTERACTIONS AND EVOLUTION

As positive interactions can be such a strong force, it is hardly surprising that it has played an important role in evolution as well. In the course of deep time, life itself has made our planet hospitable in many ways. This process has not been smooth. Instead, biological innovations triggered revolutionary shifts into novel states (Lenton & Watson 2013). Although in evolution there is no way back to demonstrate hysteresis, such new states can often be seen as alternative stable states. For example, the great oxygenation event, about 2·4 billion years ago, was the result of the emergence of photosynthesis interacting with a positive feedback in atmospheric chemistry leading to an alternative stable state (Goldblatt, Lenton & Watson 2006). This high-oxygen state subsequently facilitated the Cambrian explosion of life (Lenton & Watson 2013).

Massive changes in the aspect of global vegetation may also be related to facilitative effects, where certain plant forms alter conditions that promote their own success. For instance, it is thought that such ecosystem engineering may have been central to one of the most spectacular evolutionary radiation events in life, the explosion of flowering plants (angiosperms) in the mid-Cretaceous (Berendse & Scheffer 2009). Several groups of angiosperms were already around about 130 million years ago. However, they remained a minor component of the gymnosperm-dominated vegetation of the Earth for many millions of years until they finally rose to massive dominance around 70–100 million years ago. Innovations such as seed dispersal and pollination by animals may have contributed to the sudden angiosperm radiation. However, another mechanism that has likely played a role is the fact that angios-

perms created conditions that facilitated their own growth. Angiosperms need higher soil nutrient levels than gymnosperms. However, angiosperms also promote nutrient levels because they produce litter that is easily decomposed compared to the litter of gymnosperms. Angiosperms thus facilitate angiosperm growth through an improvement of growing conditions. This positive feedback may have been important in driving the runaway process that may have unleashed this new plant type once a critical threshold was passed (Berendse & Scheffer 2009).

An even more rapid change of global vegetation was invoked by the evolution of C4 grasses that rapidly concurred large parts of the Earth during the Miocene and Pliocene (3–8 million years ago) (Edwards *et al.* 2010). The success of these grasses was in part due to their flammability which implied a facilitative loop. Fire favours grass over trees as grass bounces back from fire better. The massive global change upon the spread of C4 grasses also had important cascading evolutionary effects. For instance, upon the global spread of C4 grasses, fire-adapted savanna tree species have evolved from the forest species, and now there is hardly any overlap between the species pool of savanna and of the neighbouring forests (Hoffmann, Orthen & Nascimento 2003).

Future directions: towards an ecological theory of positive interactions

What we mostly see in terms of alternative states in ecosystems is a shift in dominance from one functional group to another (and in a few cases from absence or presence of all biomass; Table 1). Those can often be understood from positive feedbacks between organisms and the physical environment (Fig. 1b–d), where a functional group promotes conditions under which it grows better than the competing group (Table 1). In other terms, the contrasting

ecosystem states have stabilizing feedback mechanisms that keep them persistent. Those feedbacks can cause threshold-like responses to changing conditions if they are strong enough relative to the other processes occurring in the ecosystem.

In a number of now classical examples in the literature, the core of these positive feedbacks are positive interactions occurring through the abiotic environment (Bertness & Callaway 1994; Holmgren, Scheffer & Huston 1997; Bruno, Stachowicz & Bertness 2003; Callaway 2007), which thereby contribute to the possible emergence of alternative stable states. However, positive interactions occurring through the abiotic environment may only have the potential to trigger self-reinforcing feedbacks under certain conditions. We hypothesize that this is more likely to occur when the facilitative effects (i) involve a modification of the physical environment that favour the facilitating species or group of species, such as amelioration of atmospheric conditions (e.g. temperature or wind), changes in soil conditions (e.g. water infiltration or drainage); (ii) the facilitative effects are sufficiently strong to expand across relatively large patches in an ecosystem; (iii) the facilitative effects interact with changes in disturbance regimes that further favour the establishment of a new community. These conditions may more likely occur at intermediate levels of environmental severity in some ecosystems. The best examples we know are semi-arid ecosystems (e.g. Rietkerk *et al.* 1996; Holmgren & Scheffer 2001), grasslands (e.g. Le Bagousse-Pinguet *et al.* 2014), peatlands (e.g. Eppinga *et al.* 2009; Holmgren *et al.* 2015) and marshes (e.g. Bertness & Hacker 1994; van de Koppel *et al.* 2005a).

Going through the literature, it is striking how much has been done at the micro-scale level of interactions between individuals (Table 1). Bridging this vibrant field to the important question of alternative stable states seems an obvious opportunity for progress, but requires scaling up results from the individual level to the community and the ecosystem scale. Recent work, using simple individual based models, provides insights into the conditions under which individual plant effects may scale up to cause alternative stable states on a landscape level (Xu *et al.* 2015b). On the empirical side, as remotely sensed images are quickly improving, the possibility to infer the strength of positive interactions from large scale patterns (Xu *et al.* 2015a) is another opportunity to scale up from plant–plant interactions to landscape dynamics.

Further theory development as well as empirical work across scales may help bridge that gap between the different organizational levels. Ultimately, getting a clearer understanding of the links between individual-level facilitation, positive feedback loops, alternative stable states and ecosystem-level catastrophic shifts may rely on investigating whole networks of interactions between species and their abiotic environment, that is on merging ecosystem and community approaches (Kéfi *et al.* 2012). Indeed, a limitation of the ecosystem models which have been used to study ecosystem shifts so far is that they often ignore species diversity and the diversity of their interactions and usually simulate one or a few nurse species (e.g. Noy-Meir 1975; May 1977; Rietkerk *et al.* 1996; van de Koppel *et al.* 2001, 2005a,b; Kéfi *et al.* 2007b). In such cases, a positive interaction is almost equivalent to a positive feedback loop (such as in Fig. 2a). Conversely, community ecology models, which integrate species diversity, do not generally take positive interactions into account despite their potential functional importance for community functioning and resilience (Bruno, Stachowicz & Bertness 2003). When complex interaction networks have been studied (e.g. pollination networks; Lever *et al.* 2014), positive interactions have usually been studied in isolation from other types of interactions (but see Gross 2008; Kéfi *et al.* 2012).

The link between positive interactions and positive feedback loops is not trivial because it increases the complexity of the models used, but also because we know that ecosystems in which positive interactions are present and abundant do not necessarily exhibit alternative stable states. In many cases, positive interactions could be more important in linking, transmitting and modulating effects within ecosystems rather than in causing changes per se. This suggests that, despite an increasing interest about the implication of facilitation at community and ecosystem levels (e.g. Kéfi *et al.* 2007b; Gross 2008; Lever *et al.* 2014; Xu *et al.* 2015b), there is still a need for a further integration of positive interactions into ecological theory, more than a decade after the call of Bruno, Stachowicz & Bertness (2003). A better understanding of the role of positive interactions could be essential for smart ecosystem management (and in particular, the prevention of catastrophic shifts) as well as for ecosystem restoration (e.g. a better use of positive interactions to trigger positive feedback loops).

Acknowledgements

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