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Interspecific facilitation and critical transitions in arid ecosystems

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Climate change and intensified land-use impose severe stress on arid ecosystems, resulting in relatively rapid degradation which is difficult to reverse. To prevent such critical transitions it is crucial to detect early warning signals. Increased 'patchiness' – smaller and fewer vegetated patches – is thought to be such a signal, but the underlying mechanisms are still poorly understood. Facilitation between plants is known to be an important mechanism driving the patchiness of the vegetation, but we lack understanding of how interactions between plants change in response to combined effects of drought and consumer pressure – the main stressors in many arid ecosystems. Over the last decade numerous experimental studies have tested how intensity of facilitation between plants changes with increasing stress. The most recent synthesis predicts a decline in facilitation intensity at the severe end of a drought stress gradient. Adding consumer pressure may result in even earlier and faster declines in facilitation intensity. So far, studies on critical transitions and plant–plant interactions have developed separately. The relationship between stress and facilitation intensity has been overlooked in critical transition theory, while facilitation intensity may determine the position of a critical transition threshold. In this study, we incorporate experimental studies on the relation between stress and facilitation intensity into the critical transition framework, to improve our ability to predict critical transitions. Moreover, we propose that a decline in facilitation intensity at the severe end of a stress gradient may occur prior to a critical transition. Inclusion of consumer pressure will speed up this process, leading to earlier and faster degradation. In-field monitoring of seedling–facilitator associations and declines in facilitator recruitment can indicate declines in facilitation intensity and may thus provide additional early warning signals for imminent critical transitions, besides increased patchiness.

Human population growth, intensified land use and climate change are posing increasing stress on earth's ecosystems (Adeel et al. 2005). Especially prone are arid ecosystems because gradual build up in stress by drought or grazing can result in a critical transition from a vegetated to a non-vegetated state (Rietkerk et al. 1996, Rietkerk and Van De Koppel 1997, Scheffer et al. 2001). Critical transitions can result from bistability meaning that two alternative stable states are possible given the same environmental conditions. After a threshold is reached vegetation cover will decline more rapidly than expected, which may have negative impacts on ecosystem multifunctionality through reduced plant diversity (Maestre et al. 2012). Because critical transitions are hard to reverse there is a high need for early warning signals, indicating an imminent transition. Recent modelling and observational studies identified the rapid loss of relatively large vegetated patches with increased environmental stress as a possible warning signal prior to a critical transition (Kéfi et al. 2007a, b), but the exact mechanisms remain so far unclear. More insight into the relevant mechanisms and a stronger link with experimental studies is currently highly needed to improve our ability to predict critical transitions (Scheffer et al. 2009).

Interspecific facilitation is the mechanism whereby a 'facilitator' plant species ameliorates the environment for 'protégé' plant species. Facilitators can relief abiotic stress for protégés by protecting against extreme temperatures and high irradiance, increasing water availability, improving nutrient availability or by reducing soil compaction and erosion (Callaway 2007). Next to that, facilitators can lower consumer pressure (disturbance, i.e. biotic stress sensu Smit et al. 2009) by protecting protégés against herbivores, a process known as associational resistance (sensu Hay 1986). These two types of facilitation (relief of abiotic stress and associational resistance) shape a wide range of ecosystems and the significance of facilitation in structuring plant communities is now fully recognized (Callaway 2007). However, there is much discussion on how the direction and intensity of facilitation respond to increased abiotic stress and consumer pressure and thus far, interspecific facilitation has not yet been explicitly considered in the framework of critical transitions in arid ecosystems.

Here we aim to combine insights from the theories on critical transition and on interspecific facilitation in plant communities along stress gradients (stress gradient hypothesis framework) to improve our ability to predict the onset of critical transitions in arid ecosystems. These two important ecological theories have thus far developed separately and the relation between environmental stress and facilitation intensity has until now been overlooked in critical transition theory. Firstly, we discuss most recent insights in plant–plant interactions along abiotic and biotic stress gradients. Secondly, we link these insights to the framework of critical transitions, by emphasizing that changes in facilitation intensity can affect the position of a critical transition threshold. Finally, we propose a conceptual framework for critical transitions in arid ecosystems based on the notion that not only the density of facilitator species will decline with increasing abiotic stress and consumer pressure, but also the intensity of facilitation will change. We discuss the possibilities for ecological applications and give future directions for essential field and modelling studies.

Current knowledge on species interactions along stress gradients

Classic conceptual models on direction and intensity of plant–plant interactions along stress gradients predict that the frequency and intensity of facilitative interactions increase with higher abiotic stress or consumer pressure (Bertness and Callaway 1994, Callaway 1995, Holmgren et al. 1996, Callaway and Walker 1997, Brooker and Callaghan 1998). This conceptual framework was later called the stress gradient hypothesis (Lortie and Callaway 2006, SGH). The reasoning behind the SGH (Fig. 1, grey line) is that both competition and facilitation act simultaneously upon species but shift from net competitive to facilitative with increasing environmental stress. Since its formulation, multiple studies have tested the SGH experimentally by assessing the interaction intensity for species pairs at several abiotic or biotic stress levels. Interaction

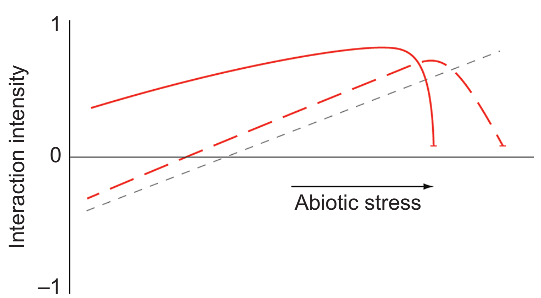

Figure 1. Possible shapes of the relation between stress and interaction intensity for arid ecosystems with (red solid line) and without (red dashed line) inclusion of consumer pressure along an abiotic stress gradient. Negative values represent competition and positive values facilitation. The original SGH (grey dash-dot line) predicted a monotonic increase from competition to facilitation. The revised SGH predicts a hump-shaped relation.With inclusion of consumer pressure we predict overall higher interaction intensity but an earlier and faster decline in interaction intensity at the severe end of the abiotic stress gradient. These hypotheses predict the shape of the relationship between stress and interaction intensity in a qualitative way, we do not intend to make quantitative predictions.

intensity is typically measured as the performance of a target plant (protégé) close by a facilitator compared to its performance without a facilitator. Interaction intensity can range from negative (often called competition intensity) to positive (often called facilitation intensity). While several studies found supporting evidence for the SGH (Callaway et al. 2002, Gómez-Aparicio et al. 2004, Lortie and Callaway 2006) others found evidence against it (Tielbörger and Kadmon 2000, Armas and Pugnaire 2005). These contrasting results have led to debate (Lortie and Callaway 2006, Maestre et al. 2005, 2006) and calls for new studies, (Michalet 2007, Brooker et al. 2008, Brooker and Callaway 2009), and as a consequence several refinements of the SGH have been proposed (Kawai and Tokeshi 2007, Maestre et al. 2009, Holmgren and Scheffer 2010, Le Roux and McGeoch 2010, Smit et al. 2009, Malkinson and Tielbörger 2010, Soliveres et al. 2011a). These proposals consider the length of the stress gradient studied, the type of stress imposed (resource or non-resource based, consumer pressure and their combinations), and the life-strategies (competitor vs stress tolerant) and life-stages of facilitators and protégés. For example, in arid ecosystems where stress is mainly resource driven (stress tolerant facilitator, stress intolerant protégé), interaction intensity is predicted to show a hump shaped relation with stress (Fig. 1, dashed line). Plant–plant interactions first shift from competition to facilitation from high to low rainfall levels, but facilitation intensity wanes again at even lower rainfall levels (Maestre and Cortina 2004, Maestre et al. 2005). The reason for a decline in facilitation intensity at high stress is that the level of resources become so low that positive effects of a facilitator on the micro-environment cannot outweigh competitive interactions by the canopy, such as rainwater interception or belowground root competition (Michalet et al. 2006, Anthelme et al. 2007, Valladares et al. 2008, Holmgren and Scheffer 2010).

Furthermore, abiotic stress and consumer pressure (e.g. grazing) will interact in driving plant–plant interactions (Smit et al. 2009). It has even been suggested that consumer pressure is the primary driver of a decline in facilitation intensity at the severe end of a stress gradient consisting of both biotic and abiotic components (Michalet et al. 2006, Forey et al. 2009). Indeed, such declines in facilitation intensity at high consumer pressure have been observed in both terrestrial (Brooker et al. 2006, Graff et al. 2007, Smit et al. 2007) and aquatic ecosystems (Levenbach 2009, Le Bagousse-Pinguet et al. 2012a) where the facilitator was no longer able to protect protégés because it got damaged itself at very high consumer pressure. Hence for improved understanding, studies are needed that investigate the combined effects of both stress types on facilitation intensity in arid ecosystem. Studies attempting this are very scarce (but see Soliveres et al. 2011b, Maalouf et al. 2012) and are especially needed as consumer pressure has a large impact on the formation of spatial vegetation patterns and on the onset of critical transitions (Kéfi et al. 2007a).

Expanding theory: combining abiotic and biotic stress gradients

Since studies that cross both biotic and abiotic stress gradients are still very scarce for arid ecosystems, we propose the following testable predictions on how plant–plant interactions may change if consumer pressure is superimposed on an aridity gradient. Adding consumer pressure may result in three important changes in the shape of the relation between facilitation intensity and abiotic stress (Fig. 1, solid line). Firstly, facilitation intensity may be higher over the whole aridity gradient (until a threshold is reached), because facilitators simultaneously protect against herbivory (i.e. associational resistance) and ameliorate the microenvironment (e.g. shading) (Smit et al. 2009). With inclusion of consumer pressure, we hypothesize higher overall and a higher maximum in facilitation intensity as traits (e.g. spiny or waxy leaves) resulting in microhabitat amelioration often also result in protection against herbivores, leading to additive facilitative effects if both stress types operate simultaneously. Secondly, the importance of associational resistance relative to microenvironment amelioration may decrease with increasing abiotic stress (Fig. 1, smaller distance between the solid and dashed line with increasing abiotic stress). This is based on the idea that environments with low abiotic stress are able to support more consumers than harsher environments (Grime 1977) and therefore associational resistance should be of higher importance at low abiotic stress. Two studies, one in rocky reef (Bulleri et al. 2011) and one in salt marshes (Crain 2008) already have found support for this idea. Thirdly, the decline in facilitation intensity will occur at lower abiotic stress levels and will be faster when biotic and abiotic stresses operate simultaneously instead of separately (Fig. 1, earlier and faster drop of solid line): these interacting stress types will lower the facilitator's ability to ameliorate the micro-environment or effectively protect against herbivores.

Critical transitions in arid ecosystems and patch sizes as an early warning signal

Over the last decade much research has focused on providing warning systems for critical transitions to a degraded state in arid ecosystems (Kéfi et al. 2007a, Rietkerk et al. 2004, Scheffer et al. 2009). Spatial explicit modeling studies showed that when vegetation is regulated by local facilitation in combination with overall limitation of resources, the patch-size distribution of the vegetation is irregular and best described by a power law (Kéfi et al. 2007a, Scanlon et al. 2007). Local facilitation was modeled by inducing a positive effect of vegetated cells on neighboring bare soil cells, increasing the probability of vegetation recruitment close to a vegetated cell. A decrease in the intensity of local facilitation or an increase in the consumer pressure resulted in the disappearance of the largest patches from the ecosystem, prior to a critical transition to a bare state. This model outcome was confirmed by field observations of vegetation patchiness at field sites situated along a grazing gradient (Kéfi et al. 2007a). Therefore, it was concluded that deviations in the power law – a deficiency in large patches – can be used as an early warning signal prior to critical transition to a desert state (Kéfi et al. 2010, but see debate Maestre and Escudero 2009, 2010). However, more recent analysis showed that models without local facilitation also show a similar disappearance of the largest patches during gradual transition from vegetated to a desert state (Kéfi et al. 2011). So, more insight is still needed on how changes in plant–plant interactions along stress gradients relate to spatial patterns in vegetation, and in turn to the onset of critical transitions.

Kéfi et al. (2007b) also showed that whether a system will undergo a sudden collapse (i.e. discontinuous transition) or a gradual change (i.e. continuous transition) with increasing stress depends on the intensity of the local facilitative mechanism (Kéfi et al. 2007b). Strong local facilitation intensity diminishes the risk of discontinuous transitions, because patches of vegetation can more easily form, spread and maintain themselves. The appearance of few vegetated patches in the system is already sufficient for vegetation recovery when facilitation intensity is very high. Hence, when facilitation intensity is very high, an ecosystem is predicted to undergo a continuous (i.e. gradual) transition with increasing stress. However, when facilitation intensity was decreased in their model, the system became bistable and the chance for critical transition from a vegetated to a desert state increased. With low facilitation intensity, the density of facilitators needs to be higher to effectively result in facilitative effects, as degraded sites need more than one neighbouring facilitator or need to be in closer proximity to the facilitator to receive the same benefit. So, a higher initial vegetation density is needed to lead the vegetation in the desired vegetated state, increasing the overall probability for a critical transition to occur.

Integrating changes in species interactions into the critical transitions framework

Facilitation intensity is predicted to change in a testable manner in response to multiple drivers of stress (Fig. 1). Moreover, facilitation intensity may determine the position of a critical transition threshold (Kéfi et al. 2007b). From this, we will now describe how the shape of the relation between stress and facilitation intensity can be incorporated in critical transition theory in order to better predict the onset of critical transitions.

We propose that state transitions in arid ecosystems can be described by a plane that is very similar to a cusp catastrophe plane (Fig. 2). This way we can account for the notion that the nature of a state transition (gradual or discontinuous) and the position of a critical transition threshold may depend on the facilitation intensity. The use of a cusp catastrophe to describe vegetation dynamics in arid ecosystems has been previously proposed for transitions from perennial to annual vegetation types (Rietkerk et al. 1996) and for transitions from grassland to shrubland (Turnbull et al. 2008). The essential element of a cusp catastrophe model is that it can explain both continuous and discontinuous transitions in vegetation states with increasing abiotic stress, dependent on a third variable, facilitation intensity in our case.

Changes in the facilitation intensity will result in a different nature of the transition (Fig. 2). With high facilitation intensity, the system will show continuous transitions, because even very low vegetation densities are able to exert strong enough positive feedback for vegetation to recover. With intermediate facilitation intensity, the system will show discontinuous transitions, but with a relatively small

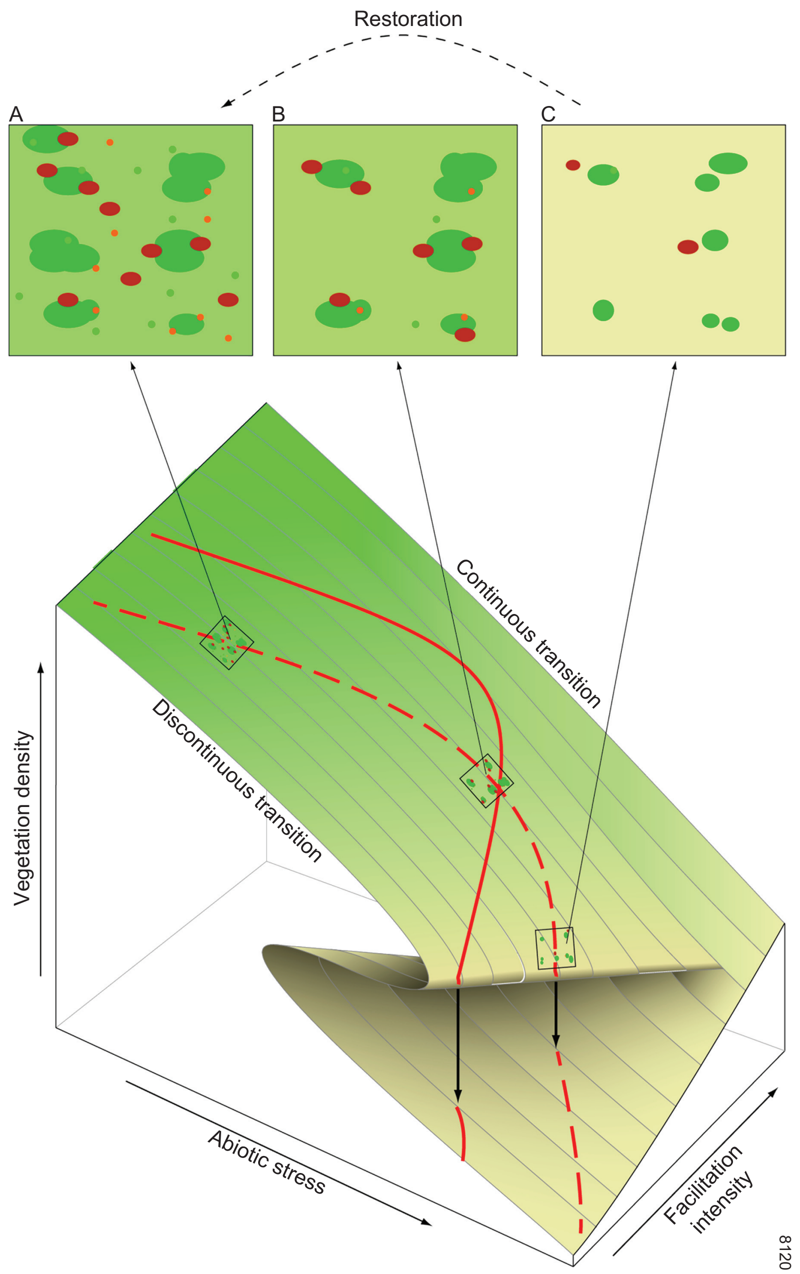

Figure 2. State transition from low to high facilitation intensity (i.e. positive interaction intensity) along a gradient of abiotic stress, with (red solid line) and without (red dashed line) inclusion of consumer pressure. Vegetation density is the amount of plants (both protégé and nurse species) per surface area. The downward arrows represent sudden jumps in the vegetation state. Panel A, B and C represent snapshots of the patch size distribution and coinciding changes in spatial association strength along a stress gradient. Dark green represents mature facilitator species, light green small dots represents facilitator seedlings. Dark brown represents mature protégé species. Light brown small dots represents protégé seedlings. The figure is adapted after Rietkerk et al. (1996) and Turnbull et al. (2008).

sudden jump. With even lower facilitation intensity the system will show discontinuous transitions with relatively large sudden jumps. Whether a system will remain in a vegetated state or will converge to a bare state is thus dependent on both the density of vegetation and the intensity of interactions. Higher intensity may partly compensate for low density of vegetation, maintaining the system in a vegetated state. Conversely, lower facilitation intensity will only effectively maintain vegetation if vegetation is abundant at a higher density. This is reflected in the position of the critical transition threshold: with higher facilitation intensity the point of collapse occurs at higher abiotic stress levels (lower density), because higher facilitation intensity can compensate for a lower density of plants.

We thus hypothesize that the abiotic stress level at which a critical transition occurs is partly dependent on the shape of the relation between stress and facilitation intensity. We illustrate this by following two possible shapes of this relation, one with and one without inclusion of consumer pressure. Without inclusion of consumer pressure, the relation is hump-shaped (Fig. 1, red dashed line). At low abiotic stress (Fig. 2, red dashed line, panel A) the ecosystem is in the upper part of the plane. The system is far from collapse, as while facilitation intensity is low, the vegetation density is still high enough to maintain itself. If the stress is moderate (Fig. 2, red dashed line, panel B), the system still has a low probability of collapse, because the decline in facilitator density is partly compensated by an increase in facilitation intensity. However, if stress becomes even higher (Fig. 2, red dashed line, panel C) and facilitation intensity begins to decline, the system will approach the threshold for critical transition very quickly, because now both the facilitator density and the facilitation intensity will decline with further increasing stress. With inclusion of consumer pressure (Fig. 1, red solid line), the relation between stress and facilitation intensity is also hump shaped, but the decline in facilitation intensity will occur at lower abiotic stress levels and will be faster. Therefore the collapse of vegetation will occur at lower abiotic stress levels and the sudden jump will be larger, as facilitation intensity will reach a lower level (Fig. 2, red solid line).

New early warning signals? Spatial species associations and facilitator recruitment

As facilitation between plants plays a crucial role in the prevention of critical transitions, declines in positive interactions may provide an additional warning signal prior to critical transitions, in addition to a deficiency of large patches in the patch size distribution (Kéfi et al. 2007a) or changes in cover (Maestre and Escudero 2009). In the following paragraphs we describe possible ways to monitor declines in facilitation intensity and predict how facilitator–protégé associations may change prior to the onset of a critical transition.

Previous studies showed that facilitation intensity is highest during recruitment and the earliest life stages of plants (Franks 2003, Lortie and Callaway 2006, Soliveres et al. 2010), since tolerance and protection against stress have not fully developed yet. So, if shifts from facilitation to competition occur at very high stress, they will be most pronounced during the seedling and sapling stages of plants. Changes in spatial association strength (how often plants are co-occurring) between seedlings and nurse plants could thus effectively serve as a possible early warning sign that positive interactions are weakening.

Recent studies employing a network approach to map plant–plant interactions in arid ecosystems showed that community stability is determined by few very abundant species that have strong interspecific facilitative effects within the whole community (Saiz and Alados 2011, Verdú and Valiente-Banuet 2008). Given the key-role of these particular facilitator species, it is of crucial importance that viable populations of these species are maintained via consistent and frequent recruitment of new seedlings. Recruitment failure inevitably leads to local extinction of species which, in the case of a facilitator, may have dramatic consequences for the entire ecosystem. Seedlings of facilitators often still lack effective defense mechanisms against herbivores in their first life stage and can therefore be considered as protégés (Smit and Ruifrok 2011). So, if facilitation wanes this may result in recruitment failure of facilitator species, which over time will make a system converge to a state without facilitative effects. Recruitment failure of facilitator species could thus indicate that a system is converging towards a degraded state. The speed at which this occurs is dependent upon the life span of the still present mature facilitator species, with fast degradation when facilitators are short-lived.

Therefore, we propose that a decline in nurse-seedling association strength and failure of facilitator recruitment can be used as additional warning signs for a nearby critical transition. If with increasing stress spatial associations strengthen, it may indicate that a system is not yet close to a critical transition or even that the system is not bistable due to high facilitation strength. However, if with increasing stress spatial association strength declines and facilitator recruitment declines, this might indicate that facilitative interactions are weakening and thus that an ecosystem might be approaching the critical transition threshold quickly. If facilitator recruitment fails, this can indicate that a system has passed a threshold and is converging to a degraded state over time.

More specifically, we predict the following sequential change in spatial association strength when an ecosystem is approaching a critical transition, illustrated along the abiotic stress gradient presented in Fig. 2 (red dashed line). When stress is low, spatial association strength between facilitators and seedlings will be moderate and facilitator recruitment will be high enough to maintain the facilitative vegetation and to form new patches (Fig. 2, panel A). When stress becomes higher, the spatial association between mature facilitators and seedlings will become stronger, as sole standing seedlings from both protégés and facilitators species are no longer able to survive (Fig. 2, panel B). When stress becomes even higher and facilitation intensity starts to decline, the largest patches will disintegrate as facilitation intensity wanes (Fig. 2, panel C). Both protégé and facilitator recruitment will become very low and facilitator–seedling associations will become weaker, as a result of the waning facilitation intensity. This is the point where a deficiency in the largest patches occurs as observed by Kéfi et al. (2007a). We thus propose that the disintegration of largest patches is coincidental with a decline in spatial association strength between facilitators and seedlings and a decline in facilitator recruitment. With further increasing stress facilitator recruitment becomes too low to maintain the vegetation and a critical transition occurs. Moreover, we predict that with inclusion of consumer pressure this critical point is reached at lower abiotic stress as facilitation intensity might decline earlier (Fig. 2, red solid line).

Both changes in facilitation intensity and recruitment success of facilitator species can be obtained by field observations (transect or quadrat sampling of vegetation) to determine the spatial association strength and recruitment success of important facilitators. If facilitation intensity is observed to decline at increasing stress, tools to restore facilitative effects, such as revegetation with nurse plants (Pueyo et al. 2009), should be applied in time to prevent further irreversible degradation. Moreover, by implementing removal or planting experiments, the stress level at which facilitation intensity wanes can be assessed more accurately. Experimentally assessing declines in facilitation intensity on crossed gradients of abiotic stress and consumer pressure could provide additional information for determining optimal land use under different drought scenarios.

Synthesis and future directions

In sum, many observational and experimental studies over the last decades showed that interactions between plants change along stress gradients. For arid ecosystems, most current syntheses predict a hump shaped relation between facilitation intensity and stress. This interplay between stress and facilitation intensity has been largely overlooked in critical transition theory, while the shape of the relationship between stress and facilitation intensity may importantly determine the position of a critical transition threshold. We therefore propose that assessing the shape between facilitation intensity and multiple drivers of stress (biotic and abiotic) may improve our ability to predict the onset of critical transitions. Furthermore, we propose that monitoring declines in facilitation intensity can be used to predict whether a system is approaching a critical transitions threshold. More specifically, we propose that this decline in facilitation intensity can be observed in the field by monitoring facilitator–seedling associations and recruitment of facilitator species. A similar approach to predict critical transitions (focusing on declines in facilitation intensity) might be applicable to other systems as well. For example, indirect facilitation between macrophytes has been linked to a critical transition from a clear water state to a eutrophicated turbid state in freshwater ecosystems (Le Bagousse-Pinguet et al. 2012b).

We now need experimental studies that test predictions on facilitation intensity for the dominant facilitator species at several levels of combined abiotic and biotic stress. Next to that, observational studies are needed that monitor regeneration patterns of facilitator species to observe declines in facilitation intensity and to prevent chronic recruitment failure. Moreover, spatial explicit modeling studies are needed that integrate the interplay of facilitation intensity and multiple stress types in a mechanistic way, to better understand the implications of this interplay on spatial vegetation patterns and the onset of critical transitions. Such modeling studies could also add to the recent and ongoing discussion on facilitation importance (facilitation's relative impact, Brooker and Kikividze 2008) by exploring the relationship between facilitation intensity and facilitation importance along stress gradients. Facilitation importance expresses the role of plant interactions compared to the role of other abiotic factors and may thus be a more direct indicator for declining positive interactions than facilitation intensity. While facilitation intensity and importance need not be related (Brooker et al. 2005), both indices have shown to be positively related along a complex stress gradient, consisting of both water stress and disturbance (Maalouf et al. 2012). More insight is needed on how facilitation intensity and importance change along combined stress gradients and how changes in both these indices relate to the onset of critical transitions.

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